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The Structure
of the Wool Follicle with
special reference to the
Growth & Form of the Fibre.

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THE STRUCTURE OF THE WOOL FOLLICLE WITH SPECIAL REFERENCE

TO THE GROWTH AND FORM OF THE FIBRE

The difficulty which attaches itself to the various problems connected with fleece characters is aggravated by the lack of fundamental knowledge concerning the mechanism of follicle activity. Information on the growth forces would very considerably assist the interpretation of the complex structural variations in the forest of fibres, upon which many observations have already been made. Detailed studies of follicle form were undertaken with a view to throwing further light on the factors governing fibre production. Not only does this work have a value in correcting our ideas on the meaning of the form of the fleece, but it gives important information on the limitations of follicle activity and on the sources of irregularity in the fleece. As a result we are brought into more intimate contact with the potentialities of the fleece. In the last few years discussions on the physiology of development, growth, the nervous system etc., have conspicuously dwelt on the necessity for a more detailed basis of morphological knowledge, without which physiological ideas on what is and what might have been are not readily obtained.

An outline is given below of the information resulting from a study of wool follicles in New Zealand Romney sheep.

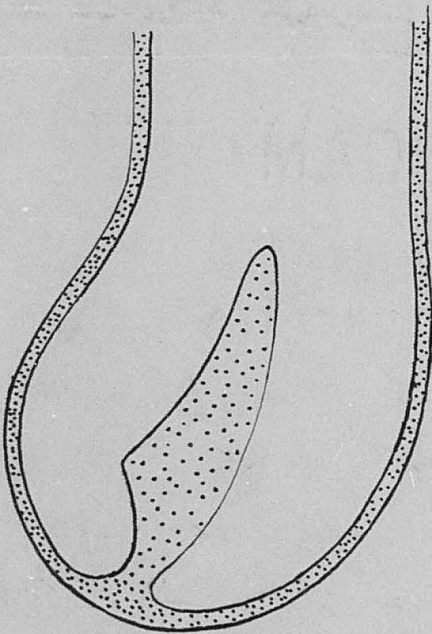
1. MAJOR DIFFERENCES BETWEEN FOLLICLES.

From a previous work it was known ^{that} some follicles only possessed a sweat gland and arector pili muscle while others were without either of these structures. All follicles possessed sebaceous glands. One might therefore create a division into two

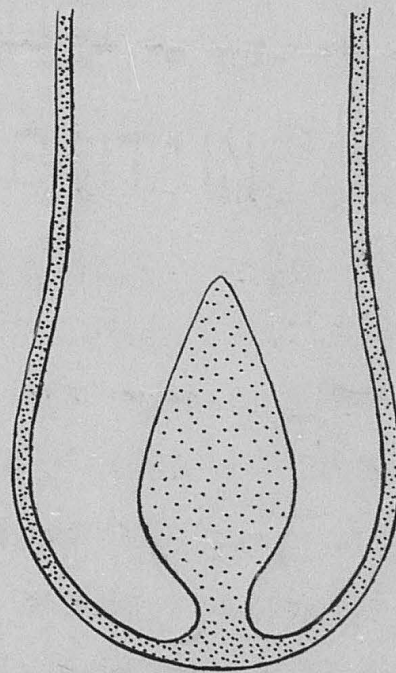
classes of follicles namely, those possessing sweat glands and those without them. However, detailed histological work on skin taken from very different types of Romney sheep, has revealed the existence of vestigial sweat glands. These are by no means rare and occur as very small columns of cells extending parallel with the follicle and being about a quarter its length. They enter the mouth of the follicle by an open duct quite as in the case of a normal sweat gland. In such follicles there is no arector muscle. The vestigial glands cannot be considered as due to the effect of a prenatal check. They are as common in animals vigorously hit by such a check as in those which according to their fibre development would appear to be unaffected by a prenatal check. The upshot of this discovery is to place more reliance in the hypothesis that all follicles are essentially the same and are to be considered in a continuous series.

Additional observations have been made that point out a correlation in the development of the two follicular glands. Follicles possessing a sweat gland possess an arector muscle. In follicles possessing an arector muscle the sebaceous glands are always well developed. Where there is no arector muscle the sebaceous glands are conspicuously smaller often being minute. Hence in the sheep, the two yolk secreting glands are linked together in their development. Whether this association occurs per medium of the follicle muscle or by some

FIGURE 1



A. Asymmetrical face of the papilla, showing the minor diameter.



B. Symmetrical face of the papilla, showing the major diameter.

FIGURE 2

TYPES OF PAPILLA.



