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BIOLOGICAL AND STATISTICAL STUDIES ON THE NEW ZEALAND ROMNEY LAMB WITH REFERENCE TO RELATIVE GROWTH GRADIENTS.

by

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I. INTRODUCTION

It was known that there was considerable variation in the coats of sheep, both from animal to animal as well as from breed to breed. Studies on fibre-types occurring in the coat of the New Zealand Romney lamb led to the discovery (Dry$_2$) that these were arranged in a definite order which he termed fibre-type arrays.

Different fibre-type arrays were found to occur on different positions of the body. It was then found that there was a posterior-anterior fibre-type array gradient, fibre-type arrays with coarse fibres being situated posterior to those with fine fibres.

Preliminary studies on pre-natal material revealed the fact that the different positions of the body developed their wool coats at different times. It also showed that follicle development was orderly, passing through three marked stages:-

<u>An initial follicle stage</u> - when follicles of two types - X and Y - appeared and arranged themselves in alternate rows. The difference between X and Y follicles was only in the time of their appearance. The linear arrangement followed immediately on the appearance of the Y follicles.

<u>A trio follicle stage</u> - when each of the X and Y follicles have two small follicles-xx and yy-developing one on either side of them i.e. xXx -yYy.

<u>A nine stage of follicle development</u> which was not so marked as the other two stages of development, it arose as a secondary trio stage from the first trio stage, by two small follicles appearing one on either side of the

follicles of the trio stage. Quite often the nine stage was not perfect - one or two of the follicles failing to appear. Following on the completion of the nine stage the first fibres pierced the skin.

The check to follicular activity affecting the early growing pre-curly-tip fibres, it was suggested, was due to overcrowding of follicles at the trio stage, while the check causing the decrease in coarseness of the late curly-tips was thought to be due to the high fibre population density at the nine stage. Overlapping of the two stages of overcrowding was thought to produce a fine even coat showing little variation in coarseness.

An attempt has been made to correlate the density counts at the different stages of development with the growth of the foetus to show that regions with coarser fibre-type arrays passed through a phase of rapid growth during critical stages in follicle development, the follicular density consequently being relatively decreased.

II. MATERIAL and METHODS

A. Natal lambs.

I. Breed and Sampling

Wool samples were taken from a number of New Zealand Romney lambs, a few Southdown, and a few Ryeland lambs. In addition a few Cheviot and Scottish Blackface pelts were examined. Samples were taken from the following positions. See figure I.

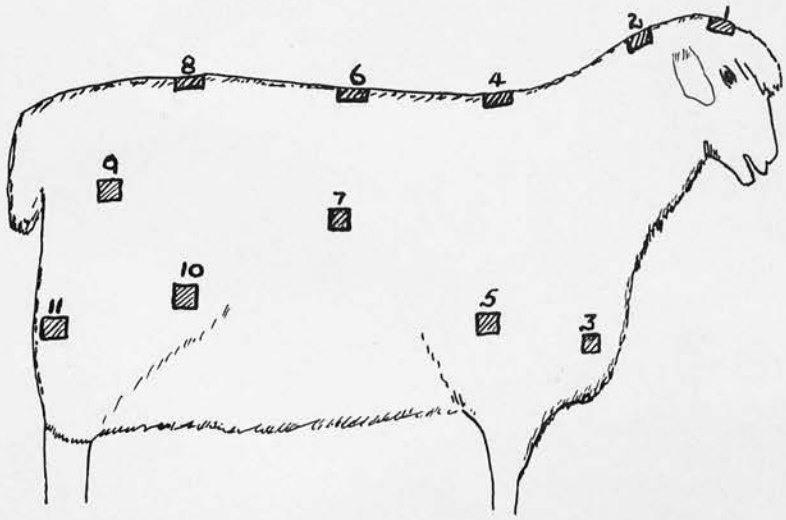


Figure I

I. Poll. - on the mid-dorsal line between the ears and the position of the horns.

2. Neck. - on the mid-dorsal line midway between the ears and the last cervical vertebrae.

3. Shoulder-point. - on the point of the shoulder bone.

4. Withers. - On the mid-dorsal line level with the fifth rib.

5. Fifth rib - on the fifth rib - ventro-lateral to the withers in a line with the shoulder-point position and dorsal to the point of the olecranon (elbow).

6. Back - on the mid-dorsal line level with the last rib.

7. Side. - on the side at the distal end of the last rib.

8. Superior ileum. - on the mid-dorsal line on the medial angles of the ilea.

9. Hip joint. - on the junction of the femur and pelvic bones(acetabulum) and ventro-lateral to the superior ileum position.

10. Superior flank. - midway and slightly anterior to an imaginary line drawn between the stifle and the hip joint.

II. Britch. - Immediately posterior to the stifle joint and midway across the thigh.

The samples were taken as near the skin level as was possible when using fine curved scissors. They were then stored in envelopes for sorting in the laboratory. These samples were the same as those used to determine the fibre-type array distribution over the body.

2. Technique of Sorting and Counting.

The samples were sorted on black velvet; blunt-tipped forceps were used. The fibres of each sample were separated into two groups - pre-curly-tips and curly-tips. The pre-curly-tip group consisted of all fibres which commenced growth before the curly-tips.

i.e. - halo-hairs.
sub-halo-hairs.
sickle fibres.
super-sickle fibres.

The curly-tip group comprised the later growing fibres and in the sheep studied, was never less than two thirds of the total fibres counted.

In the curly-tip group were curly-tips - both coarse and fine, -histerotrichs - usually a very small proportion of the fibres of each sample.

A representative portion of a sample was taken and all the fibres in that portion were placed in one or the other of the two groups. The number of fibres in each group was then counted and the result expressed as the number of pre-curly-tips to curly-tips in a hundred fibres. The counts from the different regions were found to group themselves in the following way.

Table I.

Group A.	Poll	- highest number of pre-curly-tips per hundred fibres.
Group B & C.	Neck Shoulder point	
Group D.	Withers Fifth rib. Britch	
Group E.	Back Side	
Group F.	Superior ileum Hip joint Superior flank	- lowest number of pre-curly-tips per hundred fibres.

The names of the groups have been taken from the area to which regions sampled would be allocated XXXX in the foetus. Appendix. Paper I - Galpin.

B. I. Foetal Material.

Eighty-three New Zealand Romney foetuses were obtained at definite stages of development. The ewes were all Romney ewes but were not pedigreed. They were all fairly coarse but it was possible to divide them into two classes according to wool characters - a finer and a coarser class. The ewes of the finer class were mated with a fine woolled ram while those of the coarser class with two very coarse woolled rams. Dates of service were taken and the ewes were killed in the local abattoirs on prescribed dates. The foetuses were taken from the uterus carefully labelled and immediately placed in a five per cent formalin solution. After twenty-four hours they were removed to storage tanks filled with a five per cent formalin solution.

Foetuses were collected at the following ages:- <u>ages in days</u>

42; 46; 49; 52; 56; 60; 68; 72; 76; 80; 83; 87;
90; 93; 97; 101; 104; 108; 112; 118; 122; 127; 136; 143;

2. <u>Technique</u>.

a) <u>Measuring</u> - Before any sampling for staining was done the foetuses were measured with callipers to determine the relationship between the measurements obtained with the callipers and the skin surface measurement. A few were measured with a flexible copper wire and the relationship worked out. This has been placed in the appendix.

The following measurements were taken with callipers - <u>see figure 2</u>.

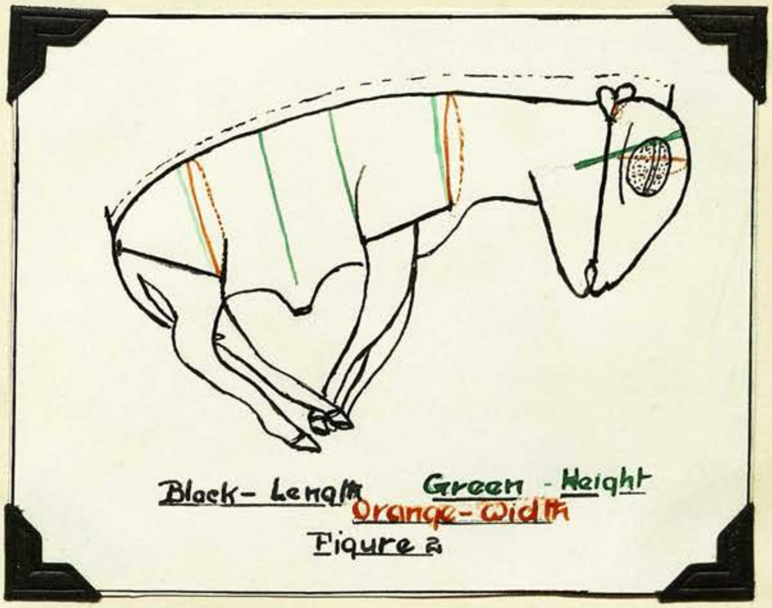


Figure 2

LENGTH MEASUREMENTS.

I. Crown to rump - i.e. C.R. - from the highest point of the head to the root of the tail.

2. Maxilla length.

3. Humerus length. - Long-bone measurements.

4. Femur length.

HEIGHT MEASUREMENTS.

I. Crown to mandible - in a straight line from the highest point of the crown to the **Ventral** edge of the lower jaw bone.

2. Mid-dorsal line to Humerus head. - i.e. M.D.L. to humerus head.

3. Mid-dorsal line to the Point of the Olecranon. - i.e. M.D.L. to elbow.

4. Mid-dorsal to the Navel. - i.e. M.D.L. to navel.

5. Mid-dorsal line to the Femur head. - i.e. M.D.L. to femur head.

WIDTH MEASUREMENTS.

I. R.eye to L.eye.

2. R.ear to L.ear.

3. R.humerus head to L.humerus head.

4. R.femur head to L.femur head.

b) Sampling.

Skin samples were taken from the following regions. - See figure 3.

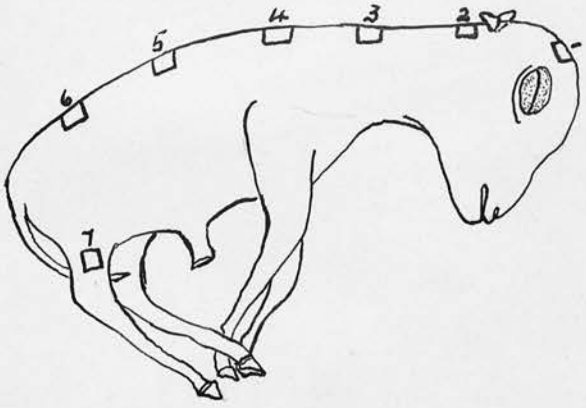


Figure 3.

I.	Poll	- on the mid-dorsal line half-way between the ears and the positions of the horns.
2.	Neck.	- on the mid-dorsal line halfway between the ears and the last cervical vertebra.
3.	Neck Base.	- on the mid-dorsal line at the level of the last cervical vertebra.
4.	Withers.	- on the mid-dorsal line level with the fifth rib.
5.	Back.	- on the mid-dorsal line level with the last rib.
6.	Superior ileum.	- on the mid-dorsal line on the medial angles of the ilea.
7.	Britch	- Immediately posterior to the stifle joint and midway across the thigh on the lateral aspect.

These regions were chosen because they were representative of the six Areas into which the skin of the foetus can be divided according to developmental stages - see Paper I Galpin, in appendix.

Poll	represents	A	area,	the	first	to	develop	follicles.
Neck	"	B	",	"	second	"	"	"
Neck base	"	C	",	"	third	"	"	"
Withers Britch	represent	D	",	"	fourth	"	"	"
Back	represents	E	",	"	fifth	"	"	"
Superior ileum	"	F	",	"	sixth	"	"	"

c) Bulk Staining.

From each animal on which the fibres were not through the skin a complete series of skin snippet samples was taken for examination in bulk. The foetuses had been fixed in five per cent formalin. Each snippet was therefore washed in distilled water and then treated in the following way:-

I. Stained in haemalum, for six hours - made by dissolving 100 grams of potash alum in 2000 mls. of water and adding 2 grams haematoxylin crystals and allowing the mixture to ripen.

2. Differentiated in 70 per cent alcohol for at least 36 hours; the acid alcohol was made by adding 5 drops of hydrochloric acid to 100 ccs. 70 per cent alcohol.

3. Dehydrated in diethylene dioxide for at least 48 hours - one change after first 24 hours.

4. Partially cleared in a solution of 1 part methylsalicylate to 2 parts diethylene dioxide for 2 hours.

5. Further cleared in a solution of 2 parts methylsalicylate to 1 part diethylene dioxide for 2 hours.

6. Finally cleared in methylsalicylate about 12 hours.

7. Mounted in Euparal or xylol balsam.

These snippets were then ready for the examination and the counting of follicles under the microscope. In addition to haemalum, borax carmine, and picro-indigo-carmine were tried. Borax-carmine was quite a good stain for the younger foetuses when follicle density was still low but was poor when the density became high. Picro-indigo-carmine gave a poor differentiation before keratinisation of the fibres had begun.

d) Section Cutting.

For sectioning the skin, samples were treated in the following way:-

I. Washed in distilled water.
2. Dehydrated in alcohol.
3. Cleared in alcohol.
3. Cleared in cedarwood oil.
4. Placed in equal parts cedarwood oil and paraffin overnight.
5. Transferred to 52° paraffin for two hours.
6. Changed to a fresh 52° paraffin for 1½ hours.

The skin snippets were small and longer periods of hot infiltration with paraffin hardened them.

After sections of 10 μ thick had been cut they were attached to the slide with albumen fixative and the paraffin removed with xylol.

They were then passed through a descending series of alcohols to distilled water and stained in the following way:-

I. Stained 10 minutes in Delafield's Haematoxylin - overstaining resulted.
2. Washed in running tap water - 10 minutes.
3. Stained five minutes in Unna's water.
4. Washed in distilled water.

5. Stained 5 minutes in a 1 per cent aqueous solution safranine.
6. Washed in distilled water.
7. Stained 0·5 per cent potassium bichromate solution for 10 to 15 minutes.
8. Washed in distilled water.
9. Passed through an ascending series of alcohol to zylol.
10. Mounted in xylol-balsam.

This method of treating and staining was found to be the most satisfactory. Various other methods were tried. Mayer's muci-carmine was experimented with but owing to the early stage of development of the glands was found to give poor differentiation. Picro-indigo-carmine gave good keratin stains but was of no use for sections from young foetuses. Mann's methylene-blue-eosin method was tried but was found to be too diffuse for high power examination. Heidenhain's haematoxylin was good but the differentiation not so varied as in the Unna's water method used.

The actual method used was an adaptation of Shapiro's Unna's water method-see *Carlton* p. 288, 1926 Edit. It was found that using the method given the nucleii did not stain very clearly. The sections, were therefore, first overstained in Delafield's haematoxylin. The acid in the Unna's water removed the excess stain and the nuclei appeared black. The composition of the Unna's water used was:-

Wasser blau	1 gram.	Solution A
Orcein (Grubler)	1 gram.	
Glacial acetic acid	5 ccs.	
Glycerine	25 ccs.	
Absolute alcohol	100 ccs.	
Distilled water	100 ccs.	
Eosin (Alcohol soluble)	1 gram.	Solution B
Absolute Alcohol	80 ccs.	

1 per cent Aqueous solution Hydroquinone Solution C.

These were freshly mixed before use in the following proportions:-

A.	B.	C.
10	3	3

The following method of Shapiro was also tried but did not give such good results as the first one.

I. Stained with Orth's Lithium carmine 20 to 30 mins.

2. Differentiated in Acid Alcohol.

3. Washed in tap water

4. Stained in an Orcein solution 24 hours.

Solution		
	Orcein D (Grubler)	1·5 grams.
	96 per cent Alcohol	120 ccs.
	Distilled water	60 ccs.
	Nitric acid	6 ccs.

Add sufficient of the solution to a 3 per cent nitric acid in 80 per cent alcohol solution to make it a dark brown colour.

5. Differentiated in 80 per cent alcohol.

6. Stained in a Picro-indigo-carmine solution.

Solution		
	Saturated Aqueous solution picric acid	200 ccs.
	Indigo carmine	0·5 grams.

7. Rinsed in a 3·5 per cent acetic acid solution.

8. Passed through Alcohol 96 per cent.
Xylol.

9. Mounted in balsam

This gave good differentiation of muscle and elastic fibres but did not give a good general differentiation until the foetuses were at least 97 days old.

C. .Examination of Samples.

I. Bulk samples

These were used to gain a knowledge of the general arrangement and distribution of the follicles and for counting follicular density. The lines of follicle growth and the arrangement of the follicles were easily seen. Counts were made from each skin snippet. For counting, a 5 mm. square was inserted in the eye piece and the field magnified a hundred and three times. The follicles were orientated and arranged in lines.

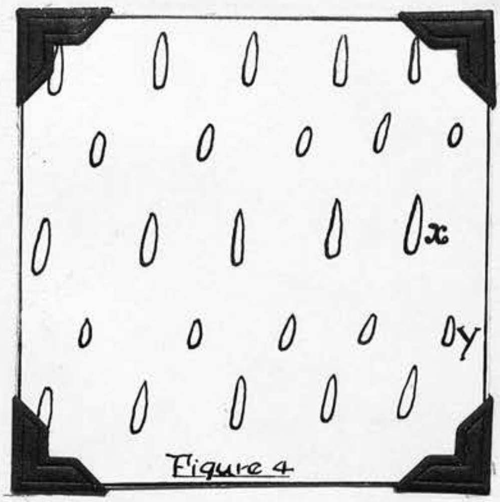


Figure 4

The number of follicles to a line - i.e. the number of follicles on a dorso-lateral line - were counted and the number calculated from the other two counts. The counts were expressed thus:- $\frac{\text{Area}}{24} = \frac{\text{D.L.Line}}{6.} \times \frac{\text{C.R. Line}}{4.}$

D.L. Line = Dorso-lateral Line
C.R. Line = Crown-rump Line.

2. Skin Sections.

The follicular arrangement was compared with that found in the bulk samples. The successive stages of follicle development were compared with those found in the bulk samples.

Glandular development on the different regions was followed by means of serial sections. The times of appearances of the sebaceous and sudoriferous glands, and of the root sheaths as well as the fibre itself were also noted.

Table 2.

To show the Arrangement of the Foetuses in Groups

Group	Age in Days.	No.	Av. Age.	Stage of Follicle Development.
I	42, 46, 49	7	46	No follicles on any area.
II	52, 56, 60, 64	10	59	Follicles present, A, B & C Areas. No follicles present D, E & F Areas.
III	68, 72, 76, 80	14	74	Completed trio stage development - A,B & C Areas. Follicles present D, E & F Areas.
IV	83, 87, 90	14	86	Nine stage development A, B & C Areas. Completed trio stage development - D, E & F Areas.
V.	93, 97, 101	14	97	Fibres through skin A, B, & C Areas. Nine stage development D, E, & F Areas.
VI	104, 108, 112	10	108	Fibres through skin, A, B & C Areas. Fibres through skin, D, E & F Areas.
VII	118, 122, 127	8	122	Fibres through skin on all Areas.

D. Statistical Methods.

I. The measurements representing length, height and width had been taken. To find the growth gradients all measurements at each age were then plotted against time on one way logarithmic graph paper - see Fisher (Statistical methods for Research Workers) pp. 28-32 - 1925 Edit.

The number of measurements at each age was too few and the difference between the ages not more than four days so it was decided to group the measurements. The average size of the group was then plotted against the average age of the group on one way logarithmic graph paper; this gave the relative growth gradient for a region. This was done for the C.R. measurements, the long bones, the dorse-lateral measurements and the width measurements. For the grouping see Table 2.

This grouping was somewhat arbitrary and the follicle development not so clear-cut as it would appear from the table. There was a tendency for the D area to be somewhat in advance of the E and F areas and for the C area to lag behind the A.and B ones.

From the differences between the successive naperian logarithms of the size of each of the groups, the decrease in relative growth rate per cent per day was calculated. See Fisher (Statistical Methods for Research Workers pp. 28-32 - 1925 Edit.) Graphs of the decrease in the relative growth of each region were then drawn. To compare with these graphs the increase per cent per day was calculated from the increase in size from one group to the next.

2. The Equilibrium Constant of Huxley (6)

Huxley in "Problems of Relative Growth" (1932), has given the formula $y = bx^k$ when y = the measurement of the part and x = the measurement of the whole. "The measurement of the whole" used as the standard in this study, was the C.R. measurement.

In a personal communication, Professor Huxley suggested that the new terminology for relative growth - to be published soon by Professors Huxley and Teissier - should be used. They have suggested that the term equilibrium constant should replace growth co-efficient k.
is Isometry was the term used to indicate that two regions were growing at the same rate? time. Allometry -
s negative or positive - was the term used to show that two regions were growing at different rates. The formula now reads $y = bx^{\alpha}$.

The measurements for all regions were plotted against the C.R. measurement on a double logarithmic grid to give comparable values. From the graphs, the average value for the three main lines of growth were obtained. These were then plotted against body position to show the change in equilibrium constant from the anterior to the posterior end of the body.

From the formula $\alpha = \dfrac{\log.y_1 - \log.y}{\log.x_1 - \log.x}$

α was calculated for each period of growth. The calculated values of α were then plotted against time to show the minor variation in the equilibrium constant.

3. 'α-with-time'.

Richards (7) in a recent paper refers to the fact that small differences in the rate of growth though significant are lost in the general trend. He points out that a single average α value is misleading.

It was thought that the minor changes in α value as well as the growth gradient might throw light on changes in follicle density in relationship to growth rate. The decrease in relative growth rate per cent per day had been calculated - see Fisher (5)

From the formula

$$\alpha = \frac{\dfrac{\log._e y_1 - \log._e y}{t} \times 100}{\dfrac{\log._e x_1 - \log._e x}{t} \times 100}$$

An equilibrium constant which allowed for the lapse of time was calculated.

When the graphs from the α calculated from the above formula were compared with the graphs drawn for the α from Huxley's (6) formula

$$\alpha = \frac{\log. y_1 - \log. y}{\log. x_1 - \log. x}$$

it was found that both graphs showed the same general trend; the α-with-time graphs, however, increased the importance of the variations in the equilibrium constant.

4. Follicle counts.

The follicle counts for each position at each age were averaged to give the average follicular density at that stage of development, and the averages plotted to show a correlation between follicular density and growth increase.

III. RESULTS

A. The proportion of Pre-curly-tips to Curly-tips in the Lamb's Coat.

The following table 3 gives the number of pre-curly-tip fibres per hundred fibres in the coat of some New Zealdnd Romney, Southdown and Ryeland lambs.

It will be seen that there was no correlation between the distribution of high pre-curly-tip counts and fibre type-array distribution.. See paper 2 in appendix on "The Occurrence of a Britch-poll Fibre-type-array Gradient"

From the prenatal studies, however, it can be seen that the earlier follicle initiation took place on a region, the more pre-curly-tips were present in that region of the lamb's coat. See paper I in appendix on the "Prenatal Development of the New Zealand Romney Lamb".

It will be seen that the distribution of pre-curly-tips varied considerably from lamb to lamb, but the general trend was for early developing areas to have more pre-curly-tips than later developing ones. There was a general trend for the proportions to begin in the following ratio.

AREAS A & B   AREAS B & C   AREA D   AREA E   AREA F
4 : 3 : 2 : 2 : 1

These ratios were in no way fixed and were only of use for general analysing on a broad basis.

The pre-curly-tips, it was found, could constitute about one third of the total fibre population of some regions - notably the poll regions - but were rarely more than one third. From a personal communication - Rudall on the Suffolk Down finds over half the fibre population of the poll region belonging to the pre-curly-tip group. He also found that the shoulder point and withers

Table 3. To show the number of precurly-tips occurring on the different positions; the positions have been allocated to the Areas to which they belong according to their time of follicle initiation - see paper I in appendix.

Positions sampled.	AREA	NO. OF PRE-CURLY-TIPS PER 100 FIBRES.												
		Romney									South-down		Rye-land	
		Sheep Numbers												
		607	619	622	628	638	641	745	755	763	80	85	50	63
Poll	A	No samples				32	30	20	24	25	19	32	31	31
Neck	B	No samples					25	14	21	22	No samples			
Shoulder point	C	22	19	20	27	25	20	10	20	20	15	29	24	24
Withers	D	17	13	17	21	22	18	7	14	13	12	27	19	20
Fifth rib		No samples						8	14	14	—		18	20
Britch		15	15	16	21	22	16	9	14	13	9	26	18	19
Back	E	14	10	10	18	18	13	6	12	9	7	25	14	13
Side		14	11	12	19	20	14	7	11	8	5	23	11	13
Superior ileum	F	8	8	8	15	8	10	5	8	5	5	17	6	7
Hip joint		10	9	9	17	7	8	5	-	6	No samples			
Superior flank		8	8	8	17	7	9	No samples						

The lambs whose numbers are given here are the same lambs used in the fibre type-array gradient studies. See paper 2 in appendix.

regions had fewer pre-curly-tips than were found on the lambs for which the figures have been given. This may be due to a difference in technique as the pre-curly-tips on the Down breeds examined have been found to be very fine and short and unless the sample was carefully examined may not be seen at all or casually grouped with the histerotrichs.

B. Relative Growth Gradients.

Graphs I, 2 and 3, - Tables 4 to 15 give the measurements - were drawn to show the growth gradients of the various regions of the foetal lamb. See figure 2.

Graph I was drawn to show the relative growth gradients for the C.R., the maxilla, the humerus, and the femur - all length measurements.

Graph 2. showed the relative growth gradients for the dorso-lateral regions of the body:-

the M.D.L. to the mandible.
the M.D.L. to the humerus head
the M.D.L. to the elbow.
the M.D.L. to the femur head.

Graph 3. was to show the relative growth gradients from one side to the other:-

the eye to the eye.
the ear to the ear.
the humerus head to the humerus head.
the femur head to the femur head.

It will be seen that with increasing age there was, with the exception of the hind limb, a general decrease in growth rate. The dorso-lateral regions - with the exception of the head region grew rapidly till the 86 day stage was reached, after which there was a considerable decrease in the relative growth rate. The growth rate of the head region began to decrease earlier at about the 74 days stage. The growth rate of the maxilla decreased at approximately the same time as the dorso-lateral regions of the head. The femur and humerus, however, - the humerus less markedly than the femur - showed considerable increase in their growth rates from the 86 days to the 122 days stage.

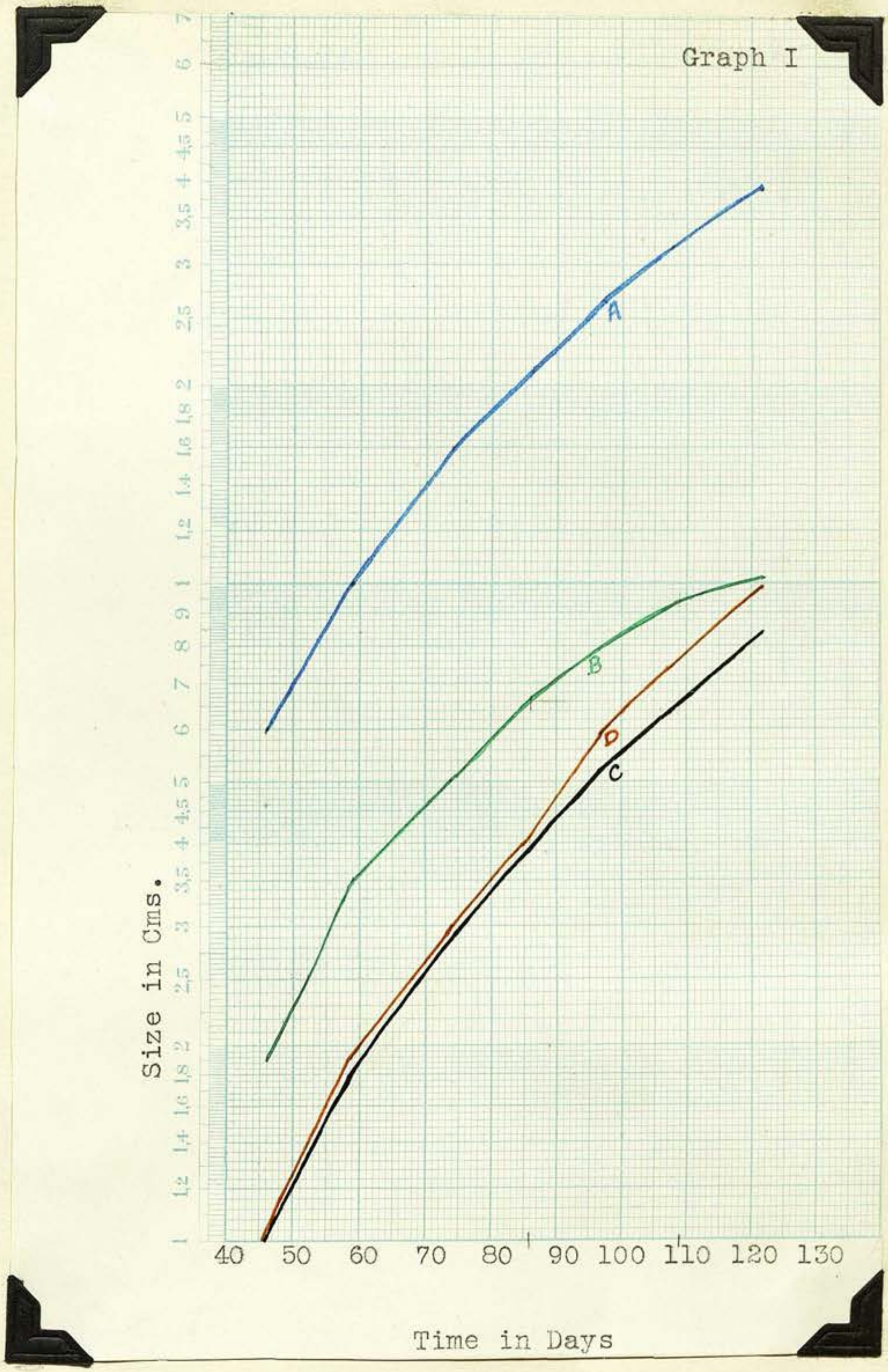
The curves for the increases in body width behave in a manner similar to those for the length increases of long bones but the increases in the body width growth rates for the fore and hind were not so marked as for the humerus and femur lengths. The head regions, showed the decrease in the magnitude of the growth rates again taking place about the 74 day stage. Examination of the C.R. growth gradient reveals that the growth rate of the length of the foetus as a whole gradually diminished with increasing age.

Therefore, we find that the relative growth rate of the foetus as a whole decreases with age. The head region decreases its relative growth rate along all three lines of growth after the 74 day stage. The fore limb region decreases its relative growth rate dorso-laterally after the 86 day stage,but its width and length relative growth gradients do not decrease, the length tending, if anything, to increase from the 86 days to the 108 days stage. The hind limb also showed a decrease dorso-laterally in its relative growth rate but at the 86 days stage in width and length the relative growth rate increased.

Graphs I, 2, and 3 show the curves for the relative growth gradients of the head, forelimb and hindlimb regions in length, height and width, and for the foetus "as a whole" from the crown to rump measurements. The actual average size of a group of foetuses has been plotted against the average age of the group on one-way logarithmic graph paper. For figures see Tables 4 to 15.

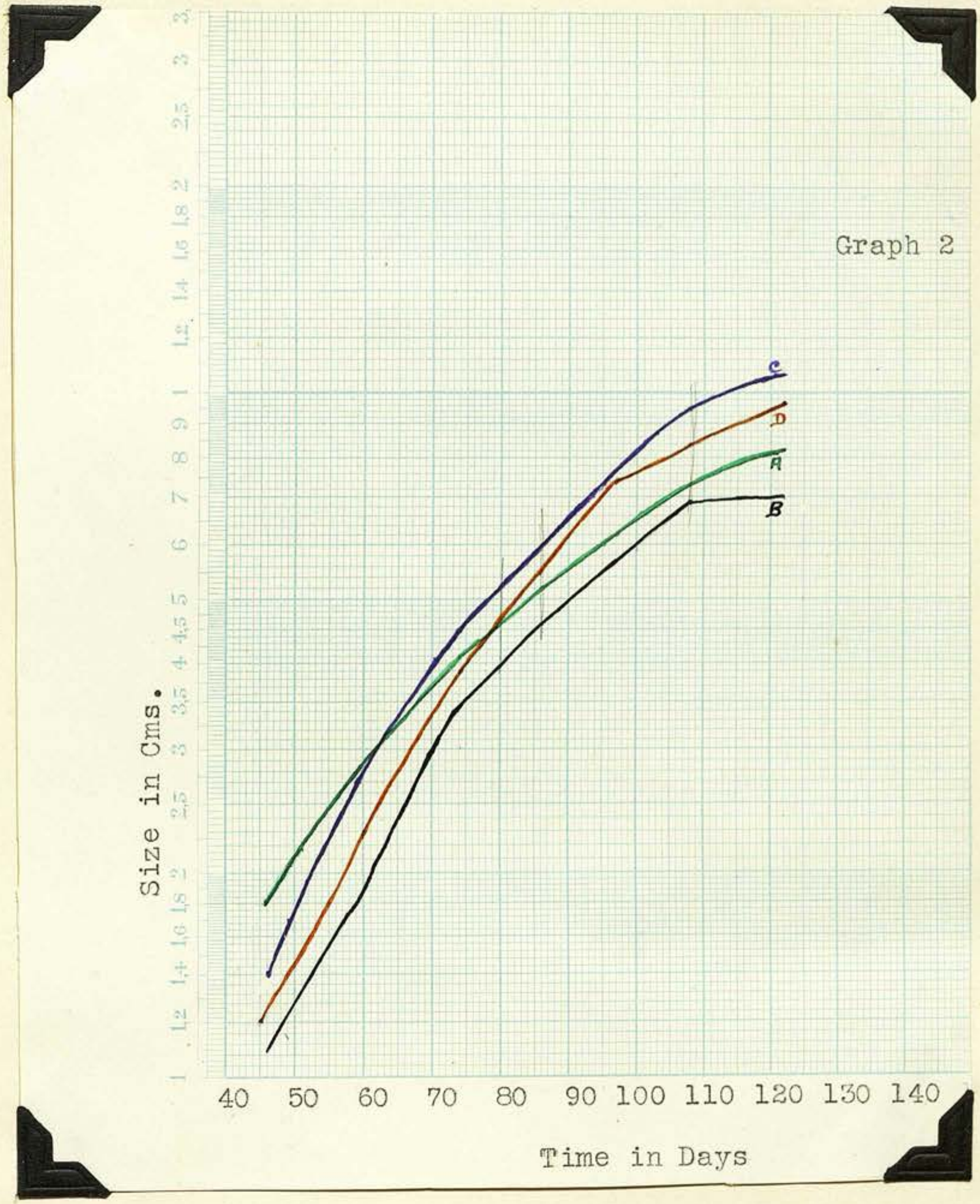
The colours on all three graphs have been arranged thus:-

Blue - C.R.
Green - length, height and width of the head region.
Red - width " " " "
Black - length, height and width" " forelimb region.
Purple - height of the forelimb region.
Orange - Length, height and width of the hindlimb region.



Graph I The Relative Growth Gradients for the increase in foetal length.

Curve A - C.R. - blue
Curve B - Maxilla length - green
Curve C - Humerus length - black
Curve D - Femur length - orange



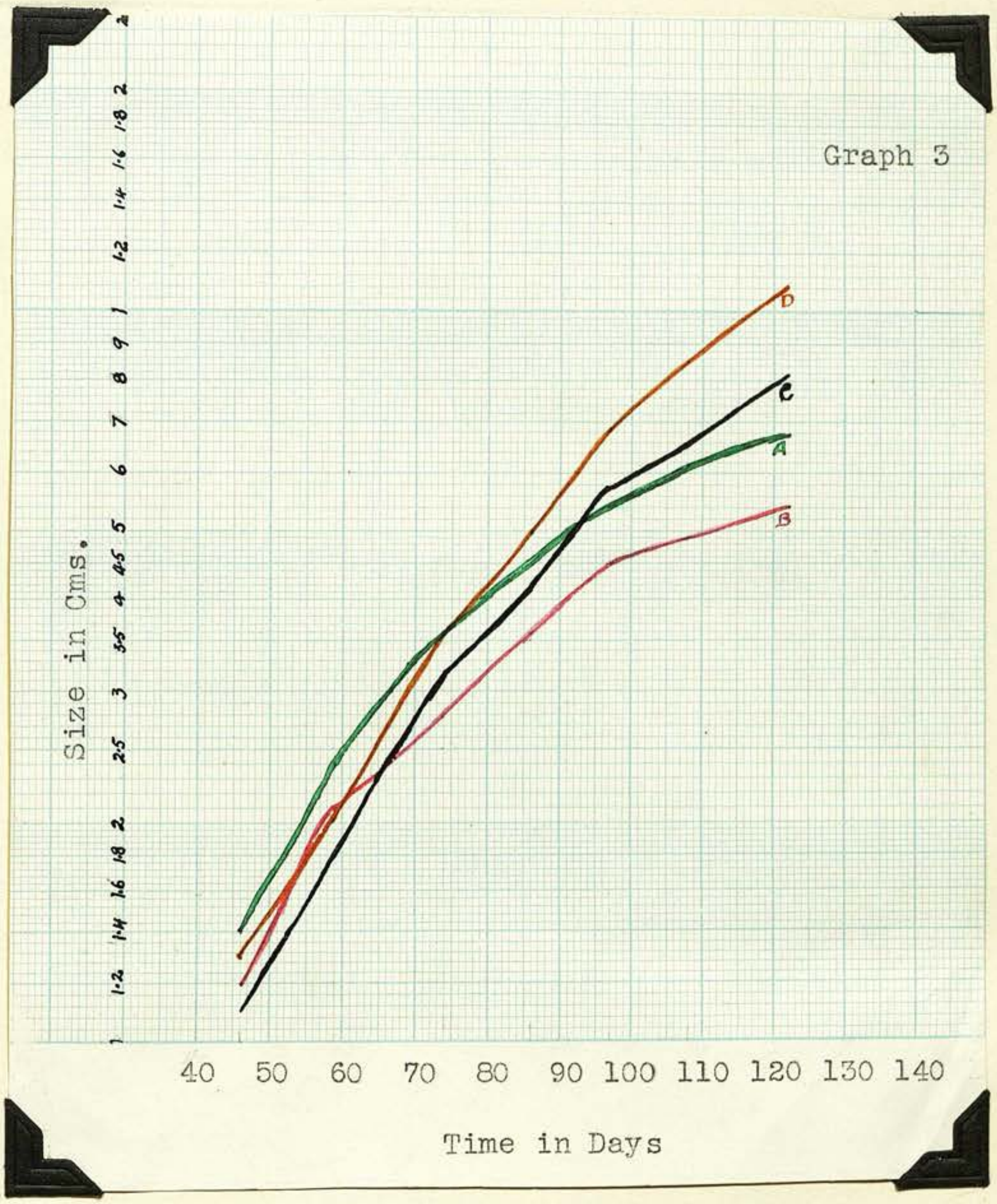
<u>Graph 2</u> The Relative Growth Gradients for the increase in the height of a foetus.

Curve A - Crown - mandible - green

Curve B - M.D.L. - humerus head - black

Curve C - M.D.L. - elbow - purple

Curve D - M.D.L. - femur head - orange.



<u>Graph 3</u> The Relative Growth Gradients for the increase in foetal width.

<u>Curve A</u> - Eye - eye - green

<u>Curve B</u> - Ear - ear - red

<u>Curve C</u> - Humerus head - humerus head - black

<u>Curve D</u> - Femur head - orange

The following tables 4 to 15 give the measurements for the different regions of the foetus at different times, and the groupings adopted.

The ages of the foetuses are given in days, the measurements in millimeters. The increase in actual size is given in millimeters.

The naperian logarithm of the average size of each group is given. The $\log._e$ increase is given as the difference between each successive naperian logarithm - see Fisher(5) pp.28-32. The relative growth rate per day per cent is the

$$\frac{\log._e \text{ increase}}{\text{time}} \times \frac{100}{1}$$

α was calculated from the formula

$$\alpha = \frac{\log.y_1 - \log.y}{\log.x_1 - \log.x} \quad - \text{ see Huxley(6)}$$

When y = the part and x = the whole (C.R. in these calculations). 'α with-time' was calculated from the formula

$$\alpha = \frac{\dfrac{\log._e y_1 - \log._e y}{t} \times 100}{\dfrac{\log._e x_1 - \log._e x}{t} \times 100}$$

when y = the part and x = the whole - C.R. in these calculations.

The increase/per day per cent was calculated from the $\frac{\text{increase per cent}}{\text{time}}$ = increase per cent per day.

Table 4. is for the standard Crown-Rump measurements.

Tables 5, 6, 7 and 8 are for the measurements of the head region.

Table 5 the maxilla length - length

Table 6 the crown - mandible - height

Table 7 the R. eye to L. eye - width

Table 8 the R. ear to L. ear - width

Tables 9,10,11,12 are for the measurements of the fore-limb region:-

Table 9 the humerus length - length

Table 10 M.D.L. - humerus head - height

Table 11 M.D.L. - point of the olecranon (elbow) - height

Table 12 Humerus head - humerus head - width

Tables 13,14,15, are for the measurements of the hindlimb region:-

Table 13 the femur length - length

Table 14 M.D.L. - femur head - height

Table 15 Femur head - femur head - width

The measurements for six foetuses are not given. Three of these foetuses were very much distorted so that their measurements were useless and the remaining three were a set of triplets whose measurements did not correspond with those of other foetuses of the same age.

Table 4

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	Increase per cent	Increase per cent per Day
42		44,44	60		1·79176				
46	46	58							
49		70,60,80,71							
				40		·51083	3·929	66·7	5·1
52		90,85	100		2·30259				
56	59	100							
60		108,105,106,108,110							
64		120,119							
				60		·47000	3·133	60	4
68		134,155,149	160		2·77259				
72	74	163,161,164,154							
76		169,174,176,162							
80		200,183,194							
				50		·27193	2·266	31·2	2·6
83		190,185,214,214,205	210		3·04452				
87	86	225,225,231,221,230							
90		237,237,235,229							
				60		·25132	2·284	28·6	2·6
93		246,253,253	270		3·29584				
97	97	266,254,250,255) 270,276,253,255)							
101		305,302,293							
				50		·16990	1·544	18·5	1·7
104		303,272,278,286,300	320		3·46574				
108	108	310,							
112		320,328,320,315							
				70		·19782	1·413	21·9	1·6
118		333,333	390		3·66356				
122	122	400,408,395,							
127		435,447,362							

Crown-rump

Table 5

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day.	γ with-time	γ	Increase per cent	Increase per cent per Day.
42 46 49	46	15,15 18 20,20,22,22	19		·64185						
				16		·61091	4·853	1·23	1·1	84	6·5
52 56 60 64	59	30,26 30 34,36,35,32,34 43,49	35		1·25276						
				15		·35668	2·378	·75	·89	42·9	2·9
68 72 76 80	74	41,42,44 44,50,48,48 56,54,51,50 58,57,59	50		1·60944						
				17		·29267	2·439	1·07	1·02	34	2·8
83 87 90	86	61,63,60,58,64 64,70,69,67,74 72,75,67,74	67		1·90211						
				13		·17733	1·612	·706	·92	19·4	1·7
93 97 101	97	76,70,78 81,78,80,86,80) 82,78,76) 80,84,84	80		2·07944						
				13		·15057	1·368	·88	·97	16·3	1·5
104 108 112	108	95,90,87,85,93 94 93,93,105,94	93		2·23001						
				13		·07856	·561	·4	·93	13·97	·99
118 122 127	122	103,104 100,100,105 120,110,106	106		2·30857						

The Maxilla length

Table 6

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ-with-time	γ	Increase per cent	Increase per cent Per Day
42		15,16	18		·58779						
46	46	18									
49		19,18,19,19									
				10		·43183	3·322	·84	·93	55·5	4·3
52		23,22	28		1·02962						
56	59	24									
60		30,28,28,24,29									
64		32,28									
				13		·38137	2·542	·81	·91	46·4	3·1
68		34,36,37	41		1·41099						
72	74	37,38,40,40									
76		42,42,45,40									
80		42,48,46									
				11		·23767	1·98	·87	·96	26·8	2·2
83		48,50,46,46,51	52		1·64866						
87	86	52,52,53,54,57									
90		53,62,50,59									
				10		·17589	1·599	·7	·93	19·2	1·7
93		56,55,60	62		1·82455						
97	97	63,58,64,64,)									
		64,62,59,58)									
101		64,70,69									
				11		·16332	1·439	·93	·99	17·7	1·6
104		76,69,69,68,72	73		1·98787						
108	108	75									
112		74,70,78,78									
				9		·11626	·830	·59	·92	12·3	·88
118		75,79,70,85,80	82		2·10413						
122	122	95,90,84									
127											

Crown-mandible - height

Table 7

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ - with-time	γ	Increase per cent	Increase per cent per Day
42		12,12	14		·33647						
46	46	12									
49		17,15,14,16									
				10		·53900	4·145	1.06	1·03	71	5·5
52		22,20	24		·87547						
56	59	22									
60		24,24,24,23,23									
64		32,30									
				12		·40546	2·703	·86	·94	50	3·3
68		32,32,33	36		1·28093						
72	74	34,34,34,36									
76		37,38,39,36									
80		38,38,37									
				9		·22315	1·859	·82	·95	25	2·1
83		44,42,40,38,43	45		1·50408						
87	86	46,45,48,46,46									
90		50,52,45,48									
				9		·18232	1·657	·73	·93	20	1·8
93		50,50,52	54		1·68640						
97	97	56,52,53,54)									
		54,54,55,51)									
101		63,58,58									
				8		·13815	1·256	·82	·97	15	1·4
104		64,58,54,60,62	62		1·82455						
108	108	62									
112		64,68,61,64									
				5		·07756	·554	·39	·88	8	·57
118		66,66	67		1·90211						
122	122	64,65,68									
127		66,70,67									

R.Eye to L.eye - width

Table 8

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ - with-time	γ	Increase per cent	Increase per cent per Day
42		10,10	12		·18232						
46	46	10,									
49		15,14,12,16									
				9		·55962	4.304	1·09	1.05	75	5·8
52		18,18	21		·74194						
56	59	18									
60		22,22,20,21,20									
64		24,23									
				7		·28768	1·917	·61	·83	33	2·2
68		26,25,24	28		1·02962						
72	74	24,24,26,26									
76		28,29,30,31									
80		32,31,30									
				8		·25131	2.094	·92	·97	29	2·4
83		35,32,36,34,36	36		1·28093						
87	86	36,38,40,38,36									
90		41,36,35,36									
				9		·22315	2.028	·89	·97	25	2·3
93		38,43,40	45		1·50408						
97	97	47,46,45,44) 42,45,48,42)									
101		55,46,52									
				4		·08516	·774	·50	·98	8.8	·8
104		50,49,50,47,46	49		1·58924						
108	108	45									
112		50,51,50,50									
				5		·09716	·694	·49	·904	16	·7
118		50,52	54		1·68640						
122	122	50,50,52									
127		55,65,61									

R.Ear to L.ear - width

Table 9

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ- with-time	γ	Increase per cent	Increase per cent per Day
42 46 49	46	8,8 9 12,11,9,11	10		·00000						
				8		·58779	4·521	1·15	1·08	80	6·2
52 56 60 64	59	14,15 14 19,18,19,15,16 25,20	18		·58779						
				11		·47692	3·179	1·01	1·00	61	4·1
68 72 76 80	74	23,27,23 26,26,29,26 30,32,32,28 32,33,32	29		1·06471						
				10		·29627	2·468	1·09	1·02	34·5	2·9
83 87 90	86	35,39,35,32,34 38,36,42,40,45 38,46,45,47	39		1·36098						
				13		·28768	2·615	1·15	1·03	33·3	3
93 97 101	97	40,50,48 46,56,51,54) 56,54,50,49) 56,56,68,	52		1·64866						
				11		·19189	1·744	1·13	1·02	21·2	1·9
104 108 112	108	62,60,58,62,59 58 65,72,74,60	63		1·84055						
				21		·27571	1·969	1·4	1·08	33·3	2·4
118 122 127	122	85,77 76,77,75 90,100,89	84		2·11626						

Humerus length

Table 10

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day.	γ - with-time	γ	Increase per cent	Increase per cent per Day.
42		10,10	11		·09531						
46	46	10									
49		14,10,10,10									
				7		·49248	3·788	·96	·98	63·6	4·9
52		15,13	18		·58779						
56	59	16									
60		20,16,18,18,18									
64		21,22									
				16		·63699	4·246	1·36	1·18	89	5·9
68		26,32,32	34		1·22378						
72	74	35,32,30,30									
76		33,41,35,40									
80		38,38,36									
				12		·29228	2·435	1·07	1·03	35	2·9
83		38,42,35,41,44	46		1·52606						
87	86	42,46,50,46,47									
90		47,56,49,55									
				11		·21441	1·949	·85	·96	23·9	2·2
93		54,46,52	57		1·74047						
97	97	58,64,62,58,)									
		48,55,50,57)									
101		70,56,66									
				12		·19105	1·736	1·13	1·02	21	1·9
104		73,62,63,67,60	69		1·93152						
108	108	80									
112		76,73,69,66									
				1		·01439	·103	·073	·83	1·45	·103
118		73,65	70		1·94591						
122	122	66,68,70									
127		80,73,72									

M.D.L. - humerus head - height

Table 11

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per day	γ-with-time	γ	Increase per cent	Increase per cent per Day
42		10,11	14		·33647						
46	46	16									
49		16,15,15,18									
				13		·65678	5·052	1·28	1·15	92·9	7·1
52		22,20	27		.99325						
56	59	22									
60		28,28,29,27,26									
64		34,30									
				18		·51083	3·405	1·09	1·04	66·7	4·4
68		33,36,35	45		1·50408						
72	74	42,42,42,40									
76		48,52,42,46									
80		52,56,50									
				14		·27087	2·257	·99	·99	31·1	2·6
83		57,62,45,51,44	59		1·77495						
87	86	59,58,62,58,62									
90		62,68,58,67									
				18		·26627	2·420	1·06	1·01	30·5	2·8
93		72,76,79	77		2·04122						
97	97	74,75,70,74)									
		78,79,75,76)									
101		85,85,80									
				18		·21007	1·909	1·24	1·04	23·4	2·1
104		96,88,90,77,89	95		2·25129						
108	108	103									
112		91,109,91,101									
				11		·05728	·409	·29	·92	11·6	·8
118		107,91,	106		2·30857						
122	122	102,102,105									
127		105,115,119									

M.D.L. - point of olecranon - height

Table 12

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ - with-time	γ	Increase per cent	Increase per cent per Day
42		8,8	11		·09531						
46	46	10									
49		14,10,12,13									
				7		·49248	3·788	·96	·96	64	4·9
52		16,15	18		·58779						
56	59	15									
60		20,19,17,18,18									
64		19,19									
				14		·57536	3·835	1·22	1·1	78	5·2
68		28,27,27	32		1·16315						
72	74	35,29,34,27									
76		34,31,36,34									
80		38,35,36									
				10		·27193	2·266	1	1	31	2·6
83		36,41,36,39,37	42		1·43508						
87	86	44,40,40,46,40									
90		46,42,54,46									
				15		·30539	2·776	1·2	1·05	36	3·3
93		48,49,50	57		1·74047						
97	97	56,56,63,58)									
		50,50,62,62)									
101		66,62,65									
				9		·14660	1·332	·86	·97	16	1·5
104		62,64,64,68,66	66		1·88707						
108	108	60									
112		72,72,65,68									
				16		·21706	1·550	1·1	1·01	24	1·7
118		80,80	82		2·10413						
122	122	70,70,75									
127		92,95,95									

Humerus head - humerus head - width

Table 13

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ-with-time	γ	Increase per cent	Increase per cent per Day
42		8,8	10		·00000						
46	46	10									
49		12,10,10,11									
				9		·64185	4·937	1·25	1·14	90	6·9
52		14,15,	19		·64185						
56	59	17,[illegible]									
60		18,20,20,19,20									
64		26,22									
				11		·45676	3·045	·97	·99	57·9	3·8
68		28,24,24	30		1·09861						
72	74	24,28,26,28									
76		36,36,34,35									
80		34,36,32									
				10		·28768	2·397	1·06	1·01	33·3	2·8
83		38,37,40,35,44	40		1·38629						
87	86	44,40,45,46,44									
90		40,52,45,51									
				19		·36767	3·342	1·47	1·14	47·5	4·3
93		52,56,57	59		1·77495						
97	97	64,54,62,59)									
		56,57,54,53)									
101		64,70,71									
				15		·22653	2·059	1·33	1·05	25·4	2·3
104		73,74,68,66,62	74		2·00148						
108	108	80									
112		75,80,83,73									
				24		·28090	2·006	1·42	1·1	32·4	2·3
118		93,93	98		2·28238						
122	122	95,93,94									
127		100,115,108									

Femur length

Table 14

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	with-time γ	γ	Increase per cent	Increase per cent per Day
42		8,8	12		·18232						
46	46	12									
49		13,13,13,16									
				11		·65059	5·004	1·27	1·15	91·6	7·04
52		18,18	23		·83291						
56	59	21									
60		23,25,24,23,24									
64		22,28									
				16		·52807	3·52	1·12	1·06	69·6	4·64
68		33,36,32	39		1·36098						
72	74	37,36,38,39									
76		45,43,35,39									
80		40,41,46									
				16		·34377	2·86	1·26	1·07	41	3·41
83		48,49,45,45,54	55		1·70475						
87	86	46,49,60,58,60									
90		66,65,60,60									
				18		·28312	2·573	1·13	1·05	32·7	2·97
93		68,72,76	74		2·00148						
97	97	68,75,74,76,)									
		72,72,72,65)									
101		81,80,80									
				11		·12675	1·152	·75	·98	15·1	1·4
104		80,80,77,84,82	84		2·12823						
108	108	80									
112		93,97,80,87									
				13		·14390	1·038	·74	·94	15.5	1·11
118		89,89	97		2·27213						
122	122	90,96,96									
127		96,104,115									

M.D.L. - femur head - height

Table 15

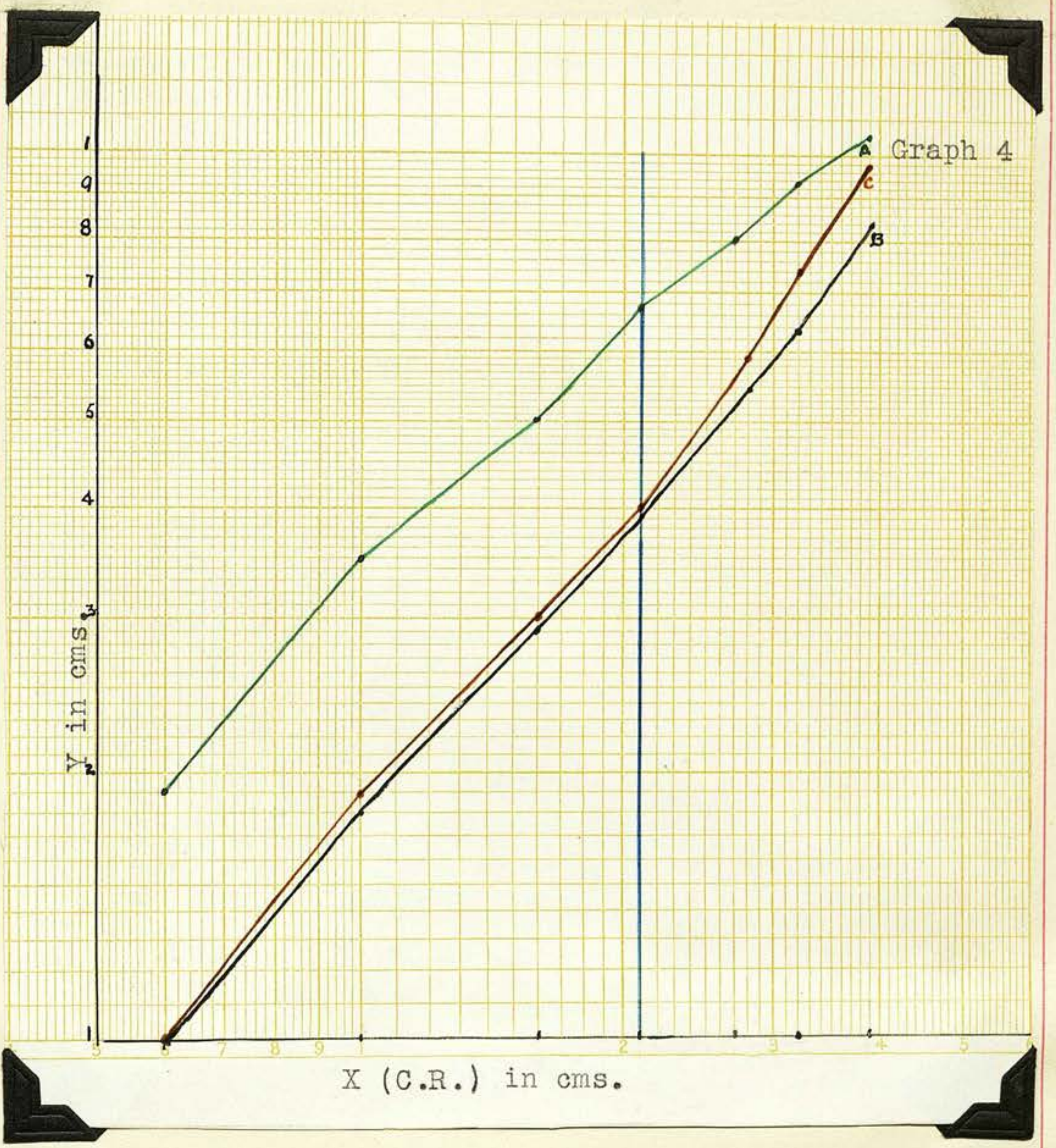
Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ with-time	γ	Increase per cent	Increase per cent per Day
42		8,8	13		·26236						
46	46	15									
49		17,16,14,16									
				7		·43079	3·313	·84	·92	53·8	4·1
52		18,16	20		·69315						
56	59	20									
60		19,18,19,20,18									
64		28,25									
				16		·58778	3·918	1·25	1·125	80	5·3
68		30,29,34	36		1·28093						
72	74	37,36,32,27									
76		37,38,46,37									
80		38,39,40									
				14		·32851	2·737	1·2	1·05	38·9	3·2
83		48,40,43,46,40	50		1·60944						
87	86	56,55,52,48,56									
90		52,48,64,48									
				19		·32118	2·919	1·28	1·07	38	3·5
93		58,60,62	69		1·93152						
97	97	70,64,66,74)									
		70,75,66,67)									
101		84,75,80									
				16		·20855	1·895	1·23	1·01	23·2	2·1
104		82,80,80,75,80	85		2·14007						
108	108	88									
112		104,92,88,85									
				25		·25783	1·841	1·3	1·06	29·4	2·1
118		105,95	110		2·39790						
122	122	90,109,92									
127		125,122,140									

Femur head - femur head - width

Graphs, 4,5 and 6 are for determining the equilibrium constant α . The size of the part is plotted against the size of the whole. (C.R. measurement used as standard) on a two-way logarithmic grid. A line is drawn through the graph at 86 days to show the change in α value after this period.

As the length, height and width measurements are plotted on different graphs the Colours on the graphs have been arranged so that the length, height and width measurements of the same region are in the same colour.

