

Merino Evolution, Skin Characteristics and Fleece Quality

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¹The scientific theories and interpretations of data in this report are those of the authors only and are not necessarily associated with CSIRO or its stakeholders.

Contents

1 Acknowledgement	2
2 Abstract	3
3 Introduction	4
4 Methods	5
5 Results	6
5.1 Characteristics of Primitive Sheep and Modern Merinos	6
5.2 Incidence of Primitive Individuals in Industry Flocks	16
5.3 Incidence of Primitive Individuals in Research Station Flocks .	22
5.4 Evidence of Primitive Trends from Genetic Parameter Estimates	32
5.5 Evidence from Developmental Studies of the Importance of Size of Primary Follicles in Evolution of Merinos	36
5.6 Evidence from Historical Accounts of Incidence od Primitive In- dividuals in Spanish Merino Flocks	41
5.7 Direct Evidence of Increased Incidence of Primitive Characteris- tics in a Feral Merino Population	44
6 Conclusion	45

1 Acknowledgement

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2 Abstract

The Australian Merino population contains animals which manifest traits characteristic of primitive domestic sheep. Such animals occur in selection experiments, in random-bred control lines, in industry flocks of all strains, and in all environments. These observations are taken as evidence confirming the supposed evolution of the Merino direct from primitive sheep (Ryder [44]). Primary fibre diameter is shown to be a critical parameter in assessing degree of regression toward primitive type of fleece. Developmental considerations show that other factors (such as S/P ratio and follicle number), which differ between advanced and primitive sheep, are a consequence of the size of primary follicles. Primary fibre diameter is shown to be closely correlated with fitness, and it is suggested that natural selection might account for the observed widespread occurrence of primitive individuals. Regression is shown to be associated with deterioration of fleece quality, particularly with poor handle and fabric prickle. It is suggested that selection for reduced ratio of primary fibre diameter to secondary fibre diameter may change a Merino population in the opposite direction to regression, and may therefore lead to a more advanced Merino with improved wool quality. Full implications for fleece quality in breeding programs require further investigation.

3 Introduction

The Merino breed is considered to have evolved directly from either wild sheep or primitive two-coated domestic sheep (Fraser [17]; Ryder [44]; Ryder [46]); "primitive" here means domesticated but not developed for any narrow special purpose by artificial selection. Evidence for this assertion is indirect; for example breed comparisons of follicle characteristics (Carter [10]; Carter [11]) show that relative number of secondary to primary follicles (S/P ratio) is an order of magnitude greater in the Merino than in any other breed, so there is no obvious *Merino ancestor* among existing breeds. The Australian Merino population is divided into those strains in which some introduction of English Longwool genes is acknowledged and those for which pure Spanish Merino ancestry is claimed (Hogan, 1979). There is also a possibility that Cape or Bengal sheep introduced to Australia during early settlement may have contributed genetic material to the early Australian Merino (Turner [51]; Turner [52]; Garran and White [21]; Massy [30]). No-one seems to have considered the possibility of uncovering direct evidence of Australian Merino ancestry, by searching modern Australian Merino flocks for individual animals that resemble the putative primitive ancestor. This study shows that such individuals do occur at a high frequency in various industry flocks, and that their occurrence may be increased by certain breeding practices. We outline a method for identifying such animals based on a combination of follicle and fibre characteristics. There are interesting implications in the area of breeding methods for fleece quality control, as well as in direct confirmation of Ryder's evolutionary theories.

4 Methods

The paper makes use of a symbolic notation for measured characteristics. Symbols, their meaning, and unit of measurement, are given in Table 1.

Table 1: Symbols Used for Observed Characteristics

Symbol	Definition	Units
D _p	Average diameter if primary fibres	micron
D _s	Average diameter of secondary fibres	micron
D _p /D _s	Ratio of diameter of primary fibres to diameter of secondary fibres	-
N _p	Number of primary fibres per unit area of skin	no per mm ²
N _s	Number of secondary fibres per unit area of skin	no per mm ²
S/P	Ratio of number of secondary fibres to number of primary fibres	-
CWW	Clean wool weight per head (12 months growth)	kg
BW	Body weight at hoggett shearing	kg
dNLW	Number of lambs weaned by an animal's dam, at the current lambing	count

Techniques for skin biopsy sampling, tissue processing, and microscopic evaluation are described by Maddocks and Jackson [27]. The present results have been made possible by recent advances in automated evaluation using image analysis, particularly for measurement of diameter of primary and secondary fibres (Jackson and Maddocks [25]).

5 Results

5.1 Characteristics of Primitive Sheep and Modern Merinos

It is essential to define those characteristics of skin and fleece that indicate degrees of resemblance to the primitive type before searching for traces of primitive characteristics in Australian Merino flocks. In this regard we rely heavily on work of Ryder ([43], [44], [45], [46]), which in turn relies on quantitative histological studies of Carter [6]. Table 2 lists characteristics which may be of assistance in ranking sheep on an evolutionary scale ranging from wild sheep to the modern Merino.

Table 2: Skin and Fleece Characteristics which may Reflect Stages in Merino Evolution

Line of evolution	Approx. time scale	Congenetic sheep	Dp (microns)	Ds (microns)	Medullation	S/P Ratio	Follicle Arrangement	Fleece structure
Wild Sheep	9000 B.C.	Mouflon, Barbary	150	15	latticed	3-5	S between P, P in straight lines	Two coated, long medullated guard hairs and fine underwool
Primitive Domestic Sheep	3000-1000 B.C.	Soay, Asiatic	42	17	non-latticed, continuous	4-5	S in two groups, point of wedge between P	III defined staples with curly tips and fine fibres
Ancient Fine to Medium Wool	500 B.C.-	Dead sea scroll material, ancient textiles	38	21	interrupted	5-7	S wedges merged, closer and in staples?	Heterotype hairs, fine/medium fibres
True Fine Wool	1500-1850 A.D.	Spanish Merino	19-24	17-21	nil?	20	So further from P, Sd between So and P	Well defined wool staples, blocky tips, uniformly fine/medium diameter and uniform length
Australian Merino	C.1830-1988 A.D.							
Fine			16-22	16-21	-	16-24	-	-
Medium			21-29	16-24	-	19-27	-	-
Strong			29-32	22-25	-	15-18	-	-
Other ?								

We illustrate the evolutionary series presented in Table 2 with samples from its extreme points. Figure 1 shows a transverse skin section from a Barbary sheep - a primitive north African breed ([29]) considered by the authors to be representative of original wild sheep before domestication. Note the coarse medullated primary fibres, the small number of very fine secondary fibres, and the position of groups of secondary follicles on a line between the primaries. Figure 2 shows a fibre diameter histogram from the same Barbary specimen. Figure 3 shows a transverse skin section of a modern medium Australian Merino with no evidence of primitive characteristics. Note the large number of secondary fibres, uniform fibre diameter, lack of medullation, and arrangement of secondaries to one side of rows of primaries. Figure 4 shows a fibre diameter histogram from the same medium Merino specimen.

The most easily quantified characteristics in Table 2 are average diameter of primary and secondary fibres (D_p and D_s) and S/P ratio. We illustrate quantitative variation along the evolutionary series in Figures 5 and 6. The position of British Longwool breeds in Figures 5 and 6 is of interest in relation to their suspected role in evolution of some Australian Merino strains. The Merinos are as close to the primitive Soay as they are to the Longwools in Figures 5 and 6.

Figure 7 illustrates changes in follicle group arrangement and fibre medullation through four stages of Merino evolution described in Table 2. These changes are more difficult to quantify but are of value in visual examination of skin sections. The changes in follicle arrangement are obviously a consequence of increased occurrence of compound secondary follicles (Hardy and Lyne [22]) as one moves down the evolutionary series. One cannot see compound follicles in a single transverse skin section, but follicle arrangement reflects their presence.

Considerable caution needs to be applied in interpreting D_p and D_s data from skin biopsy material, because fibres are sectioned at a single point in their growth cycle. If, for example, primary fibres are of a seasonal shedding type, then the point at which they are cross-sectioned could be:-

- a brush-end (unmedullated and coarse)
- a regrowth tip (unmedullated and fine)
- an actively growing fibre (medullated and coarse)

so that D_p and medullation data would depend on the season in which the sheep was sampled. If, on the other hand, primary fibres were shedding asynchronously, then a specimen taken at a given season might exhibit all three above possibilities simultaneously, resulting in a very wide distribution of primary fibre diameters, ranging from fine regrowth tips of less than 15 microns to heavily medullated fibres of greater than 50 microns. Since skin characteristics are subject to environmental effects (Short [49]), it is not sound practice to sample sheep from one flock at one time and to draw conclusions regarding the genetic merit of that flock, absolutely or relative to other flocks. However it is valid to compare animals within a flock grazed under similar conditions,

or to compare flocks in a common environment. These requirements cannot be strictly met across vast expanses of time and space, so some of the material presented in this report depends on an unverifiable assumption that the sheep sampled grazed under comparable conditions. Where possible we have taken steps to ensure this, by sampling ewes rather than rams, by taking a random sample of sheep from a mob, by avoiding drought or hand-fed conditions and by correcting for environmental differences where these could be estimated.

