A STUDY OF THE FOLLICULAR ORIGIN OF THE FIBRE TYPES OF N-GRADE ROMNEY LAMBS.

G.A. WICKHAM

- May 1958 -

A thesis presented at Massey Agricultural College in partial fulfilment of the requirements for the Degree of Master of Agricultural Science in the University of New Zealand.

ACKNOWLEDGMENTS

Special thanks are due to Dr F.W. Dry without whose assistance and encouragement the project would never have been started.

Professor A.L. Rae's guidance in the final stages has resulted in considerable improvement to the thesis.

Appreciation is expressed to Dr F.R. Cockrem for general discussion; Dr D.S. Flux for advice on histological techniques; Mr M.F. McDonald for assistance in correcting errors in the script; the library staff for locating much of the reference material; and Miss V. Wagstaff for her patience in preparing the typescript.

The work was carried out while the author held a New Zealand Wool Board Scholarship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

It has long been realised that a greater understanding of the physiology of wool follicles and the various processes involved in the growth of fibres might reveal simple, economic methods to improve the quantity and quality of wool produced by a sheep.

In physiological studies of wool growth, workers unable to observe directly the functioning of the follicle have used certain features as criteria.

The chief criteria used have been the following: -

i A measure of wool growth.

ii The morphology of the fibre.

iii Anatomy and changes in the anatomy of the skin and the follicles.

In an attempt to explain the morphological differences between birthcoat fibre types, workers have formulated several hypotheses about the forces in the skin during the period of follicle development. (Dry 1933, Sutherland 1939, Goot 1940). Some workers (Galpin 1935, 1936b, Fraser 1951, 1952a 1953) have postulated that changes in the follicle population is the chief cause of these differences. If this is true there should be some relationship between the class of follicle and the type of fibre which it produces. While the relationship between the type of follicle and the fibre it produces has been widely discussed in the literature, little experimental work has

been carried out to find the true origin of the different fibre types.

Experimental accounts of relationships so far published, have with the exception of the work of Fraser and Hamada (1952), all arisen from studies originally designed to provide data on other problems. Consequently our knowledge is not great and the reliance which can be placed on the published relationships is limited.

In a study of the fibre type arrays of sheep of the N/+ nr/nr genotype, a large number of arrays were found in which the distribution of fibre types was difficult to reconcile with what would be expected if the relationships of birthcoat fibres and follicles suggested for the N-type Romney by Fraser, Ross and Wright (1954), held true. Further work on the arrays of Romney N/N and Cheviot and Lincoln cross N-types cast further doubt on whether Fraser et al's relationship could be applied as generally as had been at first supposed.

The problem is of importance for two reasons; firstly certain workers (Dry, Burley and Speakman 1952, Burley and Speakman 1953) have used Dry's fibre type classification as an index of the class of follicle from which the fibre is derived. These fibre types have then been compared in their physical properties, and the results published in terms of the differences between

fibres produced by the different classes of follicles.

Secondly, the morphology of the birthcoat fibres, the expected order of development of birthcoat fibres and the expected relationship between the follicle and the fibre type produced in it, have been used in formulating theories on the physiology of the wool follicle. If the suspected relationships do not hold we may be led into formulating false theories, while conversely if there are relationships of which we do not know the existence, we may miss chances of further advancing our knowledge of follicle physiology.

II DEFINITION OF TERMS AND ABBREVIATIONS

A Follicles.

1. Definitions

Primary follicles : (P) Follicles,* each of which possess a complete set of accessory glands consisting of: -

(a) a tubular sudoriferous gland
(b) an arrector pili muscle
(c) an acinous sebaceous gland (generally bilobed)

Secondary follicles : (S) Follicles which do not possess the full complement of accessory glands. Generally secondary follicles possess only a unilobar sebaceous gland, but Burns (1949) has observed follicles classified secondaries having either a sudoriferous gland or an arrector muscle as well as a sebaceous gland.

Primary central : (PC) The central member of a trio of primaries.

Primary lateral : (PL) The lateral primaries of the trio.

Trio : The three P follicles of the normal follicle group.

Trio Group - follicle group. : In sheep it consists typically but not exclusively of a basic group of 3 primaries and a variable number of secondaries (Carter 1955).

*The insertion of each means that only one follicle of a primary bundle (Lyne 1957a) would be considered to be a P follicle.

Bundle : A group of two or more follicles, the fibres of which share a common follicle neck.*

Immature follicles : Follicles which have not produced a fibre which is keratinised at the level of the primary sebaceous glands. (i.e. at the level of sectioning).

2. Abbreviations

The abbreviations used are those suggested by Hardy and Lyne (1956a) as an extension of the abbreviations put forward by Wildman and Carter (1939).

PCX early formed primary central follicle

PCY late formed primary central follicle.

* Duerden and worker at Torridon have generally referred to the follicle group as a "follicle bundle."

PIx primary, lateral to a PCX follicle

PIy primary, lateral to a PCy follicle

SOU unbranched original secondary follicle

SOB branching original secondary follicle

SD secondary follicle derived by branching from the neck of a SOB

Within each type two states of development are recognised.

i incompletely developed (p or s of Carter & Hardy 1947)

f containing a keratinised fibre (P or S of Carter and Hardy).

These symbols are used after the letter denoting the type of follicle, for example Sf: a mature secondary follicle.

n signifies density per square millimetre

$\bar{n}$ signifies mean density per square millimetre

d signifies diameter of the fibre in the follicle

$\bar{d}$ signifies the mean diameter.

For example $\bar{d}P$ signifies mean diameter of primary fibres while $\bar{d}S$ signifies the mean diameter of secondary fibres.

B Fibres.

The fibre types have been described so often in the past (Dry 1935, Sutherland 1939, Goot 1940, Stephenson 1952, 1956) that it is not necessary to detail them fully. However since they are fundamental to the present study a short summary will be given.

1. Pre-curly-tip fibres (pre-CT)

Halo-hairs (HH) Long fibres coarsely medullated throughout

Halo-hair´ (HH') As above but with a short break in the medulla at the birth point

Super-sickle A (SSA) Similar to HH but less robust with a sickle shaped tip

Super-sickle A´ (SSA') As above but with a short break in the medulla at the birth point

Super-Sickle B (SSB) Similar to SSA' but with a longer break in the medulla

Sickle (SK) Have a sickle shaped tip which may or may not be medullated, followed by a thinner, non medullated pre-natal region

2. Curly-tip fibres

Hairy-tip-curly-tips (HTCT) Medullated in the pre-natal region

Checked curly-tips (ChCT) The longest curly tips with a

large number of curls in the tips. No medulla throughout and followed by medullated CT.

Ordinary curly-tips (CT) Curly tipped fibres non medullated in the pre-natal region

3. Post curly-tips

Histerotrichs (Hi) Straight or waved short fibres

Where it is desired to differentiate on the basis of the post-natal medullation the terms "fine" or "medullated" (med) are used. (med = chalky)

Dry (1935) has called the largest, pre-precipice curly tips, peak curly-tips (peak - CT).

Baby fibres Short shed fibres which do not grow after birth

Infant fibres Shed fibres which grow for a short time after birth.

Ribbon-shaped fibres Fibres flattened in cross section. Also called "infilled" or "collapsed" fibres (Elphick 1932) "squeezed" fibres (Sutherland 1939), "partially air-filled" fibres (D.A. Ross 1950) "squashed" fibres (Dry personal communication).

Precipice "Precipice is the term given to the sudden change along the array from the coarse to the fine CT fibres without intermediates". (Galpin unpublished; cited by Sutherland 1939). Fine is not interpreted as non-medullated in this case.

Pre-precipice fibres (pre-pr.) Fibres of size greater than that at which the precipice is judged to occur.

Post-precipice fibres (post-pr.) Fibres of size smaller than that at which the precipice is judged to occur.

"Toughness" Freedom from the pre-natal check as measured in terms of the fibre type array. Plateau is considered "tougher" than saddle which is in turn considered to be "tougher" than ravine etc.

TABLE 1

Fibre types in the different arrays (Based on Stephenson's 1956 graph)

Array	HH	SSA	SSA'	SSB	Sk	Fine pre-CT	ChCT	HTCT	Med CT	Fine CT	Med Hi	Fine Hi
Plateau P_0	+							+	+	*	+	+
Plateau P_1	+	+						+	+	*	+	+
Plateau P_2	+	+	+					+	+	+	+	+
Plateau P_3	+	+	+	+				+	+	+	*	+
Saddle	+	+	+	+	+			+	+	+	*	+
Ravine	+	+	+	+	+	+		+	+	+	o	+
Valley	*	*	+	+	+	+	+		+	+	o	+
Plain	*	*	*	*	*	+	?			+	o	+
Escarpment	+	+	+	+						+		+
All in	+	+	+	+	+	+	+	+	+	+	o	+
Incline	+	+	+	+	+				+	+	o	+

\+ Probably present
* Only occasionally present.
o Presence would not affect classification but never found.
? Some CT present which would be classified as ChCT if med CT were present.

III REVIEW OF LITERATURE

A The History of Follicle Group Studies.

1. Before 1939.

Knowing the difficulties of sectioning skin satisfactorily and failing to recognise the importance and significance of certain features in the skin, the majority of earlier wool biologists avoided the use of histological techniques. Most of these early workers did not realise the importance of trying to assess differences quantitatively to limit the scope of the human imagination and to allow the application of statistical methods to the data. However a great deal of descriptive work on follicle histology and development was accomplished in these early days.

von Nathusius (1866) was the first to use histological preparations of skin to estimate fibre density and he noted the group pattern of follicles. Various other German workers, contemporaries of von Nathusius had shown the group pattern to exist in many other mammals and de Meijere (1894) reviewing this work, found that although there was considerable variation between species the groups appeared to be phyllogenetically related.

Little further advance took place until the very detailed studies of Spöttel and Tänzer (1923) and Tänzer (1926). (cited by Frölich, Spöttel and Tänzer 1929 and

Carter 1943). These workers made a very detailed study of the skin histology of European breeds of sheep. They recognised two different types of follicles, named after Toldt's (1910) fibre types, "Leithaare" and Gruppenhaare". These corresponded to Wildman and Carter's (1939) primary and secondary follicles. Also they referred to the existence of a group which, (since they thought the trio only existed as a passing phase), consisted of one Leithaar with its associated cluster of Gruppenhaare. In calculating the number of Gruppenhaare per Leithaar as an index of group size, they were the first to make use of what is now called the S/P ratio. In recent years this has become the main numerical criterion in studying, the development of the follicle group.

Duerden and Ritchie (1924) studied follicle development in Merino foetuses. In relating the development of individual follicles, they described only the first to begin growth, apparently not realising that these, being primary follicles, made up only a small proportion of the total population. They also noticed clusters of ten to thirty follicles separated by bands of connective tissue.

Wildman (1932) could find no differences between the foetal follicle development of various British breeds and the Merino, as described by Duerden and Ritchie. He also described the development of a primary follicle only,

although he stated that not all follicles possessed sweat glands. He made reference to trios but did not stress the importance of this occurrence, while he classified follicles on the basis of their order of appearance into "primary" and "secondary" follicles, comparable to PCX and PCY. All other follicles fell into his "later" class.

Teodoreanu (1934) compared Rambouillet Merinos, Tsigais and Rambouillet-Tsigai F1s in such characteristics as fibre density, sebaceous and sweat gland density, and size of the hair group (1P+ xS). However the value of this approach was not recognised by other workers at the time.

Galpin (1934)(1935) working on the prenatal development of the New Zealand Romney lamb emphasised the importance of the "trio" and also suggested that a "nine" stage followed the trio stage. However later workers, (Duerden 1939, Carter 1943, Ross 1945, Ryder 1956) have not been able to find this stage. She also classified follicles into the following: -

X	(PCX)
Y	(PCY)
x	(PLx)
y	(PLy)
x'	(S associated with PCX)
y'	(S associated with PCY)

Terentjeva studied follicle development in the Kirgiz Fat-rumped breed (1937) and in the Askanian Ramouillet and Précoce (1939). Follicle development showed a similar pattern in all three breeds. Terentjeva stated that there was more rapid development of fine follicles in the fine woolled breeds, but it seems that this finding is at least partly due to his considering the primary lateral follicles of the Rambouillet and Précoce to be fine follicles. He is the only worker who has used a large enough sample of foetuses to give a good indication of the variation between sheep, but unfortunately he did not go into histological detail.

2. 1939 Onward

Since 1939 the pattern of research in wool science has changed markedly, Carter and his colleagues in Australia being the main instigators of these changes.

Firstly Wildman and Carter (1939) presented a new classification of follicles, into "primary" and "secondary" depending on whether they grew in the trio or the post-trio phase. They further classified primaries into: -

Primary X, Primary Y	Central trio follicles
Primary x, Primary y	Lateral trio follicles

They stated that smaller follicles grew in association with the original trio to complete a "follicle bundle" (follicle group).

This classification was first used by Wildman in compiling the results of a study by Deurden (1939), of pre-natal follicle development in many British breeds and the Blackhead Persian. The importance of the trio was again stressed and it was stated that in many cases secondaries developed from a wedge of "primordial fibro-genetic tissue", situated between the central and lateral members of the trio.

The large scale use of histological techniques for studying follicle populations was made feasible by Carter (1939a), when he described a relatively simple method of taking sections and estimating relevant facts about the populations. Carter (1939b, 1940, 1942) stressed the importance of the follicle group as one of the basic units for production of the fleece, showing how the make up of the follicle group could affect the character of the subsequent fleece produced, although density remained constant. He advocated the use of P : (P+ S) ratio as a measure of the follicle group size.

Carter (1943), led the way in the application of these techniques, with a study of the timing of pre-natal development in the Merino, while Carter and Hardy (1947) followed the

study to a further stage by describing regional variations in the timing, and determining the foetal age at which the different stages of follicle development occurred. Various other workers have studied foetal development, generally doing a comparison with the Carter (1943) or the Carter and Hardy (1947) description of Merino development. Ross (1945, 1954) worked on the N/+ Romney, Margolena (1954) the Karakul, Diomidova (1955) the Precoce - Northern short-tail cross, and the Soviet Merino, Ryder (1956) the English Romney, Hardy and Lyne (1955a, 1956b) the Merino and Stephenson (1957) on the N/N, N/+ and +/+ New Zealand Romney.

Unfortunately none of these workers has used a big number of foetuses. (Carter, 12, Carter and Hardy, 20, Ross 37, Margolena 21, Hardy and Lyne, 24, Ryder, 7, and Stephenson 53, of three different genotypes). These numbers spread over a period of about a hundred days, have been insufficient to give an accurate idea of variation between individuals of a similar foetal age, and implications from one foetus, separated from its neighbours in the series by a large time gap, have often been applied to a whole breed. In particular the study of Ryder (1956), which included two sets of twins in the seven foetuses examined, was on such a small number as to make it of very limited value.

Within the limits imposed by the number of foetuses used, and our limited knowledge of intra-breed variation,

it has been shown that the timing of follicle initiation, and follicle development generally, is remarkably similar, when the wide variation in fleece types between the breeds studied is considered. Ross (1945, 1954), suggested that after 92 days, follicles grew faster in the N-type Romney than the Merino. This however was refuted by Stephenson (1957), who was not able to find any differences. He did find however that variation between sheep was high after 90 days, and he considered that the differences found by Ross were due to this factor. Also he could find no differences, except in size of the primary follicles, between N-type and non-N Romneys.

This information on intra-breed variation has only become available recently and is contained in graphs drawn by Hardy and Lyne (1956b) and Stephenson (1957) showing follicle development stages at different ages for individual foetuses of the Merino and non-N and N-type Romney. Stephenson also presented a graph of the limits of variation for the main body positions in the Romney.

Hardy and Lyne (1955a, 1956b) reappraised Carter's divisions of the stages of development of individual follicles, and of the follicle population as a whole. The stages which they defined for individual follicles were a modification of those first defined by Hardy (1949) for the mouse. They described the development of both primary and

secondary follicles in terms of this classification. Thus they were the first workers to give a detailed description of individual secondary follicles in the sheep. Hardy and Lyne accepted the eighteen stages of development of the follicle population defined by Carter but in the light of more recent work they were able to give a more precise account of these stages.

While it does not go into statistics of the follicle population or regional variation over the body, Hardy and Lyne's (1956b) paper is the clearest and most concise account available, of the development of the follicles of the Merino foetus.

Hardy and Lyne stressed the importance in the development of the secondary follicle population of an early formed secondary (SO) branching to produce a number of "derived" (SD) follicles. de Meijere (1894) described situations in several species in which a number of follicles shared a common neck, and he put forward two theories as possible reasons for this.

i Necks of closely adjoining follicles fusing together.

ii Follicles arising by "budding" from another follicle."

Tänzer (1926) observed budding in the Karakul and in other breeds (unpublished quoted by Frölich Spöttel and Tänzer

1929), but he apparently considered that this was an anomalous condition, and that most of the bundles, which he observed to be quite common, were formed by fusion of the necks. Höfer (1914) carried out a detailed study of budding in the skin of the cat, and showed this to be a normal occurrence in the development of the coat. Other workers including Duerden and Ritchie (1924), Duerden (1939) Communal and Adrover (1953) Auber and Ryder (1955) noted bundles in the sheep, but they considered these to be an anomaly resulting from fusion of follicles. Dry (unpublished, quoted by Goot 1940) has suggested that the second wave of histerotrichs grow in follicles which bud from the follicles of the first wave.

Lyne (1957a) reported finding bundles of 2-6 fibres associated with a single sweat gland and arrector muscle. He postulated that follicles develop by budding from an original primary (PO), something which has been found to occur in the bandicoot. He called the associated follicles derived primaries (PD). Although it is rather difficult to decide into which class the follicles should fall, without any knowledge of the actual timing of development of these follicles, it seems that since the so called "derived" follicles do not possess sweat glands, or arrector pili

muscles of their own, they would be better classed as secondaries. Wildman (1957) stated they could not be classified clearly as either primary or secondary.

Hardy and Lyne (1956a) also reappraised Wildman and Carter's (1939) classification of follicles, in the light of more recent knowledge. The resulting classification is described in the definition of terms at the commencement of this thesis.

In the last ten years many workers have studied the post-natal development of the secondary population and changes in follicle density. Most of these investigations have been on the normal pattern of development. Burns described several English breeds including the English Leicester and Romney (Burns 1949), the Scottish Blackface (Burns 1954), the Suffolk (Burns 1954a) and the Herdwick (Burns 1954b). Margolena (1954) included some post-natal material in a study of follicle development in the Karakul, while Sugai (1954) worked on the Corriedale. All these observations were unfortunately carried out on a rather small number of sheep, although much useful data can be gained from them. Schinckel (1953, 1955a, 1955b), Fraser (1954) and Short (1955a) working on the Merino used rather larger numbers of sheep and hence the changes in the follicle population shown by the S/P ratio are more readily applicable to the whole breed.

B Development of the follicle group.

As a result of the previous studies it is possible to formulate a generalised pattern of follicle group development applicable to all breeds of sheep. It must be remembered when thinking of the times given in this pattern, that they are only approximate averages, and that between foetuses up to eighty days old variations of ten days in attaining a certain stage of development are quite common, while between older foetuses of the same breed variation can be as high as twenty days.

The three periods of Carter (1942) are still a useful division of the stages of foetal development, but it is doubtful if these are clear cut for the foetus as a whole, there being some overlapping between regions.

1. Pre-trio period :

A number of PCX follicle plugs appear around the muzzle and eyes at about 45 days. More of these appear over the poll, then legs, and gradually over the rest of the body until at around 60 days it is completely covered. PCY follicles first appear on the poll 55 to 60 days after conception and spread over the rest of the body in a wave similar to that of the PCX follicles, the wave being complete at about 70 days. There is however no rigid boundary between PCX and PCY follicles.

2. Trio period :

This period commences with the appearance of the first PLx follicle in the region. This generally occurs on the poll somewhere near 65 days. The rest of the body becomes covered with these follicles from about 70 days onward, all PL follicles having appeared by approximately 80 days.

3. Post-trio period :

The first secondary follicles commence development on the head at approximately 80 days, but the post-trio period does not really commence until 85-90 days, when secondaries start appearing over the rest of the body. In each region there is a gap of 8-10 days between the initiation of the last PL and the first S. Before 100 days SO only are initiated, these first follicles being situated at the secondary margin of the group, but after 100 days SD follicles begin to bud from the ental side of the neck of SOB follicles. Little is known as to the actual proportion of later formed secondaries which develop in this way, but it seems that in the Merino the proportion is fairly high (Hardy & Lyne 1955a, 1956b). Since bundles have been observed in other breeds with a lower S/P ratio, some secondaries at least are probably formed by budding, and Lyne (1957b) has stated that the frequency of common follicle openings becomes progressively

greater from the Moufflon to the Merino.

