CRIMP IN WOOL: GROWTH CHARACTERISTICS OF WELL-CRIMPED AND ABNORMALLY CRIMPED FIBRES

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Summary

Poorly crimped fibres are shorter than fibres with good or intermediate crimp within staples of medium Merino wool, irrespective of the degree of abnormality in staple crimp. As staple crimp deteriorates, poorly crimped fibres are progressively thicker and to some extent heavier than well-crimped fibres. The cortical cells in poorly crimped fibres are thicker and larger in volume than cells in well-crimped fibres, irrespective of staple crimp abnormality, but become progressively shorter as staple crimp deteriorates.

It is inferred that cell number in abnormally crimped fibres, relative to that in well-crimped fibres, changes as staple crimp deteriorates and that hyperplasia of the follicle bulb accompanies hyperplasia of the outer root sheath when staple crimp is slightly doggy. Increase in the regression coefficients of thickness on length of abnormally crimped fibres also occurs in slightly doggy staples. This suggests that the hyperplasia of the follicle bulb which occurs at this stage of crimp deterioration has relatively more effect on fibres thickness than on length.

The majority of the correlation coefficients between fibre thickness and length within crimp grades are positive and significant when the fibres are separated on the basis of crimp definition. These coefficients are lower than is usual within staples for fibres not previously separated on crimp definition.

The lengths of the keratogenous zone in fibres, as depicted by staining for protein-bound sulphydryl groups, do not differ significantly in follicles with normal, enlarged, or cystic outer root sheaths. The rate of the keratogenous process may be slightly affected in follicles with cystic outer root sheaths.

I. INTRODUCTION

Among sheep with different degrees of staple crimp abnormality (or "dogginess"), the frequency of follicles with gross hyperplasia of the outer root sheath tissue increases with staple crimp deterioration (Chapman, Short, and Hyland 1960), and the proportion of fibres lacking crimp likewise increases (Aiken and Ryder 1962). Also within staples of wool, poorly crimped (doggy) fibres are produced by follicles with gross hyperplasia of the outer root sheath tissue (Chapman, Short, and Hyland 1960). Such fibres are shorter and thicker than adjacent crimped fibres (Aiken and Ryder 1962).

In the present study, fibres were separated on the basis of their crimp definition within wool samples with different staple crimp gradings, and fibre length, weight, thickness, and cortical cell size were measured. Dimensions of the keratogenous zone of fibres within follicles with different outer root sheath conditions were also

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measured. These data provide evidence of an effect of follicle outer root sheath tissue on fibre architecture.

A strong positive correlation exists between the length and thickness of fibres within staples when there has been no prior separation of fibres on the basis of crimp definition (Duerden and Bosman 1931; Darlow and Craft 1935; Oczan 1956). To ascertain whether such a strong correlation still exists for fibres in different crimp grades the relationship between fibre length and thickness in each grade was examined.

II. Materials and Methods

(a) *Wool Samples*

Samples of wool from the rump of 12 medium-wool Merino ewes were examined for fibre length, weight, thickness, and cortical cell dimensions. Using the staple crimp classifications shown in Plate 1 samples 1–3 were normally crimped, Nos. 4–6 had secondary waves, Nos. 7–9 were slightly doggy, and Nos. 10–12 were doggy to very doggy. The samples were degreased in solvent ether which facilitated later separation of the fibres but caused little disturbance of fibre crimp. Individual fibres were graded into three crimp classes: (1) with well-defined crimp, (2) with intermediate crimp, and (3) with poor crimp, as illustrated in Figure 1, until at least 100 fibres were obtained for length, weight, and thickness measurements and 40–50 fibres for cortical cell measurements in each class from each sample. The distinction of one fibre type from another was subjective and depended on the range of crimp frequencies present in the sample. The most difficult boundary to set was between the categories of good and intermediate crimp.

(b) *Fibre Length*

The lengths of individual fibres were measured on a fibre-measuring board calibrated in intervals of 2 mm (Oczan 1956), and the fibres were retained for subsequent weighing.

(c) *Fibre Weight*

The fibres were conditioned at 68(±2)°F and 65(±2)% R.H. and were weighed individually under these conditions on a Mettler microbalance. The weights were recorded in length classes so that an examination could be made of the relationship between length and the expression $(w/l)^{\frac{1}{2}}$, where w = weight and l = length of individual fibres. When w is measured in micrograms and l in centimetres, $(w/l)^{\frac{1}{2}} \times 10 \div d$, where d = diameter, expressed in microns, of an equivalent circular fibre cross-section. Therefore, the expression $(w/l)^{\frac{1}{2}}$ can be considered proportional to fibre thickness.

(d) *Fibre Thickness*

After being weighed, the fibres were placed across strips of adhesive cellulose tape and mounted in liquid paraffin on microscope slides. This procedure was similar in principle to the "long fibre" method of fibre thickness measurement described by the American Society for Testing Materials in "Standards in Textile Materials"

(1956). One measurement per fibre was made on the fibre profiles on a Reichert Lanameter at a magnification of ×500 as the slide was traversed lengthwise. Precautions concerning focusing were observed as described in the British Standards specification B.S. 2043 (British Standards Institution 1953), and in the Draft Specification of the International Wool Textile Organization (1952).

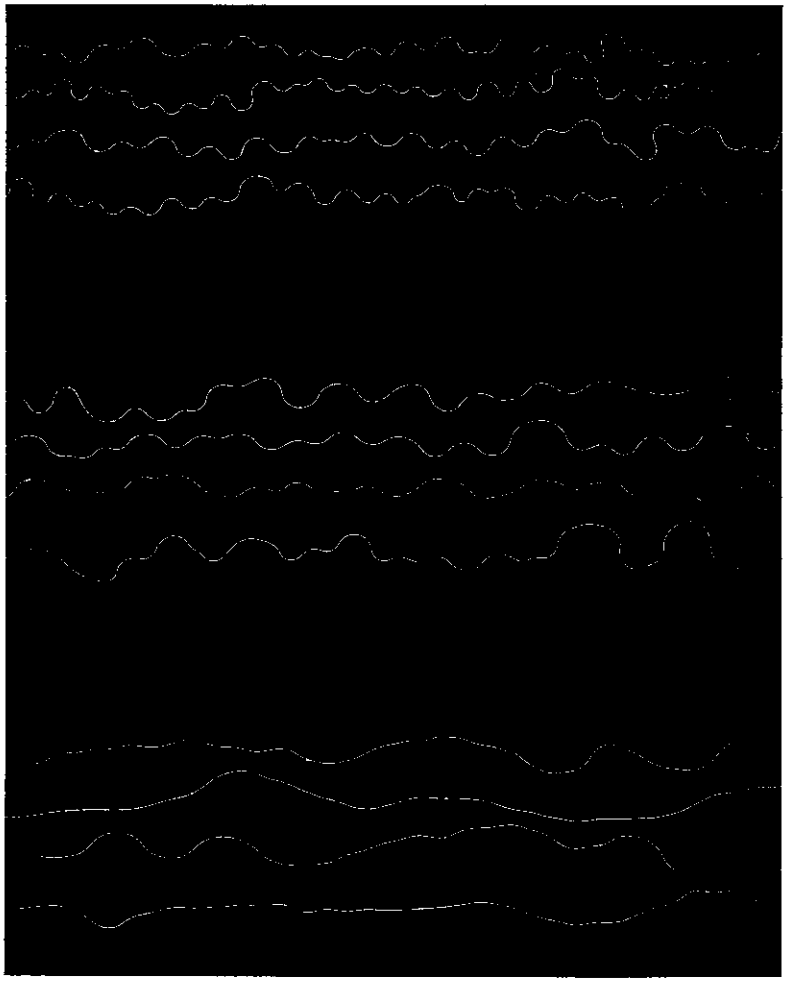


Fig. 1.—Three grades of fibre crimp into which the fibres within staples were graded: good crimp (top), intermediate crimp (centre), and poor crimp (bottom). ×2·4.