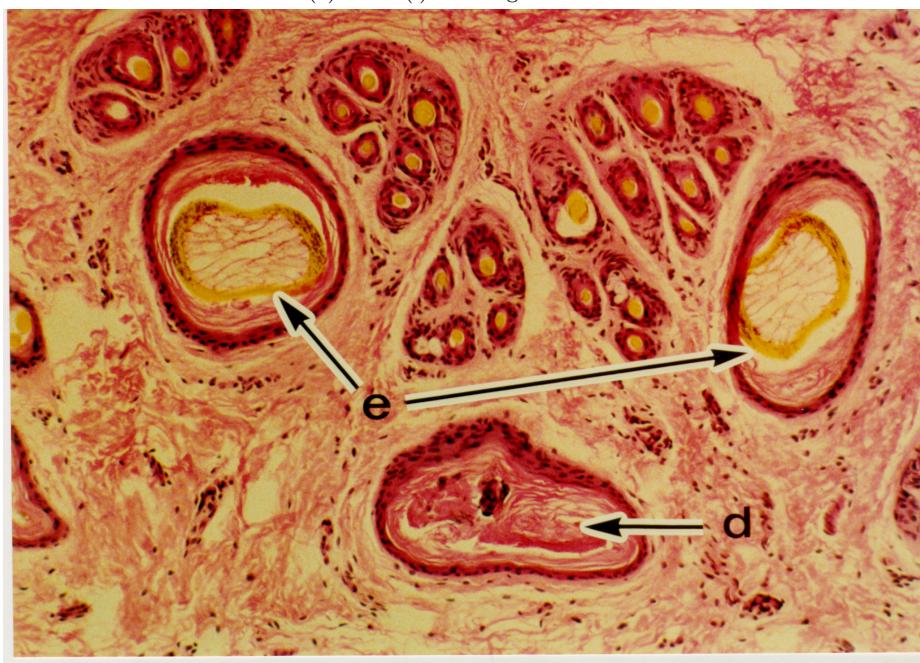
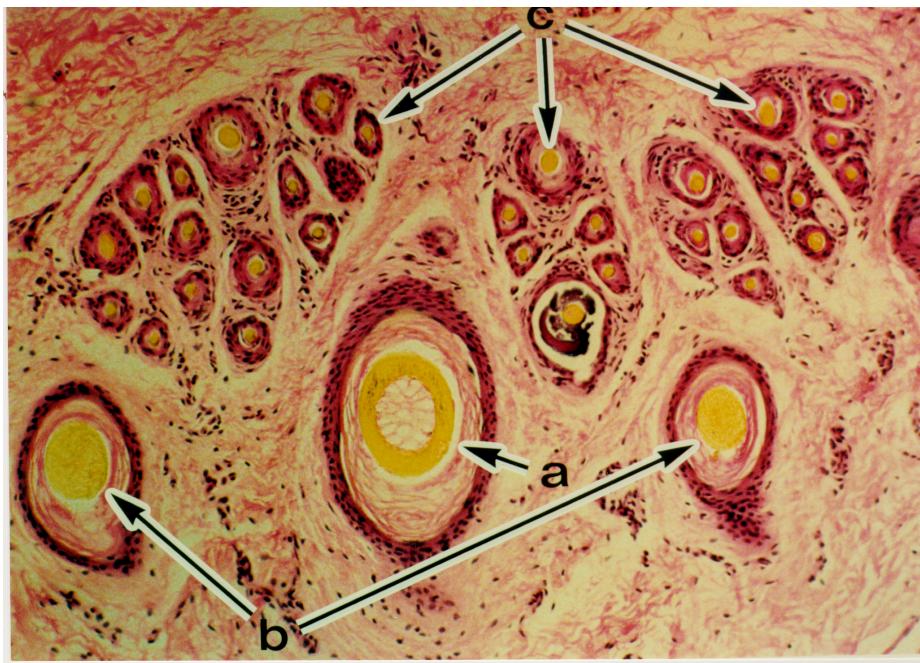


Figure 1: Transverse sections of skin from a primitive Barbary sheep showing (a) medullated central primary fibre ($150\mu m$), (b) large primary lateral fibres ($80\mu m$), (c) groups of fine secondary fibres ($15\mu m$), (d) primary central follicle which has shed its fibre showing collapsed follicle wall, (e) medullated primary lateral fibres ($100\mu m$). The follicle groups have an average of nine secondaries per primary and the 'wedge shaped' arrangement of secondaries is a consistent feature.

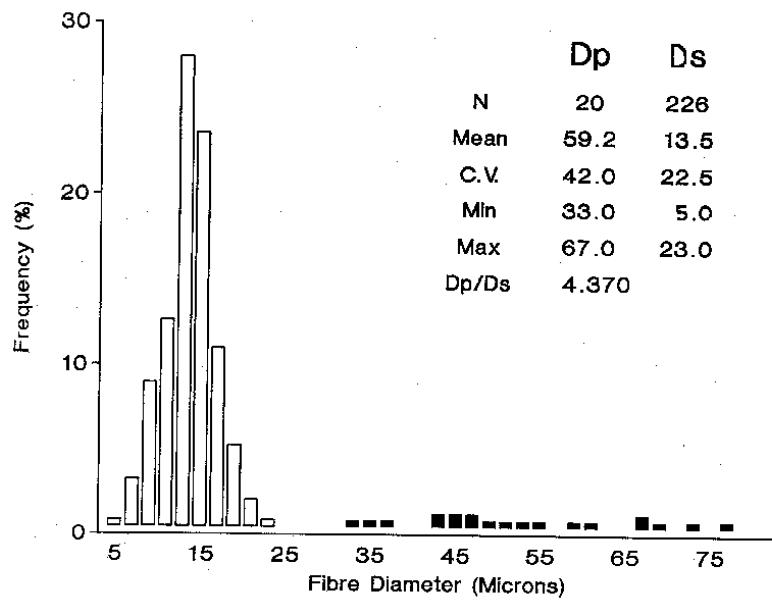


Figure 2: Fibre diameter histogram for the Barbary specimen of Figure 1. Primary fibre frequencies are shown as shaded classes.



Figure 3: Transverse section of skin from a modern medium Australian Merino with no evidence of primitive characteristics, showing (a) primary fibres ($20 \mu m$) (b) secondary fibres ($20 \mu m$). Plate (i) x magnification.

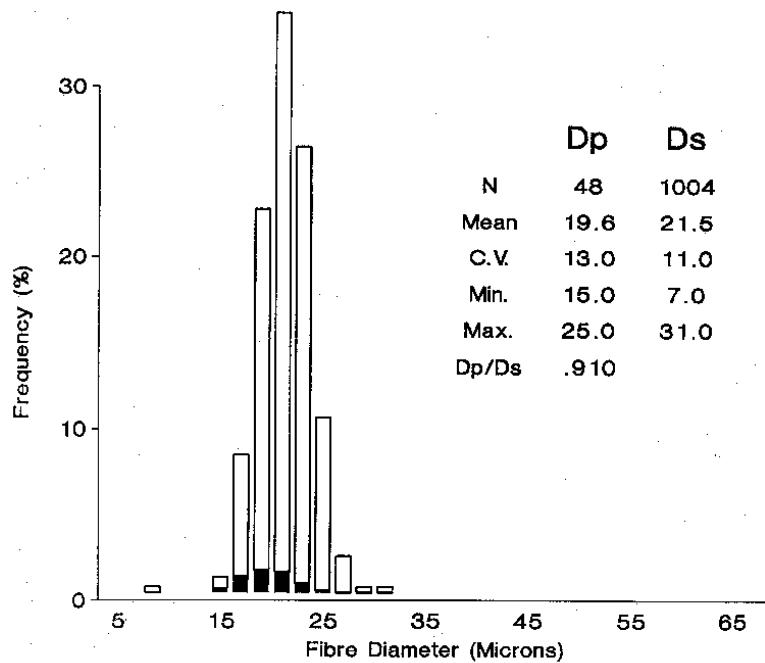


Figure 4: Fibre diameter histogram for the Merino specimen of Figure 3. Primary fibre frequencies are shown as shaded classes.

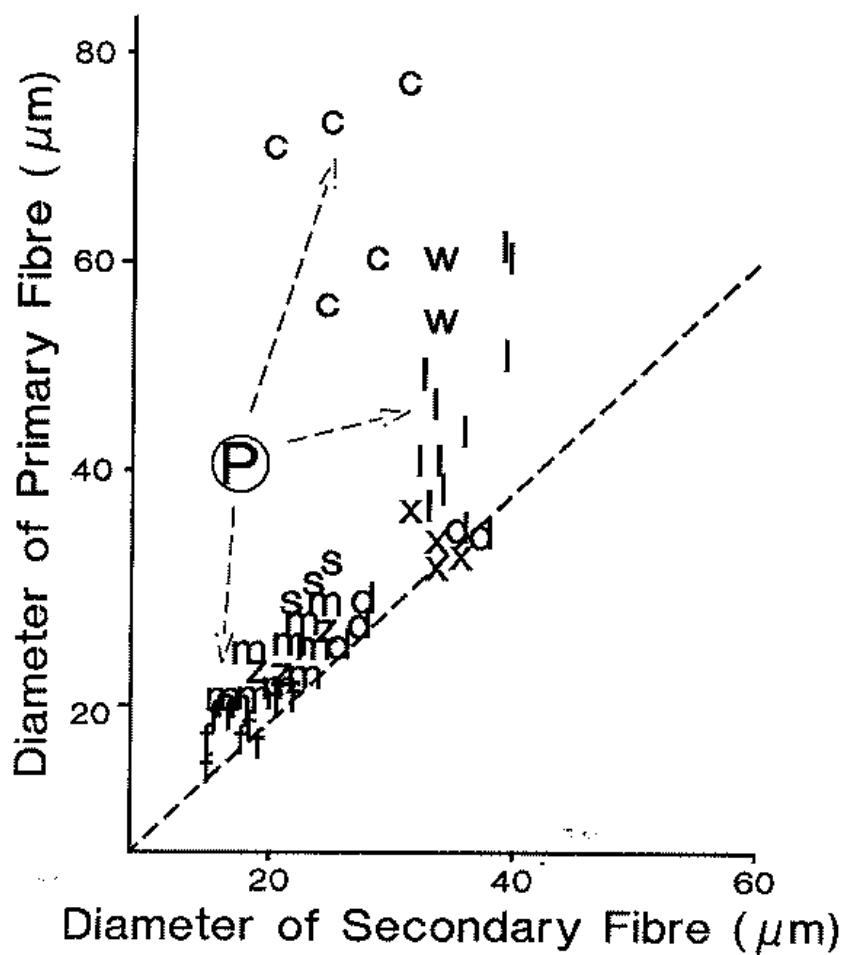


Figure 5: Relationship of primary fibre diameter (D_p) to secondary fibre diameter (D_s) across a range of breeds. Data from Carter (1968) and CSIRO (unpublished). Suggested lines of evolution of the major breeds shown \dashrightarrow . D_p/D_s ratio = 1 shown $\cdots\cdots\cdots$. Letter codes denote breed; f, Fine Merino; m, Medium Merino; s, Strong Merino; z, Polwarth; x, Corriedale; l, Longwool; d, Downwool; c, Carpet Wool; P, Primitive; w, Wiltshire Horn.