Possibly the rapid increase in $\frac{P+S}{P}$ found by Carter and Hardy (1947) in Merino foetuses from 100 days onward is due to the commencement of budding. This rapid increase continues until shortly before birth. Ryder's (1956) data from Romney foetuses suggested that S/P ratio increased fairly rapidly from 100 to 110 days but was then fairly stable.

While Short (1955a) and Schinckel (1955b) in the Merino, and Margolena (1954) in the Karakul, have found potential Sf/Pf ratio to be determined before birth, the low $\frac{Sf+Si}{Pf+Pi}$ found in new-born Blackface lambs by Fraser and Hamada (1952), and Burn's (1954a) data on Suffolks, seems to suggest that this might not be the case in British breeds.

Our knowledge of post-natal changes of the follicle population is rather sketchy in breeds other than the Merino, and because of the small number of animals observed it is not possible, except in the case of the Merino, to formulate any pattern of development on which much reliance can be placed.

In the Merino it seems that for a period of about one week after birth development is limited to the maturation of a few Si to Sf. However after this period of lag in development there is a sudden spurt lasting about 21 days during which the majority of the secondaries mature. Following this

wave the rate of follicle maturation slows and continues at a low level for a period of up to twelve months. Burns (1955) stated that follicle development is limited to the first 2-3 months of the lamb's life and suggested that Carter & Hardy's earlier finding of maturation of follicles up to 12 months was due to failure to recognise follicles which were regenerating following shedding. However in the face of other evidence from Australian workers showing increase in Sf/Pf ratio up to 9 months in Merinos, it seems that we must accept the longer period of development as the true picture. Burns's results could be due to differences between the British breeds and the Merino, to the slightly different method of approach used or possibly to the few lambs involved, many of which were not thriving at the time of sampling.

Carter (1943) combined the pre-trio and trio periods into the protophase, while the post-trio period he called neophase. He pictured the phases as two entirely separate periods of development, with primary follicles only being produced in protophase and secondary follicles only being produced in neophase, the primaries having a complete set of accessory structures while the secondaries possessed at the most a sebaceous gland. However Burns (1949) found follicles at the secondary margin of the group which possessed the full complement of accessories, while other

follicles in a similar position were found to have either a sweat gland or an arrector muscle. These findings with Lyne's (1957a) report of P bundles, seem to indicate that the phases are not as distinct as Carter imagined.

C. Factors affecting follicle development.

Lately several workers have studied the effect of different treatments during the development of the follicle population. Schinckel (1953) was the first to present evidence on the effect of nutrition on the follicle population when he showed that twin lambs and lambs from young ewes had a lower Sf/Pf ratio in all stages of development and that the correlation between birth weight and birth Sf/Pf was high. He stated that rate of maturation of S follicles was proportional to the general growth rate and later (Schinckel 1955b) enlarged on this when he worked out correlations between such factors as potential S/P, birth weight, live weight increase over different periods and Sf/Pf at 15 months.

Short (1955b) furthered this investigation by feeding ewes at different levels during pregnancy. He found 168 day old lambs from the ewes fed on a low plane were significantly

lower in Sf/Pf ratio and in fibre density than ewes fed at a higher level. These differences showed up in the 200 day fleeces which were coarser, longer and less dense in the low plane group. Panfilova (1955) carried out a similar study comparing lambs from normally fed Soviet Merino, "Precoce" and semi fine woolled Dagestan Mountain ewes, with lambs from similar ewes which were fed supplementary concentrate during pregnancy. At birth, lambs from the concentrate fed ewes showed a significantly greater fibre length and density, the differences being largest for the finer woolled sheep.

Hugo (1953) fed Merino ewes at two treatment levels during pregnancy and lactation. After weaning, some lambs were switched from the high to the low plane treatment and vice versa. The only significant differences between the groups in the skin and fleece were those attributable to the high plane feeding following weaning, and apparently follicle development had not been affected. Ryder (1955) reported a similar trial in which feeding Cheviot ewes supplement during pregnancy and lactation had no effect on S/P ratio of the offspring. Ryder (1957a) however stated that a later trial, not at the time completely analysed, suggested that differences of S/P ratio of Romney lambs, had been induced when a lower unsupplemented diet was used.

Galpin (1948) and Henderson (1953) have shown that the better Romney lambs grow in the early period of life,

the denser will be the resultant fleece. Cockrem (1956) suggested that the greater staple length and hairiness of twins was the result of impaired development of the S follicles.

Ferguson et al (1956) and Labban (1957a) showed that thyroxine and growth hormone affected the development of the secondary follicle population. Ferguson et al found that Merino lambs thyroidectomised at birth but with enough thyroid tissue left to maintain life showed very little increase in Sf/Pf up to 11 weeks. Thyroxine injections then brought about a wave of secondary maturation which almost brought the ratio up to that achieved by the control animals. Ceasing replacement therapy after 11 weeks in another group of lambs thyroidectomised at birth, caused a reduction in the Sf/Pf ratio and a fall in body weight. Another group, given injections of sheep pituitary extract containing growth hormone and thyrotropic hormone while apparently showing a greater rate of secondary follicle maturation did not differ significantly from the controls in any feature. Wool growth in thyroidectomised animals not given any replacement therapy was at a very low level. From this it was suggested that requirements of thyroxine for wool growth and for follicle development are greater than that for growth in general.

Labban (1957a) injected Suffolk lambs 3-4 weeks of age

with growth hormone and found the treated animals were significantly higher in secondary density and in Sf/Pf.

D. Follicle populations.

As a result of these developmental processes the skin of the adult sheep is covered with a large number of fibres each growing from a follicle. The follicles vary in type and are not arranged randomly over the area but congregate in groups, separated in the upper levels of the skin by bands and connective tissue, the trabeculae.

The normal type of follicle group consists of one PC follicle associated with two PL follicles, one being situated on each side of the PC. All these primary follicles have a complete set of accessories, the sebaceous gland being bilobar. These accessories are situated roughly at right angles to a line running through the three primary follicles. On the side of the primaries opposite the accessories, (i.e. on the ectal side of the primaries) are situated a variable number of secondary follicles, the largest secondary fibres being those furthest from the primary margin of the group. Generally these secondaries possess a unilobed sebaceous gland, but in many cases these are absent.

Despite earlier work, notably by Spöttel & Tänzer

(1923) and Teodoreanu (1934), the value of comparative studies of adult follicle populations in sheep breeding and in providing a criterion for tracing the evolution of the domestic breeds, has not been generally realised. The only extensive comparative work on follicle populations is that of Carter and Clarke (1957a 1957b), although some work has been done on British breeds by Ryder (1957b) and Sugai (1953, 1955) has described the follicle populations of Corriedales. A certain amount of knowledge on adult follicle populations has been gained from the final samples observed in studies of post-natal development. The majority of this work has been reviewed by Carter (1955), while Ryder (1957b) reviewed the work on British breeds.

Carter and Clarke (1957a) examined the follicle populations in young ewes from a number of Australian Merino stud flocks and found large differences existed between flocks in the characteristics of the follicle groups. While age and general body condition at sampling could influence density, and the early environment could influence S/P ratio, it seemed that since the sheep involved were in most cases given a fairly high plane of nutrition, the differences were chiefly genetic. In comparing the flock averages while density and fineness seemed to be fairly closely related there did not seem to be any relationship between S/P ratio and either of these characters. This does not fit in with

most of the earlier formulated ideas on the relationship between the fleece and the follicle population.

Carter and Clarke (1957b) compared the different breeds of sheep, the most outstanding feature in the comparison being the large difference in S/P ratio between Merino and non-Merino breeds with the Corriedale and Polworth breeds intermediate. This suggests that the Merino breed is distinct from other breeds, although probably some genes have been introduced into the modern Merino from the British breeds and vice versa. This is further evidence for the suggestion that the evolution of the Merino has been almost entirely divorced from that of the other domestic sheep breeds. Also it seems clear from this paper that the carpet breeds of sheep differ from the other breeds chiefly in the ratio of the diameter of primary fibres to the diameter of secondary fibres ($\bar{d}P/\bar{d}S$), although they generally have only a low S/P ratio. This is best demonstrated in a comparison of the N-type (carpet wool type) and ordinary Romney, where the influence of the N gene on the follicle group is to increase $\bar{d}P/\bar{d}S$; S/P not being affected significantly. (Ross 1945, Carter 1955). High $\bar{d}P/\bar{d}S$ values are also associated with coarse birthcoats, all carpet woolled breeds being very hairy at birth (Fraser and Hamada 1952 and various other workers) while Lockart (1956a) and Carter and Clarke (1957a) have demonstrated the relationship within the Merino breed. Lockart (1956a) found a highly significant correlation ($r=0.83$) between birthcoat grade (scored 1-7) and adult $\bar{d}P/\bar{d}S$.

The other outstanding feature of Carter and Clarke's interbreed comparison was that the short woolled mutton breeds (Southdown, Dorset Horn, Suffolk and Ryeland) and the Cheviot differed little from the other British breeds in S/P and density, but the fibres were considerably finer. It seems therefore that the fine, light fleeces of these breeds are due to the follicles not competing efficiently with other tissues for the available nutrients. Ryder's (1957b) review also shows the same tendency.

Lockart (1956a) calculated the correlations between different features of the follicle population of Merino ewes.

E. Fibre populations.

Nineteenth century German workers were amongst the first to publish macroscopic descriptions of individual wool fibres.

Toldt (1910, 1912, 1935) expanded this approach by classifying the fibres into groups, the main types being Leithaare (outer, thick hairs) Grannenhaare (over hair) and Wollhaare (fine hairs). He then compared the fibre populations of different species of wild mammals by

placing the fibres in the different classes.

Crew and Blyth (1922) classified fibres from Scottish Blackface lambs into three groups corresponding to kemps, hairs and wool, while many workers about this period carried out similar studies of adult fleeces from many sheep breeds.

Duerden and his associates, (Duerden 1927, 1929 Duerden and Seale 1927, Duerden and Boyd 1930, Boyd 1927), studied several breeds of sheep by these methods, and on the basis of their findings theorised as to the paths of evolution of the different breeds. Duerden and Seale (1927) first drew attention to sickle fibres and Duerden (1932) stated that they might be of importance phylogenetically. He also suggested (personal communication quoted by Dry 1931) that the thinning of the neck might be the criterion of important changes in the follicle.

Following up this lead Dry was able to develop a system for classifying all the fibres in the birthcoat of the New Zealand Romney lamb into a number of separate types. This classification (Dry 1935a) depended firstly on the shape of the tip and secondly on presence or absence of medulla in various regions of the fibre. The basic types of fibres recognised at this early stage were: -

Halo-hairs

Super-sickle fibres

Curly-tip fibres

Histerotrichs

Various divisions were recognised among the individual fibre types. Sickles were classified as "baby" sickles, "infant" sickles, (depending on stage of shedding) chalky sickles, and fine sickles. Curly-tip fibres were divided into hairy-tipped-curly-tips, checked curly-tips, peak curly-tips and others.

To assess the "toughness" of the lambs birthcoat Dry practised dividing a small sample from the lambs birthcoat into the different classes of fibres. Then on the basis of presence or absence of the different fibres types he classified the sample into an array. The original arrays recognised by Dry and defined earlier, were, in order of toughness.

the plateau array

the saddle array

the ravine array

the valley array

the plain array

Galpin (1934, 1936a) added the "escarpment" array to this series, being of the same order of toughness as "plain", while Dry (1935a) refers to the "all in" array. Burns (1955) refers to a rather similar array, the "incline" array which does not have a precipice and shows a straight

transition from HH to Hi. The occurrence of the different fibre types in these arrays is shown in table 1.

Dry (1934) made some suggestions as to the relationship between the birthcoat and the adult fleece, and also described the effect of some environmental factors on birthcoat and later hairiness. Dry (1935b) suggested that poor growth of the lamb caused a reduction in the shedding of hairy sickle fibres and failure to add the normal number of histerotrichs. The first of these features he considered to be due to lowered vigour of the follicles, associated with the idea that shedding is generally a function of the more vigorous follicles. The failure of the normal number of histerotrichs to appear, under poor nutritional conditions was also found by Henderson (1953) the reason probably being failure of secondaries to develop. (Short 1955b).

Leslie (1935) showed that lambs from ewes fed on a high plane during pregnancy averaged a higher score for halo distribution than lambs from ewes fed on a lower plane. A non significant tendency for twins to be higher than singles does not seem to fit in well with this picture. Cockrem (1956) showed significant differences in favour of twins in halo density.

Galpin (1934, 1936a) studied the variation of fibre type arrays between twelve positions in Romney lambs and between nine positions in Ryeland and Southdown lambs.

Five of these positions were along the back while four were low on the side. As a result of the study Galpin (1934) concluded: -

> ".....the array on any position either posterior or inferior to another position in a straight line, limits the array on either the anterior or superior position to being no less depressed than the array on either the posterior or inferior position."

While Galpin has made an overgeneralisation not taking into account such features as shoulder patches and other sudden changes this conclusion is a useful statement of the general tendency. Galpin also found that the Romney lambs had the "toughest" arrays and were most variable from position to position, followed by the Ryelands then Southdowns. Galpin (1934) also studied the abundance of pre-curly-tip fibres and found that the regions of percentage of pre-CT were similar to the regions of development of the follicles. Taking abundance on the rump as unity the numbers of these fibres in other regions were: -

Poll	4-5
Withers	2-4
Neck	2-4
Side	1-2
Back	1-2

From an examination of foetuses Galpin (1934, 1935) concluded that the fibre types developed in the skin in the order that they are listed above.

Sutherland (1939) studied each fibre type in detail, drawing conclusion on the physiology of the follicles from the morphology of the fibres. On the basis of his finding that plateau arrays had a low proportion of CT and a high proportion of Hi he suggested that at birth lambs with plateau arrays had not attained the same stage of follicle development as lambs with finer arrays. Stephenson's (1957) work seems to disprove this theory.

Finding occasional fibres the presence of which did not seem compatible with the remainder of the fibre population, Sutherland stressed the importance of "in parallelism" first suggested by Dry (unpublished, quoted by Sutherland 1939). This concept is that small areas of skin may be subject to forces which do not affect neighbouring areas. Sutherland suggested this could be due to local variation in the density of follicles causing a pre-natal check in a small area. Sutherland also studied the position of the precipice in the array and found this to be rather variable, sometimes occurring in the histerotrich series and even in the pre-curly-tip fibres.

Goot (1940), also discussed physiological implications of the shape of the different fibre types. He suggested that crisis thinning was a repetition of the pre-natal check. Goot also suggested that HTCT develop about the same time as super-sickles, while he did some work on shedding

of the different fibre types. Goot (1940, 1941) also commented on the evolution of the birthcoat of the lamb.

Dry (1940) reviewed work done by Sutherland, Goot, McMahon, Galpin and himself and described some relationships between features of the birthcoat and later characters of the fleece, chiefly shedding of kemps.

Goot (1945) reported a highly significant correlation (99 samples) between fibre type array and medullometer reading, -

$$r = 0.75$$

J.M. Ross (1945) and Ross and Wright (1954) followed on with the kemp succession work, studying the succession of the different birthcoat fibres in the various N genotypes. Ross (1945) concluded that the abundance of G2. kemp was related to proportion of HTCT fibres present in the array and to the toughness of the array, these two factors being interrelated. Ross and Wright (1954) stated that shedding of the different fibre types was similar in all genotypes studied. They also presented data on the proportions of the different fibre types shedding, the order being, HH, SSB, SSA', Sk, HTCT.

D.A. Ross (1950) presented much data from measurements of the various fibre types and complete samples taken from lambs in November and January. He found in N-type lambs the range of fibre diameter was,

pre-CT 70-140 μ.

pre-precipice-CT	40-75 μ.
post-precipice-CT	0-50 "

There was considerable overlapping of fibre diameter between fibre types, and although the precipice was readily distinguishable by eye, it was not clear in graphs illustrating the distribution of fibre diameters. Ross found that fibre diameter variability was greatest on the back, and he suggested that the coefficient of variation for all fibres approached a constant for each lamb. In surveying the relationship between medulla diameter and fibre diameter Ross suggested that the relationship was not simple, although it was apparently linear above 70 μ. His measurements showed that in practically all the samples examined (N-type), the average post-natal fibre and medulla diameters were greater than the average pre-natal diameters, the fibre diameter increasing gradually from birth until the time of the November sampling. When studying fibre length Ross found a trimodal distribution, the first mode consisting of fibres produced in P follicles, the second mode fibres produced in the first wave of secondaries, with the third mode, fibres produced in the second wave of S follicles. Another aspect of the fibre length study was that although HTCT were generally finer than HH, their post-natal growth in length was faster.

Stephenson (1952, 1956) furthered the work of Galpin

(1934, 1936a) on array gradients, studying seven positions on lambs of different N genotypes. In all genotypes the most heavily checked sample found was that from the shoulder patch. Since this position is almost immediately posterior to the shoulder position it seems that Galpin's (1934) statement, that positions anterior or inferior to another, are always less heavily checked, does not always hold. Also Stephenson (1952) reports one case of a lamb with "tougher" arrays on the back and side than on the britch.

Stephenson (1952) stated that as the arrays became "tougher" the precipice became more noticeable in the CT fibres. This he ascribed to an increasing difference between P and S fibres. In studying percentages of the different fibre types, Stephenson (1952, 1956) was unable to find the high proportions of pre-CT fibres on the britch reported by Galpin (1934, 1936a), although this area did tend to have the highest proportion. He found very low percentages of pre-CT on the shoulder patches of +/+ lambs however. Stephenson (1952) was also unable to find a higher proportion of histerotrichs in N-types than in non-N. Sutherland (1939) and Goot (1940) had reported that "tougher" arrays had more histerotrichs.

Stephenson (1952) applied a discriminant function analysis to his data from the shoulder patch position, to

separate the genotypes. The analysis showed N/N to be significantly different from all genotypes with N/+ and nr/nr only barely significantly different at the 5% level and +/+ significantly different from the others. In view of the laborious calculation involved with the computing techniques generally available, it seems that the method is of little use for fibre type array work.

Stephenson gave the average arrays for the different genotypes in each position, N/N being the "toughest" in all samples with N/+, nr/nr and N/+ +/nr having similar arrays, and +/+ the "weakest."

Dry, Burley and Speakman (1952) and Burley and Speakman (1953) studied the plasticity of the different fibre types of Romney, Lincoln and Merino hoggets and found quite large differences between fibre types. The order of plasticity was the inverse of the order of development, histerotrichs being highest and sickles lowest in plasticity.

Henderson (1953) used fibre type array analysis to estimate the post-natal development of fibres and follicles. On the basis of finding highly significant differences in histerotrich numbers between lambs of the high plane and low plane groups, he concluded that nutrition up to 20 weeks of age was a factor influencing the ability of lambs to increase fibre numbers post-natally.

While the New Zealand Romney has been the main breed examined in fibre type work, our knowledge of the arrays of other breeds has been added to in recent years. Deshpande (1948) studied Scottish Blackface lambs, Short (1951) Welsh Mountain while Fraser and Hamada (1952) presented some data on the birthcoats of Scottish Blackface, Welsh Mountain, Halfbred (Cheviot x Border Leicester), Blackface x Cheviot, Oxford x Halfbred and Suffolk x Halfbred. Dry (1952) reported some Wensleydale arrays in which no pre-CT fibres were present, checked CT being apparently the earliest fibres to commence growth. Burns has studied the fibre types of the Suffolk (Burns 1954a), the Herdwick, the Herdwick x Swaledale (Burns 1954b), the Merino and the Herdwick x Merino (Burns 1955). Burns showed that the Merino x Herdwick sheep had arrays varying from coarse plateau to fine plain, the most common being a new array, the "incline" array.

Burns (1955) presented data on the accuracy to be achieved from counting different numbers of fibres suggesting that a count of 500 fibres would be desirable. She stated that the adult fleece characters most closely related to the fibre type array were uniformity of length and diameter of fibres in the staple and hairiness.

F. The relationship between fibre types & follicle types.

Our knowledge of which fibres grow in the different types of follicles is very limited, despite much discussion of the relationship. de Meijere (1894) provided the background for much of the discussion, when he stated that generally the first follicles to appear produced the most robust fibres.

Dry (1935a) presented the different fibre types in what he stated to be their order of appearance, his evidence being chiefly robustness with some observations of foetuses, mainly by Hefford and Galpin. Dry (1933, 1935a) expanded Duerden & Boyd's (1930) idea of a birth check into the pre-natal check concept as an explanation of the thinning in sickle fibres. Dry (1933) stated that the pre-natal check had several effects.

i Narrowing of the basal part of sickle ends and shedding of babies.

ii Fineness of the tip of CT and basal portion of checked Sk and CT.

iii Sub apical thinning of HH.

iv Causing persistent growth.

v Reduced size and presence of sweat glands. (Hefford, unpublished).