(e) *Cortical Cell Size*

Using conditions similar to those of Leveau (1956), each group of fibres was treated in 6N hydrochloric acid at 60°C for 1 hr, the optimum time of treatment (Stewart, unpublished data). The fibres were then washed thoroughly with water and ground in water to produce a suspension of cells. Small quantities of this sus-

pension were placed on microscope slides which had been smeared with egg albumin. When the cells were air-dry, coverslips were sealed on to the slides with paraffin wax. Lengths and maximum widths of 250 cells, chosen at random, were measured for each group of fibres at a magnification of $\times 850$ on a Mipro microprojector.

(*f*) *Skin Samples*

Skin samples were taken with a biopsy punch from the rump of four fine-wool Merino ewes, of which two had normal staple crimp (Nos. 1, 2) and two had doggy fleeces (Nos. 3, 4). The samples were fixed in 1% trichloroacetic acid in 80% ethanol for 24 hr and then embedded in paraffin wax.

(*g*) *Dimensions of the Keratogenous Zone*

Serial longitudinal sections of 10 μ thickness were cut from the paraffin-embedded skin samples and protein-bound sulphydryl groups were demonstrated by the Barrnett and Seligman technique (1952, 1954). The lengths of the zone of sulphydryl staining, considered to be the keratogenous zone, were measured in fibres at a magnification of $\times 225$ on a Reichert Lanameter, and the outer root sheaths of the corresponding follicles were assessed as normal, enlarged, or cystic. Wherever possible 10 fibres were measured in follicles of each type per sample. This was done by tracing on paper those fibres in which the limits of the purple colour of the keratogenous zone could be found either in a single section or when tracked through several sections. At the lower limit of the zone the staining was confined mainly to the material near the surface of the cortical cells, and appeared as fine strands in the thin skin sections.

Fibre thickness was measured at a magnification of $\times 500$ at the lower and upper limits and along the length of the zone on those fibres for which zone lengths were obtained. Cortical cell boundaries at the lower limit of the zone were traced at a magnification of $\times 1420$ using an oil-immersion lens on a modified Reichert Lanameter, and the mean cell width at this level was determined for each fibre examined. In addition, 100 well-crimped and 100 poorly crimped fibres (as in Fig. 1) were separated from within each of the samples of wool clipped from the sheep at the time the skin biopsies were taken. The length and thickness of these fibres were measured.

(*h*) *Statistical Analysis*

Analyses of variance were performed to compare the mean lengths, weights, thicknesses, and cortical cell dimensions of fibres in the three crimp grades, and the mean lengths of the keratogenous zone, the mean thickness at the upper limit of the zone, the percentage reductions in cross-sectional area of the zone, and the mean cell widths at the lower limit of the zone of fibres in follicles with normal, enlarged, and cystic outer root sheaths.

For the three grades of fibre crimp in each wool sample, correlation and regression coefficients were calculated for $(w/l)^{\frac{1}{2}}$ against l.

III. Results

(a) *Fibre Length, Weight, Thickness, and Cortical Cell Size*

Tables 1–5 show, respectively, the mean lengths, weights, and thicknesses and mean cortical cell lengths and widths (and their coefficients of variation) of fibres separated into the three crimp grades. The corresponding analyses of variance are summarized with each table.

When sheep Nos. 1–3 (with normal staple crimp), 4–6 (with secondary waves), 7–9 (slightly doggy), and 10–12 (doggy to very doggy) are considered as separate groups, the trends in mean fibre length, thickness, and weight and cortical cell length and width are as shown in Figure 2.

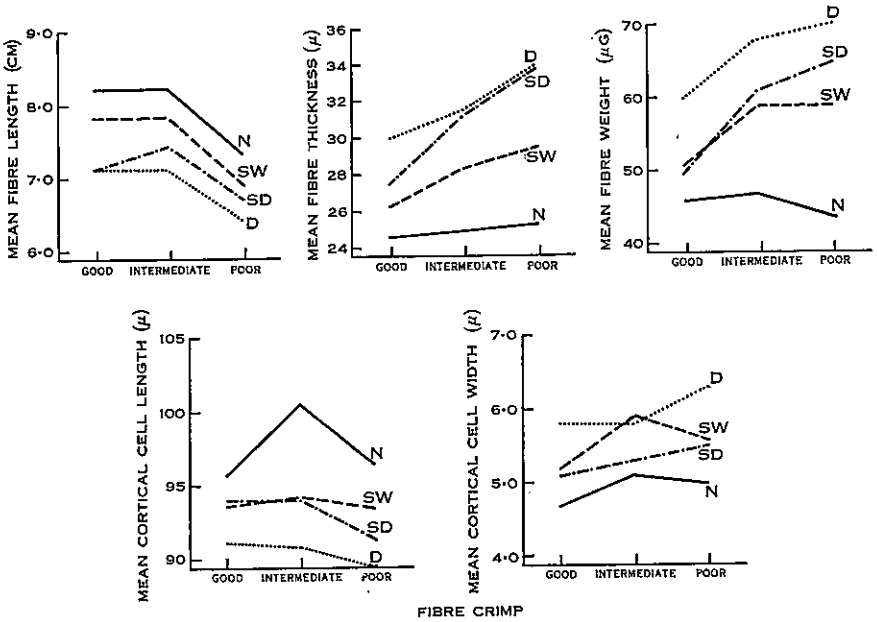


Fig. 2.—Mean fibre length, thickness, and weight, and mean cortical cell length and width in relation to fibre crimp. Staple crimp grading: *N*, normal; *SW*, with secondary waves; *SD*, slightly doggy; *D*, doggy and very doggy.

These data reveal rather marked differences among the three fibre crimp categories. Mean fibre lengths (Table 1) differ significantly ($P < 0{\cdot}001$), poorly crimped fibres being shorter than fibres with good or intermediate crimp, irrespective of the state of the staple crimp (Fig. 2). However, within any one fibre crimp category, mean fibre length decreases with progressive deterioration of staple crimp (Fig. 2), the differences between staple crimp grades being significant ($P < 0{\cdot}05$, Table 1). Variation in fibre length increases with deterioration of fibre crimp, the differences between the crimp grades being significant ($P < 0{\cdot}05$, Table 1).