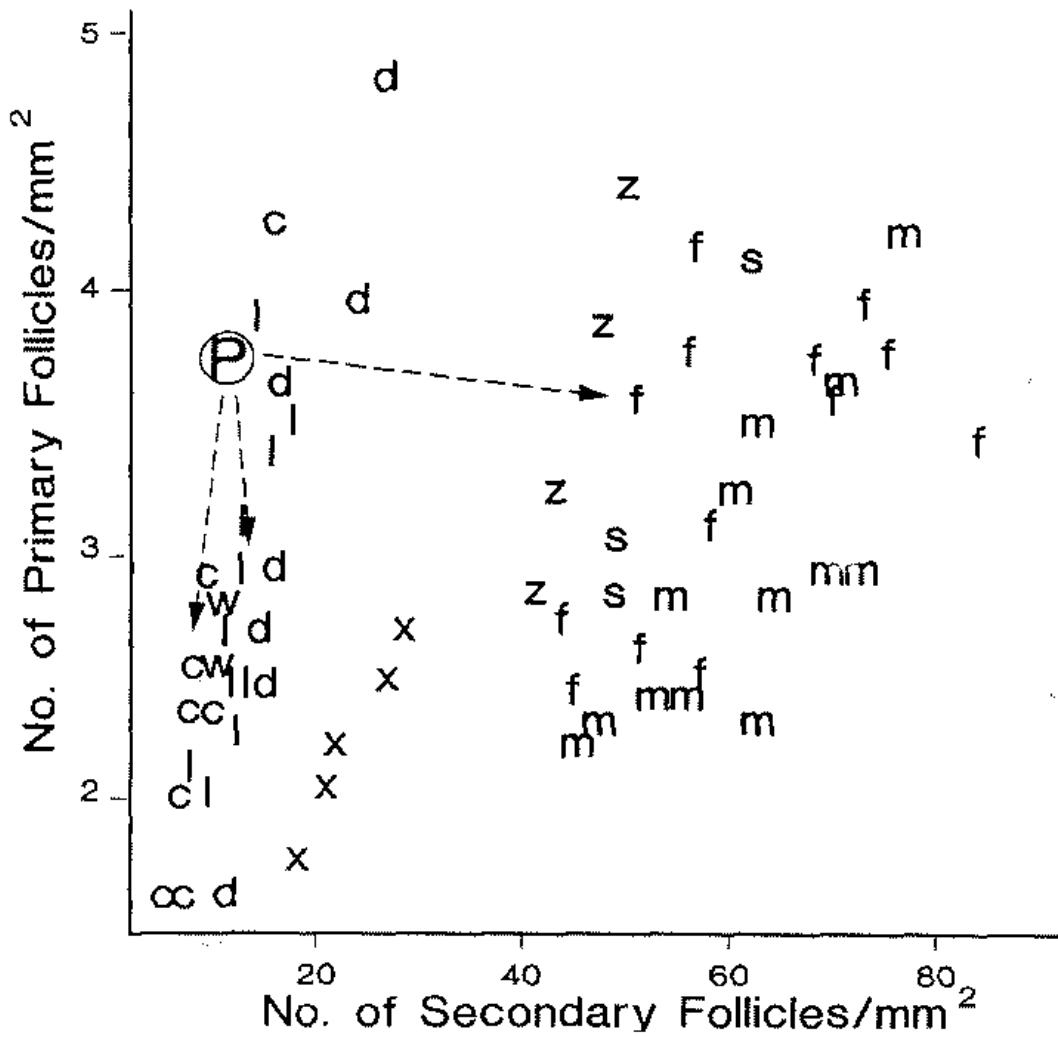
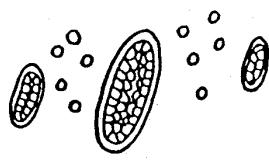


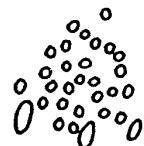
Figure 6: Relationship of primary fibre density (N_p) to secondary fibre density (N_s) across a range of breeds. Data from Carter (1968) and CSIRO unpublished. Suggested lines of evolution of major breeds shown \dashrightarrow . Letter codes for breeds as in Figure 5.



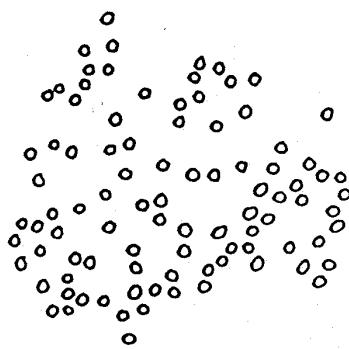
(a)



(b)



(c)



(d)

Figure 7: Tracings of fibre outlines showing changes in follicle group arrangement, fibre diameter and medullation through the four stages of Merino evolution described in Table 1. (a) wild sheep, (b) primitive domestic sheep, (c) ancient fine/medium wool, (d) true fine wool. Magnification x

5.2 Incidence of Primitive Individuals in Industry Flocks

In the 1940's and early 1950's CSIRO sampled hogget ewes from a number of leading Australian Merino studs. Results have been summarized by Carter and Clarke [10] and Carter [8]. We have re-examined these data and are representing it, in Table 3, to highlight individual variation in Dp/Ds ratio.

Table 3: Variation in Diameter of Primary and Secondary Fibres in Sheep from a Number of Leading Australian Merino Studs Sampled by CSIRO over the Period 1948-52. Data from Carter (unpublished and 1968).

Strain	Flock	Mean	Dp/Ds	> 1.2	> 1.5	> 1.8	Number Sampled
		Dp	Ds	Dp/Ds	Dp/Ds	Dp/Ds	30
Early Fine Merino	1	19.2 ± .34	17.2 ± .19	1.11 ± .021	26.7	0.0	0.0
Tas. Fine Merino	2	18.4 ± .49	17.8 ± .30	1.03 ± .023	9.5	0.0	0.0
	4	19.2 ± .47	16.2 ± .21	1.15 ± .022	36.4	0.0	0.0
	6	19.3 ± .40	16.7 ± .28	1.15 ± .028	33.3	0.0	0.0
	7	19.9 ± .56	18.8 ± .42	1.02 ± .031	8.7	0.0	0.0
	8	20.6 ± .83	18.1 ± .60	1.15 ± .05	37.5	6.3	0.0
Vic. Fine Merino	10	20.2 ± .55	18.0 ± .37	1.12 ± .025	28.6	0.0	0.0
	11	18.3 ± .52	15.9 ± .33	1.16 ± .037	27.3	0.0	0.0
	12	15.8 ± .59	15.7 ± .45	1.01 ± .039	7.7	0.0	0.0
	13	22.7 ± .89	19.9 ± .45	1.15 ± .041	38.1	4.8	0.0
NSW Fine Merino	14	19.0 ± .54	17.1 ± .68	1.13 ± .032	19.0	0.0	0.0
Non-Pepin Medium Merino	15	23.0 ± .50	22.6 ± .42	1.02 ± .026	6.0	0.0	0.0
	16	22.3 ± .72	21.0 ± .43	1.07 ± .036	22.7	0.0	0.0
	17	26.6 ± .79	22.3 ± .45	1.20 ± .038	38.1	9.5	0.0
Peppin Medium Merino	18	29.8 ± .96	23.7 ± .28	1.26 ± .038	56.7	20.0	0.0
	19	25.1 ± .97	17.8 ± .53	1.43 ± .53	80.0	25.0	15.0
	20	28.0 ± .80	22.8 ± .54	1.23 ± .025	60.0	0.0	0.0
	21	25.7 ± .80	23.2 ± .51	1.11 ± .036	30.0	0.0	0.0
	22	21.6 ± .63	17.1 ± .36	1.27 ± .050	42.9	19.0	4.8
	23	25.5 ± 1.14	19.9 ± .38	1.25 ± .052	66.7	13.3	0.0
	24	21.1 ± 1.21	16.8 ± .41	1.27 ± .096	54.5	9.1	9.9
	25	22.5 ± .66	19.2 ± .43	1.18 ± .031	38.1	0.0	0.0
Strong Merino	26	29.7 ± 1.25	22.5 ± .42	1.33 ± .061	71.4	14.3	9.5
	27	30.8 ± .78	23.7 ± .38	1.30 ± .035	76.2	19.0	0.0
	28	32.6 ± 1.11	24.7 ± .44	1.33 ± .046	66.7	14.3	4.8

If one arbitrarily regards sheep with $Dp/Ds > 1.5$ as showing primitive characteristics then Table 3 shows that they occur in all strains of Merino, and in all environments, and that individual flocks vary in the frequency of occurrence. Gallagher and Yeates [19] studied the incidence of coarse fibres in two Merino flocks of Tasmanian and Peppin origin. They found percentages of fibres exceeding 30 microns of 5.4, 4.7 and 11.5 at the neck, mid-side and breech regions in flock 1, and 3.6, 3.9 and 10.0 respectively in flock 2. Corresponding percentages of medullated fibres were 0.17, 0.15 and 0.28 flock 1, and 0.11, 0.11 and 0.20 discussion that "one Merino ewe in flock 1 exhibited long coarse largely non-medullated fibres projecting beyond the staple tip, a fleece characteristic which Marston [28] described as being reminiscent of the coarse outer and fine inner coat of the primitive sheep".

In a later paper Gallagher [18] surveyed 1014 bales of Merino wool, finding a 1.1% incidence of medullation (up to 3.3% in individual lots) and noting that this constituted an increase over estimates of previous workers. The average incidence of fibres over 30 microns in this survey was 2.4%. Unfortunately figures for individual lots were not published. We have recently sampled sheep from a small number of today's leading Merino studs. Individual variation in Dp/Ds ratio is shown in Table 4.

Table 4: Variation in Diameter of Primary and Secondary Fibres in a Random Sample of Ewes from a Number of Leading Merino Studs Sampled by CSIRO in 1987-88, and from two Studs and two Commercial Flocks Sampled by CSIRO in 1977.