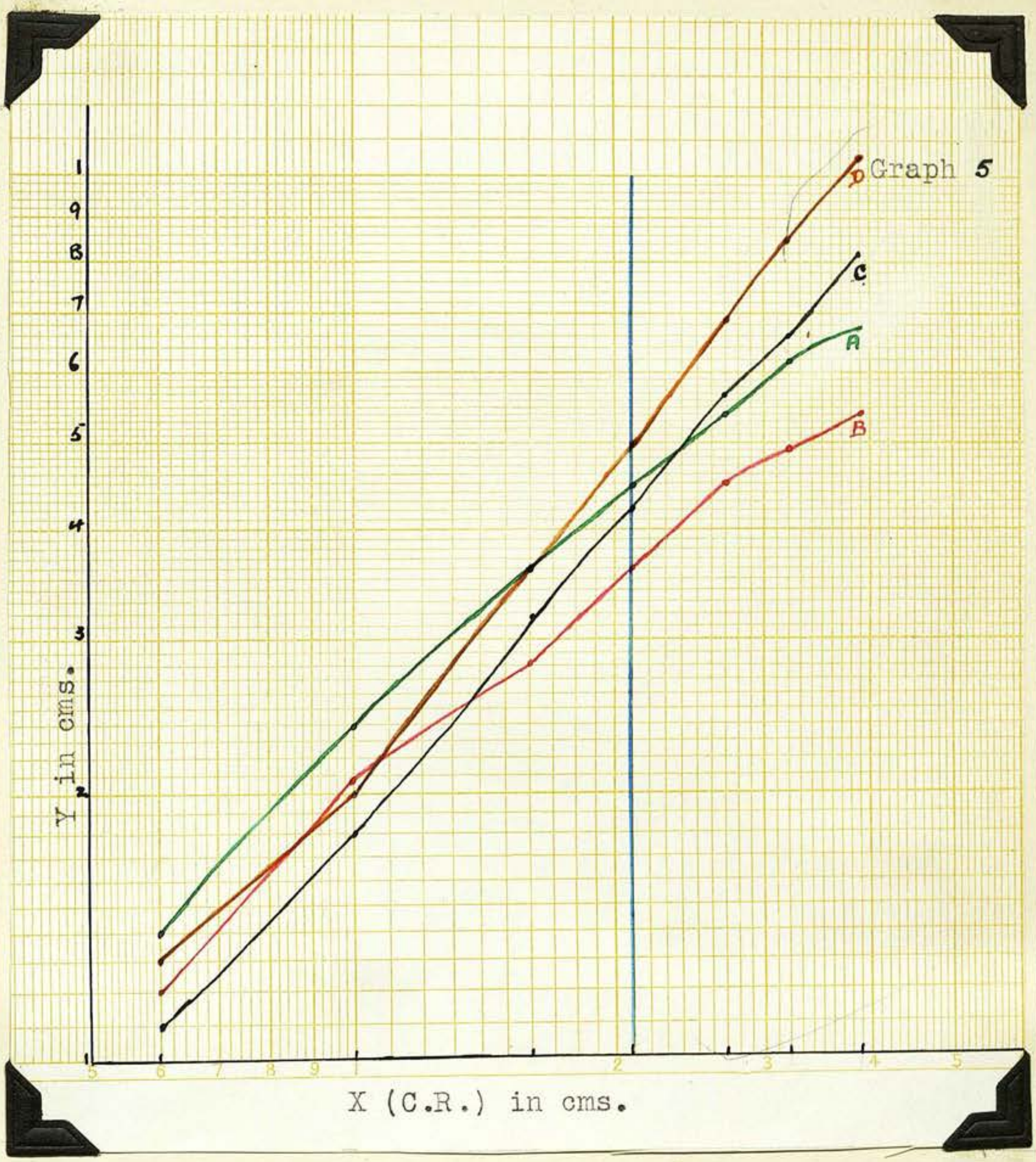
Green - length, height,and width of the head region.
Red - width " " " "
Black - " " " " " "forelimb "
Purple - " " " " "
Orange - " " " " " "hindlimb ".



Graph 4. Increase in the logarithm of the length y of the maxilla, humerus and femur against the increase in the logarithm of the C.R. measurement x see Table 16.

Curve A - maxilla - green	α for 60 - 390 = ·93
	α for 60 - 210 = 1
	α for 210- 390 = ·8
Curve B - humerus - black	α for 60 - 390 = 1·13
	α for 60 - 210 = 1·15
	α for 210- 390 = 1·35
Curve C - femur - orange	α for 60 - 390 = 1·25
	α for 60 - 210 = 1·19
	α for 210- 290 = 1·5

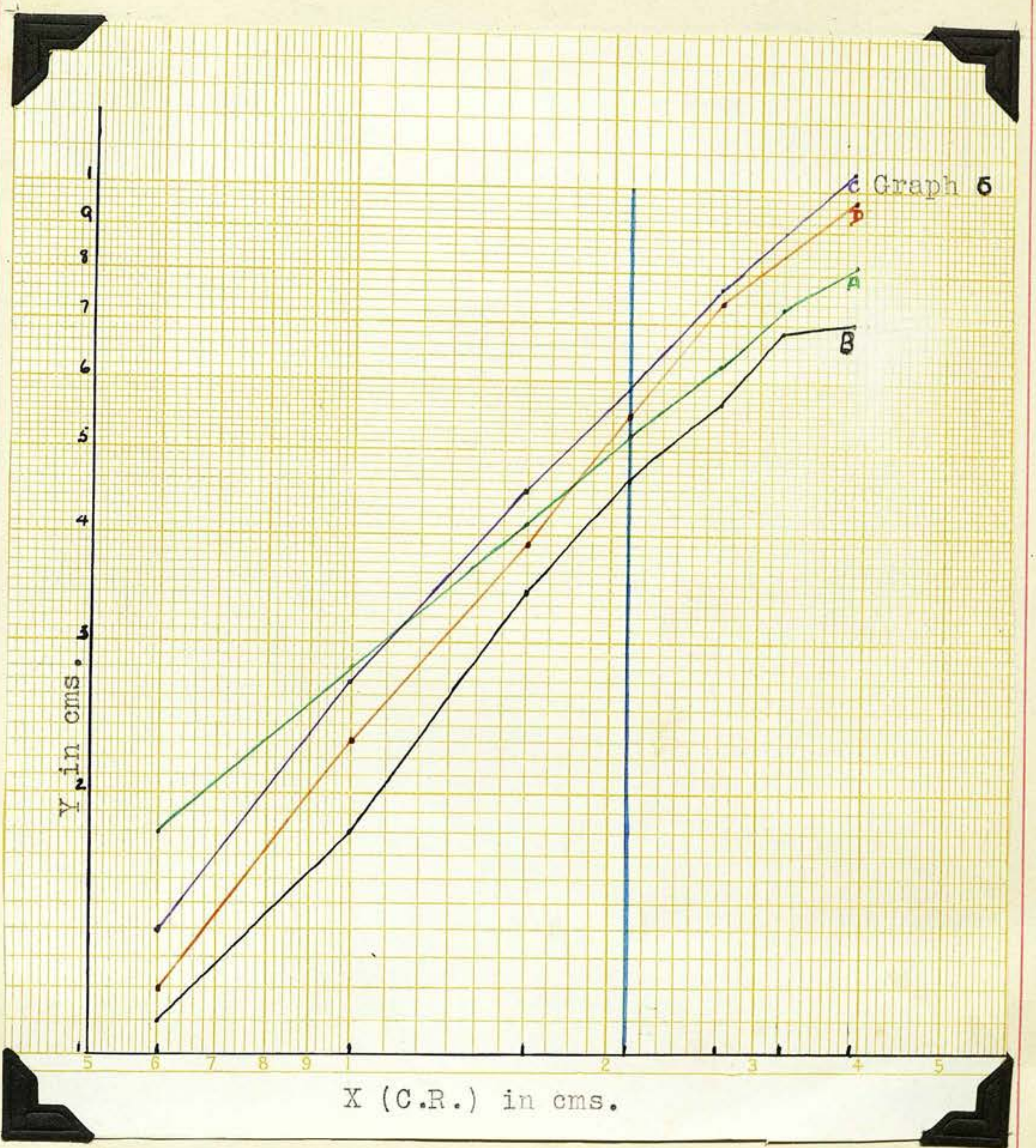
The blue line drawn through the graphs denotes the change from one α value to another at 86 days.



Graph 5. The increase in the logarithm of the width-y- measurements eye - eye, ear - ear, humerus head - humerus head, and femur head - femur head against the increase in the logarithm of the C.R. measurements-x- see Table 17.

Curve A -	eye - eye — green	α for 60 - 390 = ·84 α for 60 - 210 = ·92 α for 210 - 390 = ·65
Curve B -	ear - ear — red	α for 60 - 390 = ·8 α for 60 - 210 = ·87 α for 210 - 390 = ·65
Curve C -	humerus head to humerus head - black	α for 60 - 390 = 1·08 α for 60 - 210 = 1·07 α for 210 - 390 = 1·07
Curve D -	femur head to femur head — orange	α for 60 - 390 = 1·15 α for 60 - 210 = 1·07 α for 210 - 390 = 1·39

The blue line drawn through the graph shows the change from one α value to another at 86 days.



Graph 6 The increase in the logarithm of the height -y- measurements for the crown-mandible, M.D.L. - humerus head, M.D.L. - elbow, and M.D.L. femur against the increase in the logarithm of C.R. measurement-x.- See Table 18.

Curve A. - crown-mandible _ green	α for 60 - 390 =	·78
	α for 60 - 210 =	·74
	α for 210- 390 =	·77
Curve B. - M.D.L. - humerus head-black	α for 60 - 390 =	1
	α for 60 - 210 =	1·15
	α for 210- 390 =	·77
Curve C. - M.D.L. - elbow - purple	α for 60 - 390 =	1·08
	α for 60 - 210 =	1·15
	α for 210- 390 =	·95
Curve D. - M.D.L. - femur head - orange	α for 60 - 390 =	1·13
	α for 60 - 210 =	1·2
	α for 210- 390 =	·95

The blue line drawn through the graph shows the change from one α value to another at 86 days.

C. The Equilibrium constant α of Huxley (6)

Graphs 4, 5 and 6.

$$y = bx^{\alpha}$$

From plotting the measurements for the different regions against the standard C.R. measurement and two-way logarithmic grid and reading off the graph, the α value for the whole region was obtained.

Inspection of the graphs, however, showed that a single α value was incorrect, so the graphs were divided into two parts and two α values taken - one from the 46 days to the 86 days stage and the other from the 86 days to the 122 days stage.

The following tables give α values for the different regions.

Table 16.

The α values for the long bones.

	Maxilla	Humerus	Femur
46 to 122 days.	·925	1·125	1·25
46 to 86 days.	1·0	1·149	1·185
86 to 122 days.	·8	1·345	1·5

Table 17.

The α values for the width measurements.

	Eye-Eye	Ear-Ear	H.head-H.head	F.Head-F.head.
46 to 122 days.	·838	·8	1·075	1·15
46 to 86 days.	·92	·87	1·07	1·07
86 to 122 days.	·65	·65	1·07	1·385

Table 18.

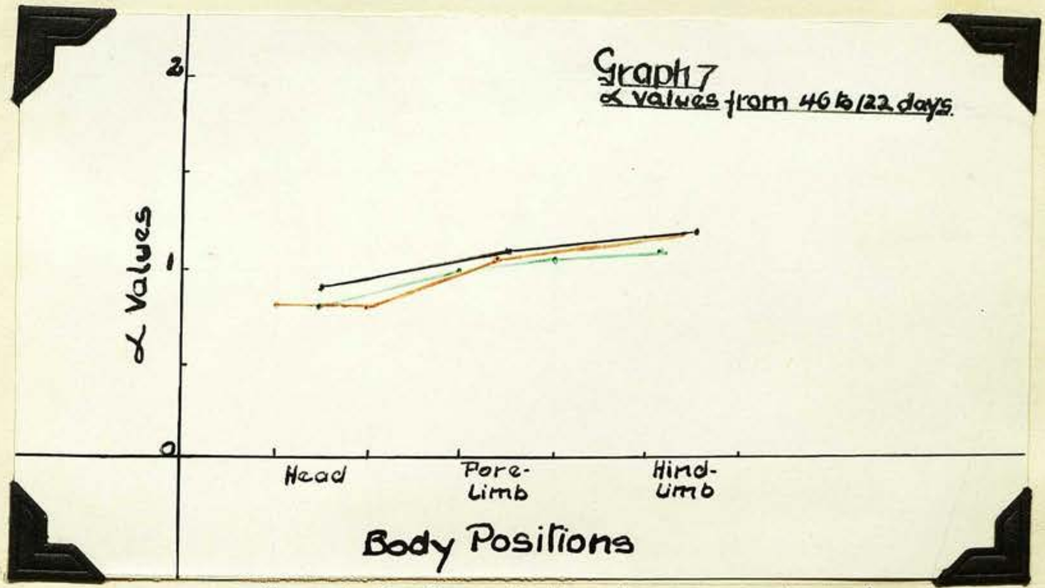
The α values for the dorso-lateral regions.

	Crown-mandible	M.D.L. - H. head.	M.D.L. - Elbow	M.D.L. - Femur head.
46 to 122 days	·78	1·0	1·075	1·125
46 to 86 days	·74	1·148	1·148	1·2
86 to 122 days	·769	·769	·95	·95

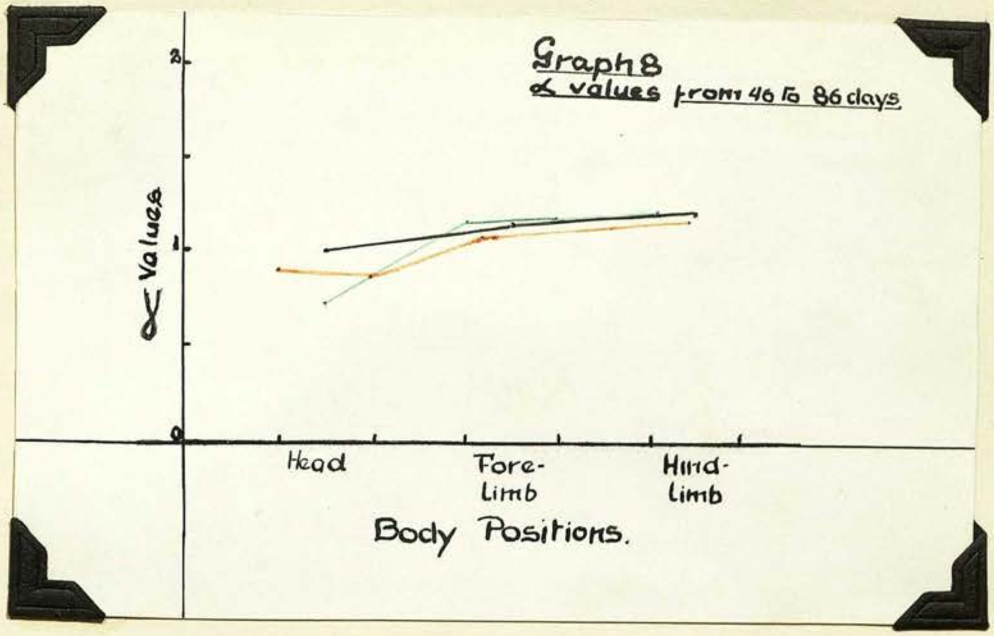
H.head = Humerus head. F.head = Femur head.

From these tables together with the graphs it will be seen that the single α value gave the general trend of growth down the body. It masked, however, the significant change in growth rate taking place at 86 days, in both long bone and width growth rates.

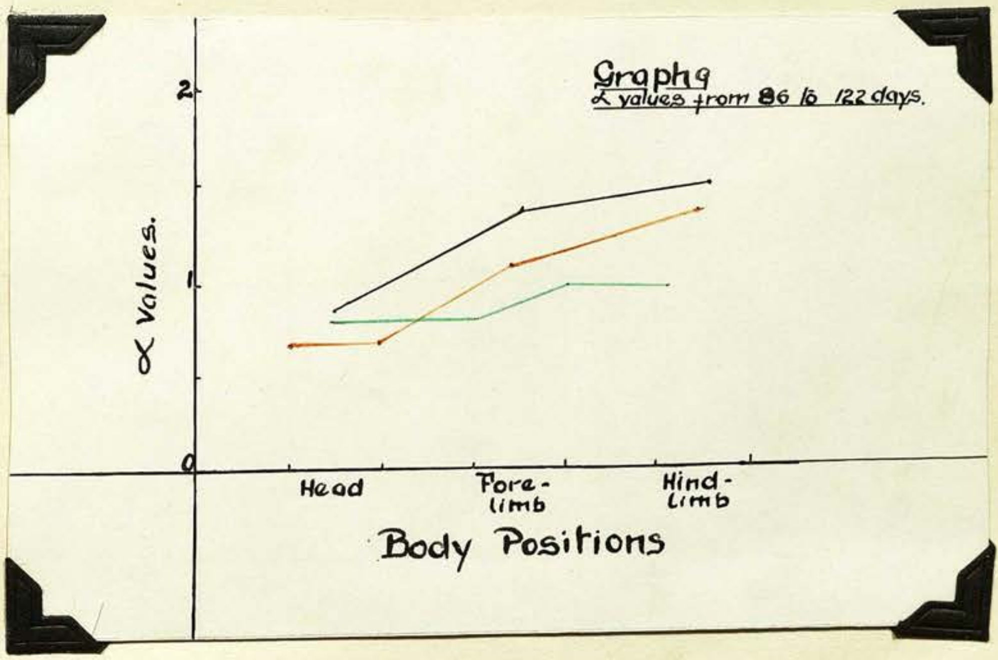
To compare the relative growth rates of the different regions of the body, the α values for these regions were plotted against body position - Graphs 7,8,9.



Graph 7 showed the increase in α value from the anterior to the posterior end of the body when a single α value was used. The long bones showed the highest α values, and the dorso-lateral growth the lowest.



Graph 8 showe~~d~~s the increase in α value from the anterior to the posterior end of the foetus from 46 days to 86 days. The dorso-lateral regions at this stage were growing at about the same rate as the long bones, while the increase in width was considerably less than the increase in height or length. The allometry of all growth, with the exception of the growth in width and height of the head region, was positive. The head length showed a state of isometry.



Graph 9. Here was a marked change in the relative growth rate of the dorso-lateral regions - a change from positive to negative allometry taking place for the fore and hind limb growth so that the allometry of all dorso-lateral growth became negative.

Long bone growth on the head had now reached a stage of negative allometry but the fore and hind-limbs had increased their relative growth rate and were now growing considerably faster than before. The rate of increase in the width of the head had decreased, the allometry of this part remaining negative. The width of the fore-limb was increasing at the same rate as it did from 46 to 86 days. The allometry was positive.

The hind-limb, however, showed a marked increase in width comparable with the increase in femur length. The increase in the value of α was marked.

Graphs 7, 8 and 9 should be compared with the graphs showing the fibre-type-array gradient in the coat of the Romney lamb - Paper 2 in appendix. It will be seen that there was a general correlation between fineness and slow growth and coarseness and quick growth.

D. The Decrease in Relative Growth Rate

Graphs 10 11 12

Tables 4 to 15

The relative growth rate per cent per day was calculated from the following formula. See Fisher (5)

$$\frac{\log._e m_1 - \log._e m}{t} \times 100$$

When m = a measurement taken at time$_1$ and m_1 a measurement taken at time$_2$. t = the difference in time between t_1 and t_2.

Graphs 10, 11 and 12 show the decrease in relative growth rate per cent per day plotted against time. The figures used are given in Tables 4 to 15.

Graphs 13, 14 and 15 show the change in allometry in length, height and width for the different regions at different periods of time. The 'α -with-time' value has been plotted against time. Further graphs 13, 14 and 15 show the changes in follicle density on different positions plotted against time. Follicle counts are given in Table 19 page 63.

The time used is a stage midway between the beginning and the end of a period. E.g. The 46 - 59 days period = 53 days stage or period.

Graph 10 is the decrease in relative growth rate per cent per day for the head region and the C.R. measurement plotted against time.

Curve A. is the graph for the C.R. - blue

Curve B. is the graph for the maxilla length - black

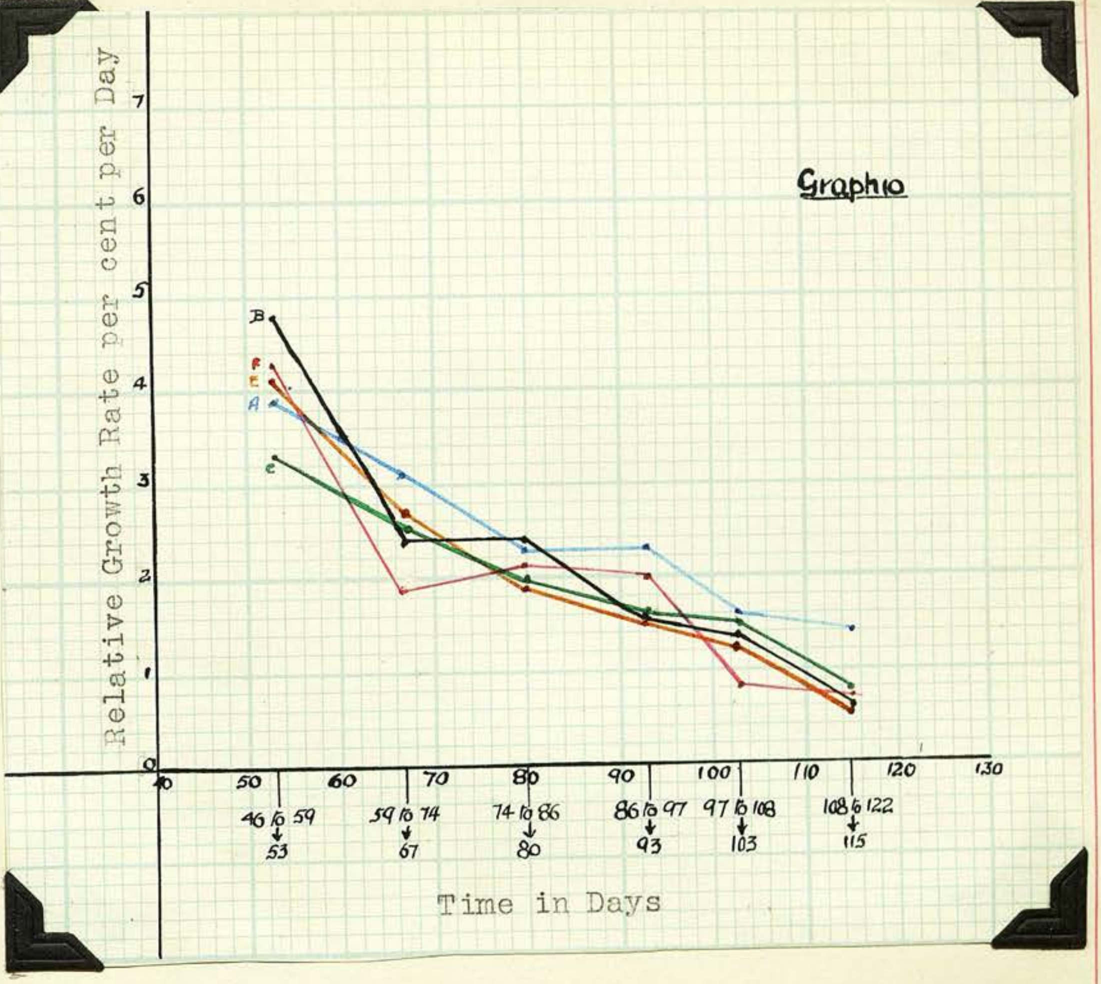
Curve C. the graph for the crown-mandible—height measurement - green

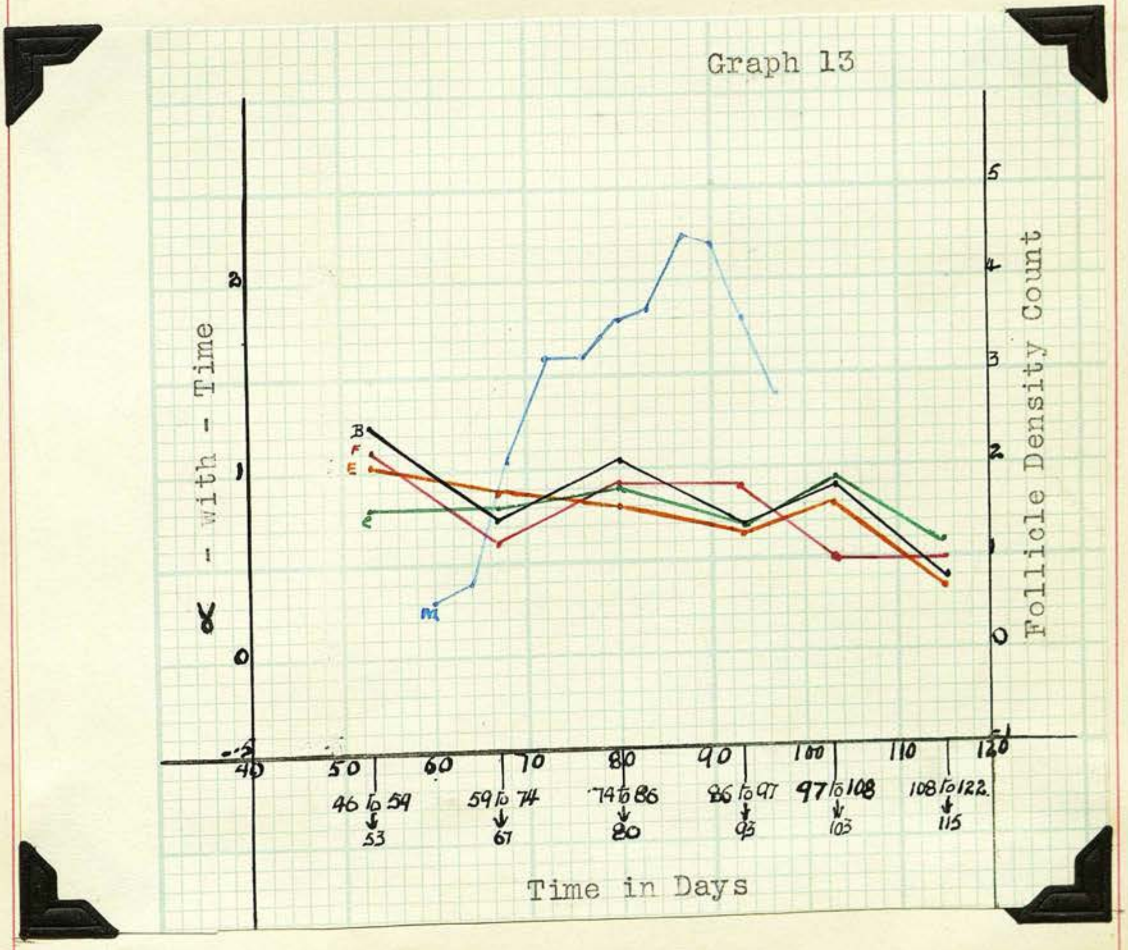
Curve E. the graph for the eye - eye measurement - width - orange

Curve F. the graph for the ear - ear measurement - width - red

Graph 13 is the change in allometry of the head region.plotted against time, together with the changes in follicle density plotted against time.

Curve B - maxilla length - black
Curve C - crown mandible - green
Curve E - eye - eye - orange
Curve F - ear - ear - red
Curve M - poll position follicle density counts - blue


Graph10
Relative Growth Rate per cent per Day
0
1
2
3
4
5
6
7
B
F
E
A
C
40
50
60
70
80
90
100
110
120
130
46 to 59 → 53
59 to 74 → 67
74 to 86 → 80
86 to 97 → 93
97 to 108 → 103
108 to 122 → 115
Time in Days


Graph 13
γ - with - Time
-.5
0
1
2
Follicle Density Count
0
1
2
3
4
5
B
F
E
C
M
40
50
60
70
80
90
100
110
120
46 to 59 → 53
59 to 74 → 67
74 to 86 → 80
86 to 97 → 93
97 to 108 → 103
108 to 122 → 115
Time in Days

Graph 11 is the decrease in relative growth rate per cent per day for the forelimb region and the C.R. measurements plotted against time.

Curve A is the graph for the C.R. - blue

Curve B is the graph for the humerus length - black

Curve C is the graph for the M.D.L. - humerus head — height - green

Curve D is the graph for the M.D.L. - elbow — height - purple

Curve E is the graph for the humerus head - humerus head — width - orange

Graph 14 is the change in the allometry of the forelimb region plotted against time, together with the changes in follicle density plotted against time.

Curve B - Humerus Femur length - black

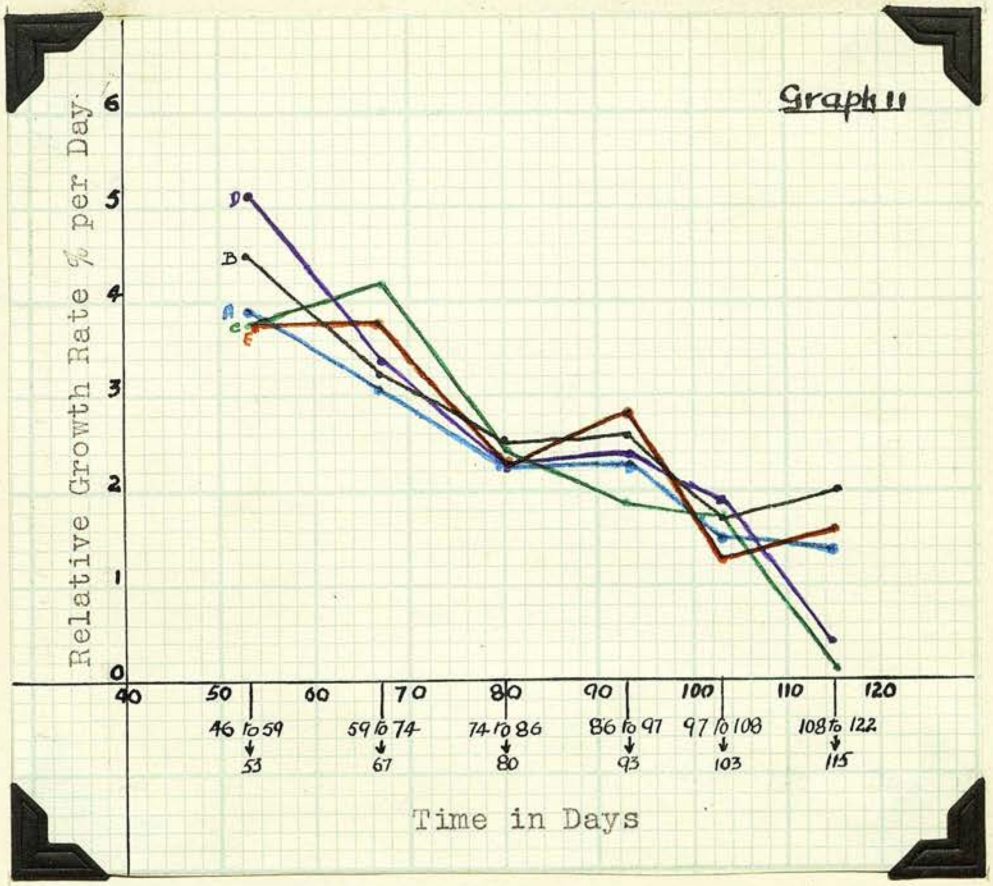
Curve C - M.D.L. - humerus head - green

Curve D - M.D.L. - elbow - purple

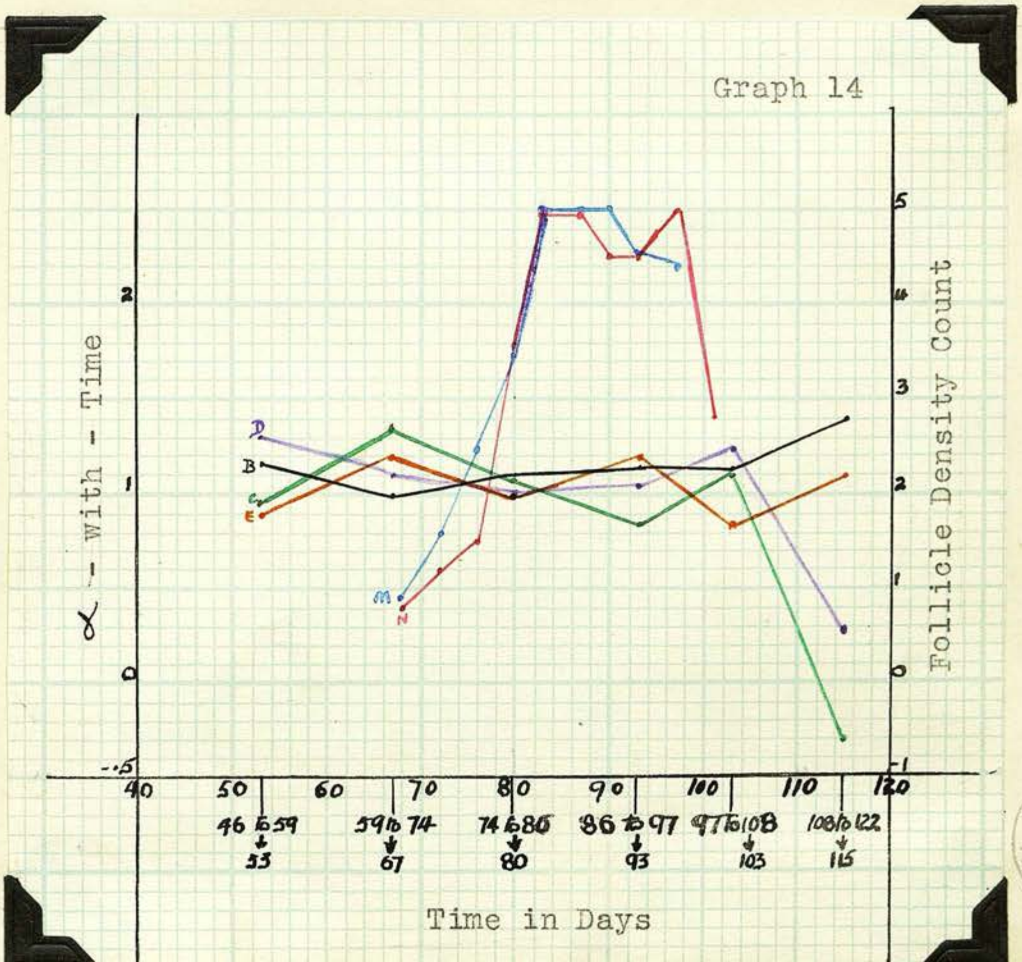
Curve E - Humerus head - humerus head - orange

Curve M - Neck base position follicle density count - blue

Curve N. - Withers position follicle density count - red



Graph 11



Graph 14

Graph 12 is the decrease in relative growth rate per cent per day for the hindlimb region and the C.R. measurements.

Curve A is the C.R. graph - blue

Curve B is the graph for the femur length - black

Curve C is the graph for the M.D.L.- femur head — height - green

Curve E is the graph for the femur head - femur head — width - orange

Graph 15 shows the change in allometry of the hindlimb region plotted against time, together with changes in follicle density plotted against time.

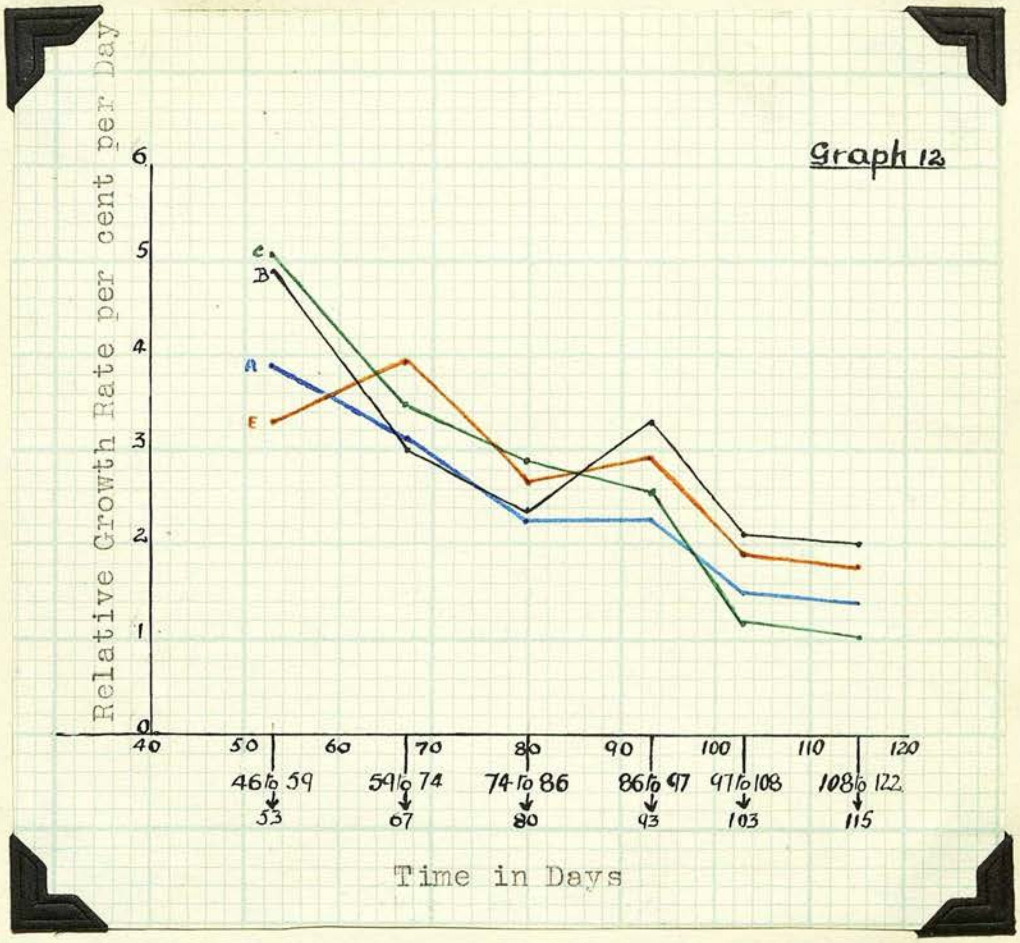
Curve B is the Femur length - black

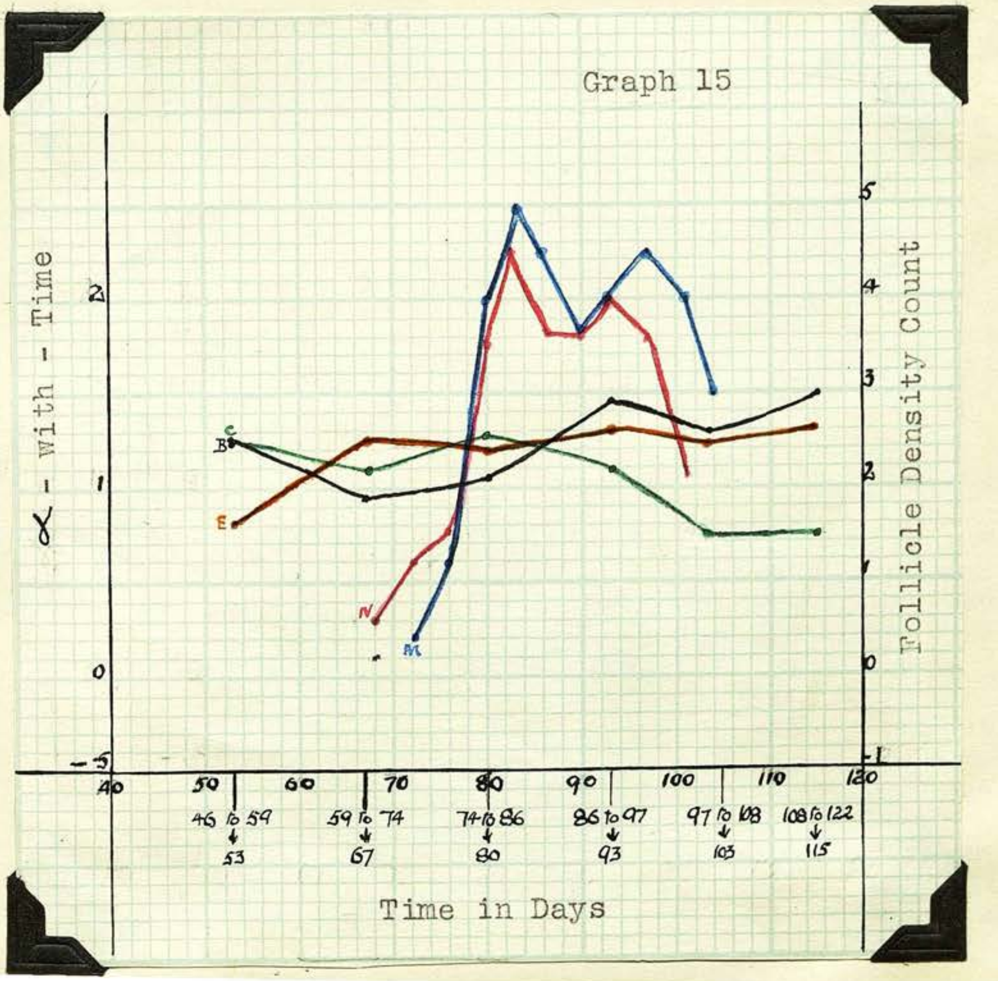
Curve C is the M.D.L. - femur head - green

Curve E is the Femur head - femur head - orange

Curve M Superior ileum position follicle density count - blue

Curve N Britch position follicle density count - red


Graph 12
Relative Growth Rate per cent per Day
6
5
4
3
2
1
0
C
B
A
E
40
50
60
70
80
90
100
110
120
46 to 59
53
59 to 74
67
74 to 86
80
86 to 97
93
97 to 108
103
108 to 122
115
Time in Days


Graph 15
α - With - Time
2
1
0
-5
Follicle Density Count
5
4
3
2
1
0
-1
C
B
E
N
M
40
50
60
70
80
90
100
110
120
46 to 59
53
59 to 74
67
74 to 86
80
86 to 97
93
97 to 108
103
108 to 122
115
Time in Days

The calculations were then plotted to show that the relative growth rate per day decreased.

Equilibrium Constant α with-time.

$$y = bx^{\alpha}$$

From the decrease in relative growth rate per cent per day the α with reference to the factor time was calculated from the following formula.

$$\alpha = \frac{\dfrac{\log_e y_1 - \log_e y}{t} \times 100}{\dfrac{\log_e x_1 - \log_e x}{t} \times 100}$$

See Tables 4 to 15 for the value of α so calculated. Graphs 13 14 15 showed the change in α value for the different lines of growth of the head, fore-limb and hind-limb regions.

Graph 10 was the graph of the decrease in relative growth rate per cent per day of the head region. The C.R. decrease in relative growth rate per cent per day was plotted on the same graph to give a standard for comparison.

	Graph	A	C.R. decrease in relative growth rate.
Length	"	B	Maxilla " " " " "
Height	"	C	Crown-mandible decrease in relative growth rate.
Width	"	E	Eye to eye decrease in relative growth rate.
	"	F	Ear to ear " " " growth rate.

It will be seen that there was a general decrease in relative growth rate. With the exception of the maxilla it will be noticed there was no marked decrease between the 80 and 93 days period. The C.R. relative growth rate it will be seen does not decrease at this period.

B. twice - at 53 days and 80 days, and F once - at 53 days showed a positive allometry. The allometry at all other periods for all head measurements was negative.

The change in the α value with time for the head region has been shown on Graph 13 - Graph B represents the length, C the height, E and F the width. It will be seen that the α value decreases with the increase in age of the foetus.

Graph 11.

For the fore limb regions was the graph of the decrease in relative growth rate of-

Length	Graph B	Humerus decrease in relative growth rate.
Height	Graph C	M.D.L. to humerus head decrease in relative growth rate.
	Graph D	M.D.L. to elbow decrease in relative growth rate.
Width	Graph E	Humerus head to humerus head decrease in relative growth rate.

Graph A was the standard C.R. graph for purposes of comparison.

On this region there was considerable diversity in the relative growth rate. The allometry of B was always positive; the allometry of C, on the other hand, changed from negative to positive at 67 days and back to negative at 93 days. It became positive at 103 days but was again negative at 115 days. D, with the exception of a period of isometry at 80 days, had an allometry that was positive until the 103 day period when it also became negative. The allometry of E was positive with two exceptions - at 53 days and 103 days. The allometry of all three lines of growth - length, height and width was with the exception of C and E at 53 days positive until the 80 day period. After this period the dorso-lateral region C became negative at 93 days; B, D and E, however, remained positive. At 103 days, all except E were positive; at 115 days the length - B- and the width-E-were positive, while the height C and D were negative. At the 80-93 days period when the C.R.(A) does not decrease, the relative growth rate of B and E increased, that of D remained constant and C decreased to show negative allometry.

From Graph 14 can be seen the change in the value of 'α-with-time' for the forelimb region lines of growth - length (B), height, (C) and (D), and width (E).

<u>Graph 12</u>. showed the decrease in relative growth rate of the hindlimb regions.

Graph A showed C.R. decrease in relative growth rate.

" B " Femur " " " " " - length

" C " M.D.L. to femur head decrease in relative growth rate - height.

Graph E showed Femur head to femur head decrease in relative growth rate - width.

Here again there was considerable variation in the allometry of the different regions. The allometry of B became negative at 67 days but otherwise was positive throughout. C showed a positive allometry till 93 days after which it became negative and remained so. The allometry of E was negative at 53 days but had become positive at 67 days and remained so throughout.

From this then it will be seen that the allometry of the length, height and width lines of growth of the hind limb was mainly positive; the dorsal-lateral regions, however, became negative at the 103 day period. Graph 15 showed the change in the value of 'α-with-time' for the lines of growth of the hind limb - length(B) height(C) and width(E).

From these graphs - 10 to 15 - it will be seen that the allometry of the head was nearly always negative; that of the forelimb was more often positive than negative but with low values for the equilibrium constant α . The allometry of the hindlimb was almost entirely positive with high α values. The allometry of the femur head to femur head line of growth was negative at 53 days, that of the femur length at 67 days and dorso-lateral growth showed constant negative allometry after the 93 days period.

Comparison of 'α-with-time' with α of Huxley.

The α of Huxley(6) calculated from the following formula.

$$\alpha = \frac{\log . y_1 - \log . y}{\log . x_1 - \log . x}$$

was compared with that of Richard's(7) calculated from the formula

$$\alpha = \frac{\dfrac{\log ._e y_1 - \log ._e y}{t} \times 100}{\dfrac{\log ._e x - \log ._e x}{t} \times 100}$$

Graphs 16, 17, 19, 20, 21, 22, 23, 24, 25, and 26 show the difference between α values calculated from

$$\alpha = \frac{\log.y_1 - \log.y}{\log.x_1 - \log.x}$$

and with-time calculated from the formula

$$\alpha = \frac{\dfrac{\log._e y_1 - \log._e y}{t} \times 100}{\dfrac{\log._e x_1 - \log._e x}{t} \times 100}$$

and 'α-with-time' for the length, height and width of the head, fore and hindlimb regions were plotted against time.

On graphs 16 to 26 curve A - black - is for α

curve B - red - is for 'α-with-time'

Graph 16 - maxilla length

Graph 17 - crown-mandible height

Graph 18 - eye - eye width

Graph 19 - ear - ear width

Graph 20 - humerus length

Graph 21 - M.D.L. - humerus head height

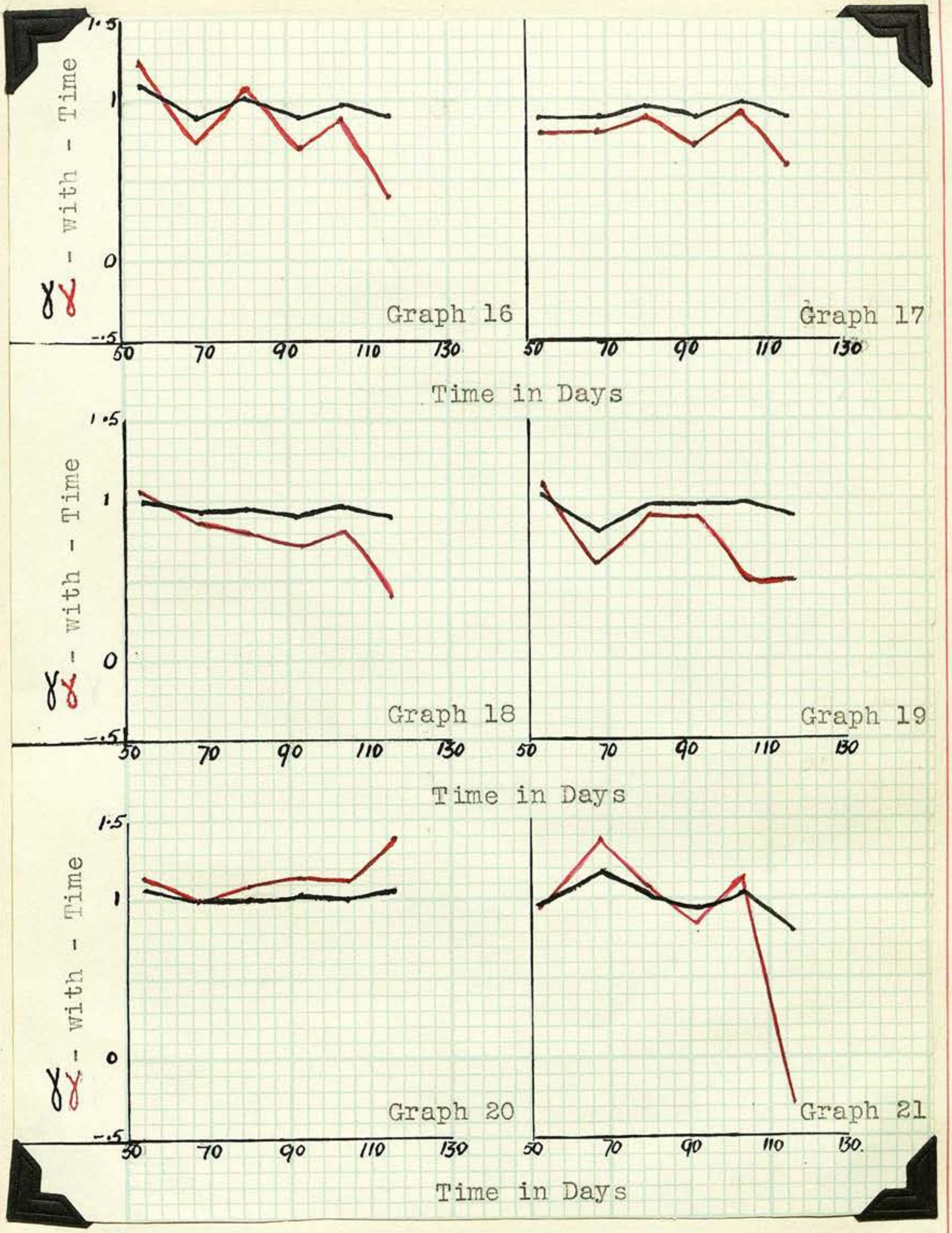
Graph 22 - M.D.L. - elbow height

Graph 23 - humerus head - humerus head width

Graph 24 - femur length

Graph 25 - M.D.L. femur head height

Graph 26 - Femur head-femur head width



Graph 16 - Maxilla length

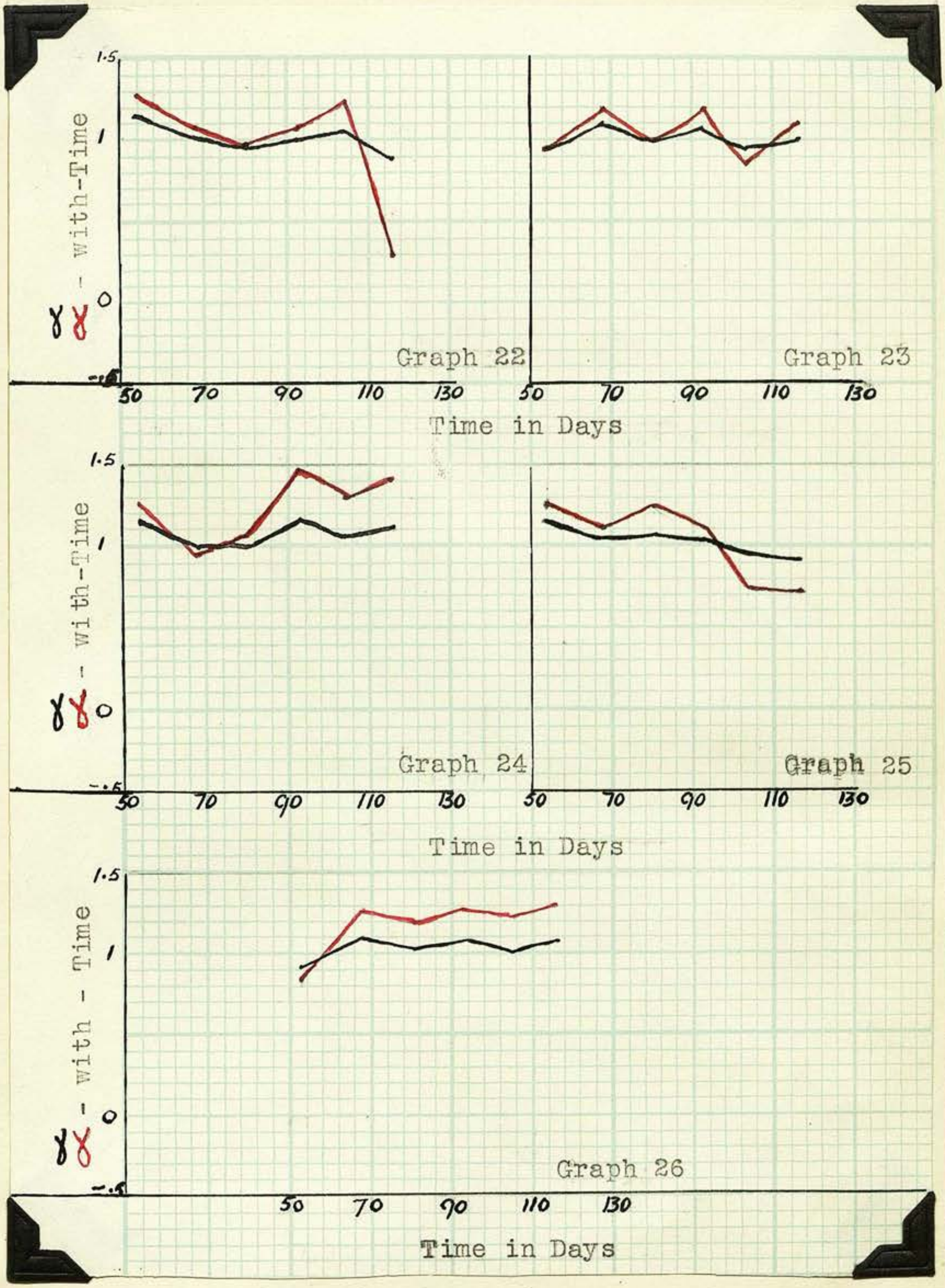
Graph 17 - Crown-mandible

Graph 18 - Eye - eye

Graph 19 - Ear - ear

Graph 20 - Humerus length

Graph 21 - M.D.L. - humerus head.



<u>Graph 22</u> - M.D.L. - elbow

<u>Graph 23</u> - Humerus head - humerus head

<u>Graph 24</u> - Femur length

<u>Graph 25</u> - M.D.L. - femur head.

<u>Graph 26</u> - Femur head - femur head.

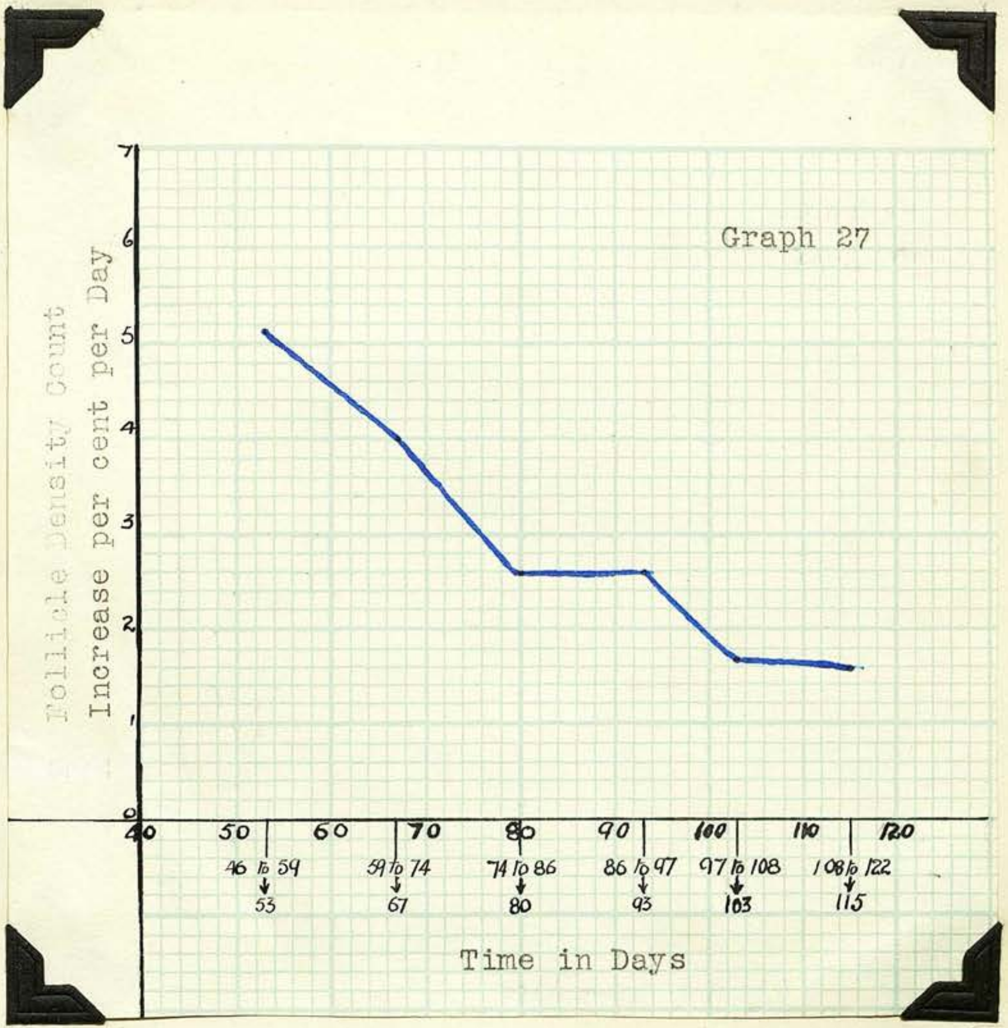
Graphs 27, 28, 29, and 30 show the decrease in the increase per cent for the head, forelimb, and hindlimb regions plotted against time. For the figures see Tables 4 to 15. The changes in follicle density counts for the various positions were plotted against time on the same graphs - See Table 19.

Note the britch and withers positions began follicle initiation at approximately the same time.