Mean fibre weights of the three crimp grades also differ significantly ($P < 0{\cdot}01$, Table 2), the fibres with intermediate or poor crimp being heavier than well-crimped fibres, except in normally crimped staples (Fig. 2). As staple crimp deteriorates from

TABLE 1

MEAN LENGTHS AND COEFFICIENTS OF VARIATION IN LENGTH OF FIBRES IN THREE GRADES OF FIBRE CRIMP FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good		Intermediate		Poor	
		Mean Length (cm)	Coefficient of Variation (%)	Mean Length (cm)	Coefficient of Variation (%)	Mean Length (cm)	Coefficient of Variation (%)
Normal	1	8·4	8·4	8·1	9·7	7·2	17·0
	2	7·9	6·2	8·0	7·6	7·4	15·8
	3	8·2	9·2	8·6	9·7	7·2	11·4
Mean		8·2	7·9	8·2	9·0	7·3	14·7
Secondary waves	4	7·7	8·8	7·5	10·0	6·8	10·4
	5	7·9	8·5	8·0	8·2	6·8	9·3
	6	7·8	7·6	8·0	7·4	7·2	9·9
Mean		7·8	8·3	7·8	8·5	6·9	9·9
Slightly doggy	7	7·2	11·1	7·4	9·3	6·6	9·3
	8	7·0	8·7	6·9	8·6	6·1	9·0
	9	7·0	8·1	7·8	11·9	7·4	12·9
Mean		7·1	9·3	7·4	9·9	6·7	10·4
Doggy	10	7·1	10·0	6·9	10·4	6·1	10·2
	11	6·5	14·3	6·8	11·4	6·3	15·1
	12	7·8	11·2	7·7	10·6	6·9	8·0
Mean		7·1	11·8	7·1	10·8	6·4	11·1
All grades Mean		7·5	9·3	7·6	9·6	6·8	11·5
S.E.		0·2	0·6	0·2	0·4	0·1	0·9

Analyses of Variance

Source of Variation	D.F.	Mean Fibre Length S.S.	Mean Fibre Length M.S.	Coefficient of Variation S.S.	Coefficient of Variation M.S.
Between fibre grades	2	4·6606	2·3303***	34·611	17·305*
Between staple grades	3	5·5389	1·8463*	26·989	8·996†
Between sheep within staple grades	8	2·5533	0·3192**	41·640	5·205†
Fibre × staple	6	0·2994	0·0499†	53·449	8·908*
Error	16	1·0734	0·0671	45·780	2·861
Total	35	14·1256		202·469	

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$; †, not significant.

TABLE 2

MEAN WEIGHTS AND COEFFICIENTS OF VARIATION IN WEIGHT OF FIBRES IN THREE GRADES OF FIBRE CRIMP FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good		Intermediate		Poor	
		Mean Weight (μg)	Coefficient of Variation (%)	Mean Weight (μg)	Coefficient of Variation (%)	Mean Weight (μg)	Coefficient of Variation (%)
Normal	1	48	23·8	47	23·1	45	36·2
	2	45	20·4	47	22·8	42	33·8
	3	45	27·1	48	20·2	45	34·4
Mean		46	23·8	47	22·0	44	34·8
Secondary waves	4	55	23·1	59	22·2	59	20·7
	5	48	23·3	58	23·4	51	30·6
	6	49	23·3	59	20·5	68	35·1
Mean		51	23·2	59	22·0	59	28·8
Slightly doggy	7	44	27·5	49	28·4	59	30·2
	8	58	23·4	62	24·2	59	27·5
	9	47	30·0	73	32·9	78	36·3
Mean		50	27·0	61	28·5	65	31·3
Doggy	10	57	21·9	64	21·7	60	25·8
	11	47	27·7	52	27·3	61	31·8
	12	75	20·7	88	21·3	89	21·8
Mean		60	23·4	68	23·4	70	26·5
All grades Mean		52	24·3	59	24·0	60	30·3
S.E.		3	0·9	4	1·1	4	1·6

Analyses of Variance

Source of Variation	D.F.	Mean Fibre Weight S.S.	Mean Fibre Weight M.S.	Coefficient of Variation S.S.	Coefficient of Variation M.S.
Between fibre grades	2	484·66	242·33**	305·780	152·890***
Between staple grades	3	1874·44	624·81†	119·489	39·830†
Between sheep within staple grades	8	1981·56	247·70***	232·717	29·090**
Fibre × staple	6	249·56	41·59†	108·011	18·002†
Error	16	459·78	28·74	112·663	7·041
Total	35	5050·00		878·660	

** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; †, not significant.

normal to doggy, mean fibre weight for each crimp category tends to increase (Fig. 2), although the differences between staple crimp grades are not significant, due to the considerable differences between sheep within staple crimp grades (Table 2). Coefficients of variation in fibre weight are significantly different ($P < 0{\cdot}001$) among the fibre crimp grades, poorly crimped fibres being more variable than fibres with good or intermediate crimp (Table 2).

The three grades also differ significantly ($P < 0{\cdot}001$) in mean fibre thickness, well-crimped fibres being finer than fibres with intermediate or poor crimp (Table 3). However, the differences are less for fibres from within normally crimped staples than for fibres from within staples with abnormal crimp (Fig. 2). Similar to mean fibre weight, mean fibre thickness of each crimp category increases as staple crimp deteriorates (Fig. 2), the differences between staple crimp grades being significant ($P < 0{\cdot}01$, Table 3). Unlike the coefficients of variation in fibre weight, the coefficients of variation in fibre thickness of the three fibre crimp categories are not significantly different for these sheep (Table 3).

The mean lengths and widths of cortical cells in fibres in the three fibre crimp grades differ significantly ($P < 0{\cdot}05$, Table 4, $P < 0{\cdot}01$, Table 5, respectively), the cells in poorly crimped fibres being shorter and thicker than cells in fibres with good and intermediate crimp. Variations in both cortical cell length and width show upward trends as fibre crimp deteriorates although the differences between the fibre grades are not significant (Tables 4 and 5). As staple crimp deteriorates from normal to doggy, cortical cell lengths decrease within each fibre crimp category, as do fibre lengths, and cortical cell widths increase as do fibre thicknesses (Tables 4 and 5; Fig. 2).

(*b*) *Dimensions of the Keratogenous Zone*

In follicles of the fine-wool Merino sheep the lower limit of the keratogenous zone, as depicted by the presence of protein-bound sulphydryl groups, occurs just above the follicle bulb at a distance of about 80 μ (range 70–90 μ) above the tip of the papilla. In Table 6 are presented the mean fibre thicknesses at the lower and upper limits of the zone, the mean percentage reduction in fibre cross-sectional area in the zone, the mean lengths of the zone, and the mean cortical cell widths at the lower limit of the zone. Using the assumption that the reduction in cross-sectional area which occurs in the zone is the same for both cells and fibre, the mean cell widths at the upper end of the zone, i.e. in the keratinized fibre, have been estimated and are also listed in Table 6.

In the majority of fibres, the zone thickness remains the same in the lower half of the zone. About the mid-point of the zone the presence of protein-bound sulphydryl groups is maximal, as judged by the intensity of the purple colour. Above this level both the zone thickness and intensity of staining decrease until keratinization is complete. The shape of the zone, therefore, is a cylinder capped by a frustrum of a cone. The surface area and volume of the zone, also listed in Table 6, have been calculated on the basis of this shape.