Strain	Flock	Mean	Dp	Ds	Dp/Ds	Percent with Dp/Ds > 1.2	> 1.5	> 1.8	Number Sampled
Vic. Fine Merino	1	20.7 ± .31	19.1 ± .24	1.08 ± .014	17.3	0.0	0.0	0.0	81
NSW Fine Merino	2	21.3 ± .45	20.2 ± .34	1.06 ± .015	10.9	0.0	0.0	0.0	46
	3	20.3 ± .43	20.1 ± .27	1.02 ± .023	6.25	0.0	0.0	0.0	32
Non-Peppin Medium Merino	4	21.1 ± .27	19.0 ± .18	1.07 ± .014	18.7	2.7	0.0	0.0	150
Peppin Medium Merino	5	27.6 ± .41	24.6 ± .17	1.13 ± .017	26.0	5.0	0.0	0.0	100
	6	29.3 ± .46	25.0 ± .28	1.18 ± .019	37.0	3.7	1.2	1.2	81
	7	24.0 ± .35	22.5 ± .20	1.07 ± .015	18.3	0.0	0.0	0.0	60
	8	25.6 ± .47	22.6 ± .21	1.12 ± .021	19.7	7.6	0.0	0.0	66
	9	24.4 ± .35	20.7 ± .21	1.18 ± .016	32.9	1.3	0.0	0.0	76
Strong Merino	10	30.1 ± .39	23.8 ± .25	1.32 ± .022	68.0	16.0	4.0	4.0	50

Animals showing a primitive Dp/Ds ratio continue to occur in our Merino population, and the extent of the problem continues to vary between studs. There were no individuals with $Dp/Ds > 1.5$ in the fine-wool flocks sampled this time. Figures 8 and 9 show fibre diameter histogram and skin section of a primitive individual from one of today's leading Australian Merino studs. It remains to be established whether there has been a significant change since Carter's survey of the 1940's, but the phenomenon is certainly still visible. It would be of considerable interest to locate skin and fleece specimens dating from before 1940, to obtain some indication as to whether recurrence of the primitive type has always been a feature of the Merino.

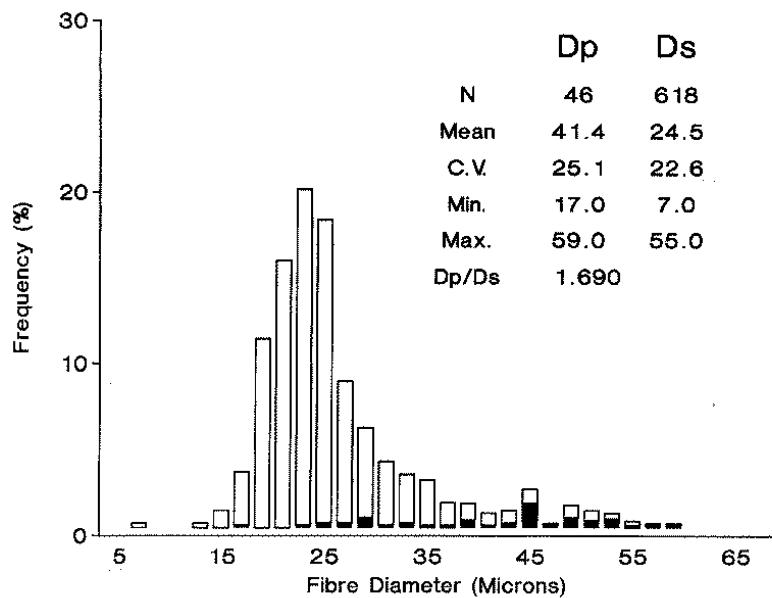
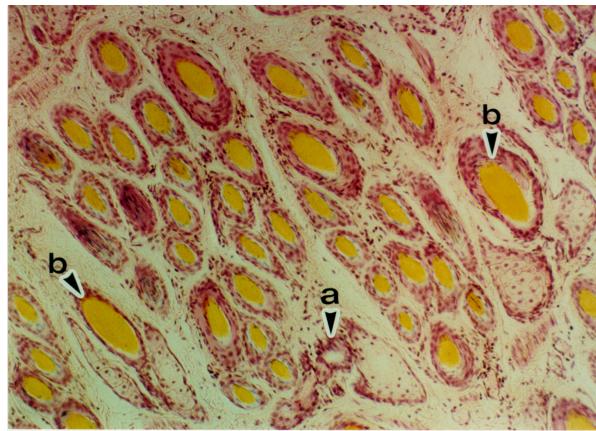
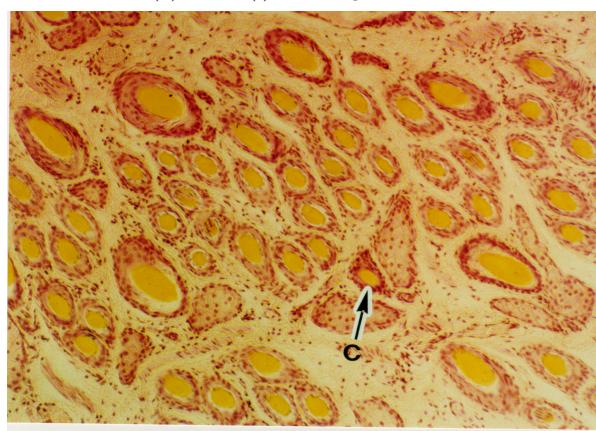


Figure 8: Fibre diameter histogram of a hogget ewe from a leading Australian Merino stud. Note the high frequency of large primary and secondary fibres and the simultaneous presence of fine primary fibres. The fine primaries are probably regrowth tips indicating shedding.

Because industry flocks do not have experimental controls, one cannot draw conclusions from the above observations as to why sheep showing primitive characteristics occur. One cannot even say whether the cause is genetic or environmental. We turn to research flocks for an indication of possible causes.



(a) Plate (i) x... magnification.



(b) Plate (ii) x... magnification.



(c) Plate (iii) x... magnification.

Figure 9: Transverse section of skin from the Australian Merino specimen of Figure 8. Note (a) central primary follicle from which fibre has shed, (b) large lateral primary fibres ($40 \mu\text{m}$), (c) central primary fibre with fine fibre regrowth tip ($78 \mu\text{m}$), (d) wedge shaped arrangement of secondary follicles extending between the row of primary follicles, ²¹ similar to the ancient fine/medium wool in Figure 7.

5.3 Incidence of Primitive Individuals in Research Station Flocks

Occurrence of animals showing primitive characteristics was first noted in CSIRO selection experiment no. 32. This experiment was designed to mimic visual classing methods which place emphasis on skin thickness or "productive skins" (Coy [14]. This experiment consisted of three lines selected for: increased follicle depth (Nay 1973) (line 1) increased number of follicles per head (line 2), and simultaneous increase in follicle depth and follicle number per head (line 3) over the period 1978-85. The animals grazed with an unselected control line. Foundation animals for experiment 32 were CSIRO experimental sheep upgraded by mating with rams from a Victorian fine Merino stud. Control line animals were of medium Peppin origin, thus providing an environmental trend control, assuming that both strains would react equally to environmental change. Observations of distribution of diameter of primary and secondary fibres were only available on the 1982-85 drop animals; that is for the years in which automated image analysis was employed. Table 5 summarizes performance of 1982-85 drop animals.

Table 5: Variation in Diameter of Primary and Secondary Fibres of 1982-85 Drop Animals in CSIRO Experiment No. 32.
 (Means obtained as drop x line effects in a linear model adjusting for sex and age of dam)

Line	Drop	Mean		Percent with Dp/Ds			Number Sampled
		Dp	Ds	Dp/Ds	> 1.2	> 1.5	
High follicle depth	1982	24.4 ± .74	21.1 ± .42	1.16 ± .037	38.5	4.6	0.0
	1983	21.9 ± 1.08	20.1 ± .62	1.09 ± .054	10.9	2.2	0.0
	1984	25.7 ± .84	23.3 ± .48	1.10 ± .041	19.4	0.0	0.0
	1985	25.7 ± .72	20.5 ± .41	1.26 ± .036	61.5	11.5	0.0
High follicle number	1982	21.9 ± .72	20.0 ± .41	1.09 ± .036	26.7	3.3	0.0
	1983	20.6 ± .90	20.1 ± .51	1.03 ± .044	14.3	2.9	0.0
	1984	22.4 ± 1.12	21.5 ± .64	1.05 ± .055	0.0	0.0	0.0
	1985	22.0 ± .79	19.8 ± .45	1.12 ± .039	19.1	2.9	0.0
High depth and number	1982	25.0 ± .77	20.5 ± .44	1.23 ± .039	53.7	14.6	1.2
	1983	26.1 ± .65	19.5 ± .52	1.16 ± .045	30.8	0.0	0.0
	1984	24.6 ± .86	20.8 ± .49	1.18 ± .043	37.5	3.6	0.0
	1985	25.2 ± .72	20.0 ± .41	1.27 ± .036	62.5	11.4	2.3
Unselected control	1982						82
	1983						39
	1984						56
	1985						88

One would not expect to be able to detect a trend over these four years; one can only compare lines at this point in time. The result of greatest relevance here is the higher frequency of animals with high Dp/Ds ratios in lines 1 and 3, particularly in the 1985 drop. In a closely controlled experiment of this nature, one can conclude that the higher frequency of primitive animals was caused by selection for increased follicle depth. While the change in line average Dp/Ds is not large, some very extreme individuals (with Dp halfway between a fine Merino and a primitive Soay) were produced. One of these is illustrated in Figures 10 and 11.

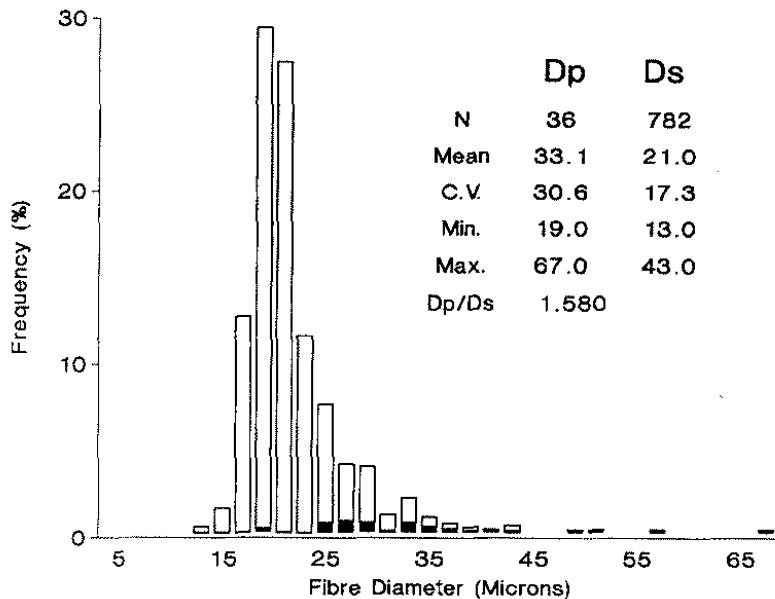


Figure 10: Fibre diameter histogram of a 1985 drop hogget ewe from the high follicle depth selection line of CSIRO experiment No. 32. In this case most of the large fibres are primaries.