Papilla in histerotrich follicle
X150



Papillae in fine curly-tip
follicle X150

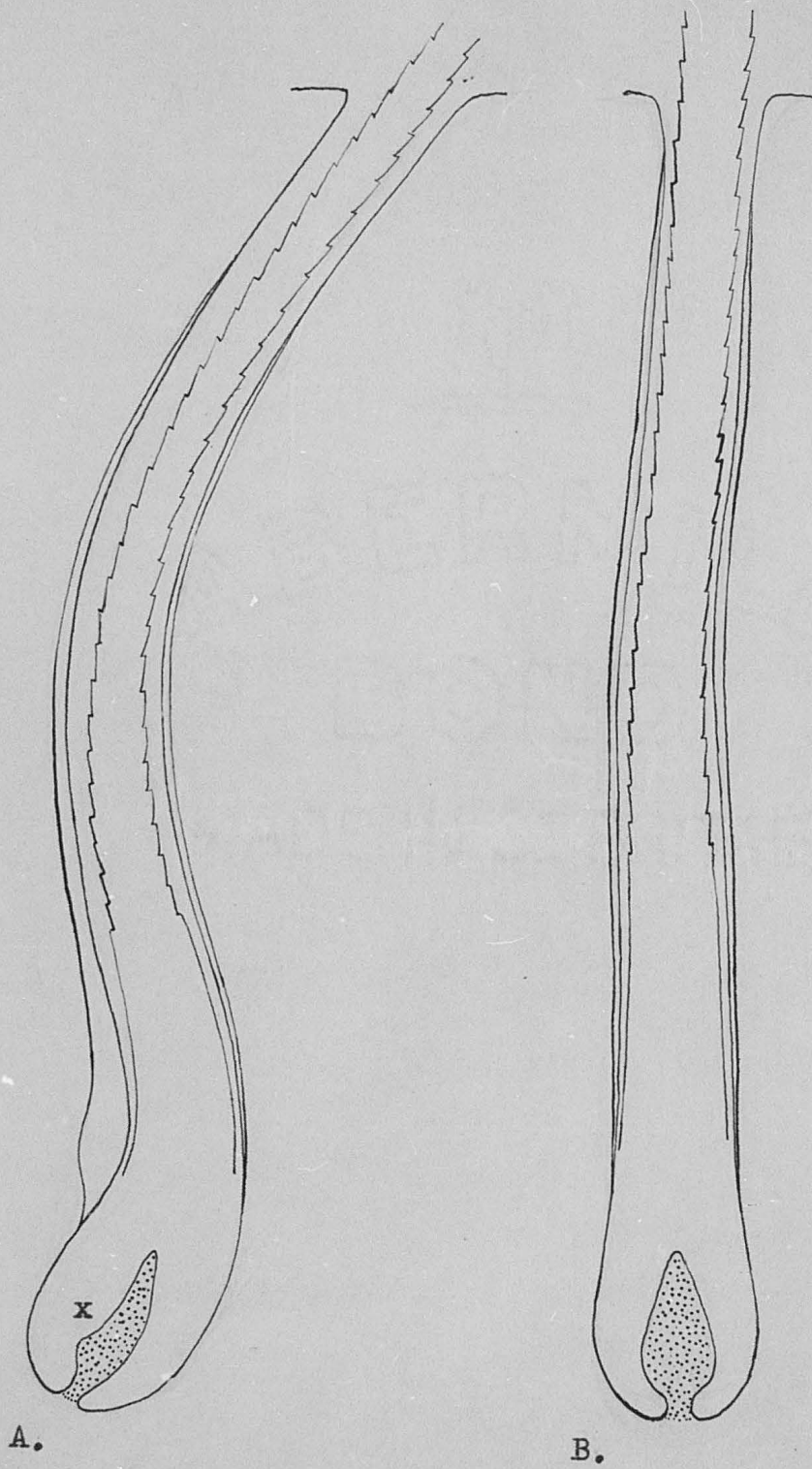


Papilla in stout curly-tip follicle
X175



Views of papillae from
different angles. X150

FIGURE 4



other correlating influence is a matter for separate study.

Depth of Follicles. At a given area follicles producing coarse fibre extend deeply into the skin, while those producing fine fibre are much more superficially placed. Correlated with this it is common to find very greatly elongated follicles at the britch of an animal, but much less gross follicles on back and shoulder. Kemp follicles which have ceased growing will also be found situated quite superficially in the skin, the papilla being on a level with or even shallower than the bases of fine fibre follicles. With the recommencement of growth the fibre resumes a deeper position. However, as is pointed out below, it is the size of the follicle bulb and growing point that influences the coarseness and medullation of the fibre in the most important manner.

2. DETAILED DIFFERENCES BETWEEN FOLLICLES.

Attention to date has been largely focussed on the papillae or growing points which exhibit great variation in their gross form and in their detailed structure. Hitherto no intensive study has been made on the papillae of mammalian hair follicles. This is to be regretted when it is realized that the papilla is the source of nourishment to the fibre and might be expected to have a major influence in fibre production.

A. Gross Form of the Papilla.

Although there are a few follicles possessing papillae that are nearly symmetrical, in general a marked asymmetry about the long axis is to be observed *Fig. 1 A & B.* . Recognition of this asymmetry is a point fundamental to any measurements

FIGURE 3



Twisted condition of the dermal fibres at the base of the papilla, where it is thinned to a neck-like portion.

that may be made on the size of the papilla. Other observations, which are quite fundamental to this work have been made depicting differences in papilla type associated with the various fibre types. These show a general serial arrangement with large stout, nearly symmetrical papillae at the 'halo' end of the array (1) and smaller, thin, markedly asymmetrical papillae at the fine curly-tip and histrotrichs end. Special features distinguish the papillae of sickle fibre follicles notably a reduction in the height of the papilla.

Measurements on the diameter of the papilla.

A large number of measurements have been made on the two diameters of the papilla in follicles from various types of Romney cross-bred sheep. These data have been collected with a view to comparing the size of the papilla at different regions of the body, at different seasons of the year and before and after shearing. As a result it has been possible to establish the concept that the papilla can change its size and form. Furthermore these changes can be correlated with the coarseness of the fibre and, where hairiness was in evidence, with the coarseness of the medulla.

In view of the fact that small follicles possess small papillae and large follicles large papillae, the measurements have been expressed as ratios of

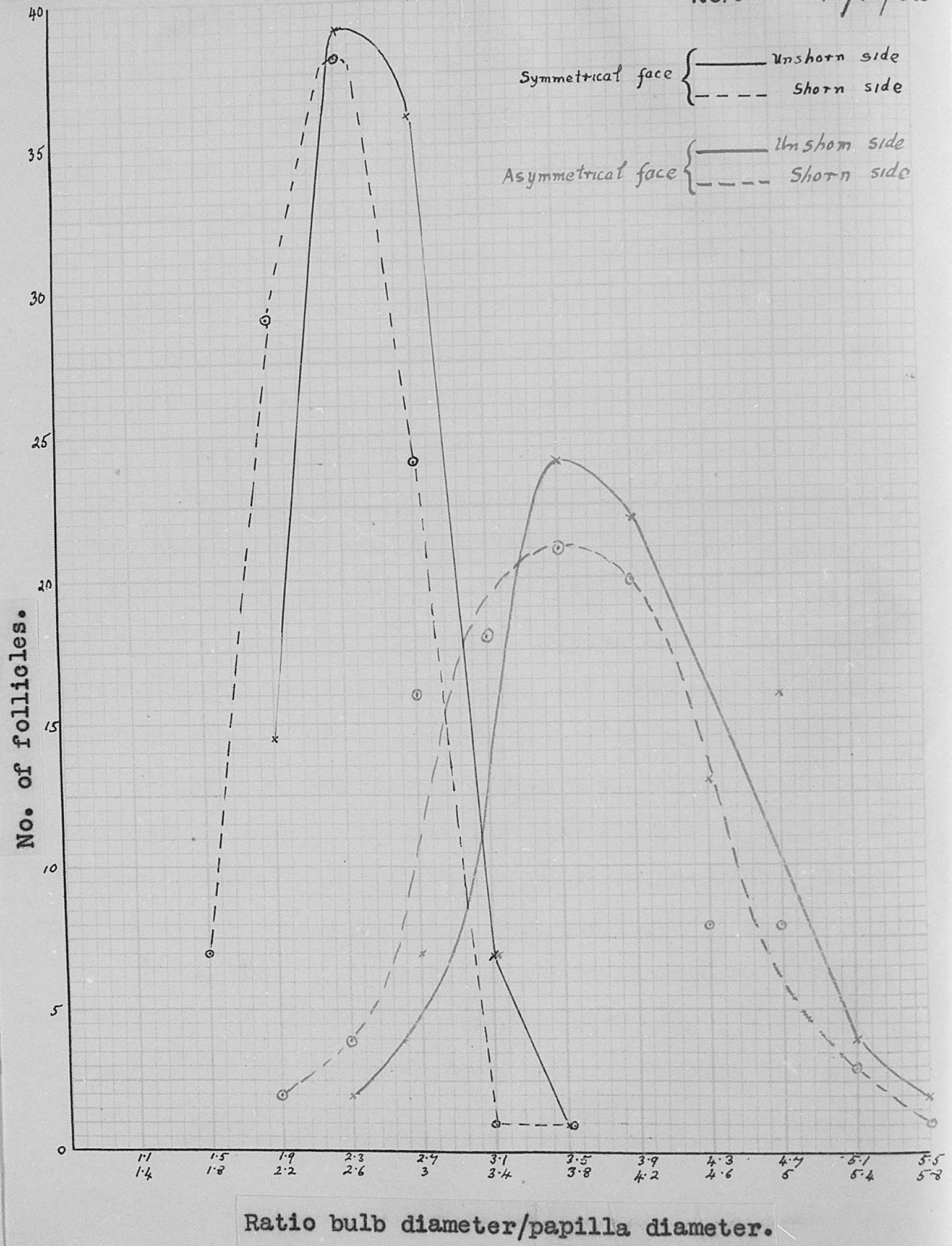
$$\frac{\text{Maximum diameter of the follicle bulb}}{\text{Maximum diameter of the papilla}}$$