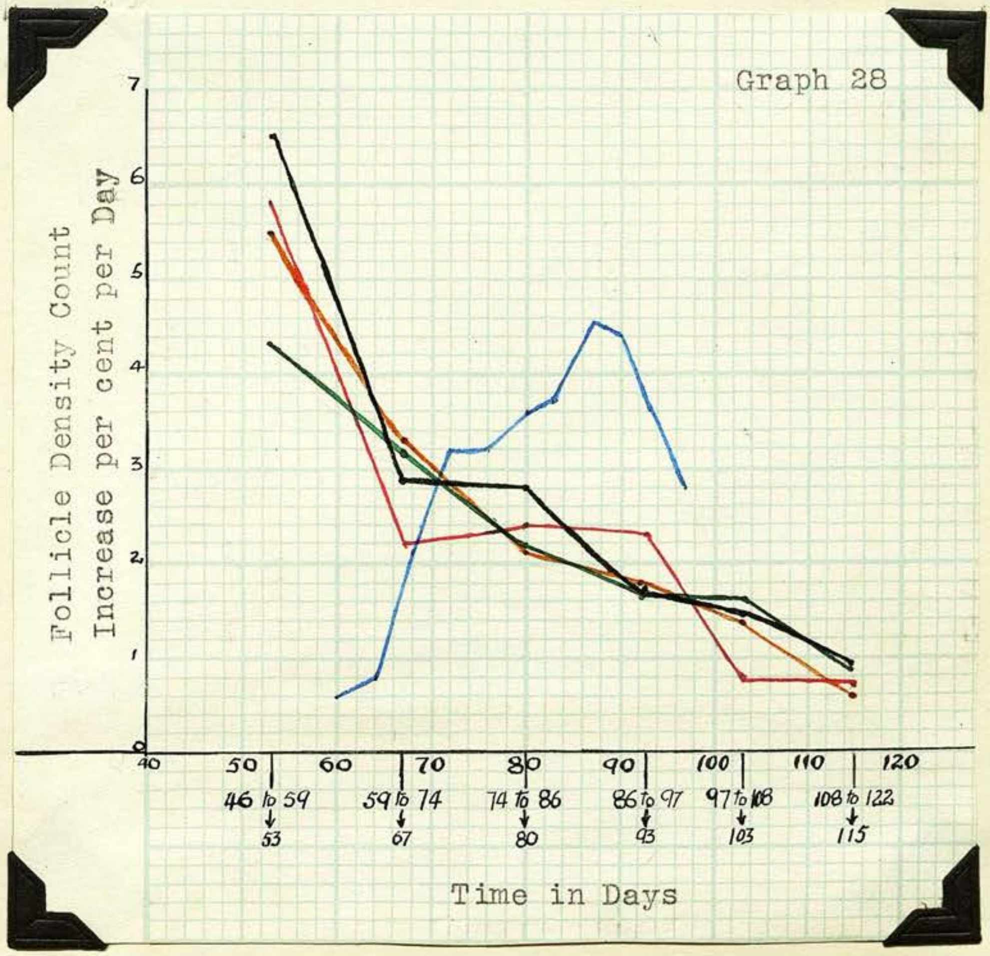
Graph 27 is the increase per cent per day of the measurement for the C.R. plotted against time.

Graph 28 is the increase per cent per day for the head region and the follicle density plotted against time.

Curve B - Maxilla length - black
Curve C - Crown - mandible — height - green
Curve E - Eye to eye — width - orange
Curve F - Ear to ear — width - red
Curve M - Poll position density count - blue



Graph 27



Graph 28

Graph 29 is the increase per cent per day for the hind-limb regions and the follicle density plotted against time.

Curve B - Humerus length - black

Curve C - M.D.L. humerus head — height - green

Curve D - M.D.L. - elbow — height - purple

Curve E - Humerus head - humerus head — width - orange

Curve M - Neck Base position density count - blue

Curve N - Withers position density count - red

Graph 30 is the increase per cent per day for the hind-limb regions and the follicle density plotted against time.

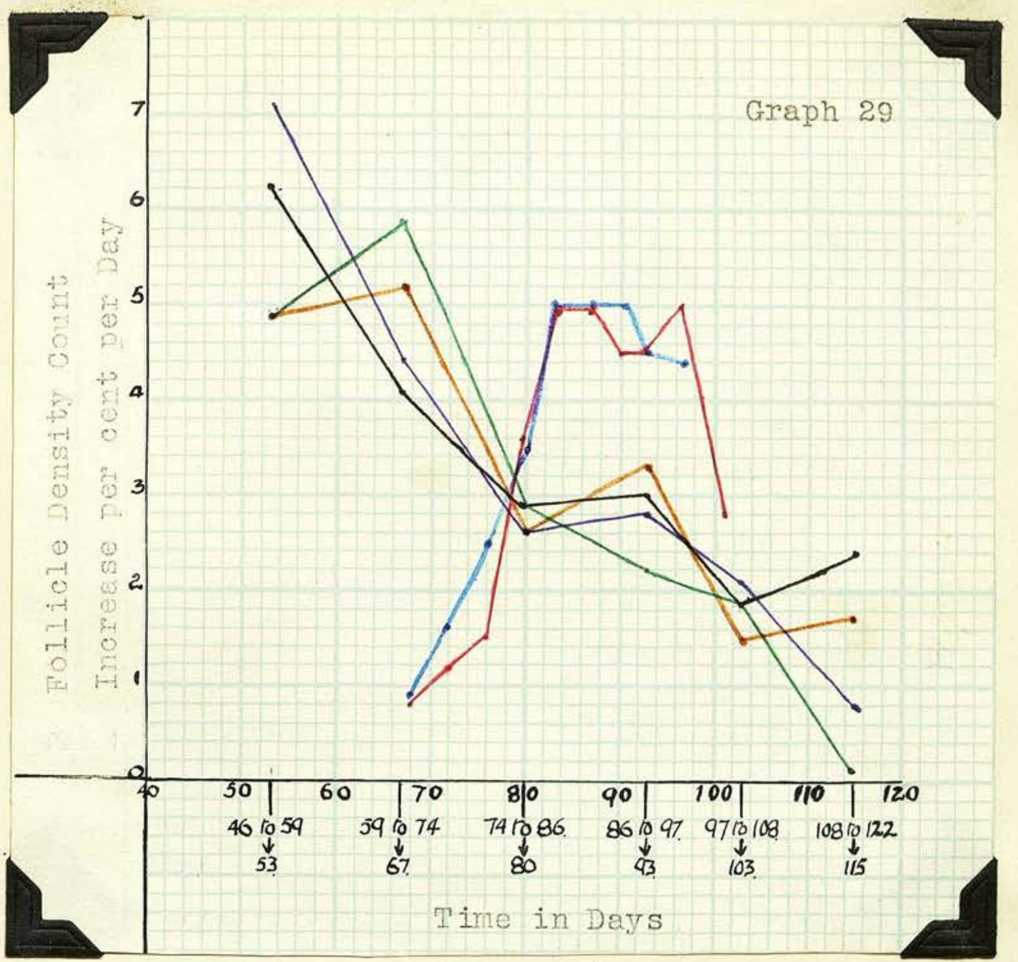
Curve B - Femur length - black

Curve C - M.D.L. femur head — height - green

Curve D - Femur head - femur head — width - orange

Curve M - Superior ileum position density count - blue

Curve N - Britch position density count - red


Graph 29
Follicle Density Count
Increase per cent per Day
0
1
2
3
4
5
6
7
40
50
60
70
80
90
100
110
120
46 to 59 ↓ 53
59 to 74 ↓ 67
74 to 86 ↓ 80
86 to 97 ↓ 93
97 to 108 ↓ 103
108 to 122 ↓ 115
Time in Days

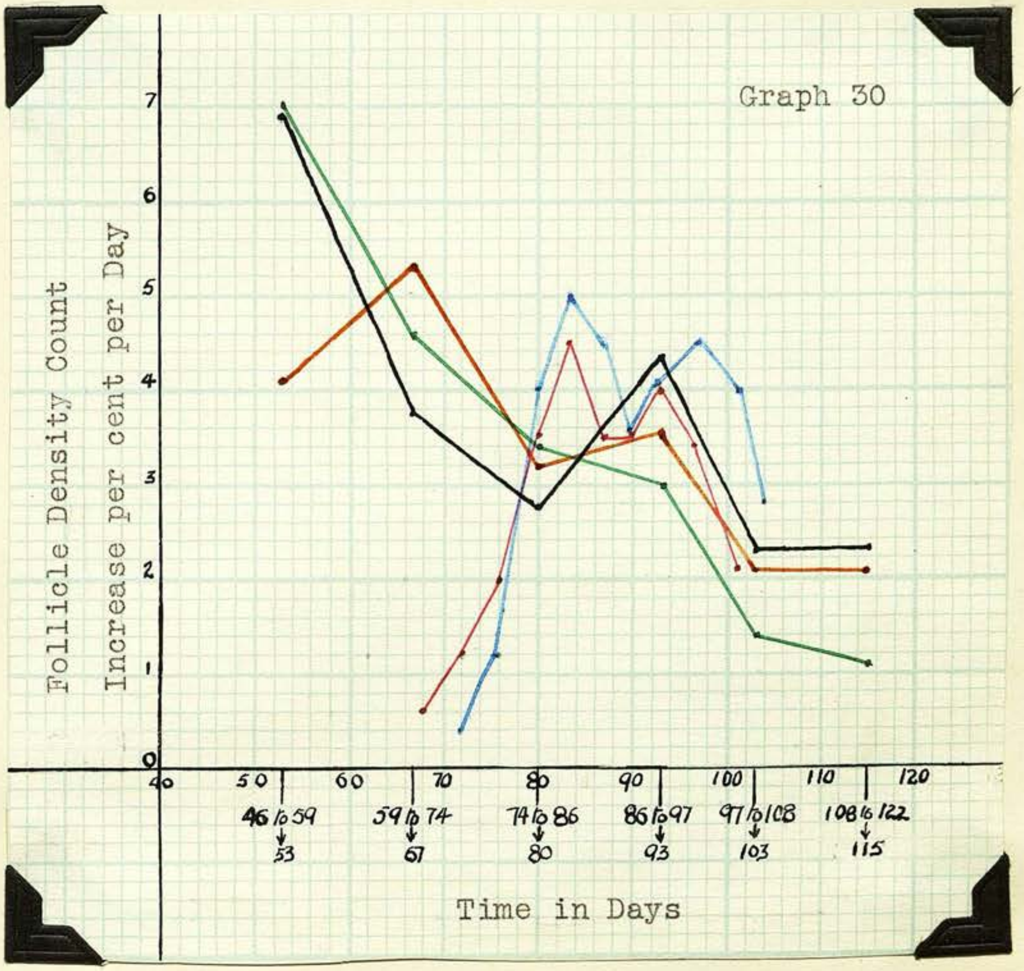

Graph 30
Follicle Density Count
Increase per cent per Day
0
1
2
3
4
5
6
7
40
50
60
70
80
90
100
110
120
46 to 59 ↓ 53
59 to 74 ↓ 67
74 to 86 ↓ 80
86 to 97 ↓ 93
97 to 108 ↓ 103
108 to 122 ↓ 115
Time in Days

Table 19 shows the follicle density counts on the different positions at different ages of foetal development.

Area = No.of follicles to $\frac{25}{103}$ sq. mms.

DL is the no. of follicles to a line and L is the no. of lines of follicles in $\frac{25}{103}$ sq. mms.
See page 14.

Time in Days

		60	64	68	72	76	80	83	87	90	93	97	101	104
Position							Follicle Counts							
Poll	Area	6	8	21	32	32	36	37	45	44	36	28		
	DL	3	4	7	8	9	9	9	9	9	9	7		
	L	2	2	3	4	4	4	4	5	5	4	4		
Neck Base	Area			9	16	25	35	50	50	50	45	44		
	DL			3	4	5	7	10	10	10	11	11		
	L			3	4	5	5	5	5	5	4	4		
Withers	Area			8	12	15	36	50	50	45	45	50	28	
	DL			3	4	5	9	10	10	9	9	10	7	
	L			3	3	3	4	5	5	5	5	5	4	
Britch	Area			6	12	20	35	45	36	36	40	36	21	
	DL			3	4	5	7	9	9	9	10	9	7	
	L			2	3	4	5	5	4	4	4	4	3	
Superior ileum	Area				4	12	40	50	45	36	40	45	40	28
	DL				2	4	8	10	9	9	10	11	10	9
	L				2	3	5	5	5	4	4	4	4	3

Graphs 16 to 26 were drawn to show the two values calculated for α from the two different formulae. The α from Huxley's(6) formula was less variable than the α from the second formula given. The general trend of the graphs was the same and for general growth gradients there was little advantage to be gained from using the formula including the time factor. Minor variations were, however, more easily demonstrated by using the second formula -

$$\alpha = \frac{\dfrac{\log._e y_1 \;-\; \log._e y}{t} \times 100}{\dfrac{\log_e x_1 \;-\; \log.\,x}{t} \times 100}$$

Graphs 27, 28, 29 and 30 of the decrease in increase per cent per day were drawn to show the absolute increase in size from one stage to the next. The trend of each graph was the same as that of the graphs 10, 11 and 12, showing the decrease in relative growth rate per cent per day.

On the same graph to show the correlation between increase in size and increase in follicle density were plotted the follicle density counts.

Table 19 gives the follicle density counts for the positions sampled.

From graphs 27, 28, 29 and 30 showing the increase per cent it will be seen that the foetus showed a decrease in its rate of increase, but the absolute size always increased.

Graphs 31, 32, 33, 34, 35, and 36 showed the variation in the change in α value for growth in length, height, and width from the anterior to the posterior end of the body at different stages of foetal development correlated with

Graphs 31, 32, 33, 34, 35, 36 are graphs showing the change in the antero - posterior gradient in growth rate from one period to the next. α values for length, height and width at the different periods of time were plotted against body position.

The follicle density at the different periods has also been plotted against the body position on the same graphs.

Curve A	length	black
Curve B	height	green
Curve C	width	orange

Curve M - follicle density - blue

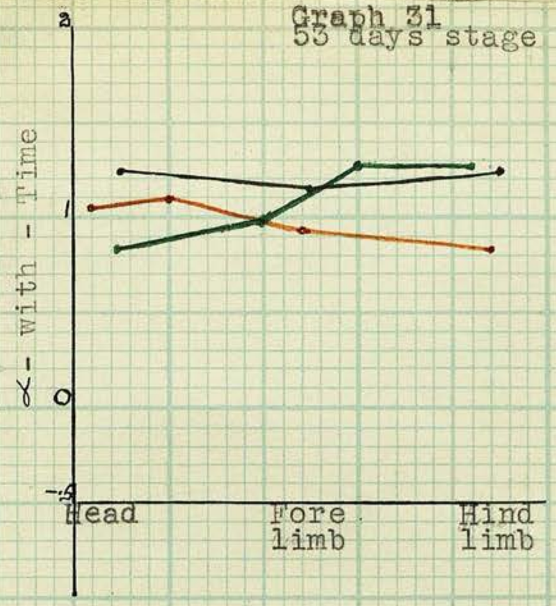
Curve N - number of follicles to a line in a $\frac{5}{103}$ mms. square - red

Curve O - number of lines of follicles in a $\frac{5}{103}$ mms. square - purple

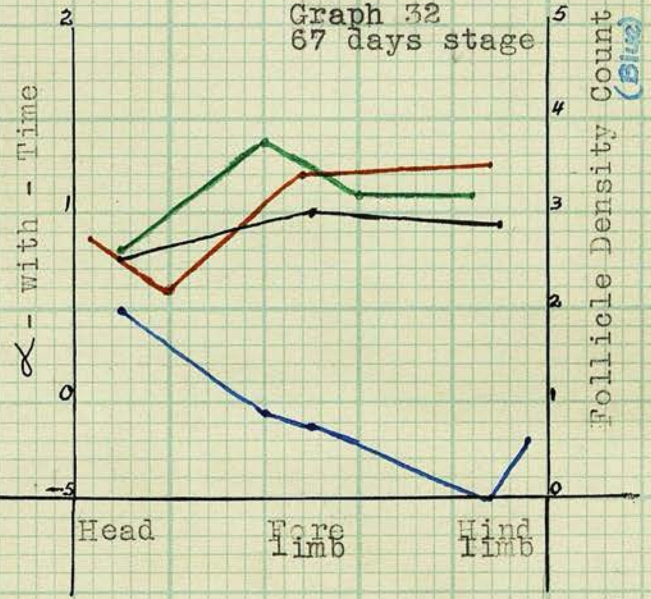
Graph 31 is for the 46 days to 59 days period -
Average 53 days.

Graph 32 is for the 59 days to 74 days period -
Average 67 days.

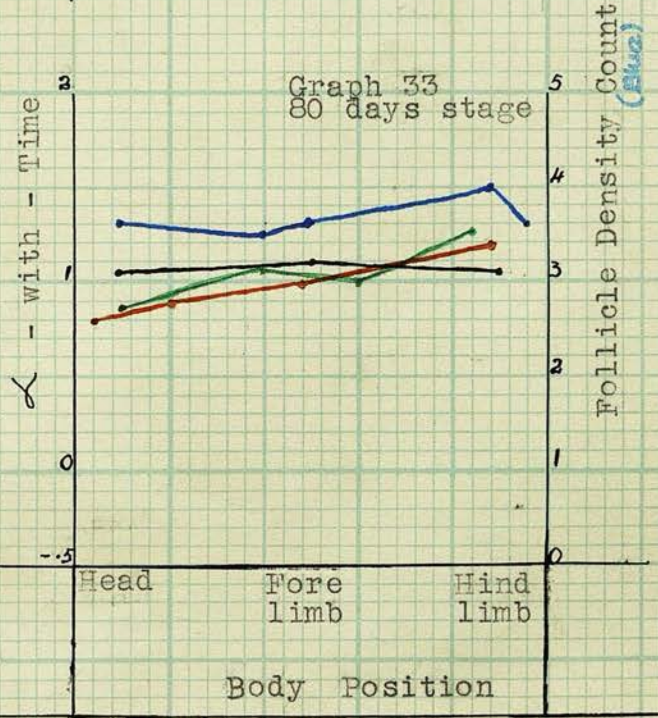
Graph 33 is for the 74 days to 86 days period -
Average 80 days.



Graph 31
53 days stage



Graph 32
67 days stage



Graph 33
80 days stage

γ-with-time. Length - black; Height - green; Width - orange.

Graph 34 is for the 86 days to 97 days period -

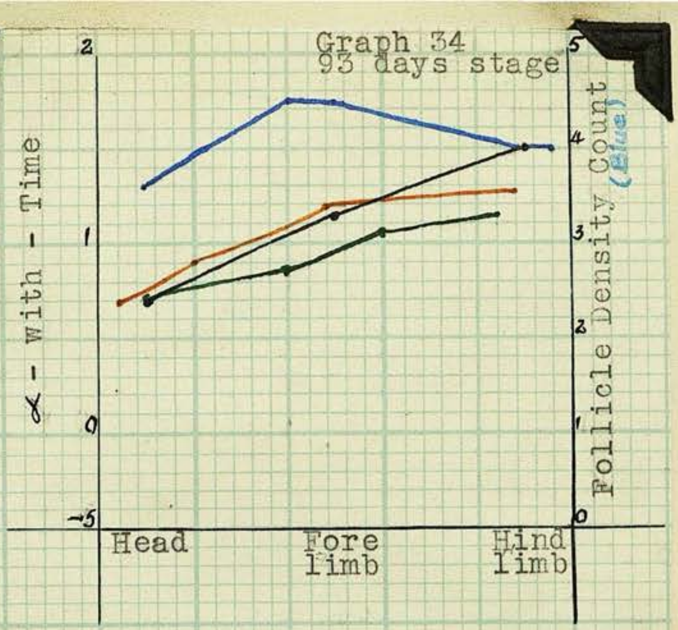
Average 93 days.

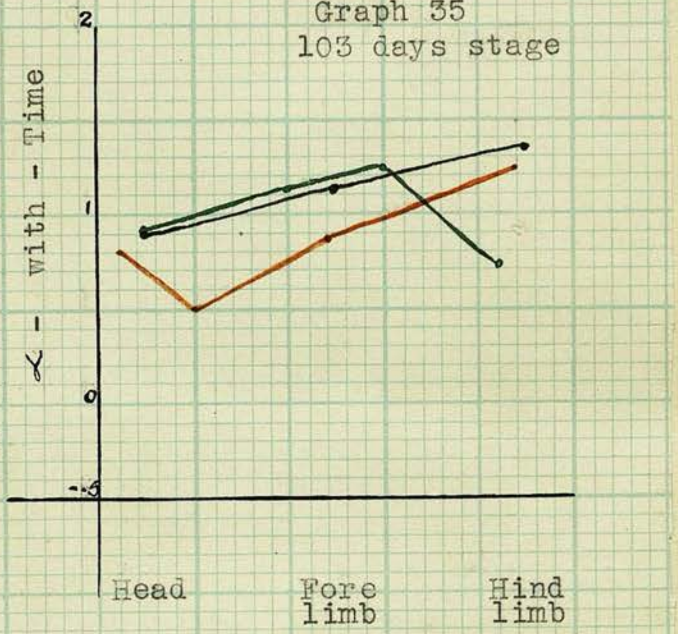
Graph 35 is for the 97 days to 108 days period -

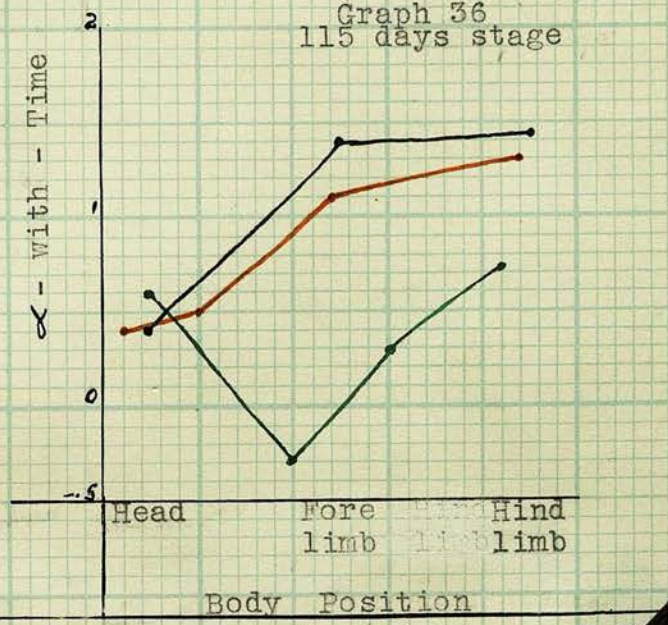
Average 103 days.

Graph 36 is for the 108 to 122 days period -

Average 115 days.


Graph 34
93 days stage


Graph 35
103 days stage


Graph 36
115 days stage

'α-with-Time' Length- black; Height-green; Width- orange.

changes in follicle density.

From the graphs of the decrease in increase per cent per day, it can be seen that there was always an increase in actual size.

At the 53 day stage of development - graph 31

Length

Maxilla α = 1·23

Humerus α = 1·15

Femur α = 1·25

The allometry of all three was positive and all three regions were increasing at approximately the same rate of relative growth.

Height.

$$\left.\begin{array}{ll} \text{Crown-mandible} & \alpha = \cdot 84 \\ \text{M.D.L.-humerus head} & \alpha = \cdot 96 \end{array}\right\} \text{allometry negative}$$

$$\left.\begin{array}{ll} \text{M.D.L-elbow} & \alpha = 1\cdot 28 \\ \text{M.D.L.-femur head} & \alpha = 1.27 \end{array}\right\} \text{allometry positive}$$

The crown-mandible was growing a little slower than the M.D.L.-humerus head. The M.D.L. - elbow and the M.D.L. femur head were increasing at about the same rate of relative growth.

Width.

$$\left.\begin{array}{ll} \text{Eye-eye} & \alpha = 1\cdot 06 \\ \text{Ear-ear} & \alpha = 1\cdot 09 \end{array}\right\} \text{allometry positive}$$

$$\left.\begin{array}{ll} \text{Humerus head-humerus head} & \alpha = \cdot 96 \\ \text{Femur head-femur head} & \alpha = \cdot 84 \end{array}\right\} \text{allometry negative}$$

The head region was growing faster than the trunk regions - the forelimb region growing a little faster than the hindlimb one. From this, it can be seen that head, fore, and hindlimb regions were all increasing in size at appromixately the same relative rate of growth, the positive allometry in body width balancing the negative allometry in height for the head region and the vice-versa for the fore and hind-limb regions.

At the 67 day state of development - Graph 32

Length

Maxilla α = ·75
Humerus α = 1·01
Femur α = ·97

The allometry of the maxilla and femur were negative. The humerus was in a state of isometry. There was, however little difference between the rate of growth of the humerus and femur. The maxilla was growing somewhat slower. The relative rates of growth of all three had dropped considerably.

Height.

Crown-mandible α = ·81 allometry negative
$$\left.\begin{array}{l}\text{M.D.L.-humerus head } \alpha = 1{\cdot}36 \\ \text{M.D.L.-elbow } \alpha = 1{\cdot}09 \\ \text{M.D.L.-femur head } \alpha = 1{\cdot}12\end{array}\right\}\ \text{allometry positive}$$

The M.D.L. - elbow and the M.D.L. femur head both showed a decrease in relative growth rate, the crown-mandible was growing at approximately the same rate while the M.D.L. - humerus head showed a marked increase.

Width

$$\left.\begin{array}{l}\text{Eye-eye } \alpha = {\cdot}86 \\ \text{Ear-ear } \alpha = {\cdot}61\end{array}\right\}\ \begin{array}{l}\text{allometry}\\ \text{negative}\end{array}$$
$$\left.\begin{array}{l}\text{Humerus head-humerus head } \alpha = 1{\cdot}22 \\ \text{Femur head-femur head } \alpha = 1{\cdot}25\end{array}\right\}\ \begin{array}{l}\text{allometry}\\ \text{positive}\end{array}$$

There has been a decrease in the relative growth rate of the head region with a change from positive to negative allometry. An increase in relative growth rate of the fore and hindlimb regions resulted in a change from negative to positive allometry. From this, it will be seen that the relative increase in size of the head has decreased, of the forelimb increased, while that of hindlimb has remained about constant. Both fore and hindlimb regions were increasing at a faster rate than the head region; the forelimb region was growing the fastest. Follicles had appeared on all positions except on the skin over the superior ileum. The trio stage was foreshadowed on the poll and neck and neckbase regions. Only X and Y follicles had appeared elsewhere.

<u>At the 80 day stage of development</u> - Graph 33

<u>Length</u>.

$$\left.\begin{array}{l}\text{Maxilla } \alpha = 1{\cdot}07\\ \text{Humerus } \alpha = 1{\cdot}09\\ \text{Femur } \alpha = 1{\cdot}06\end{array}\right\}\text{ allometry positive}$$

There has been an increase in the value of α for all three regions - that of the head region being the greatest. All three regions were now increasing at approximately the same rate.

<u>Height</u>.

Crown-mandible α = ·87 allometry negative
M.D.L.-humerus head α = 1·07 allometry positive
M.D.L.-elbow α = ·99 isometry - nearly
M.D.L.-femurhead α = 1·26 allometry positive

The crown-mandible showed a slight increase in α value, the forelimb region a decrease, the decrease of the M.D.L to the humerus head being marked. The hindlimb regions had a higher α value than at the 67 day period.

Width

Eye-eye $\alpha = \cdot 82$ } allometry negative
Ear-ear $\alpha = \cdot 92$ }
Humerus head-humerus head $\alpha = 1$ isometry
Femur head-femur head $\alpha = 1 \cdot 2$ allometry positive

There has been, with the exception of the ear-ear region, a slight decrease in the α values of all three regions - that of the forelimb being the most marked.

The head region at this stage has increased its rate of relative growth since the 67 day stage. Apart from a slight increase in the α value of the humerus length the forelimb region showed a decrease in its relative rate of increase. The hindlimb region was growing faster than the other regions and a little faster than it was at the 67 day stage - with growth in both length and height showing an increase, while increase in width showed a relative decrease.

Follicles had appeared on all positions; the trio stage of development had been completed on the poll, neck, and neckbase positions between 74 and 78 days. The withers and britch regions were at the trio stage of development; the superior ileum position showed some trio follicles but many of the initial follicles were still without the additional two of the trio.

At the 93 day stage - Graph 34

Length.

Maxilla $\alpha = \cdot 706$ negative allometry
Humerus $\alpha = 1 \cdot 15$ } allometry positive
Femur $\alpha = 1 \cdot 47$ }

When compared with the 80 day values for α the α value of the maxilla showed a marked decrease, that of the humerus and femur an increase; the femur increase being very marked.

Height.

$$\left.\begin{array}{ll}\text{Crown-mandible} & \alpha = \cdot 7\\ \text{M.D.L.-humerus head} & \alpha = \cdot 85\end{array}\right\}\text{allometry negative}$$

$$\left.\begin{array}{ll}\text{M.D.L.- elbow} & \alpha = 1\cdot 06\\ \text{M.D.L.-femur head} & \alpha = 1\cdot 13\end{array}\right\}\text{allometry positive}$$

With the exception of the α value for the M.D.L.— elbow, α value for relative increase in height showed a consistent decrease; α value for the M.D.L. — elbow was higher than at the 80 day stage.

Width.

$$\left.\begin{array}{ll}\text{Eye-eye} & \alpha = \cdot 73\\ \text{Ear-ear} & \alpha = \cdot 89\end{array}\right\}\left\{\begin{array}{l}\text{allometry}\\ \text{negative}\end{array}\right.$$

$$\left.\begin{array}{ll}\text{Humerus head-humerus head} & \alpha = 1\cdot 2\\ \text{Femur head-femur head} & \alpha = 1\cdot 28\end{array}\right\}\left\{\begin{array}{l}\text{allometry}\\ \text{positive}\end{array}\right.$$

From the 80 day to the 93 day stage α values for the head region decreased while those of the fore and hindlimb increased. When compared with the 80 day stage it was seen that the head region decreased in its rate of relative increase in size; the forelimb region remained approximately the same - with a tendency to increase rather than to decrease its rate of relative growth, while the hindlimb region showed a marked increase in its rate of relative growth. The increase in the actual size was somewhat greater than the increase in relative size indicated, for there was no decrease in the relative growth rate of the C.R. at this stage.

Follicle density has increased for all

positions. The nine stage of follicle development was completed on the poll and neck regions at approximately 87 days; on the neck-base at about 90 days; on the withers and britch positions follicle development was then approximately at the nine stage; while on the superior ileum most of the follicles of the nine stage were formed but not all.

<u>At the 103 day stage</u> - Graph 35.

<u>Length</u>.

Maxilla α = ·88 allometry negative

$$\left.\begin{array}{l}\text{Humerus } \alpha = 1{\cdot}13\\ \text{Femur } \alpha = 1{\cdot}33\end{array}\right\}\text{ allometry positive}$$

The maxilla showed a slight increase in α value at this stage - due probably to the fact that the marked decrease at the 93 day stage was caused by there being no decrease in the relative growth rate of the C.R. at this stage. Both the humerus and the femur showed a decrease in their α values, that of the humerus being less than that of the femur.

<u>Height</u>.

Crown-mandible α = ·93 negative allometry

$$\left.\begin{array}{l}\text{M.D.L.-humerus head } \alpha = 1{\cdot}13\\ \text{M.D.L.-elbow } \alpha = 1{\cdot}24\end{array}\right\}\text{ positive allometry}$$

M.D.L.-femur head α = ·75 negative allometry

With the exception of that of the M.D.L.-femur head there was a general increase in the values of α at this stage. The M.D.L.-femur head showed a marked decrease, a change from positive to negative allometry taking place.

Width.

$$\left.\begin{array}{ll}\text{Eye-eye} & \alpha = \cdot 82 \\ \text{Ear-ear} & \alpha = \cdot 50 \\ \text{Humerus head-humerus head} & \alpha = \cdot 86\end{array}\right\}\text{ allometry negative}$$

$$\begin{array}{ll}\text{Femur head-femur head} & \alpha = 1\cdot 23 \text{ allometry positive}\end{array}$$

The α value for growth in width from eye-eye showed a slight increase, for all other/ width growth there was a decrease in α values, particularly marked for the growth in width from humerus head-humerus head.

There was a slight increase in the relative growth rate of the head and forelimb regions and a marked decrease in the relative increase in the size of the hind-limb region.

By the time the 103 day stage was reached the fibres had pierced the skin on the poll, neck and neckbase regions and were quite obvious. Fibres had just pierced the withers and britch positions. Development on the superior ileum which was later than that of the others showed the fibres well developed in the follicles and nearly ready to pierce the skin. Fibres were first found piercing the skin on this region at about 106 days.

At the 115 day stage - Graph 36

Length.

$$\begin{array}{ll}\text{Maxilla} & \alpha = \cdot 4 \text{ negative allometry}\end{array}$$

$$\left.\begin{array}{ll}\text{Humerus} & \alpha = 1\cdot 4 \\ \text{Femur} & \alpha = 1\cdot 42\end{array}\right\}\text{ positive allometry}$$

The maxilla value for α decreased while those of the humerus and femur increased. The increase in the α value for the humerus was marked.

Height.

$$\left.\begin{array}{ll} \text{Crown-mandible} & \alpha = \cdot 59 \\ \text{M.D.L. - humerus head} & \alpha = \cdot 073 \\ \text{M.D.L. - elbow} & \alpha = \cdot 29 \\ \text{M.D.L. - femur head} & \alpha = \cdot 74 \end{array}\right\} \begin{array}{l}\text{negative}\\ \text{allometry}\end{array}$$

There has been a decrease in all α values for relative increase in height, the forelimb region showing particularly marked decrease.

Width.

$$\begin{array}{ll} \text{Eye-eye} & \left.\begin{array}{l}\alpha = \cdot 39 \\ \alpha = \cdot 49\end{array}\right\} \begin{array}{l}\text{negative}\\ \text{allometry}\end{array} \\ \text{Ear-ear} & \\ \text{Humerus head- humerus head} & \left.\begin{array}{l}\alpha = 1\cdot 1 \\ \alpha = 1\cdot 3\end{array}\right\} \begin{array}{l}\text{positive}\\ \text{allometry}\end{array} \\ \text{Femur head-femur head} & \end{array}$$

The head region showed a decrease in its relative growth rate, while the fore and hindlimb regions both showed an increase - the increase of the forelimb region being greater than that of the hind, the α value for the hindlimb region, however, remaining higher than that of the forelimb region.

The relative increase in size had decreased for the head and forelimb region and remained approximately the same for the hindlimb region. The forelimb region was growing faster than the head region but considerably slower than the hindlimb one.

E. Follicle Density Counts correlated with Changes in Relative Growth Rate

In a previous paper it has been suggested that the check causing fineness in some of the sickle, super-sickle fibres and early curly-tips was due to crowding of follicles at the trio stage, and that the second check causing the decrease in coarseness in the later growing curly-tips was due to crowding at the nine stage. Variations in the extent of the crowding were thought to be expressed in the natal lamb by different types of fibre-type-arrays which varied from position to position in a lamb's coat as well as from lamb to lamb. From lambs of the New Zealand Romney breed taken at random it was found in their fleeces that the most general dorso-lateral fibre-type-array gradient was from Saddle array on the britch regions to Plain array on the poll - see paper 2 in appendix. Ravine and Valley arrays were encountered on positions anterior to the britch and posterior to the poll; Valley arrays occurred on positions anterior to the positions on which Ravine arrays were found.

From graphs, 1,2,3,13,14,15,28,29,30,32,33, 34 and 35, it will be seen that follicle formation takes place at varying times on different positions. On the poll position where a fine fibre-type-array is usually found together with a high pre-curly-tip count it has been found that the initial follicle density was not very high - trio formation beginning when the density of initial follicles was about 8 to $\frac{25}{103}$ sq.mms. Density at the trio stage was also relatively low and perhaps accounts for the large number of pre-curly-tips - see graphs 1,2,3,13,28,32, 33 and 34. At the 80 day period the trio stage - i.e. at the beginning of the nine stage - the density remains approximately the same, while the relative rate of increase in size of the head region increased. With the completion of the nine stage follicular density increases while the relative rate of growth of the head region decreases - from the increase per cent per day graphs it will be seen, however, that there is a considerable increase in actual size at this period. No great increase in follicle density takes place and with increase in the size of the head region the density falls at about 97 days to 28 follicles to $\frac{25}{103}$ sq. mms. On the poll area a series of phenomena were found which exhibited themselves in the following way:-

A. At 60 days The initial X and Y follicles were formed; the head region was growing rapidly; the density was low.

B. At 67 days The trio stage was developing most of the X follicles now having two small follicles one on either side of them. The rate of growth of the head region had decreased but it was still increasing rapidly; density was low.

C. At 74 days The trio stage was completed; the relative growth rate of the head region was increasing. The density was increasing but was low for the trio stage.

D. At 80 days The nine stage of follicle development had commenced - the head region was still growing comparatively rapidly but had begun to decrease. The density was increasing.

E. At 87 days The nine stage was completed. The relative growth rate of the head region had decreased; the density was high.

F. At 93 days The fibres were ready to pierce the skin; the density had decreased. A few additional follicles had appeared but the greates number were already laid down. The relative growth rate was much the same as at 80 days.

The neckbase position - graphs 1,2,3,14,29, 32,33 and 34 - which developed a little later than the poll and neck positin but earlier than any other area, was also found to have a relatively low density at the beginning of trio formation. Density at the trio stage was about the same as that of the neck position.

The development of the trio follicles took place during a stage of decrease in the relative growth rate of the forelimb but the decrease was not marked and the actual increase in size fairly great. The nine stage, completed about 90 days, began to develop during the period when the relative growth rate was decreasing and follicle density increased markedly. The high density was maintained for a short time; a marked increase in relative growth occurred about this time but it will be noticed that though the forelimb as a whole increased in size the dorso-lateral line of growth affecting the neckbase position M.D.L. - humerus head decreased its relative growth rate. The density fell, however, when the 93 day stage was reached; the forelimb regions continuing to grow rapidly, the M.D.L. - humerus head increasing its relative rate of growth. The relatively low initial density was probably responsible for the high proportion of pre-curly-tips found while the high nine stage density may have affected the later growing follicles and may account for the fineness of the fibres of this position.

On the neckbase position the following phenomena occur successively:-

A. <u>At 67 days</u> Follicle initiation was nearly completed and the forelimb region was growing rapidly; follicle density was low.

B. <u>At 80 days</u> The trio stage was completed and the nine stage had just begun. During this period the relative growth rate of the forelimb was decreasing. The density was low at the trio stage but became high when the nine stage follicles appeared.

C. <u>At 90 days</u> The nine stage was completed; the relative growth rate of the forelimb region was increasing but not markedly. There was a definite decrease in the M. D.L.-humerus head rate of growth; the density was high.

D. <u>At 97 days</u> Fibres were ready to pierce the skin. The density had fallen but not much and the forelimb growth rate was approximately the same with a tendency to decrease a little.

The withers position - Graphs 1,2,3,14,29,32,33 34 and 35.

On this position follicle initiation began during a period of rapid growth and was completed during a phase of decreasing relative growth. Trio formation was completed at about 80 days when the relative growth of the forelimb was approximately in a state of isometry. The nine stage began while the increase in relative growth was not yet marked and resulted in a high density which fell, however, during the period; marked increase in growth rate for all three dimensions affecting the withers - the humerus length, M.D.L. - elbow, and the humerus head-humerus head. A slight decrease in the rate of the increase in size of the forelimb region occurred after the 93 days stage and with the completion of the nine stage the density again rose to fall again at about 101 days. There was no marked addition of follicles after the completion of the nine stage. The density of the trio stage not being very high may account for the number of pre-curly-tips present on the withers, the density at the nine stage probably caused the extreme fineness of some of the sickle fibres and early "checked curly-tips" (3) usually found on this region. The drop in density after the beginning of the nine stage probably resulted in the coarser curly-tips which were often found in the fibre-type-arrays of this position - valley array/being the most frequent - succeeding finer curly-tip fibres ("checked curly-tips" - see Dry(3)).

In the withers position, therefore, the following stages of development were found:-

A. At 67 days Follicle initiation was taking place. The growth rate of the forelimb region was rapid but was beginning to decrease . Density was low but higher than that of the previously mentioned regions at the same stage of development.

B. At 80 days The trio stage of development was completed. The growth rate of the forelimb had decreased till the region was nearly in a state of isometry. Density was higher at the trio stage on the withers position than on the poll and neckbase positions at the same stage.

C. At 93 days The nine stage was almost completed; the growth rate of the forelimb region had increased. The density was high but a slight drop had occurred at 87 days.

D. At 97 days The nine stage had been completed. The rate of increase in size of the forelimb was decreasing slightly; the density was high.

E. At 101 days The fibres were ready to pierce the skin. The density had fallen; only a very few new follicles were appearing. The growth rate was decreasing a little but was approximately the same as before.

The Britch position - Graphs 1,2,3,15,30,32, 33,34 and 35, commended growth at about the same time as the withers. Trio stage density on this position was much the same as on the withers; trio formation occurred before the hindlimb region had shown any marked increase in relative growth. It was, however, growing more rapidly than the rest of the foetus. The commencement of the nine stage resulted in a density increase but almost immediately a marked increase in relative growth rate caused a decrease in density. Completion of the nine stage at about 94 days resulted in a slight increase which was also coincident with a slight decrease in the growth rate of the hindlimb region, the decrease being most marked in height. After the completion of the nine stage the density falls fairly rapidly; the hindlimb was still continuing to increase its size at a relatively rapid rate. The density at the trio stage being much the same as that of the withers may account for the fact that the number of pre-curly-tips was usually about the same as those of the withers - the smaller increase in relative growth of the withers probably accounting for the fact that the pre-curly-tips on the withers region were usually finer than those of the britch. The marked drop in density and slight increase even at the nine stage may be responsible for the fact that the curly-tip fibres of the britch were often very coarse, frequently showing coarse peak curly-tips (Dry 3) succeeding some finer ones.

The britch, therefore, passes through the following stages of development:-

A. <u>At 67 days</u> Folliole initiation was taking place; the hindlimb region was growing comparatively slowly. The density was low but high for this stage - approximately the same as the withers at this stage.

B. <u>At 80 days</u> Trio formation was completed. The relative growth rate of the hindlimb had shown a very slight increase; the region was growing rapidly. A marked increase in growth rate followed this stage. Density was approximately the same as on the withers and was high for this stage of development.

C. <u>At 93 days</u> The nine stage was nearly completed. There had been a drop in follicle density after the nine stage due to the rapid increase in the growth rate; increase in size of the hindlimb region was very marked. The density had dropped after the completion of the trio stage. The completion of the nine stage resulted in a slight increase in density but the density was low for nine stage development.

D. <u>At 97 days</u> The nine stage had been completed. The growth rate had decreased a little but the hindlimb region was still growing rapidly; the density had decreased.

E. <u>At 101 days</u> Fibres were ready to pierce the skin; the density had fallen considerably for only a very few new follicles were appearing. The hindlimb region was growing rapidly.

The superior ileum position - Graphs 1,2,3, 15,30,33,34 and 35 - was the last position on which follicles developed. Initial density was fairly high and with the formation of the trio stage a comparatively high density count occurred which, however, dropped at 87 days - i.e. at the completion of the trio stage. The drop in density occurred during a period of rapid relative growth. With the commencement of the nine stage the density gradually increases till the completion of the stage at 97 days, after which it drops. From the completion of the trio stage to the completion of the nine stage the size of the hindlimb was increasing rapidly.

The high density of the initial stage during the development of the trio stage may account for the small number of pre-curly-tip fibres present on this region. The drop in density at approximately 87 days may be responsible for the prevalence of Ravine arrays on the superior ileum position - the drop in density resulting in increased follicular vigour with a resulting increase in fibre coarseness. The gradual increase in density after the drop will account for the gradual decrease in fineness of the later fibres of the array.

On the superior ileum position, therefore, we have a series of phenomena which behave successfully:-

A. At 72 days Follicle initiation was taking place; the number of initial follicles was high. The growth rate of the hindlimb was much the same as that of the rest of foetus at this period. The density was low but higher than it was on other positions at this stage of follicle development.

B. At 80 days The trio stage was just beginning. The relative growth rate of the hindlimb region showed a slight increase and it was then growing a little faster than the rest of the body. The density was high at this stage.

C. At 87 days The trio stage was completed; the hindlimb was growing very rapidly; a drop in follicle density took place after the 83 day stage and there was no rise till after the 90 days stage.

D. At 97 days The nine stage was completed. The growth rate of the hindlimb region was decreasing slightly; the follicle density on the superior ileum had increased.

E. At 104 days The fibres were just about to pierce the skin; new follicles were rare. The hindlimb region was still growing rapidly but there was a tendency for the growth rate to decrease; density had fallen.

Counts were made for the neck and back positions but owing to the difficulty of getting a standard position to measure from these positions have not been included in the graphs. A mid-dorsal to mid-ventral line measurement was taken but was not comparable with any of the othe measurements. The counts for the back and neck positions are given in the appendix with the table for the mid-dorsal—mid-ventral line measurement.

F. Follicle Development and Arrangement.

Follicular development has been described by many people in many different animals; Duerden(4) and Wildman(8) have given the details of this development in the sheep. It is unnecessary, therefore, to describe follicular development in any detail, but is necessary to emphasise that they do not describe follicle arrangement in any detail. A fuller account of this will be found in Galpin(I) in appendix.

A series of photo-micrographs showing the main stages of development have been included.

The first four - figures 5 to 8 - show the arrangement of follicles from the initial follicle stage to the nine stage of follicle development.

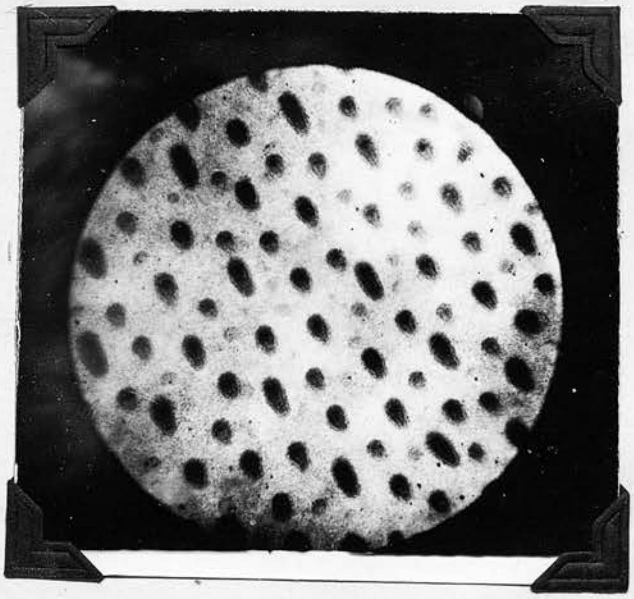
The vertical sections show the development of follicles. Figures 9 to 15.

It was found that from the time of initiation of a follicle till its fibres pierced the skin was approximately six weeks. The time elapsing between the first aggregation of cells forming fibre rudiments and the arrangement of follicles in lines was approximately a week. A fortnight later the trio stage was completed; all follicles in surface view then appeared to be much the same size.

New follicles coming in formed a nine stage which was completed about ten days after the completion of the trio stage. It was thought that no marked increase in follicle density occurred after this stage.

The sudoriferous glands appeared just after the completion of the trio stage - about three weeks after the initiation of the follicle. The first cells of the sebaceous glands were seen a few days (four at most) after the appearance of the sudoriferous glands.

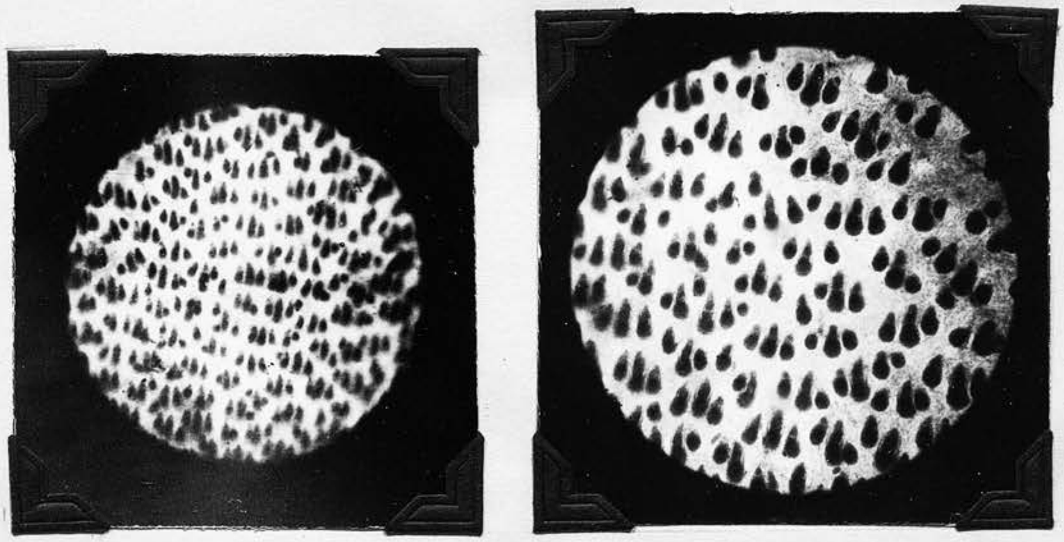
The first appearance of root sheaths and the commencement of the dermal papilla took place just after the trio stage had been completed - i.e. about three and a half weeks after follicle initiation began. The first appearance of fibres was between ten and twelve days after the trio formation, the first fibres piercing the skin approximately three weeks after the formation of the trio stage. A fortnight after fibres pierced the skin the type of fibre could be determined by an examination of its free tip.



H. P.

Figure 5

Initial follicle stage showing large X follicles and smaller Y follicles in lines.

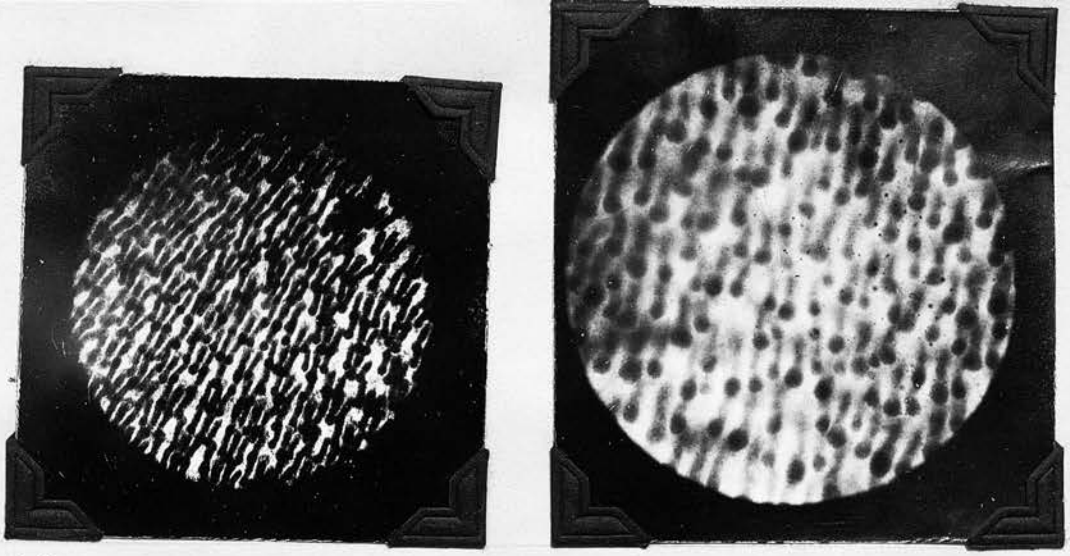


X 60 -approx.

H. P

Figure 6

Trio arrangement of follicles. The small follicles have not ~~yet~~ developed as yet beside some of the Y follicles.



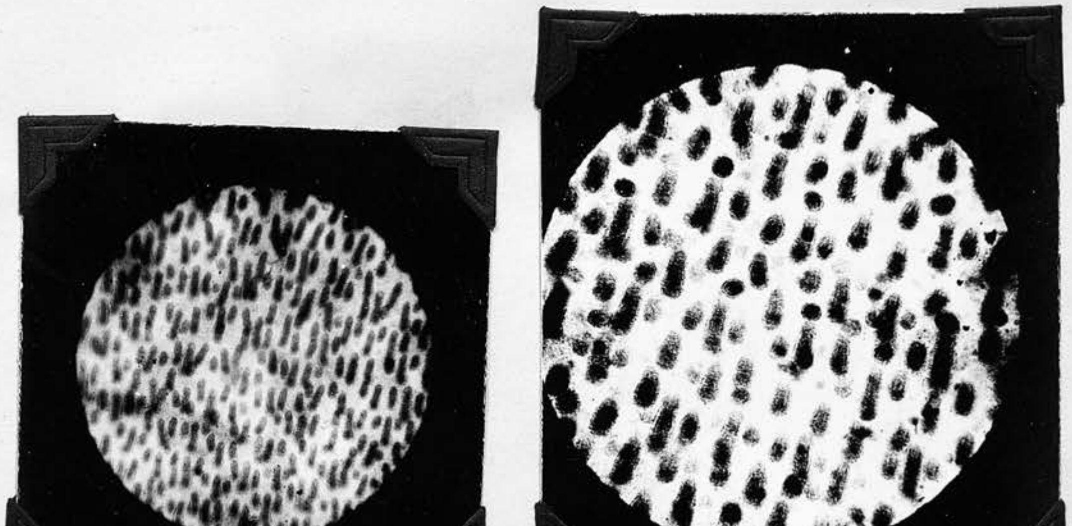
X 60 approx.

H.P.

Figure 7

The follicles of the trio now have two small follicles one either side of them making a secondary trio appearance.

- the nine stage

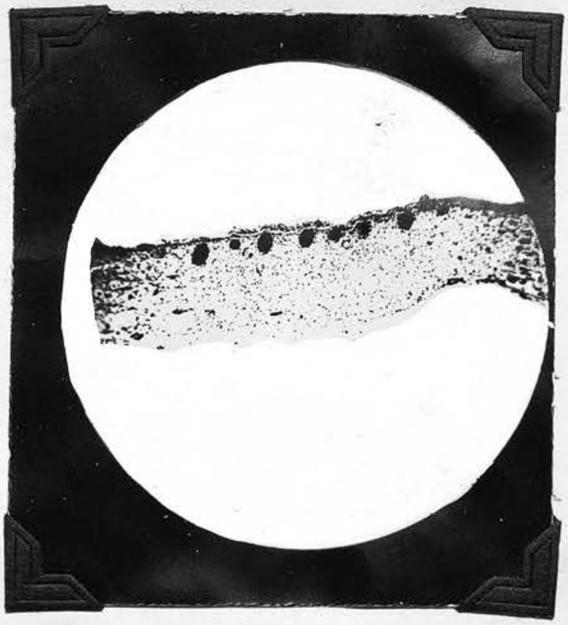


X 60 approx.

H.P

Figure 8

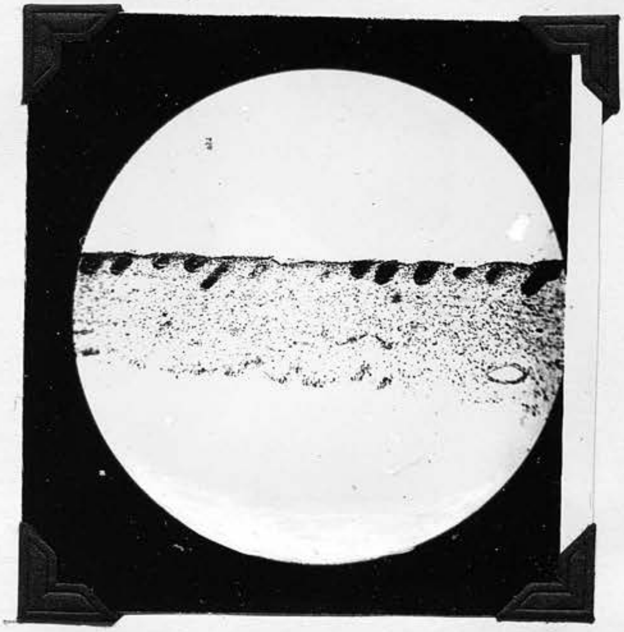
Stage intermediate between the trio and nine stages of follicle development.



L.P

Figure 9

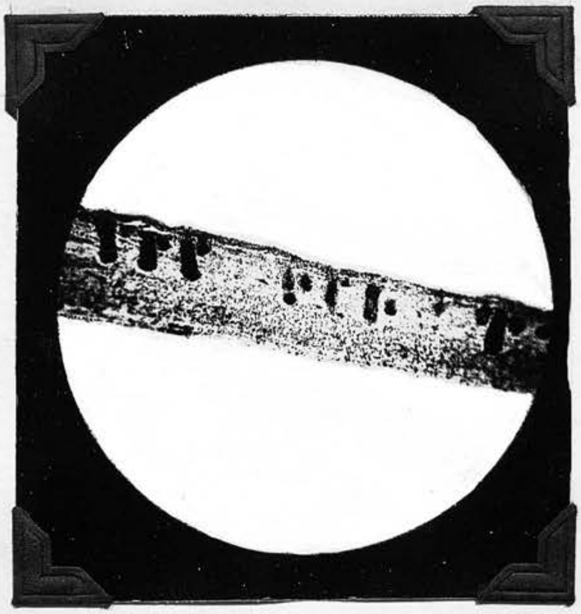
Back 80 days - had the hair rudiment just appearing - follicles fairly close together and a foreshadowing of trio stage.



L.P

Figure 10

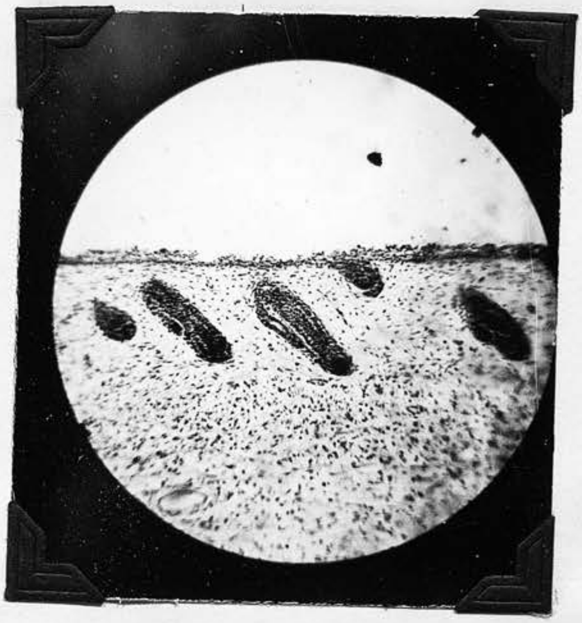
Back 83 days - a perfect trio stage of development on which no glands had appeared as yet.



L.P.

Figure 11

Withers 76 days - The trio stage was just breaking up. Sweat glands were forming as a bud at the side of the follicle. Whether they came from the malpighian layer as a separate bud was not certain. They arise about the trio stage of development.



H.P.

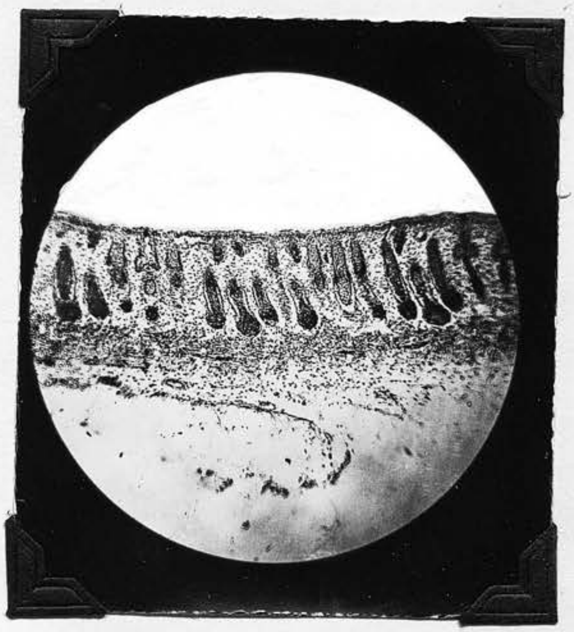
Figure 12

Poll 76 days was an advanced trio stage of development showing the trio breaking up and the sweat glands growing downwards.

H.P

Figure 13

Withers 83 days - Post trio stage with the original trio follicles fairly widely apart and new follicles coming in between. Arrector pili muscles were appearing.



L.P

Figure 14

Back 94 days - A later stage ~~between trio and~~ almost a nine stage development- showing groupings of follicles and the appearance of sweat and sebaceous glands. Arrector pili muscles have appeared.

L.P

Figure 15

Withers 94 days - Late ~~Almost a~~ nine stage of development. with sebaceous glands and sweat glands present. Arrector pili muscles were well developed.

L.P.

Figure 16

94dys Poll - Just prior to the time when fibres pierced the skin.

All photography by Williams

IV. DISCUSSION

From the relative growth gradients it has been found that the relative growth rate of the foetus "as a whole", as determined from the C.R. measurement, decreased as the foetus became older. The head, fore and hindlimb regions also showed decreasing relative growth as the age of the foetus increased. The relative growth rate of the head region was shown to decrease more rapidly than that of the other regions, and the decrease began earlier on this region than elsewhere.