We have one further piece of evidence from experiment 32. If primary fibres are coarser in the adult fleece, one would expect a correlated increase in *hairiness* of the lamb birthcoat (Schinckel [47]. Figure 12 shows that there has been an increase in birthcoat score in lines 1 and 3 of experiment 32. These data are particularly valuable as they span the whole period of selection, and show that the changes referred to have only become obvious in the last few drops.

If a mere 8 years of selection could expose this amount of variation in primitive characteristics, one is led to ask whether other selection regimes could do better (or worse depending on one's point of view)? This led us to ask whether primitive sheep could be found in industry flocks. Data already presented show that primitive sheep are not peculiar to research flocks - they occur throughout



Figure 11: Transverse section of skin from the specimen of Figure 10. Note (a) large medullated central primary fibre and (b) large non-medullated lateral primary fibre. Plate (i) x... magnification.

the Australian Merino industry in all strains. We looked also at CSIRO selection experiment no. 10 selection for high clean wool weight with no culling to prevent increase in average fibre diameter), over the period 1958-88. Table 6 summarizes performance of 1979 and 1982 drop animals.

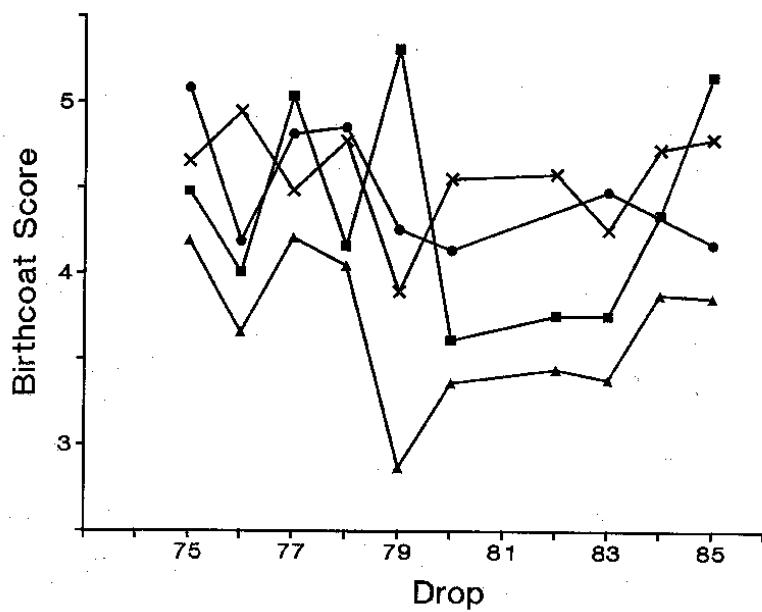


Figure 12: Average birthcoat scores of successive drops in CSIRO experiment 32. ■ - - - ■ line 1; ▲ - - - ▲ line 2; X - - - X line 3; ● - - - ● unselected control line.

Table 6: Variation in Diameter of Primary and Secondary Fibres in Sheep from CSIRO Experiments No. 10 (high clean wool weight) and No. 1 (high clean wool weight with average diameter and wrinkle held constant)

Drop	Flock	D _p	Mean D _s	D _p /D _s	Percent with D _p /D _s > 1.2	Percent with D _p /D _s > 1.5	Number Sampled
1979	expt 1	28.4 ± .82	23.1 ± .30	1.23 ± .037	60.0	0.0	10
	expt 10	35.5 ± 1.15	15.1 ± .47	1.41 ± .076	40.0	20.0	10
	control	26.5 ± .96	21.2 ± .44	1.25 ± .045	50.0	10.0	10
1982	expt 10	31.7 ± .45	26.6 ± .26	1.21 ± .020	39.8	5.7	88
	control	-	-	-	-	-	-

Figures 13 and 14 show one extreme individual. These animals are different from experiment 32. In experiment 10 the entire fibre diameter distribution has become coarse, not just the primary fibres. The animals in experiment 10 resemble British Longwools more than primitive two-coated sheep. This may be a reflection of their different origin; foundation animals in experiment 10 were Medium Peppin Merino, or of the different selection regime.

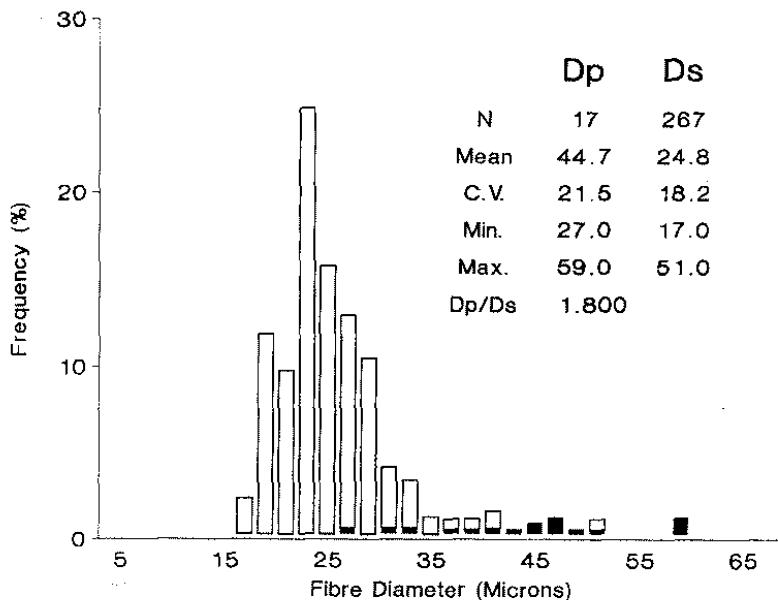


Figure 13: Fibre diameter histogram of a 198? drop hogget ewe from CSIRO experiment No. 10. Note the high frequency of large primary and secondary fibres.

We would also like to have looked at CSIRO selection experiment no. 1 -selected for high clean wool weight, with culling to prevent increase in average fibre diameter or wrinkle. Unfortunately, this experiment was abandoned in 1977 and there are few surviving skin specimens. There were some primitive characteristics shown in 6 of 10 surviving specimens (Table 6). An individual with $D_p/D_s = 1.4$ is illustrated in Figure 15.

Barlow [2] published mean values of D_p and D_s for three drops of ewes in high and low clean fleece weight and random flocks at NSWDA, Trangie, NSW. These data are summarised in Table 7.

All three flocks exhibit higher D_p/D_s ratios than the average industry medium Peppin flock in Tables 3 or 4, and similar D_p/D_s ratios to the CSIRO research flocks in Table 6. There is also an obvious effect of selection - the highest D_p/D_s ratio in each drop occurred in the Fleece Plus group. From the above observations on research flocks we can conclude that the occurrence of sheep showing

Table 7: Variation in Diameter of Primary and Secondary Fibres in three Drops of Ewes from Trangie High and Low Fleece Weight and Random Flocks.

Flock	Drop	Mean		
		Dp	Ds	Dp/Ds
Fleece plus	1962	29.6	19.4	1.53
	1963	29.6	20.6	1.44
	1964	28.1	20.9	1.34
Random	1962	27.1	18.6	1.46
	1963	28.8	21.2	1.36
	1964	26.3	20.5	1.28
Fleece minus	1962	24.7	19.7	1.25
	1963	27.2	22.2	1.23
	1964	22.8	20.4	1.12

primitive characteristics has a genetic basis. It is not clear which types of artificial selection criteria will lead to increased frequency of primitive characteristics, and it is not clear whether natural selection or non-additive gene action are involved. It is also obvious, from Table 5, that characteristics such as Dp/Ds are influenced by environment as well as inheritance, so that one has to be wary of drawing conclusions from uncontrolled observations on a single flock. There does seem to be a general trend for research flocks, particularly random-bred flocks, to display more extreme primitive characteristics than industry flocks of the same strain. We turn to more precise studies of quantitative variation for a prediction of what is likely to occur under particular breeding objectives.



(a) Plate (i) x... magnification.



(b) Plate (ii) x... magnification.

Figure 14: Transverse section of skin from the specimen of Figure 13. Plate (i) shows a trio group with large primary and secondary fibres. Plate (ii) shows (a) a shed primary follicle, and (b) all unlabelled arrows show secondary follicles in various stages of shedding.

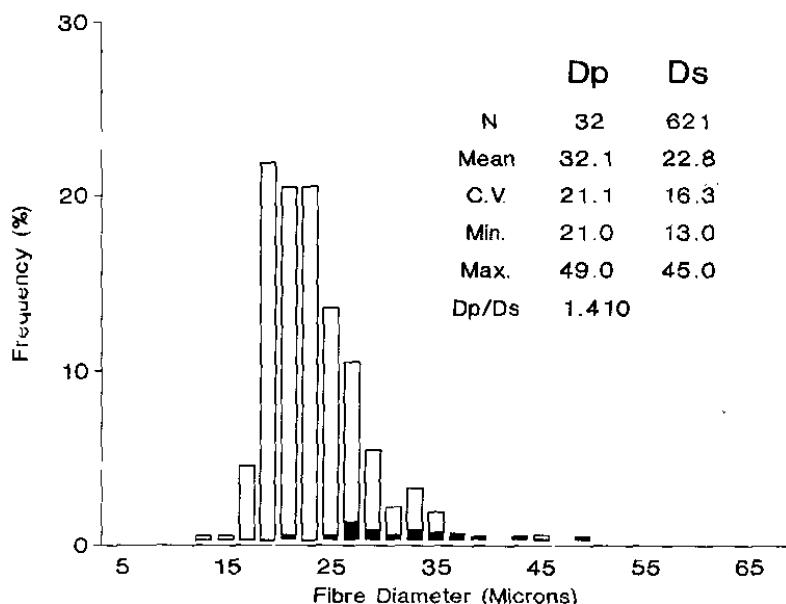


Figure 15: Fibre diameter histogram of a 1976 drop hogget ewe from CSIRO experiment No. 1. Note that the frequency of large primary and secondary fibres is not as large as in Figure 13, but is higher than in Figure 4.