This has an added advantage in that errors of measurement (and due to the condition such as the state of swelling)

I

Graphs of frequency of bulb/papilla ratio for Symmetrical and Asymmetrical faces of the papilla taken on each side of a differentially shorn lamb.

No. 659 16/12/32



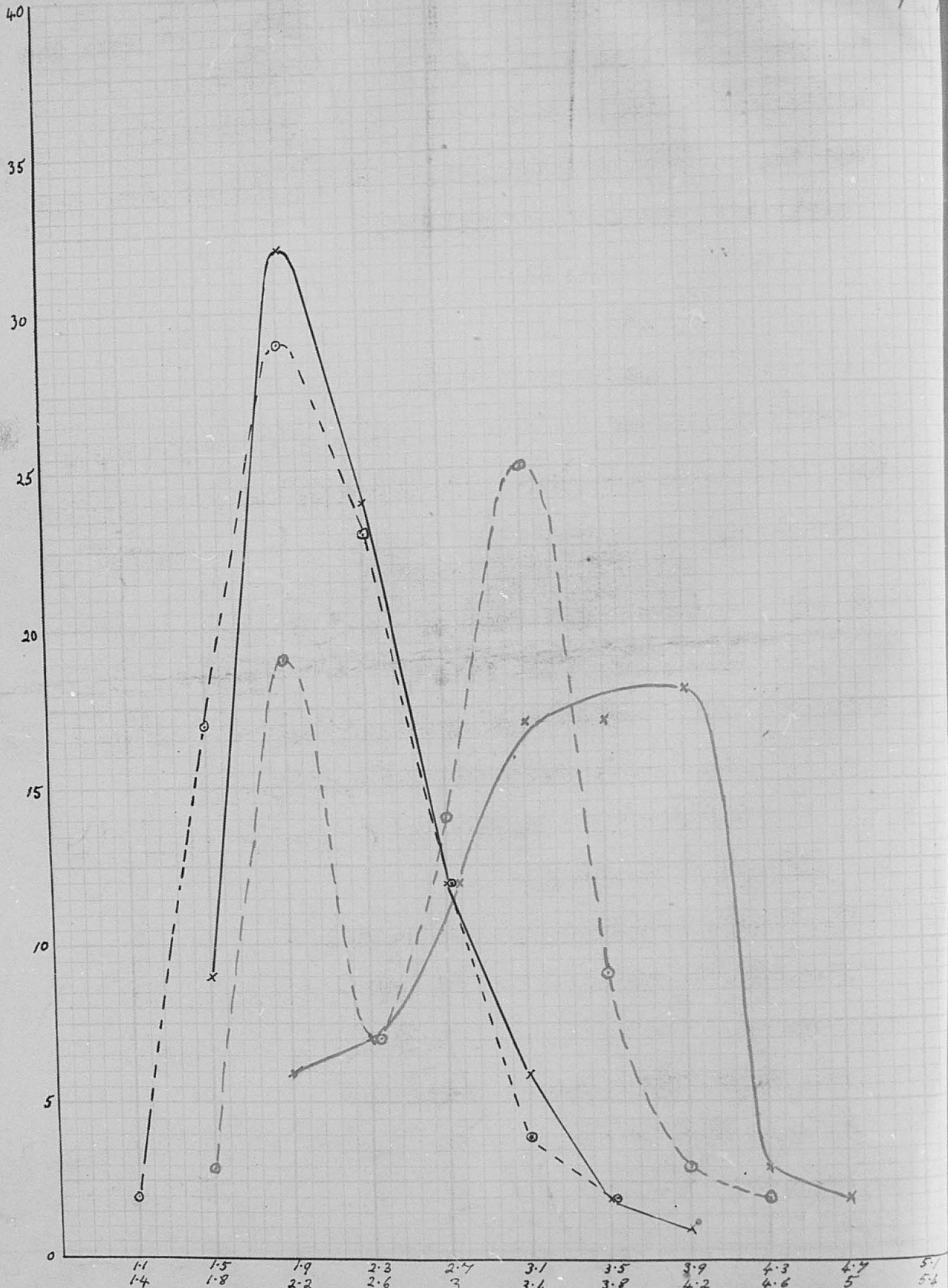
Ratio bulb diameter/papilla diameter.

II

Graphs of frequency of bulb/papilla ratio for Symmetrical and Asymmetrical faces of the papilla taken on each side of a differentially shorn lamb.

No. 659 30/12

No. of follicles.



Ratio bulb diameter/papilla diameter.

are greatly reduced in their resultant effect upon the ratio. In the case under consideration measurements were taken with a micrometer eyepiece working at a magnification of 60 diameters. For the purpose of drawing graphs the ratios were placed in fairly large groups as follows:-

1.1 - 1.4

1.5 - 1.8

1.9 - 2.2 etc.

Sets of graphs I - III, each drawn from measurements of 100 such follicles are presented below for cases of differentially shorn lambs. Graphs show the varying frequency of the ratio:-

$\frac{\text{Maximum bulb diameter}}{\text{Maximum Papilla Diameter}}$

for (a) the symmetrical face of the papilla

(b) the asymmetrical face of the papilla

taken at i. 18 hours after shearing one side of the animal

ii. 2 weeks after the above shearing

iii. 6 months later during mid winter when fine pure wool was being produced.

From these graphs it is seen that:-

The symmetrical face of the papilla is distinctly wider in reference to the width of the approximately circular bulb than is the asymmetrical face. Graph 1.