In width and height the forelimb region behaved in much the same manner as the C.R. did; there was, however, an increase in growth rate between 80 and 93 days, especially in the humerus length. After 93 days the growth rate of the humerus showed only a slight decrease, while the decrease in the growth rate of the increase in width was more marked. In height the forelimb region showed a marked decrease in growth rate after the 103 day period.

The hindlimb region until the 80 day period was growing a little more rapidly than the foetus as a whole. After the 80 days stage there was a marked increase in the growth rate of the hindlimb, especially in length and in width. The relative growth rate of the increase in height continued to decrease. From the equilibrium constant values it can be seen that there was a definite gradient for relative growth in length, height, and width from the anterior to the posterior end of the body. The hindlimb region was growing the fastest, the head region the slowest.

It will be noticed that from these measurements there was no indisputable evidence that periods of rapid growth were preceded by periods of arrested growth. It is thought that perhaps measurements do not give this phenomenon when changes in weight from age to age do.

Richards(7) had said that a single α value masked small but significant changes in relative growth. α -with-time - was therefore calculated from the decrease in relative growth rate per cent per day and compared with the α of Huxley(6) calculated from

$$\alpha = \frac{\mathrm{Log.}y_1 - \mathrm{Log.}y}{\mathrm{Log.}x_1 - \mathrm{Log.}x} .$$

When plotted, these were found to give graphs with similar curves. It was found that small changes in the value of α were significant and were able to be correlated with changes in follicle density.

could

From the changes in the values of the equilibrium constant α, calculated from -

$$\alpha = \frac{\dfrac{\mathrm{Log.}_e y_1 - \mathrm{Log.}_e y}{t} \times 100}{\dfrac{\mathrm{Log.}_e x_1 - \mathrm{Log.}_e x}{t} \times 100} ,$$

from period to period, fluctuations in the general trend of relative growth were obtained.

When the α values for each region at definite periods of time were plotted against body position it was seen that an anterior-posterior gradient in growth did not occur during the early stages of foetal growth. At 53 days it is found that head, fore and hindlimb regions were all growing at approximately the same rate. The growth rates gradually change till, at 80 days, the fore and hindlimb regions were growing at approximately the same rate while the head region was growing more slowly.

At 93 days the anterior-posterior gradient in growth rate was obvious, the head region growing slowly the hindlimb region very rapidly. The gradient became less marked at 115 days stage but there was still an anterior-posterior gradient.

Arrangement of follicles in the foetal skin showed an early stage when follicle initiation was taking place, followed by a trio stage when the older follicles had two small follicles one on either side of it and a nine stage arising from the trio stage by the appearance of two new follicles either side of each of the trio follicles. This stage was not always completed, some follicles being suppressed. Follicle development showed that fibre growth and differentiation of the associated glands took place after the formation of the trio stage.

Fibre types could be recognised from the tips of the fibres about fourteen days after the fibres pierced the skin. It was found that the coats of the New Zealand Romney, the Southdown and the Ryeland Breeds had more pre-curly-tip fibres on positions on which follicle development began early than on the positions on which follicles developed later.

The fibre-type-arrays, however, showed a posterior-anterior gradient - coarse-fibred arrays occurring on the britch and fine-fibred ones on the anterior positions.

Comparison with the anterior-posterior gradient in relative growth-rate will show that the fine fibre-type-arrays occur on regions where the relative growth-rate was slower in the later stages of follicle development and that coarse fibre-type-arrays occurred on the regions where the growth rate was still rapid, during the later stages of follicle development.

It was also found that the high pre-curly-tip counts occurred on regions on which follicle initiation and trio stage arrangement took place when the regions were growing more rapidly than they did in the later stages of foetal development. Low pre-curly-tip counts - found on the posterior regions were thought to be due to the fact that the comparatively high density counts occurred on these positions until the trio stage of development was nearly complete. The marked increase in growth rate during the nine stage of development, however, resulted in low nine stage density which was thought to account for the coarse curly-tips.

The britch position was unique in that it had a pre-curly-tip count as high as that of the withers and also coarse curly-tips. This is thought to be due to the fact that the britch and withers commenced follicle initiation at approximately the same time. The hindlimb regions and forelimb regions were at this stage growing at approximately the same rate. The density at the trio stage accounted for some of the trio stage follicles not developing into pre-curly-tips and the marked increase in growth rate of the hindlimb at the commencement of the nine stage probably accounts for the coarse curly-tips found on the britch - especially the peak curly-tips (Dry3) This marked increase in growth rate was also thought to account for the prevalence of coarse-fibred-fibre-type-arrays.

Only one breed of sheep has been studied and this breed is well known to have a coat with great variation in fibre length, fibre fineness and fibre diameter.

In a fine-coated breed of sheep, such as the Merino, where there is little variation in fibre characters, it is possible that the initial follicle density ~~was~~ is sufficiently great to allow the incoming new follicles to maintain a high density throughout follicle development, the fleece of the sheep being as a result fine and even.

From these results, however, it is suggested that in the New Zealand Romney lamb the coat characterisation of a region ~~was~~ is dependent upon the relationship between the local initial follicle density and the effect of the growth rate of the region upon it. No opportunity has arisen to determine whether there may be a direct effect upon the characterisation of the foetal coat, and therefore subsequently upon the characterisation of the adult fleece, caused by maintaining pregnant ewes at different levels of metabolic activity during the gestation period, but is well-known that in New Zealand there is frequently difficulty in providing a supply of adequate food during the winter months (i.e. when the majority of ewes are pregnant). It is logical to assume that a proportion of the variation which is known to exist in New Zealand Romney wool may have as its basis the irregularity of the nutritive supplies taken in by the gravid ewe, and a promising line of further research work is envisaged.

V. SUMMARY

I) A series of eighty-three dated foetuses of the New Zealand Romney breed of sheep have been used to provide material for a study of the relationship between increase in body size and development and arrangement of wool follicles and the effects of these on the characterisation of the fleece in different body regions.

2) The results of preliminary studies made on fibre-type-arrays, and on follicle arrangement are incorporated in two papers, which are presented in support of this thesis: viz: Galpin I and Galpin II in appendix.

3) It has been shewn that different regions of the body show different growth-rate increases relative to crown-rump measurements. The foetal head showed a decrease in relative growth-rate from the 74th day to the 122nd day of intra-uterine life; the forelimb region showed a slight increase in relative growth-rate for length and width after the 86th day and continued to grow at approximately the same rate until the 122nd day; the hind-limb showed a marked increase in relative growth-rate from the 86th day and continued to grow at approximately the same rate until the 122nd day.

4) The formula $y = bx^{\alpha}$, which has been proposed by Huxley to replace $y = bx^{k}$, has been used to determine differences in rates of growth of different body regions.

5) It was found that the equilibrium constant 'α-with-time' exaggerated the magnitude of small but significant variations in growth rates, which might be somewhat obscured by results calculated from the formula

$$\alpha = \frac{\log.y_1 - \log.y}{\log.x_1 - \log.x}$$

6) From the values of the equilibrium constant α for the head fore and hindlimb regions, it was found that there was an antero-posterior gradient for relative growth-rates - the anterior regions growing more slowly than the posterior ones. Further it was determined that this antero-posterior gradient was slightly previous to the 86 days stage of development and marked after the stage.

7) The antero-posterior growth-rate gradient was found to be comparable with the postero-anterior (Britch-poll) fibre-type-array gradient; coarse-fibred arrays occurred posterior to fine-fibred arrays.

8) It has been shown from the changes in value of 'α-with-time' for the different regions, from period to period, that the antero-posterior gradient for relative growth-rate was not obvious in the early stages of development and did not become important until about the 80 days stage. There was a gradual change from stages with no gradient to stages with a marked gradient.

9) In each region the varying growth rates have been correlated with local fibre population density, and it has been shown that acting together these may both have an effect upon the general character of the wool grown on a region.

10) It has been shown that positions on which follicle initiation begins early have higher percentage counts of pre-curly-tip fibres than those on which follicle initiation begins later. Correlation with relative growth-rates showed that the former regions grew more rapidly until the completion of the trio stage than they did after it. Positions with low pre-curly-tip counts showed an

initiation of follicle growth at a time when the growth rate of the region was slower than it would be during the later stages of follicle development.

11) Coarse curly-tip fibres were found on regions which grew rapidly after the completion of the trio stage - notably the britch and superior ileum positions. The britch had a pre-curly-tip count the same as the withers, i.e. midway between that of the poll and superior ileum positions; this may be explained by the fact that, though on both britch and withers follicles commence to grow at the same time, the forelimb regions did not show an increase in growth rate after the completion of the trio stage comparable with that of the hindlimb regions where the increase in growth rate was very marked.

12) It has been shown that formation of glands and ducts takes place about three weeks after initiation of follicle growth, and that fibres pierce the skin between six and seven weeks after their follicles were first laid down.

13) The evidence accumulated permits the enunciation of the hypothesis that there is a direct correlation between rates of growth and follicle densities in each region, and that the ultimate local characterisation of the fleece depends upon the relative degrees to which these operate. The faster a region grows after follicles are first laid down and the less the follicle density, the coarser is the wool grown upon it; similarly, the slower the growth and the greater the density, the finer is the wool produced.

To Dr. Dry, Dr. Duerden, Dr. Irwin and Mr. Rudall for their helpful suggestions I wish to acknowledge my indebtedness. My thanks are especially due to Professor Huxley and Professor Miller for many helpful suggestions and much constructive criticism. I am also indebted to Professor F. A. E. Crew for granting facilities to carry out this work.

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Appendix

Table I - Page 2 - is a table, similar to Tables 4 to 15 in the thesis, for the M.D.L. to navel.

Table 2 - Page 3 - is for the follicle density counts for the neck and back regions. See Table 10 in thesis.

Tables 3 to 8 - Pages 4 to 10 - are tables to show the correlation between calliper and wire measurements.

Table I

Age of Foetuses	Av. Age of Foetuses	Size of Foetuses	Av. Size of Foetuses	Increase	Natural Log. Size	Increase	Relative Growth Rate per cent per Day	γ with-time	γ	Increase per cent	Increase per cent per Day
42		14,14	17		·53063						
46	46	16									
49		21,16,19,21									
				10		·46262	3·558	·91	·95	57·7	4·4
52		27,22	27		·99325						
56	59	25									
60		30,30,29,30,28									
64		35,35									
				19		·53281	3.552	1.13	1·06	70·4	4.7
68		37,42,37	46		1·52606						
72	74	42,38,44,45									
76		47,52,54,46									
80		53,51,50									
				15		·28223	2·352	1.04	1	57·2	4·8
83		52,62,52,52,55	61		1.80829						
87	86	58,64,60,64,65									
90		70,74,60,70									
				14		.20661	1·878	·82	·96	23	2·1
93		70,66,68	75		2·01490						
97	97	84,69,72,73,)									
		72,72,76,72)									
101		79,84,85									
				16		.19337	1·757	1·14	1·02	21·3	1·9
104		90,80,85,78,90	91		2·20827						
108	108	99,									
112		100,105,95,90									
				20		·18866	1·347	·95	1	22	1·6
118		108,106	111		2·39790						
122	122	102,112,115									
127		120,120,107									

M.D.L. to Navel

Table 2 in appendix shows the follicle density counts for the neck and back positions at different ages of foetal development.

Area = no. of follicles to $\frac{25}{103}$ sq. mms.

DL is the no. of follicles to a line and L is the no. of lines of follicles in $\frac{25}{103}$ sq. mms.

See page 14

Position		Time in Days Follicle Counts 60	64	68	72	76	80	83	87	90	93	97	101	104
Neck	Area		2	15	18	28	40	44	45	44	36	32		
	DL		2	5	6	7	10	11	9	11	9	8		
	L		1	3	3	4	4	4	5	4	4	4		
Back	Area			1	10	16	28	45	50	50	36	55	36	21
	DL			1	3	4	7	9	10	10	9	11	9	7
	L			1	3	4	4	5	5	5	4	5	4	3

Tables 3 to 8 show that the relationship between calliper measurements and measurements with a flexible wire is approximately constant - the length and height measurements behaved in a similar way and the calliper measurements were approximately between ·7 and ·8 of the measurements with wire. The width measurements showed the calliper measurements to be between ·55 and ·65 of the wire measurements.

Plotting the measurements made with a flexible wire against the dorsal neck curvature measurement was found to give an α value similar to that obtained from plotting the measurements made with callipers against the C.R. Therefore, it has been assumed that from calliper measurements a fairly accurate idea of the relative growth rate of a foetus might be obtained.

Table 3

Dorsal Neck Curvature from the crown to the root of the tail.

Age of Foetus	Calliper measurement	Wire measurement	Correlation from calliper measurement [illegible] wire measurement
49	70	80	·8
56	100	110	·9
64	120	140	·8
68	134	150	·8
72	163	190	·8
76	169	200	·8
83	190	225	·8
90	237	300	·78
97	266	320	·8
122	395	430	·9
127	435	490	·88

The calliper measurements were approximately ·8 of the wire measurements.

Table 4

Femur Length

Age of Foetus	Calliper measurement	Wire measurement	Correlation from $\frac{\text{calliper measurement}}{\text{wire measurement}}$
49	10	13	·76
56	17	18	·9
64	22	28	·78
68	24	29	·82
72	28	37	·76
76	36	43	·83
83	44	56	·78
90	52	70	·74
97	62	75	·82
122	94	110	·85
127	108	125	·86

The calliper measurements were approximately ·8 of the wire measurements.

Table 5

Humerus Length

Age of Foetus	Calliper measurement	Wire measurement	Correlation from calliper measurement / wire measurement
49	12	15	·8
56	14	18	·8
64	20	27	·77
68	27	34	·79
72	29	35	·82
76	28	37	·76
83	39	50	·78
90	38	50	·76
97	50	63	·79
122	76	94	·8
127	90	118	·76

Calliper measurements were approximately ·8 of the wire measurements.

Table 6

Eye to Eye

Age of Foetus	Calliper Measurement	Wire Measurement	Correlation from calliper measurement wire measurement
56	22	32	·68
64	30	39	·76
68	32	45	·71
72	36	50	·72
76	39	60	·65
83	44	70	·62
90	50	75	·66
97	56	85	·65
122	64	100	·64
127	70	120	·58

Calliper measurements were approximately ·65 of the wire measurements.

Table 7

Femur head to Femur head

Age of Foetus	Calliper measurement	Wire measurement	Correlation from calliper measurement / wire measurement
49	14	26	·54
56	20	40	·5
64	27	54	·52
68	34	68	·5
72	37	70	·52
76	46	80	·57
83	48	100	·48
90	64	120	·53
97	75	150	·5
122	109	175	·62
127	125	200	·62

Calliper measurements were approximately ·55 of the wire measurements.

Table 8

M.D.L. to the point of the olecranon

Age of Foetus	Calliper measurement	Wire measurement	Correlation from calliper measurement / wire measurement
64	34	45	.75
68	36	50	·72
72	42	56	·75
76	48	60	·8
83	57	70	·8
90	68	93	·73
97	74	105	·7
122	102	135	·74
127	115	162	·7

Calliper measurements were approximately ·75 of the wire measurements.

Paper I

Thesis DSc. Galpin 1936

THE PRE-NATAL DEVELOPMENT OF THE COAT OF THE NEW ZEALAND ROMNEY LAMB

BY

NANCY GALPIN, M.Sc.

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THE PRE-NATAL DEVELOPMENT OF THE COAT OF THE NEW ZEALAND ROMNEY LAMB.

BY NANCY GALPIN, M.Sc.

(Massey Agricultural College, Palmerston North, New Zealand.)

(With Ten Text-figures.)

CONTENTS.

I. INTRODUCTION.

THE classification of fibre type arrays (Dry (2)) is based on postulated pre-natal events. Very little is known about the pre-natal development of the coat of the sheep, and the work that has been done has been of histological (3, 6) rather than of morphological importance. It was therefore desirable to study the development of the coat of the sheep with a view to interpreting post-natal morphological expressions from pre-natal events.

II. MATERIAL AND METHODS.

The material consisted of a series of dated New Zealand Romney foetuses from the Massey Agricultural College flock and a number of undated ones from various sources.

Macroscopic examination was carried out with the aid of a hand lens, and more detailed knowledge was gained by taking snippets of skin from definite areas and mounting these for microscopic examination.

The earlier foetuses were fixed immediately they were taken from the uterus by immersion in a formol-alcohol bath—5 per cent. formalin, 30 per cent. alcohol; this bath was changed after 24 hours and the foetuses were stored in a second similar bath. This was found to be a satisfactory method of preserving the earlier foetuses—the tissues remaining in a suitably stretched condition. The later foetuses—from 112 days—were immersed in a 5 per cent. formalin bath instead of the formol-alcohol one. They were changed to a similar solution in which they were stored in the same way as for the earlier ones.

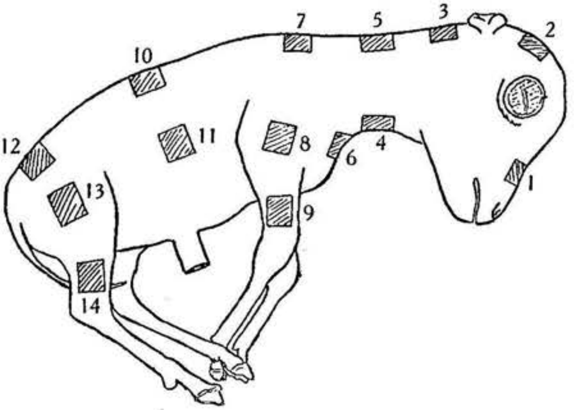


Fig. 1. Diagram of foetus to indicate positions from which skin snippets were taken. 1, nose; 2, poll; 3, neck; 4, ventral neck; 5, anterior withers; 6, shoulder point; 7, withers; 8, h.-r.j.; 9, forearm; 10, back; 11, side; 12, superior ileum; 13, hip joint; 14, britch.

Skin samples were regularly taken from the following positions:

(1) *Nose.* Across the bridge of the nose just anterior to the eyes.

(2) *Poll.* On the mid-dorsal line between the ears and the positions of the horns.

(3) *Neck.* On the mid-dorsal line half-way between the ears and the last cervical vertebra.

(4) *Ventral neck.* On the mid-ventral line comparable to the anterior withers position.

(5) *Anterior withers.* On the mid-dorsal line about the level of the sixth cervical vertebra.

(6) *Shoulder point.* On the point of the right shoulder.

(7) *Withers.* On the mid-dorsal line level with the fifth rib.

(8) *Humero-radial joint.* Ventro-lateral to the withers, on the right side, in a line with the lateral aspect of the shoulder point and slightly anterior to the elbow.

(9) *Forearm.* Half-way down the right forearm.

(10) *Back.* On the mid-dorsal line level with the last rib.

(11) *Side.* On the right side at the distal end of the last rib.

(12) *Superior ileum.* On the mid-dorsal line on the medial angles of the ilea.

(13) *Hip joint.* Ventro-lateral to the superior ileum position at the junction of the femur and pelvic bones (acetabulum).

(14) *Britch.* Immediately posterior to the stifle joint and midway across the thigh.

In addition skin snippets were taken from many other positions, but not from every foetus. The skin snippets were stained with borax carmine, cleared and mounted in xylol balsam. This staining proved most effective, the follicles staining a deeper red than the skin generally.

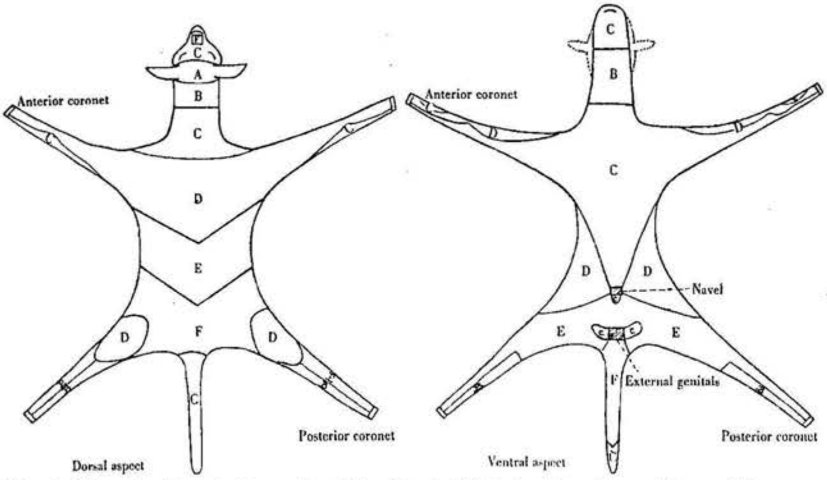


Fig. 2. Dorsal and ventral aspects of the skin, laid flat, to show the positions of the areas referred to in the text. The sensory follicles around eyes, mouth, ears and nostrils and those of the anterior and posterior coronary regions do not belong to any area.

Examination of skin snippets revealed the fact that the body naturally divided itself into regions that developed at different times. These regions were not all contiguous, and for the purposes of description all regions that develop at the same time have been grouped together and termed an area. There are six of these areas and they have been described as areas A, B, C, D, E and F, respectively—area A including the regions that develop first, area F those that develop last. These areas do not include the sensory follicles around the eyes, mouth, ears and nostrils, nor those on the anterior or posterior coronary regions; these are referred to by name when mentioned in the text.

The areas include the following regions (see Fig. 2):

Area A. The poll region.

Area B. The anterior neck region—dorsal and ventral. The posterior aspect of the hind-limb inferior to the hock joint.

Area C. The dorsal and ventral portions of the posterior neck region. The carpal areas and the posterior aspect of the fore-limb. The large ventral region between the fore-limb extending laterally to the anterior coronary region and mid-ventrally a short distance behind the navel. The small regions on either side of the external genital organs. The dorsal surface of the tail and the posterior third of the ventral surface. The face region. The ventral aspect of the lower jaw.

Area D. The withers region extending laterally to the anterior coronary region and mid-dorsally to a short distance anterior to the last rib. The cranial face of the fore-limb inferior to the carpal region. The lateral regions of the ventral surface as far posterior as the navel. The britch region.

Area E. The dorsal and lateral regions of the back. The lateral limb regions inferior to the britch. The ventral surface posterior to the navel and extending down the limbs.

Area F. The ventral anterior two-thirds of the tail. The dorsal surface of the hind-quarters posterior to E area. The bridge of the nose.

III. DEVELOPMENT OF THE COAT.

The development of the coat of the New Zealand Romney lamb was found to correspond in the main with that described by Wildman (6) for certain British breeds. The principle of crown-rump measurement as normally employed has been used in this paper and has been given for each foetus along with its age.

It will be noticed, however, that considerable importance was attached to the stage of development termed "trio" (4, 5), which Wildman (6) made reference to but did not stress. Further, reference has been made to a "nine" stage—a derivative of the trio stage—which has been considered of equal importance to the trio stage; this stage when completed might well be mistaken for a complete trio stage—description appears later in the text (see Figs. 6 and 10). This nine stage was not mentioned by Wildman (6) in his description of British breeds, but along with the trio stage it has been found a very satisfactory stage by which to date foetuses approximately. A discussion as to its importance will be given later.

At 42 *days*. The earliest dated foetus taken was a 42-day one (6 cm. crown-rump measurement). Follicles were present around the eyes, nostrils and mouth, both upper and lower lips; these were the follicles of tactile fibres. The follicles around the eyes were very prominent, being evident as large white rounded spots. No follicles were to be seen elsewhere on the body.

At 49 *days* (Fig. 3). On the 49-day foetus (7½–8 cm. crown-rump measurement) a few scattered single follicles had appeared on the poll (A area), and isolated ones on the anterior portions of the neck (B area). Posterior and anterior coronary regions both had follicles. With the exception of sensory follicles mentioned as occurring in the 42-day foetus on no other regions of the body could follicles be found.

At 56 *days* (Figs. 3 and 4). The 56-day foetus (11 cm. crown-rump measurement) had isolated follicles over most of the body, but they were more difficult to find on the E and F areas than elsewhere. On the A areas it was possible to distinguish two types of first follicles, X being the term applied to the larger and older, and Y to the later and smaller of these (see Figs. 3 and 4). The follicles were numerous on the A area. The B area had a number of follicles but it was not possible to distinguish X and Y follicles. The B area was, however, at a more advanced stage than the other areas, the most noticeable differences being the greater size of the follicles and the greater numbers.

At 64 *days* (Figs. 3, 4 and 5). At 64 days the foetus was 14 cm. in crown-rump measurement, and had follicles all over the body. Variation in density was quite marked, density here signifying the number of follicles per unit area, that is, population of fibres per unit area of skin surface (6). On the A area, the X and Y follicles were numerous, and the larger X follicles had now two small follicles, one on either side, giving the trio arrangement mentioned previously (Fig. 5). These small follicles have for convenience been termed x and y, so that the trios may be written xXx and yYy. The X and Y follicles of the A area had arranged themselves in lines. The trio grouping did not disturb this arrangement (see Fig. 5). On the B area both X and Y follicles were apparent but no trio grouping had appeared as yet. On the C area large X follicles and small Y ones were found; D area had X follicles with Y ones just appearing; E and F areas had isolated follicles scattered over the field. The follicles on the E area, however, were slightly more pronounced than those on the F area. Linear arrangement of follicles was to be seen on the A and B areas, but nowhere else on the body.

At 68 *days* (Figs. 3, 4, 5 and 6). The 68-day foetus (15 cm. crown-rump measurement) had all the follicles of the A area in trio groups xXx and yYy. The B area had X and Y follicles which were assuming a linear distribution—appearing much the same as the poll did at 56 days. The C area was similar, but the follicles were smaller, especially, the Y ones.

The D area had the same follicles present and the same follicular arrangement as the D and C areas, but the follicles were noticeably smaller. Only

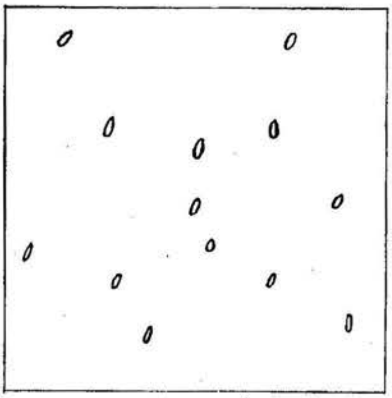
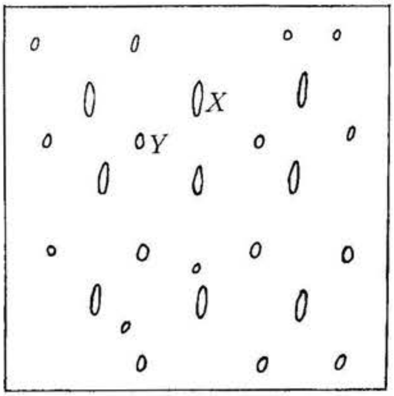


Fig. 3.



First stage

Fig. 4.

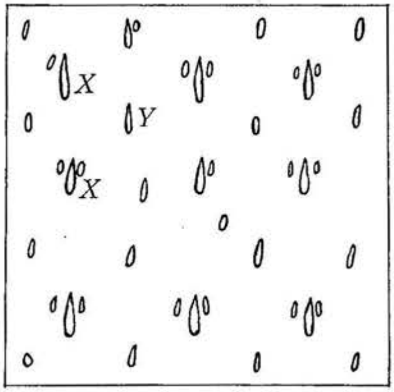
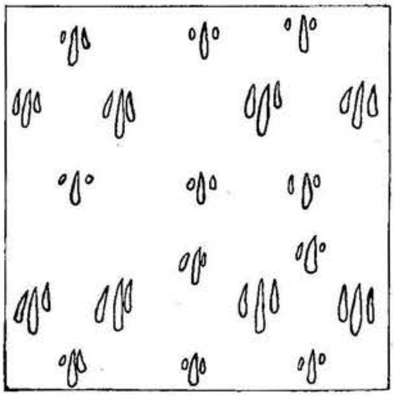


Fig. 5.



Trio stage

Fig. 6.

Figs. 3–6. Diagrams to illustrate earlier stages of follicle distribution in the pre-natal skin.

Fig. 3. First follicles just appearing.

Fig. 4. Two types of follicles; the larger ones are *X* follicles, the smaller ones *Y* follicles.

Fig. 5. Shows commencement of trio stage. The *X* follicles show trio arrangement, but the *Y* follicles have not yet reached this stage. Note the linear arrangement.

Fig. 6. Complete trio stage.

X follicles were found on the F area, while *X* and suggestions of *Y* follicles were to be seen on the E area.

At 72 *days* (Figs. 4, 5, 6 and 7). The 72-day foetus (19–20 cm. crown-rump measurement) showed the trio arrangement disappearing on the A area. This was apparently due to the fact that at or about the 68-day stage X and Y follicles on this area had completed their earliest development and were about to commence fibre growth. When the 72-day stage is reached the x and y follicles of the trio have also nearly completed development and are about to commence fibre growth, so that at 72 days all follicles of the trio—xXx and yYy—look much the same. At this stage it was impossible to differentiate between trio groups of the xXx and yYy types. Grouping in threes was, however, still detectable (Fig. 7). Among the follicles of the trio grouping a number of new small follicles were found. They did not necessarily appear close to the middle or oldest follicles of the trio group but were situated indiscriminately beside either X or x, or Y or y. In the B area all the follicles were at the trio stage of development; on the C area the X and most of the Y follicles had reached the trio stage of development, while on the D area only the X follicles had reached this stage. The number of follicles on the E and F areas had increased; the E area showed a linear follicular arrangement, while on the F area there were still a number of Y follicles just appearing.

At this stage the follicles around the eyes and nostrils and on the upper and lower lips were very prominent, and tactile fibres were nearly ready to burst through the skin.

At 76 *days* (Figs. 4, 5, 6, 7 and 8). The next foetus was 76 days old (20 cm. crown-rump measurement). The A area now retained only a suggestion of the trio arrangement, it being impossible to distinguish between any of the xXx or yYy follicles of the trio except by their position. Additional new follicles, $x'y'$, were developing (Fig. 8) rapidly beside the various members of the trio. The B and C areas had completed their trio stage of development (Figs. 6 and 7). The B area had the trio stage disappearing, and odd new x' and y' follicles were appearing as on the poll at 72 days (Fig. 7). The C area, though not so advanced as that of B, also had suggestions of the new x' and y' follicles. The D area had a few yYy trios to be completed (Fig. 5); the F area follicles were linearly arranged (Fig. 4).

At 83 *days* (Figs. 6, 7, 8 and 9). At 83 days the foetus (22–23 cm. crown-rump measurement) had the tactile eyelash fibres through the skin. The A area on casual inspection were much the same as at 76 days, but closer examination revealed further development of x' and y' follicles about the old xXx and yYy trio groups. These new follicles were becoming arranged in groups about either the X or x, the Y or y follicles of the original trio group in a manner suggestive of the original trio grouping which had now completely disappeared. This was the foreshadowing of the nine grouping—which was due to each of the follicles of the trio group becoming the central follicle of a group of three follicles—making each trio the forerunner of a nine group. At this stage groups of seven and eight could be found. The x' follicles were still small (see Fig. 9). On the B, C and D areas the trio arrangement of follicles was no longer obvious, but close inspection revealed the remains of such grouping. New x' and y' follicles were appearing, B and C areas showing groups of five and six follicles. An odd group of seven might be detected on the B area. On the E area the suggestion of a trio arrangement still persisted, but now x' and y' follicles were appearing. The F area were in the late stage of trio development, the follicles of x and y type being of the same size as the X and Y.

At 90 *days* (Figs. 7, 8, 9 and 10). On the 90-day foetus (29–30 cm. crown-rump measurement) the fibres round the nostrils, and on upper and lower lips, the horn and posterior coronet regions, had all burst through the skin, while the hairs around the eyes were quite long.

The follicles of the A area were now grouped in nines, each nine originating from an original trio group. There were thus three groups of three, one about the X follicle of the trio group and one about each x follicle. This grouping $x'xx'$, $x'Xx'$, $x'xx'$ (which may very easily be mistaken for an advanced trio grouping) showed on closer inspection the nine grouping and the origin of the group (Fig. 10). In addition new follicles were beginning to appear beside the nine-stage follicles. Some of the follicles on this area were ready to burst through the skin. B, C and D areas showed a further increase in the number of x' and y' follicles, the B area having very nearly reached the complete nine-grouping stage. On the E area remains of the trio arrangement could still be detected, but the number of x' and y' follicles was increasing. On the F area, the suggestion of the trio arrangement still persisted though it was rapidly disappearing.

At 97 *days* (Figs. 8, 9 and 10). At 97 days (30 cm. crown-rump measurement) the foetus had quite a number of regions on which the fibres had emerged through the skin. The hairs were quite long on those regions where fibres had been found through the skin at the 90-day stage. The fibres on the anterior coronet region were through.

The fibres had emerged through the skin on the A area and were just piercing it on the B area. The C area showed the completed nine groups, though there were still a few groups of seven and eight to be completed. No complete nine groups occurred on the D area, but there was a number of groups of eight; on the F area the remains of the trio stage could with difficulty still be detected. The E area had a number of groups of five, six and seven follicles, while the F area had the x' follicles appearing, groups of four and five being quite common.

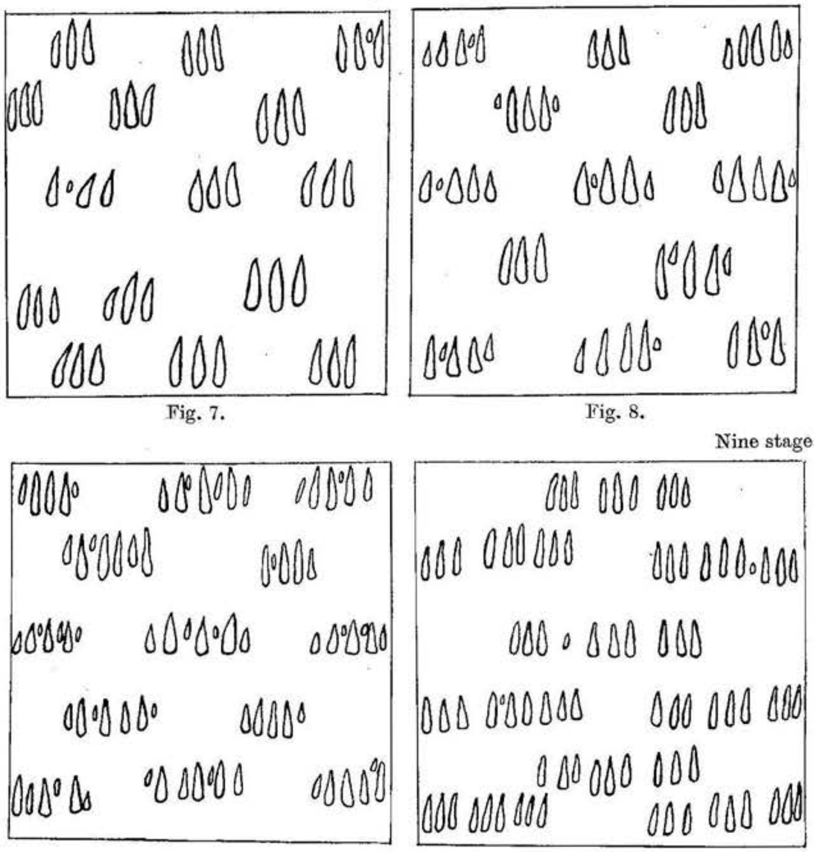

Trio stage

Fig. 7.

Fig. 8.

Nine stage

Fig. 9.

Fig. 10.

Figs. 7–10. To illustrate the later stages of follicle distribution.
Fig. 7. Complete trio stage. Follicles all approximating each other in size.
Figs. 8 and 9. Stages intermediate between the trio and nine stages.
Fig. 10. Complete nine stage. Linear arrangement is still perceptible.

Owing to the sterility of one ewe no foetus intermediate between 97 and 111 days was secured.

At 111 *days.* The next foetus was aged 111 days (32–33 cm. crown-rump measurement). This had fibres through on all areas except E and F.

The fibres of the A and B areas were quite long and had commenced to curl, while on the C area the fibres were through the skin. The D area had the fibres just piercing the skin. On the E area fibres were not through. The nine grouping was complete and some of the follicles were just ready to pierce the skin. On the F area the nine grouping was very nearly complete.

At 122 *days*. The 122-day foetus (40–43 cm. crown-rump measurement) was completely covered with fibres. On the early regions—the A and B area—it was possible to distinguish the halo-hairs and sickle fibres. On the C and D areas suggestions of sickle fibres could be detected, while on the E and F areas the fibres were short and straight. This ewe had triplets, and the wool characters of the lambs were somewhat different, two having a large number of halo-hairs while the third had very few.

At 127 *days*. The 127-day foetus (47–50 cm. crown-rump measurement) had relatively long fibres present. On the earlier areas—A, B and C—there was quite a marked curl effect, the region about the shoulder point being the most tightly curled. Pre-curly-tip fibres were easily recognisable from A, B and C areas, and also some curly-tip ones were distinguishable. As well as these there were some fine, straight, short fibres not able to be distinguished as yet as belonging to any definite fibre type. On the E and F areas, all the fibres were uncurled and were not able to be sorted into definite fibre types. On the earlier regions it was possible at this stage to find representations of all fibre types, except histerotrichs.

At full term (146 days average). No dated foetuses were secured older than 127 days, but some lambs that died at birth were secured. These were from 50 to 54 cm. crown-rump measurement. The wool was found to be curled on all regions, the halo-hairs standing up rather stiffly. The fibres had grown considerably longer in the time intervening between 127 days and birth. Samples taken from various regions on these when sorted gave halo-hairs, super-sickle, sickle and curly-tip fibres and a few short fibres which might have been histerotrichs but in all probability were late curly-tip ones.

Undated foetuses. From the dated material in my possession no definite information could be gathered as to whether the fibres on the E or F areas pierced the skin first. From the relative times at which fibres in the two areas began to grow it was surmised that in E area they pierced slightly in advance of F. Undated material confirmed this. An undated foetus (33 cm. crown-rump measurement) had fibres in the E areas just piercing the skin, while those in F area had not emerged. Two other foetuses (33–36 cm. crown-rump measurement) had their E areas with fibres well through and their F areas with just a few scattered fibres piercing the skin. In addition there were a number of white papilla-like spots which were follicles with the fibres just ready to pierce the skin.

Another foetus of 32 cm. crown-rump measurement showed the mid-dorsal line of the E area in advance of the side regions of the same area. This was also found on the 33–36 cm. long foetuses which had only a few fibres piercing the skin on the F area, the number of fibres through on the mid-dorsal line being greater than elsewhere.

One whole skin of an undated foetus (21 cm. crown-rump measurement) was stained with borax carmine and cleared in cedar-wood oil. On this foetus the trio arrangement could still be detected on the D area, while on the B and C areas the new follicles coming in were beginning to mask the arrangement. On E area the trio grouping was obvious, but new x' and y' follicles were appearing. The F area was still at the trio stage.

Study of the skins of the dated series suggests that the approximate age of this foetus was 83 days. Study of the arrangement of the follicles revealed a linear arrangement similar to that figured for the Masham foetus in Wildman's paper ((6), p. 267).

Examination of the undated foetus illustrates the fact that fibres burst through the skin in the order that they were laid down—that is, in accordance with the directional currents—halo-hairs appearing first, followed by sickle fibres, curly-tips, and last of all histerotrichs.

In the account of the development of the coat it will be noted that after the nine stage there was no further mention of development in threes. Odd follicles were mentioned as appearing alongside members of the nine stage which may suggest that a further stage—a twenty-seven stage—was possible. From post-natal observations, however, this was unlikely. In a paper now being prepared for publication will be found an account of the distribution in the coat of the Romney lamb of the pre-curly-tips, that is, the halo-sickle group of fibres. It was found that the earlier an area commenced follicle development, the more numerous were the pre-curly-tip fibres. The proportion of pre-curly-tip fibres was never more than 33 per cent. of all fibres; on the poll region they usually approximated to this number. We thus find that pre-curly-tips constituted about a third of the coat. The remaining two-thirds were curly-tips and a few histerotrichs. From this we might assume that the pre-curly-tips were from the trio stage follicles and the curly-tips from the additional follicles constituting the nine stage. The histerotrichs might be from

Table I. *Showing the stage of development of different areas at different ages.*

Age of foetus (days)	Area A	Area B	Area C	Area D	Area E	Area F
42	—	—	—	—	—	—
49	X	—	—	—	—	—
56	X and Y	X	X	X	X	X
64	xXx and Y	X and Y	X and Y	X and Y	X	X
68	xXx and yYy (trio stage)	X and Y	X and Y	X and Y	X and Y	X
72	xXx and yYy (late trio stage)	xXx and yYy (trio stage)	xXx and Y and yYy	xXx and Y	X and Y	X and Y
76	$xXx'x$ and $y'yYy'y$	xXx and yYy (late trio stage)	xXx and yYy (trio stage)	xXx and yYy and odd Y (trio stage)	xXx and Y	X and Y
83	$x'xx'Xx'x'xx'$ and $y'yy'Yy'yy'$ (trio gone)	$x'xXx'xx'$ and $yy'Yy'yy'$ (trio gone)	$xx'Xx'x$ and $y'yYy'yy'$ (trio gone)	$xXx'x$ and $yy'Yyy'$ (trio disappearing)	$xXx'x$ and yYy (late trio stage)	xXx and yYy (late trio stage)
90	$x'xx', x'Xx', x'xx'$ and $y'yy', y'Yy', y'yy'$ (nine stage)	$x'xx', x'Xx', x'xx'$ and $y'yy', y'Yy', y'yy'$	$x'xx'Xx'x'x$ and $y'yy'Yy'y'yy'$	$x'xx'Xx'x$ and $y'yy'Yy'yy'$ (trio gone)	$xx'Xx'x$ and $yYy'y$ (trio still detectable)	$xXx'x$ and $yYy'y$ (trio disappearing)
97	Fibres through the skin	Fibres piercing the skin	$x'xx', x'Xx', x'xx'$ and $y'yy', y'Yy', y'yy'$ (nine stage)	$xx'Xx'x'xx'$ and $yy'y'Yy'y'yy'$	$xx'Xx'xx'$ and $yy'Yy'y'yy'$ (trio gone)	$xXx'x$ and $yYy'y'y$ (trio gone)
111	Fibres begun to curl	Fibres begun to curl	Fibres through the skin	Fibres piercing the skin	$x'xx', x'Xx', x'xx'$ and $y'yy', y'Yy', y'yy'$ (nine stage)	$x'xx'x'Xx'xx'$ and $y'yy', y'Yy', y'yy'$
122	Halo-hairs and sickle fibres recognisable		Fibres begun to curl, sickles present	Fibres begun to curl, sickles present	Straight fibres	Straight fibres
127	All pre-curly-tip and some curly-tip fibres recognisable		Pre-curly-tip and a few curly-tip fibres recognisable		—	Straight fibres

the few extra follicles appearing after the nine stage. If a twenty-seven stage appeared one would expect that the histerotrichs would be twice as numerous as the pre-curly-tips and curly-tips together.

Further, if any stage later than a nine stage occurred, the post-natal density of the Romney—not a very densely-woolled sheep—would necessarily be very high, or the sheep very much larger than it is. It is conceivable, however, that on a dense-woolled sheep such as the Merino there might be a complete twenty-seven stage of development.

A point of considerable interest was the comparatively long time taken between the laying down of the follicle and the piercing of the skin by the fibre. On the poll region, the first follicles are laid down at about 7 weeks, while the first fibres do not pierce the skin surface till after 13 weeks. The time from the initiation of the follicle till it had attained its full length was between 2½ and 3 weeks. The remaining period—2½–3 weeks—was taken up with the formation of the fibre.

Rudall (in a personal communication) mentioned that it took over 2 weeks for the regeneration of a fibre.

When the lapse of time between follicle initiation and the fibre piercing the skin was considered, it was not inconceivable that there was a delay between the causal event determining the pre-natal check and the resultant expression.

Dry (1) in the mouse found that the length of a zigzag fibre could be prophesied within narrow limits by examining the length of the distal segments of some fibres. This indicated that total length was determined at an early stage of development. In the sheep he found expressions that suggested that they were the delayed result of a causal event. Such expressions were the percentage of chalky sickles shed and the nature of the halo-hair successors (Dry, unpublished paper).

The nature of the succession of the first lot of secondary kemp was evidence of a very much delayed result of a past causal event (Dry, unpublished paper).

IV. DISCUSSION.

Before summarising the account of the follicular development, it will be necessary to discuss the trio and nine groupings which have figured somewhat prominently in the above account. The present work emphasises the fundamental importance of the number three, the importance of which in hair arrangement was first recognised by de Meijere (5).

The trio stage of development was referred to by Wildman ((6), p. 272) as occurring on the Down and Scottish Blackface breeds on certain specialised regions. In his account he has not, however, attached the same importance to it as has been done in this account of the New Zealand Romney. On the Romney this trio stage was a definite stage in the pre-natal development of the follicles of the coat. It occurred on all areas, and was a means of determining the stage of development of an area. It was considered that it might be a method of determining the approximate ages of undated foetuses. Examination of undated material, of dated twins, and of two dated foetuses of the same age, suggests that although length and width may vary the stages of development are comparatively constant for the same age. The nine grouping succeeded the trio stage of development, through the development of two follicles, one on either side of each follicle of the trio. This stage might be useful for dating older foetuses.

From this account of the development of trio and nine stages it follows that all the first follicles—the X and Y follicles—are forerunners of eight additional follicles, giving the following groupings: xXx and yYy at the trio stage, $x'xx'$ and $x'Xx'$, $x'xx'$ and $y'yy'$, $y'Yy'$, $y'yy'$ at the nine stage.

At the completed nine stage we see additional small follicles appearing which as far as can be ascertained at present do not develop in any regular way, appearing haphazardly beside any of the follicles of the nine group. From both pre- and post-natal observations it was thought that these follicles were not very numerous and never resulted in a twenty-seven stage of development. It was suspected that these follicles were the follicles of the histerotrich fibres. The number of histerotrichs in post-natal material apparently varied considerably, but was not usually high. We found, therefore, that the bulk of the coat was made up of fibres which grow from the follicles of the nine stage.

We had the following pronounced stages in the follicle development:

(1) The foundation, or X and Y follicle, stage.

(2) The trio stage.

(3) The nine stage.

This arrangement of three successive stages emphasised the fact that the number and distribution of first X and Y follicles was perhaps the chief factor determining the density of the coat of the adult animal. It was known that at 17 weeks, halo hairs, sickle fibres and curly-tip ones could be seen on the advanced areas. From post-natal work it was known that the proportion of pre-curly-tip fibres per hundred fibres was higher on the advanced than on the later areas (see p. 354). Thirty-three pre-curly-tip fibres per hundred fibres was the highest proportion found.

From this we must assume that in such cases all trio stage follicles produced pre-curly-tip fibres. On the other hand, on some of the later areas we must assume that only the *X* and *Y* follicles became pre-curly-tip fibres and not necessarily all of these.

From this we can make the general assumption that there was an original density which varied from position to position.

It has been postulated that the fibre type arrays (2) were due to the action of two variables: (1) the pre-natal check, and (2) the reduction of inherent coarseness. These two variables it was suggested were two expressions of the same kind of balance, the increasing of the varying original (*X* and *Y*) densities as opposed to skin expansion at different times, viz. the trio and nine stages. These two variables, however, cannot be separated, but according to the extent of their interaction do we get the varying fibre type arrays. It now seems as if we may regard the pre-natal check as a trio depression[1] and the reduction of inherent coarseness as a nine depression.

The follicles that appear after the nine stage have not been considered as affecting the fundamental fibre type array, being only additional follicles which may or may not comprise all the histerotrich fibres.

It is hoped that future more detailed work on density variation and skin expansion will further test this view.

V. SUMMARY.

For the purpose of describing the development of the Romney lambs' coats it was found convenient to divide the skin into six areas, A, B, C, D, E and F, each being formed by the grouping of all regions that develop at the same time and rate.

These areas are determined by the following methods:

(1) All regions where *X* and *Y* follicles begin growth at the same time belong to the same area.

(2) All regions attaining the trio stage of development at the same time belong to the same area.

(3) All regions reaching the nine stage of development at the same time belong to the same area.

(4) All regions on which follicles pierce the skin at the same time belong to the same area.

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[1] The word "depression" is here used in a general way to mean that combination of two or more influences tending to cause the earliest formed follicles to produce coarser fibres than the later formed ones in which, therefore, the potentiality for fibre growth is depressed.

These are the four main stages in the development of the coat and might be termed:

(1) The foundation, or *X* and *Y* follicle, stage.
(2) The trio stage.
(3) The nine stage.
(4) The skin-piercing stage.

These four stages take place on different areas at different times, but never more than three stages could be recognised on a foetus at one time. Further, it was possible to detect marked differences in the extent to which a stage was developed; for example, two areas might both be at the trio stage, but one area might be at an advanced stage and the other at an early stage of trio development. It was a study of these differences in the stages of development of the trio group that was most useful in defining the areas.

From this work we can state: (1) that different areas develop at different times; (2) there is orderly progression in development from A to F areas; (3) there are certain marked stages of development that enable one to judge the approximate age of the foetus by a study of the different stages of follicle development occurring over the foetus at the same time; (4) that each region is a local governor of its own development, this last fact supporting the view that the depression is a local phenomenon.

It has been shown that the first follicles formed were the first from which fibres pierced the skin, and that certain areas were always in advance of other areas in the following order of developmental progress, A, B, C, D, E, then F areas. The time elapsing between the foundation of a follicle and the fibre piercing the skin was between 6 and 7 weeks.

The first fibres (sensory fibres) to come through were on areas carrying sensory hairs. The next regions in which fibres pierce the skin were those around the horns and posterior coronets. The order of development of fibres on areas was found to be the order given above: A, B, C, D, E, and then F.

The particular variety of fibres produced from these first follicles depended upon the pre-natal check (trio depression). In the New Zealand Romney, on all areas except B and C and the withers portions of D they were often halo-hairs; on the finer-woolled breeds, however, they were usually sickle fibres.

The later fibres continue emerging from the skin, and what they become depends upon the time and extent of the reducing of inherent coarseness (nine depression).

In future work it is hoped to correlate these results with post-natal growth. It is proposed to test the theory that the fibre type array is determined by the original density of X and Y and its relationship to skin expansion.

I wish to acknowledge my indebtedness to Dr F. Dry, Prof. W. C. Miller and Mr K. M. Rudall for their helpful criticisms. My thanks are also due to the donors of the Farmers' Union Scholarship for the opportunity to carry out this investigation.

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NATIVE PRODUCTION OF COFFEE ON KILIMANJARO

A. J. WAKEFIELD

(*Deputy Director of Agriculture, Tanganyika Territory*)

WITH PLATES 7, 8

History of Coffee in Tanganyika Territory.—Wild coffee is indigenous to Tanganyika Territory, the varieties *C. arabica* h. var. *Stuhlmannii* Warb (= *C. bukobensis* Zimmerii = *C. robusta* L. Linden), *C. arabica* h. var. *intermedia* Fraehner (this also is very probably *C. robusta*), being found in the region of Lake Victoria Nyanza; *C. zanguebarica* along the coast; *C. Schumanniana* W. Busse in the Rovuma valley on the southern border of the territory, and *C. mufindiensis* Hutch. M.S. in the southern highlands.

Coffea robusta has been grown for many generations by natives in the Bukoba district on the west shore of Lake Victoria Nyanza; its cultivation is mentioned by the early explorers Speke and Grant, and some of the existing trees are reputed to be over 100 years old. It is only in comparatively recent times, however, that the crop has been cultivated for export on an extensive scale; formerly the bean was used solely for chewing. *Coffea arabica* is also cultivated in Bukoba, whence it was introduced by missionaries about the year 1896. To-day the exports of native-grown coffee from Bukoba amount to about 7,000 tons of the *robusta* type and 3,500 tons of *arabica*. In this area the coffee is prepared by the Brazilian method of drying the whole cherry, and the native separates the bean by hand-hulling and winnowing. The coffee is regarded as a low-grade type, equivalent to Brazils, but, possibly owing to bulk-marketing at the port of export and grading, the prices obtained have not fallen in proportion to the fall sustained by the higher-grade mild coffees, prepared by the more skilful wet method of pulping and fermenting.

In the northern part of the territory, on the slopes of Mount Kilimanjaro, *arabica* coffee was introduced by Father Auguste, of the Kilema Mission. The seed was obtained from Réunion (Bourbon) and was first planted in 1883 near Morogoro (the present head-quarters of the Department of Agriculture), but after several years it was cut out owing to the high incidence of *Anthores*, the white stem-borer. In 1893, seed from these trees was planted at Kilema on the southern slopes of Kilimanjaro; some of the trees of this planting are still bearing well. (In 1896 or 1897, seed was taken from Kilema to the Bura and Nairobi localities of Kenya Colony.) The crop soon established itself on Kilimanjaro, where it was cultivated by the missions, their native followers, and by the early European settlers. In 1899 coffee to the value of £4,817 was produced, and in 1934 the production of European and native-grown coffee on the mountain amounted to 1,361 and 1,530 tons, respectively; in 1935 it is estimated that the production of native coffee on Kilimanjaro will amount to 2,000 tons. The coffee is prepared by the wet method of pulping and fermentation and is well regarded as a good-quality mild coffee on the London market.

There are other coffee areas at Arusha, Babati, and Oldeani in the Northern Province, and in the southern highlands; in these areas production is mainly European, but natives are taking an increasing interest in the crop. It is, however, with coffee grown by natives of the Chagga tribe on Kilimanjaro that this article is mainly concerned, especially in regard to the influence which the European has had in the development and improvement of native agricultural practice in regard to coffee.

Coffee on Kilimanjaro.—The coffee-belt of Kilimanjaro lies between the altitudes of 3,000 and 5,500 ft., the most favourable areas being on the southern slopes. Coffee also extends to the western and eastern slopes, and decreases towards the northern slopes, which are without permanent water and are uninhabited. The rainfall varies between 35 in. at the lower levels to 80 in. and more at the upper limits of coffee-cultivation. There is abundant water, which is used by the Wachagga for irrigating their food crops, and by both natives and Europeans for irrigating coffee. Although, generally speaking, the estates owned by Europeans are confined to the lower and medium elevations, with the majority of the native holdings above them, there is no definite line of demarcation, and some estates are practically surrounded by plots of native-owned coffee.

Thus we have a position where a cash crop is successfully grown by native and European agriculturalists without segregation, and, whilst there is no doubt that the initial example set by the European has been a dominant factor in establishing the valuable native coffee industry, it is not correct to hold, as some do, that the cultivation of coffee on Kilimanjaro was actually initiated by the European settler. As stated above, missionary enterprise first demonstrated that coffee was a suitable crop, and, although few in number, natives were the first to follow their lead. It was, however, the European planter who first exploited the economic possibilities of this crop, and it was not until 1902 that natives began to see its commercial possibilities. White influence of the benevolent kind was seen, for the headmen of the early settlers were encouraged by their employers to grow coffee: seed was given out to natives, notably by an Italian, de Croce, and by Dr. Forster, a German. The German Government also appears to have given some encouragement, since native growers of wheat, European potatoes, and coffee were exempt from certain forms of communal labour.

The influence of missions was also extended in the direction of preaching industriousness to the people, particularly to the menfolk, whose activities in the agricultural sphere prior to coffee-growing must have been much less than to-day. In former years the European grower relied chiefly on the local native tribe for his labour-supply and the habit of working, and a sense of orderliness, which is essential to coffee culture, was instilled into many Wachagga during their employment on coffee estates. The comparative affluence of the European, especially during the times of high prices, was attributed by the natives to coffee, and an ever-increasing number imitated their employers' example and grew coffee for sale. A result of this was that, as with sisal, it became necessary to recruit labour in such districts as Songea, and again the effect is that to-day many natives from the Matengo highlands of Songea, before undertaking recruitment, stipulate that they shall be employed on coffee estates, with a view to being coffee-growers on their own account. The influence of the planter in extending the cultivation of a staple product is thus seen to be potent, and spreads far beyond the confines of the locality in which he lives. In 1916 the number of native-owned coffee-trees is given as 14,000 only, and in 1922 the total was 125,000. Natives knew of the high prices obtained for coffee at that time, and there was a rapid increase in their plantings. One of the earlier growers started a nursery for the supply of seedlings to his fellow tribesmen, and planting material was readily offered by, and purchased from, European coffee-growers. At this time the influence of Government became predominant, and Major Dundas, the administrative officer in charge of the Moshi District, did much to encourage coffee-growing by natives on Kilimanjaro.

Thus we see the establishment of a now important native coffee industry by the efforts of missionaries and by the early benevolent influence of planters. The prosperity of the European coffee-grower during the period 1920–28 was a considerable incentive to native coffee-growing, and from 1922 Government took an increasing interest in the industry and supplied white supervision: the latter influence was, and remains, most important.

The political aspect.—With the rapid extension of coffee-growing by natives in the past decade, the European producer feared that native plantings would be a source of pest- and disease-infection, and would be a menace to his own crop in which much capital was invested. Opposition to native coffee-growing became vocal, and this, strangely enough, further energized native plantings. It is generally and historically true that there is no object more desirable than that which is forbidden, and when the Wachagga realized that the European settler would at least like to restrict their coffee crop, they became all the more determined to have and to hold it. In the face of such opposition, the temper of the native coffee-planters in the early years of the technical supervision given to the crop was such that they came to regard their coffee jealously as a precious possession; almost every European who had anything to do with the crop was regarded with suspicion, and strenuous objections were always advanced against the uprooting of any native coffee under the Plant Pest and Disease Regulations, as they suspected such action to be the thin end of the wedge to eliminate all native coffee. Consequently the work of the Agricultural Officer was difficult, and it became more or less police work.

At the same time certain leaders were wise enough to realize that there was truth in the European allegations. To counter these, they set about forming the Kilimanjaro Native Planters' Association for the purchase of spray-equipment and chemicals for communal use. The effectiveness of spraying had been amply demonstrated to them on European plantations, and natives would work on such estates merely to obtain knowledge of pest- and disease-control, as well as of pruning and coffee culture generally. The leaders of the Association also adopted the tactics of complaining of the state of certain European coffee estates whenever propaganda against their own plantings was advanced. The critical attitude of the white planters thus went far towards causing the natives to endeavour, for their own protection, to put their house in order. The extent of such influence was seen a year or two ago when an article was published in a local paper containing serious adverse statements about native coffee; the effect of this was that the leading natives of the area concerned convened meetings of growers. It was admitted that there was a certain amount of truth in the description given of their coffee, and a time limit was set by their leaders for all offenders to place their coffee in a satisfactory state. A rapid clean-up was effected. There is no doubt that the criticisms to which the native coffee-grower has been subject over the past decade have given an impetus to the industry and have assisted in raising the standard of coffee culture.

The spread of European practice.—In addition to the knowledge gained from the European planter concerning the methods of pest- and disease-control, the native has learnt to give careful attention to the production of seedlings in the nursery, to planting out in orderly fashion, and to pruning. In fact, pruning, as well as irrigation, until fairly recently was rather overdone by the European, and the fault has also occurred with much native coffee. Such careful culture is not seen in Bukoba, where there are only a few European planters, and where the coffee has been allowed to grow, often to advantage, in a comparatively uncared-for condition.

Again, in the preparation of the coffee-bean, in Bukoba, partly because of water shortage but mainly because it is the line of least resistance, the cherry is dried and a low-grade coffee is produced, whereas on Kilimanjaro the native has followed the European idea of pulping the fresh coffee-fruits and fermenting the seeds to remove the mucilaginous matter from the parchment covering the bean. At one time there were a number of locally made wooden pulpers in use, but, following the more efficient use of up-to-date equipment by the European coffee-grower, these have been almost entirely replaced with imported metal pulpers of the breast type. Approximately one coffee-grower in ten has one of these modern pulpers, and those who have not make arrangements for the use of one at a rental based on the amount of the cherry which is pulped. Following this operation, each grower ferments and washes his own coffee in wooden boxes, or occasionally, following the European idea, in cement tanks. The parchment coffee is then dried on wire trays, when some hand-picking of defective beans is carried out.