Analyses of variance in zone length, fibre thickness at the upper limit of the zone, percentage reduction in fibre cross-sectional area in the zone, and cell width

TABLE 3

MEAN THICKNESSES AND COEFFICIENTS OF VARIATION IN THICKNESS OF FIBRES IN THREE GRADES OF FIBRE CRIMP FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good		Intermediate		Poor	
		Mean Thickness (μ)	Coefficient of Variation (%)	Mean Thickness (μ)	Coefficient of Variation (%)	Mean Thickness (μ)	Coefficient of Variation (%)
Normal	1	24·5	12·4	24·6	15·0	24·4	17·0
	2	24·9	16·0	25·5	13·7	25·0	17·3
	3	24·3	13·4	24·7	13·2	26·1	18·4
Mean		24·6	13·9	24·9	14·0	25·2	17·6
Secondary waves	4	26·6	13·3	28·6	15·4	27·4	13·6
	5	25·8	17·1	28·5	16·1	29·7	14·8
	6	25·8	14·5	27·9	12·2	31·1	18·8
Mean		26·1	15·0	28·3	14·9	29·4	15·7
Slightly doggy	7	26·4	14·7	28·3	15·2	32·2	17·6
	8	29·4	14·9	32·0	15·2	33·4	13·9
	9	26·8	16·2	33·3	15·7	35·1	19·8
Mean		27·5	15·3	31·2	15·4	33·6	17·1
Doggy	10	29·5	15·5	30·2	13·8	31·5	13·0
	11	28·3	13·7	28·6	12·1	32·8	14·2
	12	32·2	14·5	35·5	13·4	37·4	12·2
Mean		30·0	14·9	31·4	13·1	33·9	13·1
All grades Mean		27·0	14·7	29·0	14·2	30·5	15·9
S.E.		0·7	0·4	1·0	0·4	1·2	0·7

Analyses of Variance

Source of Variation	D.F.	Mean Fibre Thickness S.S.	Mean Fibre Thickness M.S.	Coefficient of Variation S.S.	Coefficient of Variation M.S.
Between fibre grades	2	72·427	36·213***	17·183	8·591†
Between staple grades	3	258·984	86·328**	25·266	8·422†
Between sheep within staple grades	8	64·197	8·025**	17·713	2·214†
Fibre × staple	6	24·303	4·050*	21·670	3·612†
Error	16	21·957	1·372	47·534	2·971
Total	35	441·868		129·366	

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$; †, not significant.

TABLE 4

MEAN LENGTHS AND COEFFICIENTS OF VARIATION IN LENGTH OF CORTICAL CELLS IN FIBRES IN THREE GRADES OF FIBRE CRIMP FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good — Mean Length (μ)	Good — Coefficient of Variation (%)	Intermediate — Mean Length (μ)	Intermediate — Coefficient of Variation (%)	Poor — Mean Length (μ)	Poor — Coefficient of Variation (%)
Normal	1	97·6	13·3	104·4	12·3	98·7	13·6
	2	91·3	14·2	96·8	15·6	94·8	15·1
	3	97·8	11·4	100·4	12·9	95·5	14·9
Mean		95·6	13·0	100·5	13·6	96·3	14·5
Secondary waves	4	92·6	11·8	93·4	11·5	92·1	12·5
	5	94·2	14·9	92·1	13·7	93·4	12·8
	6	93·9	13·0	97·1	13·7	95·1	13·2
Mean		93·6	13·2	94·2	13·0	93·5	12·8
Slightly doggy	7	93·4	11·8	91·9	12·8	88·9	14·7
	8	93·5	10·6	91·3	12·6	90·9	13·7
	9	95·1	13·1	98·7	11·6	94·4	11·1
Mean		94·0	11·8	94·0	12·3	91·4	13·2
Doggy	10	91·4	13·3	88·1	13·9	88·5	13·7
	11	90·6	13·4	93·6	11·7	91·4	13·5
	12	91·4	14·3	90·6	14·0	88·7	15·3
Mean		91·1	13·7	90·8	13·2	89·5	14·2
All grades Mean		93·6	12·9	94·9	13·0	92·7	13·7
S.E.		0·7	0·4	1·4	0·3	0·9	0·4

Analyses of Variance

Source of Variation	D.F.	Mean Cell Length — S.S.	Mean Cell Length — M.S.	Coefficient of Variation — S.S.	Coefficient of Variation — M.S.
Between fibre grades	2	28·543	14·271*	3·980	1·990†
Between staple grades	3	224·929	74·976*	9·761	3·254†
Between sheep within staple grades	8	114·840	14·355**	19·133	2·392†
Fibre × staple	6	32·764	5·461†	4·120	0·687†
Error	16	41·420	2·589	17·614	1·101
Total	35	442·496		54·608	

* $P < 0·05$; ** $P < 0·01$; †, not significant.

TABLE 5

MEAN WIDTHS AND COEFFICIENTS OF VARIATION IN WIDTH OF CORTICAL CELLS IN FIBRES IN THREE GRADES OF FIBRE CRIMP FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good		Intermediate		Poor	
		Mean Width (μ)	Coefficient of Variation (%)	Mean Width (μ)	Coefficient of Variation (%)	Mean Width (μ)	Coefficient of Variation (%)
Normal	1	5·1	18·6	5·9	22·0	5·2	22·7
	2	4·7	20·0	4·8	22·0	4·7	25·0
	3	4·2	25·0	4·6	17·9	5·1	20·9
Mean		4·7	21·2	5·1	20·6	5·0	22·9
Secondary waves	4	5·3	17·8	6·2	18·5	5·8	18·4
	5	4·9	21·4	5·3	17·3	5·3	20·0
	6	5·3	20·0	6·2	20·8	5·8	16·3
Mean		5·2	19·7	5·9	18·9	5·6	18·2
Slightly doggy	7	4·6	20·5	5·3	20·3	5·3	20·0
	8	5·3	20·0	5·4	19·6	5·1	22·3
	9	5·3	20·0	5·2	20·5	6·1	21·2
Mean		5·1	20·2	5·3	20·1	5·5	21·2
Doggy	10	5·4	19·6	5·5	21·1	5·4	19·6
	11	6·0	17·6	6·2	17·1	6·9	18·6
	12	6·0	17·6	5·8	18·4	6·6	19·6
Mean		5·8	18·3	5·8	18·9	6·3	19·3
All grades Mean		5·2	19·8	5·5	19·6	5·6	20·4
S.E.		0·2	0·6	0·2	0·5	0·2	0·7

Analyses of Variance

Source of Variation	D.F.	Mean Cell Width		Coefficient of Variation	
		S.S.	M.S.	S.S.	M.S.
Between fibre grades	2	1·2872	0·6436**	3·661	1·830†
Between staple grades	3	5·3656	1·7885*	47·139	15·713**
Between sheep within staple grades	8	3·5066	0·4383**	14·104	1·763†
Fibre × staple	6	0·5994	0·0999†	11·416	1·903†
Error	16	1·4868	0·0929	62·910	3·932
Total	35	12·2456		139·230	

* $P < 0·05$; ** $P < 0·01$; †, not significant.