It seems that with regard to "v" the effects of the pre-natal check and the type of follicle were confused.

Dry (1933) suggested that increasing density of follicles was the cause of the check and he stated that variation in arrays was due to differences in onset, intensity, and decline of the check.

Galpin (1934, 1935) suggested that the pre-natal check was a "trio depression" brought about by the sudden increase in density when the PL follicles developed. She suggested that there was a further check, the "nine depression", caused by increasing density at the commencement of development of follicles of the nine stage which she had postulated. Overlapping of the two depressions caused the fibres to be fine thereafter. On the basis of these ideas she suggested combinations of forces which would produce the different fibre type arrays.

Galpin (1934, 1936a) found the earlier an area commenced development, the higher the proportion of pre-CT fibres to be found on that area. She concluded that while in the earlier areas to commence development, all trio follicles could produce pre-CT fibres, on later developing areas pre-CT fibres were limited to the central trio follicles. Further, she suggested that fibres growing in "nine stage" follicles would be limited by the "nine depression" to Hi.

Galpin (1936b) enlarged on these ideas, studying the foetal growth rate of different areas at the time when the follicles were developing. She found that fine arrays

occurred where the relative growth rate was slower in later stages of foetal development, while high pre-CT counts were associated with regions where follicle initiation and the trio stage occurred when the region was growing most rapidly. It seemed from this that the faster growth rate kept the density lower, so minimising the check.

Hefford (unpublished) dissected follicles growing checked CT fibres out of the skin and found that while in most cases they were associated with a sweat gland, these glands were often lacking. She also found sweat glands were associated with pre-CT fibres.

Sutherland (1939) suggested that the fibre type array was the result of two independent but interacting forces.

i An inherent drive towards hairiness (base)

ii The pre-natal check.

These two forces acted antagonistically to one another, a strong base resulting in coarse medullated fibres which could withstand a fairly intense check without undue fining, although some thinning would result (e.g. a P3 array).

Goot (1940), also discussed base and check at length. He suggested that crisis thinning was a repetition of the pre-natal check and consequently called the pre-natal check "head check" and crisis thinning "tail check." Goot also suggested that the check acts on individual follicles and not all follicles which have been initiated are affected

by the check. He believed HTCT to begin development at the same time as super-sickles and even perhaps halo-hairs. Goot quoted Dry (unpublished) that the second wave of histerotrichs grew in follicles developed by budding from the first wave histerotrich follicles. Dry did not think follicles producing other fibre types gave rise to daughter follicles. Goot however suggested that small CT follicles might produce daughter follicles.

J.M. Ross (1945, 1954) examined the fibres through the skin in a 113 day old N/+ foetus. She found four types of fibres.

i Large tips with a long unmedullated apical region. (HH)

ii Shorter tips with medulla to the extreme end. (SS)

iii Small curved tips with a little medullation at the base. (HTCT)

iv Small tips with no medulla. (CT)

As the S fibres had not pierced the skin at this stage, all the above must come from P follicles. Ross (1945) stated that the appearance of HTCT was often just as early as super-sickles and hence she suggested they should be considered as part of the pre-CT series. Ross also noted that follicles were very crowded at the 113-119 day stage.

Fraser and Hamada (1952) compared frequencies of the different classes of follicles and fibre types in birth

coats of individuals of several different breeds and crosses of British sheep.

They calculated "expected" Sf/Pf and PL/PC ratios from fibre type frequency by assuming certain fibre types to grow in certain follicle types. It was found that the "expected" and actual ratios agreed reasonably well when it was assumed that in coarse birthcoats PC follicles grew HH, PL grew HTCT and S grew plain CT and Hi, while in fine birthcoats, PC grew sickle tips, PL grew chCT and S grew plain CT and Hi. Agreement was not very good in many cases and Fraser and Hamada suggested that in coarse birthcoats some PL follicles grew plain CT fibres. Numbers of fibres counted were not great in many individuals, and the accuracy of the estimation cannot be very high in these cases.

Fraser, Ross and Wright (1954), from observation on PL/PC ratio in N/+ foetuses and Sf/Pf ratio in N/+ and +/+ new born lambs, calculated the mean percentages of the different follicle types. Fibre type distributions were determined from 33 N/N, 65 N/+ and 17 nr/nr hoggets, frequencies were corrected for differences in histerotrich populations between ages, genotype and total mean percentages were obtained and the percentages were compared with the standard follicle frequencies calculated as above. The ratios best fitted the following hypotheses.

i In N/N, PC grew pre-CT, PL grew HTCT and S grew CT and Hi.

ii In N/+, PC grew pre-CT, PL grew HTCT and CT, S grew CT and Hi.

iii In nr/nr, PC grew pre-CT and possibly some HTCT, PL grew HTCT and CT, while S grew CT and Hi.

From this and other data, Fraser et al concluded that in N-type, CT fibres never grow in PC, although this occurs in some non-N lambs. If this occurs many, if not all are ch CT. Data from fibre length supported the above assumptions.

Rudall (1955) published work carried out in the early 1930s relating fibre types to papilla morphology. His evidence seemed to suggest that the rate of growth of a fibre was proportional to the papilla volume/papilla surface ratio. Also there seemed to be a relationship between medullation and the bulb volume/papilla volume ratio. Rudall observed that halos had papillae of large diameter, and sickles very short papillae 2/3 the length of those of curly-tips to which it was similar in other respects. Rudall ascribed this shortening to the action of the pre-natal check. Rudall also found a relationship between eccentricity of the papilla and the fibre. This agrees with Teodoreanu and Derlogea's (1956) statement that the cross section of ribbon shaped fibres was similar to that of the "roots" that produced them.

Fraser (1951, 1952a, 1952b 1953) expanded on suggestions of Galpin (1934, 1935, 1936b, 1947, 1948), formulating

a theory that the birthcoat and later fleeces were dependent on the interaction of two forces.

i Competition between follicles for fibre forming substrate

ii The relative "efficiency" of the different follicles.

This theory can be considered to be a variation of the check and base concept.

Galpin (1947) stated (the statement has since proved erroneous; Morley, Lockart and Davis 1955, Lockart 1956b) that under good conditions the output of wool weight per unit area is a constant, independent of density. She suggested that this was due to a limited amount of substrate available to the follicles.

Fraser theorised that the follicles were in competition with one another for this substrate and that mean fibre diameter was related to follicle density via this pathway. To explain differences between carpet type and other wools, Fraser suggested that in carpet breeds, the earlier a follicle developed, the greater its relative efficiency in competing for substrate. Hence the length and diameter of P fibres would be much greater than that of S fibres.

Fraser (1951, 1952a) made the suggestion that the sickle end was the result of competition from the developing PL follicles slowing the growth rate of fibres already growing

in PC follicles. These fibres were subject to a constant amount of crimp per unit of time, but since the rate of increase in length was declining, the result was an increasing degree of curvature in more proximal regions. The thickening of the fibre in the post-natal region was explained in terms of decreased competition as a result of skin expansion. Fraser (1952a) also stated that the earlier CT fibres differed from those commencing growth later, by having more crimps.

According to Fraser (1952a) the equation

$$(e) = f(T)$$

or efficiency of a follicle is a function of its time of development, gave a statement of the pre-natal check. Since Fraser (1951) had previously stated that the shape of the sickle end was due to competition and Dry had said the sickle end was the result of the pre-natal check, it seems that competition would be the critical factor in the check. The above equation approaches much more nearly a statement of the base concept.

Fraser (1952b) found that in the birthcoats of ordinary Romneys the length distribution was bimodal, the modes corresponding to

i Primary and early secondary fibres

ii Late secondary fibres.

In N-types however there were three modes, with the primary

and early secondary fibres occurring in separate modes. Fraser (1953) elaborated on these ideas demonstrating how they could be fitted into a plan to explain all aspects of fleece growth. He suggested that the type of fleece which a sheep grows was determined by three factors

i The amount of substrate available

ii The relative efficiencies of the different types of follicles

iii Density of follicles and the resultant competition.

Fraser and Short (1952) calculated the regression of size of a central fibre on the sum of sizes of other fibres within a certain radius. In Ryeland, Lincoln and Merino skin samples they found significant regressions for a radius of up to 173μ, 283μ and 147μ respectively. They suggested that these radii were the effective distances of competition in the three breeds. Fraser and Short stated that while a certain amount of bias would result from the method of analysis, using every fibre in an area as a central, other data (Short unpublished) supported their findings.

Padfield and Bell (1957) obtained similar regression coefficients in a study of some idealised Lincoln follicle groups which were drawn with primaries of one diameter, secondaries at the secondary margin of another diameter and inner secondaries of a still smaller diameter. On the strength of these findings Ryder (1957b) suggested that Fraser and Short's (1952) results were due to the structure of the follicle group and that hence their data did not

provide any evidence for the competition theory. However it can just as easily be argued that the differences in the size of the fibres in the group are due to competition, not to any inherent property of the group itself. Hence Padfield and Bell's results could be considered to be evidence favouring the competition theory.

Possibly the main argument which can be levelled against Fraser and Short's technique, is that the measurements were apparently obtained at the level of the sebaceous glands while the fibres are keratinised and fixed in diameter at levels below this. The distribution of follicles is more diffuse and does not conform rigidly to a group pattern in these lower, prekeratinisation regions where competition, if it does occur, will be taking place. Ryder (1957b) also argued against the competition theory, on the grounds that since each follicle had its own, individual blood supply (Ryder 1955b), he did not see how the competition could take place. This argument does not seem valid however, since systems "in parallel" (physics terminology) can compete with one another, and competition is not the sole property of systems arranged "in series".

In conclusion, the literature shows that while much theory has been brought forward to relate fibres to follicles, our factual knowledge is limited. While the competition theory certainly provides a useful concept as a basis for study it still remains only a theory and many workers in the field doubt its validity.

IV DEVELOPMENT OF TECHNIQUES

No really satisfactory method of determining the origin of the fibre types has as yet been used. Hefford (unpublished work) dissected out complete follicles with the fibres still intact. Galpin (1934, 1935) based her conclusions on frequencies of fibre types and the order of development of fibre types which she reported. Dry (unpublished) had based his conclusions on the order of development of fibre types and follicles and also on fibre morphology. Goot (1940) also drew some conclusions from fibre morphology, while J.M. Ross (1945, 1954) studied the fibre types present on the skin of foetuses. The most comprehensive studies however, those of Fraser and Hamada (1952) and Fraser, Ross and Wright (1954), were based on a comparison of the frequencies of follicle classes and of fibre types.

These methods, variations of these methods and several untried methods gave promise at the start of the project that a really satisfactory technique could be developed.

The simplest and most satisfactory method described in the literature was the frequency comparison method of Fraser and his colleagues (Fraser and Hamada 1952, Fraser Ross and Wright 1954). Frequencies of fibre types were fitted to the frequencies of follicle classes by assuming

certain types of fibres to grow in a certain class of follicle. While it was thought that a better planned approach could probably supply more accurate information than the studies already mentioned, doubts about the accuracy of the results from previous frequency studies stressed the desirability of having proof of these findings by an independent method.

Most of the methods originally thought to be possibilities, on further consideration proved to be impossible. However four new methods were thought to be worthy of trial. They were: -

1. Dissection.

Dissection of complete fibres with follicles from a piece of skin had been used by Hefford (unpublished). However although P and S follicles could be separated on the basis of presence or absence of sweat glands, it would be impossible to go beyond this stage in the follicle classification. Clearing a piece of skin, then observing through a microscope from which follicles the different sorts of fibres were withdrawn, seemed to have possibilities.

As a preliminary investigation, two pieces of skin from which the wool had been removed prior to fixation, were lightly stained using haematoxylin and eosin. They were dehydrated by passage through increasing concentrations

of alcohol and cleared in cedarwood oil. While Galpin (1935) had used a similar method on foetal skin, it was found to be impossible to recognise the different types of follicles in this study. After removal of much of the lower layers of the skin by hand leaving approximately 500-1000μ, it was still impossible to recognise most of the follicles, although some primaries could be identified. Since follicles are generally classified in fairly thin (below 50μ) transverse sections, and because of the extreme difficulties in obtaining such a section with the fibres still attached, it was decided to abandon the method.

2. Fibre Removal.

It was suggested that pulling all of a certain fibre type from a piece of skin and then studying the empty follicles following sectioning might have possibilities. However the difficulty in removing all of a certain type of fibre, coupled with the loss of quite a few fibres during sectioning, appeared likely to reduce the accuracy of the method to the point where the results obtained would not justify the extremely laborious technique involved.

3. Cortical staining.

Horio and Kondo (1953) reported bilateral differentiation of fine wool fibres by staining with Janus

green and Ponceau 2R. Auber (1952) had earlier suggested that progress of the final phase of keratinisation was diametrically across the fibre (segmental) while that of straight fibres was periphero-axial. Fraser and Rogers (1955a, 1955b) and Dusenbury and Menkart (1955) had shown that as fibres became coarser the differentiation of the two regions of the cortex tended to become periphero-axial. It was thought that possibly there might be differences between the fibre types and between follicle types of N-type sheep in fibre segmentation, and that the staining reaction with Janus green might be a possible means of relating the fibres and follicles. Also the findings could possibly be of interest for their own sake. Consequently two slides of skin sections from an N/N lamb sample were stained with Janus green using the technique of Horio and Kondo (1953) with the exception that an ordinary microscope was used in place of a polarising microscope.

Despite very good differential staining of tissues of the follicles only a few of the finer fibres showed any indication of division of the cortex into two parts. A similar case of failure of Janus green to differentiate cortical regions had been reported by Lang (Discussion, Proc. Int. Wool Text. Res. Conf. Aust. 1955 F) and because of limited time, no attempt was made to try the methylene blue staining technique reported by Fraser and Rogers (1955a).

4. Comparing fibre diameters.

It was thought that possibly in N-type sheep there was a reasonably strict relationship between the type of follicle and the diameter of the fibre produced in that follicle. This could perhaps be related to the diameters of the fibre types. Ross (1950) had shown that there was a tendency for the fibre diameters of the fibre types to decrease greatly from HH to Hi., but the amount of overlap between similar fibre types seemed to suggest that the method would be far from perfect. In some sheep it did seem however that fairly rigid boundaries existed. Carter (1955) presented data indicating that there were wide differences in diameter between P and S fibres of adult N-type sheep but no data was available on differences between PC and PL fibres. However the method presented worthwhile possibilities and it was decided, to attempt to define the relationship on the basis of diameters.

V MATERIALS AND METHODS

A Sampling

In mid October 1956, skin and wool samples were taken from a number of N/N lambs (Dry 1955, 1956) varying in age from 8 to 63 days. The sampling procedure was based on that described for cattle by Carter and Dowling (1954). The use of this method on sheep has subsequently been described in detail by Carter and Clarke (1957a). The procedure was as follows: -

i The wool was removed from a small area on Dry's standard back position by cutting with scissors as close to the skin as practicable.

ii The wool sample was placed in an envelope.

iii The area was rubbed with a 50:50 absolute alcohol-ether mixture to remove wool grease.

iv A 1 cm. diameter circle was cut in the skin of the cleared area by pressing a trephine to the back and rotating it clockwise and anticlockwise once.

v The disc of skin was lifted with forceps and freed from the subcutaneous tissue with scissors.

vi The disc was pressed, subcutaneous surface downwards, onto a piece of cardboard, to which it adhered.

vii Cardboard and skin sample were placed in a jar of 5% formalin in isotonic saline for fixation.

viii The wound was treated with antiseptic.

The method proved entirely satisfactory provided the operator was resolute in applying the trephine. In preliminary trials half heartedness in the first cut had often led to the reapplication of the trephine. If the two cuts did not coincide, the samples obtained were rather smaller than the prescribed 1 cm. diameter.

B Skin Sections

Skin samples were treated using a method modified slightly from that used by the Department of Agriculture and Stock, Brisbane (Anon. 1955). This is very similar to the technique reported by Carter and Clarke (1957a).

1. Processing

The majority of the samples were processed automatically with an Elliot automatic tissue processor but prior to the arrival of this machine a few samples had been prepared manually. The samples were washed in tap water to remove formol-saline, most of the excess connective tissue beneath the follicles was removed with scissors (removal of too much makes the skin rather more "plastic"

than is desirable), and the identification number of the lamb was written on the subcutaneous surface with indian ink. The samples were then placed on the tissue processor trays, one in each compartment, with a small cardboard strip showing the identification number in case the number on the sample became illegible. Processing was as follows, the processor automatically moving the samples on to the next bath at the end of each period.

i	50% alcohol	-	2 hours
ii	70% "	-	3 hours
iii	70% "	-	3 hours
iv	95% "	-	3 hours
v	95% "	-	2 hours
vi	Abs. "	-	2 hours
vii	Abs. "	-	2 hours
viii	Abs.alcohol-xylol	-	2 hours
ix	Xylol	-	1 hour
x	Xylol	-	1 hour
xi	Paraffin wax	-	3 hours
xii	Paraffin wax	-	3 hours
			27 hours

2. Embedding

Prior to embedding, the gauze trays containing the samples, were stored in a dish of molten wax in a thermostatically controlled oven. Wooden blocks, approximately 1" x 5/8" x 5/8", were placed in a shallow dish of molten wax to allow the wax to be absorbed.

Each sample was then treated in the following way: -

i A pair of brass, L shaped embedding moulds were smeared with glycerol-alcohol to prevent wax adhering to them.

ii The moulds were placed together on a small sheet of glass.

iii Molten wax was poured into the space between the two moulds.

iv The sample was placed, subcutaneous surface uppermost in the molten wax. If fast congealing made it necessary, the wax in the central portion was warmed by applying a low bunsen flame to the undersurface of the glass.

v The soaked end of a wooden block was warmed slightly in the bunsen flame, introduced slowly into the wax on an angle to prevent air bubbles remaining between the block and the sample, and the block was then pressed lightly onto the disc of skin to flatten it.

vi After blowing on the wax for a short time until a film of solidified paraffin formed, the piece of glass with moulds, sample and block were placed in cold water to hasten cooling.

vii After allowing adequate time for setting, the block and wax were separated from the glass and moulds and excess wax was trimmed off with a razor blade or scalpel.

This method, using a block of wood to flatten the skin, proved extremely satisfactory when the technique was finally perfected. Most other workers have pressed a small piece of glass onto the skin to flatten it but hitting this glass with the microtome knife could make this rather an expensive procedure if care was not exercised. Further,

having the paraffin block attached to the wood meant that to change blocks on the microtome, all that was necessary was to unscrew a clamp and slip another block into the clamp in the place of the previous block.

Most of the impregnating and blocking was carried out using a 54.5 °C melting point paraffin to which ceresin had been added. In the case of some sections cut during a series of hot days, a switch was made to a 58°C melting point wax. This gave much improved results but ribbon formation was not good.

3. Sectioning

Skin is one of the most difficult tissues to section satisfactorily and many workers have been forced to use celloidin embedding to get satisfactory sections (Carter 1939a). A large number of trials were carried out before sectioning of the actual thesis material was attempted, but still several modifications giving better results were made during the sectioning of these latter samples. The microtome used was a "Jung" rotary model. Most of the sections were cut at 8μ, but in some of the earlier attempts it was found necessary to cut sections somewhat thicker.

The method used in the later stages was as follows: -

i The wax was scraped from the area over the sample to expose the skin.

ii The block was soaked in 1% Teepol solution, for a period of one to three days.

iii The block was dried with filter paper and placed in the microtome.

iv The sample was oriented carefully with regard to the microtome knife, to cut sections parallel to the surface.

v The first few cuts were made with an old microtome blade. This was replaced with a first class blade and a series of sections were cut at 8μ.

vi As the paraffin ribbons were formed they were removed with camel hair brushes and laid on the surface of water thermostatically controlled at about 50°C.

vii Sections were selected from the ribbons in the bath and were floated onto microscope slides which had been smeared very lightly with albumen adhesive.

viii Slides were identified with glass marking ink.

ix The slides were dried by placing them in a 48°C oven for at least 24 hours.

Soaking in 1% detergent (suggested by Pearlman and Cole 1951) allowed sections to be cut much more readily. Without this softening the tissue tended to shatter before the blade. Another unsuccessful attempt to improve sectioning involved cooling the block in a refrigerator.

The sections tended to become rather badly compressed during sectioning, and flattening was difficult. In the earlier work sections were floated in water on the microscope slides. These were then warmed gently over a bunsen.

The final technique of floating the ribbons in a bath proved much more satisfactory.

4. Staining

The staining technique, a haematoxylin, eosin, picric acid method, was based on that used by most Australian workers. The slides, held in a rack, were transferred through a series of rectangular jars. The reagents, and the time spent in each jar are as follows: -

Xylol	2 baths of 7 min. each.
Absolute alcohol	7 min.
95% alcohol	5 min.
70% alcohol	5 min.
50% alcohol	5 min.
Water	1 min.
Haematoxylin	8 min.
Water	5 min.
Picric acid	4 min.
Water	3 quick changes.
Bluewash	1 min.
Water	2 baths of ½ min. each.
Eosin	3 min.
95% alcohol	3 baths of 2 min. each.
Abs. alcohol	3 baths of 5 min. each.
Xylol	4 baths of 3 min. each.