Native methods of agriculture.—Not all the methods adopted by the native grower from plantation practice have been to his benefit, but better to appreciate this it is first necessary to refer briefly to his other crops; at the same time the opportunity for, and the extent of, the influence given by technical supervision will be seen. The staple food of the Chagga is the banana, which also supplies him with thatching material and food for his cattle, which are stall-fed. His banana plot is usually his main consideration. Apart from small areas of beans, yams, &c., the only other crops of importance are maize, which may be grown some distance away below the main coffee-belt, and eleusine for the manufacture of beer. The banana plots are situated in the coffee-belt, and each family occupies a hut amongst his bananas. The basis of this system, which allows of no rotation for the main banana crop, is the cattle population. There is practically no vacant land for grazing, frequently insufficient even for the beasts to exercise; therefore the Chagga stall-feeds his stock. He feeds them on bananas and on veldt grass, the latter being carried by his womenfolk over long distances from the plains. Formerly, most of the manure went back to the bananas, but with the inclusion of coffee into the system an increasing share of the manure is made available for the coffee. The Chagga is ready to adopt any measures which will establish his coffee more firmly and make it more productive, and his line of reasoning is that, if it pays the European to purchase cattle dung for his crop, it must be good practice. It is becoming increasingly difficult for Europeans to purchase cattle manure from natives.

The greater part of the native-owned coffee has been planted among the bananas and, where the necessity for thinning out the latter to make room for the coffee has been recognized, the coffee has flourished under what are almost ideal conditions. The heavy mulch of decaying organic matter is effective in preventing soil wash on even comparatively steep slopes, soil moisture is maintained, weed-growth is controlled, and the bananas themselves provide shade and protection from wind. Generally the indigenous forest trees (particularly *Albizzia* spp. and *Rauwolfia inebriens*) have been left in, and with bananas to provide an excellent soil mulch no other cultivation is necessary. That farm-yard manure should be the basis of this system is evident when one sees coffee in a banana plot which, perhaps because the owner is a bachelor and has not built and stocked his house, is unmanured; in this case the coffee makes very poor, spindly growth and is unable to carry even a small crop without showing signs of distress.

Unfortunately the ambitious Chagga is often tempted to extend his coffee beyond the limits of his banana plots, and perhaps opens up land some distance away. Following the example of many European planters, he may not put in shade trees, or not enough; he often maintains a more or less clean state of cultivation tending to the loss of much of his unprotected top soil through soil wash, and then endeavours to stimulate his flagging trees with excessive irrigation. Couch grass may become established and the disheartened owner either practically abandons the coffee, or mutilates its root-system beyond recovery in an endeavour to eradicate the couch grass. He may not be a cattle-owner or be in the position of the European who has been able to purchase supplies of manure from native neighbours; nor is he sufficiently advanced to endeavour to keep up or replace the lost humus of the soil with green manures, cover crops, or composts, to which planters are now giving their attention. These are the extremes of conditions of coffee cultivation by the Wachagga. Fortunately, the greater part approximates to that first described and the proportion of really poor coffee is on the decrease; in fact, public opinion among the native coffee-growers is often exerted towards the eradication of very unhealthy and uneconomic trees.

There are, however, many natives owning coffee plots, some of them 5 to 15 acres in extent, whose methods approximate very closely in every respect to those of the better European planter, but such a slavish imitation of plantation methods by peasant cultivators is not encouraged. The aim is that the native should be a peasant farmer in the real sense, with his food crops and his cattle plus a small plot of coffee which cannot become beyond his capacity to manage.

Although concerned also with propaganda for improved methods of cultivation, the staff of the Department of Agriculture, responsible for the care of native coffee, endeavoured at first to secure improvement through the enforcement of the Plant Pest and Disease (Coffee) Regulations. Under penalty of a fine, planters (both European and native) were obliged to maintain their coffee reasonably free of noxious weed-growth and to take appropriate action against pests.

During the last five years a sounder appreciation of the requirements of the coffee-plant, particularly with regard to soil conditions and development of the root-system, has led to some change of policy. A change in mind and temper of the native coffee-growers, and, generally, a change in the attitude of European planters towards them, have facilitated this change, thus enabling Agricultural Officers to devote more time to the teaching and demonstration of cultural methods without neglecting the control of plant-pests and diseases.

The Influence of the Native Authority.—It was realized that the planting of coffee by natives frequently led to the choice of exhausted or otherwise unsuitable land, the use of inferior planting material, and careless planting methods; and that such conditions resulted in weakly coffee, particularly liable to pest and disease. It also became evident that to enforce the cultivation of neglected coffee was uneconomical, since the digging necessary to eradicate deep-rooted grasses left the tree with a mutilated root-system, and under Kilimanjaro conditions such plants seldom, if ever, fully recovered. By means of rules enacted by the Native Authority on the advice of the Agricultural Officer, further plantings of coffee by natives were brought under strict control. For the last two seasons a permit has had to be obtained from the Agricultural Officer, or his nominee (usually the African Instructor of the sub-district), before a native could add to his existing coffee or open up a new plot. This permit is given only when the planter demonstrates that he has suitable land which is free from couch grass. The observance of certain conditions such as the completion of anti-erosion measures (terracing, or contour-trenching, with hedges) and the planting of shade trees, may be insisted upon. At the same time the native is instructed in planting methods. In the event of failure to comply with these conditions the coffee may be summarily uprooted by order of one of the European departmental officers, of which there are three concerned with native coffee on Kilimanjaro. All nurseries are subject to inspection and all unsuitable planting material is destroyed. By the control thus exercised it is possible to avoid at the outset those conditions which are conducive to the establishment of weakly and unproductive trees. Where coffee becomes derelict as the result of abandonment, or for other reasons, it is uprooted.

Pests and Diseases.—The three most important pests are thrips, which may cause heavy leaf-fall followed by die-back, the coffee bug (*Antestia lineaticollis* Stal.), which is the carrier of Coffee-bean Disease, and the White Stem-borer (*Anthores leuconatus*). Fortunately, the greater part of the native coffee lies above the altitude below which thrips causes most damage, so all that is required is to maintain supplies of pumps and lime-sulphur at strategic points and spray small areas that may be attacked, particularly in years of low rainfall. The coffee bug is a serious pest throughout the coffee-belt, causing considerable loss of crop wherever it is unchecked, and for the past three years an annual spray campaign has been carried out, requiring three sprayings at intervals of ten days. Some 18,000 of native-owned coffee plots are so treated. This is only possible by making use of the native co-operative organization, which has been mentioned above and is described below, for the movement of spray materials and the supervision of spraying, under the general direction of departmental officers. The stem-borer, like thrips, is confined to the lower altitudes, but approximately one-sixth of the native coffee is found in this belt. Every year, prior to the emergence of the adult borer-beetles from the coffee at the onset of the short rains, every coffee-tree in the borer-belt is examined; severely bored trees are uprooted and burned, and the borer-grubs removed from those only superficially bored. This work is also carried out by the individual growers under the supervision of departmental African instructors and field secretaries of the native co-operative society, who co-operate closely in all matters concerning coffee. It was established in 1932 that the coffee was being re-infected with borer from three species of wild shrubs that were common throughout the coffee areas of Kilimanjaro. In view of this, by communal effort, over 1½ million of these shrubs were uprooted and burned, with the object of reducing the danger of re-infestation of the coffee.

It has been amply demonstrated that the disease *Hemileia vastatrix* is mainly induced by cultural errors affecting both plant and soil; it invariably occurs on badly eroded soils. The rules made under the Native Authority for the control of plantings go far to avoid coffee which is conducive to Hemileia attack. Hemileia can be dealt with by spraying with Bordeaux mixture; this also appears to assist in the maintenance of leafage with subsequent increase in crop yields. Here again the influence of the European in demonstrating the value of Bordeaux spraying will be a valuable support to the propaganda and demonstrations of the Agricultural Officer.

The Co-operative Society.—This account would not be complete without some reference to the Kilimanjaro Native Co-operative Union, Ltd., of which every native coffee-grower on Kilimanjaro is a member through one or other of the twenty-seven affiliated subsidiary societies. All coffee grown by the members is marketed through the Union. The reason for the formation of the first society, mainly for defence purposes, has been described: it was not a co-operative society in a recognized sense and soon got into difficulties, which became so serious about 1930 that Government stepped in to assist in its reorganization. Mr. Strickland visited Kilimanjaro to report on the question of co-operative societies, and the Co-operative Societies Ordinance was the outcome; under this the existing native association was reorganized with a European manager, and since then the society has gone from strength to strength. Of the 45,000 males over 18 years of age inhabiting Kilimanjaro, nearly 20,000 are coffee-growers and are members of the Union; some 10,000 males live in areas which are not suitable for coffee-growing. Not more than 10 per cent. of the cultivable land owned by the Chagga tribe is under coffee. The influence of the European manager is best seen from the following extract from the Annual Report of the Department of Agriculture for Tanganyika Territory for 1934:

> '*Native Coffee.*—The production of native-grown coffee on Kilimanjaro reached the record output of 1,530 tons. The position of this industry must be regarded as good when compared to the unsatisfactory state of affairs of three to four years ago. In the Annual Report for 1931 it was stated that "the Kilimanjaro Native Planters' Association has been of little or no use to the department in the work of cultural improvement, neither have they been satisfactorily equipped with spray pumps and chemicals to deal with coffee pests and diseases". Again in regard to the marketing of the native-grown coffee crop it was noted that "departmentally we have been completely impotent to effect an improvement in this matter, which has greatly handicapped our work to effect improvements in both the culture and preparation of native coffee". All this has been changed, and the credit for the more satisfactory state of affairs is mainly due to Mr. A. L. B. Bennett, the manager of the Kilimanjaro Native Co-operative Union, and to Mr. C. Harvey, District Agricultural Officer, and his assistants, who in their work of the past four years have contributed largely to that close co-operation now existing between the society and the department, and which is so essential to our work and the aims and success of the society.
>
> 'In addition to marketing, the society has undertaken to carry out with our advice the organization of anti-pest and disease-control measures. The keenest interest is taken by all the native officials of the society in the regulations affecting coffee, and in all agricultural matters generally. They are invaluable and active in their assistance to the agricultural staff in the field, and form one of the best media for getting the peasant coffee-grower to react favourably to our advice. The force of public opinion alone is now sufficient in many areas to cause the eradication of derelict and pest-ridden coffee. In many areas there is similar close co-operation with the native chiefs. Where the native chiefs are not interested one may find the greatest obstacles to improvement, and there conditions are most backward.
>
> 'The two agricultural assistants concerned with native coffee have with their native staff made 20,467 inspections of bearing coffee, in addition to 6,242 inspections of newly planted coffee.'

The reorganization of the native association was primarily for the purpose of marketing the crop, as this had been carrried out in a competitive and most unsatisfactory manner, and at present marketing is still an important function of the Union. With the realization of the effect of united effort, the societies now take an active part in the promotion of better agricultural methods, and it is considered that these works, together with the collection of the crop, will become the most important functions of the Union, and that the actual disposal and realization of the crop will be left to some more specialized body.

Co-operation of the European with the Native.—The influence of the white coffee-producer passed from a benevolent phase to one of malevolence, but has now arrived at the stage where there is a real desire for co-operation with the native coffee-producer. This was expressed at a meeting, held in Nairobi in 1934, of representatives from Kenya, Uganda, and Tanganyika of European coffee-growers in a resolution which, in general terms, stated that there should be no racial discrimination whatsoever between coffee-producers, and that coffee, whether grown by natives or non-natives, should receive similar treatment. It was inevitable that such an attitude should come about, but the present depression pervading the coffee markets of the world has caused a more ready acceptance of the position, for it was obvious that in the reorganization of marketing methods so ardently desired by the European grower it was impossible to leave out a class of producers whose output amounts this year to some 2,000 tons of coffee from Kilimanjaro, as well as over 10,000 tons of the Bukoba coffee, even though the latter is of a different class to the Kilimanjaro native and European-grown coffee. The value of bulk-marketing, especially of the lower grades, has been amply demonstrated by the Kilimanjaro Native Co-operative Union, prices being obtained this season which would have been impossible to achieve if the produce had been sold in small and uncontrolled lots, as the European produce is usually sold. By this means indiscriminate competition with European-grown coffee and dumping on over-loaded markets should be avoided. It is interesting to note that the European coffee-growers in East Africa are studying the methods by which bulk and controlled marketing, of their lower grades especially, can be achieved. The point of competition of native-grown coffee can be over-stressed, however, for although Tanganyika, including Bukoba, produces about one-quarter of the amount of coffee grown within the Empire, the amount of coffee grown by natives on Kilimanjaro in 1934 was but one-fortieth of this, or one-half of one per cent. of the total effective world stocks.

Research and Investigation.—The interest shown by the Wachagga in the Coffee Research and Experiment Station, recently opened on Kilimanjaro, is in accordance with his general attitude towards his coffee. He will not accept what is told him without careful thought and, maybe, argument; but, once he is satisfied that what is proposed will benefit his coffee, he will support the proposal to the limit of his resources of labour or actual cash. The natives assist equally with Europeans in financing the station, and they are showing keen interest in its work.

Perhaps the best tribute that has been paid to the Kilimanjaro native coffee-grower is that of an experienced European planter from a neighbouring colony, who, being a little fearsome at the extent of native production, on account of competition, made a tour of the native coffee areas and summed up his opinion in four words: 'It is disappointingly good.' It can be said that the European planter himself has been, perhaps unwittingly, the strongest influence of all in achieving this not unsatisfactory standard of native coffee culture, for sustained and continued contact and example, as is given by the European coffee industry to that of the native, is most effective.

Tribal customs may also become affected by the influences which have made the native coffee industry what it is to-day. The crop has considerably enhanced the value of land in the eyes of the native; at the present time the land is the property of the tribe, held in trust by the chiefs, who act with the advice of their councils. A tribesman is allotted a plot to utilize to the best advantage; such allocation does not confirm ownership of the land but only the crops and buildings thereon. If the cultivator fails to make good use of the holding, it may revert to the pool and be re-allocated. This custom ensures that the land is used advantageously, as a lazy occupier is always in fear of losing his plot to a more competent man, and, where coffee is grown, there is even greater incentive to better agricultural methods and possibly a desire for a more permanent form of tenure and individual ownership of land.

In conclusion I desire to acknowledge my indebtedness to Mr. A. L. B. Bennett, the manager of the Kilimanjaro Native Co-operative Union, to Mr. R. M. Davies, Senior Agricultural Officer, Moshi, and especially to Mr. C. Harvey, District Agricultural Officer, all of whom have materially assisted in the preparation of this paper.

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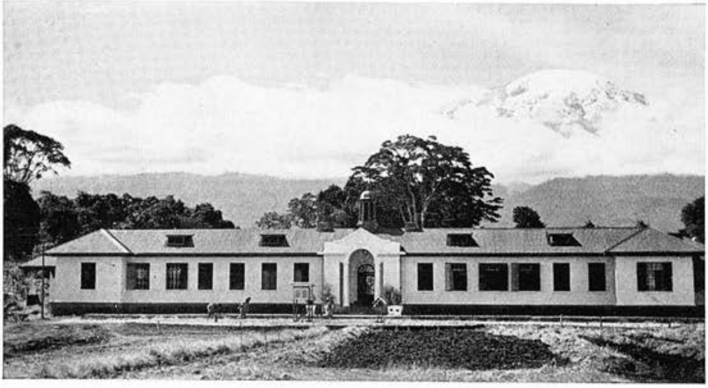


Laboratory of the Coffee Research and Experiment Station, with Kilimanjaro in the background

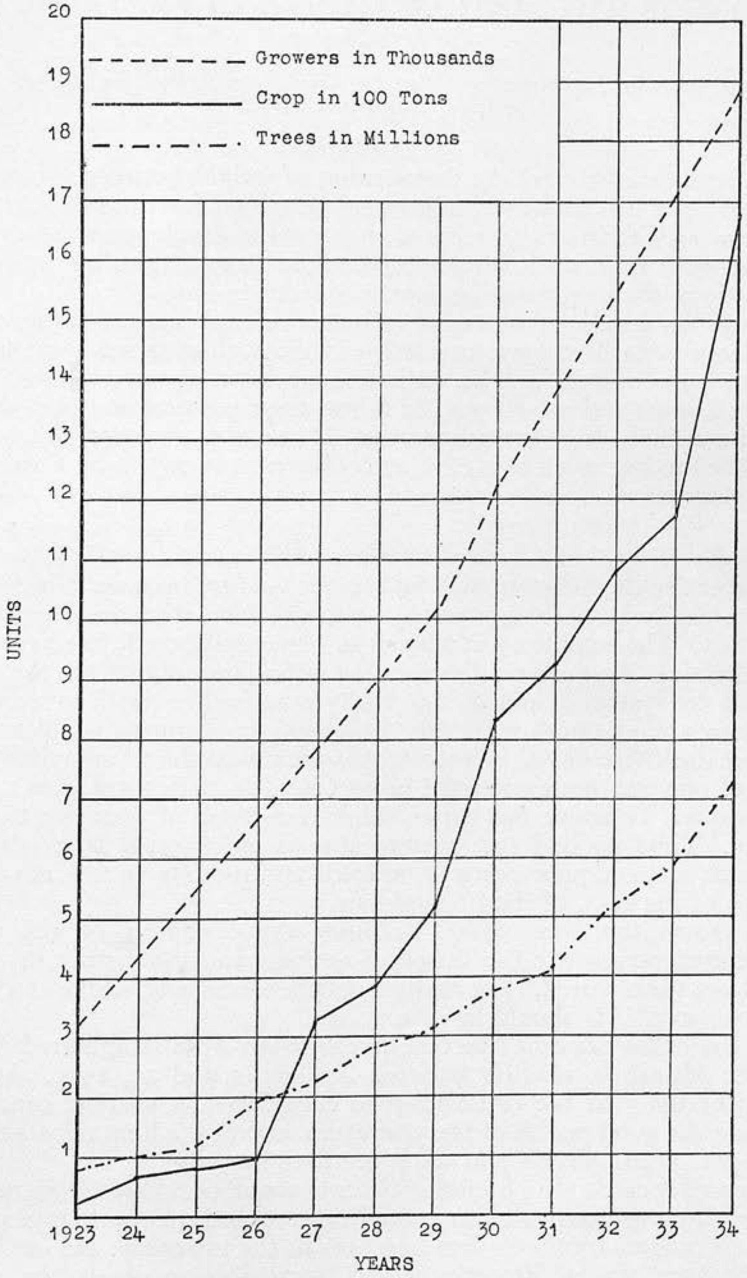
Young native-planted coffee on sloping land which has been terraced or contour-hedged

Young coffee with light banana shade. (Contour-trenches are being made)

An example of good native coffee on Kilimanjaro

Branch Office of the Kilimanjaro Native Co-operative Union

PROGRESS OF NATIVE COFFEE PLANTING AND PRODUCTION ON KILIMANJARO



THE WEIGHTS OF THE CARCASS AND OF THE INDIVIDUAL ORGANS IN THE BODY OF CATTLE IN KENYA COLONY

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WITH PLATE 9

IN a previous article [1] the distribution of weight between the carcass and the other parts of the body was determined for the zebu cattle in Tanganyika Territory. In view of the possible development of an East African meat industry it was thought advisable to get similar figures for the cattle in the neighbouring colony of Kenya.

Kenya has developed into a 'white man's colony' very much more than has Tanganyika Territory, and much of the highlands has been settled by European farmers. The natives have been removed from these alienated areas and are allowed to follow their pastoral and agricultural pursuits only in their native reserves. It becomes necessary, therefore, to divide the live stock of Kenya according as it is owned by Europeans or by natives.

Native-owned Cattle

The native-owned stock will be considered first because it is of pure zebu origin and closely comparable with the zebu stock in Tanganyika Territory. The conditions in which the Tanganyika cattle live have been described [1]. As one would expect, the importance of cattle in the social life and the system of animal husbandry practised in the Kenya Native Reserves are identical with the conditions in Tanganyika Territory, because the international boundary does not follow the tribal boundaries, parts of one and the same tribe being found in both territories. As in Tanganyika Territory the native thinks far more of quantity than of quality. Thus we find that overstocking is common; it is responsible for much erosion, poor pastures, stunted and thin stock, and, at certain periods of the year, of starving animals.

As shown for Tanganyika Territory the condition of the cattle slaughtered varies with the season of the year and the district in which they have been reared. For further details concerning native stock the previous article [1] should be consulted.

All the cattle examined in this investigation were slaughtered in the Nairobi Municipal abattoir between August 11 and 23, 1935. At this period of the year the cattle may be considered in average condition between the good period of the year at the end of the long rains and the worst part when grazing and water are both scarce.

The native cattle slaughtered in Nairobi are all purchased from natives at the collecting stock-markets in the Reserves, and are eventually bought from the traders by the Indian butchers in the township. As cattle are bought from several Reserves it was impossible to divide the cattle slaughtered according to their place of origin. Generally, however, it appeared that the Machakos cattle were smaller than the Masai, and the Boran cattle were much larger than those from any other Reserve. If the large Boran stock be excluded the remainder resembles in size the cattle in Tanganyika Territory, though perhaps they are usually a little larger.

As in Tanganyika the Kenya natives are very reluctant to part with female stock, and during the period of the present examination so very few female cattle were brought to the abattoir that they were not recorded.

The parts of the body weighed and recorded below are the same as for the Tanganyika stock, and reference to the article quoted [1] will explain the various headings.

No estimations were made of the weight of blood in the cattle because of the delay that would have been caused in the abattoir, and because of the difficulty of accurately collecting blood from an animal slaughtered by having its throat cut. As there is little difference in size between the majority of the Kenya zebu cattle and the Tanganyika cattle it can be expected, from measurements on Tanganyika cattle, that the blood-weight of Kenya cattle will be approximately 20 lb. per beast.

No weigh-bridge is attached to the Nairobi abattoir, so that live-weights before slaughter could not be ascertained. The cattle after slaughter were examined by the Meat Inspector, and the carcass and organs were weighed before they had become cold. This means that the loss in weight due to cooling must have been very small, and so a very close approximation to the actual live-weight can be obtained by adding all the body components and allowing a 2 per cent. loss due to cutting up the carcass, &c.

TABLE 1. *Average Weights in Pounds of Carcass and Individual Organs of Native Zebu Cattle*

Type of stock	*2-Tooth cattle*	*4-Tooth cattle*	*6-Tooth cattle*	*Full-mouth cattle*	*Full-mouth oxen, carcass over 350 lb.*
No. recorded	21	20	23	214	58
Carcass	183·2	205·5	222·8	308·5	384·8
Head	16·4	19·0	20·9	23·9	28·5
Hide	29·2	31·5	35·5	43·4	52·0
Feet	9·4	10·5	12·3	12·8	13·4
Tongue	1·6	1·6	1·9	2·5	3·0
Tail	1·1	1·2	1·3	1·6	2·1
Liver	5·5	5·6	6·9	8·3	10·0
Lungs	4·2	4·5	4·8	7·0	8·3
Kidneys	0·9	1·0	1·1	1·2	1·5
Spleen	1·0	1·3	1·5	1·8	1·9
Heart	1·2	1·3	2·2	2·3	3·1
Suet fat	1·4	2·3	3·0	3·9	5·0
Caul fat	3·0	2·8	3·9	5·6	7·4
Contents of alimentary canal	53·3	64·7	67·8	90·4	108·4
Stomachs and intestines	26·0	25·5	34·2	40·4	42·6
Hump	2·6	3·9	4·8	5·1	7·2

From the figures in this table we calculate that the average live-weight of the full-mouthed native cattle slaughtered in Nairobi is 590 lb. This is about 80 lb. heavier than for similar cattle in Tanganyika. The carcass-weights varied from 212 to 475 lb., and the average of 308·5 lb. is over 40 lb. heavier than for the zebu cattle measured in Tanganyika. Further comparisons between the cattle of the two territories show that the Kenya cattle have much the heavier hides but the lighter heads. The feet, stomachs, intestines, tongue, liver, and omental fat are all heavier in the Kenya stock. The hump, on the other hand, is larger in the Tanganyika animals.

Table 2 shows the average live-weight of the full-mouthed stock from the two territories, together with the proportional distribution of weight in the body.

TABLE 2. *The Live-weights and their Distribution in the Body of the Zebu Cattle in Kenya and Tanganyika Territory*

	Kenya Colony				*Tanganyika Territory*			
	Full-mouthed cattle		*Full-mouthed cattle over 350 lb. carcass*		*Full-mouthed cattle*		*Full-mouthed cattle over 350 lb. carcass*	
	Weights (lb.)	*Weights as % of live-weight*	*Weights (lb.)*	*Weights as % of live-weight*	*Weights (lb.)*	*Weights as % of live-weight*	*Weights (lb.)*	*Weights as % of live-weight*
Live-weight	590	100	715	100	510	100	700	100
Carcass	308·5	52·3	384·8	53·8	260·4	51·1	381·1	54·4
Head and horns	23·9	4·0	28·5	4·0	28·1	5·5	34·7	4·9
Hide	43·4	7·3	52·0	7·3	31·6	6·2	43·6	6·2
Feet	12·8	2·2	13·4	1·9	10·6	2·1	11·8	1·7
Stomachs and intestines	41·4	7·0	42·6	6·0	34·1	6·7	44·3	6·3
Contents of alimentary canal	90·4	15·2	108·4	15·2	84·4	16·5	91·3	13·0
Tongue	2·5	0·4	3·0	0·4	2·2	0·4	2·7	0·4
Tail	1·6	0·3	2·1	0·3	1·5	0·3	1·7	0·2
Liver	8·3	1·4	10·0	1·4	7·1	1·4	8·8	1·2
Lungs	7·0	1·2	8·3	1·2	7·4	1·4	9·3	1·3
Heart	2·2	0·4	2·3	0·3	2·1	0·4	2·9	0·4
Kidneys	1·2	0·2	1·5	0·2	1·4	0·3	1·6	0·2
Spleen	1·8	0·3	1·9	0·3	1·8	0·3	2·0	0·3
Suet fat	5·6	0·9	7·4	1·0	4·1	0·8	9·4	1·3
Caul fat	3·9	0·7	5·0	0·7	3·8	0·8	9·5	1·4
Hump	5·1	0·9	7·2	1·0	5·9	1·2	12·0	1·7
Blood	20·0	3·4	25·0	3·5	18·1	3·5	25·0	3·6
Loss	..	1·9	..	1·5	..	1·1	..	1·5

The figures in this table show that the tongue, tail, liver, lungs, heart, spleen, and kidneys form the same proportional weight of the total body of the cattle in both territories. The average carcass-percentage of the full-mouthed cattle in Kenya is slightly above the percentage yield for the average of the Tanganyika full-mouthed animals, but the reverse holds true for the bigger cattle yielding a carcass of over 350 lb. The most striking differences are the heavier hide of the Kenya stock, and the heavier head of the Tanganyika cattle.

Beyond nutritional retardation of growth-rate there does not appear to be any obvious reason for these differences, yet a difference of over 10 lb. in the average green-weight of the hides will cause a marked increase in the value of the hides sold annually. It is also noteworthy that the percentage weight of the hide in these Kenya native cattle is higher than is usually met with in improved breeds, and is higher than is found in the grade European stock of the Colony. The native cattle of Kenya are slightly heavier than those in Tanganyika, but the increased surface area, calculated as proportional to the (weight)$^{\frac{2}{3}}$, is sufficient to account for a 0·1 per cent. increase in the area of the hide. From a few measurements on animals chosen at random it appears that the skin thickness is greater for cattle in Kenya than it is in Tanganyika (Table 3).

TABLE 3. *Average Thickness of Skin of Zebu Cattle in Tanganyika Territory and Kenya*

Place	Breed	No. of cattle measured	Skin thickness (cm.)		
			Shoulder	Flank	Over 13th rib
Tanganyika Territory	Zebu	50	0·26	0·30	0·39
Kenya Colony . .	Zebu	50	0·37	0·44	0·65
Kenya Colony . .	European zebu grade	39	0·43	0·52	0·84

Trowbridge, Moulton, and Haigh [2] found that as a steer fattens the percentage-weights of carcass and fat increase, whilst the proportional-weight of other organs, with the exception of the stomach and liver, decreases. The figures in Table 2 for the average full-mouthed and the heaviest cattle in both Kenya and Tanganyika Territory are in general agreement with these American findings. However, the proportion of liver in these zebu cattle falls slightly in the Tanganyika stock, and the percentage of stomachs and intestines falls very decidedly.

The figures also indicate that the large Boran cattle and the biggest of the Masai oxen, which together represent the cattle yielding carcasses of over 350 lb., yield almost as high percentage returns of carcass and edible offal as do the improved animals, i.e. the zebu cattle graded up by bulls of European breeds. The slow-growing and smaller zebu cattle are usually regarded as much inferior to the improved grade European beasts for beef-production, but these figures suggest that, were the zebu cattle reared under the same good conditions as the 'grades', then the percentage returns would be the same or very little less.

It was not possible to divide the carcasses of the cattle slaughtered at Nairobi into quarters, as was done in Tanganyika Territory. The Indian butchers at Nairobi sell much of the forequarters as 'soup' meat, and the cut dividing the fore- and hind-quarters is made as far forward as possible; usually, however, 6 ribs were left on the hind-quarters. In 50 animals, however, the carcass was divided between the 10th and 11th ribs, and in these cases the hind-quarters represented 50 per cent. of the total carcass-weight. This compares very closely with the figure, 50·7 per cent., found in Tanganyika Territory.

European-owned Cattle

The European-owned cattle of Kenya can be divided into zebu and grade European breeds. A few farmers are rearing pure zebu cattle under ranching conditions. These animals usually mature faster and grow into larger animals than do native-owned zebu stock, because they do not suffer such a severe degree of starvation as do the native-owned animals in the overstocked areas of the Native Reserves. Some of these European-owned zebu animals, chiefly of the Boran type, found their way into the Nairobi abattoir during the period of the present investigation. These have, however, been grouped with the full-mouthed zebu cattle yielding over 350 lb. carcasses.

The majority of European settlers own graded cattle. Zebu cows are bought and then graded up to a European bull, often of a dairy breed, such as the Friesian, Ayrshire, or Shorthorn. The female half-grade animals from one of these bulls are then crossed with pure or grade European bulls, not necessarily of the same breed as their father. Many of the grade animals slaughtered during this investigation were progeny of such mixed breeding. It was, therefore, impossible to group these grade animals according to the amount of European blood in their make-up, or to the European breed to which they had been graded up. It is important to remember, when examining the figures below, that these cattle were graded in the majority of cases to a dairy and not to a beef bull. Such grade dairy oxen grow quicker and develop into larger animals than do the zebu cattle, but they can never yield such good carcasses as could be obtained from cattle graded to a bull of an improved beef-breed.

The majority of the European settlers are marketing their slaughter stock through the agency of the Stock Breeders' Association. All the best European-owned cattle are bought by European butchers in Nairobi from this agency, whilst the Indian butchers buy only the poorer, older, or female stock left by the European butchers. In this investigation the grade cattle have been subdivided according to the butcher killing them, and those killed by the Indian butchers represent cattle rejected as not up to market requirements.

The average weights of the various tissues and organs of 100 grade stock slaughtered at Nairobi are given in Table 4.

We see at once the striking superiority in carcass-weight of these grade animals over the native zebu cattle: all their organs weigh more than the corresponding organs in the zebu breed. The figures also illustrate the tremendous difference that exists between the poor quality and the average grade stock. Even the average of the poorer grades killed by the Indian butchers were much heavier than the average of the heaviest native zebu cattle recorded in Table 2.

In the following discussion only the grade stock slaughtered by the European butchers will be considered, because the others are not up to the average. The carcass-weight varied in these animals from 442 to 700 lb. each, and the average of 558·9 lb. is 1·8 times the average weight of the native zebu cattle in Kenya. The hides ranged from 50 to 80 lb. each, and the average weight of 64 lb. is very good. The deposits of internal fat in these grades were on the average about four times as heavy as in the zebu.

The 100 grade animals killed during this investigation show an average carcass-weight of 502 lb. Mr. F. Raper, the Secretary of the Stock

TABLE 4. *Average Weights in Pounds of Carcass and Individual Organs of Grade European Cattle*

Butchers	*European*	*Indian*		
Type of stock	*Full-mouth oxen*	*Full-mouth oxen*	*Full-mouth cows*	*2-Tooth stock*
No. recorded . . .	60	29	6	5
Carcass	558·9	448·28	403·9	250·60
Head	36·20	28·22	29·50	22·50
Hide	64·01	55·35	56·67	30·40
Feet	19·50	15·46	13·84	12·20
Tongue	4·04	3·22	3·58	2·60
Tail	2·55	2·25	2·41	1·15
Liver	11·33	11·14	11·50	8·20
Lungs	10·98	10·54	11·00	6·20
Kidneys	1·88	1·76	1·90	1·05
Spleen	2·25	2·11	2·00	1·50
Heart	3·28	3·18	3·67	2·10
Suet fat	14·56	9·75	6·55	2·10
Caul fat	12·78	7·62	5·33	2·90
Contents of alimentary canal .	129·76	115·72	121·50	87·60
Stomachs and intestines. .	57·87	47·44	53·00	36·60

Breeders' Association kindly let me look through his records for the last 18 months, and the average carcass-weight of the grade stock sold by this Association was 496·7 lb. for 2,363 animals. This means that the animals examined were typical of the grade animals slaughtered at Nairobi.

The hind-quarters of these grade carcasses formed 51·5 per cent. of the total carcass-weight. This compares very well with Fourie's figures [3] for South Africa (51·1 per cent.), and with the figures for the native zebu cattle (50·4 per cent.).

From the figures in Table 4 we can calculate that the average live-weight of these grade animals was 970 lb., with a blood-content of 30 lb., and a loss of about 1·5 lb. in opening up and splitting the carcass. For the Indian-killed grades the average live-weight works out at 800 lb.

In Table 5 are given percentage weights of the various tissues and organs in the bodies of these grade animals.

The carcass-percentages of the Kenya grade cattle are therefore higher than for the zebu animals. They compare well with the figures given by Chalmers [4] for Argentine (56 per cent.) and Uruguay (53·6 per cent.) cattle. The figures obtained by Hammond [5] are for animals slaughtered at the Smithfield fat-stock show, and are therefore for cattle in a much fatter condition than the market normally requires. Wentworth [6], from experience at Chicago, states that good steers yield from 56 to 59 per cent. carcass, and that cattle in show condition will yield up to 64 per cent. of their weight as carcass. The Kenya grade stock therefore kills very well, and were the animals beef-grades instead of dairy-grades there is no doubt but that they would be very suitable for export as chilled beef.

The carcasses of Kenya native zebu are very similar to those described for Tanganyika zebu cattle [1]. They are too small for export to Great

TABLE 5. *Percentage Distribution of Weight in Grade Cattle*

	Grade cattle		*Average British breeds* (4)	*Average American breeds* (5)
	European-killed	*Indian-killed*		
	Weight as % of live-weight	*Weight as % of live-weight*	*Weight as % of live-weight*	*Weight as % of live-weight*
Live-weight	100	100	100	100
Carcass	57·2	56·0	64·6	58·3
Hide	6·6	6·9	6·7	6·3
Head and horns	3·7	3·5	3·9	3·8
Feet	2·0	1·9		
Stomachs and intestines	5·9	5·9	..	..
Contents of alimentary canal	13·4	14·5	..	..
Tongue	0·4	0·4	0·8	..
Tail	0·3	0·3		
Liver	1·2	1·4	2·6	2·9
Lungs	1·2	1·3		
Heart	0·3	0·4		
Kidneys	0·2	0·2	..	..
Spleen	0·2	0·3	..	..
Suet fat	1·5	1·2	..	..
Caul fat	1·3	1·0	..	..
Blood	3·1	3·1	..	3·8
Loss	1·4	1·7	..	..

Britain as chilled or frozen meat, and are far more suited for a local packing industry.

The grade carcasses as a whole are a little too small for the frozen- or chilled-meat markets. There are, however, about 50 per cent. which weigh over 600 lb. carcass-weight, and these would be suitable. The heavier-grade carcasses are much better finished than the ordinary zebu carcass, though carcasses from good Boran or Masai oxen carry a nice covering of external fat and a fair percentage of intermuscular fat. 'Marbling', however, is not seen often, even in good zebu carcasses. The grade animal has, however, the ability to deposit fat intramuscularly.

The grade carcass generally is longer, the ribs have a better spring, the sides are deeper, and the meat is thicker than in a zebu carcass. The shins are better fleshed, there is more meat on the aitch-bone and rump-joints, and the thighs are also better developed. The insides and backs of the thighs are covered with a thin layer of fat, which extends over the rump and along the back and sides of the carcass to the shoulders. Generally, there is also a little fat covering the insides of the ribs, and a large deposit on the kidneys. It is, however, in the better distribution of fat among the muscles that the grade scores most over a good zebu carcass (Plate 9). In Kenya the slaughter stock are all grass-fed and, as was noticed in Tanganyika, there is a definite tendency for the fat covering a carcass to become very yellow, thus detracting considerably from the market value of the meat. The grade cattle examined appeared to be very heavy-boned, but no figures could be obtained to check this point.

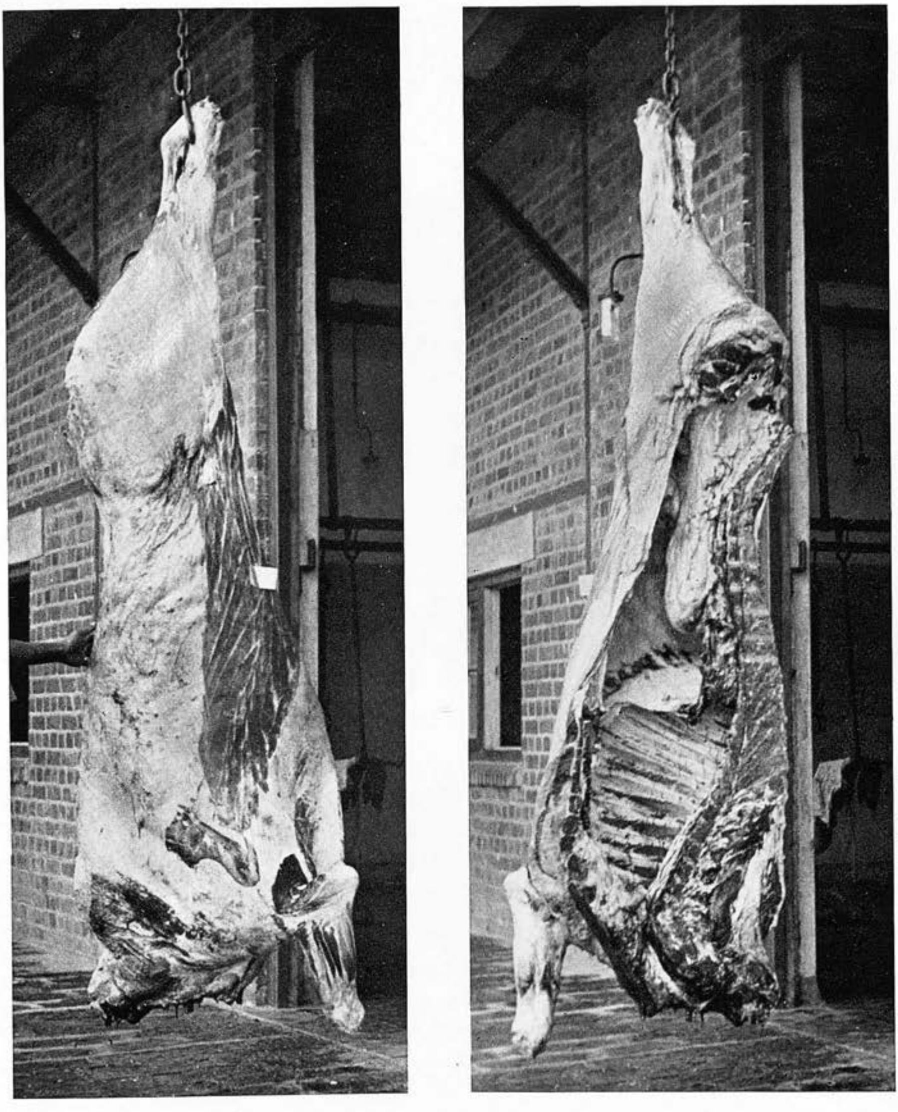

FIG. 1 FIG. 2

The carcass of an average grade ox

Much, however, could still be done to improve the carcasses of grade cattle by introducing blood of a good light-boned breed, such as the Aberdeen Angus. Such crosses will be just as early maturing, but in addition will possess a high ratio of meat to bone in the carcass, and a greater development of the higher-priced joints.

Summary

Figures have been produced to show the actual and the proportional distribution of weight in the body of zebu and grade European stock in Kenya Colony.

Comparisons have been made between the zebu carcasses of Kenya and those in Tanganyika Territory.

The grade carcasses have been compared with those from other meat-producing countries.

It has been shown that Kenya possesses grade meat suitable for export, but that an improvement would result in the use of good bulls of a beef-breed.

Acknowledgements

I acknowledge with great pleasure the help given to me by Mr. R. Daubney, Chief Veterinary Research Officer, Kenya, who suggested this work and who made all the arrangements for carrying out the measurements. I am also indebted to Mr. H. E. Hornby, Director of Veterinary Services, Tanganyika Territory, for allowing me to remain in Nairobi to make these measurements.

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THE OCCURRENCE OF A BRITCH-POLL FIBRE-TYPE ARRAY GRADIENT IN THE NEW ZEALAND ROMNEY LAMB

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IN a recent paper Dry [1] gives an account of the fibre-type arrays occurring on the back of the New Zealand Romney Lamb. Preliminary observations had suggested that orderly relations existed between the fibre-type arrays on the back and britch positions. These observations were extended and a comparative study of the fibre-type arrays occurring in the coat of the Romney lamb was made.

Material and Methods

The Romney lambs used for this work were from Dry's experimental Romney flock [2]. They were sampled from the following positions, which have been conveniently named (Fig. 1):

1. *Poll*: on the mid-dorsal line between the ear and horn positions.
2. *Anterior withers*: on the mid-dorsal line at the level of the last cervical vertebrae.
3. *Point of shoulder*: on the point of the right shoulder-bone.
4. *Withers*: on the mid-dorsal line, level with the fifth rib.
5. *Fifth rib*: on the right fifth rib, ventro-lateral to the withers in a line with the lateral aspect of the shoulder-point and dorsal to the elbow.
6. *Elbow*: on the elbow-joint of the right forelimb.
7. *Back*: on the mid-dorsal line, level with the last rib.
8. *Side*: on the right side, at the distal end of the last rib.
9. *Superior ileum*: on the mid-dorsal line on the medial angles of the ilea.
10. *Hip-joint*: on the junction of the femur and pelvic bones (acetabulum) and ventro-lateral to the superior ileum position.
11. *Stifle*: midway and slightly anterior to an imaginary line drawn between stifle and hip-joint.
12. *Britch*: immediately posterior to the stifle joint and midway across the thigh.
13. *Brisket*: on the mid-ventral line between the forelegs.
14. *Point of sternum*: on the mid-ventral line level with the shoulder-point position.
15. *Epigastric*: on the mid-ventral line immediately opposite the back position (No. 7).

The last three ventral positions were not taken regularly and the gradients given are for the dorsal and dorso-lateral regions only.

The method of examining the samples was simple; the fibres had been protected from the weather by coats of waterproof material, as described by Dry [3], the lambs being covered before the halo hairs began shedding.

Sorting was carried out on black velvet, using blunt-tipped forceps. Each sample was sorted into the following groups of fibres:

1. Halo hairs
   Sub-halo hairs
   Sickle fibres
   Super-sickle fibres
   } Shedding group
2. Curly-tipped fibres
   Checked curly-tip
   Peak curly-tip
   Other curly-tip
3. Histerotrichs
   } Non-shedding group

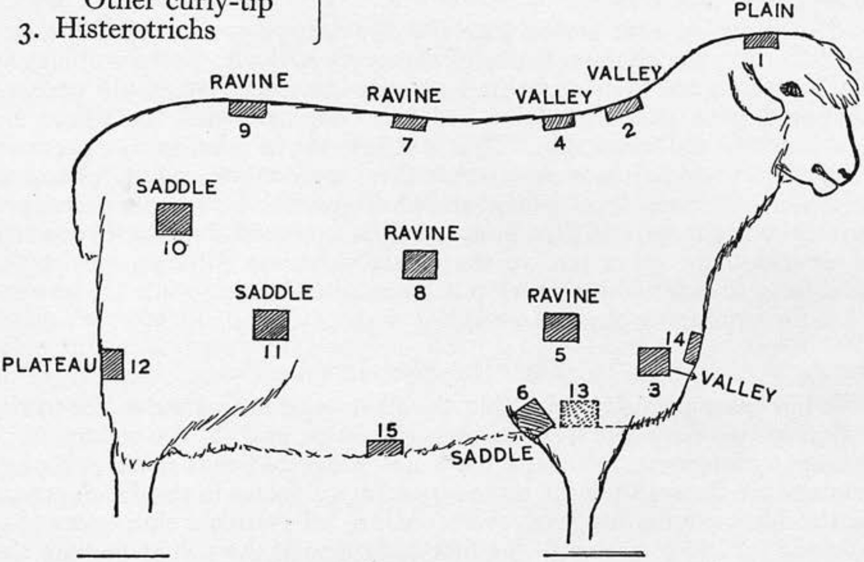

FIG. 1. Diagram to illustrate positions from which samples were taken.

1. Poll
2. Anterior withers
3. Point of shoulder
4. Withers
5. Fifth rib
6. Elbow
7. Back
8. Side
9. Superior ileum
10. Hip-joint
11. Stifle
12. Britch
13. Brisket
14. Point of sternum
15. Epigastric

On the diagram, the types of fibre-arrays found in one lamb in certain of the sampled areas (1–12) are named. The particular lamb (no. 745) is one of those shown on Graph III, which should be consulted for other types of distribution.

Halo hairs are the coarsest of the shedding fibres in the birth-coat; they are straight-tipped. The sub-halo are smaller and have a slightly curved tip. Sickle fibres have a distinct, thickened, sickle-shaped tip, demarcated from the shaft by a definite neck, but are the finest of the birth-coat fibres, which belong to the shedding group. The super-sickles are stouter and larger than the sickle fibres, possess no distinct neck, and represent a transition stage between the sickles and the sub-halo fibres. It is possible to determine a definite transition in these four fibre-types, from coarse halo hairs through sub-halos and super-sickles to the finer sickle fibres proper.

Curly tips of all varieties together constitute about two-thirds of the total fibres present in the birth-coat. Those designated 'checked curly-tips' are very fine, and have a number of curls in their tips. (It will be noted later that these fibres are found only in Valley, Plain, and Escarpment arrays.) 'Peak curly-tips' are the coarsest of the curly-tip group.

They are not found in fine arrays. Their tips have always a few curls. The remaining curly-tip fibres occur as later-growing fibres which have progressively finer tips with fewer and fewer curls.

Histerotrichs are relatively scarce, appear latest, are shorter, and are always very fine.

The samples were sorted into the above type-groups with little or no difficulty, the characteristics of the great majority being sufficiently marked to enable them to be immediately classified. It should perhaps be noted here that the above order is that in which the fibres are developed in the foetal skin. This is significant in relation to a previous study [4] in which it was shown that there are definite orderly phases of initiation of follicle-development and fibre-growth. Follicles are arranged primarily in threes, and then in nines. It is surmised that the three-stage of development gives rise to the shedding group (above), whilst the additional follicles which develop to constitute the nine-stage are responsible for producing the non-shedding type of fibres.

The Fibre-type Arrays

It has been postulated [4] that the fibre-type arrays were due to the action of two variables, (1) the prenatal check, and (2) the reduction in inherent coarseness. Prenatal work has suggested that these two phenomena are the result of the same physiological factor in the development of the fibre-population, viz. overcrowding of available skin-space due to rapid follicle-formation—the first occurring at the trio-stage, and the second at the nine-stage. The prenatal check, it was suggested, might be termed the 'trio-depression' and the reduction of inherent coarseness the 'nine-depression'.

The fibre-type arrays found have been conveniently named by Dry [1]:

Plateau (least depressed)
Saddle
Ravine
Valley
Plain and Escarpment (most depressed).

The Plateau array.—In this the trio-depression was so slight that it had no visible effect on the early fibres, no sickle fibres being present. Shed and persistent halo hairs and peak curly-tips represented the early fibres of the array-series. The nine-depression did not occur until at least half-way along the curly-tip portion of the array. There was a marked break between the fine and coarse curly-tips; this break occurred earlier in the array-series in samples from more anterior positions than in those from more posterior regions.

The Saddle array was due to weak trio- and nine-depressions. The nine-depression takes place about the same time in both Saddle and Plateau arrays.

The Ravine array had an intense, and often very intense, trio-depression of fairly short duration. There was always a marked rise in the coarseness of the post-ravine sickle fibres. The nine-depression occurred after the rise in coarseness in the post-ravine sickle fibres; there may or may not be a definite break between fine and coarse curly-tip fibres.

The Valley array showed an intense trio-depression of longer duration than in the Ravine array, there being no rise in coarseness until some of the early-checked curly-tips had been formed. The nine-depression took place shortly after the trio-depression had ceased to function.

The Plain array.—The trio- and nine-depressions overlapped in this array, and no increase in coarseness took place either in the sickle-fibres or in the curly-tip portion of the array-series.

The Escarpment array.—This new array (Fig. 2) was similar to the Plain, but no sickle fibres were present. It has been suggested that the escarpment was due to the overlapping of the nine-depression with a very intense trio-depression. This array has been found only once on any position other than the poll—on the britch of a very dense Romney; the array on the back was Plain; no other samples were preserved. It occurred frequently on the poll.

It has been suggested that the order of the fibre-type arrays was due to an increase in the intensity of the trio- and nine-depressions, those with the least intense depressions having coarse fibres, and those with more intense depressions finer fibres. Each of these arrays passed gradually into the next; all varieties intermediate between one fibre-type array and the next have been observed on different animals, and over the same animal.

Distribution of the Arrays

Preliminary examinations showed that different fibre-type arrays occurred on back and britch positions. It was known that fibre-type arrays passed gradually from one to the other (*v.s.*). From these two facts it was suspected that all fibre-type arrays separating the array on the back from the array on the britch would be found somewhere on the area intervening between these two positions. This was found to be true. Further, knowing that the arrays on the back and britch positions differed, it was expected that the arrays on the positions anterior to the back would differ from those on the back; this surmise was also found to be correct. As well as revealing that fibre-type arrays on back and britch positions differed, the preliminary examinations indicated that orderly relations existed between back and britch, the array on the back always being more depressed than the one on the britch.

More detailed work, involving the study of the fibre-type arrays occurring over the bodies of various Romney lambs, demonstrated that orderly variation from position to position was the rule for the distribution of fibre-type arrays over the body of the Romney lamb (Graphs II, III, p. 123 and Fig. 1).

This orderliness in variation was mainly due to less depressed arrays being posterior to more depressed ones, though, as explained later, some elaboration of this general statement was required.

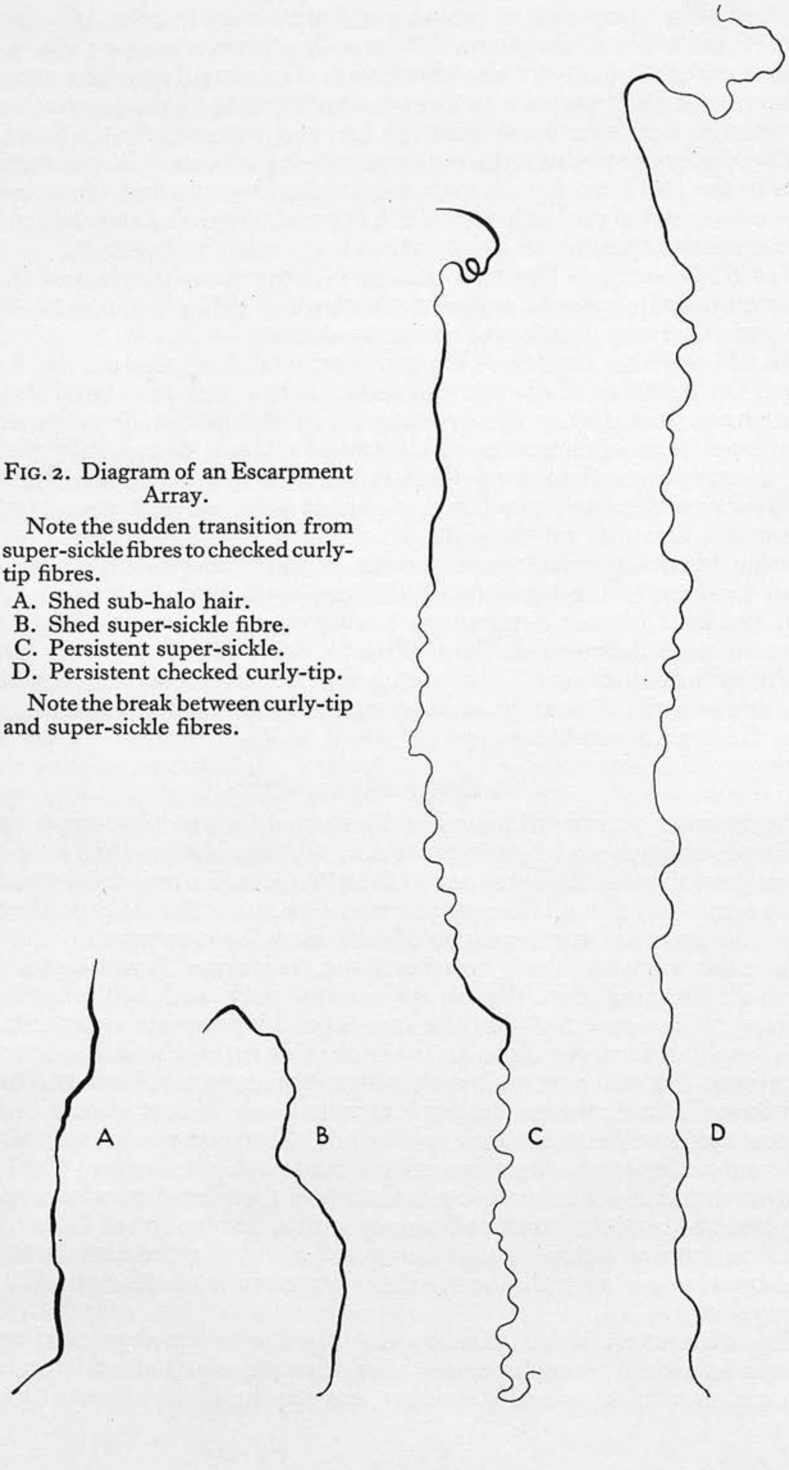

FIG. 2. Diagram of an Escarpment Array.

Note the sudden transition from super-sickle fibres to checked curly-tip fibres.

A. Shed sub-halo hair.
B. Shed super-sickle fibre.
C. Persistent super-sickle.
D. Persistent checked curly-tip.

Note the break between curly-tip and super-sickle fibres.

From these statements it was apparent that the gradual increase in fineness caused by the incidence of a check (depression in follicle-activity) from posterior to anterior regions resulted in a general posterior-anterior, or britch-poll fibre-type array gradient (Graphs II, III).

Besides the britch-poll gradient there must be kept in mind the subsidiary gradients due to gradual increase in coarseness of the fibres as one passes from dorsal to lateral positions in the coat of the Romney lamb (Graphs II and III).

It was found that the general gradients varied in steepness from animal to animal. Fine even-coated lambs and their opposites, the very coarse-coated animals, had very slight britch-poll gradients (Graphs II, III, sheep nos. 755 and 618). These two lambs resembled one another in that both exhibited slight britch-poll gradients, though at different planes. They were unlike in that No. 618 (Graph II) showed an even gradient due to an intense overcrowding occurring at the trio- and nine-stages of development, and resulting in a fine even fleece.

In no. 755 (Graph I), follicle-activity at the trio- and nine-stages of development had been very slightly affected by increasing density of the follicle-population in the skin, and the fleece in consequence was coarse, and very uneven in length and fineness. It may be noted here that this lamb, which is quite typical of its class, showed the characteristic 'break' which occurs between the coarse curly-tip and fine curly-tip groups, and all fibres developing later than the break were much shorter than the early ones.

These two sheep (Graph I, sheep nos. 618 and 755) did not exhibit such marked gradients as those given by the coats of the majority of lambs, but were indicative of the wide extremes of coarseness and fineness occurring in this breed of sheep; they also represent extremes in fibre-type arrays.

Other lambs of the Romney breed exhibited marked gradients from britch to poll (Graphs II and III, sheep nos. 641, 745, 628, 763). These graphs show general posterior-anterior gradients due to slight depressing on the britch passing to a deep depression on the poll.

These gradients were more or less characteristic of New Zealand Romney lambs. From the graphs it will be seen that the lambs can be separated into three classes, by their coat characteristic; i.e. fine, coarse, and intermediate:

Class	*Animal*	*Medullation*	*Graph*
	No.	Per cent.	No.
Coarse	755	50	I
	628	52	I
	745	54	I
	641	44	I
Intermediate	763	11	II
	619	18	..
	607	12	..
Fine	618	5	II
	638	4	II
	767	6	..

Substantiation of this grouping into three classes was supplied by the percentages of medullation found in the different coats. This medullation, though not indicative of fineness, suggested that unless the fibres were coarse medullation would not occur. The percentages of medullation were estimated by McMahon as explained in the footnote.[1]

It was found that animals of the coarse class showed not only marked variation in the fibre-type arrays occurring on the various positions but marked variation in fibre-length within an array. Also the fibre-diameter varied more in the coats of the lambs of the coarse class than in those of the fine or intermediate class. In the coats of the lambs of the fine class there was very little variation in either fibre-type array or in the length of the fibres comprising the arrays.

Thus we find that the Romney lambs can be divided into three classes: coarse, fine, and intermediate. In the coats of animals of the coarse class there is marked variation in fibre-type array, fibre-length, and fibre-diameter. In the coats of animals of the fine class there was little variation of any kind. The coats of animals of the intermediate class varied either more or less according as they approximated the fine or the coarse class.

Prevalence of the several fibre-type arrays on the various positions.—The following table gives an idea of the proportion of fibre-type arrays found on the different positions. These are from a number of animals selected at random and sampled from the same anatomical positions.