5.4 Evidence of Primitive Trends from Genetic Parameter Estimates

Additive genetic parameters can be used to predict rate of change in a population mean for a quantitative trait, under any artificial (i.e. man- applied) selection method. They cannot predict changes in mean due to natural selection, or to non-additive gene action. They also cannot alone predict changes in population variability. We have obtained estimates of parameters needed to predict genetic change in D_p and D_s from an analysis of variation between and within sire families, using all of CSIRO's currently available data which amount to 793 progeny from 90 sire families. These are summarized in Table 8.

Table 8: Parameter Estimates and Standard Errors for Dp and Associated Traits for Hogget Rams and Ewes Born in CSIRO Experiments 20 and 32.

	Dp	Ds	Dp/Ds	CWW	FD	BW	dNLW	Follicle Depth	Follicle Number	Birthcoat Score
Mean	23.9	20.6	1.17	2.5	18.5	35.4	1.34	-	73.5	3.6
Phenotypic standard deviation	3.9	2.2	0.18	0.58	1.6	6.9	0.47	-	17.1	1.6
Heterogeneity	.64 ± .15	.62 ± .14	.73 ± .15	.34 ± .11	.96 ± .16	.29 ± .11	.18 ± .10	.35	.41 ± .12	1.15 ± .16
Genetic correlation with:										
Ds	.29 ± .17									
Dp/Ds	.80 ± .07	-.35 ± .19								
CWW	.16 ± .22	.66 ± .18	-.25 ± .22							
FD	.40 ± .15	.95 ± .05	-.23 ± .17	.82 ± .14						
BW	-.35 ± .24	.04 ± .24	-.37 ± .24	.35 ± .16						
dNLW	.52 ± .25	.34 ± .28	.32 ± .26	.52 ± .38						
Follicle depth	-	-	-	-						
Follicle number	-.32 ± .22	-.86 ± .24	.23 ± .20	-.44 ± .23	-.77 ± .22	-.05 ± .27	-.37 ± .34	-		
Birthcoat score	.71 ± .01	-.03 ± .17	.70 ± .09	-.16 ± .20	.09 ± .15	-.36 ± .21	.28 ± .25	-		
Phenotypic correlation with:										
Ds	.39 ± .03									
Dp/Ds	.77 ± .02	-.28 ± .04								
CWW	.08 ± .04	.22 ± .04	-.08 ± .04							
FD	.40 ± .03	.62 ± .03	-.02 ± .04	.32 ± .04						
BW	-.04 ± .04	.16 ± .04	-.15 ± .03	.17 ± .04						
dNLW	.20 ± .04	.08 ± .04	.16 ± .04	.19 ± .04						
Follicle depth ¹	.16	.19	.06	.20						
Follicle number	-.23 ± .04	-.44 ± .03	.06 ± .04	.14 ± .04	-.51 ± .03	.21 ± .04	-.17 ± .04	.03		
Birthcoat score	.37 ± .03	-.02 ± .04	.50 ± .03	.01 ± .04	.13 ± .04	-.04 ± .04	-.03 ± .04	-	-.03 ± .04	

These parameters should be used with caution for two reasons:

- some of the sires were not chosen at random,
- one needs about twice the data available to achieve acceptable standard errors, particularly for genetic correlations.

However, there is reason for some confidence in the estimates of Table 8 because:

- heritability of CWW,BW,dNLW agree closely with other published estimates. Heritability of FD is high compared with estimates of Brown and Turner (1968) and Morley (1955) but the Armidale environment is known to differ in heritability of diameter and traits associated with it (Watson et al., 1977),
- genetic and phenotypic correlations among CWW,FD,BW,dNLW agree, at least in sign, with other published estimates.

The most obvious result in Table 8 is that traits Dp, Ds and Dp/Ds are all highly heritable. If fleece hairiness due to a high Dp were a problem in any flock, one should be able to breed it out quite rapidly. The fact that hairiness is not so easily controlled in practise (several breeders have commented to the authors that many years of visual selection against fleece hairiness has not removed it from their flocks) suggests that there are forces operating in Merino flocks which tend to favour recurrence of primitive hairy sheep. These forces could be:

- natural selection may favour sheep with a high Dp, either through greater survival rates, enhanced reproduction rates, or better maternal ability,
- artificial selection (whether by classing or objective measurement) may favour sheep with a high Dp as a correlated response due to genetic correlation between Dp and the trait(s) selected. This may be what has occurred in the various selection experiments discussed in the previous section; however, the above results could also be explained if the selection applied did not oppose natural selection for high Dp,
- non-additive gene action may lead to reversion toward the *wild type* of fleece when artificial selection is relaxed. This may be a factor explaining occurrence of primitive sheep in various industry flocks, as selection in industry flocks is not concentrated on a small number of traits as is the case in selection experiments,
- changes in degree of heterozygosity, through inbreeding or outcrossing may favour sheep with a high Dp, if Dp is correlated with fitness. The magnitude of the genetic correlation between Dp and dNLW would suggest that this is a possibility. This hypothesis would explain occurrence of primitive sheep in industry flocks which have recently crossed strains. It may also explain the general high incidence of primitive sheep in Australian Merino flocks, as the large Australian flocks would have a lower rate of inbreeding than their original Spanish Merino ancestors.

- Segregation of a single recessive gene with low frequency. This possibility is considered unlikely because animal-to-animal distributions of Dp are continuous, with no trace of bimodality.

One cannot distinguish between these possibilities from present data. In the discussion we consider the type of experiments needed to resolve these issues. The second important result from Table 8 is that Dp and Ds are under somewhat separate genetic control, as evidenced by a 0.2 genetic correlation between them, and differing genetic correlations with the other traits. For example CWW has a low positive correlation with Dp, but has a high positive correlation with Ds. Thus, from a genetic point of view, the fleece consists of two partly independent fibre populations, and it is not surprising that they occasionally respond independently in selection experiments and in commercial flocks, as reported above. The third result from Table 8 is obtained by placing an evolutionary interpretation on the correlations. If Dp/Ds is an index of *degree of primitiveness* then the correlations imply that primitive sheep have a lower CWW, higher Dp, lower Ds, lower BW, and higher dNLW, than the modern Merino. All of these inferences make sense at a breed comparison level. Compared with a primitive Soay the Merino is larger, less fit reproductively, and has a more uniform fleece of greater weight. It is well known that within-flock genetic parameters are not necessarily the same as between breed genetic parameters; but they may be if they reflect strongly buffered developmental processes. The development of primary follicles is common to all animals with warm-blooded metabolism - eutherian mammals, marsupials, monotremes, and debatably birds (Carter [7]; Rawles [39]). It is not surprising that such an ancient developmental process would be strongly buffered by many generations of selection of modifying genes, and would be strongly correlated with fitness (Note high genetic correlation of Dp with dNLW) - we interpret this correlation as a reflection of a developmental link between follicle development and homeothermy, temperature regulation being a well known factor affecting fertility (Brown and Hutchinson [4]). The final result from Table 8 is that the genetic correlation between Dp and total follicle number is negative. Note that the only experimental flock in which we have not noted an incidence of primitive sheep is the high total follicle number line (line 2) of CSIRO experiment no. 32 reported above. We believe this reflects a developmental cause and effect relationship, for which there is evidence from other CSIRO studies of the developmental process of follicle formation, outlined below.

5.5 Evidence from Developmental Studies of the Importance of Size of Primary Follicles in Evolution of Merinos

CSIRO has undertaken extensive studies of prenatal follicle development in Merino sheep (e.g. Hardy and Lyne [22]; Moore [32]; Moore and Jackson [33]; Moore et al. [34]. Three types of follicles are initiated in the foetus: primary (P), secondary original (SO) and secondary derived (SD) follicles. These begin to appear in midside skin at about 60, 85 and 100 days of gestation, respectively. P and SO follicles form at separate initiation sites, but SD follicles, which are the last to appear, develop as branches from SO and other SD follicles and perhaps from P follicles also (Lyne [26]). The Merino sheep has a greater proportion of SO + SD follicles than any other breed. Recent work supports a new hypothesis explaining follicle and fibre formation in the developing foetus in a different way from the competition hypothesis of Fraser and Short [17]. This has been alluded to in Moore et al. [34] and is based on observations of (1) the relationships between the dermal papilla component of the wool follicle and the productive activities of the follicle, (2) the effects of single character selection on the distribution of the three follicle types in the skin of the Merino and (3) the effects of such selection on wool weight and its components. The dermal papilla of each follicle arises during foetal life and is first recognisable as an aggregate of cells, adjacent to an epidermal condensation, formed by migration of fibroblastic cells within the surrounding mesenchyme. These cells remain associated with the growing epidermal plug during development and eventually become incorporated into a pocket at the base of the mature follicle. Unlike the follicle epithelium, proliferation of papilla cells is low during development and absent in the mature follicle, suggesting that absolute size of the papilla cell population may be determined early during follicle development. The close physical association maintained between the papilla and epithelial components of the follicle, during periods of active fibre growth, indicate a functional relationship. Morphometric, genetic and transplantation studies have confirmed that presence of a papilla is necessary for fibre production and that its size is correlated with fibre dimensions (Rudall [42]; Ibrahim and Wright [24]). Genetic studies have established that many skin and fleece characters may be modified using appropriate selection procedures. Selection for a single character induced, not only the desired response, but also large correlated changes in other, unselected follicle or skin traits. For example, changes in follicle density were always accompanied by inverse responses in fibre diameter. Alterations in correlated character(s) always tended to compensate, at least in part, for expected changes in wool weight (Turner et al. [53]; Rendell and Nay [40]), the overall effect of selection seeming simply to be a redistribution of wool fibre-producing tissue in the skin. Our hypothesis explains these observations by postulating that the amount of fibre-producing follicular tissue that forms in foetal skin is under the control of a population of committed cells that eventually become incorporated into the dermal papillae of the whole follicle population. The numbers of papilla precursor cells, or pre-papilla cells, that differentiate during foetal life defines