TABLE 6

MEAN DIMENSIONS OF THE KERATOGENOUS ZONE OF FIBRES IN FOLLICLES WITH DIFFERENT OUTER ROOT SHEATH STATES IN THE SKIN OF FINE-WOOL MERINO SHEEP WITH NORMAL AND DOGGY FLEECES

Staple Crimp Grade	Sheep No.	State of Outer Root Sheath	Thickness		Reduction in Cross-sectional Area (%)	Length (μ)	$10^{-3}\times$ Surface Area‡ (μ^2)	$10^{-3}\times$ Volume‡ (μ^3)	Cell Width at Lower Limit (μ)	Estimated Cell Width at Upper Limit§ (μ)
			Lower Limit (μ)	Upper Limit (μ)						
Normal	1	Normal	22	18	30	225	17·2	93·7	5·1	4·2
		Enlarged	24	20	29	214	15·9	96·9	5·1	4·4
		Cystic	26	22	29	237	19·4	133·0	5·0	4·2
	2	Normal	24	21	19	257	18·7	110·1	5·5	4·9
		Enlarged	28	23	34	273	23·2	161·4	6·1	4·9
		Cystic	29	24	26	300	26·2	185·8	6·0	5·1
Means		Normal	23	19	24	256	17·9	101·9	5·3	4·5
		Enlarged	26	21	31	243	19·6	129·2	5·6	4·6
		Cystic	27	23	27	268	22·8	159·4	5·5	4·6
Doggy	3	Normal	27	23	25	288	23·7	158·6	6·1	5·3
		Enlarged	26	23	25	285	23·0	148·6	6·3	5·5
		Cystic	32	27	28	298	28·9	224·2	7·5	6·4
	4	Normal	22	21	8	250	17·1	93·0	5·2	5·0
		Enlarged	25	21	24	261	19·3	116·6	5·4	4·7
		Cystic	24	22	17	239	17·8	106·6	5·8	5·3
Means		Normal	24	22	16	269	20·4	125·8	5·6	5·1
		Enlarged	25	22	24	273	21·1	132·6	5·8	5·1
		Cystic	28	24	22	268	23·3	165·4	6·6	5·8
Overall means		Normal	24	21	20	262	19·2	113·8	5·5	4·8
		Enlarged	26	22	28	258	20·3	130·9	5·7	4·9
		Cystic	28	24	25	268	23·1	162·4	6·1	5·2

Table 6 (*Continued*)

Analyses of Variance

Source of Variation	D.F.	Zone Length		Fibre Thickness		Reduction in Fibre Cross-sectional Area		Cell Width at Lower Limit	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Between outer root sheath states	2	212·1	106·0†	18·667	9·333*	114·00	57·00†	0·7267	0·3633†
Between staple grades	1	602·0	602·0†	6·750	6·750†	133·33	133·33†	1·0208	1·0208†
Between sheep within staple grades	2	5002·9	2501·4†	24·167	12·083*	153·67	76·83†	3·0017	1·5008**
Outer root sheath state × staple	2	437·3	218·6†	2·000	1·000†	4·67	2·33†	0·4867	0·2433†
Error	4	1474·6	368·6	3·333	0·833	129·33	32·33	0·3333	0·0833
Total	11	7782·9		54·917		535·00		5·5692	

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; †, not significant.

‡ Estimated as explained in Section IV.

§ Based on the assumption that reduction in cross-sectional areas is the same for fibres and cells.

at the lower limit of the zone in follicles with normal, enlarged, and cystic outer root sheaths are summarized in Table 6.

Differences in the mean zone lengths in follicles with the three outer root sheath states are small and not significant. However, the thicknesses at the upper limit of the zone in fibres produced by the three types of follicle differ significantly ($P < 0{\cdot}05$), fibres in cystic follicles being thicker than those in follicles with normal outer root sheaths. The trends in the overall mean thicknesses of fibres in follicles with the three different outer root sheath states are similar to the trends in the overall mean thicknesses of fibres with good, intermediate, and poor crimp in Table 3.

TABLE 7

REGRESSION COEFFICIENTS (b)† OF $(w/l)^{\frac{1}{2}}$ ON l AND CORRELATION COEFFICIENTS (r)† BETWEEN $(w/l)^{\frac{1}{2}}$ AND l FOR FIBRES IN THREE CRIMP GRADES FROM WITHIN MEDIUM-WOOL MERINO STAPLES WITH FOUR GRADES OF STAPLE CRIMP

w = fibre weight in micrograms; l = fibre length in centimetres

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade: Good		Intermediate		Poor	
		b‡	r	b‡	r	b‡	r
Normal	1	0·127	0·401***	0·079	0·260**	0·085	0·297**
	2	0·167	0·402***	0·117	0·306**	0·056	0·211*
	3	0·154	0·417***	−0·002	−0·007	0·168	0·376***
Secondary waves	4	0·085	0·222*	0·025	0·068	−0·019	−0·049
	5	0·077	0·204*	−0·058	−0·124	0·194	0·339***
	6	0·058	0·131	0·136	0·346***	0·290	0·465***
Slightly doggy	7	0·073	0·218*	0·177	0·417***	0·175	0·287**
	8	0·147	0·317**	0·102	0·194*	0·275	0·449***
	9	0·235	0·409***	0·251	0·613***	0·322	0·617***
Doggy	10	−0·012	−0·031	0·061	0·158	0·147	0·247*
	11	0·088	0·318**	0·120	0·311**	0·097	0·243*
	12	0·004	0·011	0·025	0·065	0·239	0·418***

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

† Based on degrees of freedom ranging from 103 to 129.

‡ $b \times 10 \doteq$ change in fibre thickness in microns per centimetre change in length.

Although the percentage reductions in cross-sectional area in the keratogenous zone in follicles with normal, enlarged, and cystic outer root sheaths do not differ significantly, there is a tendency for the percentage reductions to be greater in follicles with enlarged and cystic outer root sheaths. Also, cell widths at the lower limit of the zone do not differ significantly among the three conditions of follicles, but the differences between sheep within staple crimp grades are significant ($P < 0{\cdot}01$). It is of interest that the trends in mean cortical cell widths within the normal and

doggy staple crimp grades and in the overall means of fine-wool Merinos (Table 6) are very similar to the trends in mean cell widths of medium-wool Merinos (Table 5). The lack of significance for the differences in cell width between the three outer root sheath states in Table 6 is probably due to the smaller number of sheep examined.

(c) *Regression and Correlation Coefficients*

The regression and correlation coefficients of $(w/l)^{\frac{1}{2}}$ on l for fibres in each crimp grade are grouped according to staple crimp in Table 7. The majority of the correlation coefficients are positive and small, but significant. Both the regression and correlation coefficients of fibres with good crimp are higher in normal and slightly doggy staples than in the other staple crimp grades. For abnormally crimped fibres with either intermediate or poor crimp the coefficients are highest in slightly doggy staples.

IV. Discussion

(a) *Changes in Fibre Properties accompanying Hyperplasia of Follicle Outer Root Sheaths*

The observation by Aiken and Ryder (1962) that, within wool samples with staple crimp abnormalities, fibres lacking crimp are shorter and thicker than crimped fibres has been confirmed. Therefore, hyperplasia of the outer root sheath tissue of follicles which produce poorly crimped fibres (Chapman, Short, and Hyland 1960) also has an effect on fibre growth characteristics in addition to crimp.

While reduction in length of poorly crimped fibres is a consistent feature irrespective of staple crimp grading (Table 1), poorly crimped fibres become progressively thicker than well-crimped fibres as staple crimp deteriorates (Table 3). On the other hand, cortical cells in poorly crimped fibres are consistently thicker than in well-crimped fibres, irrespective of staple crimp grading (Table 5), whereas reduction in cell length in poorly crimped fibres only becomes apparent as staple crimp deteriorates (Table 4). Since the changes in cell dimensions do not account for all of the changes in fibre dimensions which accompany staple crimp deterioration, it appears that there must also be a change in cell number.