As a result of shearing there is no very apparent change in the diameter ratio of the symmetrical face, but a distinct decrease in this ratio is shown for the asymmetrical face. This denotes a relative increase in the minor diameter of the papilla.

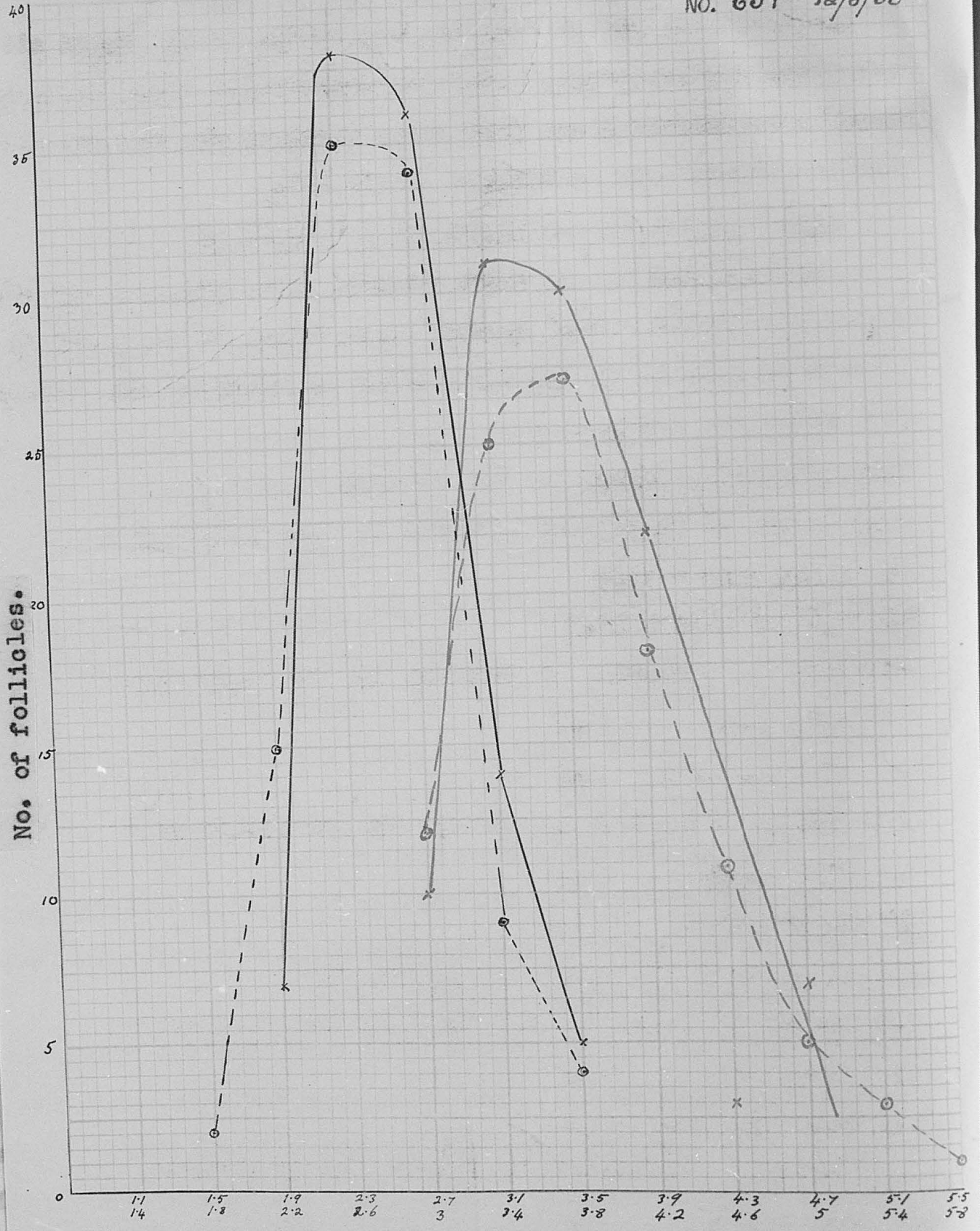
Graph 11.

III

Graphs of frequency of bulb/papilla ratio for Symmetrical and Asymmetrical faces of the papilla taken on each side of a differentially shorn lamb.

Graph

No. 659 12/6/33



Ratio bulb diameter/papilla diameter.

At the winter period the diameter ratios on the shorn side have returned to normal, being comparable with those shown 18 hours after shearing and with those taken on the unshorn side some two weeks after shearing. Graph 111.

Measurements in the Height of the Papilla.

Coincidentally with the above diameter measurements, the height of the papilla was noted in each case, viz., for skin cut 18 hours after shearing, two weeks after shearing and in midwinter six months after shearing:-

Case of a hairy tipped animal (No 659)

Mean height of papilla at 16/12/32 for 100 follicles:-

- (a) Shorn side = 18.3
- (b) Unshorn side = 19.0

Mean height of papilla at 30/12/32 for 100 follicles:-

- (a) Shorn side = 18.3
- (b) Unshorn side = 18.3

Mean height of papilla at 12/6/33 for 100 follicles:-

- (a) Shorn side = 13.5
- (b) Unshorn side = 13.8

Case of a non-hairy tipped animal (No 624)