the quantity of follicular tissue that will develop and hence the innate capacity to produce fibre. The distribution of numbers of papilla precursor cells among the follicles determines individual follicle characteristics and thus their capacity to produce fibres of particular types. In simple terms, genes manipulate fleece weight and fibre quality by changing the numbers and distribution of pre-papilla cells. Studies of the distribution of follicle types in sheep has provided evidence that is consistent with this hypothesis. In selection lines with different follicle densities, P and SO numbers were found to be similar (Moore, unpublished observations). Since P and SO follicles are the only types to occupy separately identifiable initiation sites, the implication is that site number is invariant among the lines. All variation in follicle-forming potential was realised only at sites that were already occupied. Thus observed differences in follicle numbers must be almost exclusively confined to the SD type. Although these form last, as stated above, they are the most numerous. The fact that they branch from pre-existing follicles suggests that the capacity of the skin to form follicles is not confined by the apparent limitation in site number, initiation continuing in the absence of a mechanism to specify further initiation sites. Thus, site number and pre-papilla cell number and distribution are specified and under direct genetic control, whereas follicle number and S/P ratio are unspecified and are not under direct genetic control. We have postulated from these observations that follicle formation ceases only when the skin "runs out" of the capacity to generate follicular tissue, that is, becomes depleted of pre-papilla cells. The fundamental developmental process being modified during artificial selection of animals for different follicle densities, or during evolution of sheep breeds, is the genetic specification of the numbers of pre-papilla cells that leave the committed cell population, thereby depleting it, accumulate at the epidermis, and participate in the initiation of each follicle. Figure 16 quantifies the above argument. It attempts to illustrate in a diagrammatic way, the essential difference in follicle development between a Merino and a primitive sheep. It should be stressed that cell numbers and division rates in Figure 16 are probably not correct in absolute terms. It is meant only as a demonstration of the principle that primary follicle development affects the subsequent coarse of events in such a way as to explain most aspects of the Merino-primitive difference.

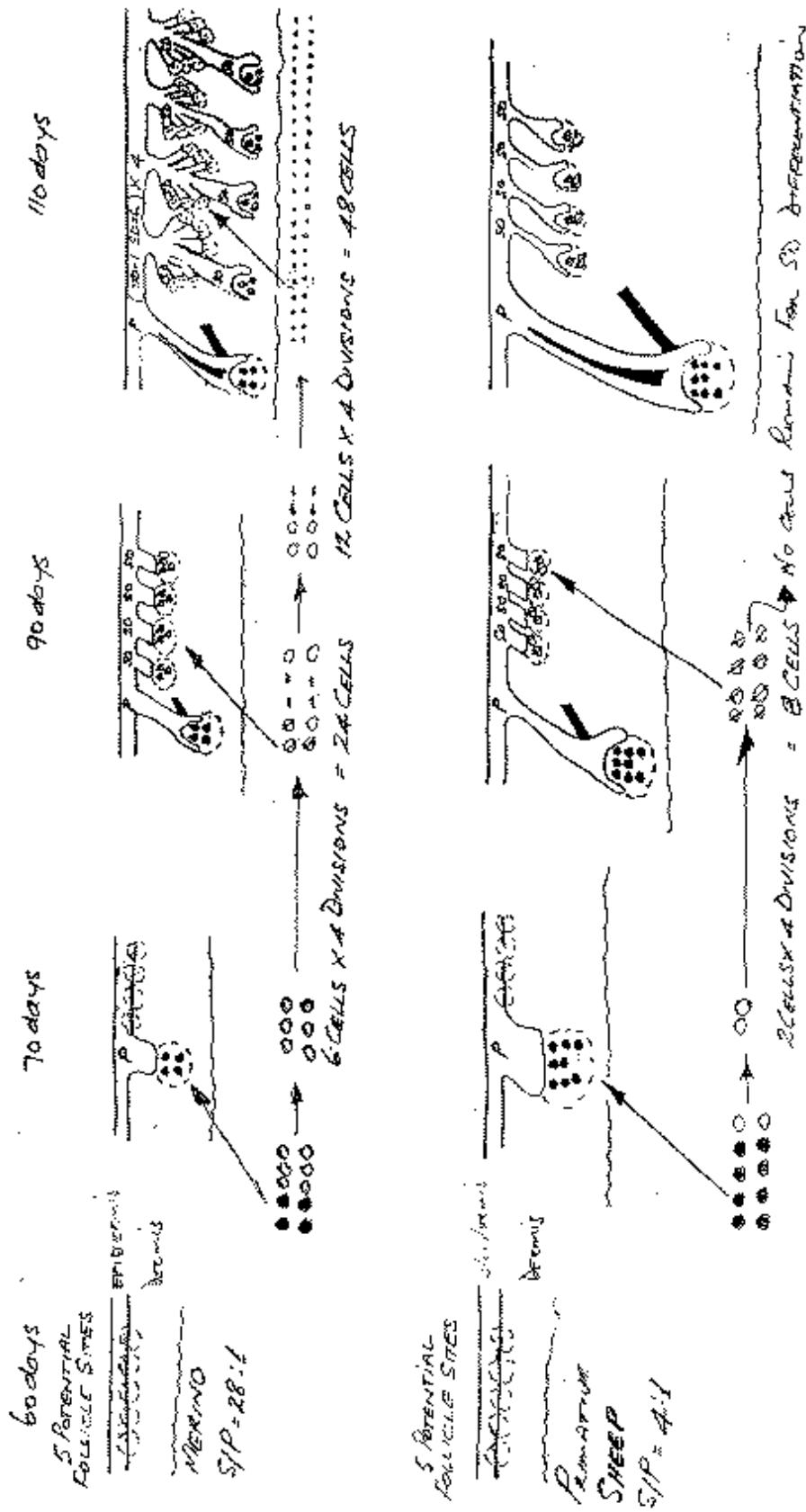


Figure 16: A quantitative illustration of predictions which can be made with the Moore hypothesis regarding the role of primary follicle size in determining comparative development of Merino and primitive foetal skin over the period 60-110 days of gestation. Note that this presentation is diagrammatic - relative sizes and shapes of follicles are not able to accurately represent reality, and cell numbers and division rates should not be absolute. For a complete explanation see text.

Take an arbitrary area of skin containing 5 potential initiation sites and 10 pre-papilla cells, in both Merino and primitive, at some time prior to 70 days. Let the cell division rate (of pre-papilla cells) be 4 divisions per 20 days in both Merino and primitive. At 70 days let the Merino develop one primary follicle, using 4 pre-papilla cells and one site; let the primitive also develop one primary follicle, but using 8 pre-papilla cells and one site. Let this difference (4 versus 8 cells) be the only pre-determined difference between the two development processes. In the Merino development continues as follows: the 6 remaining pre-papilla cells divide to form 24 cells over the period 70-90 days. At 90 days, 4 SO follicles form, using 3 pre-papilla cells each and the 4 remaining sites, leaving 12 cells undifferentiated. The twelve remaining cells divide again over 90-110 days, making 48 cells. At 110 days, 24 SD follicles form using 2 pre-papilla cells each, and exhausting the supply pre-papilla cells, thus halting follicle formation. Because all sites were used at 70 days the SD follicles form as branches from existing sites, mainly the S0 sites, thus forming branching or compound follicles. There are 28 (SD + S0) follicles altogether, giving an adult S/P ratio of 28:1, typical of a Merino-like skin. In the primitive sheep development proceeds as follows. The 2 remaining pre-papilla cells divide to form 8 cells over the period 70-90 days. At 90 days 4 SO follicles form, using 2 pre-papilla cells each, and the 4 remaining sites. There are no pre-papilla cells remaining, so development ceases, no SD follicles being formed. There are 4 (SD + S0) follicles altogether, giving an adult S/P ratio of 4:1, typical of a primitive skin with coarse hair and fine down. There are obviously shades of grey between the extremes illustrated. In reality all secondary follicles are not of equal size, or equal number of symmetrically arranged branches, as shown in Figure 16. It would detract from comprehension to show such variation. We postulate that, during evolution of the Merino, a resource (the population of pre-papilla cells) has been redirected by selective forces from forming large primary follicles to forming many compound secondary follicles. The key observation is that the initial event (formation of the primary follicle) in this developmental process influences its later course. We therefore conclude that adult Dp is an observation representing the earliest event of the follicle development process which we can measure, and suggest it is likely to be the basic cause of the quantum difference between the Merino and other breeds in fleece quality characteristics. This is a modification of the view of Dr Carter, who suggested that S/P ratio was the basis of the difference between Merino and other breeds (Carter and Clarke [10] [11]). Our view is that differences in S/P are a consequence of earlier differences in Dp. It would be quite likely that the original Merino occurred as a mutant gene with a major effect on primary follicle and fibre size, and that its effect was subsequently masked by selection of modifying genes, so that its segregation is not now obvious in crosses. Genes of similar effect occur in other species (Fraser [16]; Searle and Jude [48]) and are commonly known as *rex* mutants. If the Merino is a *rex* mutant sheep it should be possible to make its segregation visible in crosses by selecting Merinos in a way which would suppress the action of modifying genes. A new CSIRO experiment (no. 73) may allow us to test this prediction. Conversely, if the *rex* hypothesis is accepted, one would not expect

pure Merino populations to exhibit segregation at the *rex* locus, so segregation could not be used to explain occurrence of primitive individuals in purebreds. Purebreds may have other modifying genes segregating, but these would be more than one and small in effect.

5.6 Evidence from Historical Accounts of Incidence of Primitive Individuals in Spanish Merino Flocks

There is some evidence that the original Merino flocks in Spain had an incidence of primitive hairy individuals. An anonymous author, discussing Merino lambs introduced into England from Spain (*A Practical Treatise on the Merino and Anglo-Merino Breeds of Sheep*, London, 1809; cited by Ryder [46]), states that:

'There is occasionally a peculiarity in the wool of the lamb when first dropped, differing from any breed in this country (if indeed it may be termed wool), many of them being entirely covered with hair, which I do not find mentioned by any author except Dr Parry (*Communication to Board of Agriculture*, vol. 5, p. 346) who observed that the wool of Merino lambs, in general, is evidently coarser and harder than that of the sheep. It seems, however, that the different flocks vary in this respect. The lambs of the Infantado and Paular races are covered with a coarse sort of hair, which afterwards changes into very fine wool. The same appearance is sometimes to be found among lambs of the Negrete breed in England.'