TABLE I

Positions	*No. of sheep examined*	*Fibre-type Arrays in Proportion to One Another*				
		Plateau	*Saddle*	*Ravine*	*Valley*	*Plain and Escarpment*
Britch . .	100	30	**45**	13	9	Infrequent
Hip-joint . .	39	3	6	**26**	3	"
Superior ileum .	30	1	5	**18**	4	2
Back Side . .	100	Infrequent	4	35	**42**	18
Withers Fifth rib . .	46	"	Infrequent	4	**21**	18
Shoulder point .	44	"	"	2	19	**20**
Poll . . .	35	"	"	Infrequent	3	**30**

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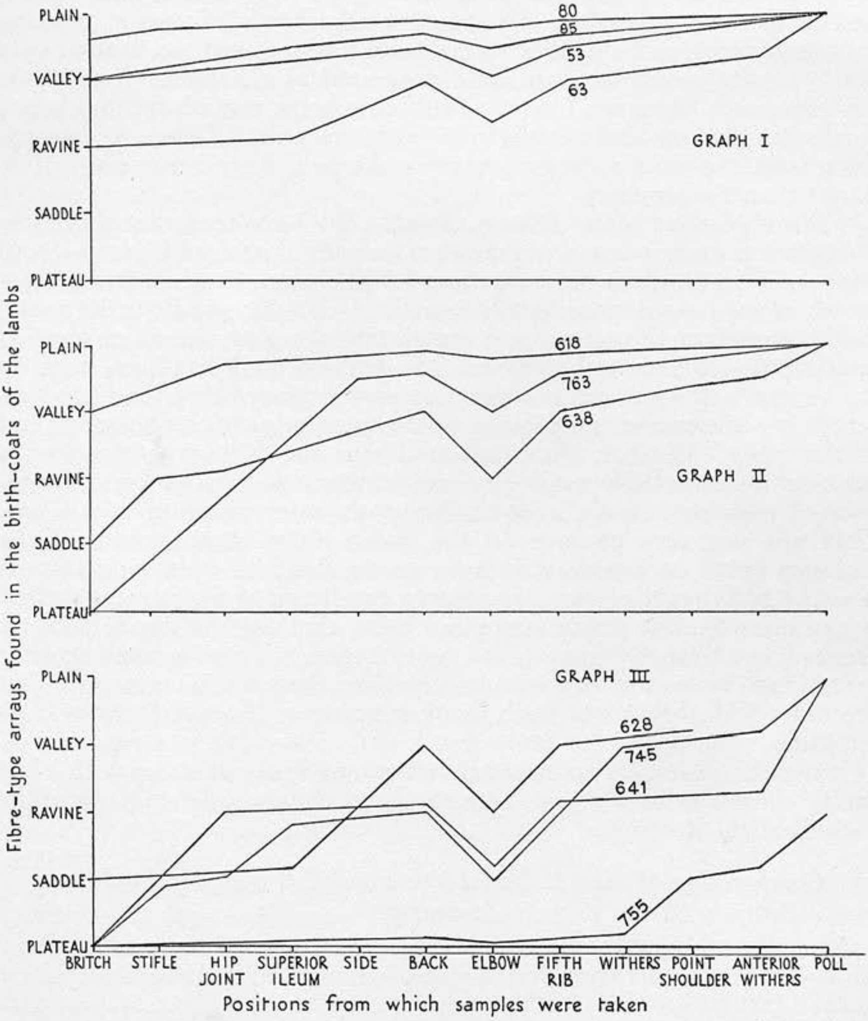
[1] *A method of estimating the medullation revealed in benzol.* By P. R. McMahon. When comparing samples the average percentage of fibre-material affected by medullation may be taken as an index of the degree of hairiness revealed by the benzol test. The following technique was evolved to obtain such a figure:

1. The staple is teased out to a standard thickness of 300 fibres to each inch of width by comparison with a standard staple obtained by direct counting.
2. The staple is immersed in benzol and with the aid of a photograph of a lock in benzol, spread to the same thickness and showing zones where 10 to 90 per cent. of the fibres are medullated, estimations of the percentage of fibres affected are made at ¼ in. intervals.
3. Taking these figures as representative, the average percentage of medullated fibre over the lock is calculated and expressed as one figure.

The technique is slow and cumbersome, but has been shown to be reasonably accurate for normal samples of wool. In the case of lamb's wool, however, the accuracy is considerably reduced by rapid changes in hairiness from one level in the staple to another, and also by the parallel placing of the fibres, which hinders accurate teasing. Differences of 7 per cent. would be significant.



To illustrate the general posterior-anterior (britch-poll) fibre-type array gradient in the Southdown, Ryeland, and Romney lambs studied.

GRAPH I

Southdown lambs nos. 80 and 85
Ryeland lambs nos. 53 and 63

Note the gradients are not very marked; the gradients of the Ryeland lambs, however, are slightly more marked than are those of the Southdowns.

GRAPH II. *The fine and intermediate class*

Romney lambs nos. 618, 638, 763

No. 618. *Fine Class.* Note the very slight britch-poll gradient and the very slight ascending gradient of the fore-limb.

No. 638. *Fine Class*, has a more general type of coat than that of No. 618; fine and

On the britch among the sheep examined it was found that Plateau was far more common than at first suspected. Dry [2], however, working on animals with no halo hairs on the back, found that these animals very rarely have a britch array so little depressed as a Saddle. Two of the Plateau arrays had a few halo- and sub-halo hairs, but a large number of super-sickle fibres and coarse Peak curly-tip ones. Plain and Escarpment were the most common arrays on the poll, Plain being more often found than Escarpment.

Ventral gradient of the Romney breed.—We have seen that there was a gradual posterior-anterior gradient over the dorsal and dorso-lateral regions of the Romney lamb due to gradual change from coarser to finer arrays as we passed from britch to poll. This same gradient, however, does not apply to the ventral and ventro-lateral region, for which another gradient would have to be drawn. No detailed work has been done on the ventral surface, but a few examinations indicated that the fibre-type arrays became coarser on passing from the anterior to the posterior end of the body. Further, they indicated that the fibre-type array on a position on the mid-ventral line was inclined to be slightly more depressed than one on a corresponding position on the mid-dorsal line. This was not very obvious on the sheep more characteristic of the Romney breed on positions anterior to the shoulder-point position. It is suspected that the posterior-anterior gradient for the ventral surface was similar to, but rather less steep than, that for the dorsal surface. Hence it can be seen that there is a general tendency for the more anterior positions to have more depressed arrays than the posterior ones, and that the most typical Romney lamb was a member of the intermediate class of lambs.

It was then necessary to ascertain whether a breed of sheep with a less variable fleece exhibited fibre-type array gradients similar to those of the New Zealand Romney.

Comparative Studies in Two Finer-woolled Breeds, Ryeland and Southdown

A small number of samples was taken from Southdown and Ryeland lambs—nine samples from four sheep of each breed and less from others

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even but with a fairly marked gradient from the britch to the side. The fore-limb gradient is also more pronounced.

No. 763. *Intermediate Class*, has a marked britch-side gradient, but anterior to this the gradient is slight.

GRAPH III. *Coarse Class*

Romney lambs nos. 628, 641, 745 and 745

No. 755. Very coarse-coated, showing very little change in coat fineness till the shoulder-point position; gradient posteriorly is very slight but fairly marked anteriorly.

No. 628 }
,, 745 } All show marked britch-poll gradients.
,, 641 }

No. 628. (No anterior withers or poll sample taken.) Note the side-back gradient.

No. 745 }
,, 641 } Both very uneven-coated sheep.

—with the idea of determining the fibre-type array gradients for purposes of comparison with the Romney lambs.

Southdown lambs (Graph III, sheep nos. 80, 85).—The Southdown coat was very much finer and more uniform than the Romney coat; medullation rarely occurred. Air in the cortical cells, termed 'smokiness' by Rudall [5] and Elphick [6], occurred frequently. A few had halo hairs on the poll and a rather larger number on their britch margins; on many, however, halo hairs did not occur at all.

The arrays showed a very even distribution with very little gradient in the array-depression. Two animals with less depressed arrays on their britches than the others (Graph I, sheep no. 85) had some sickle fibres with medullated ends: these did not comprise the greater number of sickle fibres, there being far more very fine non-medullated ones. Some of these very fine sickle fibres were shed, but those with medullated ends were not shed; a few of the fine curly-tip fibres were also shed.

The animals with more depressed britch arrays (Plain arrays on the britch, Graph I, sheep no. 80) had few fibres with medullated sickle ends. Sickle fibres were numerous but extremely fine. On no sheep examined was an array less depressed than a Plain found anterior to the superior ileum position.

On one animal an Escarpment array was found on the poll. This animal had halo- and sub-halo hairs—short stout kemp fibres—and very fine super-sickle fibres succeeded by checked curly-tip ones.

The Southdowns examined were from one flock only and did not represent the extremes of coarseness or fineness that might be found in the breed. They can, however, be compared with those Romneys more characteristic of the breed. The Southdown gradients were not unlike the gradients of the extremely fine Romney lamb no. 618, Graph II, but they were generally far more even in array-distribution than those more typical Romney lambs (Graphs II and III, sheep nos. 641, 745, 628, 638, 763).

The Ryeland lambs (Graph I, sheep nos. 53, 63)—In many ways the wool of the Ryeland lambs was not unlike that of the Romney lambs (Graph II).

In the Ryeland the sickle fibres were like those of the Southdown but were perhaps a little coarser; sickle fibres with medullated ends were by no means restricted to the posterior regions. The sheep examined had fewer halo hairs than the Romney, and they were not so long. They were not, however, so free of these fibres as were the Southdown lambs. Shedding of fine sickle fibres took place as in the Southdown, but to a lesser extent.

In the curly-tip fibre portion of the array the resemblance to the coat of the Romney was quite marked. A considerable amount of medullation was present in some cases and in most there were traces of it. Compared with the curly-tip portion of the Romney, however, the Ryeland curly-tip fibres presented a more even series and exhibited less variation in length from fibre to fibre within the array; very coarse-tipped curly-tips were not found. The fibres as a whole were somewhat shorter than those of Romney lambs of the same age.

A Plain array was not found on the Ryeland britches studied, but Valley was common; Ravine arrays were found on two of the britches examined but nothing coarser was seen. The distribution of the arrays of these Ryeland lambs resembled the distribution of the arrays on the lambs belonging to the fine class of New Zealand Romneys (Graph II, sheep nos. 638, 618), but there was apparently far less variation in the fibre-type arrays occurring on different positions on the more average Ryeland lambs than there was in the more characteristic Romney lambs.

As in the case of the Southdown, the Ryeland lambs sampled were from one flock, and were therefore not indicative of possible extremes of either coarseness or fineness.

Though the numbers of sheep of these breeds examined were small, the observations made indicated that in both these breeds the distribution of fibre-type arrays was far less variable than in the Romney, and their coat generally finer and with less variation in fibre-length. The coat was shorter than that of the Romney, especially in the case of the Southdown.

Medullation was more common in the Romney, but not uncommon in the Ryeland lamb; the Southdown had very little of it, but those examined were inclined to show a considerable amount of 'smokiness' [5, 6].

Of the two breeds studied, the Ryeland more nearly approximated the Romney than did the Southdown in type of array and in character of fibre.

Shedding of Fine Fibres

Both Ryeland and Southdown lambs exhibited a marked tendency to shed their finer sickle fibres. Coarse super-sickle fibres and halo hairs were shed in a manner similar to the shedding of coarse fibres in the Romney breed. The Southdown also shed a few early fine curly-tip fibres. This shedding of fine sickle fibres was in marked contrast to the shedding of these fibres in the Romney, where shedding of all but those sickle fibres shed at birth, or very soon after, has been regarded as an expression of vigour [2]. Roberts [7], and Darling [8], in their papers on the Welsh mountain and the Scottish Blackface breeds, respectively, mentioned that shedding of fine fibres occurred, and dissociate it from the shedding of kemp. In their work on the Blackheaded Persian of South Africa, Duerden and Boyd [9] referred to a spring shedding of wool fibres as distinct from kemp fibres. In the Blackheaded Persian, however, all fibres of the coat were apparently shed. In the Southdown and Ryeland only the early fibres of the fibre-array type, the sickles and early curly-tips, were shed. In the Welsh Mountain breed [7], from the accounts given, the shedding was apparently similar to that of the Romney. In the Romney [2], shedding of kemp fibres was common. In addition to this, however, there was 'smoky' shedding due to the damaging of fibres [5]. Further, in one animal examined by Rudall it was found that there was shedding of the histerotrich fibres, possibly 'hunger' shedding. The manner of shedding of these differed from that of the early kemp fibres. Here the shed fibres did not have a bulb-like swelling forming a sheath round the brush, nor did they have a 'smoky' swelling, as in fibres where the shedding was caused by the damaging of follicles. The brush was small, and the proximal portion of the shaft of the fibre very thin. In the Scottish Blackface the shedding of the fine fibres was apparently more nearly related to the shedding in the Blackheaded Persian than to that in the Romney breed.

The fine fibres shed by the Southdown and Ryeland were the early fibres of the array, the fibres that might form kemp in more hairy breeds. They were shed in a manner similar to that of the kemp of the Romney; each fibre had a bulb-like sheath about its brush, the bulb being visible to the naked eye when sorting on black velvet. These fibres were not those sickle fibres shed at birth or very soon after, though both these types were found in the Southdown and Romney breeds. Some of the shed curly-tip fibres of the Southdown had 'smoky' swellings, but not all, some being shed in the normal way.

From this we can say that the shed fibres of the Southdown and Ryeland lambs were of the same type as those fibres that constituted the kemp of the Romney, i.e. halo hairs, and coarse super-sickle fibres when present, and fine super-sickle and sickle fibres, and, as in the Romney, occasional curly-tip ones. The shedding of the fine curly-tip fibres of the Southdown was more common than the shedding of coarse curly-tip fibres of the Romney, which usually takes place to any extent only in Plateau and very occasionally in Saddle and Ravine arrays.

In a personal communication, Dry reported that one fine-woolled Romney lamb exhibited shedding of fine sickles in a manner similar to that of the Southdown and Ryeland. This was accompanied by the shedding of coarse kemps as well.

The method of shedding in these two breeds was similar to that of the kemp of the Romney, a thinning of the fibre succeeded by a brush in a sheath forming a bulb-like swelling. 'Smoky' shedding occurred in all three breeds.

Summary and Discussion of the Distribution of the Fibre-type Array

1. *Britch-poll gradient.*

In the New Zealand Romney, the Southdown, and the Ryeland, the extent to which the fibre-type arrays were observed to be depressed varied over the body, giving a general gradient from britch to poll, i.e. a posterior-anterior gradient; this gradient was gradual, no sudden transitions, such as Plateau on the britch to Plain on the superior flank position, taking place.

2. *Subsidiary gradients.*

The gradients up the sides of the body were subsidiary to the general posterior-anterior gradient, but accompanied it; they were most noticeable up the limbs. In these gradients the array on the inferior position limited the array on the superior position; thus the array on the britch limited the arrays on the rest of the body to being no less depressed than that on the britch.

3. *Variation in fibre-length*

The length of the fibres comprising the array series varied from the anterior to the posterior end of the body in accordance with the fibre-type array. Variation in fibre-length was less in the more depressed arrays, Plain and Valley, than in the less depressed Plateau and Saddle arrays.

4. *Shedding*

Shedding of the kemp in the Romney is regarded as an expression of vigour. Similar shedding affecting the coarser fibres was observed in the Ryeland and Southdown lambs. Shedding of the fine fibres also occurred in these breeds.

5. *Medullation*

Some medullation occurred in all of the Romney coats examined, but there was marked variation in the percentages found in different coats. A higher percentage of medullation was found in coats with slightly depressed arrays and a lower percentage in those coats where the arrays were more depressed. In the Southdown breed, medullation was negligible; it was more common in the Ryeland breed.

Acknowledgements

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IRRIGATION-DEVELOPMENT IN AUSTRALIA WITH SPECIAL REFERENCE TO IRRIGATION-SETTLEMENTS OF THE STATE OF VICTORIA

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WITH PLATE 10 AND MAP

THE conservation of water for irrigation purposes, and the construction of irrigation-systems for distributing the water, have proceeded steadily in Australia since 1886. The rate of progress is illustrated by reference to the State of Victoria. The total capacity of storage within the State at June 30, 1934, was 1,243,870 acre-feet, and on completion of works in course of construction will amount to 1,290,570 ac.-ft., as compared with 172,000 ac.-ft. in 1902. Furthermore, the Hume reservoir on the Upper Murray is completed to a capacity of 1,250,000 ac.-ft., and is designed for an ultimate capacity of 2,000,000 ac.-ft., half of which will be credited to the State of Victoria. In addition, considerable quantities are drawn direct from the Murray river. On completion of the Hume reservoir and other storages being provided by minor River Murray works, the total capacity of the storages available for the State will amount to 2,367,570 ac.-ft. The storages in New South Wales, existent and projected, are referred to later. The locations of the main irrigation-districts on the Murray river and its tributaries are shown in the accompanying map.

IRRIGATION IN THE STATE OF VICTORIA

The schemes already constructed and under construction provide for supplies of water to thirty-two irrigation-districts. The supply of irrigation-water is mainly drawn from the head-works constructed on the Murray river, and from the Goulbourn and Loddon rivers, which are tributaries of the Murray.

The Goulbourn irrigation-system.—The Goulbourn system comprises chiefly two main channels and a diversion-weir which raises the summer level of the water 45 ft., giving 408 ft. above sea-level. The principal storage-reservoir within the system is Waranga Basin, from which water for irrigation is distributed to a distance of 230 miles. Additional storage is provided by the Eildon reservoir (Plate 10, Fig. 1), which provides also an outlet for State hydro-electric works. An interesting feature of the Eildon reservoir is the dam across the Goulbourn, which is constructed to a height of 140 ft. above the river-bed, with a foundation, in places, 75 ft. below the surface, and an overall length of 3,000 feet. This wall, excepting 700 ft. of mass concrete forming a flood spillway, consists of a rock-fill bank with a reinforced concrete-core wall (Plate 10, Fig. 2).

The main channels of the Goulbourn system have an aggregate length of 340 miles, in addition to which there are 2,300 miles of distributaries and 500 miles of drains, a total of 3,140 miles for the whole system.

The various irrigation-areas of this system total approximately

1,293,500 acres, and produce mainly fodder-plants and irrigated pastures, and also fruits. Among the latter, stone-fruits predominate, the aggregate production of the three co-operative canneries (Shepparton, Ardmona, and Kyabram) being 24 million cans in 1933.

River Murray irrigation-systems.—Several irrigation-works for service of frontage lands on the Murray are in operation between Echuca and the South Australian border. The districts between Echuca and Swan Hill are supplied from the Torrumbarry weir and lock, by means of which the summer level of the Murray river can be raised 16 feet, which is sufficient to permit diversion by gravitation. The districts of Nyah, Red Cliffs, Mildura, and Merbein are supplied by pumping from the Murray river.

The gravitational scheme from the Torrumbarry weir serves 202,500 acres in the Leitchville, Cohuna, Gonnawarra, Koondrook, and Swan Hill districts, and, when supplemented by the Kow Swamp reservoir, about 114,000 acres farther south in the Kerang and Mystic Park districts. The major portion of the land watered wholly by gravitation (excepting Woorinen) is used for fodder-crops and pastures, whilst the settlements supplied by pumping are used almost entirely for fruit-growing.

The main fruit-growing areas comprise Tresco (1,100 acres), Nyah (3,800), Red Cliffs (11,000), Mildura (11,000), and Merbein (8,400). All of these are under the control of the State Rivers and Water Supply Commission, excepting Mildura, which is controlled by the First Mildura Irrigation Trust. The River Murray settlements served by pumping are compact, consisting of small-holdings, usually 15 to 20 acres, which adjoin. The chief products are grapes and citrus fruits, with grapes for drying purposes greatly predominating. The more recent of these settlements (Red Cliffs) is described in detail later.

Loddon-river systems.—This is a gravitational system, used for fodder-crops, the head-waters comprising a regulating weir on the Loddon at Laanecorie, with a capacity of 6,650 ac.-ft. This serves an area of 79,200 acres for domestic and stock purposes and partial irrigation varying in extent from year to year.

Werribee system.—There are two reservoirs, Pyke's Creek (21,000 ac.-ft.) and Melton (17,000 ac.-ft.) in this system. These serve respectively 3,495 and 8,141 acres of land for annual crops and pastures relatively close (25 miles) to the city of Melbourne.

Macallister-river (Maffra) system.—The head-works of this system comprise a storage-reservoir of the Macallister river at Glenmaggie in south-eastern Victoria. The ultimate storage-capacity is designed at 150,000 ac.-ft., commanding by gravitation some 80,000 acres of rich flats on the Macallister, Ovens, and Thomson rivers. The area first supplied was 8,000 acres, and was constituted the Maffra Irrigation District in 1927. More recently, extensions have been made in the Sale district, and the total irrigable area of the Maffra-Sale district is now about 41,900 acres, of which some 20,000 acres are being irrigated. The chief products of the district are sugar (from beet), butter, and condensed milk, for which factories have been established.

The Irrigation-Settlement of Red Cliffs

(i) *General.*—The settlement at Red Cliffs is hereunder described in special detail, as an example of the intensification of industry and population achieved by the application of irrigation-water to lands of low rainfall. Prior to irrigation, the land of the settlement depended on an average rainfall of 10 in. Such land is marginal in respect to wheat-growing; in an unimproved condition it has a carrying capacity of approximately one sheep to ten acres.

(ii) *Irrigation-system and settlement.*—The Red Cliffs irrigation-settlement is situated on the Murray river in north-western Victoria. The settlement comprises a total area of 18,000 acres, of which approximately 11,500 acres are now served with irrigation-water. The land was acquired by the State for the settlement of ex-soldiers, and the scheme of works for the district ranks first in importance among Victoria's pumping-systems. The works include a pumping-plant capable of delivering 500 ac.-ft. of water per day. The water is lifted 105 ft. along a reinforced-concrete rising main, 6½ ft. in diameter and 34 chains long. Thereafter, the water is distributed by gravitation, except at two points where it is necessary to re-lift by relatively small motor-driven pumps. A system of main and distributing channels commands each of some 670 holdings. The length of channelling is now 133 miles, of which all portions adjoining irrigated holdings (114 miles) have been lined with concrete to decrease wastage of water and to preserve soil fertility.

The individual holdings average approximately 17 acres, and are occupied by some 670 settlers under the provisions of the Closer Settlement Act of Victoria. Approximately 500 of the present settlers are repatriated ex-soldiers of the Great War.

The Red Cliffs township is placed centrally and includes the offices of the government departments concerned, fruit-packing houses, and the usual private residential and business premises. The settlement is compact, the holdings being within a three-mile radius of the township, thus giving electric lighting and power facilities to settlers, as well as daily deliveries of household necessities. Approximately 2,750 persons reside permanently in the district, with the addition of about 1,500 migrating workmen who visit the district for a period of about six weeks at harvest.

(iii) *Produce.*—The major plantings in 1934 were, in acres: Vineyards (vines and citrus), 11,133; Lucerne, &c., 400; and Miscellaneous, 112: total, 11,645.

The principal product of the district is dried fruit, the production of which for the past five seasons has varied from 13,000 to 17,000 tons. The sale of dried fruits constitutes the principal source of income for the settlement, supplemented by fresh fruits (grapes and citrus), and annual crops (peas). Poultry, cattle, and pigs are secondary, being limited practically to domestic requirements.

The value of the dried fruits may be computed fairly accurately, since all the fruit goes into a common pool. The annual income of the settlement naturally varies with production and sales. As the dried fruit is pooled, it has been found possible to compute total returns from the various markets with reasonable accuracy. These may be stated as follows:

Value of Sales of Dried Fruit

	United Kingdom	*Canada New Zealand The East*	*Australia*	*Total*
	£	£	£	£
1931 . . .	364,000	67,000	160,000	591,000
1932 . . .	183,000	214,000	227,000	624,000
1933 . . .	411,000	73,000	119,000	603,000
1934 . . .	248,000	143,000	165,000	556,000

Average annual realization for dried fruits: £593,500.

It is estimated that the settlement-income from dried fruits is supplemented by approximately 7 per cent. of its total from other sources.

(iv) *General finance*.—The settlement was undertaken by the Victorian Government. The main works, channelling, clearing, &c., were constructed immediately after the War, at a time when costs were further raised by the necessity for employing ex-soldiers, who were naturally excluded from experience in such work during the War period. These abnormal conditions have resulted in a capital debt of £780,379 on June 30, 1934, for the Red Cliffs settlement of 11,000 acres, in contrast with a capital debt of £227,972 on the same date for the Merbein settlement of 8,400 acres. A general charge of £3 10*s*. per acre per annum is made for irrigation-water over the whole of the settlement. A portion of the rates collected (approximately 54 per cent. of the total revenue derived from this source) is absorbed in annual costs, the remainder contributing towards the annual interest on expended capital. The irrigation-rate is not sufficiently high to cover the whole interest on the capital expended in addition to annual expenditure.

At June 30, 1934, £481,799 of the total capital indebtedness was allocated to the settlement, the remaining portion being placed in a suspense account, and the interest met from general State revenue. The economic relations of the irrigation-settlement of Red Cliffs to the State of Victoria cannot be accurately computed, as other sources of State revenue, including railway freight and income-tax, are favourably affected.

(v) *Individual finance*.—The majority of the individual settlers had little or no funds when the land was taken up, and were financed mainly by the Victorian Government. Within five or six years, the value of the individual holdings rose very rapidly, up to, say, an average capital value of £2,500 for holdings of 17 acres. The increased value was due to the erection of buildings, plant, and the development of horticultural plants, and represented reproductive expenditure with little unearned increment. Government collections have been satisfactory in that the individual indebtedness to the Government is being steadily decreased, with a consequent increase in the settler's equity. In general, the Government collections from all sources have been calculated to permit a satisfactory income for the settler, plus a satisfactory increase in his equity in the holding.

(vi) *Production methods.*—The experiences of the adjoining older settlements of Mildura and Merbein, in respect of horticultural and irrigation practice, and especially the organized sale of the principal produce, dried fruit, were of immense value to the settlement of Red Cliffs. In particular, it was found possible to minimize soil wastage and the consequent reduction in capital value hitherto associated with the introduction of irrigation-water to soils of these types. From the inception of the settlement, the lay-out and the method of irrigation were designed to prevent harmful accumulations of the free subsoil water associated with soil wastage. The precautions, with the addition of agricultural drainage where free water has accumulated, are proving successful. At the present time, after fourteen years of occupation, every one of the original holdings is occupied and supporting a family.

The advance of experience in irrigation is such that continued productivity may be anticipated, with improvement in irrigation-distribution, and the installation of community drainage-schemes now in course of construction. The preservation of soil productivity, and the improvement in soils that show signs of wastage, constitute the chief research problems of the district. Horticultural practices, including the processing of the fruit, appear satisfactory in comparison with the methods used in other countries.

The cultivated area under irrigation in Victoria.—The total extent of irrigation and variations for the years 1929–34 are shown in the following table. A detailed statement of all the irrigated areas and of the crops cultivated thereon may be found in the Annual Report of the State Rivers and Water-Supply Commission of Victoria for 1933–4.

	Area under Irrigation (acres)				
Source of Supply	*1929–30*	*1930–1*	*1931–2*	*1932–3*	*1933–4*
Goulburn State Works .	322,039	242,435	212,284	243,378	217,105
River Murray State Works .	173,642	156,169	136,254	158,223	151,714
Loddon and other Northern State Works . . .	12,486	12,067	11,120	11,621	14,496
Southern State Works. .	25,831	22,662	28,094	31,042	23,687
Mildura and Private Diversions	32,579	29,765	30,663	30,452	28,322
Totals . .	566,577	463,098	418,415	474,716	435,324

IRRIGATION IN THE STATES OF AUSTRALIA (*Other than Victoria*)

For comparison with the irrigated areas in the State of Victoria, the extent of irrigation in New South Wales and South Australia, and the crops grown there, are briefly discussed. Irrigation in Western Australia and Queensland are relatively unimportant. Queensland irrigates about 22,000 acres for market-garden and other crops, and 4,000 acres of orchards and vineyards. Western Australia has about 2,500 acres of irrigated fodder and market-gardens with approximately a similar acreage for fruit-production.

New South Wales.—The Murrumbidgee irrigation areas are first in importance. The water is supplied by gravitation from the Burrinjuck reservoir, which is situated in the upper reaches of the Murrumbidgee river. The capacity of the storage is 771,640 ac.-ft. at full-supply level, and in 1934–5 irrigation water from this reservoir served 87,374 acres of land in the Murrumbidgee area for the following crops:

Crops	*Acres*	*Tree-fruits*	*Acres*
Oats	8,996	Citrus	5,640
Wheat	16,077	Vines	5,477
Maize	99	Deciduous, &c.	6,213
Barley	233		
Lucerne	3,356	*Miscellaneous*	
Millet and grasses	7,283	Vegetables	1,668
Rice	20,411	Tobacco	16
Pastures	2,674	Other sundries	63
		Fallow, &c.	9,168
Total	59,129	Total	28,245

In addition to the Murrumbidgee irrigation area, there are three irrigation areas controlled by the State. Two of these, Curlwaa (2,208 acres) and Coomealla (2,106 acres), are fruit-growing settlements near Mildura on the north side of the River Murray, from which the irrigation-water is obtained by pumping. The Hay settlement (1,040 irrigable acres) is on the Murrumbidgee river, and the water is used principally for fodder-crops. There are also several irrigation districts controlled by private irrigation-trusts. Two of these, Goodnight (1,364 acres) and Koraleigh (1,785 acres), are fruit-growing settlements on the Murray river near Nyah; there is one fruit-growing settlement, Pomona (1,224 acres), near Wentworth, on the Darling river, and a number of relatively small areas, chiefly on the Murray, which supply irrigation-water for fodder-crops.

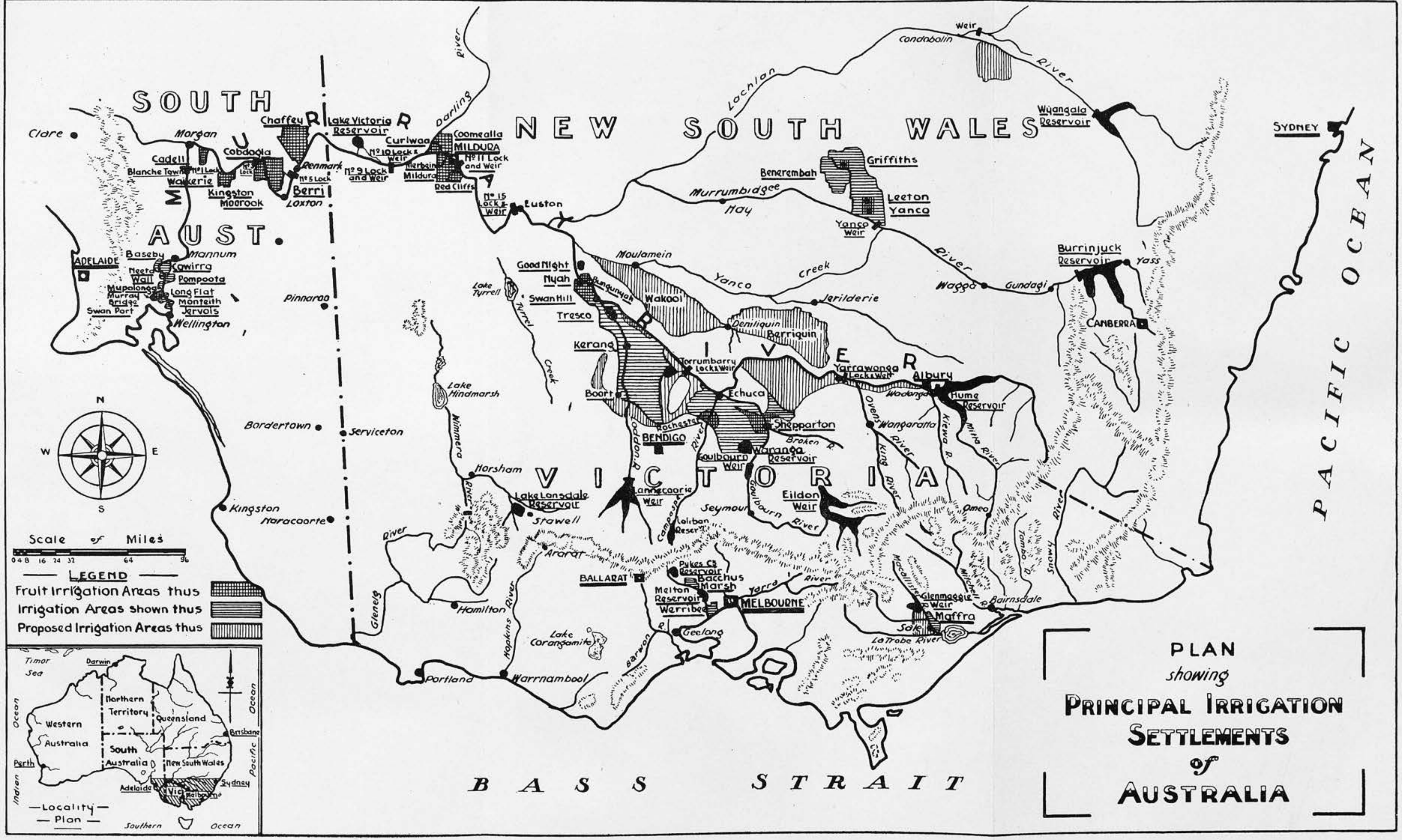
Great extensions in irrigation in New South Wales are projected. During the year 1935 the work of constructing a supply-channel to the Berriquin district was started. This supply-channel (the Mulwala canal) leads from the site of a projected weir at Yarrawonga, on the Murray, to the Berrigan district, the main channel being 96 miles in length and 125 ft. wide at the bottom. Channels of total length of 500 miles are also projected. These works are designed to supply water for domestic and stock purposes, a limited amount for irrigating some of the large holdings covering a total area of 618,000 acres, with an ultimate extension to an additional area elsewhere.

A somewhat similar scheme is planned for the Wakool district, supplying an area of 540,000 acres. As the supply of water at Albury, as regulated by the Hume storage, will be shared equally by New South Wales and Victoria, subject to reserved supplies for South Australia, very considerable extensions of irrigation in the Berrigan and Wakool districts may be anticipated.

South Australia.—The South Australian irrigation-settlements are of two types: fruit-growing settlements, which obtain irrigation-water by pumping direct from the Murray river, and low-lying flood-plains near the mouth of the Murray, protected by levee-banks, and used

FIG. 1. Eildon Reservoir. General view of bank during remedial work 1929–30. From lower slopes of Mt. Pinniger

FIG. 2. Goulbourn Weir, Victoria



PLAN
showing
PRINCIPAL IRRIGATION SETTLEMENTS
of
AUSTRALIA

for fodder-crops. There is a group of six irrigation-settlements producing fruit within a distance of about 35 miles on the Murray river. These comprise Renmark (9,000 acres), Berri (7,416), Cobdogla (4,104), Moorook (614), Kingston (502), and Lyrup (500 approx.).

The Renmark settlements are controlled by local trusts, whilst the remaining four settlements in this group are administered by the South Australian Department of Lands. There are three other fruit-producing settlements of similar type on the Murray river in South Australia, Waikerie (3,282), Cadell (1,000), and Mypolonga (855). Approximately 73 per cent. of these irrigated lands are planted with vines, 21 per cent. with orchards, principally citrus, and 6 per cent. with fodder-crops.

The irrigated lands on the lower Murray are distinct from other irrigated lands in Australia. They are situated near the mouth of the Murray, for a distance of about 50 miles from Wellington, at the mouth, to Mannum. The irrigated areas comprise swamps reclaimed from the Murray by levee-banks close to the main stream, pumps, and a drainage-system to reduce the level of the water-table to a depth of about 30 in. Irrigation-water is obtained direct from the Murray by sluice-gates in the levee-bank, or by a syphon initially operated by a small pump and engine.

Dairying is the main industry, the major plantings being lucerne and other fodders. Approximately 13,000 acres have been reclaimed by the drainage-system, in areas ranging from 60 to 3,800 acres, and are in various stages of development. At the time of writing, 7,167 acres of these swamp-lands are planted, 2,238 acres of which are under lucerne and 4,929 acres under fodder-crops, with a growing tendency to develop permanent pastures. The planted areas carry 6,500 head of cattle, of which approximately two-thirds are milking-cows.

Conclusion.—Brief reference only has been made to production methods and soil type. Systematic soil surveys are relatively recent in Australia, and the present position of this work is given in publications of the Australian Council for Scientific and Industrial Research.

Although development of additional irrigation-areas is still in progress, there has been in recent years a growing tendency to improve irrigation-methods, particularly with a view to avoid soil wastage, so manifest in the early settlements. There is evidence that, in districts where irrigation methods are being modified as a result of research, there has been considerable success in maintaining and improving the fertility of the irrigated land.

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FISH-POISON PLANTS AS INSECTICIDES

A REVIEW OF RECENT WORK

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Introduction

IN recent years widespread attention has been given to the control of insect pests by chemical means. The literature on the subject has already grown to very large dimensions and covers fields of great extent and variety. Mineral products, such as the arsenicals and fluorine derivatives, synthetic organic derivatives, products of the oil and coal-tar industries as well as many plants, have been used as insect poisons and deterrents, and in addition much attention has been given to the preparation of adjuvants and to the physical and mechanical factors leading to more effective application of insecticides.

The search for plants having insecticidal properties, and the production of the more potent of these on a large scale, have not been the least important phases of the work. The main object has been to discover and, if possible, cultivate plants which, whilst containing poisons highly potent to insects, are relatively harmless to man. Although this ideal objective has not been completely realized, a large measure of success has been attained. Most of these plant products belong to the group of insecticides known as contact insecticides, which on being brought into external contact with the organism either penetrate the chitin or find access to some vulnerable part via the tracheal system, although there is evidence to show that some of them, e.g. nicotine and rotenone, may act as stomach poisons, and kill by ingestion. Recent research has been chiefly devoted to three classes of these plants:

1. Certain leguminous plants used by natives of tropical countries for stupefying fish.
2. Pyrethrum.
3. Plants containing alkaloids of the nicotine class, e.g. anabasine.

This article deals with the first-named class.

Fish-Poison Plants[1]

Whereas many natural orders of plants are used as fish poisons, only those of the order *Leguminosae* have so far proved of importance as insecticides, although *Cocculus indicus* (Menispermaciae) containing a neutral active principle 'picrotoxin' has some reputation as a parasiticide, and it has been reported that the bark *Barringtonia racemosa* has insecticidal properties. By far the most important groups from this point of view are the leguminous plants which contain active principles closely

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[1] A valuable account of these plants with an excellent bibliography is given by F. N. Howes (*Kew Bull.* (1930), No. 4, p. 129). Roark has published a very full digest of the literature of *Derris* (*Deguelia*) species used as insecticides 1747–1931 (U.S. Dept. Agric. Misc. Pub., No. 120, 1932).

related in structure to each other, of which rotenone is the most important. Many of these plants are exceedingly potent insecticides. They occur mainly within a tropical and semi-tropical belt and are widely distributed. The chief among them are species of *Derris* (*Deguelia*), *Lonchocarpus*, and *Tephrosia* (*Cracca*). Each of these genera contains species having little or no insecticidal properties, and there appears to be a wide range of activity for each of the species and varieties known to be toxic. It seems highly probable that only the more potent plants will find a ready market in Europe and America, although this conclusion may require qualification in cases where the material is to be used for dusting, and when the price of the poor-quality material more than counterbalances the cost of inert diluents used with high-quality material.

Nomenclature.—It appears to the writer that the use of local native names for these plants in the past has proved a darkening of counsel, and the recent work of M. R. Henderson [1], in which he attempts to distinguish the different kinds of derris in the field by leaf characters and habit of growth, is timely. It is hoped that it will be expanded for *Derris* and other genera in order to enable us to ascertain whether the chemical characteristics and insecticidal potencies are associated with particular varieties, and whether and to what extent they are dependent upon environmental conditions of soil and climate. Before this can be adequately carried out some means of chemically evaluating these roots, more reliable than those we now have, would appear to be necessary.

Active principles.—Several crystalline products of different degrees of insecticidal activity have been isolated from these plants and their structure ascertained by the labours of teams of workers in different parts of the world. They are rotenone, deguelin, toxicarol, the tephrosins, and a new compound isolated by Cahn and Boam [2]. Of these rotenone is so much the most active that for some time it was thought that its determination would be sufficient to ascertain the relative potencies of these plants and, as it was more easy to isolate it than the other constituents, a ready and rapid method of evaluation seemed to be in sight. This hope, however, has receded during the last two years. It is now pretty clear that deguelin, toxicarol, and tephrosin do not exist in derris and cubé root in the form in which they are isolated. Takei and his co-workers [3] have by a simple oxidation process converted deguelin into tephrosin and *iso*tephrosin. The isolation of deguelin and toxicarol from *Derris* and *Lonchocarpus* spp. as well as from *T. toxicaria* has usually been accomplished by the use of alkali. Clark [4], who first isolated deguelin and determined its structure, considered that it was in some form of combination, but an alternative view is that at least part of the deguelin is present in an optically active form, and that since the deguelin so far isolated in a pure state has shown no optical rotation, racemization caused by the process of extraction has lowered its insecticidal power. F. B. LaForge and H. L. Haller, who in association with L. E. Smith first published the chemical structure of rotenone [5], universally accepted to-day, have prepared [6] what they term a 'deguelin concentrate' from which dihydro-deguelin was isolated after hydrogenation. Campbell and Fink found this active compound more toxic than inactive dihydro-deguelin when used against mosquito larvae. It is thus at least probable that the relatively feeble toxicities found for deguelin (and possibly toxicarol), as isolated, are not a measure of the toxic properties of their precursors in the root.

There is a great deal of converging evidence demonstrating that rotenone is not wholly responsible for the toxicity of derris and cubé. It has been shown by Jones *et al.* that a derris extract from which only 25 per cent. of rotenone could be isolated was as toxic to mosquito larvae as pure rotenone. Campbell and his collaborators [7] found deguelin to be nearly as effective against house-flies as rotenone, and that a kerosene extract of a sample of derris from which no rotenone could be isolated was also effective against this insect. Fryer *et al.* [8] found the resins, freed as far as possible from rotenone, toxic to insects. Many other observations of the same nature have been made. There is, however, the possibility that the amount of rotenone separated by present methods from the resins does not represent the whole amount in the root. Cahn and Boam [9] have shown that the so-called Sumatra-type roots, from which no rotenone is obtainable by the Jones method[1] [10] may yet contain up to 2·4 per cent. of rotenone in a 'hidden' condition, and that the standard method of determination may be seriously in error if the extracted resins contain less than 10 per cent. of rotenone. The work of Takei and his co-workers [3] also indicates that crystallization from an ether solution of the resins does not yield the whole of the rotenone present. It is therefore possible that some part of the insecticidal activities of the uncrystallizable resin may be due to rotenone in this 'hidden' state, but the evidence at present available shows that one or more highly toxic substances, one of which may be optically active deguelin, play an important part. Cahn and Boam's conclusion [2] 'that the value of derris root or resin can only be assessed by its rotenone-content is quite unjustified' is borne out by all the recent work.

Chemical evaluation.—In two recent papers by Jones, Campbell, and Sullivan [11] and Tattersfield and Martin [12] the problem of the chemical evaluation of these plants is examined in some detail, and although neither paper proposes what can be regarded as a final solution of this difficult problem, suggestions are made which may be of value towards that end. The chief value of these papers is perhaps to be found in the presentation of two different criteria by means of which the validity of a chemical method can be determined. There is substantial agreement between them that the percentage amount of rotenone, as at present determined, the total extractives in benzene or ether, and the methoxyl-content of the total benzene or ether extract cannot be correlated with the activity of all the samples examined by these workers. The American investigators found that for a number of their samples, but with marked exceptions, the estimation of rotenone and deguelin by the Gross and Smith test [13] showed a fair agreement with toxicity, and Tattersfield and Martin found that an estimation of the dehydro compounds (mainly

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[1] This method of estimating rotenone has been modified by C. D. V. Georgi and G. L. Teik (Bull. Dept. Agric. Straits Settlements and F.M.S. Sci. Series, 1933, No. 12), and by Cahn and Boam (loc. cit.).

rotenone and deguelin) by Takei's method gave a relatively good comparative assessment of the insecticidal power of a more limited number of samples of derris root. Jones, Campbell, and Sullivan found a sample of a type, termed by Cahn the Sumatra-type derris root, exceptional, and recent (unpublished) work by the writer and Dr. Martin has indicated that the determination of the dehydro compounds by Takei's method in the case of a similar sample gave an erroneous estimate of its toxicity. Jones, Campbell, and Sullivan found that the estimation of a value termed 'rotenone based on the methoxyl-content minus toxicarol' gave, with one or two exceptions, a fairly close correlation with the potency of the root. It has, however, not been found by the author that the alkali-extractable material of derris resin has in all cases a methoxyl-content of the same order as toxicarol, and the part played by this compound in the insecticidal properties of derris and cubé roots is at present obscure. The necessity for studying roots of different types and the resins obtained from them in greater detail is clear. It would, moreover, seem to be important that the biological data should be subject to statistical analysis; the recent work of C. I. Bliss [14] on the comparison of dosage-mortality data may prove a useful instrument for testing the validity of any chemical method of evaluating these plants.

Effect of genetical and environmental factors.—To ask what part these compounds play in the economy of the plant, or by what metabolic process they arise, is not likely to elicit any answer of value for a considerable time. But the query, whether the relative amounts of the active principles, particularly the proportion of rotenone to uncrystallizable resin, are determined by genetical factors, or can be altered by environmental conditions of soil, manuring, and climate, are important. Georgi and Teik [15] and several observers have noted a higher proportion of rotenone to ether extractives in the case of *D. elliptica* than of *D. malaccensis*, but certain analyses of the latter variety, grown on the Belgian Congo [16], showed a high proportion of rotenone to ether extract. The question therefore arises whether a rough demarcation of these species can be made by chemical means. The number of varieties and sub-varieties of both *D. elliptica* and *D. malaccensis*, as given by Henderson [1], render the problem a difficult one. It is not made any easier by the fact that a sample of wild roots, vouched for as *D. elliptica*, was found at Rothamsted to have no rotenone, a low ether-extract, and no toxicity to insects. The question whether any of these varieties are capable of showing under one set of cultural conditions results given by the Sumatra type, and under another a high rotenone-content, is one of no little importance. That these plants are leguminous should not be lost sight of, and specific root-nodule-forming bacteria may play some part in their economy. Weber [17] found that lupin plants bearing nodules had a higher alkaloid-content than those without them, and although the elaboration of a non-nitrogenous compound of the type of rotenone may not be comparable with that of the nitrogenous alkaloids, the matter may be worth inquiry, as may also be the critical study of the effect of manures and the effect of the presence or absence of traces of such elements as boron, which is known to have an important effect upon the growth of many plants of this order.

Koolhaas [18] reports that 32 samples of derris from the Dutch East Indies ranged in rotenone-content from 0·3 to 10·9 per cent., and the selection of roots of high rotenone-content for planting in the Dutch East Indies is being made. There are also reports of the planting of derris in the Philippines, where a number of species and varieties are found ranging in rotenone-content from 0·02 to 1·68 per cent. The experimental cultivations of certain varieties of *D. elliptica* and *D. malaccensis* on the Belgian Congo [16] and of *D. elliptica* on the Gold Coast have been successful. Samples of the latter submitted to the Rothamsted Experimental Station contained 2·5 and 2·8 per cent. of rotenone. It is obvious that the cultivation of *Derris* can be undertaken over a large area. Whatever method for evaluating these plants is finally elaborated, there would appear to be no doubt of the sales value of a high content of rotenone, particularly if it is to be coupled with high ether-extract.

Cubé, Haiari, and Timbó.—Much work seems to have been done in Peru in the cultivation of cubé or barbasco (*Lonchocarpus nicou*), and Brazil is becoming increasingly interested in timbó, a species of *Lonchocarpus*. Roark [19], in discussing the relative merits of derris and cubé, considers it as well established that, for a given rotenone-content, derris contains, in general, larger quantities of ether extractives than does cubé, and since these extractives are toxic, in general, derris will be more toxic. Jones, Campbell, and Sullivan [11] obtained rather variable results for some samples of equivalent rotenone and total-extract contents. For one pair of samples toxicity was about equal, whilst for another cubé proved slightly less toxic than derris. They consider that no general conclusions can be drawn from their data. Some samples of cubé and timbó have been found with very high rotenone-content, occasional specimens of the former containing as much as 12 per cent. rotenone and of the latter one as high as 15–16 per cent. have been reported, but these are exceptional. Commercial samples of cubé examined at Rothamsted have usually ranged from 5–6 per cent. and good samples of *Derris elliptica* have touched 8–9 per cent. There is, however, little or no question that these South American plants are being produced in continually increasing amounts and that in course of time competition with derris is likely to be severe.

It has been recently established that the White Haiari of British Guiana is *Lonchocarpus nicou* (Aubl.) D.C. and conspecific with cubé of Peru; thus there are obviously several strains of this plant which differ somewhat widely in rotenone-content. Haiari plants taken from forests of British Guiana, and from their appearance of many years' growth, analysed at Rothamsted, showed appreciable amounts of rotenone. Black Haiari roots contained over 3 per cent. and the stems about 0·8 per cent. White Haiari roots gave 1·8 and the stems 0·6 per cent. of crude rotenone by the carbon tetrachloride method. Cultivated specimens, six years old, of Black Haiari gave 1·4 per cent. and of White Haiari 0·9 per cent. rotenone, the stems in both cases containing only traces. A further search for other and richer strains of *Lonchocarpus* in that colony would appear to be worth while. There is always the possibility, as Killip and Smith [20] point out, that in Peru the cubé plant, cultivated for centuries as a fish-poison, may represent a selected strain in which the content of toxic principles of the roots is at a maximum.

Tephrosia species.—Of the species of *Tephrosia* (*Cracca*) the most important are *T. macropoda*, *T. toxicaria*, *T. virginiana*, and *T. vogelii*. The first-named, a plant deriving from Natal, has been reported by Tattersfield and Gimingham [21] as possessing insecticidal properties, and recent (unpublished) work at Rothamsted has shown it to contain rotenone (0·3–0·4 per cent.), and other derivatives of an insecticidal nature are undoubtedly present. *T. toxicaria* appears to be widely distributed over the more tropical parts of South America. A sample of the roots tested at Rothamsted proved to have insecticidal properties [22]. The yellow crystalline compound isolated from it was named toxicarol by Clark [23]. Its toxicity to insects is not due to this compound as isolated. *T. virginiana* and *T. latidens* are of interest as being North American plants, showing both the properties of poisoning fish and insects. The insecticidal properties of the roots of *T. virginiana* were pointed out by Little [24]. Jones, Campbell, and Sullivan [25] have published a valuable report of the chemical composition and insecticidal value of the species of *Tephrosia* (*Cracca*) occurring in the United States. In the two species mentioned they have found rotenone present to the extent of 0·2 to 0·5 per cent. It is interesting that the most effective samples of *T. virginiana* came from Texas; samples from other sources were not so effective. *T. vogelii* is of considerable interest, as its leaves and seeds contain the active principles. Only one other fish-poison plant, said to be a species of *Derris* from the British Solomon Islands, and sent to Rothamsted by Mr. H. T. Pagden, has in the experience of the author possessed leaves with insecticidal properties.[1] It is obvious that such leaves and seeds could be more readily harvested than roots. In potency, however, the *Tephrosia* species are hardly in the same class as the richer roots of *Derris* and *Lonchocarpus* spp., but that they might be improved by selection and hybridization should not be lost sight of. Worsley [26] has confirmed and extended the earlier observations of Tattersfield, Gimingham, and Morris [22] on the insecticidal properties of *T. vogelii*. He finds that as a contact insecticide against aphis, thrips, and similar soft-bodied insects, extracts of *T. vogelii* are effective, and considers that it might displace nicotine for use against these insects in East Africa. He has noted its effectiveness in the form of paraffin extracts against flies and mosquitoes, if directly hit by the spray. Wilbaux [27] has found that, in addition to their insecticidal properties, extracts of *T. vogelii* are bactericidal. The plant is widely spread on the African continent and, like the other species of this genus and such other legumes as *Neorautanenia fisifolia* and *Mundulea suberosa*, may find a local use.

Chemical structure.—Of the crystalline derivatives isolated from fish-poison plants, structural formulae have been ascribed to rotenone and deguelin and tephrosin. A summary of much of the work upon the chemical structure of rotenone is given by LaForge, Haller, and Smith

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[1] Jones *et al.* (loc. cit.) found the seeds of *T.* (*Cracca*) *lindheimeri* effective.

[5] and by Takei [28]. The structures given by Clark to deguelin and tephrosin are now generally accepted [29]. In the case of tephrosin there appears to exist a complicated isomerism [30]. The structure of toxicarol has been the most difficult of these compounds to unravel, but recently Heyes and Robertson [31] have suggested two alternative formulae to account for its reactions. In view of the fact that rotenone contains three asymmetric carbon atoms, and that its insecticidal potency probably depends in some obscure way upon its particular molecular orientation, it appears at present unlikely that it will be synthesized so as to be able to compete in price with the natural product.

Toxicity to insects.—A body of knowledge is gradually being built up of the insecticidal usefulness of these plants, particularly of cubé and derris. Kelsall and his collaborators [32] have given a series of interesting notes on the toxicity of derris to various species of insects. Roark [19] gives also a list of insect pests in America, controlled by it, and mentions that during 1933, 300,000 lb. of ready-prepared derris dusts were sold on Long Island as substitutes for arsenicals. Much work has been done on the control by derris of caterpillar pests on *Cruciferae*. Campbell [33] has also reported tests on fifty-five species of insects. De Bussy, van der Laan, and Jacobi [34] have published results of the control value of derris powder and rotenone on Netherlands insects. For the control of Warble-fly the observations of Wells, Bishopp, and Laake [35], of McDougall [36], and of Gaut and Walton [37] have been confirmed by later experimenters, as have those of Steer [38] on the control of *Byturus tomentosus* on Raspberry and Loganberry. Bishopp and his co-workers [39] have given accounts of the control of various animal-infesting pests, and Crane [40] has tested the utility of rotenone against a number of internal parasites of dogs. Buckingham [41] claims rotenone to be non-toxic to warm-blooded animals administered *per os* and Crane (loc. cit.) found it non-toxic to dogs up to 0·2 gm. per 1 kg. body-weight. Such internal usages should be carried out with care, as this compound has been known to give rise to intestinal irritation and death in mice in some experiments carried out at Rothamsted. Several patents have been taken out for its use as sheep-dip and vermifuge.

Physiological action.—The active principles of these plants are usually slow in their paralysing and lethal effect upon insects, in marked contradistinction to the pyrethrins, but it has been noted that rarely does an insect recover from the narcotic effects if they are at all deep. Often the effects of the pyrethrins are fugitive. and it would appear as if these two insecticides might supplement each other's action. It is interesting to note that patents covering such mixtures have been taken out in the United States of America.

The physiological action that derris and its active principles have upon insects is as yet not exactly known, but Miller [42] considers that its supposed action as a stomach poison needs re-investigation. Miller's paper contains an interesting report by Dr. Buckley of an analysis of the excreta of the cockroach *Periplaneta americana* L. after being fed upon, but apparently not seriously affected by, a diet containing rotenone. The conclusion was drawn that these cockroaches, though excreting a certain amount of rotenone unchanged, were able to build up a derivative insoluble in carbon tetrachloride, but capable of yielding rotenone again on treatment with sulphuric acid. The total rotenone consumed was far more than that recovered from the excreta, thus indicating some nutritive function.

Loss of activity.—Like pyrethrum, derris and cubé lose their activity under certain conditions. Spoon [43] concludes that they will keep for reasonable periods if properly stored, but there is little doubt that sprays made with soap solutions do deteriorate after a time. However, Miller (loc. cit.) regards the loss of activity to be less rapid than it is generally considered to be. Durham observed a change in rotenone on exposure to light. Tattersfield and Roach [44] noted the formation of yellow-coloured derivatives when rotenone solutions were exposed to sunlight and ultra-violet light. A detailed study of the detoxication of rotenone in light has been made by Jones, Campbell, and their co-workers [45], and it was concluded that the loss was sufficiently rapid to limit its use as a stomach poison but probably not as a contact poison. So far, no really adequate means has been discovered for overcoming this drawback. The drawback, however, is only a partial one, and although it may account for the failure to control codling moth, there is a countervailing advantage that when used on market-garden crops the spray residue left, unlike the arsenicals, causes apparently no anxiety from the point of view of public health.

Some insects are immune to the effects of derris and cubé, certain boring beetles, indeed, constituting a major pest of these products in store; nevertheless, as knowledge of their range of usefulness grows, there seems to be an expanding market for them in both Europe and America for some years to come.

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THE EFFECTS OF PARTIAL FIELD-DRYING ON THE COMPOSITION OF FRESHLY CUT GRASS

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Introduction.—The costs of conserving grass by artificial drying depend very much upon the ratio of water to dry matter (technically termed the 'water ratio' of the grass) present in the grass fed to the drier. It is the more general practice to feed the grass to the drier immediately or shortly after cutting, to avoid possible losses and changes by respiration and fermentation, but it is obvious that some preliminary removal of water by partial drying in the field would considerably improve efficiency by reducing carting and drying costs and by increasing the output of the drier.

The object of this investigation was to gain information on the amount of water removed from freshly cut grass by preliminary drying in the field under natural conditions for periods up to 54 hours, and on the actual extent of the losses and changes occurring in the contents of dry matter, nitrogen, and carotene. The results presented were obtained under one particular set of climatic conditions, which proved to be favourable for field-drying. Since climatic conditions must obviously play a major part in determining the effects of field-drying in any particular instance, the results cannot be taken as being necessarily applicable to other climatic conditions without further investigation.

A preliminary investigation carried out by S. J. Watson at this Station on October 21, 1931, had shown that drying freshly cut grass in the field for six hours reduced the moisture-content from 81 to 74 per cent. in fine, calm weather (unpublished data); otherwise, no data would appear to be available concerning the preliminary drying of grass for subsequent artificial drying under British conditions. Preliminary field-drying of lucerne, before artificially drying, however, is practised successfully in Germany and in the United States of America.

Outline of Investigation.—The investigation was carried out between May 22 and 24, 1935, on pasture grass, 6 to 8 in. high, which was being cut at the time for artificial drying. The herbage consisted largely of perennial rye-grass (34 per cent.) and meadow foxtail (35 per cent.), with some of the former and much of the latter in flower. The yield was about 19 cwt. dry matter per acre, with a crude-protein content of about 16 per cent. The grass was cut between 9 and 10.30 a.m. on May 22 by a horse-drawn mower with a 40-in. cutting knife, and three different methods of field-drying were employed:

(i) in swaths as cut;
(ii) in windrows consisting of 4 swaths raked together;
(iii) in heaps consisting of 100 lb. fresh grass.

These treatments were replicated three times in random blocks.

Randomized samples of the herbage were examined initially on cutting, and at intervals of 6, 9, 24, 30, 48, and 54 hours thereafter from the swaths and windrows, and of 6, 24, 30, and 54 hours from the heaps. No material was raked over or disturbed in any way during the field-drying period. The samples were taken in the following manner:[1]

(i) From the swaths. The whole of the herbage from a measured strip of 2 ft. along the swath and extending over four adjacent swaths was collected and weighed. The percentage of dry matter in the herbage was determined by oven-drying duplicate sub-samples of 200 gm. each.

(ii) From the windrows. The whole of the herbage from a measured strip of 2 ft. along the windrow was collected, weighed, and its percentage of dry matter determined as in (i).

(iii) From the heaps. The whole heap was weighed, thoroughly mixed, and duplicate samples taken for determining the percentage of dry matter as in (i) and (ii).

Determinations were made, on individual samples, of total nitrogen, and, on weighted composite samples, of 'Stützer' (or 'true protein') and pepsin-digestible nitrogen. Determinations of carotene were made on composite samples of the fresh grass.

Climatic Conditions.—The daily meteorological readings for the period May 21 to 24 are given in Table 1. The 24 hours prior to cutting were fine, and the grass when cut held a little external moisture from a light dew. During the period of the test no rain fell, and a moderately strong and drying wind from between NE. and E. prevailed the whole time. May 22 was a cool day with considerable sunny periods, May 23 was appreciably warmer and mainly sunny, and May 24 was slightly warmer still but mainly cloudy.

In brief, the weather conditions were conducive to efficient drying, and probably also to minimum losses and changes by respiration and fermentation.

TABLE 1. *Meteorological Readings during Field-drying*

Date	*Barometer*	*Relative humidity*	*Screen Temperature*		*Sunshine hours*
			Max.	*Min.*	
	in.	Per cent.	°F.	°F.	
May 21 .	29·98	73	57	39	10·9
May 22 .	30·05	60	54	36	5·9
May 23 .	29·77	72	64	40	9·4
May 24 .	29·83	67	66	48	2·8

Effects of Preliminary Drying on the Water and Dry-matter Contents of the Grass

(*a*) *Yield of dry matter.*—Although preliminary drying will normally result mainly in loss of water from the grass, some loss of dry matter may also occur under certain conditions, and this, if appreciable, might

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[1] (*a*) Adequate precautions were taken to prevent side and edge effects in the swath and windrow methods of drying.