Mean height of papilla at 5/1/33 for 100 follicles:-

- (a) Shorn side = 20.4 \pm .20
- (b) Unshorn side = 17.9 \pm .12

Mean height of papilla at 12/6/33 for 50 follicles:-

- (a) Shorn side = 13.4
- (b) Unshorn side = 13.7

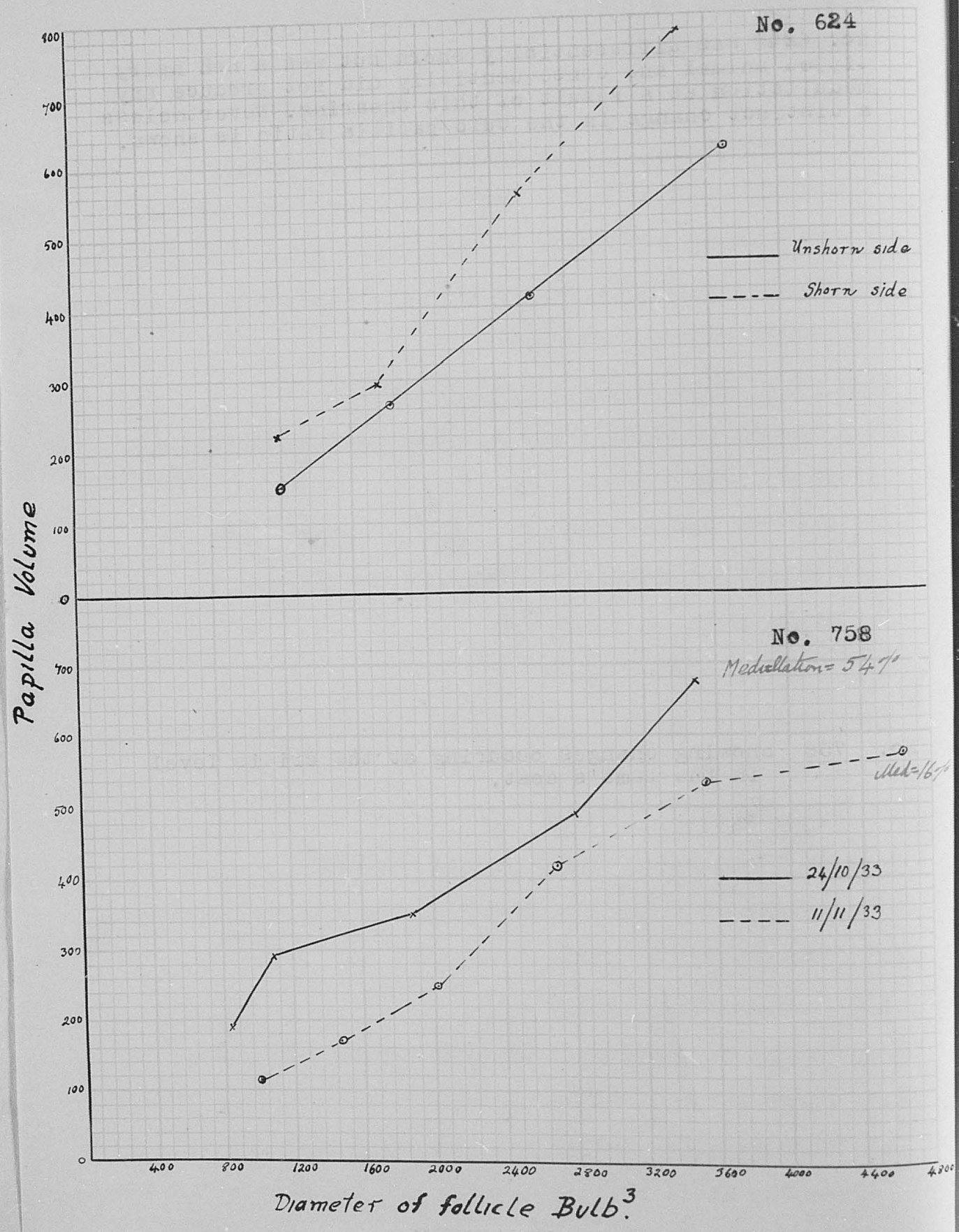
From the above results the two animals show a difference

No. 624 was differentially shorn but was a non hairy tipped animal and consequentially did not produce any medullation as a result of this shearing. Nevertheless a distinct change in the bulb/papilla ratio is shown.

No. 758 Showing changes occurring at the crisis level in the lamb's coat.