In Table 8 are listed for the different staple crimp grades the differences in mean fibre weight, fibre volume, and cell volume between abnormally crimped and well-crimped fibres, expressed as percentages of the values for well-crimped fibres. The fibre (or cell) volume has been calculated as being proportional to ld^2, where l = mean fibre (or cell) length and d = mean fibre (or cell) thickness. Also listed in Table 8 are the percentage differences in cell number which are the differences in fibre volume not accounted for by the differences in cell volume.

There are discrepancies between the percentage differences in fibre weight and fibre volume, but these are slight except in the slightly doggy staples. However, the trends in the percentage differences in fibre weight and fibre volume are similar, so that an assessment of the trends in the percentage differences in cell number from a comparison of fibre volume and cell volume seems valid.

Compared with well-crimped fibres, fibres with intermediate or poor crimp increase in volume when staple crimp deteriorates, and attain a maximum difference

when staple crimp is slightly doggy (Table 8). The extent of these changes is somewhat greater for poorly crimped fibres which in normally crimped staples are initially smaller in volume than well-crimped fibres.

By comparison with cell volume in well-crimped fibres, cell volumes in fibres with intermediate and poor crimp exhibit different trends with staple crimp determination. Cells in fibres with intermediate crimp are considerably larger than cells in well-crimped fibres in staples with either normal crimp or secondary waves, but this difference disappears when staple crimp becomes doggy. Cells in poorly crimped fibres, however, are consistently larger than cells in well-crimped fibres irrespective of the state of the staple crimp. In spite of these different trends in cell volume, the trends in cell number are apparently similar for fibres with either intermediate or poor crimp. By comparison with well-crimped fibres, abnormally crimped fibres contain fewer cells when staple crimp is normal or has secondary waves, considerably more cells when staple crimp is slightly doggy, and about the same number or slightly more when staple crimp has severely deteriorated (Table 8).

TABLE 8

PERCENTAGE DIFFERENCES IN MEAN FIBRE WEIGHT, MEAN FIBRE AND CELL VOLUMES, AND CELL NUMBERS BETWEEN ABNORMALLY CRIMPED AND WELL-CRIMPED FIBRES FROM WITHIN STAPLES OF WOOL WITH DIFFERENT GRADES OF STAPLE CRIMP

Staple Crimp Grade	$\left[\frac{\text{Intermediate}-\text{Good}}{\text{Good}}\right]$ (%)				$\left[\frac{\text{Poor}-\text{Good}}{\text{Good}}\right]$ (%)			
	Fibre Weight	Fibre Volume	Cell Volume	Cell No. [Col. (3) − Col. (4)]	Fibre Weight	Fibre Volume	Cell Volume	Cell No. [Col. (7) − Col. (8)]
Normal	+2	+3	+24	−21	−4	−7	+14	−21
Secondary waves	+16	+18	+30	−12	+16	+12	+16	−4
Slightly doggy	+22	+34	+8	+26	+30	+41	+13	+28
Doggy	+13	+10	0	+10	+17	+15	+16	−1

From these changes in cell number which accompany crimp deterioration, it may be inferred that when hyperplasia of follicle outer root sheath tissue first commences there is an altered partitioning of the currently available nutrients between the outer root sheaths and the bulbs of affected follicles. This new partitioning is indicated not only by hyperplasia of the outer root sheath tissue, but also by an increase in cell volume in abnormally crimped fibres, presumably as a result of increased cell growth, and an apparent decrease in cell number (Table 8) from a reduced proliferation of bulb matrix cells.

There is evidence that the early stages of crimp deterioration are not accompanied by an increase in fleece weight, whereas fleece weight increases when dogginess becomes apparent (Chapman, unpublished data). Extra nutrients apparently become available to the follicles at this stage, and this could account for the increases in cell

volume and cell number in poorly crimped fibres within slightly doggy staples (Table 8). In other words, in some follicles the matrix is apparently hyperplastic when staple crimp is slightly doggy and this demand for nutrients is being met in addition to the requirements of the enlarged outer root sheaths.

When wool growth is doggy, matrix cell hyperplasia apparently decreases, although cell size is maintained (Table 8). This could result from nutrients not being available in unlimited supply, so that eventually when a large proportion of follicles have grossly hyperplastic outer root sheaths, a situation again apparently exists in which the nutrient demand of the outer root sheaths has preference.

(*b*) *Thickness–Length Relationships for Fibres Separated on the Basis of Crimp*

Previous workers have found a strong positive correlation between thickness and length of fibres within staples (Duerden and Bosman 1931; Darlow and Craft 1935; Oczan 1956). However, in this study of fibres separated on the basis of crimp definition, the correlation coefficients are much lower (Table 7). An inspection of Tables 1 and 3 reveals that the correlation between thickness and length tends to be negative between fibre crimp grades.

The increases in the regression coefficient of thickness on length of fibres with intermediate and poor crimp in slightly doggy staples (Table 7) produces a pattern in the coefficients for these fibres similar to that in the percentage differences in cell number as staple crimp deteriorates (Table 8). Therefore, the hyperplasia of follicle matrices, which is considered to accompany hyperplasia of the outer root sheaths when staple crimp is slightly doggy, apparently affects the thickness of abnormally crimped fibres to a greater extent than it does the length.

(*c*) *Comparative Rates of the Keratogenous Process in Follicles with Different Outer Root Sheath States*

The keratogenous zone, as depicted by histochemical staining for protein-bound sulphydryl groups, commences where there is marked cellular elongation. A region of increase in sulphydryl groups is followed by a region in which sulphydryl groups are oxidized to disulphide bonds during keratinization. The keratogenous zone, as described here, is equivalent to the zone F of cellular elongation together with the zones G and H of prekeratinization described by Auber (1950), and is similar to the combined D and E zones of keratinization described by Mercer (1961).

The similarity in length of the keratogenous zone of fibres growing in follicles with different outer root sheath states (Table 6) would at first sight suggest that the rate of the keratogenous process is unaffected by the outer root sheath. However, the length growth rate of poorly crimped fibres, grown by follicles with grossly enlarged and cystic outer root sheaths (Chapman, Short, and Hyland 1960), is less than that of well-crimped fibres (Table 1). Therefore, the time for cells to pass through the length of the keratogenous zone would be greater in fibres in cystic follicles than in normal follicles. This could be interpreted as a slower rate of the keratogenous process in cystic follicles. The problem immediately arises as to what is an adequate definition of the rate of the keratogenous process, in view of the

lack of information as to the rate-determining mechanism(s), either biochemical or biophysical, of the process.

The only evidence, as far as the authors are aware, that the rate of the keratogenous process *in fibres* can vary is the extended zone with sulphydryl groups in fibres in the skin of copper-deficient sheep (Marston 1946). The length of this zone is equivalent to about 3 days' growth, indicating that in this syndrome the rate of oxidation of sulphydryl groups to disulphide bonds is reduced. There has been some speculation that the rate of keratinization differs in ortho- and paracortical cells of wool fibres (Kassenbeck 1959; Louw 1960), but no direct evidence has been presented.