The above account does not mention hairy adult fleeces, but the association of adult Dp with birthcoat is very strong in our data (Table 8), so there is a high probability Spanish Merinos were also hairy as adults. There is also one piece of direct evidence. There is a flock of Merinos at La Bergerie Nationale, Ram-bouillet, France, that descend from Spanish Merinos imported by the French Government in 1786. Their history is described by Carter [9] and Ryder [46]. They would appear to be a large representative sample of 18th century Spanish Merinos, maintained without introductions. In 1964 Dr Carter sampled 6 rams and 18 ewes from this flock. These data are still preserved at CSIRO, and are summarised in Table 9.

Table 9: Variation in Diameter of Primary and Secondary Fibres and in Percentage of Follicles Exhibiting Shedding, in Sheep from the Merino Flock at la Bergerie Nationale, Rambouillet, France

Sex	Mean			Percent with Dp/Ds			Number Sampled
	Dp	Ds	Dp/Ds	> 1.2	> 1.5	> 1.8	
Rams	19.4 ± 1.02	19.3 ± 0.41	1.00 ± 0.32	0.0	0.0	0.0	2.6 ± 1.97
Ewes	21.5 ± 0.41	19.1 ± 0.29	1.13 ± 0.03	38.9	0.0	0.0	0.6 ± 0.37

There was one ram with 12.4(D_p = 25.1, D_s = 17.6). These results are remarkably similar to the Early Fine Merino in Table 2, and to the modern fine and medium non-Peppin Merinos in Tables 2 and 3. While one should always be cautious with such comparisons of flocks in different environments, it suggests that Merino populations from the present Australian strains to the original Spanish, have an ability to generate individuals which resemble their primitive two coated ancestors. It is improbable that the flock at Rambouillet were subjected to introductions of Cape or Bengal sheep but there may have been introductions of the local European Breeds. If it is possible for the Rambouillet flock to exhibit primitive characteristics without such introductions, it is not necessary to postulate such introductions into the finer Australian strains of Merino, in order to explain a similar level of primitive characteristics. Hence, we suggest, most of the primitive characteristics which we observe in today's Australian Fine Merino, came from the Spanish Merino and its ancestors. The Cape and Bengal sheep which came to Australia with first settlement (Turner [51]; Turner [52]; Garran and White [21]; Massy [30], and/or introduction of British longwools (Cox [13]; Massy [30])), may have contributed additional primitive characteristics to the Medium, Medium Peppin and Strong Merino strains. From the point of view of the hypothesis put forward in this paper, ie that current Australian Merinos are descended from primitive two-coated sheep, it does not matter whether there is one line of descent through pure breeding or several lines of descent through various introductions. All of the documented historical introductions were also descended from primitive two- coated sheep.

5.7 Direct Evidence of Increased Incidence of Primitive Characteristics in a Feral Merino Population

The feral sheep of Arapawa Island, New Zealand, are considered to be descendants of "the commercial Merinos of the 19th century", there being no record of the introduction of any other breed to the region (Orwin and Whitaker [38]). Records of their presence on the island date back to the 1850's. Their blood types are not inconsistent with a Merino origin. Orwin and Whitaker [38] report measurements of wool and skin from Arapawa Island feral sheep. Compared with modern Merinos they produce wool high in grease content, bulk, and fibre crimp, but of similar diameter (mean 23.1, median 21.6). In these characteristics they resemble Merinos more than other commercial breeds. However their fibre diameter distributions are markedly skewed (range 9-109m) and they have a low S/P ratio (6.0) a low follicle density (26.9 per mm²) and have a tendency to shed their fleece. In these characteristics they resemble primitive breeds. Orwin and Whitaker [38] present comparative data on four other feral flocks, but in these cases strong evidence of Merino origin is lacking. They also refer to other feral Merino populations in Hawaii, the Solomon Islands, but comparative data are not available. There is ample evidence that geographically isolated feral populations evolve in the direction favoured by natural selection. What the above evidence establishes, in addition, is that in the case of Merino sheep populations, natural selection for coat type regresses the population toward the two-coated condition exhibited by primitive ancestors of the Merino. What remains to be established is whether, or at what rate, the same phenomenon occurs in domestic Merino populations.

6 Conclusion

The economic significance of primitive characteristics is difficult to establish. Whiteley [57] rates fibre diameter variability, as a parameter affecting product value, to be important only when certain limits are exceeded. He does not, however, define the critical limits, and he considers only the effect on processing wastage. Recent work at CSIRO, Division of Textile Industry (Mayfield [31]; Garnsworthy [20] shows that prickle in fabrics is the result of an excess of coarse fibres, a small percentage of fibres exceeding 30 microns in a fabric of mean diameter 21 microns being sufficient to cause discomfort in a fabric worn against the skin. Product quality is therefore predicted from fibre diameter distribution. Handle of raw wool and of wool in various stages of processing is also predicted. In addition to these textile implications there is an effect on staple structure, fleece rot resistance, and blowfly strike (Watts [56]) which in turn indirectly affect processing and product quality. There is a need to define these relationships with greater precision, and to make an assessment of the economic importance of primary fibre diameter, relative to that of other fleece characteristics. An extension of the work of Whitley and Jackson [58] and Rogan [41] is indicated. There is also a need to understand how primary and secondary fibre diameter distributions relate to other assessments of quality which are traditionally made on the live sheep. We have preliminary evidence (Lax, unpublished) to suggest that sheep classers can accurately assess occurrence of coarse fibres in the fleece from a combination of handle and visual fleece characteristics. This suggests that practical and economically feasible methods of selecting against hairiness already exist in the industry, and in many cases we believe that such methods are being applied with sufficient diligence and persistence. The worst hairiness problems were observed in selection experiments (which are selected entirely on objective measurement), in control flocks (in which there is no selection at all), and in certain studs which have dispensed with the traditional safeguards which are built into visual classing. The positive result is that there are some studs that have successfully combined objective measurement with traditional culling for faults such as hairiness. These flocks are relatively free of excessively hairy individuals. It is to these breeders that we should look for assistance in integrating the new *sharp* tools offered by objective measurement with the traditional *cautious* approach of visual assessment. For reasons of confidentiality we are obliged not to identify the studs which were involved in assembling the above observations. We conclude that some selection against hairiness is essential in any Merino breeding program. None of the above interpretations explain why sheep with primitive hairy fleeces continue to occur in Australian Merino flocks. We only know that it is necessary to exert a certain amount of selective force in order to prevent their occurrence reaching unacceptable levels. Exactly how much selection is required against hairiness has yet to be determined. The answer is unlikely to be the same for all strains. One leading breeder has advised confidentially that he expends about 30% of his available selection intensity in culling against hairiness. When so much culling is required, it is a major problem diverting selection effort away from important production traits. The

only way to eliminate such a problem is to understand the biological basis of undesirable genetic correlations. We have taken one small step towards that understanding, in the case of correlations between hairiness and production traits, firstly by demonstrating that a problem exists (though its extent has yet to be quantified) and secondly by exploring evolutionary and developmental explanations. The outstanding question which remains unanswered is why Dp should be positively correlated with reproductive fitness. Its association with lamb survival, via birthcoat, is well documented (Alexander [1]; Obst [37]), but the only reported association of coat type with adult performance is in the rock squirrel (Walsberg [54]) where solar heat gain was found to be minimized by a particular ratio of inner to outer coat depths, the outer coat being entirely coarse primary fibres. It may not be entirely unreasonable to suggest that coat type in sheep has an effect on thermoregulation; fur and warm blooded metabolism evolved together and may well be genetically linked even if there is no direct physical effect. The link between thermoregulation and reproductive performance is well documented. Heat stress affects semen quality, embryonic loss, foetal growth and lamb survival (Brown and Hutchinson [4]). There are also documented effects of heat and cold stress on adult wool production and quality (Wodzicka, 1960; Slee and Ryder [50]; Downes [15]). Of particular interest is an effect of heat stress of the pregnant ewe on secondary follicle maturation of the lamb (Cartwright [12]). The field was reviewed by Bottomley [3]. We suggest that genetic association between coat type and thermoregulation in sheep merits further investigation. The adaptive significance of coat type could be an important consideration in the formation of sheep breeding objectives for various parts of the Australian continent. It should not be assumed that all of the observations reported here are either new or original. Our interpretation of the observations may vary from that of previous workers, but the fact of occurrence of individuals of primitive coat type in Merino flocks is widely known throughout the industry, as the following citation from Country Life of 18 October 1932 clearly demonstrates.

'A freak Merino ram has come into the possession of the Department of Agriculture - a freak because of its extraordinary wool growth, which is said to have a coating similar to the original wild sheep. This freak ram - now at Trangie Experiment Farm - is a rising 4 tooth. Mr E A Elliot, Government Sheep and Wool Expert, told the writer that it will be used for breeding purposes, in order to see whether it will reproduce its kind. The ram was bred in a high class stud flock and because of this fact will be joined with selected Merino ewes. In addition to having a coating of short wool and hair, the ram is very leggy and has practically no fold development. The ram, too, has a thick jaw, and is very active ...'

This account was quoted by Cox [13] who also presents a photograph of the ram clearly showing the short fleece with protruding hair. The context of Cox's citation show that he considers this /em freak an example of reappearance of a primitive breed characteristic. There seems to be no record of further research

into this animal or its progeny. It is somewhat surprising that a phenomenon widely publicized could be ignored in breeding research for four decades. The only definite result of this study is a confirmation that sheep with primitive skin and fleece characteristics do exist in the current Australian Merino population, and have probably always been present in the Merino breed. We interpret this observation as consistent with Ryder's theory of evolution of the Merino directly from primitive two-coated domestic sheep. This interpretation led us to the hypothesis that Merino flocks tend to regress toward wild or primitive sheep, at least in so far as their coat type is concerned. The conditions under which this tendency is actualized would appear to be fairly common.

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