V

RELATIONSHIP : Diameter of follicle Bulb³ x Papilla Volume

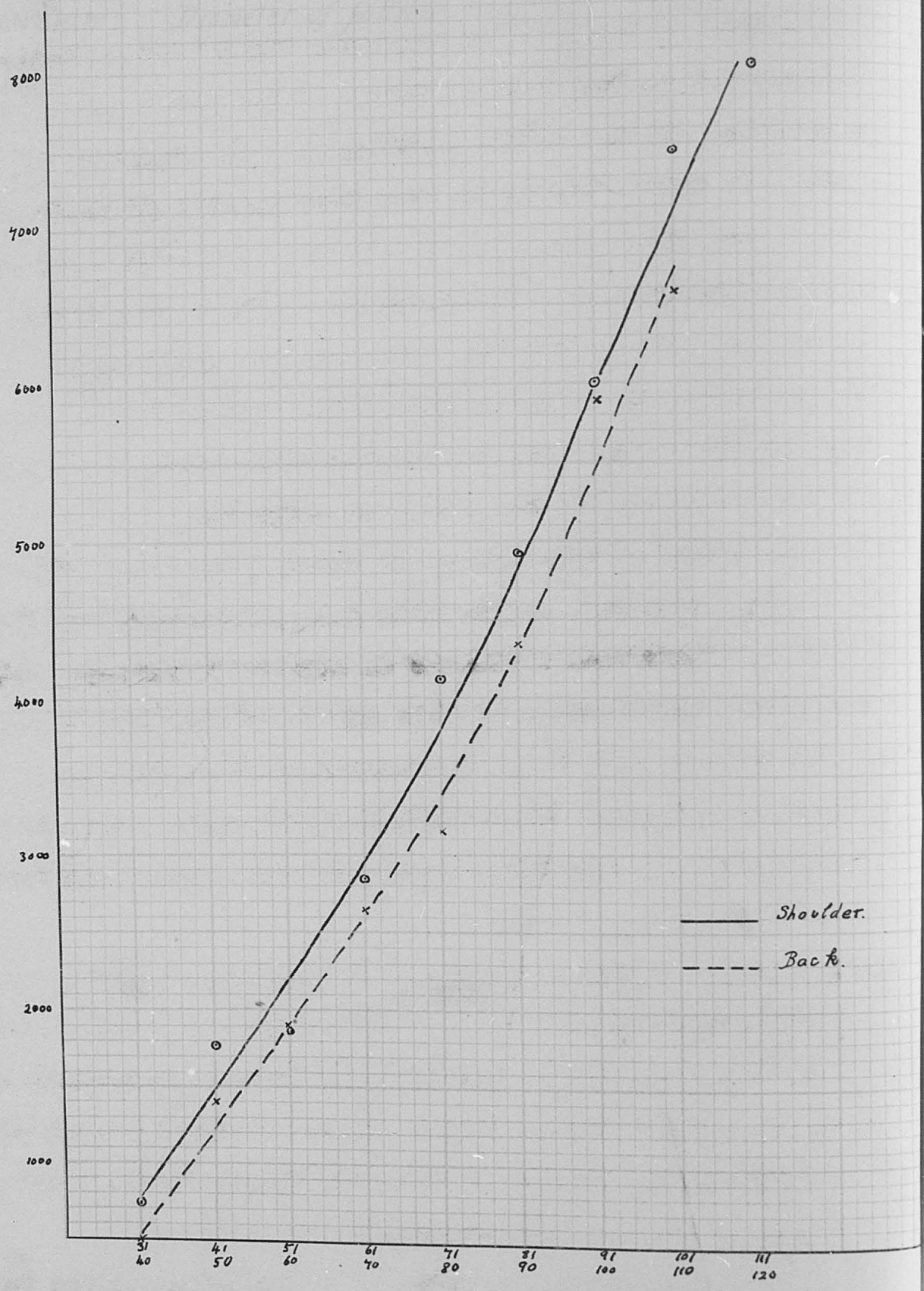


VI

RELATIONSHIP: Fibre cross-section area x Papilla Volume

No. 76

Papilla Volume
Papilla Volume



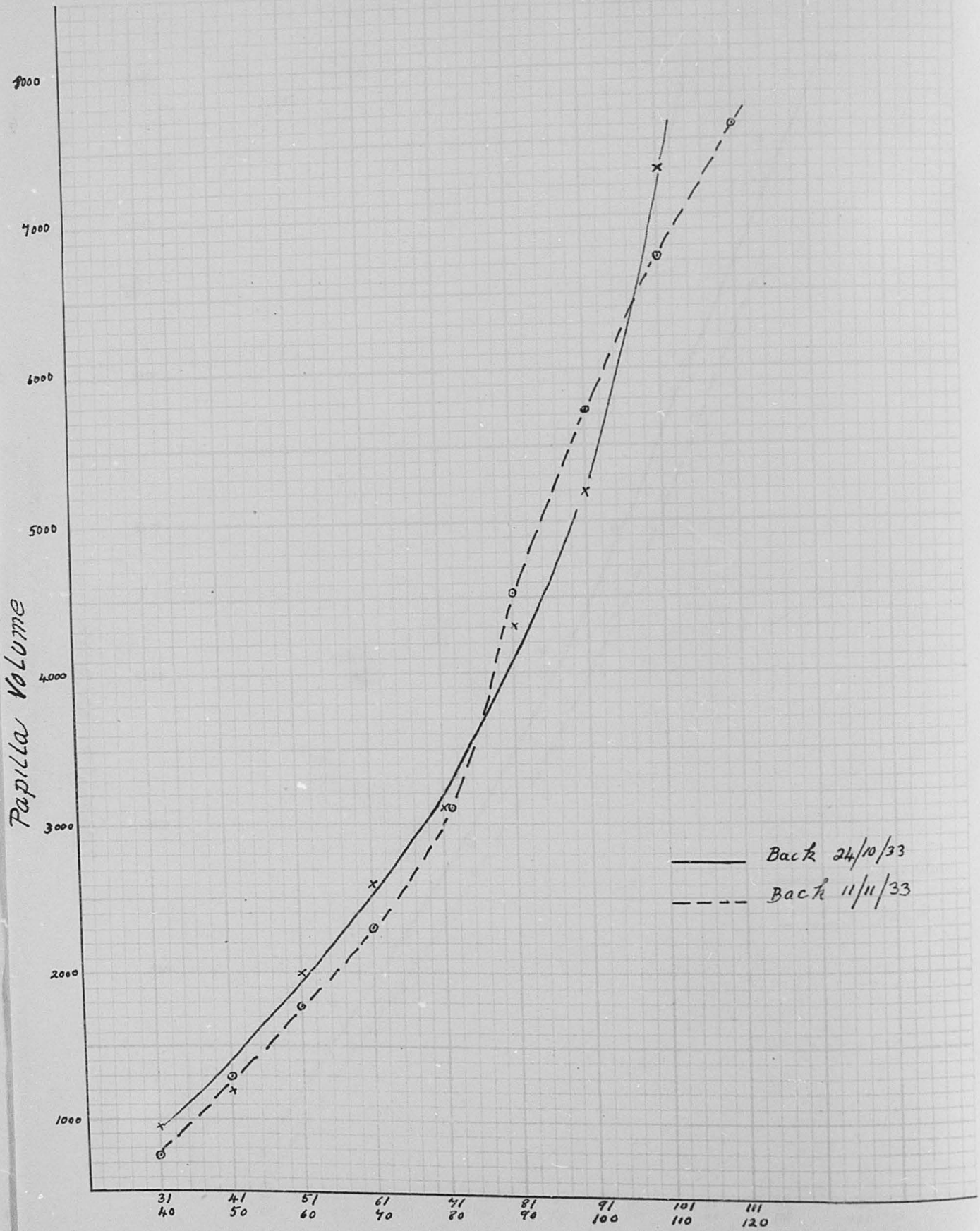
— Shoulder.
- - - Back.

Fibre cross-section area Groups

VII

RELATIONSHIP : Fibre cross-section area x Papilla Volume.