The sections were then mounted in Canada balsam and dried in a hot oven.

The Haematoxylin used, the rapid staining, iodine ripened mixture suggested by Cole (1943), produced excellent results. The picric acid consisted of a saturated aqueous solution while the eosin was a 5% aqueous solution of Eosin B.

The sections were stained rather more heavily with

eosin than is generally the case. This made the trabeculae rather more easily seen and thus it was possible to distinguish more clearly between PC and PL follicles.

5. Measurement of the follicle population

(a) S/P and density. Ten fields, scattered over the skin section were projected at 100 X and follicles falling into a 10 cm. square (i.e. follicles in a 1 mm. square area of skin) were charted using symbols for the different types of follicles. All follicles, the lumen of which touched the top or left hand edge of the square, were considered to be in the area, while all follicles with lumen touching the bottom or right hand edge were considered out and were not recorded.

The follicles of the different types were counted separately, each follicle being checked off as it was counted. The counts of all the mature P and S follicles (including those which apparently had shed fibres) were then added together to give the uncorrected P and S densities. Follicles which did not show evidence of shedding or losing a fibre by having an empty lumen, and which did not have a fully keratinised fibre (stained yellow), were classified as immature and were not included in this figure.

Corrections for shrinkage of the skin were first determined by projecting the section at 20·8x through the objective lens of the microscope alone. Measurements were

made in four directions across the image of the sections using a special direct reading scale. The average of these four measurements was squared to give the correction factor.

$$\text{Correction factor} = \left(\frac{D_1 + D_2 + D_3 + D_4}{4} \right)^2$$

This correction factor then is the ratio, area of the section/area of a circle of diameter 1 cm. The raw densities were multiplied by this factor to give the corrected densities.

Because many of the sections were far from oval or circular in shape, it seemed that possibly the above method might not be very accurate. Consequently the edges of the sections, magnified 20·8X were mapped on paper. The circle cut in a piece of paper by the trephine was similarly mapped and a planimeter was adjusted so that two traverses around the edge of this circle gave a reading of unity. The map of each of the skin sections was then placed under a large sheet of transparent paper and the edges were traced round twice with the planimeter. Then the correction factor could be read directly from the planimeter. Differences were not as great as might have been expected, the average error being only 2·8%. All densities were subsequently revised, using the correction factor determined with the planimeter.

Sf/Pf ratios were calculated from total uncorrected Pf and Sf densities from the ten counts.

6. Fibre diameters

Follicle groups with readily discernible PC and PL follicles were not a very common occurrence in most sections; in fact the method could not be used on a large proportion of the sheep because it was impossible to discern PC and PL in the sections available. Suitable follicle groups were chosen by projecting an image through the high power objective alone. Once a suitable group had been found the other lens was folded into place and the diameter of the minor axes of the fibres were measured with a scale reading directly in microns. Every follicle in the group was so treated.

Initially, in one sheep, fibre and medulla, major and minor axes were measured. These were then examined to see which measurement was likely to give the most satisfactory results. It seemed likely that the "apparent" minor diameter would be the most useful since it was unlikely to be affected by marked deviations of follicles away from the perpendicular.

Some longitudinal sections and the appearance of some follicles obviously cut at a fairly acute angle, in transverse sections, seemed to suggest that in these sheep, errors due to this cause might not be as negligible as Burns and Clarkson (1949) have suggested. It seems that the 20% deviation from right angles, on which they based their

calculations, might be an underestimate. Minor fibre diameter was expected to be of more use than minor medulla diameter, since medulla diameter can be rather difficult to measure. Standard deviations and coefficients of variation for the four characteristics of PC and PL follicles were calculated from one section. In PC fibres, standard deviations and coefficients of variation were both larger for the medulla diameters, with the major fibre diameter slightly larger than minor fibre diameter. In the case of the PL fibres there was little difference between any of the standard deviations but coefficients of variation were somewhat greater in the case of the medulla diameters, while the minor fibre diameter had a slightly greater coefficient of variation than the major fibre diameter. On the basis of this it seemed that the choice lay between minor and major fibre diameters. The greater difference between PC and PL in mean major fibre diameter (28 μ as against 23 μ in minor diameters) seemed to indicate that major diameter might be more suitable but doubts about the angle of the cut across the fibres weighed the balance in favour of the minor diameter.

C The Fibre Population

1. Fibre type arrays

A small subsample, judged to contain about 200 fibres was grasped at the butt and withdrawn from the main sample. The subsample was placed on a small (8½" x 16") sheet of three ply covered with fine black velvet. This in turn was placed on a larger piece of black velvet covering a well lit bench. The individual fibres were drawn from the sample and laid with other members of the same fibre type on the large piece of velvet. Any fibres difficult to classify because doubts existed whether or not they were medullated in a certain portion were checked by observing them in a petrie dish of benzol. If further observation was necessary a microscope was used. Having placed all the fibres into groups, the numbers of the different fibre types were then counted.

To check that the wide random variations did not enter into the count a similar subsample was obtained and was treated the same way.

2. Fibre diameters

A line of cedarwood oil was laid down one side of a microscope slide. The members of one fibre type were picked off the velvet with balance forceps and were laid with their butt ends in line, along the slide. A

cover slip was lowered gently onto the slide and the fibre diameters were measured when projected at 540 magnifications. The measurements were made close to the butt of the fibre, an attempt being made to measure the minor diameter by locating the narrowest part of the fibre in the field. Each of the fibre types were treated in this way except for the shortest histerotrichs. These were placed haphazardly in a small blob of cedarwood oil before a cover slip was placed over them. In this case no attempt was made to measure the diameter at the butt of the fibre.

D Presentation

The data is considered for individual sheep

1. Frequencies

The method is similar to that of Fraser and Hamada (1952), the assumption being made that certain fibre types grew in a certain type of follicle. Then the assumption was checked by calculating the S/P and PL/PC ratios "expected" to be found if the assumptions were correct, and comparing these with the ratios found in the skin sample. Owing to distortion of the follicle groups

during the development of the S follicle population, it becomes very difficult to recognise PC and PL in lambs as old as these. Consequently the PL/PC ratio used (1.9) is that determined by J.M. Ross (1945, 1954) in N-type foetuses.

2. Fibre diameter

The fibre diameter data is presented in the form of two series of histograms, each series consisting of the frequency distributions of fibre diameter of the different fibre or follicle types. The series for fibre types is placed immediately above the series for follicle types to allow easy comparison of the frequencies.

All fibres from a number of follicle groups were measured, data from 200-250 fibres being taken and plotted in the graph for the different follicle classes. The graph of diameter distributions of fibre types is made up of measurements of a similar number of fibres to that in the follicle class graph. The number of diameters of each fibre type included in the graph was calculated by multiplying the number of measurements for the different follicle classes by the proportion of each fibre type.

$$n_1 = N \frac{f_1}{F}$$

where n_1 = the number of diameters of fibres of type 1 plotted in the graph.

N = the total number of fibre diameters of all fibre types, plotted in the graph. (= the number in the follicle class graph)

f_1 = the number of fibres of type 1 counted in the array analysis.

F = the total number of fibres of all types counted in the array analysis.

Data for ribbon shaped fibres were omitted since the minor diameter is not a good indication of the size of the fibre and also because it is impossible to measure the minor diameter accurately. Further, the occurrence of ribbon shaped fibres has also been used separately in studying the origin of the fibre types.

By comparing fibre diameter distributions of the different fibre types with those of the follicle types it should be possible to get some indication as to which fibres grow in the different follicles. The reliance which can be placed on the method is however limited by the following factors that could possibly lead to wrong conclusions being drawn.

i Variation between different regions of a fibre.

ii Variation between fibres from adjacent pieces of skin.

iii Variation between fibres of one type in the same piece of skin.

(Studying distributions should eliminate the possibility of large errors due to this cause).

iv Variation between axes of fibres.

While an attempt was made to measure the minor fibre diameter of fibre types, reducing factor iv, the method was far from satisfactory. Measuring the diameter

in cross sections would have been much better. The importance of errors associated with measuring an axis other than the minor of a proportion of the fibres was however not realised until all the data had been collected. If the major axis of a fibre was measured instead of the minor axis the diameter could be over estimated in P fibres by approximately 20μ. This of course means that if a HTCT is found with a diameter 20μ larger than the largest PL follicle, this difference might be due to the fact that the major axis of the HTCT was measured and need not necessarily indicate that the fibre was of PC origin.

Because only a small number of samples were suitable for the application of this technique, only five samples have been treated in this way.

3. Fibre characteristics

In some samples the occurrence of ribbon shaped fibres provided a useful method for studying the origin of fibres. This characteristic of certain fibres is simply recognised from a visual inspection of the fibre itself or in cross section. Unless there have been sudden changes along the length of individual fibres, if we find only one class of follicle with ribbon shaped fibres, we can say that those fibres, ribbon shaped basally are produced by that class of follicle.

4. Summary

Finally for each sheep an attempt is made to summarise the results from all methods into a clear, concise description of the most probable origin of the different fibre types.

VI RESULTS

A Sheep 52

1. Frequencies

TABLE 2

Percentages of fibre types and ratios of fibres and follicles- Sheep 52

Type	Sample 1	Sample 2	Total
HH	-	1.1%	0.6%
SSA	-	3.7%	2.1%
SSA'	0.5%	-	0.2%
Broken pre-pr	-	1.8%	1.0%
HTCT	18.9%	13.6%	15.9%
CT	23.3%	30.4%	27.3%
Hi	57.3%	49.5%	52.8%
No. of fibre	206	273	479
"Expected" S/P	4.2	4.0	4.0
HTCT/pre-CT.	39	2.1-3.2	4.0-5.8

* The dotted line marks the position of the precipice.

$Sf_{/Pf}$ = 3.7, $\pm$0.2

$\bar{n}Pf$ = 7.4, $\pm$ 0.6

$\bar{n}(Pf+Sf)$ 34.7, $\pm$ 2.9

The "expected" S/P ratio calculated by assuming that all pre-CT and HTCT fibres grow in P follicles is not greatly different, either in total or subsample counts, from

that found in the skin. This, coupled with the occurrence of the precipice between the HTCT and CT fibres, suggests that the assumption that pre-CT and HTCT are the fibres which grow in the P follicles, is correct.

The problem of determining which of these fibres grow in PC and which in PL, is confused by the extremely large difference in the pre-CT counts of the two subsamples. The unidentified, broken tipped fibres also created a difficulty, since if they are assumed to be pre-CT fibres, the HTCT/pre-CT ratio of 2·1 for the second sample, is not greatly different from the 1·9 or 2 we would expect for PL/PC ratio. However if we assume these fibres to be HTCT the difference between the HTCT/pre-CT ratio and the PL/PC ratio (3·2 vs 1·9) would probably mean that some HTCT were growing in PC follicles. It seems certain that in the area of skin supplying the first subsample, most of the PC follicles produced HTCT fibres. Many of the HTCT fibres were very robust and approached super-sickle fibres, but under normal circumstances they would not be placed in the pre-CT group. The possibility that the lack of pre-CT fibres is due to shedding of PC fibres as "babies" in a small localised area, does not seem very likely, since if this were assumed to be the case, the "expected" S/P ratio would be 2·9 which is even further away from the skin sample Sf/Pf ratio. Also none of these fibres were found in the sample. One P

follicle in the skin section was judged to have shed its fibre while some secondaries also had apparently shed.

Even although the lamb was seven weeks old at the time of sampling a good proportion of immature secondaries (12% of total S) were present. This suggests that probably the "expected" S/P ratio should be slightly less than the true follicle ratio, since some follicles would be judged mature in the sections but would not have fibres long enough to be included as part of the sample. There is a slight possibility that many of the follicles classified as immature were in actual fact follicles cut below the level of keratinisation. Since Sf + Si/P is 4·2 this would agree better with the "expected" S/P ratio. The possibility of this being the case is however not very great since the follicles classed as immature do not resemble, to the experienced eye the appearance of follicles cut beneath the level of keratinisation in lower layers of the skin. Also since Schinckel (1955a) and Short (1955a) have shown the seven weeks old Merino to have over 20% of its follicles as yet immature, it seems that 12% of immature secondaries is a reasonable proportion for an N-type Romney.

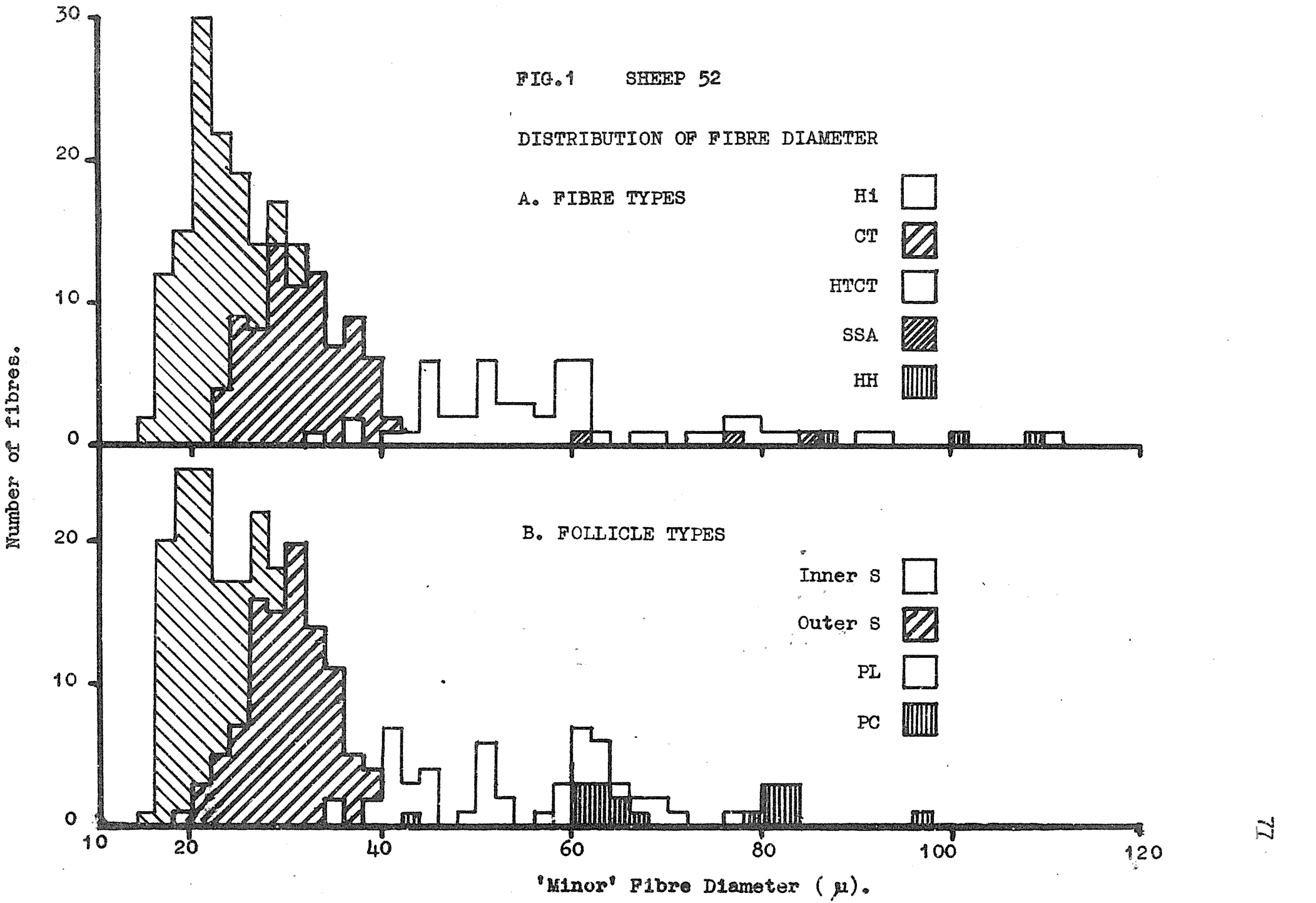


FIG.1 SHEEP 52
DISTRIBUTION OF FIBRE DIAMETER
A. FIBRE TYPES
Hi
CT
HTCT
SSA
HH
B. FOLLICLE TYPES
Inner S
Outer S
PL
PC
Number of fibres.
30
20
10
0
20
10
0
10
20
40
60
80
100
120
'Minor' Fibre Diameter (µ).

2. Fibre diameter

Figure 1, giving the distributions of the diameter of "minor" fibre axes for fibre types and follicle types tells us very little about the relationship between the fibres and follicles. Although a general tendency exists for the fibre types to vary in diameter in the order HH > SSA > HTCT > CT > Hi, while the follicles vary in the order PC > PL > S outer > S inner there is a large amount of overlap in both cases. The picture is probably complicated by the fact that some of the PC fibres were apparently thinning preparatory to shedding. This could be noticed in the follicles but not in the fibres themselves. A general impression is gained from looking at the graph that some HTCT must be in PC follicles but the evidence is not good. The one fine PC fibre contained only fragmentary medulla and was obviously shedding.

3. Fibre characteristics

It was found that a large proportion of the PC follicles were growing ribbon shaped fibres. Despite a search through the whole section, none of these flattened fibres were found in a follicle which could be recognised as a PL. Among the fibre types a number of SSA and some HTCT fibres were ribbon shaped, while one CT was described as semi ribbon shaped. This then is further evidence

that HTCT fibres are growing in PC follicles.

4. Summary

In conclusion, it seems fairly certain that in sheep 52, the pre-CT fibres are growing in P follicles. It is likely that these follicles are PC but the evidence for this is not good. HTCT fibres must be growing in both PC and PL follicles but it is extremely doubtful that any grow in S. There is a slight possibility that a few of the larger CT grow in P follicles but most grow in the outer secondaries, while Hi are apparently in the inner S.

B Sheep 80

1. Frequencies

TABLE 3

Percentages of fibre types and ratios of fibres and follicles- Sheep 80

Type	Sample 1	Sample 2	Total
SSA	5.3%	5.8%	5.5%
HTCT	11.2%	9.4%	10.2%
CT_1	-	2.6%	1.9%
CT_2	55.9%	36.6%	45.1%
Hi	27.6%	45.5%	37.1%
No. of fibres	170	191	361
Ratio CT & Hi/ HTCT and SSA	5.1	5.6	5.4
HTCT + CT_1/SSA	5.1	4.6	4.7
HTCT/SSA	2.1	1.6	1.9
HTCT + CT_1/SSA	2.1	2.1	2.2

Sf/Pf	=	5.1	± 0.7
Pf	=	5.8	± 0.7
Pf+ Sf	=	35.8	± 1.6

The study of the ratio of fibres in this lamb is complicated by the appearance of the small number of fibres designated CT_1. These fibres seem to be intermediate, between two precipices. They are longer than the rest of the CT fibres but are not as long as the HTCT fibres. Consequently they could be growing in either P or S follicles.

The "expected" S/P ratio agrees reasonably well

with the actual Sf/Pf ratio whether the CT_1 fibres are considered to be P fibres or S. Since it seems likely that the "expected" ratio should be slightly smaller than the actual ratio, possibly the figure including the CT_1 fibres, expresses the ratio of P fibres to S fibres more accurately. The "expected" PL/PC ratios provide us with little further information as to which follicles produce the CT_1 fibres. If we assume PC follicles to produce SSA and PL follicles to produce fibres of the CT group, the ratios are not markedly different from 1·9 whether or not we consider the CT_1 fibres to grow in PL.

The frequencies then suggest that SSA grow in PC, HTCT in PL and CT_2 and Hi in S. CT_1 fibres could be produced by either PL or S follicles. Possibly they are produced by P follicles at the secondary margin of groups or by follicles intermediate in character possessing only a sweat gland or an arrector muscle.