The simplest expression for the rate of the keratogenous process is that already considered above, viz. that the rate of the process is inversely proportional to the time for the cortical cells to travel through the zone. Inherent in this is the assumption that the composition of keratin produced is the same in all instances, i.e.

$$\text{Rate of keratogenous process} \propto \frac{1}{\text{Time for cells to pass through the keratogenous zone}}. \quad (1)$$

Since cellular elongation is well advanced just above the lower limit of the zone,

$$\text{Time to pass through the zone} \doteq \frac{\text{Zone length}}{\text{Length growth rate of the fibre}}.$$

When fibres within staples are being compared for sheep such as the Merino in which there is very little shedding and medullation of fibres, fibre length can be substituted for length growth rate, i.e.

$$\text{Time to pass through the zone} \mathrel{\dot{\propto}} \frac{\text{Zone length}}{\text{Fibre length}}. \quad (2)$$

Equation (1) then becomes

$$\text{Rate of the keratogenous process} \mathrel{\dot{\propto}} \frac{\text{Fibre length}}{\text{Zone length}}. \quad (3)$$

The rate of the keratogenous process can also be considered in terms of mechanisms which might be rate-limiting. For example, the rate of reaction within the cells might govern the rate of the keratogenous process. Initially this involves, *inter alia*, the rate at which sulphydryl groups are incorporated and bound in the cells, and subsequently, *inter alia*, the rate of conversion of sulphydryl groups to disulphide bonds. Thus

$$\text{Rate of the keratogenous process} = \text{Rate of reaction in the zone} = \frac{\text{Extent of reaction per unit volume of zone}}{\text{Time for cells to pass through the zone}}. \quad (4)$$

The extent of reaction in the zone would be proportional to, or a function of, the output of keratin from the zone. For a fixed composition of keratin this in turn is proportional to fibre volume when fibres within staples are compared. Using, in addition, equation (2), equation (4) can be expressed as

$$\text{Rate of the keratogenous process} \mathrel{\dot{\propto}} \frac{\text{Fibre volume}}{\text{Zone volume}} \times \frac{\text{Fibre length}}{\text{Zone length}}. \quad (5)$$

The rate of reaction in the cells or the zone might in turn be limited by the rate at which compounds containing sulphydryl groups, *inter alia*, are available for incorporation, and by the rate of removal of by-products, if the reactions in the zone are equilibrium reactions. The rate of transport by the cells of the outer root sheath and through the inner root sheath and cuticles would then become a factor limiting the rate of the keratogenous process, i.e.

$$\text{Rate of the keratogenous process} = \text{Rate of transport through the outer and inner root sheaths and cuticles}$$

$$= \frac{\text{Amount transported}}{\text{Zone surface area} \times \text{Time in the zone}}. \quad (6)$$

The amount transported would be proportional to, or a function of, the output of keratin from the zone, which, as explained above, is proportional to fibre volume when fibres within staples are compared. Using equation (2), equation (6) can be written as

$$\text{Rate of the keratogenous process} \propto \frac{\text{Fibre volume}}{\text{Zone surface area}} \times \frac{\text{Fibre length}}{\text{Zone length}}. \quad (7)$$

While equations (3), (5), and (7) do not provide absolute estimates of the rate of the keratogenous process, they do provide three alternate ways of comparing the rates of the process in normal and cystic follicles. The mean lengths and thicknesses of well-crimped and poorly crimped fibres produced by the sheep for which dimensions of the keratogenous zone were measured are listed in Table 9. The mean fibre thicknesses differ slightly from the mean thicknesses at the upper limit of the keratogenous zone given in Table 6. However, the trends are the same in that straight fibres are coarser than well-crimped fibres, while fibres in cystic follicles are coarser than fibres in normal follicles. Straight fibres are produced by grossly enlarged and cystic follicles (Chapman, Short, and Hyland 1960). Therefore, it seems valid to combine data for crimped and straight fibres with data for the keratogenous zone in normal and cystic follicles; and, using equations (3), (5), and (7), the rates of the keratogenous process in crimped and straight fibres (i.e. normal and cystic follicles) are thereby compared in Table 9. With the exception of one estimate for one sheep, these estimates are less for straight fibres than for crimped fibres. If the keratin in the fibres of both crimp types were the same, it would appear that the keratogenous process is slower in follicles with cystic outer root sheaths.

However, it has been found that staples of doggy wool have a greater proportion of paracortex than well-crimped staples (Ahmad and Lang 1957; Jones 1961), and also that straight fibres contain more paracortex than adjacent well-crimped fibres within staples (Chapman, unpublished data). This factor complicates the interpretation of the estimates of the rate of the keratogenous process (Table 9) since the extent to which the keratogenous process influences the proportions of, and differences between, ortho- and paracortex is not definitely known. The maximum alteration to the estimates of the rate of the process would occur if all the difference between the cortical segments were attributable to the keratogenous process. In these circumstances each ratio of the rates in straight and crimped fibres in Table 9 could be multiplied by the ratio of the percentages of paracortex in straight and crimped fibres. This would make the ratios in Table 9 closer to or exceed unity.

Less adjustment, however, would be required if the keratogenous process were only partly responsible for the differences between the cortical segments.

TABLE 9

MEAN LENGTHS AND THICKNESSES OF WELL-CRIMPED AND POORLY CRIMPED FIBRES AND ESTIMATES OF THE RATE OF THE KERATOGENOUS PROCESS IN FOLLICLES WITH NORMAL AND CYSTIC OUTER ROOT SHEATHS IN THE SKIN OF FINE-WOOL MERINO EWES WITH NORMAL AND DOGGY STAPLE CRIMP

Staple Crimp Grade	Sheep No.	Fibre Crimp Grade	Mean Fibre Length (cm)	Mean Fibre Thickness (μ)	Rate of the Keratogenous Process (arbitrary units)		
					A*	B†	C‡
						$\times 10^4$	$\times 10^5$
Normal	1	Crimped	9·1	21·0	357	12·01	6·56
		Straight	8·1	24·5	342	9·81	6·73
		Straight / Crimped			0·96	0·82	1·03
	2	Crimped	10·5	20·2	409	12·48	7·34
		Straight	9·3	23·7	310	6·85	4·86
		Straight / Crimped			0·76	0·55	0·66
Mean		Straight / Crimped			0·86	0·68	0·84
Doggy	3§	Crimped	3·7	23·2	128	1·267	0·849
		Straight	3·3	24·7	110	0·781	0·607
		Straight / Crimped			0·86	0·62	0·71
	4	Crimped	9·7	23·9	388	18·16	9·89
		Straight	8·6	26·4	360	15·89	9·54
		Straight / Crimped			0·93	0·88	0·96
Mean		Straight / Crimped			0·89	0·75	0·83
Overall mean		Straight / Crimped			0·88	0·72	0·84

* $A = \frac{\text{Fibre length}}{\text{Zone length}}$ (see Section IV).