No. 758



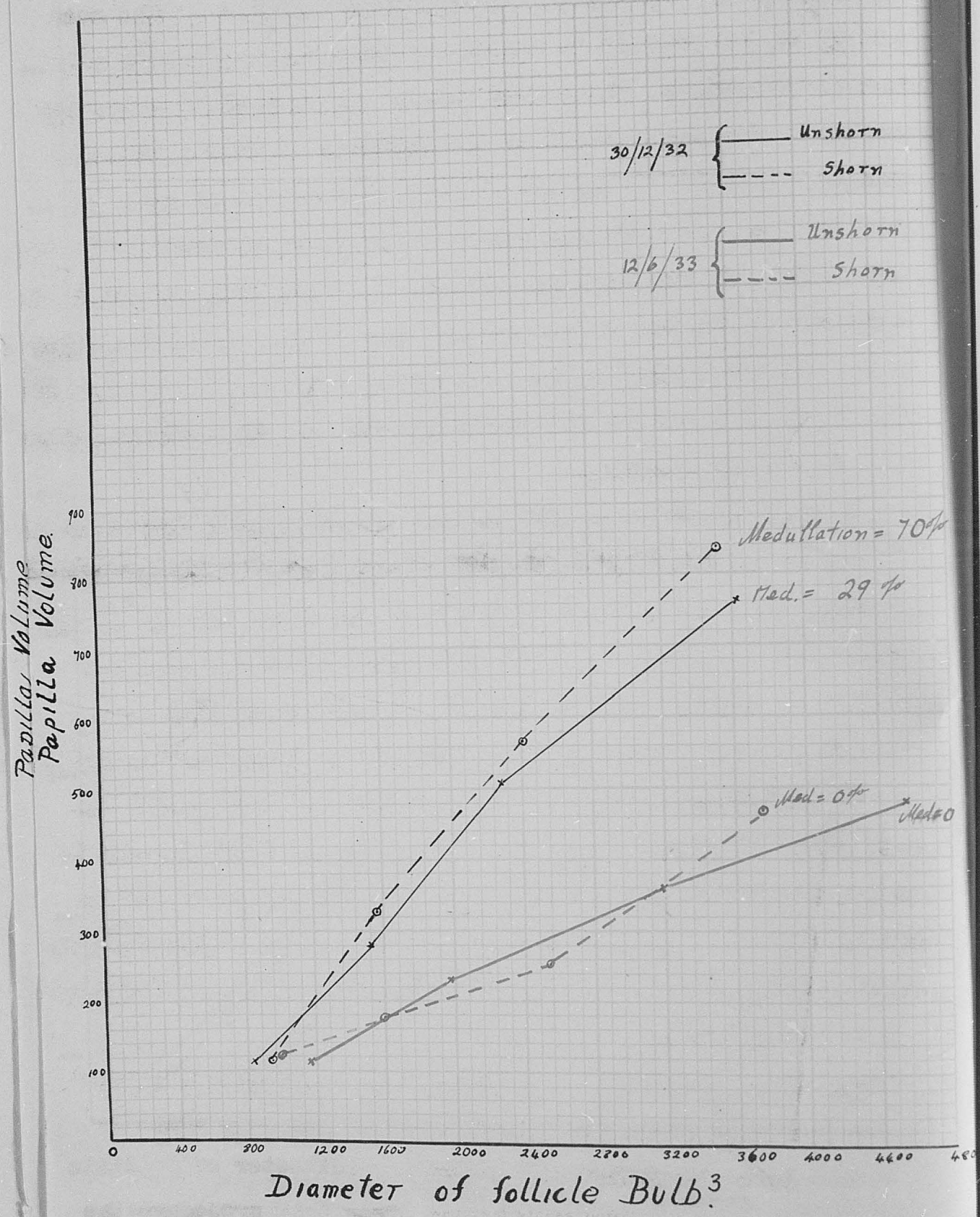
— Back 24/10/33
 - - - Back 11/11/33

Fibre cross-section area Groups.

IV

Relationship: $\text{Diameter of follicle Bulb}^3 \times \text{Papilla Volume}$

No. 659



I

of reaction to the effects of shearing. As far as the mean height of the papilla is concerned the first animal (No 659) was not affected. The second animal showed a significant increase in the mean height of the papilla. A very noticeable change was observed in both animals as a result of seasonal conditions. This change consisted of a marked decrease in the mean height of the papilla while at the same time all hairiness disappeared and the fibres became very fine. Hence it is concluded that the papilla can markedly change its shape, more particularly as a result of seasonal change and to a lesser degree as a result of shearing.

These changes in height as they affect medulla formation are significant in view of the work of King and Nichols(2) Assuming that the central portions of the fibre are fed by the upper portion of the papilla, these portions will, when the papilla is short, receive a cystine supply much more nearly similar to that of the outer layers of the fibre (fed by the base of the papilla). Hence on this cystine gradient theory the absence of medulla can be understood. In general, medulla is formed where the papilla is moderately thin and very tall, or moderately tall and very stout. In both cases there would be a distinct gradient in the supply of nutrient matter from base to tip of the papilla.

Relationship: (Diameter of follicle bulb)³ x papilla volume.

From further series of data, taken working at a magnification of 250 diameters, curves were drawn for (diameter of follicle bulb)³ against the papilla volume. From this procedure the

the slopes of the curve at shearing time, during winter conditions and at the crisis level (of the lamb's coat ⁽³⁾) can be compared. It is distinctly seen that the slope of the curves varies in such a way as to show that medulla is produced when the papilla is large compared with the follicle bulb. Graph IV. With reference to the phenomena occurring at the crisis level there is evidence that the reduction in medulla cannot necessarily be attributed to an alteration in the inherent drive towards medulla formation, but can be considered as due to changes in the dimensions of the papilla. Graph V. (No 758).

From the above considerations it appears that the dimensions of the follicle bulb relative to the papilla must be looked upon as having a profound influence on medulla formation. The physiological significance of this may be sought in the greater rate at which fibre cells will be pushed upwards thus further differentiating between the availability of cystine to cells originally near the papilla base as compared with those from near the papilla tip.

Relationship: Cross sectional area of fibre x papilla volume.

Graphs were drawn to show the relationship of the product of the two diameters of the elliptical fibre to the product of the two papilla diameters and its height. A very distinct relation is shown between increasing cross sectional area of fibre and increasing papilla volumes. Graphs VI & VII.

Further detailed measurements on the papilla and the follicle bulb will doubtless throw much light on factors that influence fibre length as well as fibre diameter. Preliminary data

comparing shoulder, back and britch, have been suggestive in explaining the gradient that is shown as a general shortening of the fleece from neck to britch. At the britch the papillae are stout in very stout follicles, but they are noticeably reduced in height as compared with the papillae at back and shoulder. We thus have a follicle constructed on a larger scale but fed by a papilla that is relatively small. It is thus reasonable to believe that the rate of growth in length will be less though the fibre cross-sectional area will be considerable.

No of Follicles	Min.Diam. of Papilla	Maj.Diam. of Papilla	Diam.of Follicle Bulb.	Height of Pap.	Min. Fibre Diam.	Maj. Fibre Diam.	Medul ^a (Max=100)
64	8.3	11.5	27	42.7	8.8	10.2	88
55	7.6	11.7	27.6	38	7.3	9.9	59
42	9	11.8	29.7	36.1	9	11.6	100

Medul. = Medullation.

At the back position a papilla of 95.4 cross section is producing a fibre of 89.7 cross section. At the britch position a papilla of 106.2 cross section is producing a fibre of 104.4 cross section. But at the back the papilla is working for a length of 42.7 whereas at the britch the working length of the papilla is only 36.1. Hence a greater length output would be well justified at the back position. Such a difference in length is observable in the samples being considered.

The Form of the Papilla and the Fibre Contour.

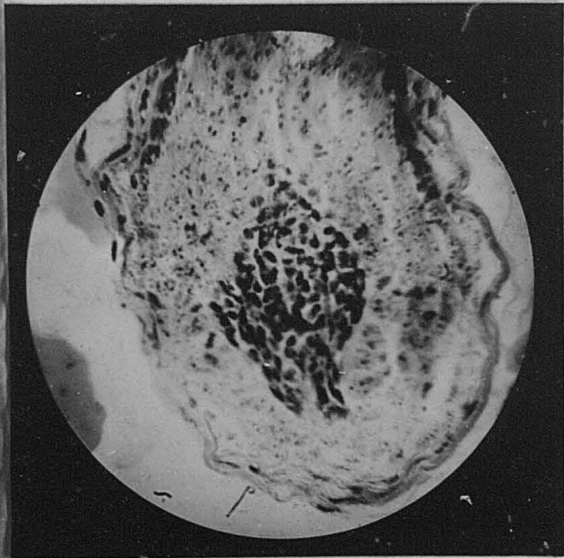
In the great majority of fibres that have been examined from Romney sheep, the contour of the fibre cross section is distinctly

elliptical. That this particular contour is correlated with the elliptical nature of the papilla cross section is supported by a considerable body of evidence. The bulb of the follicle is in each case approximately circular in cross section. The papilla on the other hand is usually markedly elliptical in section especially at its widest portion. The plastic region just above the papilla is slightly elliptical while this ellipticity increases as the fibre assumes its completely keratinized state. In the case of papillae possessing equal diameters at 90 deg. the resultant fibres are circular in cross section. A study of the circularity ratio of the papillae and of the fibres produced shows a striking parallelism between the *ellipticity* of the papilla and of the fibre produced:-