2. Fibre diameter

The histograms showing frequency of fibres of the different diameters support the theory that SSA fibres grow in PC and HTCT grow in PL. The one HTCT fibre which approaches the CT fibres much more nearly in diameter could possibly be a HTCT fibre growing in a S follicle or else it might possibly be an abnormal fibre showing a

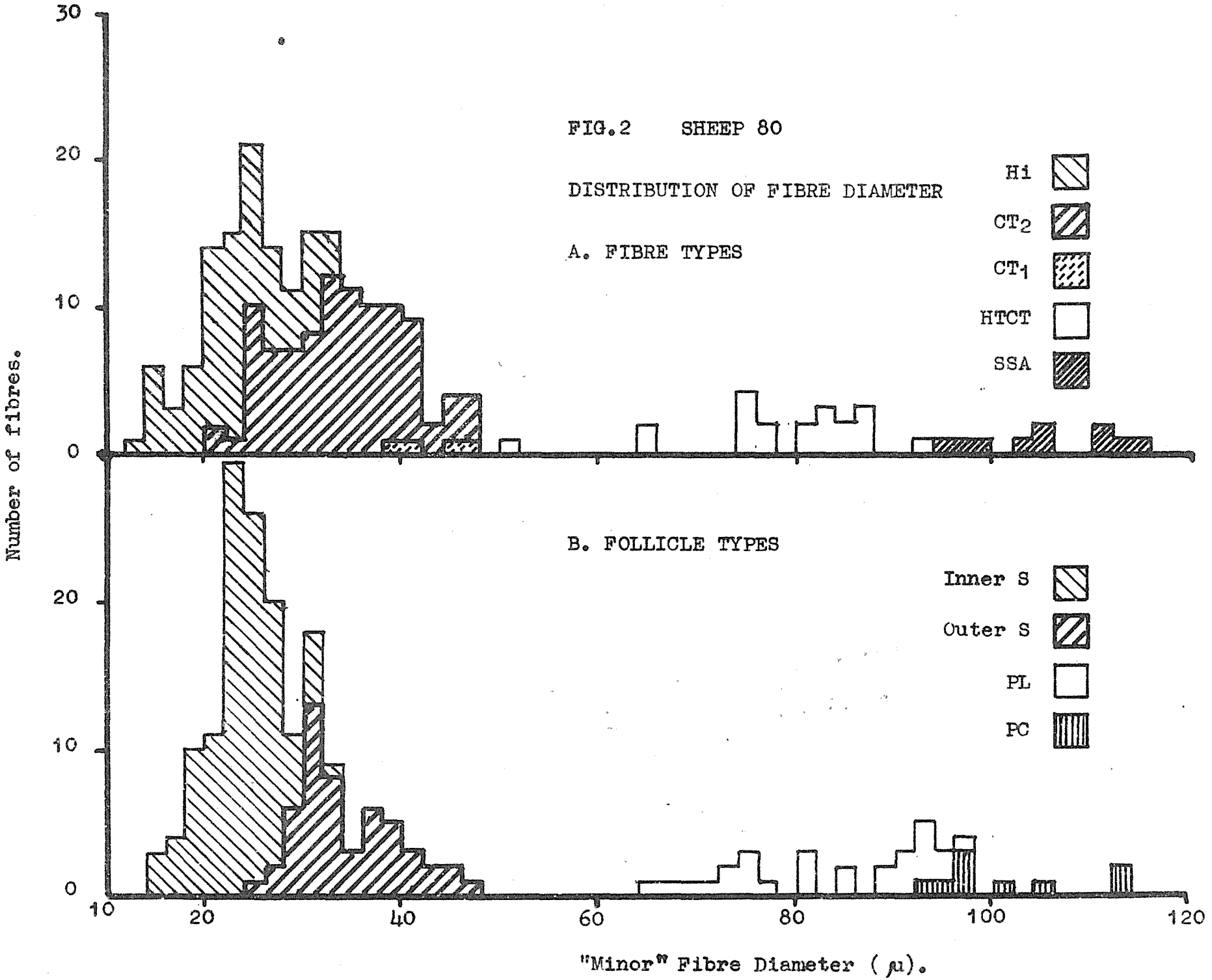


FIG.2 SHEEP 80
DISTRIBUTION OF FIBRE DIAMETER
A. FIBRE TYPES
Hi
CT2
CT1
HTCT
SSA
B. FOLLICLE TYPES
Inner S
Outer S
PL
PC
Number of fibres.
30
20
10
0
20
10
0
10
20
40
60
80
100
120
"Minor" Fibre Diameter (μ).

sudden thinning at this point. From their diameters it seems that the CT_1 fibres grow in S follicles. The division of S follicles into inner and outer does not seem to separate these into follicles producing CT and follicles producing Hi. Some of the CTs are evidently growing in inner S.

3. Fibre characteristics

A few ribbon shaped SSA fibres were present in the subsamples while a few ribbon shaped HH were present in the main samples. No ribbon shaped fibres were observed in any PL or S follicles so it seems probable that these fibres grew in PC.

4. Summary

It appears that the birthcoat of this sheep fits closely Fraser, Ross and Wright's (1954) conclusions regarding the types of birthcoat fibres produced by the follicles of N/N Romneys. While it was rather difficult to distinguish the boundary between SSA and HTCT it seems that a reasonably good distinction was made between fibres growing in PC and fibres growing in PL follicles. It seems that the relationship is fairly strictly as follows: -

PC produce SSA and a few HH

PL produce HTCT

S produce CT_1, CT_2 and Hi.

C Sheep 83

1. Frequencies

TABLE 4

Percentages of fibre types and ratios of fibres and follicles- Sheep 83

Fibre type	Sample 1	Sample 2	Total
HH	7·6%	4·5%	6·3%
SSA	3·2%	3·5%	3·4%
SSA'	-	1·5%	0·6%
Broken pre-pr	1·4%	-	0·8%
$HTCT_1$	22·4%	19·2%	21·1%
$HTCT_2$	6·5%	3·5%	5·3%
CT	30·3%	41·9%	35·2%
Hi	28·5%	25·8%	27·4%
No. of fibres	277	198	471
CT+Hi/HTCT+pre-CT+br	1·4	2·1	1·7
CT+Hi+$HTCT_2$/$HTCT_1$+pre-CT+br	1·9	2·5	2·2
$HTCT_1$/pre-CT (±br.)*	1·8-2·2	2·0	1·9-2·1
all HTCT/pre-CT(±br)*	2·4-2·8	2·4	2·4-2·6

Sf/Pf 2.9 ± 0.4

$\bar{n}$Pf 6.5 ± 0.8

$\bar{n}$(Pf+ Sf) 25.3 ± 2.7

This lamb, sampled at six weeks of age, had a fairly low Sf/Pf ratio. The fibre type array was rather complex with two sizes of HTCT fibres. The $HTCT_2$ fibres

* Separate calculations were made including the broken fibres in each group. These results were then taken as the range.

were below one precipice, yet, since the shortest $HTCT_2$ were longer than the longest CT they appeared to be above another "secondary" precipice. Since the ratio $HTCT_1$/ pre-CT approaches the 1·9 we would expect for the PL/PC ratio much more nearly than does the ratio $HTCT_1 + HTCT_2$/ pre-CT, it seems likely that the $HTCT_2$ fibres grow in S follicles. This idea is further supported by the ratios, $CT + Hi/HTCT_1 + HTCT_2 +$ pre-CT and $HTCT_2 + CT + Hi/HTCT_1 +$ pre-CT. Although both ratios are considerably smaller than the Sf/Pf ratio, including the $HTCT_2$ with CT and Hi gave a figure more nearly approaching the Sf/Pf ratio. The fact that "expected" S/P ratio is lower than Sf/Pf is possibly due to a number of secondary follicles not possessing fibres long enough to enter into the fibre samples. Since however another estimate of Sf/Pf based on a circular counting area gave a figure of 2·6 the difference is probably a sampling error.

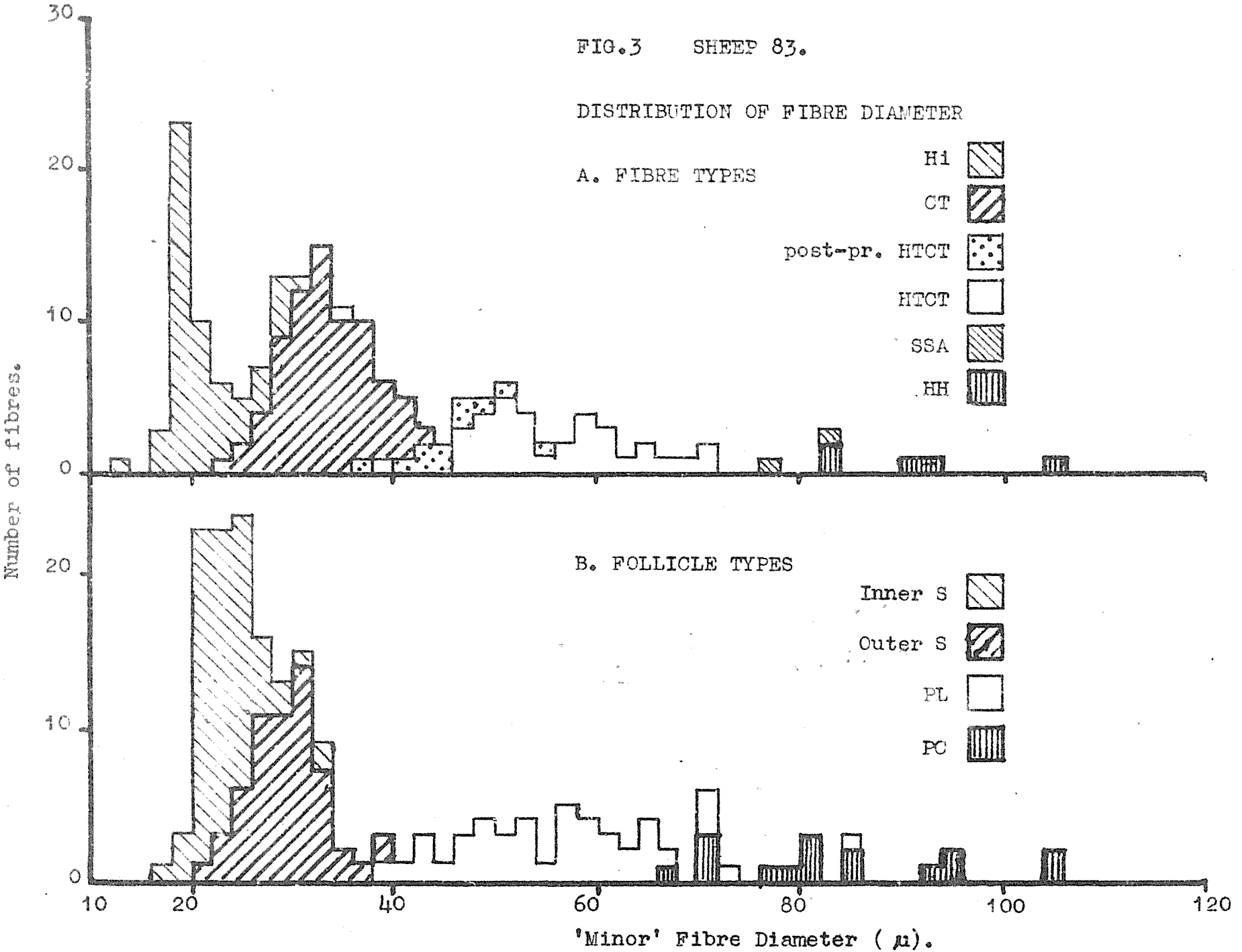
The frequencies do not provide any data suggesting that pre-CT fibres grow in follicles other than PC or that PL produce anything other than HTCT. It does seem however that as well as CT and Hi certain HTCT fibres are produced by secondary follicles.

2. Fibre diameter

The fibre diameter data was made more difficult

FIG.3 SHEEP 83.

DISTRIBUTION OF FIBRE DIAMETER



to interpret by the fact that a very large proportion of the pre-CT fibres were ribbon shaped. This means that the fibre diameter data of only a small proportion of these fibres is included in the graph. This small sample of pre-CT fibres is the probable reason why the pre-CT series does not overlap with the HTCT series. In all other cases there is a large amount of overlap between different follicle types or the different classes of follicles. This overlap does not permit the drawing of many conclusions from the diameter distribution. It does seem that the graph supports the assumptions made from the frequencies, although the position of the post-precipice HTCT fibres suggests that these fibres could possibly be growing in PL. This position however does not rule out the possibility that these fibres are growing in secondaries. CT fibres are apparently growing in the later developing secondaries as well as those around the margin of the group.

3. Fibre characteristics

A very high proportion of the pre-CT (80-90%) and a small proportion of the pre-pr HTCT (about 20%) fibres were ribbon shaped in the basal region. While 50% of the PC fibres were ribbon shaped, only one ribbon shaped PL fibre was found in the complete skin section. This suggests two possibilities.

i That the majority of the HTCT and many of the

pre-CT fibres have returned to a more circular cross sectional shape in the region of the fibre left on the skin following the removal of the birthcoat sample.

ii That some HTCT fibres are growing in PC. If this were so the deficiency of PL fibres in the ratio could be made up to some extent if $HTCT_2$ were considered to grow in PL.

If the second possibility was correct, to bring the proportion of ribbon shaped PC fibres down to correct proportions, over 50% of of the $HTCT_1$ fibres and hence over 20% of the total fibres, would have to be of PC origin. This figure cannot be fitted with either PL/PC or Sf/Pf. Consequently it seems the second possibility must be discarded.

4. Summary

While the evidence from the different methods conflicts slightly, the most probable relationship is as follows: -

PC fibres are HH, SSA and SSA'

PL fibres are HTCT "above" the precipice

S fibres are HTCT "below" the precipice, CT and Hi.

It does seem quite possible, although not probable, that some $HTCT_1$ could grow in PC follicles and some $HTCT_2$ could grow in PL follicles.

D Sheep 97

1. Frequencies.

TABLE 5

Percentages of fibre types and ratios of fibres and follicles- Sheep 97

Fibre type	Sample 1	Sample 2	Total
HH	10·7%	8·7%	10·0%
SSA	4·8%	4·0%	4·5%
SSA'	0·8%	1·7%	1·1%
HTCT	17·5%	14·5%	16·5%
CT_1	1·1%	-	0·8%
CT_2	38·6%	56·1%	44·3%
Hi^2	26·5%	15·0%	22·7%
No. of fibres	355	173	528
CT + Hi/pre-CT + HTCT	2·0	2·5	2·3
CT_2 + Hi/pre-CT + HTCT + CT_1	1·9	2·5	2·3
HTCT/pre-CT	1·1	1·0	1·0
HTCT + CT_1/pre-CT	1·1	1·0	1·1
SSA + SSA' + HTCT/HH	2·2	2·3	2·2

Sf/Pf 3.25 ± 0.20

$\bar{n}$Pf 5.4 ± 0.4

$\bar{n}$(Pf + Sf) 23.0 ± 1.3

In the array of this sheep a few CT fibres (CT_1) were apparently above the precipice. While there was a very good boundary between HH and SSA there was a continuous transition from SSA to HTCT.

It is very difficult to find any relationship between the ratios of the different types of fibres and the different types of follicles. The simple picture as envisaged by

Fraser, Ross and Wright (1954) certainly does not seem to apply in this case. Neither the ratio CT + Hi/pre-CT + HTCT nor CT_2 + Hi/pre-CT + HTCT + CT_1 fit well with Sf/Pf as determined from the skin section, the estimate from the fibre types being considerably lower. While it is possible that some HTCT are in secondaries, since a good precipice is present in the CT series, it seems likely that all the HTCT fibres grow in primaries. The low "expected" S/P ratio is probably due to the presence of a large number of recently matured secondaries which have not produced a fibre long enough to enter into the wool sample.

The differences between HTCT/pre-CT and the 1.9 we would expect for PL/PC ratio is probably more important. This difference seems to suggest that some of the pre-CT fibres must be growing in PL follicles. The ratio SSA+ SSA' + HTCT/HH approaches 1.9 much more closely but the difference probably cannot all be attributed to sampling error.

The ratios then suggest that the PC fibres are the halos and some super-sickles, the PL fibres are super-sickles, HTCT and pre-precipice CT, while the S fibres are post-precipice CT and Hi.

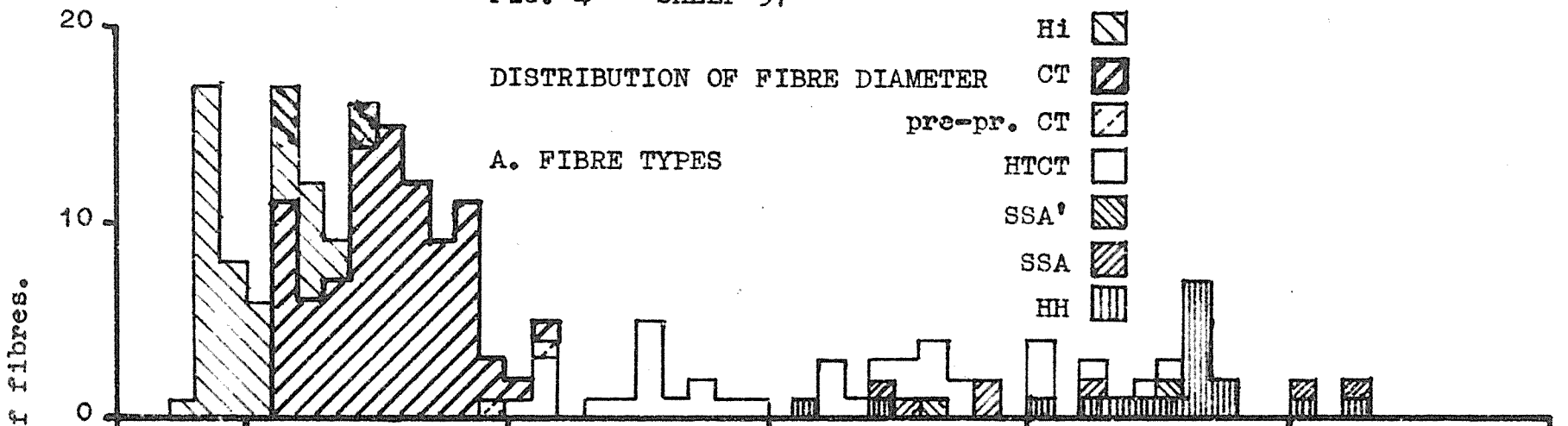
2. Fibre diameter

This sheep is of considerable interest since it is the only one to give distinct boundaries between the fibre diameters in the different classes of follicles. While there

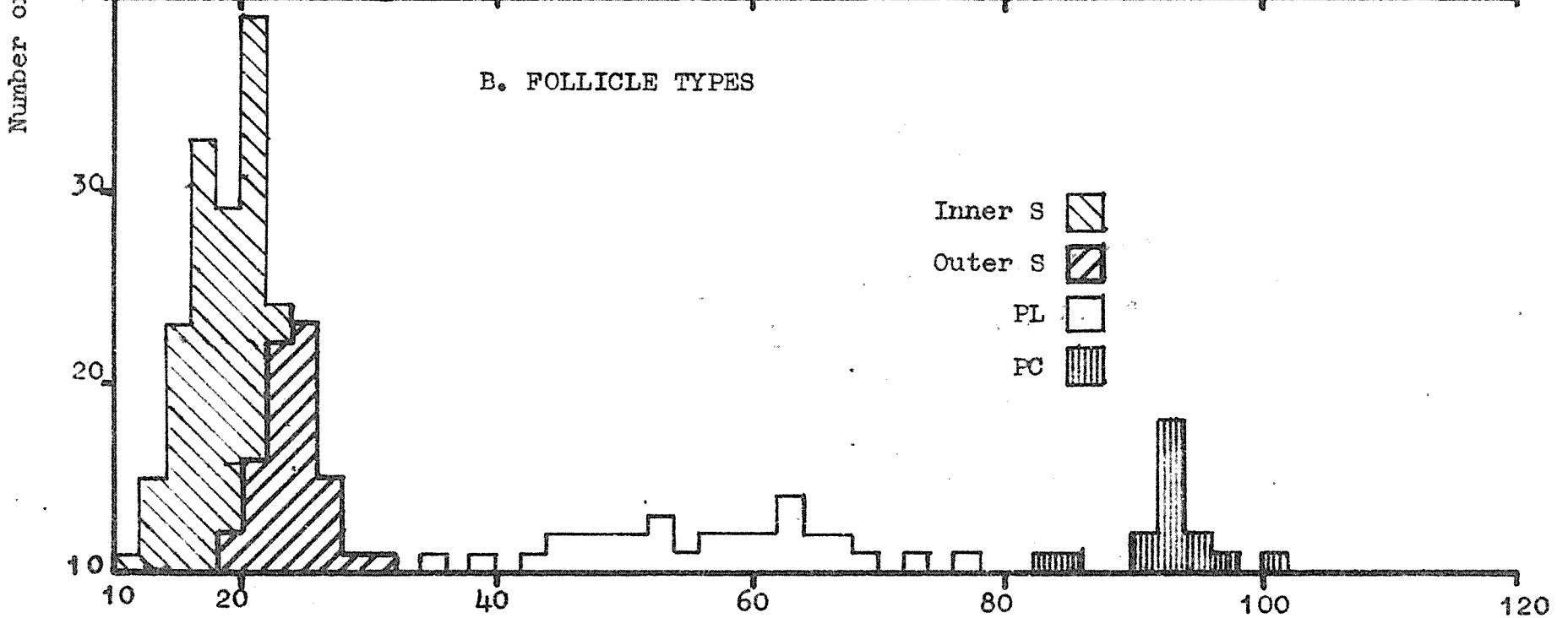
FIG. 4 SHEEP 97

DISTRIBUTION OF FIBRE DIAMETER

A. FIBRE TYPES



B. FOLLICLE TYPES



Number of fibres.