(*b*) Growth-area corresponding to samples taken from both swaths and windrows was accordingly 2 ft. × 3 ft. 4 in. multiplied by 4, or 26·7 sq. ft.

offset, to some extent at least, the advantages obtained in loss of water. In this test, however, as will be seen from the figures for average yield of dry matter given in Table 2, no significant loss of dry matter occurred in any of the methods of drying,[1] so that the losses observed may be taken to be wholly water losses. Though no heating was observed in any of the treatments at any time during the test, it is considered very probable that heating, with a loss of dry matter, might be expected to occur in the windrows and heaps at least, under the warmer weather conditions such as are not infrequently experienced during the grass-drying season.

TABLE 2. *Average Yields of Dry Matter (lb. per sample area)*

Method of Drying	*Period of Drying (hours)*							*Standard Error*	*Significant Difference**
	0	*6*	*9*	*24*	*30*	*48*	*54*		
Swaths . .	1·29	1·33	1·29	1·47	1·06	1·06	1·17	0·142	0·44
Windrows .	1·32	1·21	1·29	1·27	1·31	1·21	1·12	0·073	0·22
Heaps . .	22·8	23·1	..	25·3	22·7	..	21·5	0·568	1·9

* P=0·05

(*b*) *Percentage of dry matter in grass.*—The average values for the percentage of dry matter in the grass at the various stages of drying are given in Table 3. Drying effected a significant increase in the percentage of dry matter in the grass up to the 30-hours period for the swaths, 48 hours for the windrows, and 24 hours for the heaps, but beyond these periods no, or little, further loss of water occurred. The rate and degree of drying was greatest in the swaths and least in the heaps, which under the weather conditions obtaining was to be expected.

TABLE 3. *Average Percentage of Dry Matter in Grass*

Method of Drying	*Period of Drying (hours)*							*Standard Error*	*Significant Difference*
	*0**	*6*	*9*	*24*	*30*	*48*	*54*		
Swaths . .	26·3	30·7	31·0	35·7	46·1	51·6	50·8	1·929	5·9
Windrows .	24·4	26·9	28·1	31·4	34·2	42·5	42·3	1·496	4·6
Heaps . .	22·8	25·2	..	29·6	28·6	..	31·9	0·731	2·4

* The initial differences among the swaths, windrows, and heaps were due to a small but differential amount of drying which occurred during the period necessarily required to complete the cutting of the grass, the formation of the windrows and heaps, and the allocation of the sample areas, before the initial samples could be taken.

(*c*) *Water ratio.*—Of major economic importance in the artificial drying of grass is the amount of water to be evaporated per unit of dry matter present (the water ratio). The significance and importance of this ratio may, perhaps, best be appreciated from the following illustrative figures:

Water-content per cent. . .	80	75	67	60	50
Dry-matter content per cent. .	20	25	33	40	50
Water ratio	4	3	2	1·5	1

Thus the comparatively small reduction of the *percentage* water-content from 80 to 67 per cent. doubles the output of dry matter per unit of

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[1] The increase observed for heaps at the 24-hours period would seem to be due to some coincidence and not a real effect.

water evaporated, whilst the further reduction to 50 per cent. moisture increases the output fourfold.

Accordingly, the application of the present results to the artificial drying of grass may be more fully seen from Table 4, in which the figures for percentage dry matter (Table 3) are expressed as water ratios. These figures well illustrate the economic advantages to be derived from preliminary partial drying of the grass in the field.

TABLE 4. *Average Values for Water Ratio*

Method of Drying	*Period of Drying (hours)*						
	0	*6*	*9*	*24*	*30*	*48*	*54*
Swaths .	2·80	2·26	2·23	1·80	1·17	0·95	0·97
Windrows .	3·09	2·72	2·56	2·18	1·92	1·35	1·36
Heaps .	3·39	2·97	..	2·38	2·51	..	2·13

(*d*) *Variability of drying.*—The figures so far given for the percentages of dry matter in the grass are, of course, average values for the whole of the material in the swath, windrow, or heap at the time the sample was taken. Actually, the material, except initially, had by no means a uniform dry-matter content throughout, the grass of the outer exposed layers, of course, drying more rapidly than that of the inner less exposed layers. In all treatments, throughout the whole period, and increasingly with time, wide differences were observable in the different layers, whilst even in the swaths after 54 hours and under the favourable drying conditions obtaining, there was still a considerable difference between the top and bottom layers. At the 54-hours period samples were taken from different layers in each of the treatments and their moisture-contents determined separately; the results, which are given in Table 5, well illustrate the wide variability in the amount of drying which had taken place.

It is certain that preliminary partial drying in the field, under any method, must almost always result in producing material having a considerable variation in moisture-content, a factor which may need to be taken into account in the subsequent artificial drying of the material.

TABLE 5. *Percentage of Moisture in Grass in Different Layers after 54 Hours Field-drying*

Position of Sample	*Swaths*	*Windrows*	*Heaps*
Top layer .	40·7	39·3	39·7
Middle layer .	..	..	73·6
Bottom layer .	55·9	72·0	75·4
Average sample* .	49·2	57·7	68·1

* Representative of treatment—see Table 3.

Effect of Preliminary Drying on the Nitrogenous Constituents of the Grass

(*a*) *Total nitrogen.*—The average values for the percentage total nitrogen-content of the dry matter, which are given in Table 6, show that preliminary drying had little, if any, effect in any of the treatments on the total nitrogen or crude-protein content of the grass.

TABLE 6. *Average Values for Percentage Total Nitrogen in Dry Matter*

Method of Drying	*Period of Drying (hours)*							*Standard Error*	*Significant Difference*
	0	*6*	*9*	*24*	*30*	*48*	*54*		
Swaths . .	2·60	2·53	2·73	2·65	2·69	2·62	2·66	0·050	0·16
Windrows .	2·80	2·83	2·70	2·81	2·76	2·77	2·88	0·047	0·15
Heaps . .	2·65	2·66	..	2·67	2·68	..	2·77	0·028	0·09

(*b*) *Stützer and pepsin-digestible nitrogen.*—The values for the percentages of Stützer and pepsin-digestible nitrogen in the dry matter, given in Table 7, again show little, if any, effect of preliminary drying in any of the treatments. It may be safely assumed, therefore, that preliminary partial drying in the field, besides having practically no effect on the amount of crude protein, was also without significant effect on the nature of the main individual constituents thereof.

TABLE. 7. *Values for Percentage Stützer and Pepsin-digestible Nitrogen in Dry Matter**

Method of Drying	*Period of Drying (hours)*				
	0	*6*	*24*	*30*	*54*
	Stützer Nitrogen (per cent.)				
Swaths . .	2·38	2·20	2·29	2·31	2·22
Windrows .	2·41	2·49	2·40	2·39	2·34
Heaps . .	2·32	2·37	2·31	2·30	2·28
	Pepsin-digestible Nitrogen (per cent.)				
Swaths . .	2·22	2·14	2·23	2·28	2·26
Windrows .	2·38	2·34	2·37	2·32	2·44
Heaps . .	2·23	2·22	2·25	2·28	2·35
	Ratio Stützer: Total Nitrogen				
Swaths . .	0·92	0·87	0·86	0·86	0·84
Windrows .	0·86	0·88	0·85	0·87	0·81
Heaps . .	0·88	0·89	0·87	0·86	0·82
	Ratio Pepsin-digestible: Total Nitrogen				
Swaths . .	0·85	0·85	0·84	0·85	0·85
Windrows .	0·85	0·83	0·84	0·84	0·85
Heaps . .	0·84	0·84	0·84	0·85	0·85

* Determinations made on weighted composite samples. No determinations made at 9- and 48-hours periods.

Effect of Preliminary Drying on the Carotene-content of the Grass

Composite samples of the fresh grass for each drying treatment were examined for carotene-content initially, and after intervals of 6, 24, 30, 48, and 54 hours. No general differences in carotene-content among the three treatments were discernible at any one period, partly, perhaps, owing to a certain amount of variability among the values obtained; so only the mean values for the three treatments are given in Table 8. A moderately rapid loss of carotene occurred immediately following cutting, amounting to about 14 per cent. at the 6-hours period, and was followed by a much reduced rate of loss until after 54 hours' drying the carotene-content had been reduced by about 22 per cent. of its original value. From the nutritive point of view, however, these losses were not serious, the actual amount of carotene remaining after 54 hours still being adequate for nutrition.

It is, of course, probable that the losses in carotene from the outer layers were greater, and those from the inner layers lower, than the average values given. It was noticed that the outer layers were bleached in measurable degree, whilst the inner layers had retained better their green colour.

TABLE 8. *Average Carotene-content of all Preliminary Drying Treatments*

(mgm. per cent. of dry matter)

Period of Drying (hours)

0	*6*	*24*	*30*	*48**	*54*
42·0	36·3	35·0	35·2	32·8	32·7

* Average of swaths and windrows only.

Discussion

The main conclusions drawn from the results are as follows. Under good but comparatively cool weather conditions in May, the preliminary partial drying of freshly cut grass in the field may be undertaken successfully with an appreciable reduction in the water-content of the grass, with little if any change in the dry matter and the nitrogenous constituents, and with only a moderately small reduction in the carotene-content. Of the three methods of drying employed, drying in the swaths as cut proved more satisfactory than first collecting the grass into windrows or heaps. All forms of drying, however, resulted in grass having a very variable moisture-content.

How far similar results would obtain under other climatic conditions must be at present a matter of conjecture. The effects of rainfall and of higher temperatures in particular require study, whilst the nature and condition of the grass itself may also influence the results. Dry weather at this Station during the summer of 1935 again prevented a continuation of the investigation on the lines described.

Summary

The results are presented of a replicated experiment in which freshly cut grass, at a stage of growth suitable for conservation, was first partially dried in the field under good but comparatively cool weather conditions in May, in the form of (*a*) swaths as cut, (*b*) windrows (four

swaths raked together), and (*c*) heaps of 100 lb. fresh grass, for 54 hours, samples being taken initially and at intervals of 6, 9, 24, 30, 48, and 54 hours and examined for yield of fresh grass and dry matter, for total, Stützer, and pepsin-digestible nitrogen, and for carotene-content.

In all treatments drying was practically without effect on the yield of dry matter and on the total nitrogen and its above-named constituents. The average carotene-content was reduced by about 14 per cent. after 6 hours', and by about 22 per cent. after 54 hours' drying, in all treatments.

Drying effected a significant decrease in the average values for the percentage of water in the grass up to the 30-hours period for the swaths, 48 hours for the windrows, and 24 hours for the heaps; beyond these periods no, or little, further loss of water occurred. At these periods the original moisture-content of approximately 75 per cent. had been reduced to average values of approximately 54, 58, and 70 per cent. in the swaths, windrows, and heaps respectively. A feature in all treatments was the non-uniformity of drying; as was to be expected, the grass of the outer exposed layers dried more rapidly and to a greater degree than that of the inner less exposed layers.

The economic importance of preliminary partial drying in the field and the consequent significance of the results of this investigation in the conservation of grass by artificial drying are discussed, and the necessity for studying the effects of preliminary partial drying under other climatic conditions is pointed out. The effects of rainfall, of higher temperatures, and of the nature and condition of the grass itself are suggested as the subject of future study.

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EXPERIMENTS ON THE NITROGENOUS MANURING OF SUGAR-BEET

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IN 1925 experiments were begun at the Norfolk Agricultural Station on the following problems in the manuring of sugar-beet:

1. The economic limit in the use of (*a*) nitrate of lime, (*b*) nitrate of soda, (*c*) sulphate of ammonia.
2. Comparison of sulphate of ammonia and nitrate of soda as a source of nitrogen.
3. The time of application of sulphate of ammonia.
4. The effect of heavy dressings of muriate of potash.

The majority of the experiments were carried out on the Station's farm at Sprowston, which is typical of much land in central Norfolk, the soil being a light loam overlying brick earth and not in a particularly high state of fertility. The experiments with sulphate of ammonia were also carried out on a number of farms in the county of Norfolk.

With the exception of those carried out in 1925, all the experiments were laid down in Latin squares. The size of the plots varied from 1/40th to 1/100th acre. In the experiments carried out at Sprowston, all the beets from each plot were washed before weighing, but in the county trials the beets were weighed dirty in the field and sampled for dirt-tare. Up to 1930, sugar-content was estimated on bulked samples for each treatment, ten beets being taken from each plot. After 1930, the estimations were made separately for each plot, the sample consisting of 20 roots per plot.

The experiments cover a period of nine years, the rainfall figures for which are given in Table 1.

TABLE 1. *Rainfall at Sprowston, Norfolk, 1925–33*

Year	*April, May, and June inclusive*	*July–November inclusive*	*Total April–November*
	inches	inches	inches
1925	4·58	12·32	16·90
1926	6·18	10·56	16·74
1927	7·24	18·45	25·69
1928	5·57	9·69	15·23
1929	2·94	11·88	14·82
1930	6·15	18·15	24·30
1931	9·45	11·48	20·93
1932	7·41	13·78	21·19
1933	5·11	9·30	14·41
Normal	5·33	12·47	17·80

The rainfall at Sprowston for the eight months April to November was considerably below normal in 1928, 1929, and 1933, but in 1927, 1930, 1931, and 1932 it was appreciably above normal; 1925 and 1926 were the only two years with rainfall approximating to the normal.

The Economic Limit in the Use of Various Nitrogenous Manures

(*a*) *Nitrate of Lime.*—Nitrate of lime is not now very widely used for sugar-beet owing to its relatively low nitrogen-content and to handling difficulties. Experiments with different quantities of this fertilizer were, however, carried out at Sprowston in 1925–6–7. The quantities tested were 1 cwt., 3 cwt., and 4 cwt. per acre, and a basal dressing of 12 loads per acre farm-yard manure, 3 cwt. per acre superphosphate, and 1 cwt. per acre muriate of potash, was applied to all the plots. The results for each year are given in Appendix I and the means of the three years in Table 2.

TABLE 2. *Response of Sugar-beet to Increasing Applications of Nitrate of Lime*

	Nitrate of Lime, cwt. per acre			
	0	*1*	*3*	*4*
Washed beet, tons per acre	10·6	11·2	11·5	12·1
Per cent. of mean	93	98	101	107
Sugar-content per cent.	17·4	17·3	17·0	17·1
Sugar, cwt. per acre	36·8	39·0	39·5	41·5
Per cent. of mean	94	100	101	105
Tops, tons per acre	6·0	6·3	7·3	8·2
Per cent. of mean	87	91	105	119

The first cwt. of fertilizer gave an increase in yield of 0·6 tons, though the weight of tops was only raised slightly. The second and third cwt., on the other hand, gave only a small increase in yield of beet, but the weight of tops was raised by 1 ton per acre. It is evident that the fourth cwt. gave an economic response over the third cwt., for the weight of beet and of tops was raised by 0·6 tons and 0·9 tons, respectively.

These experiments were, however, carried out on soils not deficient in lime, and it may be that nitrate of lime would prove to be more valuable still on soils that are acid or are on the border-line of acidity.

(*b*) *Nitrate of Soda.*—The trials dealing with the use of varying quantities of nitrate of soda were begun at Sprowston in 1925 and continued in the following two years. Four quantities were tested, 1 cwt., 2 cwt., 3 cwt., and 4 cwt. per acre, the first cwt. being applied at seeding, the second at brairding, and the third and fourth immediately after singling. Thus the applications of 3 cwt. and 4 cwt. per acre were made in three separate dressings. In each year the basal manuring per acre was: 12 loads farm-yard manure, 3 cwt. 30 per cent. superphosphate, and 1 cwt. muriate of potash per acre. The yield figures for each of the three years are given in Appendix II, and the means of the three years are set out in Table 3. The rainfall in the first two years was close to the normal for the district, but from April to November in 1927 it was 45 per cent. above normal.

TABLE 3. *Response of Sugar-beet to Increasing Applications of Nitrate of Soda*

	Nitrate of Soda, cwt. per acre				
	0	*1*	*2*	*3*	*4*
Washed beet, tons per acre	10·3	11·7	12·1	12·6	12·4
Per cent. of mean	87	99	102	107	105
Sugar-content, per cent.	17·6	17·5	17·3	17·3	17·1
Sugar, cwt. per acre	36·4	41·2	42·0	43·6	42·7
Per cent. of mean	88	100	102	106	104
Tops, tons per acre	5·5	6·4	7·6	8·0	9·0
Per cent. of mean	75	88	104	110	123

The systematic lay-out of the 1925 experiment did not allow a standard error to be calculated, but the yields show the same trend as those in 1926 and 1927. In these last two years, however, there was no significant increase in yield beyond that obtained with 2 cwt. per acre of nitrate of soda, though in all three years there were indications that 3 cwt. per acre gave an economic response.

Further experiments at Sprowston have measured the response of the beet crop to 3 cwt. per acre of nitrate of soda, and the results are available for the nine years 1925–33 (Table 4). In every year after 1927, all the nitrate of soda was applied to the seed-bed, experiments [1] having shown seed-bed application to give quite as good results as top-dressing. The basal manuring per acre was the same each year, viz. 12 loads f.y.m., 3 cwt. 30 per cent. superphosphate, and 1 cwt. muriate of potash per acre.

TABLE 4. *Response of Sugar-beet to 3 cwt. per acre of Nitrate of Soda, nine years, 1925–33*

	Increased weight of washed beet per acre		*Standard error*	*Decrease in sugar-content*	*Increased weight of sugar per acre*	
Year	*tons*	*% increase*	*tons*		*cwt.*	*% increase*
1925	2·9	32	. .	0·7	8·4	26
1926	2·4	20	0·35	0·3	7·8	18
1927	1·5	15	0·28	Nil	5·2	15
1928	0·8	7	0·28	0·5	3·8	9
1929	1·7	15	0·20	0·2	5·9	13
1930	2·7	25	0·22	Nil	8·9	25
1931	1·9	17	0·32	Nil	6·4	16
1932	0·8	6	0·24	Nil	2·6	6
1933	1·0	8	0·19	0·4	2·4	5
Mean	1·8	16	. .	0·3	5·8	15

In each year (except 1925, when no error could be calculated) there has been a significant increase in yield due to the application of 3 cwt. of nitrate of soda, though there is considerable variation from year to year. The biggest increase in yield of washed beet was 2·9 tons per acre (or 32 per cent.) in 1925; the smallest 0·8 tons per acre (6 per cent.) in 1932. It is difficult to state definitely what is the reason for this variation. Season, the different fertility-levels of the fields on which the experiments were carried out, and the small variations in the date of drilling and lifting, would all tend to affect the results, and it is impossible to assess the influence of one factor independently of the others. Experiments in two of the years did show, however, that time of lifting did not materially affect the response to nitrate of soda, although, of course, the yields generally were lower with early lifting.

The drop in sugar-content also shows considerable variation, ranging from nil in four of the years, to 0·7 per cent. in 1925. The four years when the sugar-content was not depressed were 'wet' years, and in the three dry years (1928, 1929, and 1933) there was a drop in sugar-content of 0·5, 0·2, and 0·4 per cent., respectively. It appears, therefore, that the depression of sugar-content by nitrogenous manuring varies according to season, for there is a difference in the rate of maturity of the crop in the two types of season. In a dry season, the plants receiving no nitrogenous fertilizer would tend to mature more rapidly; in a wet season, maturity is delayed, as growth continues late and the unmanured plants tend to make growth as late as the manured plants. In a dry season it was usually easier to pick out the control plots than in a wet season, by the greater yellowing of the leaves in the autumn.

(*c*) *Sulphate of ammonia.*—The experiments with sulphate of ammonia were carried out in 1928 on six farms in Norfolk. The amounts of fertilizer applied were 1 cwt., 2 cwt., and 3 cwt. per acre; in each case all was applied on the seed-bed. A basal manuring of phosphate, potash, and f.y.m. was applied at each centre.

The results at the individual centres are given in Appendix III, and the means for the light-loam centres and the heavy-loam centres in Table 5.

TABLE 5. *Response of Sugar-beet to Increasing Applications of Sulphate of Ammonia*

	Sulphate of Ammonia, cwt. per acre			
	0	*1*	*2*	*3*
Washed beet, tons per acre:				
3 light loams . . .	8·6	9·2	9·6	9·7
3 heavy loams . . .	12·0	12·7	13·6	14·2
Sugar-content:				
3 light loams . . .	19·5	19·1	19·1	19·2
3 heavy loams . . .	20·2	20·3	20·1	20·0
Sugar, cwt. per acre:				
3 light loams . . .	33·8	35·3	36·9	37·7
3 heavy loams . . .	48·8	51·7	55·0	56·9

At each centre there was a gradual increase in the yield of roots with each cwt. of sulphate of ammonia up to 2 cwt. Three cwt. per acre gave no further increase in yield except at Sutton and Uphall, both heavy loam centres and well farmed. At Westacre (a light-land centre), on the other hand, there was a slight but not significant response to 1 cwt. per acre of sulphate of ammonia, and no increase in yield was obtained with additional amounts of nitrogen. From the above figures, 2 cwt. per acre of sulphate of ammonia appears to be the economic maximum, except perhaps on the more fertile soils. The year 1928, however, was a dry year, which may have prevented the fertilizer from exerting its fullest influence. Of two subsequent trials at Sprowston, only one has shown a significant response to the third cwt.

The increase in yield due to the use of 2·2 cwt. per acre of sulphate of ammonia has been measured at Sprowston during six successive years (Table 6). All the sulphate of ammonia was applied in one dressing on the seed-bed, the same basal dressing of f.y.m., superphosphate, and muriate of potash being applied each year.

TABLE 6. *Response of Sugar-beet to 2·2 cwt. per acre of Sulphate of Ammonia, six years, 1928–33*

	Increased weight of washed beet per acre		*Standard error*	*Decrease in sugar-content*	*Increased weight of sugar per acre*	
Year	*tons*	*% increase*	*tons*		*cwt.*	*% increase*
1928	0·1	1	0·23	0·4	−0·5	−1
1929	1·5	13	0·20	0·1	6·0	14
1930	1·1	10	0·22	0·1	3·3	9
1931	1·0	9	0·33	0·1	3·7	10
1932	0·1	1	0·38	0·3	1·3	3
1933	0·3	2	0·20	0·6	−0·5	−1
Mean	0·7	6	..	0·3	2·2	6

In three of the years (1929–30–31) a significant increase in yield due to sulphate of ammonia was obtained. In the remaining three years, slight responses were secured, but they were not significant. Reference to the rainfall table on page 152 does not show any marked relationship between the amount of rainfall and the response of the crop to sulphate of ammonia in these years. Of the three years in which no response to the fertilizer was obtained (1928, 1932, and 1933), the rainfall from April to November in 1928 and 1933 was below normal. Examination of the individual monthly rainfall figures also does not give consistent results. The seed was drilled and the crop lifted at approximately the same time each year, which should rule out any effects of difference in time of maturity. It is more than likely that the difference in the state of fertility of the various fields on which the experiments were laid down have influenced the magnitude of the response to sulphate of ammonia.

Also, it is possible that the potash-content of the soil influences to some extent the action of the sulphate of ammonia. If this is so, then it is not unlikely that the variation in the response to sulphate of ammonia might be due to the different potash levels of the fields on which the experiments were made. This is suggested by the fact that little response to sulphate of ammonia was obtained in 1928 at Sprowston, whereas a response was obtained on other farms (particularly the heavy-land farms) in Norfolk in that year.

Comparison of Nitrate of Soda and Sulphate of Ammonia

To provide some information on the relative efficiency of nitrate of soda and sulphate of ammonia when compared on an equivalent-nitrogen basis, experiments were carried out at Sprowston in the six years 1928–33. The rates of application were 3 cwt. per acre of nitrate of soda, and 2¼ cwt. per acre of sulphate of ammonia, these amounts giving theoretically equal quantities of nitrogen. As in the other experiments, the plots received a basal dressing of f.y.m., potash, and phosphate, all the artificials being applied before drilling. The variety in each year was Kleinwanzleben E.

The results for the six years are given in Appendix IV, these years including three years when the rainfall for the district was below normal, and three years when the rainfall was above normal. In each year the nitrate-of-soda plots have given the heavier yield, though in 1929 and 1932 the differences were not significant, and in 1931 the difference of 0·9 tons only just reached significance.

TABLE 7. *Comparison of Nitrate of Soda and Sulphate of Ammonia*

(Equivalent-nitrogen Basis)

	No Nitrogen	*2¼ cwt. per acre Sulph. of ammon.*	*3 cwt. per acre Nitr. of soda*	*Difference in favour of Nitr. of soda*
Washed beet, tons per acre . .	11·9	12·7	13·4	0·7
Per cent. of mean . . .	94	100	106	6
Sugar-content	17·5	17·4	17·4	Nil
Sugar per acre, cwt. . . .	41·7	44·3	46·6	2·3
Per cent. of mean . . .	94	100	106	6

Over the average of the six years (Table 7), 3 cwt. per acre of nitrate of soda has given 0·7 tons (6 per cent.) per acre of washed beet more than 2¼ cwt. of sulphate of ammonia. Owing to the difficulty of separating seasonal effects from other factors likely to influence the yield, it is not possible to draw any conclusions as to the relative efficiency of these two fertilizers in a wet year and in a dry year.

On equivalent cost-per-acre basis (at 1934–5 prices), nitrate of soda and sulphate of ammonia could be applied in equal quantities, i.e. 3 cwt. per acre of sulphate of ammonia would cost no more than 3 cwt. per acre of nitrate of soda. The yields from these quantities were compared in the 1932 and 1933 experiments (Table 8).

TABLE 8. *Comparison of Nitrate of Soda and Sulphate of Ammonia*

(Equivalent-cost Basis)

		No Nitrogen	*3 cwt. Sulph. amm.*	*3 cwt. Nitr. soda*	*4 cwt. Nitr. soda*	*Standard error*
Washed beet, tons	1932	13·8	14·0	14·7	15·4	0·24
per acre	1933	12·9	14·1	13·9	14·0	0·19
Sugar-content	1932	16·4	16·3	16·5	16·3	..
" "	1933	17·3	16·5	16·9	16·4	0·16
Sugar, cwt. per	1932	45·3	45·6	48·5	50·2	..
acre	1933	44·6	46·6	47·0	45·9	..

The yields from 3 cwt. and 4 cwt. nitrate of soda were significantly heavier than from 3 cwt. of sulphate of ammonia in 1932, but not in 1933. There was little difference in sugar-content in the former year, but in 1933 nitrogen, as sulphate or nitrate, lowered the percentage of sugar. These figures, however, apply only to two years, and though it would be unsafe to argue too widely from them, nevertheless, it would appear advisable, when substituting sulphate of ammonia for nitrate of soda, to effect such substitution on a cwt.-for-cwt. basis and not on an equivalent-nitrogen basis.

Time of Application of Sulphate of Ammonia

In the early years of the beet crop it was the practice to apply the nitrogenous fertilizer in two or three separate dressings, e.g. one-half at seeding and one-half as a top-dressing after singling. Experiments begun in 1927 with nitrate of soda and with a mixture of nitrate of soda and sulphate of ammonia indicated, however, that just as good results could be obtained by applying all the nitrogen to the seed-bed before drilling. If this were possible, then the labour and inconvenience of top-dressing could be avoided. Accordingly, in 1928 experiments were laid down on six farms in Norfolk, in which 3 cwt. per acre of sulphate of ammonia was applied, (*a*) all on the seed-bed, (*b*) half on the seed-bed and half at singling, (*c*) half at singling and half three weeks later. In Table 9 the yields have been averaged for the light-loam centres and the heavy-loam centres. The yields at the individual centres are given in Appendix V. The basal manuring at each centre was typical of the sugar-beet manuring at that farm, consisting of 10–12 loads f.y.m., 2–2½ cwt. superphosphate, and 1–1½ cwt. muriate of potash. There were no differences in plant-population according to the time at which sulphate of ammonia was applied, and a good plant was obtained at all centres.

TABLE 9. *Effects of Applying Sulphate of Ammonia at Different Times*

	3 cwt. per acre of Sulphate of Ammonia		
	All on seed-bed	*½ on seed-bed, ½ at singling*	*½ at singling, ½ 3 weeks later*
Washed beet; tons per acre:			
3 heavy loams	13·7	13·7	13·2
2 light loams	9·3	8·9	8·4
Sugar-content:			
3 heavy loams	20·2	20·2	19·5
2 light loams	18·8	18·8	19·0
Sugar, cwt. per acre:			
3 heavy loams	55·4	55·2	52·9
2 light loams	35·0	33·7	32·4

At three out of the six centres there was no significant difference in yield between the times of application of nitrogen, but at two of the centres (Sutton and Testerton) the very late application of sulphate of ammonia resulted in a significantly decreased yield; possibly these beets were not fully ripened when lifted, as the sugar-contents seem to indicate. At Westacre the later applications of nitrogen gave the higher yield, but at this centre the field was weedy and the seed-bed applications of nitrogen resulted in an early growth of weeds, which was not apparent with the later applications. Presumably this early growth of weeds indicated that some of the nitrogen had been taken up by them, and was therefore lost to the beet-plants. This occurred only at the one centre, however, and it would seem that its occurrence depends upon whether the land is clean at the start. If the land is weedy, then there is the risk that seed-bed applications may produce a greater early growth of weeds.

On the average, seed-bed application of sulphate of ammonia increased the yield by 3 per cent. in the light loams and by 9 per cent. on the heavier loams, when compared with the very late application. It would seem, therefore, that late applications are more deleterious on the lighter lands than on the heavier lands. It is possible that the moisture-content of the soils at the time the nitrogen is applied may affect the efficiency of the fertilizer. The year 1928 was rather dry in Norfolk, especially from June onwards, and the lighter lands might reasonably be expected to dry out more than the heavier lands, thereby affecting the efficiency of the late applications of nitrogen.

It is sometimes held that late applications of nitrogen lead to a reduced sugar-content in the beet, i.e. ripening is delayed, and at four of the centres this was so, but at one centre (Worstead) the sugar-content was unaffected.

The criticism may be made that these experiments were carried on for one year only and that one year's results cannot be very reliable, especially when the particular year, 1928, was a rather abnormal one for rainfall in Norfolk; but similar experiments with nitrate of soda [1] extending over five years showed that the efficiency of seed-bed application of nitrate of soda was in no way affected by season. Seed-bed application gave just as good results in a wet year as in a dry year, and there seems no reason why similar results should not be obtained with sulphate of ammonia—a fertilizer presumably less readily leached from the soil than nitrate of soda.

The Effect of Heavy Dressings of Muriate of Potash

It has already been mentioned that nitrogenous manuring led to a slight reduction in the sugar-content of the beet. This depression might have been due to unbalanced manuring causing late maturity, and if this were so, it is not unlikely that the application of extra potash might lead to an improvement in sugar-content.

In 1929, therefore, a trial was begun to test the effects of additional potash in the presence of 3 cwt. per acre of nitrate of soda (Table 10). The trial was continued for five years and in each year a basal dressing, per acre, of 12 loads f.y.m., 3 cwt. nitrate of soda, and 3 cwt. 30 per cent. superphosphate was applied. Two rates of potash manuring were tested, 1 cwt. per acre and 3 cwt. per acre of muriate of potash. The latter dressing is perhaps unduly high, but it was considered necessary to provide an ample supply of potash.

TABLE 10. *Effect of Additional Potash with 3 cwt. Nitrate of Soda*

	Washed beet, tons per acre		*Sugar-content*	
	Muriate of Potash, cwt. per acre			
Year	*1*	*3*	*1*	*3*
1929	13·2	13·3	18·7	19·0
1930	13·7	13·6	16·4	16·3
1931	13·3	13·4	17·0	17·1
1932	14·5	14·8	16·5	16·4
1933	13·8	13·9	16·8	17·0
Mean	13·7	13·8	17·1	17·2

In every year the effects of the additional 2 cwt. per acre of muriate of potash were negligible and in no case significant. It is possible that the action of the sodium ions from the nitrate of soda, liberating available potash from the reserves in the soil, may have provided an adequate supply of potash and the addition of extra potash had no effect and was therefore uneconomic.

In 1932 and 1933 new experiments were put down to test if extra potash would be of benefit, (*a*) if 4 cwt. per acre of nitrate of soda was applied instead of 3 cwt., and (*b*) if sulphate of ammonia was used as the source of nitrogen instead of nitrate of soda (Table 11). The former fertilizer is not presumed to have so great an effect on the reserves of potash in the soil, and therefore additional potash manuring when sulphate of ammonia is used might be more advantageous.

TABLE 11. *Effect of Additional Potash with Nitrogenous Fertilizers*

	Washed beet, tons per acre				*Sugar-content*			
Year	*1932*		*1933*		*1932*		*1933*	
Amount of M/P (cwt.)	*1*	*3*	*1*	*3*	*1*	*3*	*1*	*3*
4 cwt. nitr. soda . .	15·4	15·5	13·6	14·4	16·3	16·4	16·6	16·2
2·2 cwt. sulph. ammon.	14·1	15·1	13·1	13·4	16·6	16·4	16·6	16·8
3 cwt. sulph. ammon. .	13·7	15·2	13·9	14·3	16·6	16·1	16·7	16·3
Standard error . .	0·38		0·20		..		..	

Only two significant increases in yield due to potash were obtained in the two years, namely, an increase of 0·8 tons per acre when 4 cwt. of nitrate of soda were used in 1933, and an increase of 1·0 tons per acre when 2·2 cwt. of sulphate of ammonia were used in 1932. At the same time, however, reasonably large increases in yield due to the extra potash were obtained with 3 cwt. of sulphate of ammonia in both years. The effect of the extra potash was not reflected in the sugar percentages, for none of the differences shown in the table were significant.

In view of the difference in the response to additional potash in the two years, it would be unwise to attach too much importance to the results. At the same time, however, it is difficult entirely to disregard the evidence. The Rothamsted experiments [2] have shown that potash is likely to be beneficial when sulphate of ammonia is used, but with nitrate of soda the benefits were not so marked. Taken together, the evidence suggests that if high dressings of nitrogen are applied then additional potash will probably be advantageous, the more so if sulphate of ammonia be used, and the soil is known to respond to potash.

Summary

1. Experiments carried out in Norfolk on the nitrogenous manuring of sugar-beet are described.

2. In three-years experiments at Sprowston, the optimum amount of nitrate of lime was 4 cwt. per acre, and of nitrate of soda 3 cwt. per acre.

3. A significant response to 3 cwt. per acre of nitrate of soda was obtained each year during the nine years 1925–33.

4. In 1928 the optimum amount of sulphate of ammonia was 2 cwt. per acre at four centres. The third cwt. gave an increase in yield only on the more fertile soils.

5. Only in three of the six years 1928–33 was a significant response to 2·2 cwt. of sulphate of ammonia obtained at Sprowston.

6. In four trials at Sprowston 3 cwt. per acre of nitrate of soda gave a significantly heavier yield than 2·2 cwt. of sulphate of ammonia.

7. In experiments on six farms in 1928, 3 cwt. per acre of sulphate of ammonia applied all on the seed-bed gave at least as good results as splitting the dressing into two or three parts. Late applications of nitrogen depressed the yield at two centres and the sugar-content at four centres.

8. Additional potash did not raise the yield or sugar-content when 3 cwt. per acre of nitrate of soda was used. With 4 cwt. per acre of this fertilizer, and with sulphate of ammonia, evidence was obtained that increasing the potash manuring might raise the yield.

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APPENDIX I

Increasing Quantities of Nitrate of Lime

Amount of N. of Lime (cwt. per acre)	*Washed beet (tons per acre)*			*Tops (tons per acre)*		
	1925	*1926*	*1927*	*1925*	*1926*	*1927*
0	9·3	12·3	10·1	5·8	5·5	6·6
1	9·8	13·1	10·8	6·2	6·2	6·5
2	9·6	13·9	11·1	7·6	7·2	7·1
4	10·3	14·2	11·7	8·7	8·3	7·5
Standard error	..	0·22	0·17	..	0·32	0·31

Amount of N. of Lime (cwt. per acre)	*Sugar (cwt. per acre)*			*Sugar-content (per cent.)*		
	1925	*1926*	*1927*	*1925*	*1926*	*1927*
0	31·8	44·0	34·5	17·1	17·9	17·1
1	33·2	47·0	36·9	16·9	17·9	17·1
2	30·7	50·0	37·8	16·0	18·0	17·0
4	32·8	50·9	40·7	15·9	17·9	17·4

APPENDIX II

Increasing Quantities of Nitrate of Soda

Amount of N. of Soda (cwt. per acre)	*Washed beet (tons per acre)*			*Tops (tons per acre)*		
	1925	*1926*	*1927*	*1925*	*1926*	*1927*
0	9·3	11·7	11·0	5·0	5·3	6·1
1	11·2	13·0	11·0	6·0	5·8	7·3
2	10·8	13·8	11·7	6·8	8·2	7·7
3	12·1	14·2	11·5	7·2	9·0	7·8
4	11·1	14·6	11·5	9·0	9·3	8·6
Standard error	..	0·35	0·28	..	0·51	0·59

Amount of N. of Soda (cwt. per acre)	*Sugar (cwt. per acre)*			*Sugar-content (per cent.)*		
	1925	*1926*	*1927*	*1925*	*1926*	*1927*
0	32·6	42·1	34·6	17·5	18·0	17·3
1	38·5	46·9	38·1	17·2	18·0	17·3
2	36·5	48·9	40·5	16·9	17·7	17·3
3	40·6	50·3	39·8	16·8	17·7	17·3
4	36·2	52·0	39·8	16·3	17·8	17·3

APPENDIX III

Increasing Quantities of Sulphate of Ammonia

Washed Beet (tons per acre)

Centre: *Soil (loam):*	*Worstead* heavy	*Sutton* heavy	*Uphall* heavy	*Bridgham* light	*Westacre* light	*Testerton* light	*Mean*	*Per cent.*
Amt. of Sulph. Ammon. (cwt. per acre)								
0	11·8	11·2	13·1	11·3	7·4	7·0	10·3	92
1	12·2	11·5	14·5	11·8	8·0	7·7	10·9	97
2	13·3	12·4	15·2	12·4	8·2	8·1	11·6	104
3	13·3	13·3	16·1	12·7	8·2	8·2	12·0	107
Standard error	0·43	0·31	0·34	0·18	0·33	0·34	..	..

Sugar-content

Centre:	*Worstead*	*Sutton*	*Uphall*	*Bridgham*	*Westacre*	*Testerton*	*Mean*
Amt. of Sulph. Ammon. (cwt. per acre)							
0	20·6	19·5	20·6	20·7	19·6	18·2	19·9
1	20·2	19·8	20·8	20·1	19·1	18·0	19·7
2	20·1	19·5	20·7	20·1	19·0	18·2	19·6
3	19·9	19·7	20·3	20·6	19·1	18·0	19·6

Sugar (cwt. per acre)

Centre:	*Worstead*	*Sutton*	*Uphall*	*Bridgham*	*Westacre*	*Testerton*	*Mean*	*Per cent.*
Amt. of Sulph. Ammon. (cwt. per acre)								
0	48·6	43·7	54·0	46·8	29·0	25·5	41·3	93
1	49·3	45·5	60·4	47·5	30·6	27·7	43·4	97
2	53·5	48·4	63·0	50·0	31·2	29·5	45·9	103
3	53·0	52·4	65·4	52·4	31·3	29·5	47·3	107

APPENDIX IV

Comparison of Nitrate of Soda and Sulphate of Ammonia

Washed beet (tons per acre)

Year	*1928*	*1929*	*1930*	*1931*	*1932*	*1933*
No nitrogen . . .	11·1	11·4	11·0	11·4	13·8	12·9
2¼ cwt. S/A . . .	11·2	12·9	12·1	12·4	14·6	13·3
3 cwt. N/S . . .	11·9	13·2	13·7	13·3	14·7	13·9
Standard error	0·23	0·20	0·22	0·33	0·24	0·19

Sugar-content

Year	*1928*	*1929*	*1930*	*1931*	*1932*	*1933*
No nitrogen . . .	19·2	18·9	16·4	17·0	16·4	17·3
2¼ cwt. S/A . . .	18·8	19·0	16·3	17·1	16·5	16·7
3 cwt. N/S . . .	18·7	18·7	16·4	17·0	16·5	16·9

Sugar (cwt. per acre)

Year	*1928*	*1929*	*1930*	*1931*	*1932*	*1933*
No nitrogen . . .	42·6	43·1	36·0	38·8	45·2	44·6
2¼ cwt. S/A . . .	42·1	49·0	39·4	42·5	48·2	44·5
3 cwt. N/S . . .	44·5	49·4	45·0	45·2	48·5	47·0

APPENDIX V

Time of Application of Sulphate of Ammonia

Washed beet (tons per acre)

Centre: Soil (loam):	*Worstead* heavy	*Sutton* heavy	*Uphall* heavy	*Bridgham* light	*Westacre* light	*Testerton* light	*Mean**	*Per cent.**
3 cwt. S/A:								
All on seed-bed	12·0	13·5	15·5	11·0	7·6	7·5	11·9	102
½ on seed-bed ½ at singling	11·8	13·5	15·7	10·7	8·5	7·1	11·8	101
½ at singling ½ 3 weeks later	11·8	12·8	15·0	10·3	8·6	6·5	11·3	97
Standard error	0·17	0·21	0·40	0·57	0·31	0·18	..	..

* Excluding Westacre.

Sugar-content (per cent.)

Centre:	*Worstead*	*Sutton*	*Uphall*	*Bridgham*	*Westacre*	*Testerton*	*Mean**
3 cwt. S/A:							
All on seed-bed	20·0	19·7	20·9	19·4	19·5	18·1	19·6
½ on seed-bed ½ at singling	20·1	19·5	20·9	19·6	18·5	17·9	19·6
½ at singling ½ 3 weeks later	20·1	19·1	20·2	20·1	17·8	17·9	19·5

* Excluding Westacre.

Sugar (cwt. per acre)

Centre:	*Worstead*	*Sutton*	*Uphall*	*Bridgham*	*Westacre*	*Testerton*	*Mean**	*Per cent.**
All on seed-bed	48·0	53·2	64·9	42·7	29·6	27·2	47·2	102
½ on seed-bed ½ at singling	47·5	52·6	65·6	42·0	31·4	25·4	46·6	101
½ at singling ½ 3 weeks later	47·5	48·9	60·6	41·5	30·6	23·3	44·4	97

* Excluding Westacre.

THE INCIDENCE OF KEMP IN THE FLEECE OF SCOTTISH MOUNTAIN BLACKFACE SHEEP, WITH SPECIAL REFERENCE TO INHERITANCE

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WITH PLATES 11, 12

Introduction.—The investigations described in this paper were undertaken to determine whether hereditary factors control the presence of kemp fibres in the fleeces of Scottish Mountain Blackface sheep and, if evidence of heredity were found, to attempt to elucidate the mode of inheritance concerned.

The belief that kemp fibres depend for their expression upon hereditary factors is widely held by sheep-breeders, and in particular perhaps by owners of Scottish Mountain Blackface flocks. Barker [1] and Darling [2], dealing with Scottish Blackface sheep, and Roberts [3], dealing with the Welsh Mountain breed, *inter alia*, have put forward generalized evidence that kemp fibres are inherited in differing degrees in individual sheep. Scientific data relating to the inheritance of kemp accumulated from fleece-analyses of flocks of pedigree sheep have not, however, so far been published for the Scottish Mountain Blackface breed, with the exception of one paper by the writer [4].

Definition of kemp fibres.—In the Blackface breed the kemp fibres which are found in most fleeces do not differ markedly from those found in other breeds. They are easily recognized by their macroscopic characters, as follows:

1. The fibres have a dead-white appearance due to a large medulla, containing air, which causes light to be refracted. If pigment is present they are brown or black.
2. Typical kemp fibres show a pronounced wave in one plane only.
3. In most cases they are very coarse.
4. Their length-range varies between 1 and 3 in. when mature. The great majority of Blackface kemp fibres are included in this range; occasionally there are exceptions, but these are not sufficiently numerous to merit special notice.
5. All typical kemps exhibit a sudden thinning to a very fine tip at their distal extremities. At the proximal extremity of a completely grown fibre there is also a slight thinning immediately above the level of the follicle. This can be observed only in fibres which have been shed naturally, and the thin proximal portion of the shaft is followed by a terminal bulb. This thinned portion can seldom be seen in kemp clipped from living sheep.
6. Kemp fibres are extremely brittle.

Material and Methods

(*a*) *Distribution of kemp over the body*.—In this investigation (which was begun in the autumn of 1930 and carried out at the Institute of

Animal Genetics, University of Edinburgh) it was necessary to find some reasonably accurate method of comparing the amount of kemp present in fleeces of living sheep. Darling [2] showed that the distribution of kemp over the body varied considerably, and it was clear from this work and from general observation that in most sheep little or no kemp was present in the shoulder regions and on the thorax, even in animals which exhibited much kemp in dorsal areas.

Some important observations on the distribution of kemp in the Blackface fleece were made by Prof. Wm. C. Miller, to whom the writer is greatly indebted for permission to use the data and photographs shown in Figs. 2–5, Plates 11, 12, and described below.

One of the Blackface ewes kept at the Institute of Animal Genetics died from peritonitis and there was some delay in disposing of the carcass. Rapid decomposition set in, and about three days after death the wool fibres and long-hair fibres could be easily pulled out, but the kemp fibres were still held firmly in their follicles. All wool and long-hair fibres were removed by hand, and photographs of the carcass, with the kemp fibres *in situ*, were obtained. Subsequently, pieces of skin, each of 1 sq. in., were removed from various locations and the kemp fibres on each were counted. This procedure was repeated with other Blackface sheep which died, and with some which were slaughtered for other experimental reasons. Every carcass was not found to be satisfactory, and only those in which wool and long-hair fibres could be readily plucked without disturbing kemp fibres were used.

In each case very similar results were obtained. The kemp fibres were found to be distributed very densely over a bilaterally symmetrical area on the dorsal aspect of the sheep, extending from about the level of the eighth thoracic vertebra to the tail-head, and for about 2 in. laterally on each side of the mid-dorsal line, becoming broader posteriorly over the croup. Outside this area the density was found to decrease somewhat and, at 4–5 in. from the mid-dorsal line, the occurrence of kemp practically ceased except over the rump, where the dorsal area spread out and extended downwards over the flanks; the density, however, was considerably less in the latter region. The thorax was found to be almost free from kemp, except for one or two small tufts, but the lower parts of the abdomen showed a fair incidence of kemp fibres, though their density in this area was not high. The above description is illustrated by Figs. 2–5, Plates 11, 12. These photographs all relate to the same carcass and are included as being typical of the results obtained in this analysis of the distribution of kemp over the body.

A diagrammatic representation of the locations of the areas from which square inches of skin were removed is given in Fig. 1, and details of the actual numbers of kemp fibres counted in a typical case will be found in Table 1.

It will be seen that the variability of the density of distribution of kemp was low between areas I, II, and III, but became higher in areas IV and V. The variability between areas VI to X was clearly very high, and the density in each of these areas was lower than that of areas I to III. In other words, the variability of the density of kemp-distribution was very low in a bilaterally symmetrical area extending from a point somewhat in front of the last rib to the level of the croup and for about $1\frac{1}{2}$ in. on each side of the mid-dorsal line. Further, the density-distribution in this area was maximal for the whole skin-surface.

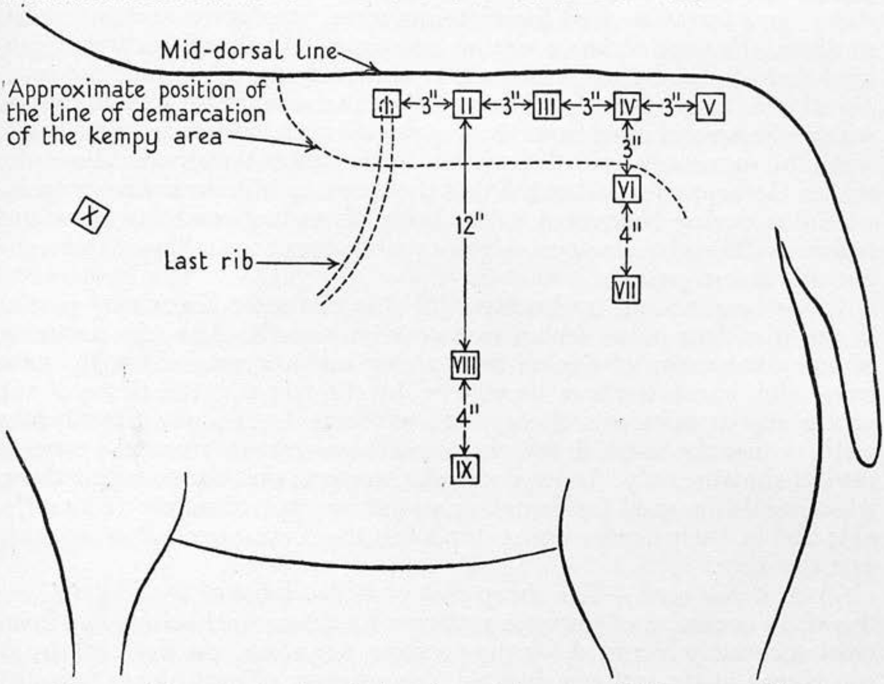

FIG. 1. Diagram showing the locations of the areas of skin removed from carcass of Blackface ewe

These observations, replicated a number of times, were found to agree closely with the results of a detailed analysis of the distribution of kemp over the body in the Welsh Mountain breed made by Roberts [5].

TABLE 1. *Number of Kemp Fibres per sq. in. of Skin in Various Locations on Carcass of Blackface Ewe**

No. of skin sample	*No. of kemp fibres*
I (over head of last rib)	706
II	646
III	696
IV	593
V	425
VI	296
VII	578
VIII	122
IX	401
X (centre of spine of scapula)	254

* Figures for the left side only are given.

(*b*) *Methods of sampling.*—Two samples of wool were removed from each sheep used in these investigations. Uniformity in sampling was assured by selecting definite anatomical points, viz. the head of the last rib on each side. These points are readily found by touch on the living sheep, and the areas used for sampling were, in every case, just medial to them. The approximate size of each sampled area of skin was $2\frac{1}{2}$ sq. cm., and the medial edge of each area was about 1 in. from the mid-dorsal line. Consequently, all samples were removed from situations well within the area of maximum kemp referred to in the preceding section.

As the maximum-growth period of kemp fibres terminates about the end of October, it was decided that the most suitable time for sampling would be during November, when kemp fibres had ceased to grow and before shedding became general; this practice has been followed throughout this investigation.

It has been shown by Lochner [6] that birthcoat-fibres may persist in the Blackface fleece for up to a year after birth. Also, the accuracy of any comparison of fleeces from sheep under a year old with those from adult sheep tends to be vitiated by the fact that the fleece of the young sheep represents the growth of fibres from some time before birth, whilst the adult fleece represents fibre-growth from the time of the last shearing only. It was decided, therefore, that the youngest sheep which could be used for sampling would be approximately 18 months old; that is, their fleeces were sampled in the November following their first shearing.

(*c*) *Material used.*—The sheep that provided most of the material for this work consisted of a private pedigree Blackface flock which had been most accurately recorded for the previous ten years. As the flock-book was placed at the writer's disposal, the ancestry of each sheep sampled was available for consideration.

In addition, wool samples were obtained from stud rams belonging to breeders in different parts of Scotland.

(*d*) *Laboratory treatment of the samples.*—Each sample was divided by hand into a non-kemp fraction and a kemp fraction, and the fractions were de-greased and scoured by the process described by Miller and Bryant [7]. Since it was shown by Barritt and King [8] that the rates of moisture re-gain for all classes of fleece-fibres are almost identical, the fractions, after scouring, were allowed to 'condition' to laboratory humidity, were then weighed, and the percentage weights of kemp were calculated. The means of the percentage weights of kemp in the two samples removed from each sheep were found, thus providing a single kemp-analysis figure for each animal.

Results

The data accumulated from the analyses of the wool samples collected as described above are set out and explained below.

Although samples were obtained from some 500 sheep in the experimental flock, owing to the impossibility of obtaining comparable wool samples from sheep less than 18 months old, comparisons between the percentages of kemp from dams and their offspring had to be limited to sheep which were adult (18 months old at least) when samples were collected. This accounts for the small number of dam-to-progeny comparisons.

Since the sires of a number of the experimental ewes sampled had been disposed of before this work was begun, it was not possible to compare the kemp-contents of some of the ewes' fleeces with those of their sires. Further, in each year of the flock-book records, the sires of about 10 per cent. of the lambs born were not definitely known, owing to accidental mistakes in reading numbers, tags being torn out of sheep's ears, and other causes. Later analyses were made only of samples from sheep of which at least one of the parents had been sampled.

The ages of the experimental sheep ranged from 1½ to 4½ years. The fleeces of sheep older than this were not analysed. The question of the influence of age on kempiness will be discussed later.

The relationship between the analysis-figures for the kemp of 11 rams and 143 of their female progeny is shown in Table 2, and of 72 ewes and their progeny (one daughter per ewe) in Table 3. To obtain reliable tests of the significance of the correlation coefficients, reference was made to Fisher [9, Table V A], where it was found that for 143 pairs of variates a correlation coefficient of 0·28 corresponds to a value of $P = 0{\cdot}01$, and for 72 pairs of variates a correlation coefficient of 0·25

TABLE 2. *Relationship between Percentage of Kemp in Rams and Percentage of Kemp in their Offspring*

CORRELATION TABLE

OFFSPRING

RAMS	0·0–0·9	1·0–1·9	2·0–2·9	3·0–3·9	4·0–4·9	5·0–5·9	6·0–6·9	7·0–7·9	8·0–8·9	9·0–9·9	10·0–10·9	11·0–11·9	12·0–12·9	13·0–13·9	14·0–14·9	15·0–15·9	16·0–16·9	17·0–17·9	18·0–18·9	19·0–19·9	20·0–20·9	21·0–21·9	22·0–22·9	23·0–23·9	24·0–24·9	Totals
0·0–0·9	14	8	2	4	4	9	1	6	3	2	4	2	1	2	3	2	2	1	1					2		73
1·0–1·9																										
2·0–2·9																										
3·0–3·9																										
4·0–4·9																										
5·0–5·9																										
6·0–6·9	1					2		2	1		1	1		1			1						1			11
7·0–7·9																										
8·0–8·9																										
9·0–9·9																										
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11·0–11·9																										
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13·0–13·9																										
14·0–14·9																										
15·0–15·9	2	2			1	3	1	2					1	1	1	1										15
16·0–16·9																										
17·0–17·9																										
18·0–18·9	2	2	1			1			1	2	2	3	1			1	2			1						19
19·0–19·9																										
20·0–20·9	1	1			1			1				1														5
21·0–21·9																										
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25·0–25·9																										
26·0–26·9																										
27·0–27·9																										
28·0–28·9				1	1			2	1	1		2	1	2	2	3			2	1					1	20
Totals	20	13	3	5	7	15	2	13	6	5	7	9	4	6	6	7	5	1	3	2			1	2	1	143

Coefficient of correlation = +0·28 ± 0·08 corresponds to a value of $P = 0{\cdot}05$. Therefore, the correlation between the kemp-analysis figures for rams and their daughters is significant, but a similar correlation for ewes and their daughters is low. However, undue weight should not be attached to the difference in the levels of significance of the two correlation coefficients, since the number of pairs in the rams' series was almost twice the number of pairs in the ewes' series. Had the number of pairs of variates not differed so widely in the two cases, this might have been regarded as evidence suggestive of sex-linkage. In the absence of recorded male progeny, it is not at present possible to determine whether for kemp-content any influence of sex-linkage inheritance exists. Some preliminary evidence would appear to have been obtained, but until opportunity for further work occurs it is not desirable to stress unduly this aspect of the problem.

TABLE 3. *Relationship between Percentage of Kemp in Ewes and Percentage of Kemp in their Offspring*

CORRELATION TABLE

OFFSPRING

EWES	0·0–0·9	1·0–1·9	2·0–2·9	3·0–3·9	4·0–4·9	5·0–5·9	6·0–6·9	7·0–7·9	8·0–8·9	9·0–9·9	10·0–10·9	11·0–11·9	12·0–12·9	13·0–13·9	14·0–14·9	15·0–15·9	16·0–16·9	17·0–17·9	18·0–18·9	19·0–19·9	20·0–20·9	21·0–21·9	22·0–22·9	23·0–23·9	24·0–24·9	Totals
0·0–0·9	5	1			1	2			1	1			1		1					1			1			15
1·0–1·9		1	1	1	2	1								1	1	1			1							10
2·0–2·9																										
3·0–3·9											1															1
4·0–4·9											2															2
5·0–5·9						1																				1
6·0–6·9																										
7·0–7·9																										
8·0–8·9		1						1							1											3
9·0–9·9																										
10·0–10·9				1		1					1															3
11·0–11·9												1														1
12·0–12·9				1												1										2
13·0–13·9		1			1	1				1									1						1	6
14·0–14·9									1						1											2
15·0–15·9							1			1				1		1							1			5
16·0–16·9																										
17·0–17·9						3		1	1			1														6
18·0–18·9			1			1										1		1	1							5
19·0–19·9																										
20·0–20·9																										
21·0–21·9												1	1													2
22·0–22·9																										
23·0–23·9											1						1			1						3
24·0–24·9																										
25·0–25·9																	1									1
26·0–26·9																										
27·0–27·9																										
28·0–28·9																										
29·0–29·9																										
30·0–30·9																										
31·0–31·9											1	1														2
32·0–32·9																										
33·0–33·9																										
34·0–34·9																										
35·0–35·9																										
36·0–36·9																										
37·0–37·9																										
38·0–38·9						1								1												2
Totals	5	4	2	3	4	11	1	2	3	3	6	4	2	3	4	4	2	1	3	2			2		1	72

Coefficient of correlation = $+0{\cdot}25 \pm 0{\cdot}11$

The distribution of the kemp-analysis figures in the experimental ewe-flock is given in Fig. 6, which should be read in conjunction with Table 4. There are 320 individual analyses included in the diagram.

It is worthy of note that the breeding sheep on this farm had been selected in such a way that individuals showing a very high proportion of kemp had been eliminated from the stock during some seven years before these investigations were started.

The distribution of the kemp-analysis figures in stud rams belonging to breeders in many parts of Scotland is given in Fig. 7 and Table 4.

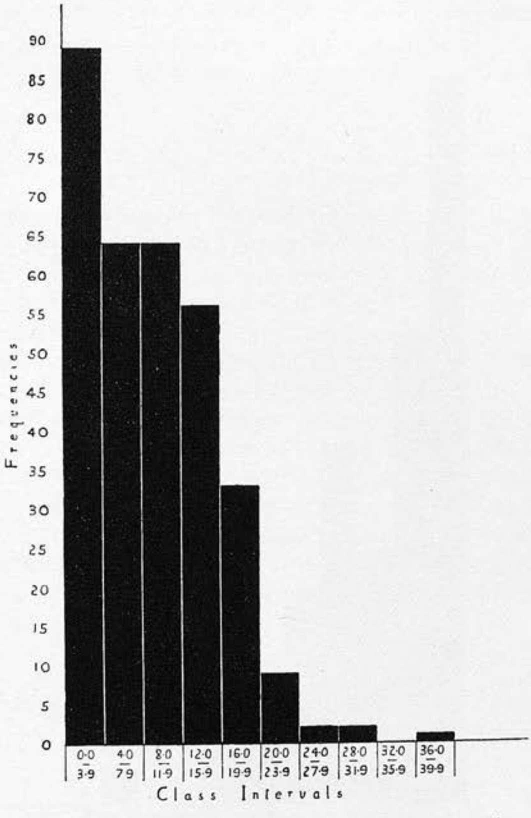

FIG. 6. Distribution of the kemp-percentage figures for the ewe-flock
Mean percentage = 8·97±0·37
No. of individuals = 320

These rams had been carefully selected for breed points, including comparative freedom from kemp. In this respect they were suitable for comparison with the ewe-flock.