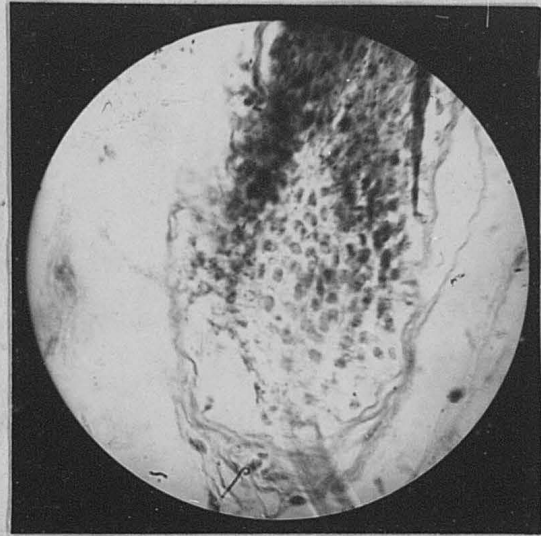
Position	No of Follicles.	<i>Ellipticity</i> of papilla section A	<i>Ellipticity</i> of Fibre section B	Ratio A/B
Back	151	1.69	1.42	1.16
"	188	1.42	1.26	1.13
"	60	1.56	1.38	1.13
Shoulder	55	1.54	1.35	1.14
Bitch	42	1.31	1.29	1.02

It is evident from the above table that the fibre is less *elliptical* than the papilla. From a general consideration of extreme cases it seems probable that there is an upper limit in the *ellipticity* of the fibre produced, whereas the papilla corresponding may be widely asymmetrical. Conversely there is, for lower *ellipticities* of the papilla, a closer parallelism, with the *ellipticity* of the fibre.

FIGURE 5



A.



B.

- A. Photomicrograph of the papilla in a medulla producing follicle. Elongated and darkly staining ovoid cells are quite numerous in the papilla.
- B. The papilla in a pure wool producing follicle. The darkly staining bodies exhibited in A. are here absent. Both follicles were observed in the same section and have consequently been treated identically.

Crimp Formation

From the work of Rossouw, Barker, Burgess, Norris and others it is clear that the characteristic form of crimped wool fibres can be analysed into two movements:-

- A. A curvative of the fibre as it grows, as if one side were growing more rapidly than the other.
- B. A periodic twisting of the fibre as it grows directing the curvative at first to one side and then to the other.

These two influences result in a wave-like structure.

S.G.Barker (4) lists several possible causes as follows:-

- (a) Dehydration of the gel with consequent application of a force along the length of the fibre, similar to that put forward by Callandreaux.
- (b) Physico-chemical forces at work in the follicle during the formation of the fibre itself.
- (c) Surface tension effects, although this is unlikely.
- (d) Wildman's rotation of the bulb.
- (e) A combination of all these.

Many of these explanations are suggested by experiments in isolated physical and physico-chemical systems. With reference to the particular biological problem at issue an exploration of the biological situation within the animal itself is being made. Concerning the follicle system the work on the orientation of the diameters of the papilla is particularly significant. This suggests that the basal portion of the follicle as a whole rotates relatively to the non-plastic upper region of the fol-

licle which contains the rigid and completely formed fibre. Evidence of such a rotation has been given by Wildman's work (5), but we are yet far from understanding the causes of such periodic twistings. Observations on the minute structure of the papilla support the view that the papilla rotates independently of the bulb of the follicle. Blood vessels enter the base of the follicle from each side. Sometimes these vessels supply that side of the papilla upon which they enter and at other times they are seen to supply opposite sides, being crossed over one another. A further significant point is that they cross over at a region where the papilla is thinned to a neck *Fig 1.* just at such a point where twisting could readily occur. In addition to the twisted nature of the blood vessels, the dermal fibres, which constitute the papilla, are also in a twisted condition (*Fig 3*) It seems necessary that there should be some periodic rotation at the base of the follicle. Anatomically there is a strong support for papilla rotations, while it is difficult to see by what other agency the stout follicle base could become twisted.

With reference to the other component in crimp formation many observations have been made on the curvative of follicles and the fibres produced. The axes of the papilla are orientated in a definite way with reference to the 'golf-club' and curved form of the follicle *Fig 4 A+B.* Viewing the 'golf-club' base of the follicle as it lies in the plane of observation, the asymmetrical face of the papilla is seen. On rotating the follicle through 90 deg. the symmetrical face of the papilla is seen but the base of the follicle is now symmetrical also i.e. without any 'golf-club' bend

(This definite orientation lends support to the view that the shape of the papilla determines in part the shape of the follicle base). In the former position, *A*, the upper part of the follicle shows far more curvature than in the case of the latter position, *B*. This is an important observation as it directs attention to the possibility of a greater rate of growth on one side of the papilla than on the other. A few observations have been made on the rate of mitotic division with reference to the axis of the papilla, the rate being greater at the position (x fig. *A*) which is on the outer side with reference to the curvature of the fibre.

The most pleasing feature of this preliminary work is the possibility of establishing an orderly relationship between the asymmetrical nature of the papilla and the contour and curvative of the fibre. From these considerations also the phenomena of twisting can be approached. As a result of such morphological work the underlying periodic forces upon which depends the form of the fibre will become more easily understood.

B. Detailed Structure of the Papilla.

Parallel with the gross form of the papilla the detailed cellular structure of the papilla is being studied with reference to the activity of fibre growth and the mechanism of medulla production. Size relationships only are insufficient to explain what have been described as different physiological potentialities for hairiness.

Just as in the case of the external form of the papilla, the internal form is equally diverse in structure. Owing to the probability of there being numerous factors which influence

medulla formation it is a difficult matter to separate out those factors which are essential to medulla formation. It is true that most conspicuous features have been associated with medullated fibres on the one hand, while on the other hand where these features have been absent wool fibre was being produced. The feature referred to consists of especially elongated and darkly staining ovoid cells in the papilla *Fig 5 A+B.* these varying enormously in numbers from follicle to follicle. In many cases such bodies are being shed from the papilla into the surrounding bulb and such a condition is more frequently associated with a decreased rate of mitotic division and no medulla production. Resting follicles of fine fibres and of shed kemps show a lack of these bodies in the papilla. Further studies on the origin of these papilla inclusions and their abundance in samples well known for their ability to (a) produce medulla (b) produce pure wool only, would probably throw considerable light on the question of the organization of cystine in the papilla.

Facts have been presented above in the scheme of work that has been undertaken on follicle structure. In this plan aiming at a conception of the fleece as a whole through a study of its elements, the interrelationship of the various characters is steadily born in mind .

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