'Minor' Fibre Diameter (μ).

is a considerable amount of overlap between diameters of the different fibre types this overlap itself is meaningful.

The diameters of most of the HH occur in the range of diameters occupied by PC fibres. Two halos have diameters which would apparently place them in PL follicles. Their diameters suggest that SSA and SSA' occur in both PC and PL follicles. The HTCT are mainly PL fibres but some have a similar diameter to PC. This is probably due to measuring the wrong axis of the fibre, giving a high estimate of fibre diameter. The diameters of the pre-pr CT indicate that these fibres may be growing in either S or PL. Other CT and Hi fibres grow in S.

3. Fibre characteristics.

All pre-precipice fibre types had a proportion of ribbon shaped fibres but since both PC and PL follicles had quite a few ribbon shaped fibres little could be inferred. The sharp boundary between HH and SSA and then the continuous transition through the SSA and HTCT series suggested there must be fairly wide differences between follicles growing SSA and those growing HH. Possibly this difference is that between PC and PL.

The distinct precipice in the CT fibres is probably caused by differential growth rates of PL and S fibres.

4. Summary

The relationship between fibres and follicles in the birthcoat of this lamb seems to be reasonably clear. The relationship however differs markedly from that found for N/N lambs by Fraser, Ross and Wright (1954) and is apparently as follows: -

PC fibres are HH, probably some SSA and SSA'

PL fibres are SSA, SSA', HTCT and pre-pr. CT.

S fibres are post-pr. CT and Hi.

It also seems a possibility that some HTCT might be growing in PC and that the pre-pr.CT could be growing in S. This is unlikely however.

E Sheep 120

1. Frequencies.

TABLE 6

Percentages of fibre types and ratios of fibres and follicles- Sheep 120

Fibre type	Sample 1	Sample 2	Total
HH	10•2%	5•4%	7•5%
SSA	0•8%	5•1%	3•2%
SSA'	-	0•3%	0•2%
HTCT appr.SS	4•5%	5•4%	5•0%
HTCT	22•3%	24•0%	23•3%
post-pr. HTCT	8•3%	-	3•7%
CT 35•6% / Hi 18•2%	53•8%	59•8%	57•2%
No. of fibres	264	334	598
CT+Hi/pre-CT+HTCT	1•2	1•5	1•3
CT+Hi+post pr.HTCT/ HTCT+pre.CT	1•6	1•5	1•6
HTCT/pre.CT	3•2	2•7	2•9
HTCT appr.SS+HTCT/pre-CT.	2•4	2•7	2•6
HTCT/HTCT appr.SS+pre. CT	2•0	1•5	1•7

Sf/Pf 2•3 ± 0•2

$\bar{n}$Pf. 9•5 ± 0•8

$\bar{n}$(Pf Sf) 31•7 ± 2•1

These fibres were very short, the lamb being only nine days old at the time of sampling. Consequently it was rather difficult to recognise a precipice. The fibre type ratios do however suggest that the HTCT fibres judged to be

post-precipice grow in S follicles. No great reliance could be placed on this however since both "expected" S/P ratios are considerably lower than the true ratio. This is probably due to a high proportion of follicles which have not produced fibres long enough to enter into the fibre sample.

The nearest approach to the 1·9 we would expect for PL/PC is given by the ratio of HTCT/HTCT approaching super-sickle, plus pre-CT. This suggests that some of the PC follicles are producing HTCT fibres, but these fibres resemble super-sickles more than the other HTCT fibres present.

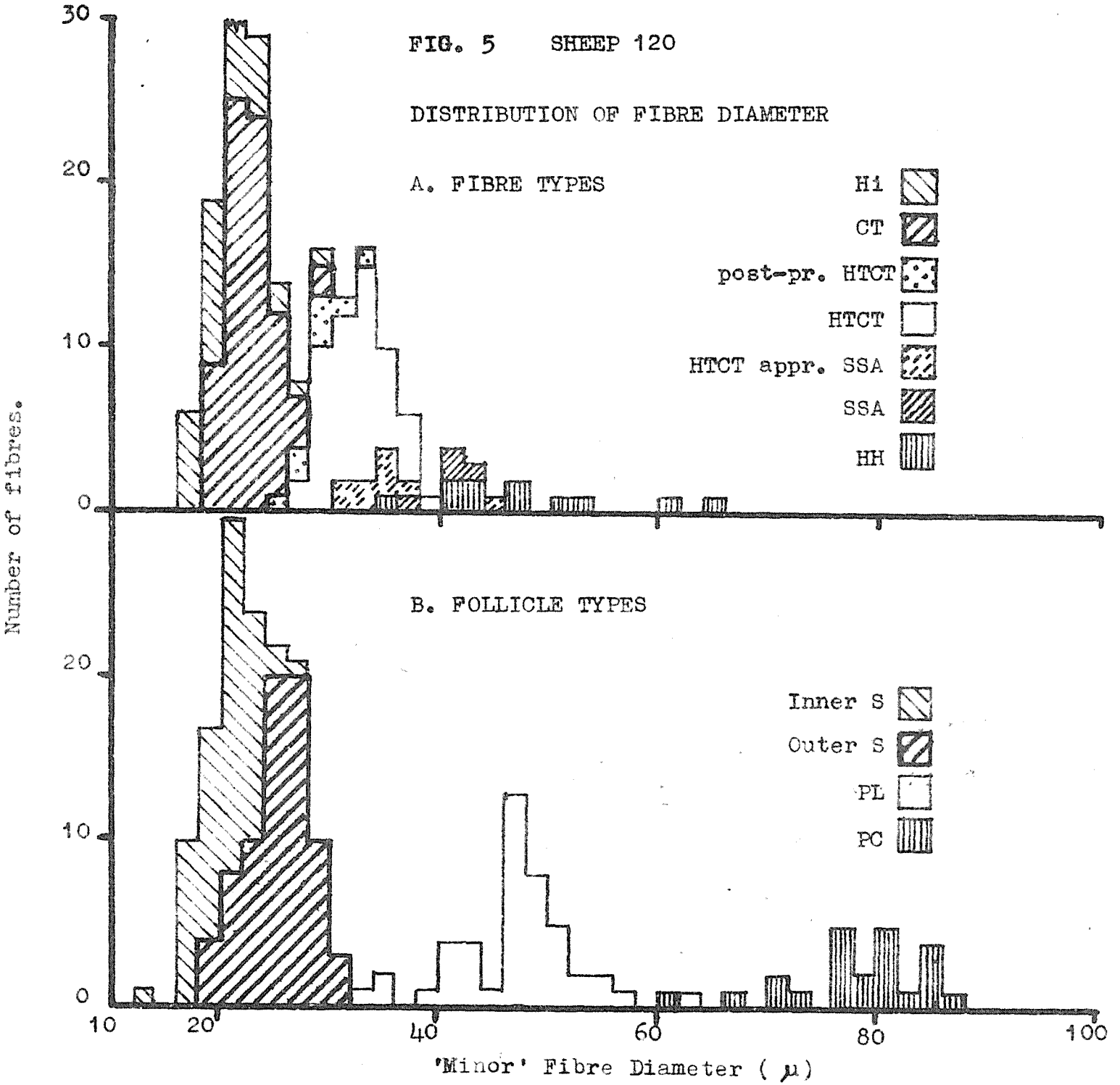
No really good relationship can be ascertained from the fibre type frequencies of this lamb. It is very difficult to decide the boundary between the P and S fibres.

2. Fibre diameter

Figure 5, the fibre diameter distributions of fibre and follicle types for this lamb tells very little about the fibre follicle relationship. The fibre diameter of the different follicle types is considerably greater than that of the fibre types. The explanation is probably that the fibre types have been measured above the thickening that occurs in the fibre at the birth point. The diameter distributions suggest the birth thickening has occurred

FIG. 5 SHEEP 120

DISTRIBUTION OF FIBRE DIAMETER



almost entirely in the P fibres, and the S follicles have been little affected. This agrees with the data of Cockrem (1956) who found that the birth thickening was much greater for the larger, more heavily medullated fibres. Taking the fibre samples at this early stage resulted in a much reduced range of fibre diameters and considerably more overlap between diameters of fibre types. This overlap prevents much inference as to which fibres are produced by the different follicles. No decision can be made on the basis of the figure as to whether HTCT appr. SS are produced by PC or PL or whether the post pr. HTCT are produced by PL or S.

3. Fibre characteristics

Little could be gained from a study of the ribbon shaped fibres since although a few HH were ribbon shaped only one fibre could be found in the skin section with a "squashed" appearance. This was a PC fibre.

4. Summary

The data will not substantiate any definite conclusions regarding the origin of the fibre types of sheep 120. It seems however that the most likely situation is as follows: -

pre-CT fibres are produced in PC follicles.

ordinary HTCT are produced in PL follicles.

CT and Hi are produced in S.

The frequency data suggests fairly strongly that the HTCT fibres approaching super-sickle form are produced in PC but there is no good evidence to support the assumption that the HTCT fibres classified as post-precipice are growing in S follicles.

F Sheep 5

With this and subsequent sheep, frequencies only have been studied as "crisis thinning" of some fibres has occurred, confusing the diameter distribution, or because it was impossible to differentiate between PC and PL.

TABLE 7

Percentages of fibre types and ratios of fibres and follicles- Sheep 5

Fibre type	Sample 1	Sample 2	Total
HH	4•9%	4•2%	4•6%
SSA	2•0%	1•7%	1•9%
SSA'	-	0•3%	0•2%
Broken pre-pr.	2•3%	1•7%	2•0%
HTCT	16•3%	12•2%	14•3%
CT	42•0%	39•5%	40•8%
Hi	32•6%	40•2%	36•3%
No. of fibres	307	286	593
post-pr/pre-pr.	2•9	3•9	3•4
HTCT/pre-CT	1•8-2•4	1•5-1•9	1•7-2•2

Sf/Pf 3•7 ± 0•5

$\bar{n}$Pf 6•0 ± 0•6

$\bar{n}$(Pf+Sf) 28•1 ± 2•6

The two figures given for HTCT/pre-CT ratio arise by including the broken fibres in each group.

The obvious assumptions from fibre and follicle

frequencies of this sheep agree with the assumptions of Fraser, Ross and Wright (1954). The good precipice which occurs between HTCT and CT fibres apparently marks the boundary between P and S fibres. Although there was no clear division between SSA and HTCT fibres no obvious departure from the PL/PC ratio of 1·9 is present in the HTCT/pre-CT ratio. It seems then that the boundary drawn between SSA and HTCT was reasonably close to the true boundary between PC and PL. It is possible of course that the agreement of frequencies is a purely chance effect, but it does seem that the relationship is as follows: -

HH, SSA and SSA' are produced in PC.

HTCT are produced in PL.

CT and Hi are produced in S.

G Sheep 6

TABLE 8

Percentages of fibre types and ratios of fibres and follicles- Sheep 6

Fibre type	Sample 1	Sample 2	Total
HH	3·3%	3·6%	3·4%
SSA	1·6%	0·8%	1·1%
SSA'	0·5%	0·8%	0·7%
HTCT	14·8%	11·9%	13·1%
pre-pr. CT	1·6%	2·0%	1·8%
post-pr.CT	48·1%	50·2%	49·3%
Hi	30·1%	30·8%	30·5%
No. of fibres	183	253	436
CT+Hi/pre-CT+HTCT	3·9	4·9	4·5
pre-pr/post-pr.	3·6	4·3	4·0
HTCT/pre-CT	2·7	2·3	2·5
pre-pr.CT+HTCT/pre.CT	3·0	2·7	2·8

Sf/Pf 3·6 ± 0·5

$\bar{n}$Pf 4·0 ± 0·3

$\bar{n}$(Pf+Sf) 18·5 ± 1·4

The precipice in the CT series of this array was not very distinct and consequently the division of fibres into pre-precipice and post-precipice curly tips might not be very real. However since the ratio of post-pr.CT + Hi/ pre.CT + HTCT + pre-pr. CT more nearly approaches the skin Sf/ Pf ratio, it seems more probable that the pre-pr.CT fibres grow in P follicles with HTCT and pre-CT.

Including the pre-pr.CT as PL fibres in calculating "expected" S/P gives a still wider deviation from 1·9 than the plain HTCT/pre.CT ratio. This suggests that the pre-pr.CT are growing in S follicles. However other possibilities are that some of the HTCT are growing in PC or that some of the pre-CT fibres have been already shed. In a search through the main wool sample two shed HTCT fibres and a small number of shed CT fibres were found but no shed pre-CT fibres were located. In the skin section the only obviously shed follicles were two PL and a number of S in the close proximity of these PLs. This is obviously an abnormal pattern of shedding and since it seems that the shed fibres are still present in the sample, shedding must disregarded as a factor causing the high "expected" PI/PC ratio. An interesting fact about this array was that the HTCT fibres were consistently longer than the HH. This could possibly mean that the reduction in output of fibre material which causes the crisis thinning has affected the HH earlier or more severely than the HTCT.

To conclude, it seems that the most likely pattern in this lamb is: -

HH, SSA, SSA' and possibly some HTCT are produced by PC follicles.

HTCT and possibly the pre-pr.CT are in PL.

post-pr.CT, Hi and possibly pre-pr.CT are in S.

H Sheep 9

TABLE 9

Percentages of fibre types and ratios of fibres and follicles- Sheep 9

Fibre type	Sample 1	Sample 2	Total
HH	7.6%	9.3%	8.3%
SSA	1.1%	1.0%	1.1%
SSA'	0.4%	-	0.2%
HTCT	15.6%	20.5%	17.7%
CT	49.0%	49.3%	49.1%
Hi	26.2%	20.0%	23.5%
No. of fibres	263	205	468
post-pr/pre-pr.	3.0	2.3	2.7
HTCT/pre-CT	1.7	2.0	1.8

Sf/Pf 2.6 ± 0.3

$\bar{n}$Pf 5.6 ± 0.4

$\bar{n}$(Pf+Sf) 20.2 ± 1.2

The fibre type array of this lamb featured a very distinct precipice between the HTCT and the CT fibres. This suggests that all the HTCT fibres are primaries while all the CT fibres are secondaries. This is supported by the good agreement between "expected" and actual Sf/Pf ratios.

Since HTCT/pre-CT is very close to 1.9 it seems reasonable to assume that the pre-CT fibres have their origin in PC follicles while the HTCT fibres have their

origin in PL follicles.

The sample from this sheep then apparently agrees with the Fraser, Ross and Wright (1954) pattern perfectly.

HH, SSA and SSA' are apparently PC fibres.

HTCT are apparently PL fibres.

CT and Hi have their origin in S follicles.

I Sheep 18

TABLE 10

Percentage of fibre types and ratios of fibres and follicles- Sheep 18

Fibre types	Sample 1	Sample 2	Total
HH	6•5%	4•6%	5•7%
SSB	-	0•6%	0•2%
Broken pre-pr	-	1•2%	0•5%
HTCT appr.HH	4•9%	1•7%	3•6%
HTCT	9•0%	11•0%	9•8%
CT	40•4%	23•1%	33•3%
Hi	39•2%	57•8%	46•9%
No. of fibres	245	173	418
pre-pr/post-pr	3•9	4•2	4•0
All HTCT/pre-CT	2•1	2•0-2•7	2•1-2•3
HTCT/pre-CT + Int.	0•8	1•4-1•8	1•0-1•1

Sf/Pf 4•0 ± 0•4

$\bar{n}$Pf 4•5 ± 2•4

$\bar{n}$(Pf + Sf) 22•3 ± 0•5

It appears that the origin of the fibres of this array are those suggested by Fraser, Ross and Wright (1954). The post-precipice/pre-precipice fibre ratio agrees closely with the Sf/Pf of 4•0, suggesting that the precipice does mark the boundary between P and S fibres and that HTCT and pre-CT fibres grow in P follicles. Since the ratio of all HTCT fibres/pre-CT fibres approaches 1•9 more closely than the ratio HTCT/pre-CT + HTCT approaching halos it seems that all the HTCT fibres grow in PL. The one SSB fibre found is

rather anomolous. While knowledge of the follicular origin of this fibre would have much interest it is impossible to judge its source from frequency data. While Fraser, Ross and Wright assumed these fibres to grow in PC there is no factual evidence that in this case the relationship holds.

Summarising the relationship for this sheep it seems: -

HH grow in PC.

HTCT appr. HH and ordinary HTCT grow in PL.

CT and Hi grow in S.

J Sheep 25

TABLE 11

Percentages of fibre types and fibre and follicle ratios - Sheep 25

Fibre type	Sample 1	Sample 2	Total
HH	3·6%	4·0%	3·8%
SSA	-	2·7%	0·9%
Broken pre-pr.	-	0·7%	0·2%
HTCT	16·0%	16·1%	16·0%
CT	60·0%	42·3%	53·8%
Hi	20·4%	34·2%	25·2%
No. of fibres	275	149	424
CT+Hi/pre-CT+HTCT	4·1	3·3	3·7
HTCT/pre-CT	4·4	2·2-2·5	3·2-3·5

Sf/Pf	$3·8 \pm 0·4$
$\bar{n}$Pf	$5·5 \pm 0·6$
$\bar{n}$(Pf + Sf)	$26·7 \pm 1·7$

In this lamb, although the precipice was not very clear, there is reasonable agreement between the ratio of post-precipice / pre-precipice fibres and the Sf/Pf ratio; hence it seems the precipice marks the boundary between P and S fibres. The agreement between the HTCT/pre-CT ratio and the PL/PC ratio is not good and it seems that the suggestion that the PC fibres produce pre-CT fibres does not hold perfectly. From the ratios it seems that some HTCT fibres must also be growing in PC follicles.

The conclusion to be drawn from these frequencies is then: -

PC follicles produce pre-CT and some HTCT.

PL follicles produce HTCT.

S follicles produce CT and Hi.

K Sheep 39

TABLE 12

Percentages of fibre types and fibre and follicle ratios - Sheep 39

Fibre type	Sample 1	Sample 2	Total
HH	8•9%	7•8%	8•5%
HTCT	16•3%	17•8%	16•9%
CT	38•2%	42•8%	40•1%
Hi	36•6%	31•7%	34•5%
No. of fibres	246	180	426
CT+Hi/HH+HTCT	3•0	2•9	2•9
HTCT/HH	1•8	2•3	2•0

Sf/Pf $3•0 \pm 0•4$

$\bar{n}$Pf $7•0 \pm 0•55$

$\bar{n}$(Pf+Sf) $27•6 \pm 1•43$

The fibre type array of this lamb was very simple,

only four classes of fibres being present. The post-pr./pre-pr. and HTCT/HH fibre ratios agree almost perfectly with the S/P and PL/PC follicle ratios. This suggests that in this lamb the origin of each fibre type is specific.

Two completely different types of HTCT fibres, one with a large curl in the tip and the other with only fine curling in the tip region occur. A possible reason for this is that one type is produced by PLx while the other type is produced by PLy follicles.

The evidence suggests strongly that the following relationship holds: -

HH are produced by PC follicles.
HTCT are produced by PL follicles.
CT and Hi are produced by S follicles.

L Sheep 60

TABLE 13

Percentages of fibre types and fibre and follicle ratios - Sheep 60

Fibre type	Sample 1	Sample 2	Total
HH	-	3.3%	1.1%
SSA	5.3%	5.3%	5.3%
HTCT-SSA	3.4%	-	2.3%
HTCT	14.0%	24.3%	17.3%
CT	32.4%	27.6%	30.9%
Hi	44.9%	39.5%	43.1%
No. of fibres	321	152	473
post-pr./pre-pr.	3.4	2.0	2.8
HTCT+HTCT-SSA/pre-CT	3.3	2.8	3.1
HTCT/pre-CT+HTCT-SSA	1.6	2.8	2.0

Sf/Pf 3.3 ± 0.4

$\bar{n}Pf$ 6.1 ± 0.5

$\bar{n}(Pf+Sf)$ 25.9 ± 1.4

Differences between the subsamples complicate the interpretation of this data. It seems that two localities, close together on the skin, must be producing rather different fibre populations. The post-pr/pre-pr fibre ratio of the first subsample agrees well with the S/P follicle ratio, but the difference between these ratios is 1·3 in the second subsample. Although only a small number of fibres were counted in the second subsample, this discrepancy is

large enough to suggest that random variation and fibres too short for inclusion cannot account for all the difference. If it is assumed that 32% of the HTCTs of this subsample are secondaries the "expected" S/P ratio becomes 3·0. This agrees well with the follicle S/P ratio. However the assumption conflicts with previous ideas about the precipice which has generally been considered to mark the boundary between P and S fibres.