From general experience gained during this work, in which visits were made to many Blackface sheep farms in Scotland, and from an examination of large numbers of Blackface ewes, it can be confidently stated that there are few commercial Blackface flocks in which the mean percentage of kemp is so low as that of the stud rams referred to above, or that of the ewe-flock, which was mainly used for the purpose of this experiment.

In Table 4 an estimate is given of an average distribution of kemp in a typical commercial flock. The percentages are necessarily approximate, but an endeavour has been made to avoid assessing the values too highly. This is included solely for purposes of comparison.

The close similarity in the distribution of the kemp-percentage figures in the ewe-flock and in the group of stud rams can be seen from the figures. This is especially noticeable with regard to the first two classes, viz. 0 to 3·9 per cent. and 4 to 7·9 per cent.

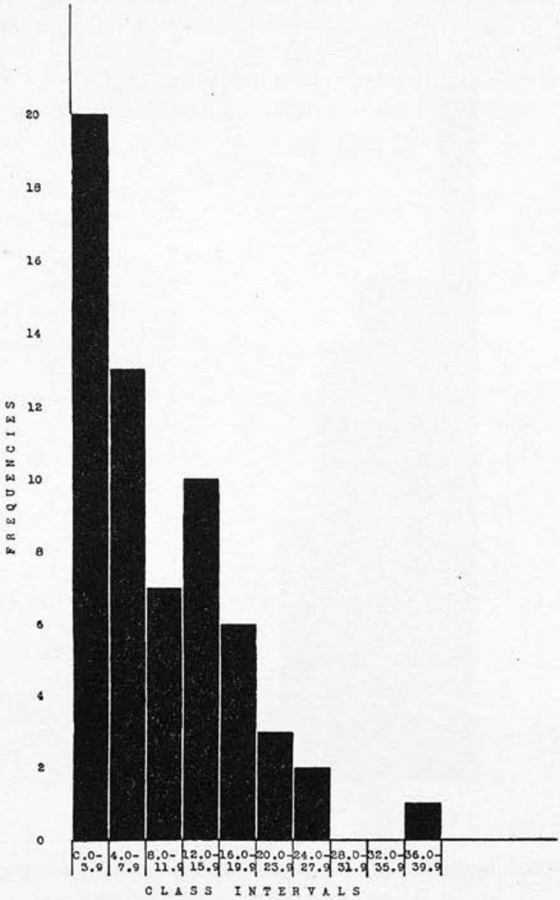

FIG. 7. Distribution of kemp-percentage figures in a group of 62 stud rams
Mean percentage $= 9{\cdot}28 \pm 1{\cdot}03$

In Table 5 and Figs. 8, 9, and 10 the kemp-analysis figures obtained from groups of the female progeny of rams A, B, and C are shown.

Figs. 11, 12 and 13 show similar details for groups of the female progeny of rams D, E, and F. These three rams were disposed of before this work was begun, so that no analysis of their fleeces could be made. The details of the progeny-groups are given here because the distribution

TABLE 4. *Average Distribution of Kemp in Experimental Flock and Estimate for Average Commercial Flock*

	Less than 4%		*4%–7·9%*		*8%–19·9%*		*20% and over*		
	No.	*Percentage of whole*	*No.*	*Percentage of whole*	*No.*	*Percentage of whole*	*No.*	*Percentage of whole*	*Mean kemp per cent.*
Stud rams	20	32·3	13	21·0	23	37·1	6	9·6	9·28±1·03
Flock ewes	89	27·8	64	20·0	153	47·8	14	4·3	8·97±0·37
Estimate for average commercial flock		18·0		16·0		50·0		16·0	

of the kemp-percentage figures for each group shows considerable divergence from that of the ewe-flock. Reference to the figures and to Table 5 shows that the kemp-figures of the progeny of rams D and E were distributed similarly, but the progeny of ram F were considerably more kempy, 75 per cent. having kemp-percentages of from 8 to 19·9 per cent. On the assumption that the ewe-groups selected for each ram during the years he was used represented a random sample of the ewe-flock as a whole—no conscious selection either for or against kempiness having been carried out in the particular matings involved—the kemp-analyses of the six progeny-groups clearly indicate that different rams transmit widely different kemp-contents to their offspring. It is extremely unlikely that the differences in kempiness shown by the various progeny groups, when compared with those of the whole ewe-flock, could have arisen by chance; and it is even more unlikely that the wide divergences displayed by the progeny of rams A, B, and F were accidental or coincidental.

TABLE 5. *Average Distribution of Kemp in Female Progeny of Rams*

	Less than 4%		*4%–7·9%*		*8%–19·9%*		*20% and over*		
Progeny of:	*No.*	*Percentage of whole*	*No.*	*Percentage of whole*	*No.*	*Percentage of whole*	*No.*	*Percentage of whole*	*Mean kemp-percentage*
Ram A (kemp analysis < 1%)	21	46·7	11	24·4	11	24·4	2	4·4	6·19±0·91
Ram B (kemp analysis 28·9%)	1	3·3	3	10·0	15	73·3	1	13·3	15·40±1·14
Ram C (kemp analysis 18·3%)	5	26·3	1	5·3	13	68·4	..	..	9·25±1·31
Ram D (not sampled)	9	19·6	7	15·2	27	58·7	3	6·5	10·63±0·98
Ram E (not sampled)	6	16·2	7	18·9	21	56·7	3	8·1	10·88±1·23
Ram F (not sampled)	2	10·0	2	10·0	15	75·0	1	5·0	13·69±1·24

In Table 6 the usual test for the significance of the difference between two means is applied for the difference between the mean kemp-percentage of each progeny-group and the mean kemp-figure of the ewe-flock.

It will be noted that the difference is clearly significant in the case of the progeny of rams B and F, and closely approaches significance for the

TABLE 6. *Significance of the Difference between the Means of the Kemp-percentage Figures of the various Progeny Groups and the Mean Kemp-percentage in the Ewe-flock*

Progeny of:	*Mean kemp-percentage figure*	*D—difference from mean kemp-percentage of ewe-flock*	*$S.E._D$—standard error of the difference*	$\frac{D}{S.E._D}$
Ram A	6·19	2·78	0·98	2·82
Ram B	15·40	6·43	1·20	5·35
Ram C	9·26	0·28	1·37	0·21
Ram D	10·63	1·65	1·04	1·59
Ram E	10·88	1·91	1·28	1·49
Ram F	13·70	4·72	1·29	3·65

progeny of ram A, but there is no indication of significance for the progeny-groups of rams C, D, and E. It would seem that these three rams, and especially ram C, were unable to influence the kemp-content of the fleeces of their progeny to the degree exhibited by, for example, ram B.

In Table 7 the kemp-analyses of rams G, H, J, K, and L, and some of their female progeny, will be found. Since the number of progeny-analyses available for each of these rams was small, and since the five rams had the same kemp-figures, the kemp-percentages of their progenies were combined in a composite diagram, Fig. 14, in which the distribution of the kemp-percentage figures for the whole group is shown. By comparison with the kemp-figures for the ewe-flock (Fig. 6) it will be observed that whereas a smaller proportion of the group under discussion had kemp-percentages of less than 4, appreciably more had analyses of less than 8 per cent.; 55·5 against 47·8 per cent. in the ewe-flock. Compared with the progeny of ram A (Fig. 8), the present group appears to be definitely more kempy. Reference to Table 7 shows, however, that the mean kemp-percentage is 8·01±1·01. It is evident that there is no

TABLE 7. *Kemp-percentage Figures of the Progeny of Rams G, H, J, K, and L*

	Kemp-percentage figures of progeny
Ram G (kemp-percentage < 1)	10·56 14·99
Ram H (kemp-percentage < 1)	1·32 4·56 5·27 5·50 5·61 7·35 7·92 9·36 10·56 15·21 15·48 16·86 18·35 Mean = 9·53±1·44
Ram J (kemp-percentage < 1)	< 1 2·94 5·52 7·75 8·89 14·76 Mean = 6·72±1·86
Ram K (kemp-percentage < 1)	< 1 1·13 5·28
Ram L (kemp-percentage < 1)	< 1 8·32 11·21
	Mean of Group = 8·01±1·01

significance in the difference between this mean and the mean kemp-figure of the progeny of ram A.

In Fig. 15 particulars are given of the kemp-analysis figures of 57 groups of sire, dam, and offspring. In the diagram the matings of each individual ram are separated by a horizontal line. The kemp-analyses of 10 rams, ewes to which they were mated, and the resulting female offspring are shown.

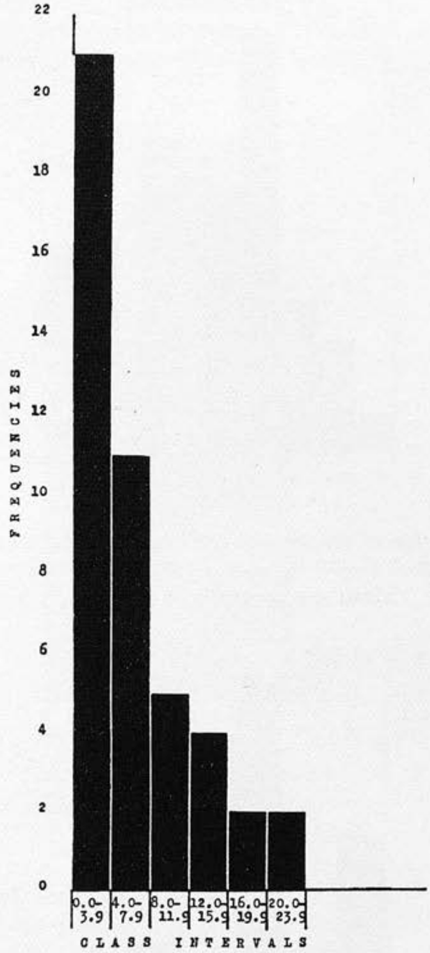

Fig. 8. Distribution of the kemp-percentage figures in 45 of the female progeny of ram A, which itself had less than 1% of kemp

Mean percentage = 6·19±0·91

In the first case the ram (ram A) had an analysis of less than 1 per cent. and figures are given for 15 individual matings. It will be noted that four of the progeny (or 26·6 per cent.) had kemp-figures of less than 4 per cent., and 10 (or 66·6 per cent.) had analyses of less than 8

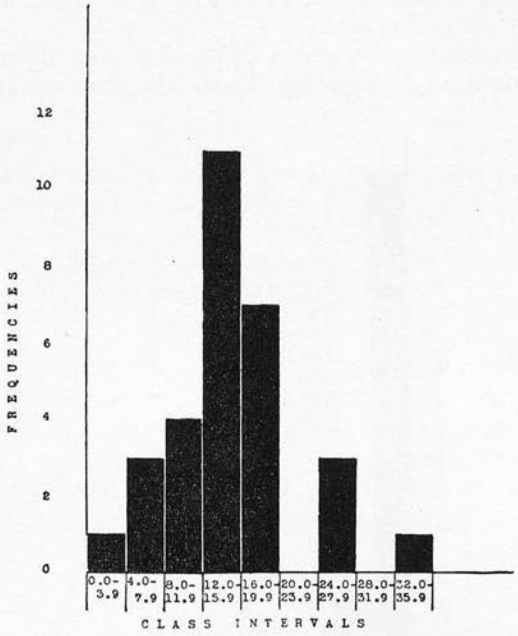

FIG. 9. Distribution of the kemp-percentage figures in 30 of the female progeny of ram B, which showed 28% of kemp

Mean percentage = 15·40 ± 1·14

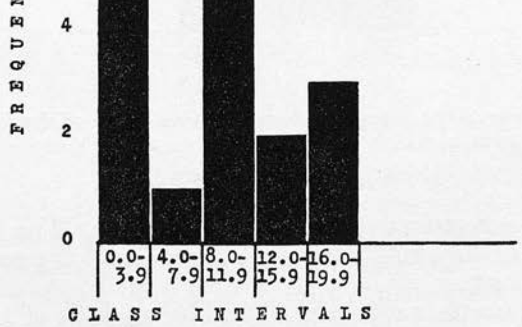

FIG. 10. Distribution of the kemp-percentage figures in 19 of the female progeny of ram C

Mean percentage = 9·25 ± 1·31

per cent., so that only 5 daughters (or 33·3 per cent.) had kemp-analyses of more than 8 per cent. Further, 9 of the progeny (or 60·0 per cent.) had kemp-figures identical with those of their parents, or intermediate between those of the sire and dams, and 6 (or 40 per cent.) had kemp-figures exceeding those of their parents.

In the second largest group of matings, those of ram B, with a kemp-analysis of 28·98 per cent., only 1 of the progeny (or 7·7 per cent.) had a kemp-analysis of less than 4 per cent., and 2 (or 15·4 per cent.) had kemp-figures of less than 8 per cent. Thus 11 daughters (or 85·4 per cent.) had over 8 per cent. of kemp in their fleeces. Eight of the progeny (or 61·5 per cent.) had kemp-values identical with those of their dams or intermediate between those of their parents, while 5 (or 38·5 per cent.) had figures below those of both parents.

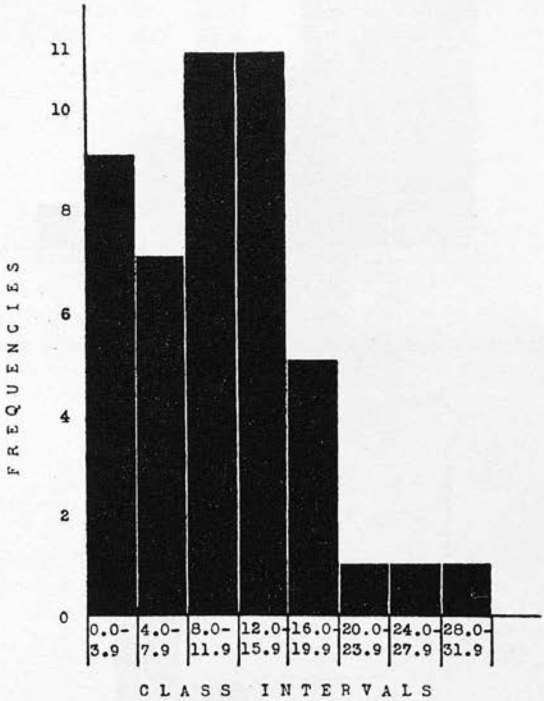

FIG. 11. Distribution of the kemp-percentage figures in 46 of the female progeny of ram D

Mean percentage = 10·63 ± 0·98

These analyses provide further evidence of the tendency shown by these rams in previous data (Figs. 8, 9) to transmit to their offspring a specific degree of kempiness.

The numbers of matings recorded of the other eight rams are too small to indicate the degree to which each transmitted its expression of kemp to its offspring. It should be noted, however, that in 18 of the 29 matings (62·1 per cent.) of these rams, the offspring had kemp-analyses identical with that of one of their parents or intermediate

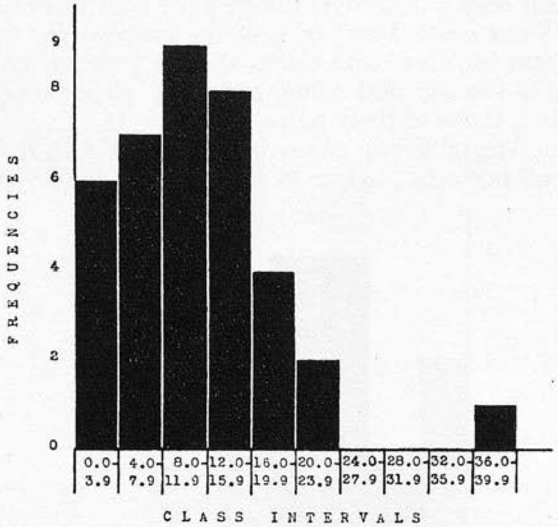

FIG. 12. Distribution of the kemp-percentage figures in 37 of the female progeny of ram E

Mean percentage = 10·88 ± 1·23

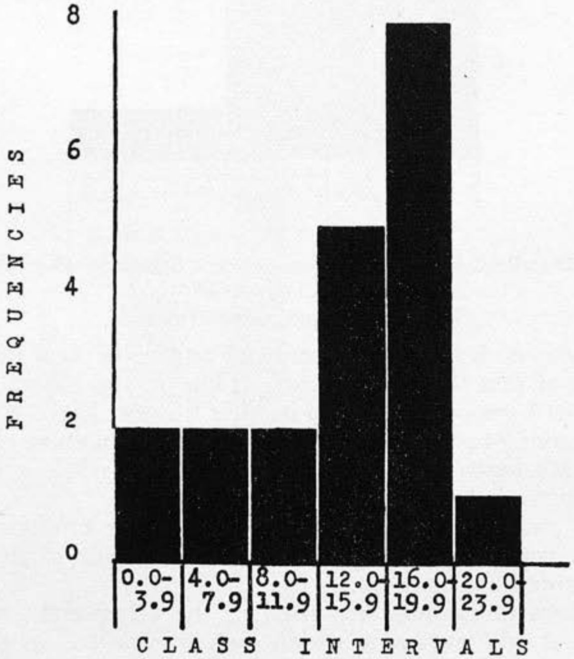

FIG. 13. Distribution of the kemp-percentage figures in 20 of the female progeny of ram F

Mean percentage = 13·69 ± 1·24

between their parents' analyses. Finally, out of the whole series of matings, in 35 cases (61·4 per cent.) the progeny had the same kemp-analysis as one of their parents or analyses intermediate between those of their parents.

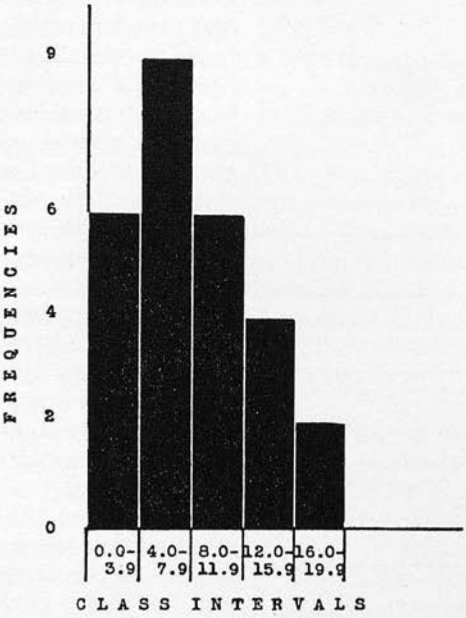

FIG. 14. Distribution of kemp-percentage figures in the progeny of rams G, H, J, K, and L, each of which had kemp-analysis figures of < 1%

Mean percentage for group = 8·01 ± 1·01

Discussion

In searching the literature, the writer has not found any published account of investigations on the inheritance of kemp carried out by analysing a large number of fleeces of adult sheep in a recorded flock. Roberts [3] states that in the majority of cases in the Welsh Mountain breed, the percentage of kemp in the adult fleece is correlated with the type of birthcoat, and that non-kempy adult fleeces correspond to a type of covering in the lamb which is definitely unsuitable for mountain conditions. Barker [10], reviewing Roberts's work, states that the type of birthcoat exhibited by the lamb is governed by heredity. He does not, however, quote any scientific proof of this. White [11] refers to the relationship between kemp in the adult Welsh fleece and the type of coat of the lamb. He states further that the type of birthcoat was found to be inherited, and that more than one factor is concerned. These authors have not published data, so far as the writer is aware, which demonstrate the mode of inheritance of kemp in the Welsh Mountain breed. Darling [2] investigated the wool–long-hair–kemp relationships in a number of selected Blackface sheep. He found that the range of variability of kemp was very great and deduces from this that kemp could be bred out of the fleece. Barker [10] alludes to the opinion held by many experienced breeders, that the presence of kemp is governed by hereditary factors. The writer has met breeders of Blackface sheep who were convinced that kemp could be practically eliminated from the breed by judicious selection of breeding-stock. Personal opinions, however, even when based on much practical experience, do not constitute scientific evidence, and of this there appears to be an almost complete absence.

The literature contains many references to cross-breeding experiments made, in many cases, with a view to producing an improved type of fleece by the use of fine-wooled rams on ewes of coarse-wooled breeds.

Dechambre [12] found that the offspring from the cross between a medium fine-wooled Berrichon ewe with a hairy-coated African fat-tailed ram had hairy coats like that of the sire. Ewart [13] mated Blackface ewes to a Southdown ram. He found there was considerable variation both in body-conformation and in fleece-characters in the F_1 and F_2 generations, but all the progeny resulting from this cross were free from kemp. Völtz [14] crossed ewes of the Pomeranian land breed with an Oxford ram. He reports that the mixed wool of the former (which contains kemp) is dominant over the Oxford-down type of wool. Spöttel [15] found that in the F_1 generations of crosses between Moufflon and Somali sheep with Merinos, a kempy type of fleece predominated, and that other fleece-characters in the F_1 were intermediate between the Moufflon or Somali and the Merino. He states further that in the F_2 generation kempiness predominates at first, but a gradual refinement occurs with advancing age. Ivanov, Belekhov, and Greben [16] in the F_2 generation from crosses of Voloshian and Chuntuk ewes with Lin-

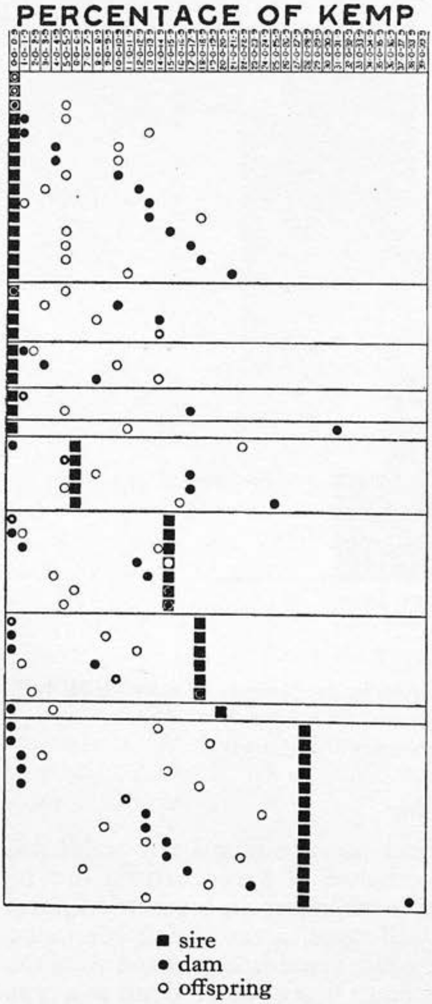

FIG. 15. Diagrammatic representation of the kemp-analysis figures of sire, dam, and offspring in matings of 10 rams

▣ = sire, dam, and offspring
▩ = sire and dam
□ = sire and offspring
⦿ = dam and offspring

coln rams, observed no segregation of fleece-characters. They state that the F_2 resembles the F_1, that there was intermediate inheritance of fleece-characters, and that in the F_2 from Chuntuk ewes none of the Chuntuk characters, such as coarse hair or kemp, were found. Among other Russian work dealing with the inheritance of fleece-characters in crosses are papers by Belekhov [17], [18], Belekhov and Greben [19], and Ivanov and Belekhov [20]. These are all concerned with the crossing of coarse-wooled breeds with Merinos. Kemp fibres were not found in either the F_1 or the F_2 generations, but there was a more marked segregation of characters in these crosses than was found, for example, in the Lincoln × coarse-wooled crosses. In summing up, the suggestion is made that the number of factors involved in the Merino crosses is smaller.

The examples quoted of observations on the occurrence of kemp fibres in crosses between non-kempy and kempy breeds of sheep indicate that, if kempiness be inherited, the inheritance is not of a simple Mendelian type, but is probably governed by multiple factors. It is doubtful, however, whether analyses of kempiness in interbreed crosses have any place in a survey of the incidence of kemp in a pure-bred flock such as the present work.

It might be argued that this investigation has not been conducted on correct genetical lines; that ewes and rams should have been sampled at the appropriate time and samples obtained from their progeny when these became adult. It is admitted that this would have been the ideal procedure, but it is emphasized that the best use had to be made of the material available in a limited time. Further, the flock of sheep which provided the bulk of the experimental material was managed on strictly commercial lines, and it was not possible to interfere with the ordinary farm routine.

It is claimed that the data produced establish beyond doubt the fact that the presence of kemp fibres in the fleece of the Blackface sheep is definitely controlled by heredity. If this were not so, the distribution of the kemp-percentage figures for the progeny-group of each of the rams would be expected to approach that of the whole flock. This has been shown not to be the case.

The ages of the experimental sheep varied between 1½ and 4½ years, and this might be thought to constitute a source of considerable error in comparisons of kemp-content. No evidence was found, however, to show that the percentage of kemp in individual sheep varied to any appreciable extent between these ages. Darling [2] showed that with advancing age the percentage weight of long hair decreases and the percentage weight of wool increases. He produced figures for groups of Blackface rams of different ages as shown on the following page.

It will be seen that the figures for mean percentage-weight of wool and long hair together are extraordinarily constant over the five age-groups both for shoulder samples and haunch samples. These figures represent the mean percentage-weight of the non-kemp fractions of the samples, and indicate that decrease in the percentage-weight of long hair with advancing age is balanced by the increase in the percentage-weight of wool. The writer has observed that sometimes very old sheep show a complete absence of long hair, thus upsetting the ratio of non-kemp to kemp. Although this seldom occurs till sheep reach a very advanced age (over 10 years), it was thought advisable to restrict the analyses to sheep not over 4½ years old. Barker [10] states that 'individual sheep examined over a period of years do not show any large differences between the proportions of kemp in different years', thus confirming the findings below.

Distribution and Percentages of Wool and Long Hair in Blackface Rams (Darling)

		Mean percentage-weight of wool	*Mean percentage-weight of long hair*	*Mean percentage-weight of wool and long hair together (the non-kemp fraction)*
Shoulder staples	Shearlings	40	57	97
	2-shear	47	50	97
	3-shear	48	48	96
	4-shear	48	50	98
	aged	53	44	97
Haunch staples	Shearlings	34	59	93
	2-shear	36	56	92
	3-shear	38	50	88
	4-shear	41	49	90
	aged	44	48	92

The influence of factors other than genetic on the expression of fleece-characters involves a wide field of investigation. This work, however, is not intimately concerned with such influences, since all the experimental sheep, with the exception of breeders' stud rams, were kept on the same farm under the same climatic conditions, and all shared the same grazing-land. It is not the practice on the farm in question to feed the stock rams intensively. These are kept out day and night until a few weeks before they are mated to the ewes, when they are brought into the house each evening and fed moderately well till they are allowed to run with the ewes. This brief period of hand-feeding has no appreciable effect on the expression of kempiness in the fleece. Not less than 3–4 months' feeding are required to effect any marked change in the length or diameter of a kemp fibre in such a way as to cause material change in the percentage of kemp to total wool-substance produced.

It is clear from the results obtained that the expression of kemp in the fleece of Blackface sheep, as measured by the percentage weight in the dorsal area of maximum density, is not controlled by a simple Mendelian type of inheritance. This statement is not, perhaps, justified with reference to the progeny groups of the various rams, where kemp-analyses of the dams were not available. By reference, however, to the kemp-analysis figures for rams, ewes, and the resulting offspring in 57 matings, shown in Fig. 15, it is evident that neither the non-kempy condition shown by the first 5 rams, nor the grossly kempy condition shown by ram B, behaves as a Mendelian dominant. The figures obtained from these matings, in fact, clearly indicate intermediate inheritance governed by multiple factors. Further reference to Fig. 15 will show that out of 25 matings of rams with kemp-analyses of less than 1 per cent., in 15 cases (60·0 per cent.) the progeny had kemp-figures of less than 8 per cent. Similarly, in 32 matings of rams with analyses ranging from 6 to 28 per cent. the progeny in 12 cases (37·5 per cent.) had kemp-percentages of less than 8 per cent. Again, it will be found that the number of ewes with kemp-analyses of less than 4 per cent. in this series is 22. Of these 12 (or 54·5 per cent.) had progeny with kemp-figures of less than 8 per cent. To consider the figures for these ewes in another way: there were 9 ewes with analyses of less than 4 per cent. of kemp mated to rams with kemp-figures of less than 1 per cent. Of these 7 (or 77·7 per cent.) had progeny with kemp-analysis figures of less than 8 per cent. There were mated to the other rams (kemp-analyses ranging from 6 to 28 per cent.) 13 ewes with kemp-percentage figures of less than 4 per cent. In only 5 cases (38·5 per cent.) did the resulting progeny have kemp-percentages of less than 8. The above figures would appear to indicate that the non-kempy condition of the fleece in the Blackface sheep is incompletely dominant over the more kempy condition. This is supported by the breeding performances of rams A, G, H, J, K, and L, as illustrated in Figs. 8 and 14.

If, then, the presence of kemp in Scottish Mountain Blackface sheep is inherited intermediately, with a tendency for non-kempiness to be dominant, eradication or reduction to negligible proportions is within reach of the practical breeder by the use of rams with fleeces of very low kemp-content, in conjunction with the rigid rejection for breeding of grossly kempy offspring. The level of kempiness tolerated in the offspring would be decreased each season. It is thus theoretically possible to establish an almost kemp-free flock in the course of a very few generations, provided an adequate supply of rams with a low kemp-content in the fleece and of good breed-type be available. It would probably take longer in practice, however, since many points other than kempiness must be considered when selecting breeding-stock, such as body-conformation, size, colour, &c.

There appear to be no great obstacles, however, to prevent breeders of Scottish Mountain Blackface sheep from first reducing by considerable proportions, and then practically eliminating, kemp fibres from the fleeces of their sheep by intelligent selective breeding, together with rigid culling of all sheep showing reversions to the kempy condition.

It seems probable that it would be extraordinarily difficult to eliminate kemp entirely from Blackface sheep. During the examination of wool samples from some 600 sheep in the course of this work, samples from the dorsal area of only one animal were encountered which contained no kemp. Each sheep among the large number classed as containing less than 1 per cent. contained a few typical kemp fibres, though it was always possible to obtain samples from the shoulder region of sheep in this class which were entirely free from kemp. If the incidence of kemp in this breed were to be reduced to such negligible proportions, however, the remaining few fibres would not be a serious objection.

In a genetic experiment involving the analysis of samples of wool, the time which must elapse before samples can be secured from progeny prevents rapid accumulation of evidence, since the sheep is essentially a slow-breeding animal. Under ideal conditions the future development of this work should follow a method which would aim at first establishing a family of sheep (rams and ewes) as nearly homozygous for absence of kemp as possible. Similarly, a definitely kempy strain would be evolved. To effect this would probably take 6–8 years of controlled breeding. Not until this has been carried out with success could reciprocal matings between kempy and non-kempy individuals be made with a view to determining what mode of inheritance is involved in the transmission of kemp; similarly the question of any influence of sex-linkage must await facilities such as are outlined above before it can be determined.

Conclusions

1. The presence of kemp fibres in the fleeces of Scottish Mountain Blackface sheep is inherited.
2. The type of inheritance is that known as Intermediate Inheritance, depending upon a multifactor basis. No form of simple Mendelian inheritance is sufficient to accommodate the results obtained.
3. The lower degrees of kempiness encountered show a tendency to behave as partial or incomplete dominants over the varying higher degrees of kempiness.
4. The presence of kemp could be reduced to negligible proportions by the use of homozygous non-kempy breeding rams, and ruthless culling of kempy progeny.
5. It is improbable that absolute elimination of kemp could be achieved.

Acknowledgements

The writer desires gratefully to acknowledge his indebtedness to Prof. F. A. E. Crew for granting facilities for the carrying out of this work. His sincere thanks are extended to Prof. Wm. C. Miller, who kept in constant touch with the investigations and gave much helpful advice; to Dr. J. A. Fraser Roberts, who allowed him free access to unpublished data and offered advice on the interpretation of the results obtained; to Dr. O. J. Robison, who afforded him much assistance in checking calculations; to Dr. I. W. Parnell for help in the collection of samples; to the many breeders who placed their sheep at his disposal, and in particular to the owner of the recorded sheep who made it possible to arrive at conclusions so rapidly; and also to Miss M. V. Cytovich, of the Imperial Bureau of Animal Genetics, for the translation of Russian papers.

The expenses incurred in this work were met in part by the Empire Marketing Board and in part by the Carnegie Trust; during the investigation the writer held a Carnegie Research Scholarship, and wishes to express his gratitude for the opportunities thus afforded him.

FIG. 2. Carcass of Blackface ewe, to show the kempy patch over the dorsal region after removal of wool and long hair.

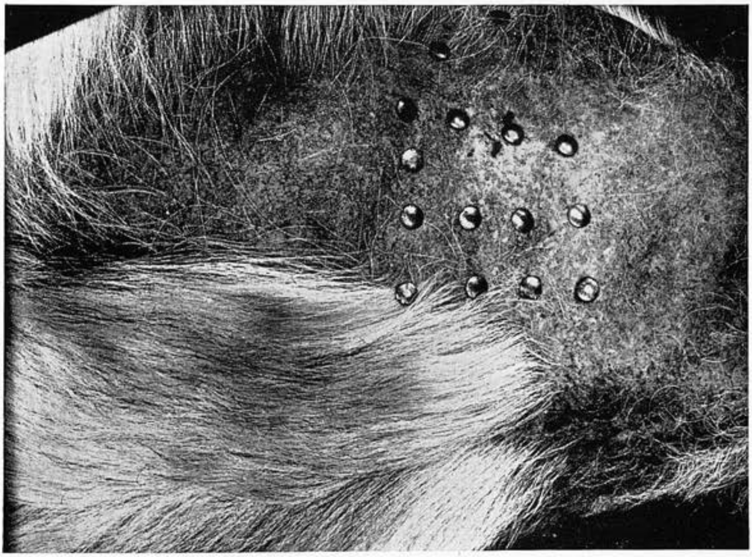

FIG. 3. Carcass of Blackface ewe, showing well-defined margin of dorsal kempy area. The drawing-pins indicate the position of the last four ribs.

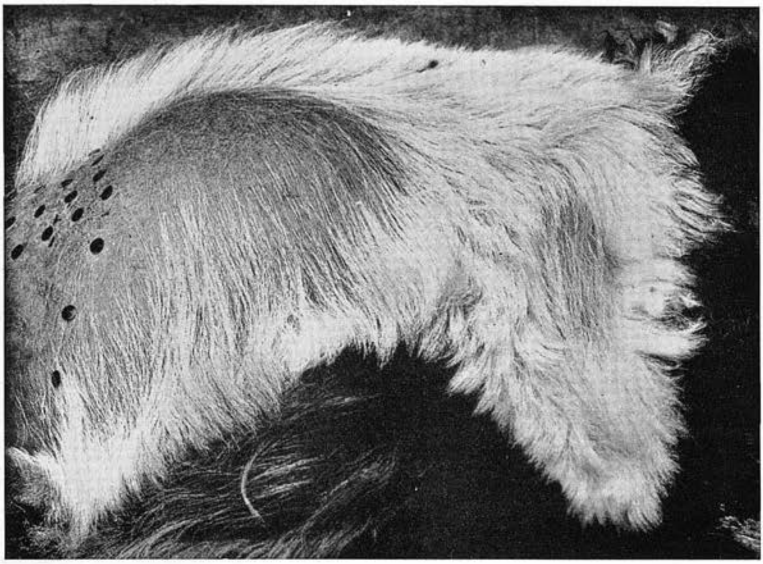

FIG. 4. Carcass of Blackface ewe, showing the dorsal kempy area, and the distribution of kemp over the flank and lower parts of the abdomen.

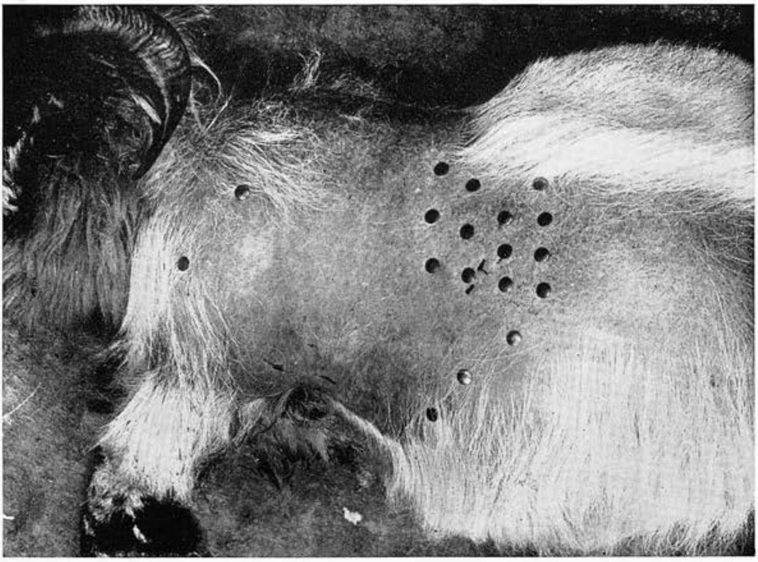

FIG. 5. Carcass of Blackface ewe, showing the beginning of the dorsal kempy area and the absence of kemp on the thorax. The drawing-pins indicate the line of the spine of the scapula, the last four ribs, and the posterior edge of the last costal cartilage.

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STUDIES ON REPRODUCTION IN CATTLE

PT. I. THE PERIODICITY AND DURATION OF OESTRUS

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IT has been observed that Zebu cattle in East Africa appear to exhibit a seasonal fertility, in that fertile matings tend to occur more particularly at a certain season of the year (unpublished results). It seemed that this apparent seasonal fertility could best be explained by assuming that conditions for the occurrence of oestrus and ovulation were more favourable at this time of the year than at any other. Considerable variation in the duration and intensity of oestrus is known to occur, and Hammond [1], working under experimental conditions, noted that in Britain the average duration of oestrus is longest in the summer months and shortest in the winter months.

Observations were accordingly undertaken, first, to ascertain if significant variation in the duration of oestrus in Zebu cattle did occur from season to season, and secondly, to investigate the relationship of any such variation in the duration of oestrus to seasonal variation in environmental conditions.

Experimental Material and Methods

In order that all seasonal changes be noted, as complete a record as possible was kept of environmental conditions, coincident with the observations on the oestrous cycle. Meteorological records—rainfall, maximum and minimum temperatures, and, as no sunshine-recording apparatus was available, observations on the amount of cloud—were made daily. Monthly analysis of the pasture was very kindly undertaken by Prof. R. G. Linton.

All the observations were made on a stock-farm in North Kavirondo in Kenya Colony. The farm is situated approximately 50 miles north of the equator (0·31° N. and 34·30° E.) at an altitude of about 4,900 ft. above sea-level. Normally there are two rainy seasons in the year: the long rains occur approximately from March to June, and the short rains in August, September, and October. The average annual rainfall for this district, recorded at two stations for 11 and 8 years, respectively, is 68·41 in. The wettest months of the year are March (av. 6·11 in.), April (av. 9·15 in.), May (av. 9·58 in.), June (av. 6·02 in.), August (av. 8·96 in.), and September (av. 6·37 in.). July with an average rainfall of 5·94 in. is the driest month between the long and short rains. January with an average of 2·26 in. is the driest month of the year, closely followed by November, December, and February. No temperature records are available for this district as a whole, but those from an adjoining district (recorded at a station approximately 50 miles from the above stock-farm and at a slightly higher altitude) show that the maximum and minimum temperature range for the year is comparatively slight. The mean of maximum and minimum temperatures for 1931 was 73·4° F. and 50·3° F., respectively; the absolute maximum temperature was 83·0° F., and the absolute minimum temperature was 43·1° F.

Originally 11 animals were chosen for the experiment, but for various reasons not connected with the experiment 6 were discarded. Of the 5 animals that were used for the observations on the oestrous cycle, 2 were cows and 3 were heifers. The cows had each borne one calf, but neither was milking during any period of the time they were under observation. The average ages of the cows and heifers were 4½ and 3 years, respectively. All 5 animals gave a negative reaction to the contagious-abortion test at the beginning of the experiment.

The experiment proper began in March 1933. It had been intended to regard the period March–April as a preliminary period and to begin the experiment in May, but unforeseen circumstances necessitated finishing the experiment in February 1934; experimental details are, however, given from March in order that a complete year may be covered. There are, moreover, no reasons why data from the period March–April should not be considered with the rest of the data. From March until the end of April two vasectomized bulls were used. The procedure adopted at this time was as follows: after a bull had served a cow he was removed from the paddock and immediately replaced by the other bull. This bull was removed in 30 min. or on service, whichever was the lesser period, and the other bull was returned. This procedure was continued until the end of oestrus. On a few occasions when a further service had not taken place in 30 min., the bull was left with the cow until service occurred, or indefinitely when no service took place. It was noted that on three occasions bull No. 22 failed to serve an oestrous cow although with her for 30 min., and on another occasion bull No. 21 did not serve an oestrous cow although with her for well over an hour. As the duration of oestrus seemed to be very short it was decided to use only one bull for further observations, and from May onwards bull No. 21 was used, except for a few occasions when two cows coming on 'heat' at about the same time necessitated the use of both bulls, and in November when bull No. 21 was suffering from phimosis and was unfit for service. As both bulls had several times been observed to take a long time to serve a cow on 'heat' the following procedure was adopted and used from May until the end of the observations in the following February. The 5 experimental animals were kept with the vasectomized bull in two paddocks, each of which was approximately four acres in extent. The animals were moved from one paddock to the other according to the state of the grazing. Owing to the scarcity of grazing during the dry season (December, January, and February) the animals were allowed to graze outside, but in the neighbourhood of the paddocks. Once a day the animals were watered at a stream half a mile away. Since the bull was with the cows all the time, a cow was noticed immediately she began to show signs of coming on 'heat'. If this occurred during the day the oestrous cow was allowed to remain with the rest of the experimental animals, but if at night, the cow was placed in a small paddock adjoining the larger ones for ease of observation. The approximate date on which a cow was due to come on 'heat' was known from previous records. If a cow had not come on heat by the seventeenth day after the beginning of the previous oestrous period she was placed in the small paddock that night and kept under observation night and day until she did. The exact time of the initiation of oestrus was thus known.

The bull was removed from the cow immediately after service had taken place. After half an hour he was put back with the cow and left with her, either until a further service took place, in which case he was again removed for half an hour, or indefinitely when no service occurred. In this way there was no possibility of service not taking place through the bull being with the cow for too short a time. The greatest number of services performed by bull No. 21 within a short period—5 in 6 hours and 8 in 28 hours—took place when 3 cows came on 'heat' within a day of each other. This number of services appeared to have no adverse effect on the sexual capabilities of the bull. Throughout the experiment bull No. 21 performed 124 services and bull No. 22 27 services. Oestrus was recognized solely by the occurrence of mating, and the duration of oestrus was estimated as the time between the first and last service in the one oestrous period. External signs of oestrus were usually so slight as to be unrecognizable. Occasionally a flow of mucus, at first clear and fairly fluid, later thicker and whitish, occurred at the time of oestrus. An animal coming on 'heat' was easily recognized by the bull following her about, standing near her, and from time to time, particularly as the onset of oestrus approached, attempting to mount her. The duration of the dioestrous cycle was taken as the interval between the beginning of one oestrus and the beginning of the subsequent oestrus.

The Periodicity of Oestrus

It is usually considered that the dioestrous cycle in cattle lasts for approximately 21 days. Hammond, who investigated 58 cycles, using a vasectomized bull, found the range of variation to be from 16·6 to 24·0 days; the mean was 19·2 days and the mode 17·8 days. Frei and Metzger [2] give a slightly greater range of variation, namely, 15 to 25 days. In their investigations the mean was 20·2 days and the mode 19·1 days.

Particulars of the duration of the dioestrous cycle, noted by different workers, are summarized in Table 1. A range of variation exceeding that of 15–25 days may possibly in some instances be due to individual differences, but very extreme variation in the length of the cycle is undoubtedly due to the inclusion of abnormal cycles. It will be seen from Table 1 that the mean length of the cycle, as observed by different workers, lies between 19 and 21 days, and the mode in those cases in which it can be accurately determined between 17·8 and 20·8 days.

Sixty-three cycles in 5 animals were investigated by the author. Details of these cycles are given in Table 2. The range of variation in the duration of the cycle is from 17·9 to 24·1 days; the mean duration is 20·1 days and the mode 20·7 days. The distribution of the cycles of various durations is given in Fig. 1.

TABLE 1. *Duration of the Dioestrous Cycle*

Breed	*Country*	*No. of animals*	*No. of cycles*	*Range of variation (days)*	*Mode (days)*	*Mean (days)*	*Authority*
Shorthorn	Britain	15	58	16·6–24·0	17·8	19·2	Hammond (1927)
Brown	Germany	..	393	8·0–32·0	20·8	21·7	Wagner (1931)
	Germany	..	59	15·0–25·0	19·1	20·2	Frei and Metzger (1926)
	Britain	11	..	17·2–21·2	19·2	19·1	Marshall (1924)
Zebu	Kenya	5	63	17·9–24·1	20·7	20·1	Anderson
	Germany	38	350	6·0–30·0	18–22	..	Struve (1911)
	Germany	12	93	..	18–24	..	Schmid (1902)
	Germany	..	..	..	21	..	Kupfer (1920)
	Germany	..	..	..	21	..	Zeitschmann (1921)
	Germany	..	..	..	21–8	..	Schmaltz (1926)
	Sicily	..	..	..	22	..	Alongi (1924)
	Italy (Umbria)	..	..	..	22–3	..	,, ,,
	Italy (Umbria)	..	..	..	21–8	..	Sanctis (1926)
	Germany	..	..	17·5–28·0	..	..	Weber (1911)
	France	..	..	..	21	..	Curot (1921)
	Germany	..	..	..	21–8	..	Franck-Albrecht (1914)

TABLE 2. *Duration of the Dioestrous Cycle in hours*
Zebu Animals

No. of animals	*1933*										*1934*	
	Mar.	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*
31	493	528	492	505	521	506	512 519	466	580	479 512	514	510
66		469 472	435		470 474	451	493 430	487 444	457	458 431	441	467
72		455 477			435 446	446 485	432 464	453 444	479	460	487 454	
80					514 506	514		493	494 457	548	542	490
90	464	497		492		473	548 531	479	484 494	549		
Av.	478·5	483	463·5	498·5	480·8	479·2	491·1	466·4	492·3	491	487·6	489
No. of cycles	2	6	2	2	7	6	8	7	7	8	5	3

The mean length of the cycle in Zebu cattle (20·1 days) is slightly greater than the figure given by Hammond for Shorthorn crossbreds in Britain (19·2 days), and the mode is also slightly greater. Both figures, however, are well within the range given for European cattle.

Hammond has noted that cows have a slightly longer oestrous cycle than heifers, the average difference being 11 hours. There is no difference in this respect in the animals examined by the author (Table 3).

TABLE 3. *Duration of the Dioestrous Cycle in Zebu Cows and Heifers*

	No. of animal	*No. of cycles*	*Duration of Cycle in Days*		
			Average	*Min.*	*Max.*
Heifers	72	14	18·8	18·0	20·3
	80	9	21·1	19·0	22·8
	90	10	20·9	19·3	22·8
Average for heifers			20·3	18·8	21·9
Cows	31	14	21·3	19·4	20·0
	66	15	19·1	17·9	20·4
Average for cows			20·2	18·7	20·2

The monthly variation in the duration of the cycle is shown in Table 2. The longest cycle—498·5 hours—occurs in June and the shortest in May. During the four months November, December, January, and February the cycle maintains a consistently high level, namely, between 488 and 492 hours.

Hammond found that on the average the cycle was about 40 hours longer in the summer than in the winter or spring. Wallace, on the other hand, states that the cycle is shorter in summer than in winter. Wagner [3] gives the length of the cycle in summer and winter as 22·3 and 22·6 days, respectively.

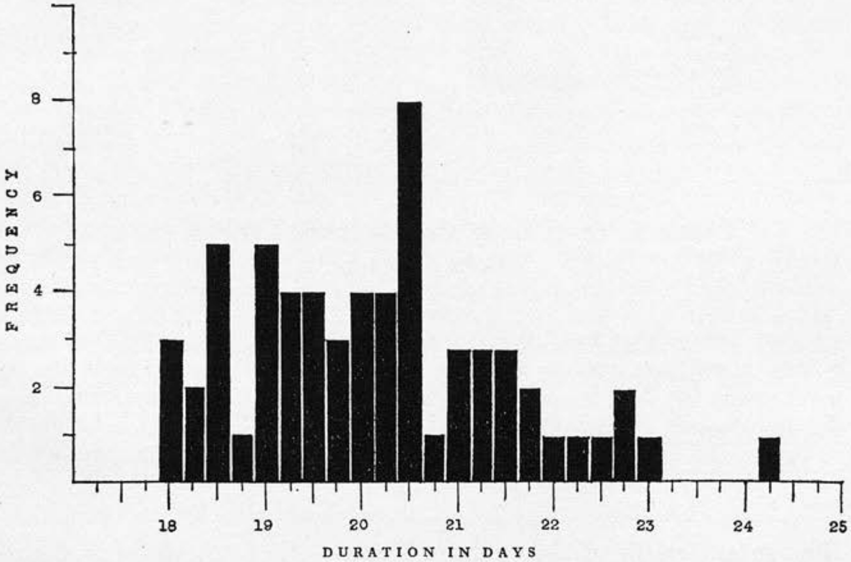

FIG. 1. Dioestrous Cycle

The Duration of Oestrus

Available records show that different workers have noted considerable variation in the duration of oestrus in the cow. It is impossible to say to what extent this is due to the methods employed in determining the existence of oestrus. The signs and intensity of oestrus vary so greatly that they are quite unreliable for this purpose. The only reliable criterion for the physiological and psychological state of oestrus is the occurrence of mating, and it is only by determining over what length of time a cow will accept the bull that the extent of oestrus can be judged.

The mean duration of 64 oestrous periods determined by Hammond in this way was 16·2 hours; the mode was 16·8 hours and the range of variation 6–30 hours. Data on the duration of oestrus in the cow is summarized in Table 4.

The most outstanding feature of the observations made by the author on the Zebu cattle was the extraordinary short duration of oestrus (Table 5). The mean length of 74 oestrous periods was 1 h. 20 min.

In 11 oestrous periods, i.e. in 14·9 per cent. of the total number of oestrous periods, single services occurred. In such cases oestrus was given the arbitrary duration of 10 min. A further check on this point is available from some of the earlier observations when two vasectomized bulls were used. At this time the procedure adopted was to remove one bull immediately after service and replace him by the other. On several occasions when this was done no second service took place, a fact which emphasizes the exceedingly brief duration of oestrus. The longest period of oestrus recorded in the 5 animals was 2 hrs. 51 min. Longer periods have, however, been recorded in two other cows, but as these animals reacted positively to the contagious-abortion test data from them have not been included with the other results. In cow No. 12 oestrus lasted for 2 hours and 7½ hours in January and February, respectively, and in No. 41 a period of 5 hours was noted in November, and single services took place in October and January. (There is no record for December in this cow, as the vasectomized bull died of rinderpest.)

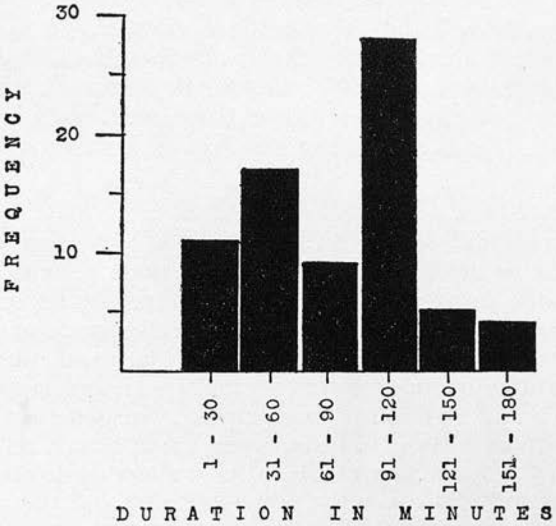

Fig. 2. Duration of Oestrus

TABLE 4. *Duration of Oestrus*

Breed	*Country*	*No. of animals*	*No. of periods*	*Range of variation (hours)*	*Mode (hours)*	*Mean (hours)*	*Authority*
Shorthorn	Britain	15	64	6–30	16·8	16·2	Hammond (1927)
	Britain	..	12	8–21	16·6	15·7	Marshall (1924)
Zebu	Kenya	5	74	0·2–2·9	1·8	1·3	Anderson
	France	..	..	..	12–24	..	Curot (1921)
	Sicily	..	..	..	24	..	Alongi (1924)
	Italy (Umbria)	..	..	..	12–24	..	,, ,,
	Germany	..	..	..	24–48	..	Franck-Albrecht (1914)
	Germany	..	..	12–120	..	..	Schmaltz (1926)
	Germany	..	155	3–36	..	..	Weber (1911)

TABLE 5. *Duration of Oestrus in minutes*
Zebu Animals

No. of animal	*1933*										*1934*		
	Mar.	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Average*
80				10	109	118 99		165 112	60	75	99 106	106	96
72	10	120	46	111	120 135	115 106	141	77 83	81	52 45	100 110		91
90	10	10 38		10 10		10 51	41	148 75	43	95	107	109	54
31	10	10 104	45	90	113	108 171	36	47 97	57	40	152 92	109	80
66	41	10 10	72	62	150	95 97	76 115	147	55 37	158	56 108	104	82
Av. to nearest figure	18	43	54	49	125	97	82	106	55	77	103	107	81
No. of eat-periods	4	7	3	6	5	10	5	9	6	6	9	4	= 74

The shortest duration of oestrus on record seems to be that of Weber [4], who states that in cows with feeble heat-periods oestrus may last 3 hours, but the same author gives the range of variation for such cows as from 3 to 36 hours. Hammond has noted heat-periods of 6 hours' duration and Marshall a period of 8·4 hours. The mean duration of Marshall's and Hammond's figures are 15·7 and 16·2 hours, respectively, and the modes 16·6 and 16·8 hours, respectively. In general the mode has been found by most authors to lie between 12–24 hours. It is therefore the exception for European cattle to have short oestrous periods. On the other hand, in Zebu cattle the mean duration and the mode are 1·3 hours and 1·8 hours, respectively.

Hammond noted that cows have on the average a slightly longer duration of oestrus (19·3 hours) than heifers (16·1 hours); however, when the differences in age were slight any effect was masked by individual differences. The difference in age between the Zebu heifers and cows is slight (3 and 4½ years, respectively); the duration of oestrus is similar in both heifers and cows.

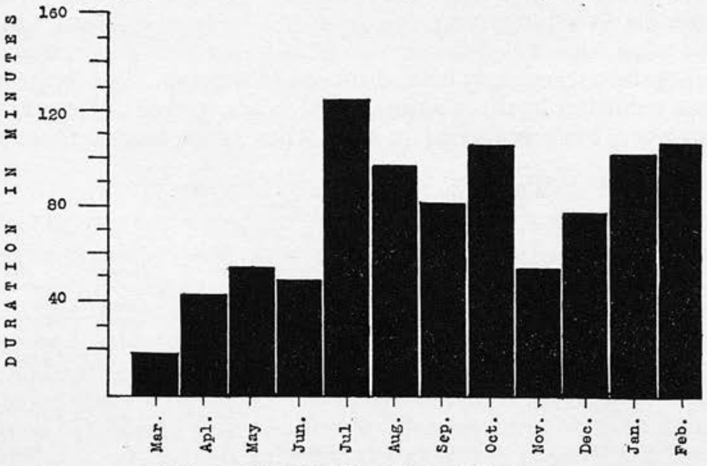

FIG. 3. Monthly Duration of Oestrus

The average monthly variation in the duration of oestrus is shown in Fig. 3 (see also Table 5). The average duration of oestrus is longest in

July (2·1 hours), October (1·8 hours), January (1·7 hours), and February (1·8 hours), and is shortest in March (0·3 hours).

Hammond has observed that the average length of oestrus is greatest in the summer months and shortest in the winter months, there being an average difference of 5–6 hours between the two extremes.

There is no evidence that cattle in different European countries exhibit a significant variation in the duration of oestrus. Suitable records are too few, however, to allow of the question being examined critically. Alongi [5] states that, with regard to the duration of oestrus, no significant differences exist between animals in Sicily, Italy (Umbria), and Germany.

Individual differences in the duration of oestrus in Zebu cattle are very slight, which is probably due to the shortness of oestrus in these animals. Hammond found marked individual differences, the heifers varying from 8 to 21 hours and the cows from 17 to 21 hours.

Relationship between Intensity, Duration, and Periodicity of Oestrus

It is a well-known fact that there is considerable difference in the intensity of 'heat' as shown by outward signs in different cows. Intensity is a factor which cannot be measured accurately and is thus liable to considerable error in interpretation. Nevertheless, variation in the intensity of 'heat' does occur. Weber [4] found that oestrus varied from 12 to 36 hours in cows with intense heat-periods, from 6 to 36 hours in cows with average heat-periods, and from 3 to 36 hours in cows with feeble heat-periods. Hammond has noted that during the winter months, when oestrus is short, the signs of 'heat' are slight. They are, moreover, more marked in the summer months when the duration of oestrus is greater. In sheep, Grant [6] has observed that in general long heat-periods were more intense than short ones; in particular the first heat-period of the season was usually shorter and less intense than subsequent periods. In the Zebu experimental animals the signs of 'heat' were scarcely recognizable. This fact is undoubtedly associated with the brief duration of oestrus in these animals.

The experimental data were examined for the existence of a relationship between the duration of oestrus and the duration of preceding and subsequent dioestrous cycles, but, as is shown in Table 6, no such relationship is evident. Hammond, on the other hand, has noted a correlation between the average length of the cycle and the average duration of the subsequent oestrous period, a long cycle being associated with a long oestrous period and a short cycle with a short oestrous period. Grant failed to find a correlation between the duration of oestrus and that of the preceding and subsequent cycles in the sheep; on the other hand he noted a definite negative correlation between the duration of oestrus and the duration of both preceding and subsequent interoestrous periods (i.e. the intervals between the end of one heat-period and the beginning of the next), in that the shorter the period of oestrus, the longer are the preceding and subsequent interoestrous periods. There is no correlation of this nature in Zebu cattle, which may possibly be due to the shortness of the oestrous period in these animals (Table 7).

TABLE 6. *Relation between the Duration of Oestrus and the Durations of Preceding and subsequent Dioestrous Cycles*

Oestrus (min.)	*Preceding cycles*	*Average (hours)*	*Subsequent cycles*	*Average (hours)*
10–39	8	482	13	485
40–69	13	489	13	484
70–99	14	477	12	488
100–29	19	487	15	480
130–59	7	476	7	464
160–89	1	(506)	2	502

In European cattle it is obvious, as Grant [6] has pointed out for sheep, that the interoestrous period is more variable than that of the whole cycle, since it is subject, not only to variation in the length of the cycle, but also to variation in the duration of oestrus. When oestrus is of short duration and the range of variation is not great, as in Zebu cattle, variation in its duration can have little effect on the length of the subsequent interoestrous period. In these animals variation in the length of the interoestrous period is due mainly to variation in the length of the dioestrous cycle.

TABLE 7. *Relation between the Duration of Oestrus and the Durations of Preceding and Subsequent Interoestrous Periods*

Oestrus (min.)	*Preceding interoestrus*	*Average (hours)*	*Subsequent interoestrus*	*Average (hours)*
10–39	8	481	13	485
40–69	13	488	13	482
70–99	14	476	12	486
100–29	19	486	15	479
130–59	6	480	6	465
160–89	1	(504)	2	499

The average length of the dioestrous cycle in British cattle is about 19½ days [1] and in Zebu cattle about 20 days; the mean duration of oestrus in these animals is 16·2 hours and 1·3 hours, respectively. It is therefore clear that a much greater range of variation occurs in the duration of oestrus than in the duration of the dioestrous cycle in the cow.

Summary

1. Records are given of 63 oestrous cycles in 5 animals. The duration of the cycle varied from 17·9 to 24·2 days with the mean of 20·1 days.

2. The mean duration of oestrus was found to be 1 hour 20 minutes.

3. Monthly variation in the duration of oestrus and the oestrous cycle was noted.

4. No relationship was evident between the duration of oestrus and either the duration of preceding and subsequent dioestrous cycles or the duration of preceding and subsequent interoestrous periods.

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