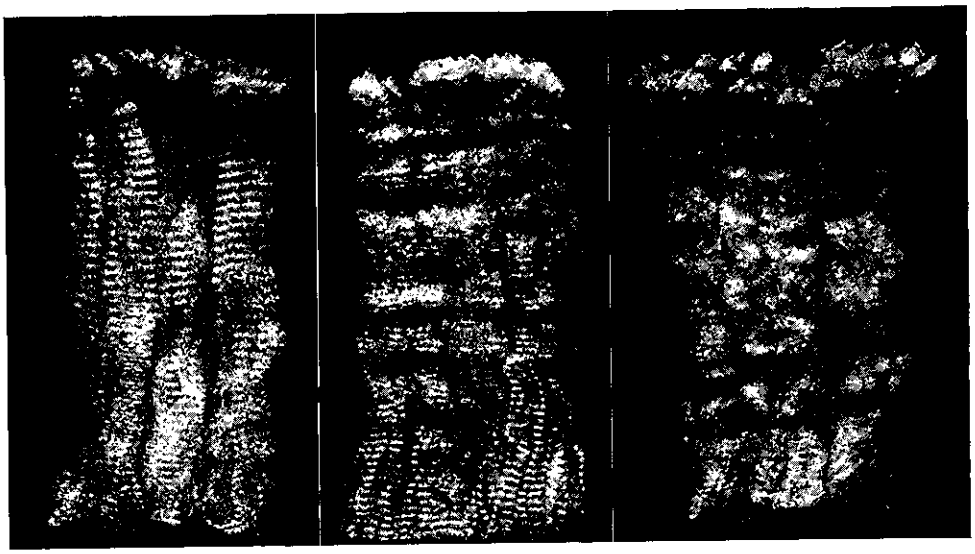
† $B = \frac{\text{Fibre volume}}{\text{Zone volume}} \times \frac{\text{Fibre length}}{\text{Zone length}}$ (see Section IV).

‡ $C = \frac{\text{Fibre volume}}{\text{Zone surface area}} \times \frac{\text{Fibre length}}{\text{Zone length}}$ (see Section IV).

§ Sheep No. 3 had been shorn more recently than Nos. 1, 2, and 4.

Unfortunately there is insufficient information to enable a decision as to which of the equations (3), (5), and (7), gives the more valid comparison of the rates of the keratogenous process in normal and cystic follicles. Nevertheless, it would appear that the keratogenous process might proceed at a slightly slower rate in follicles

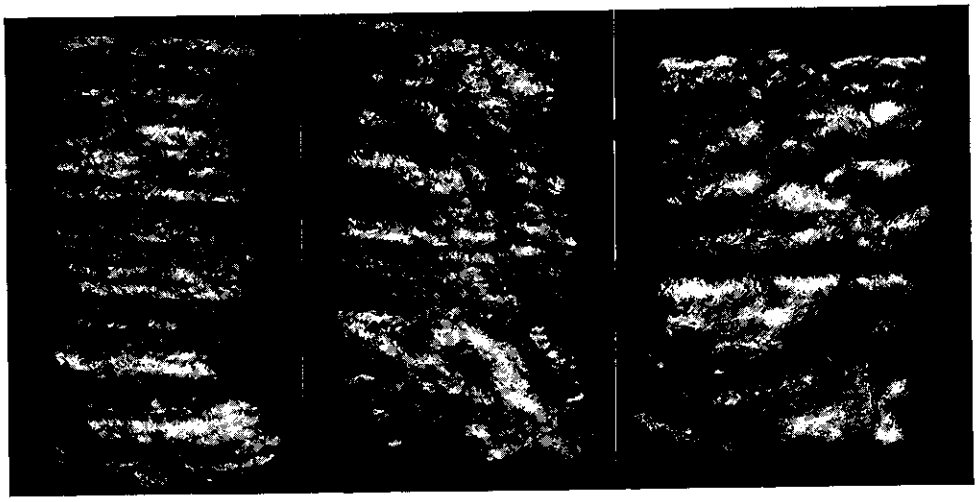
GROWTH OF FIBRES WITH DIFFERENT CRIMP



NORMAL

SLIGHT SECONDARY WAVES

SECONDARY WAVES



SLIGHTLY DOGGY

DOGGY

VERY DOGGY

Successive stages through which staple crimp passes during the change from normal wool to very doggy wool.

with cystic outer root sheaths, depending on the adjustment, at present of unknown magnitude, to allow for the differences in the proportions of paracortex in straight and crimped fibres.

As staple crimp deteriorates, it appears that fibre dimensions are affected by the extent to which hyperplasia of outer root sheaths is accompanied by hyperplasia of follicle bulbs, and possibly by the amount of reduction in cross-sectional area during the keratogenous process. Fibre dimensions, therefore, appear to depend on an interaction between the proliferative and keratogenous processes of fibre formation.

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VI. References

Ahmad, N., and Lang, W. R. (1957).—Ortho–para cortical differentiation in "anomalous" Merino wool. *Aust. J. Biol. Sci.* **10**: 118–24.

Aiken, J. D., and Ryder, M. L. (1962).—A possible method of assessing the extent of "dogginess" in Merino wools from the proportion of individual fibres affected. *Aust. J. Sci.* **24**: 484–5.

American Society for Testing Materials (1956).—"A.S.T.M. Standards in Textile Materials." (A.S.T.M.: Philadelphia.)

Auber, L. (1950).—The anatomy of follicles producing wool-fibres, with special reference to keratinization. *Trans. Roy. Soc. Edin.* **62**: 191–254.

Barrnett, R. J., and Seligman, A. M. (1952).—Histochemical demonstration of protein-bound sulfhydryl groups. *Science* **116**: 323–7.

Barrnett, R. J., and Seligman, A. M. (1954).—Histochemical demonstration of sulfhydryl and disulfide groups in protein. *J. Nat. Cancer Inst.* **14**: 769–803.

British Standards Institution (1953).—Determination of wool fibre fineness. B.S. 2043.

Chapman, R. E., Short, B. F., and Hyland, P. G. (1960).—Abnormal crimping in Merino and Polwarth wools. *Nature* **187**: 960–1.

Darlow, A. E., and Craft, W. A. (1935).—Correlation studies involving the physical characteristics of wool fibres from different breeds of sheep. Bull. Okla. Agric. Exp. Sta. No. 225.

Duerden, J. E., and Bosman, V. (1931).—Staple length and crimped and straight length of Merino wool fibres. *Rep. Vet. Res. S. Afr.* **17**: 771–87.

International Wool Textile Organization (1952).—The determination of wool fibre thickness by a projection microscope. Draft specification. Wool Sci. Rev. No. 8. pp. 57–60.

Jones, G. (1961).—Estimates of cortical differences in normal and "doggy" Merino wools. *Aust. J. Biol. Sci.* **14**: 485–7.

Kassenbeck, P. (1959).—La cinétique du processus de kératinisation et la morphogénèse des fibres kératiniques. *Bull. Inst. Text. Fr.* **83**: 25–40.

Leveau, M. (1956).—Différenciation par coloration des cellules corticales isolées de l'ortho et du paracortex de la laine. *Bull. Inst. Text. Fr.* **60**: 61–4.

Louw, D. F. (1960).—The bilateral structure of crimped and steely wools and the origin of fibre crimp. *Text. Res. J.* **30**: 606–12.

Marston, H. R. (1946).—In "Proceedings of Symposium on Fibrous Proteins". (Soc. Dyers and Colourists: Bradford.)

Mercer, E. H. (1961).—"Keratin and Keratinization." pp. 211, 220. (Pergamon Press: Oxford.)

Oczan, K. (1956).—M.Sc. Thesis, University of New South Wales.