An alternative explanation for the difference is that a small local variation in follicle Sf/Pf ratio has occurred. Since however an Sf/Pf ratio of 2·0 was not approached in any of the 1 sq. mm. areas counted this suggestion is probably incorrect.

The "expected" PL/PC ratios for the two subsamples are also very different. In the first subsample reasonably close agreement with 1·9 is obtained if the fibres intermediate between HTCT and SSA are included with the pre-CT group. It seems that these fibres probably originate in PC follicles. Halos are lacking in the first subsample and the intermediate fibres are lacking in the second subsample while the percentage of HTCT - SSAs in the first case agrees with that of the halos in the second. This suggests that possibly the intermediate fibres originate in similar follicles to the halos.

Although the small number of fibres in the second subsample limits the importance we can attach to the difference between the HTCT/pre-CT fibre ratio (2•8) and the PL/PC follicle ratio (1•9), assuming that 32% of the HTCTs are secondaries gives a primary HTCT/pre-CT ratio of 1•9.

It is suggested that: -

HH, SSA and HTCT-SSA fibres develop in PC.

HTCT develop in PL with possibly some of these fibres from subsample 2 occurring in S.

CT and Hi develop in S.

M Sheep 103

TABLE 14

Percentages of fibre types and ratios of fibres and follicles- Sheep 103

Fibre type	Sample 1	Sample 2	Total
HH	9.2%	2.6%	7.7%
SSA	0.6%	3.3%	1.2%
SSA'	0.4%	1.3%	0.6%
HTCT	29.1%	19.6%	27.0%
CT	47.0%	27.5%	42.6%
Hi	13.7%	45.8%	20.9%
No. of fibres	532	153	685
CT+Hi/HTCT+pre-CT	1.5	2.7	1.7
HTCT/pre-CT	2.9	2.7	2.8

Sf/Pf 3.5 ± 0.8

$\bar{n}$Pf 7.6 ± 0.9

$\bar{n}$(Pf+Sf) 34.2 ± 3.9

This lamb, only one month old at the time of sampling had a short coat and the precipice was not as clear as is generally the case with later samples. However the different fibre types were reasonably distinct.

While it is to be expected in a lamb of this age that a large number of follicles will possess fibres too short to enter into the birthcoat sample the "expected" S/P ratio (CT + Hi/HTCT + pre-CT) seems too low to be explained solely in these terms. The higher ratio for the second

subsample is possibly best regarded as a random effect due to the small number of fibres counted.

The high HTCT/pre-CT ratio suggests that the low "expected" S/P ratio could possibly be due to some of the HTCTs growing in the early developing secondary follicles. Calculations, based on the assumption that 33% of the HTCT fibres grew in S, gave an "expected" S/P of 2·4 and PL/PC of 1·9. 2·4 is approximately the figure we would expect for S/P taking newly matured follicles into account. The data thus agree satisfactorily with the hypothesis that some of the HTCTs are secondaries. However this evidence is not sufficient to discount completely the alternative hypothesis that the small "expected" S/P is due to follicles with very short fibres and that the large HTCT/pre-CT ratio is due to some of the HTCTs growing in PC.

In conclusion, while no really satisfactory evidence is available to determine the origin of the fibre types of this lamb, the following relations seem likely: -

PC follicles produce pre-CT and possibly some HTCT.

PL follicles produce HTCT.

S follicles produce CT and Hi and probably some HTCT.

TABLE 15

Summary of the probable origin of the fibre types.

Sheep	PC	PL	S
52	HH,SSA,SSA',HTCT	HTCT	CT, Hi
80	a few HH, SSA	HTCT	CT_1,CT_2,Hi
83	HH,SSA,SSA'	pre-pr.HTCT	post-pr.HTCT,CT Hi.
97	HH,SSA,SSA'	SSA,SSA',HTCT pre-pr.CT	post-pr.CT,Hi
*			
120	HH,SSA,SSA', HTCT appr.SS	HTCT	CT,Hi.
5	HH,SSA,SSA'	HTCT	CT,Hi.
6	HH,SSA,SSA',HTCT	HTCT,pre-pr CT	post-pr.CT,Hi.
9	HH,SSA,SSA'	HTCT	CT,Hi.
18	HH	HTCT	CT,Hi.
25	HH,SSA,HTCT	HTCT	CT,Hi.
39	HH	HTCT	CT,Hi.
60	HH,SSA,Int.HTCT-SSA	HTCT	CT,Hi.
103	HH,SSA,SSA'HTCT	HTCT	HTCT,CT + Hi.

* The relationships beneath the dotted line are not as well substantiated as those above.

N All sheep

Table 15 gives the probable origin of the fibre types for all sheep. The suggested relationships only agree with the strict relationship postulated by Fraser, Ross and Wright (1954) in five of the total thirteen lambs examined. One of the remaining eight lambs only differed slightly, having some fibres intermediate between HTCT and SSA in the primary centrals. In two sheep some ordinary CT fibres were apparently growing in PL follicles, a relationship which Fraser, Ross and Wright thought to exist in N/+ lambs. Of the five sheep with HTCTs in primary centrals, four possessed HH, SSA and SSA' fibres while the remaining one only had HH and SSA. Since these were amongst the weakest plateau arrays found, Fraser, Ross and Wright's suggestion that HTCT fibres can only occur in primary centrals in the case of strong plateau arrays is not substantiated.

Two lambs had HTCT fibres growing in secondary follicles; in one of these, there were also HTCT in the primary laterals. The remaining sheep differed radically from Fraser, Ross and Wright's findings, having super-sickle fibres growing in many of the PL follicles. Many HTCT fibres were in this case more robust than the super-sickles.

VII DISCUSSION

A Methods

1. Frequency comparison.

We must consider two features of the method: -

i its basic validity;

ii errors due to the techniques involved in assessing frequencies.

It is possible that fibre type frequencies are related to follicle class frequencies by a path other than the follicular origin of the follicle. A likely pathway is via the fibre and follicle densities, since high S/P ratios tend to be associated with high density, while if competition occurs density will have an effect on the morphology of the fibres. If such a path of relationship between fibre and follicle frequencies exists it is possible that while the frequencies of the fibre types and follicle classes agree, a fibre type which regularly occurred in similar proportions to one follicle class might not be produced by that class of follicle. Hence the method would not be valid. We have no knowledge whether any such paths of relationship exist but they probably do not. Therefore, we can draw some quite useful assumptions from frequency data, although we must remember that the validity of the method is in some doubt.

The errors due to the techniques of frequency

determinations fall into three categories: -

i differences between fibre ratios and follicle ratios due to fibres too short to include in the sample.

ii errors in estimating follicle ratios.

iii errors in estimating the fibre ratios.

Errors due to the first factor are difficult to assess but they will become progressively less as the animal becomes older. The proportion of Si follicles present will also give some idea of these errors if we consider the proportion in conjunction with a graph of secondary follicle maturation. Fiducial limits have been placed on the estimates of the follicle population means to indicate their accuracy, but the errors associated with fibre counts are more difficult to assess. Repeat counts, while giving some idea of the variation involved, do not provide enough data to derive a precise, numerical measure of it.

Burns (1955) provided a table and a formula for estimating "percentage errors" of fibre counts. These "errors" are apparently the equivalent of the standard error expressed as a percentage although the probability limits are not stated. The equation from which these "percentage errors" are calculated is derived from the formula for the variance of a binomial distribution. Consideration of the structure of the birthcoat and the differences between the repeat counts suggests that the fibres are not spread at

random throughout the coat. In this case the distribution of each fibre type in relation to the other fibres will not be binomial and will therefore not comply with the assumption made by Burns. Hence the suggested "errors" will be underestimated. To what extent the arrangement of the fibres will affect the error is rather difficult to say. It seems that as well as the grouping of the follicles affecting the arrangement there is the possibility that the longer fibres are drawn together into tufts because the tips become entangled at an early stage.

The fiducial limits of the estimates of Sf/Pf ratio and some calculations based on Burns's formula suggest that differences of fibre and follicle S/P and PL/PC ratios of one or more would probably be meaningful in most lambs. In some cases where the fiducial limits of the Sf/Pf ratio are high or where the lamb is young with many immature follicles, differences of greater than 1 between follicle Sf/Pf and "expected" S/P may not signify that the wrong relationship has been postulated in calculating the "expected" ratio.

2. Fibre diameter

The chief sources of error in the method of fibre diameter relationship used are: -

i Variation between regions over the length of fibres.

ii Variation between fibres from adjacent pieces of skin.

iii Variation between axes of fibres.

These errors could be largely eliminated by minor alterations to the technique. Variation between regions of the fibre would become of little importance if fibres were left attached to the skin and then removed close to the sebaceous gland level when making the first cut with the microtome. Variation between fibres from adjacent pieces of skin would not be encountered if all follicles in a piece of skin and all fibres removed from that piece of skin, were measured. Errors due to measuring the wrong axis of the fibre would be eliminated if the fibres were sectioned on a Hardy microtome and measured in cross section.

B Findings

The present observations do not progress very far towards providing a full understanding of the relationship between fibres and follicles but they do have a certain amount of value when considering some of the theories on the physiology of wool follicles during their development. Fraser (1951, 1952a) suggested that the sickle shaped tip was formed when fibres growing in PC follicles had their growth rate reduced because newly formed PL follicles began to compete with the PC follicles for fibre forming substrate. Results quoted previously seem to prove that in one lamb super-sickle fibres are produced in many PL follicles, while in several other lambs HTCT are produced in PC follicles. These findings indicate that follicle class per se does not determine the morphology of the fibre. Therefore while competition from PLs could cause a reduction in growth rate of PC fibres, it seems that this, if at all important, cannot be the only factor resulting in the production of the sickle tip.

Dry (1952) has also criticised Fraser's theory on the grounds that although trios occurred during the formation of the follicle population in many species, only in the case of the sheep and the Angora goat have sickle fibres been found. Possibly however Fraser and Short's (1952) suggestion that competition did not occur when follicles were more than a

certain distance apart could explain this.

Further evidence against Fraser's hypothesis is found in work carried out by Galpin (1934, 1935, 1936b) who found a very high proportion of pre-CT fibres (33% of all fibres on one lamb) on the poll. She suggested that the proportion of pre-CT fibres in an area was dependant on the earliness of development of the follicle population on that area and that in some poll samples all trio follicles produced pre-CT fibres.

Stephenson (1952, 1956) carried out a similar investigation on a limited number of positions. Between regions he found differences in pre-CT counts which are not readily explained in terms of different follicle ratios.

Not studying samples from the poll or ventral neck (Galpin's regions of highest pre-CT count) he did not find the very large pre-CT proportions as reported in the previous observations.

Although Carter and Hardy (1947) found high $\frac{Sf+Si}{Pf+Pi}$ on the poll of Merino foetuses, Stephenson (1955) has recently presented data showing that in the N.Z. Romney Sf/Pf on the head is approximately 2-3. However since these S follicles develop very early, probably all the S follicles would produce fibres large enough to be included in the fibre type counts and consequently the high pre-CT counts could not be explained solely in terms of the low Sf/Pf ratio.

If a relationship exists between the morphology of a fibre and the class of follicle producing that fibre it is obvious that the relationship must follow a less direct path than that suggested by Fraser (1951, 1952a). Carter (1943) and numerous later workers have shown that the follicle classes form an orderly series in time of development, the order being PCX, PCY, PLx, PLy, S. Dry (1935) and Galpin (1934, 1935) have suggested that fibres develop in the order HH, super-sickles, Sk, HTCT, CT and Hi, hence it seems that time of development is possibly the pathway whereby fibre type and follicle class are related.

Unfortunately our knowledge of the relative times of development of the different fibre types is limited. Dry and Galpin and later Ross (1945) based their conclusions on a few observations of the shape of the portion of fibres visible on foetuses. While they have been able to say that halos are the first fibres to commence growth, they have not been able to show conclusively that all halos have been initiated before HTCT fibres begin development. Goot (1940), on the basis of fibre morphology, suggested that some HTCT fibres develop at the same time as many of the halos and possibly before the super-sickles. While his evidence does not support the idea very effectively we have no worthwhile proof that the suggestion is false. J.M. Ross (1945) also reached the conclusion that HTCT appear just as early as super-sickles. The need for further work on the times of

development of the different fibre types was also stressed by D.A. Ross (1950) who thought the reason for arrays with robust HTCT fibres and weak SSA fibres might be that the hairy-tip-curly tips were being produced by PC follicles while the super-sickles originated in PL follicles.

Dry (1933) first suggested that the pre-natal check was due to the increasing density of follicles in the skin. Subsequently workers have concentrated on this suggestion with Galpin (1936b) and Stephenson (1958) carrying out thorough studies in attempts to prove or disprove that density changes cause the check. The recent work of Stephenson (1958) has shown that density reaches a maximum about the time of the pre-natal check. This suggests that the pre-natal check is caused by competition of an increasing number of follicles. However it is very difficult to relate the changes in density as shown by Stephenson's graphs with the variations in the intensity of the check between different regions. Also, although the N-type birthcoat is considered to show very little check while the non-N Romney birthcoat is generally heavily checked, no marked differences were found between genotypes (N/N, N/+ and +/+) in graphs of follicle density at different foetal ages.

From these results it seems that unless some other factor, such as the blood supply to follicles, allows fibres

in the less checked regions or genotypes to withstand better the changes in environment brought about by increases in follicle density, we cannot explain the check in terms of competition.

The possibility that the check is due to some cause beneath the surface layer of the foetus has been little explored, the many changes occurring in the physiology of the foetus during the later stages of pre-natal life having as yet largely escaped the attention of wool biologists interested in the pre-natal check. In particular, important changes in the endocrine balance about this time offer a very useful line of approach, especially if the studies can be related to work on the adult animal by Ferguson (1951, 1954, 1956, 1958), Labban (1954, 1957b), Maqsood (1950, 1955), Hart (1954, 1955, 1957, 1958) and Ross and Lewis (1958). Work on the adrenal steroids might prove especially interesting since Ferguson (personal communication) suggests the level of these hormones in the blood supply can be very important in limiting wool growth. Differences between regions could easily be explained since many cases in which steroid hormones cause pattern effects are already known (e.g. sex colouration), while differences between genotypes could possibly be explained in terms of different hormone levels.

Although many workers interested in the pre-natal check seem to have considered the skin to be an entity in

itself, it is really only a small part of a complex organism, and it comes under the influence of practically all the factors that affect that organism. Thus all changes taking place in the foetus from 100 days onward have possibilities as causal agents of the pre-natal check. Possibly the main reason why wool biologists have concentrated on density in studies of the check are the small local variations in the intensity of the check which Dry postulated as the agents bringing about "in parallelism" of arrays. These local effects, difficult to visualise if we consider the check to be the result of a factor operating over the whole animal, can be readily explained in terms of small local changes in density. Possibly however these effects could be due to some other cause such as a temporary break down of the blood supply to small areas. Instances of all fibres from a small area shedding were found in the skin sections. This was apparently not due to density and must have been the result of some other locally occurring factor. Of these, blood supply seems the most likely cause.

The evidence to support the idea that the check occurs at the same time in all regions of the body is not strong. The best indication is Galpin's work on the proportion of pre-CT fibres in arrays from different areas. She suggested on the basis of this work that high proportions of pre-CT fibres were found on the areas where the follicles were established earliest. The probable explanation is that

more fibres had commenced growth before the onset of the check in these regions of early development of follicles.

If it can be proved that fibres of the CT group can commence growth before some members of the pre-CT group it seems that we will have to fall back on Goot's (1940) idea that the check is the property of each individual follicle.

The results presented here do little to clarify the problem of whether the pre-natal check is a local phenomenon or whether it takes place simultaneously in all regions. The differences in fibre proportions between the two subsamples in sheep 52 and sheep 60, and the fibre diameter comparisons of sheep 97 tend to suggest that the check does not occur simultaneously in all areas. Evidently in the piece of skin supplying the fibres of the first subsample for sheep 52, almost all the PC follicles were occupied by HTCT fibres, while in the region from which the second subsample was removed almost all the PC follicles produced pre-CT fibres. The obvious explanation is that in the skin supplying the second subsample, more fibres had been growing at the time of the pre-natal check. This could be achieved by two means: -

i The check being later in the second piece of skin.

ii Follicle development not being as early in the first case.

There is a slight suggestion from the fibre diameter comparison of sheep 97 that some HTCT are of PC origin while some of the pre-CT fibres are of PL origin. If the sickle tip was due to the check this implies that the check must affect individual follicles at different times.

These ideas of course depend on the assumption that pre-CT fibres are well grown at the time of the check while in the case of HTCT fibres the check affects the fibre in a very early stage of growth. The work gives no more than an indication that the check might be a local phenomenon.

A technique offering great possibilities to further our knowledge of the check is tissue culture. Hardy and Lyne (1955b,1956c) have reported progress on culturing skin from foetuses. If finally perfected this technique will allow the study of effects of density changes and other treatments without the complication of the relationship with other tissues.

The results given here and other work suggests that the conclusions about the origin of fibre types reached by Fraser, Ross and Wright, while they may be true in many cases do not hold in a large number of N/N lambs. Work from other sources, while not specifically on the same problem, leads to similar conclusions.

Although "base" and "check" are really only vague ideas and we know very little about either, the origin of the

fibre types can be readily explained in terms of these two hypothetical forces. Those fibres which commence growth at an early stage will be relatively robust over the early stages, the robustness depending on the power of the base. At a certain stage these fibres come under the influence of the pre-natal check. This "check" causes a reduction in the fibre matter output of the follicle, this reduction being manifest in two ways.

i Reduction in length of fibre produced per unit of time.

This results in the characteristic sickle shaped tip of the pre-CT group as suggested by Fraser (1952a).

ii Reduction in the diameter of the fibre.

This reduction in diameter is controlled by the intensity of the check itself and by the power of the base. If the base is strong, as in most N-type sheep the fibre will be very coarse at the time of the check and there will proportionately be a smaller reduction in diameter. Since the medulla diameter is apparently dependent on the fibre diameter (Ross 1950, Cockrem 1956) the fibres of these sheep with a powerful base, will be strongly medullated. If, because of a weak base or a strong check, the reduction in diameter is greater than the medulla diameter before the check, the fibre will become non medullated and hence will be a sickle fibre. Those fibres which had a medulla diameter greater than the reduction due to the check will be super-sickles or halos.

The effects of the check apparently last until birth in most cases. Thus in the case of super-sickles medullation is generally weak over this period and after a while may cease altogether. Some pre-CT fibres apparently never recover from the effects of the check and remain "fine".

It seems that if only a proportion of the PC fibres are growing at the time of the check those PC fibres which develop later will belong to the CT group. In the case of N type lambs the base is powerful enough for these fibres to be hairy tipped. In many cases it seems that the check must occur when the PC fibres are all well grown but before the PL fibres have become thoroughly established. Thus all PC fibres will be pre-CTs while the PL fibres will be members of the CT group. In some cases however, such as on the poll many PL fibres as well as the PCs will be growing at the time of the check. Consequently there will be pre-CT fibres in many PL follicles as well as the PCs.

The type of CT fibre produced by those P follicles not producing pre-CT can be explained hypothetically in terms of "base". The strength of this "base" is apparently determined by

i The diameter relationship between P and S fibres (In Fraser's terms their "relative efficiency").

ii The mean fibre diameter.

iii The keratinising ability of the follicles.

If the base is very weak the primary CTs will be non-medullated. Since in these cases the check is often very strong and long lasting, in many lambs these fibres will be ch CT. If the "base" is very strong all the P follicles not producing pre-CT will have HTCT fibres. In between the two extremes there are various intermediate stages. Sheep 6 and 120 of the study apparently had weakish bases and consequently some of the later developing PL follicles were occupied by pre-precipice CT fibres.

Possibly the first of the factors which contribute to the "base" is controlled to some extent by the lasting effects of the check.

The factor controlling the hairiness of secondary fibres has not received as much attention. It probably is very similar to the "base". If the factors controlling secondary hairiness are identical to the three factors making up "base" we would expect greater hairiness of secondaries in those sheep where the size differences between P and S fibres is least. This does not seem to be the case however. It appears that associated with size differences between P and S fibres there might be a limitation of the keratinising power of the secondary follicles since in the hairy sheep studied, many of the finer curly-tips and histerotrichs were medullated.

The results did not support Burns and Clarkson's

(1949) idea that P and S medullation is independent. In both cases where HTCT fibres were apparently in secondary follicles all primaries were apparently occupied by robust pre-CT or HTCT fibres. It seems then there must be some relationship between the forces controlling hairiness in primaries and those controlling hairiness in secondaries. Knowledge of this relationship would be very valuable.

It seems then that if the drive towards hairiness is strong enough, some of the secondary follicles will produce HTCT. Where the drive is weaker a large proportion of the CT fibres and possibly some Hi will be medullated in the post-natal regions. If the drive towards hairiness is weak all secondaries will produce non-medullated CT and Hi fibres. Since Hefford found ch CT fibres in follicles without sweat glands, some of the earlier S follicles in sheep with little drive towards hairiness will produce ch CT. Other early developing secondaries will produce peak CTs and the later secondary fibres will be fine CTs and Hi. Probably many of these Hi originate in derived secondaries.

Since Burns (1949) found follicles intermediate between P and S in character, it seems that the acquisition of accessories by a follicle is controlled by it's time of development, not it's arrangement. Thus very early developing post-trio follicles can approach the trio follicles in development of accessory structures. Possibly many of the

rather anomolous fibres found are those that originate in these intermediate types of follicles.

Except in the cases of sheep 52 and sheep 60 the repeatability of the fibre type array estimate seemed reasonably good. In other cases differences between subsamples, when not attributable to normal sampling errors, were due to difficulties of differentiating between HH and SSA (Ross and Wright 1954 did not attempt any distinction) and between the smaller CT fibres and Hi (in plateau arrays the CTs tend to be rather straight). If large differences such as those that occur between the subsamples for sheep 52 are common, the value of fibre type array analysis would be limited. It appears that there is little justification for attempting to draw a boundary between HH and SSA. Probably the tip shape differences are largely due to "setting" while the fibre is fixed in position by its neighbours in the birthcoat.

VIII SUMMARY AND CONCLUSIONS

1. The possibilities of finding the follicular origin of the different fibre types were examined. Of the methods studied, a combination of frequency and fibre diameter comparisons offers reasonable possibilities for relating the fibres to the follicles when fibre diameter differences exist between classes.

2. Results suggest that the relationships derived by Fraser, Ross and Wright (1954) from mean frequencies of fibre and follicle types, are true for only a proportion of N-type lambs. Examples were found of super-sickle fibres in PL, HTCT in S and CT in PL follicles of N/N lambs.

3. Fraser, Ross and Wright (1954) suggested that in N-type sheep PC follicles produced pre-CT fibres except in some cases of sheep with Plateau arrays having very few super-sickles. These could have some primary central HTCT fibres. The present results do not support this statement. HTCT fibres apparently grow in the PC follicles of sheep with many super-sickles as readily as in other cases.

4. Since pre-CT fibres can originate in PL follicles and fibres of the CT group can grow in PC follicles slow-

ing of the growth rate of PC fibres as a result of PL competition cannot be an important factor in the formation of sickle-shaped fibre tips.

5. It is suggested that the type of birthcoat fibre produced by a follicle is dependent on

i The stage of development of the follicle at the time of the pre-natal check.

ii The output of cells from the papilla.

iii The keratinising ability of the follicle.

6. Repeatability of the fibre type array analysis was in most cases reasonable. In one sheep however large differences existed between subsamples. It seems that there is little to be gained by attemping to distinguish between HH and SSA as the difference is purely one of size.

IX BIBLIOGRAPHY

Anon. (1955) personal communication; Dept. of Agriculture and Stock, Brisbane.

Auber, L. (1952) Trans. Roy. Soc. Edinb. 62 : 191.
Auber, L. and Ryder, M.L. (1955) Proc. Int. Wool Text. Res. Conf. Aust. F : 36.

Boyd, E. (1927) S. Afr. J. Sci. 24 : 416.

Burley, R.W. and Speakman, J.B. (1953) Text. Res. J. 23 : 702.

Burns, M. (1949) J. Agric. Sci. 39 : 64.
Burns, M. (1953) J. Agric. Sci. 43 : 422.
Burns, M. (1954a) J. Agric. Sci. 44 : 86.
Burns, M. (1954b) J. Agric. Sci. 44 : 443.
Burns, M. (1955) J. Agric. Sci. 46 : 389.
Burns, M. and Clarkson, H. (1949) J. Agric. Sci. 39 : 315.

Carter, H.B. (1939a) J. Coun. Sci. Industr. Res. Aust. 12 : 250.
Carter, H.B. (1939b) Aust. Vet. J. 15 : 210.
Carter, H.B. (1940) Aust. J. Sci. 2 : 143.
Carter, H.B. (1942) J. Coun. Sci. Industr. Res. Aust. 15 : 217.
Carter, H.B. (1943) Bull. Coun. Sci. Industr. Res. Aust. no.164.
Carter, H.B. (1955) Anim. Breed. Abstr. 23 : 101.
Carter, H.B. and Clarke, W.H. (1957a) Aust. J. Agric. Res. 8 : 91.
Carter, H.B. and Clarke, W.H. (1957b) Aust. J. Agric. Res. 8 : 109.
Carter, H.B. and Dowling, D.F. (1954) Aust. J. Agric. Res. 5 : 745.
Carter, H.B. and Hardy, M.H. (1947) Bull. Coun. Sci. Industr. Res. Aust. no. 215.

Cockrem, F.R.M. (1956) Ph.D. Thesis. Massey Agricultural College.

Cole, E.C. (1943) Stain Tech. 18 : 125.

Communal, R. and Adrover, C. (1953) Bull. Acad. Vet. Fr. 26 : 471 (cited by Auber and Ryder, 1955)

Crew, F.A.E. and Blyth, J.S.S. (1922) J. Text. Inst. 13 : 149.

de Meijere, J.C.H. (1894) Morph. Jb. 21 : 321.

Deshpande, A.K. (1948) Ph.D. Thesis. University of Leeds (cited by Wildman, A.B. 1949. Rev. Text. Prog. 1 : 90).

Diomidova, N.A. (1955) Zivotnovodstvo 1955 : 64. (cited from Anim. Breed. Abstr. 24 : 42).

Dry, F.W. (1931) Nature 127 : 482.
Dry, F.W. (1933) J. Text. Inst. 24 : T161.
Dry, F.W. (1934) N.Z. J. Agric. 49 : 269.
Dry, F.W. (1935a) "Hairy fibres of the Romney Sheep". G.H. Loney, Govt. Printer, Wellington.
Dry, F.W. (1935b) N.Z. J. Agric. 51 : 229.
Dry, F.W. (1940) N.Z. J. Sci. Tech. 22A : 209.
Dry, F.W. (1952) N.Z. Sci. Rev. 10 : 69.
Dry, F.W. (1955) Aust. J. Agric. Res. 6 : 725.
Dry, F.W. (1956) Proc. N.Z. Soc. Anim. Prod. 16 : 130.
Dry, F.W., Burley, R.W. and Speakman, J.B. (1952) Nature 169 : 371.

Duerden, J.E. (1927) S. Afr. J. Sci. 24 : 388.
Duerden, J.E. (1929) S. Afri. J. Sci. 26 : 459.
Duerden, J.E. (1932) Nature 130 : 736.
Duerden, J.E. (1939) Trans. Roy. Soc. Edinb. 59 : 763.
Duerden, J.E. and Boyd, E. (1930) Bull. S. Afr. Dept. Agric. no.82.
Duerden, J.E. and Ritchie, M.I.F. (1924) S. Afr. J. Sci. 21 : 480.
Duerden, J.E. and Seale, P.M. (1927) J. Text. Inst. 18 : T265.

Dusenbury, J.H. and Menkart, J. (1955) Proc. Int. Wool Text. Res. Conf. Aust. F : 142.

Elphick, B.L. (1932) J. Text. Inst. 23 : T367.

Ferguson, K.A. (1951) J. Endocrin. 7 : lxi.
Ferguson, K.A. (1954) Nature 174 : 411.
Ferguson, K.A. (1956) Proc. Aust. Soc. Anim. Prod. 1 : 58.
Ferguson, K.A. (1958) Proc. N.Z. Soc. Anim. Prod. 18 : 128.
Ferguson, K.A., Schinckel, P.G., Carter, H.B. and Clarke, W.H. (1956) Aust. J. Biol. Sci. 9 : 575.

Fraser, A.S. (1951) Nature 167 : 202.
Fraser, A.S. (1952a) Aust. J. Agric. Res. 3 : 419.
Fraser, A.S. (1952b) Aust. J. Agric. Res. 3 : 435.
Fraser, A.S. (1953) J. Genet. 51 : 222.
Fraser, A.S. (1954) Aust. J. Agric. Res. 5 : 737.
Fraser, A.S., and Hamada, M.K.O. (1952) Proc. Roy. Soc. Edinb. 64B : 462.
Fraser, A.S., Ross, J.M. and Wright, G.M. (1954) Aust. J. Agric. Res. 5 : 490.
Fraser, A.S., and Short, B.F. (1952) Aust. J. Agric. Res. 3 : 445.

Fraser, R.D.B. and Rogers, G.E. (1955a) Aust. J. Biol. Sci. 8 : 288.
Fraser, R.D.B. and Rogers, G.E. (1955b) Proc. Int. Wool Text. Res. Conf. Aust. F : 151.

Frolich, G., Spottel, W. and Tanzer, E. (1929) "Wollkunde" (Julius Springer : Berlin.)

Galpin, N. (1934) M.Sc. Thesis. Massey Agricultural College.
Galpin, N. (1935) J. Agric. Sci. 25 : 344.
Galpin, N. (1936a) Emp. J. Exp. Agric. 4 : 116.
Galpin, N. (1936b) D.Sc. Thesis. Univ. of Edinburgh.
Galpin, N. (1947) J. Agric. Sci. 37 : 275.
Galpin, N. (1948) J. Agric. Sci. 38 : 303.

Goot, H. (1940) M.Agr.Sc. Thesis. Massey Agricultural College.
Goot, H. (1941) Nature 148 : 596.
Goot, H. (1945) N.Z. J. Sci. Tech. 27A : 349.

Hardy, M.H. (1949) J. Anat., Lond. 83 : 364.
Hardy, M.H. and Lyne, A.G. (1955a) Proc. Int. Wool Text. Res. Conf. Aust. F : 26.
Hardy, M.H. and Lyne, A.G. (1955b) Proc. Int. Wool Text. Res. Conf. Aust. F : 32.
Hardy, M.H. and Lyne, A.G. (1956a) Nature 177 : 705.
Hardy, M.H. and Lyne, A.G. (1956b) Aust. J. Biol. Sci. 9 : 423.
Hardy, M.H. and Lyne, A.G. (1956c) Aust. J. Biol. Sci. 9 : 559.

Hart, D.S. (1954) Nature 174 : 1018.
Hart, D.S. (1955) Proc. N.Z. Soc. Anim. Prod. 15 : 57.
Hart, D.S. (1957) N.Z. J. Sci. Tech. 38A : 871.
Hart, D.S. (1958) Proc. N.Z. Soc. Anim. Prod. 18 : 153.

Henderson, A.E. (1953) J. Agric. Sci. 43 : 12.

Hofer, H. (1914) Arch. Mikr. Anat. 85 : 220 (cited by Dry, personal communication).

Horio, M. and Kondo, T. (1953) Text. Res. J. 23 : 373.

Hugo, W.J. (1953) Merino Breeders J. 15 (No.3) 7, 15 (No.4) 12, 16 (No.1) 19.

Labban, F.M. (1954) J. Endocrin. 11 : v.
Labban, F.M. (1957a) J. Agric. Sci. 49 : 19.
Labban, F.M. (1957b) J. Agric. Sci. 49 : 26.

Leslie, A. (1935) Unnumbered publication, Lincoln Agricultural College.

Lockart, L.W. (1956a) Aust. J. Agric. Res. 7 : 152.
Lockart, L.W. (1956b) Aust. J. Agric. Res. 7 : 158.

Lyne, A.G. (1957a) Nature 179 : 825.
Lyne, A.G. (1957b) Wool Tech. 4 : 53.

Margolena, L.A. (1954) J. Anim. Sci. 13 : 765.

Maqsood, M. (1950) Nature 166 : 647.
Maqsood, M. (1955) Brit. Vet. J. 111 : 163.

Morley, F.H.W., Lockart, L.W. and Davis, E.C. (1955) Aust. J. Agric. Res. 6 : 91.

Nathusius, W.v. (1866) "Das Wollhaar des Schafes in histologischer und technischer Beziehung mit vergleichender Berücksichtigung anderen Haar und Haut." Wiegandt u. Hempel. (cited by Carter, 1955).

Padfield, D.G. and Bell, R.M. (1957) J. Agric. Sci. 49 : 283.

Panfilova, E.P. (1955) Dokl. Akad. Nauk. S.S.S.R. 104 : 329. (cited from Anim. Breed. Abstr. 24 : 43).

Pearlman, R.C. and Cole, B.C. (1951) Stain Tech. 26 : 115.

Ross, D.A. (1950) M.Agr.Sc. Thesis. Massey Agricultural College.
Ross, D.A. and Lewis, K.H.C. (1958) Proc. N.Z. Soc. Anim. Prod. 18 : 141.

Ross, J.M. (1945) M.Sc. Thesis. Massey Agricultural College.
Ross, J.M. (1954) Aust. J. Agric. Res. 5 : 484.
Ross, J.M. and Wright, G.M. (1954) Aust. J. Agric. Res. 5 : 503.

Rudall, K.M. (1955) Proc. Int. Wool Text. Res. Conf. Aust. F : 10.

Ryder, M.L. (1955a) J. Text. Inst. 46 : T565.
Ryder, M.L. (1955b) Proc. Int. Wool Text. Res. Conf. Aust. F : 63.
Ryder, M.L. (1956) J. Agric. Sci. 47 : 6.
Ryder, M.L. (1957a) Bull. W.I.R.A. 19 : 69.
Ryder, M.L. (1957b) J. Agric. Sci. 49 : 275.

Schinckel, P.G. (1953) Nature 171 : 310.
Schinckel, P.G. (1955a) Aust. J. Agric. Res. 6 : 68.
Schinckel, P.G. (1955b) Aust. J. Agric. Res. 6 : 308.

Short, B.F. (1951) Ph.D. Thesis. Univ. of Wales (cited by Dry, personal communication).
Short, B.F. (1955a) Aust. J. Agric. Res. 6 : 62.
Short, B.F. (1955b) Aust. J. Agric. Res. 6 : 863.

Spöttel, W. and Tänzer, E. (1923) Arch. Naturgesch 89 : 1. (cited by Frölich, Spöttel and Tänzer, 1929).

Stephenson, S.K. (1952) M.Sc. Thesis. Massey Agricultural College.
Stephenson, S.K. (1956) Aust. J. Agric. Res. 7 : 447.
Stephenson, S.K. (1957) Aust. J. Agric. Res. 8 : 371.
Stephenson, S.K. (1958) Aust. J. Agric. Res. 9 : 138.

Sugai, K. (1953) Sci. Rep. Fac. Agric. Okayama Univ. 3 : 33.
Sugai, K. (1954) Jap. J. Zootech. Sci. 25 : 155.
Sugai, K. (1955) Jap. J. Zootech. Sci. 26 : 273.

Sutherland, J.A. (1939) M.Agr.Sc. Thesis. Massey Agricultural College.

Tänzer, E. (1926) "Haut und Haar beim Karakul in rassenanalytischen Vergleich" (Otto Theile : Halle) cited by Frölich, Spöttel and Tänzer (1929).

Teodoreamu, N.I. (1934) Ann. Inst. Nat. Zootech. Rouman. 3 : 110 (cited from Anim. Breed. Abstr. 3 : 268).
Teodoreamu, N.I. and Derlogea, V. (1956) Revue de Biologie 1 : 189.

Terentjeva, A.A. (1937) C.R. (Dokl.) Acad. Sci. U.R.S.S., N.S., 16 : 189. (cited by Terentjeva 1939).
Terentjeva, A.A. (1939) C.R. (Dokl.) Acad. Sci. U.R.S.S., N.S., 25 : 557.

Toldt, K. (Jr.) (1910) Ann. Naturh. Hoffmus (Wien) 1910 : 24. (cited by Carter, 1955).
Toldt, K. (Jr.) (1912) Zool. Jb., Syst., 33 : 9 (cited by Carter, 1955).
Toldt, K. (Jr.) (1935) "Aufbau und natürliche Färbung des Haarkleides der Wildsäugetiere. (Deutsche Gesellschaft für Kleintier- und Peltztierzucht G.m.b.H and Co., Leipzig.

Wildman, A.B. (1932) Proc. Zool. Soc. Lond. 1932 : 257.
Wildman, A.B. (1957) Nature 180 : 99.
Wildman, A.B. and Carter, H.B. (1939) Nature 144 : 783.

APPENDIX

A Comparison of Square and Circular Sampling Areas in the Estimation of Follicle Population Means.

The estimation of S/P ratio and follicle density involves counting the follicles in a specific area. Various workers have employed different shapes and sizes of sampling areas. Most Australian workers charted follicles projected from a 1 mm. square area of the skin section, and averaged the counts of these. (Carter 1939a, Anon. 1955, Carter and Clarke 1957a). Burns (1955) expressed her dissatisfaction with any form of sampling area which did not take into account the group structure of the follicles and she used a method involving the charting of groups (Burns, 1949). However this method has two disadvantages.

i Separate counts are necessary for S/P and density determinations.

ii Possibly a bias could be introduced, since not all groups are clearly delineated and some selection of the groups would be necessary. If, as has been suggested, increasing density tends to obliterate the group structure and high density is associated with high S/P ratio, by selecting clear-cut trio groups we would tend to choose those groups of low S/P ratio.

Little data has been published on the errors involved in the estimation of follicle population means and no study has been made of the efficiency of different methods.

Cockrem (personal communication) found quite large "error" variances between estimations of S/P ratio from ten counts of follicles in 1 mm. square pieces of skin. He suggested that these variances were largely due to errors in the determination of $\bar{n}$ P as a result of the small number of primary follicles in each count. It seemed that possibly the errors were largely edge effects due to P follicles being just in or just out of the area. Since a circular sampling area would have a shorter margin than a square of similar area, it was thought that the circle might be more efficient. Consequently the efficiency of 1 sq. mm. circles and 1 sq. mm. squares was compared.

Primary and secondary follicles were counted in ten squqres and in ten circles for each of 15 lambs. From these data the variance components have been analysed for the Pf counts, the Sf counts, total mature follicle counts and Sf/Pf ratio. These analyses are presented in tables 16 - 23.

Tables 16 and 17 indicate that counts of P follicles on circular areas had a much lower error variance

(within sheep) than counts on square areas. In the case of the S counts however tables 18 and 19 show the squares to be the more efficient sampling area. The superiority of the squares for S counts also makes them more efficient for counts of all follicles. It is rather surprising to find the error variance higher for secondary counts than for primary counts since it was expected that the small number of P follicles would increase the error. For estimates of Sf/Pf, tables 22 and 23 indicate that squares are far superior to circles.

These results are rather difficult to interpret and should be viewed with caution until further evidence is available to substantiate them. There is no obvious reason why circles should give a better estimate of $\bar{n}$ P while squares give a better estimate of $\bar{n}$ S. It is equally as difficult to understand why squares should be giving much better estimates of Sf/Pf and it seems that the difference between squares and circles is too large to be true.

TABLE 16

Analysis of variance components for counts of P follicles in square sampling area

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	957	6•42	6•68	
Between sheep.	14	624	44•57	4•21	63•02%
Within sheep.	135	333	2•47	2•47	37•98%

TABLE 17

Analysis of variance components for counts of P follicles in circular sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	915	6•14	6•485	
Between sheep	14	802	57•29	5•645	87•05%
Within sheep	135	113	0•84	0•84	12•95%

TABLE 18

Analysis of variance components for counts of Sf follicles in square sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	6209	41·67	43·48	
Between sheep	14	4368	312·00	29·84	68·63%
Within sheep	135	1841	13·64	13·64	31·37%

TABLE 19

Analysis of variance components for counts of Sf follicles in circular sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	5941	39·87	40·85	
Between sheep	14	2603	185·93	16·12	39·46%
Within sheep	135	3338	24·73	24·73	60·54%

TABLE 20

Analysis of variance components for counts of Pf+Sf follicles in square sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	9057	60·79	63·58	
Between sheep	14	6717	479·79	46·25	72·74%
Within sheep	135	2340	17·33	17·33	27·26%

TABLE 21

Analysis of variance components for counts of Pf+Sf follicles in circular sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	7911	53·09	54·91	
Between sheep	14	4567	326·21	30·14	54·89%
Within sheep	135	3344	24·77	24·77	45·11%

TABLE 22

Analysis of variance components for estimates of Sf/Pf ratio from square sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	123.77	0.831	0.874	
Between sheep	14	102.16	7.297	0.714	81.69%
Within sheep	135	21.61	0.160	0.160	18.31%

TABLE 23

Analysis of variance components for all estimates of Sf/Pf ratio from circular sampling areas

Source	d.f.	S.S.	M.S.	Variance Components	
Total	149	147.31	0.989	1.027	
Between sheep	14	51.53	3.681	0.295	28.72%
Within sheep	135	98.78	0.732	0.732	71.28%