What are the defining characteristics of a primitive sheep relative to a modern Merino sheep

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Contents

1 Introduction

The question has arisen, in reviewing the document Jackson, Maddocks, Lax, Moore, and Watts (1990) [9], of which characteristics would be most appropriate in identifying sheep which are showing signs of reversion to a primitive two-coated fleece type.

It is obvious that we should make some use of the diameters of primary and secondary fibres, but the exact form in which these data should be used, and whether other characteristics (such as primary and secondary follicle densities, shedding follicles, birthcoat coarsness, follicle arrangement, and visibly protruding coarse fibres in the fleece) should also be used, are open to debate. To some extent the practical answer is limited by available data.

2 Terminology

We need to be consistent in using the following terms

kemp coarse heavily medullated fibres that shed anually or more often

hair coarse persistantly growing wool fibres. May be medulated but not as heavily medullated as kemp fibres. May shed but not synchronously.

wool medium to fine fibres. No medullation. Shed in undercoat of wild sheep, but not in modern fine and medium breeds.

3 Definition of a primitive fleece type

We refer to the extensive studies of Ryder(1981) [17] and Ryder(1992) [18]. In summary,

- wild sheep are two-coated, with coarse long kemp fibres and short fine underwool.

- the first domestic sheep (in the Neolithic (Stone Age) period (10000-3000BC) were similar to wild sheep. Some of the kempy sheep of Africa and India today are survivors of this type.

- in the Bronze Age (3000-1000 BC) the kemp fibres became finer , while the fine undercoat fibres became slightly coarser. Shedding of the fleece was still necessary (there were no shears in the Bronze Age), fibres were combed fro the sheep. Modern representative is Hairy Soay

- In the Iron Age (1000BC - 700AD the long kemp fibres became continuous growing long fibres termed "hair", and the fine-medium undercoat also became continuous growing. In some breeds the hairs also became finer. Modern representative is Wooly Soay.

- modern breeds (British Longwools, British Shortwools, and fine Merino) are all derived from Iron Age sheep, in the Middle Ages (700AD - 1700AD) by various modifications of the fineness and length of fibres. All these modern breeds are continuous growing

- in tropical Africa and India some survivors of the Bronze Age hairy sheep have actually further reduced the underwool, presumable as an adaptation to tropical conditions.

- in the New World (Australia and USA) present day derivatives of the modern European Breeds were developed, mainly by cross breeding followed by selection.

The extent of the changes noted above are shown in a diagram from Ryder(1992) [18] in Figure 1
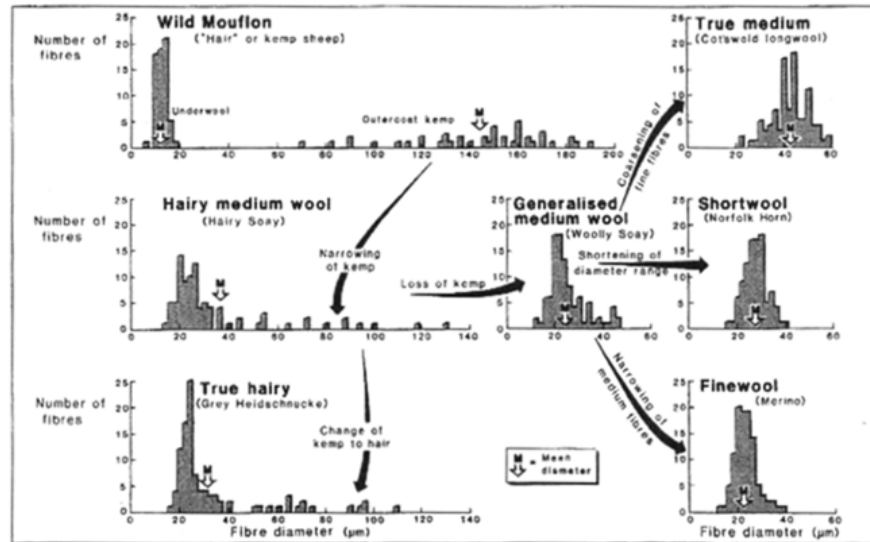

Fig. 3 : Changes in the coat during fleece evolution. Each diagram in the form of a histogram shows the distribution of fibre diameter (based on the measurement of 100 fibres), which defines fleece type. The arrows indicate the changes that occurred when breeding caused one type of fleece to change into another. The main change has been a progressive narrowing of the outer-coat kemp-hairs. These became finer as the coat of the Neolithic sheep (top left) changed into the first (Hairy-medium) fleece of the Bronze Age. Since this diagram was drawn, as shown in Table 1, evidence has been obtained for early intermediate stages with only kemp and fine wool - the Hairy-medium fleece has fibres of medium diameter (derived from the outer coat) as well as kemp and fine wool. The remaining finer kemps then changed into medium fibres to give the Generalised-medium fleece. Further narrowing changed them into the fine fibres of the Fine wool (bottom right). Other changes resulted in the Semi-fine (shortwool) and the Medium-wool (later seen in the longwool). The last three (modern) fleece types first appeared in the Iron Age and became more common during the Roman period. The Hairy type (bottom left) also appeared during the Iron Age when short kemps changed into long hairs. The breeds named are the examples used to illustrate the differente fleece types. (From RYDER, 1983a p. 46). (One micron, μ, = 0.001 mm).

Figure 1: Figure copied from Ryder(1992) [18]

So Ryder considers that Fine Merino sheep are descended from his "Generalised Medium Wool", which in turn is descended from "Hairy Medium Wool",

3

which in turn is descended from wild sheep. In other words Merinos are descended from primitive domestic sheep of the Bronze and Iron Ages, not from other medieval breeds such as the British Longwools and Shortwools.

This is basically in agreement with the description of Merino evolution given in Fraser and Short(1960) [5] which was referred to in Jackson et al(1990) [9] and used as a basis for the statement

"The Merino breed is considered to have evolved directly from either wild sheep aor primitive two-coated domestic sheep"

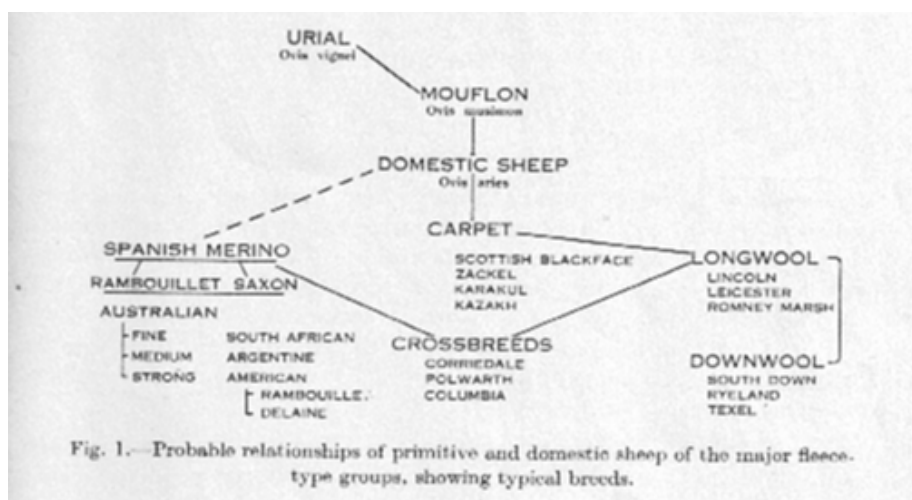We present the diagram given by Fraser and Short(1960) [5] in Figure 2.

Figure 2: Figure copied from Fraser and Short(1960) [5]

It is basically the same as Ryder, but less supported by data. It comes in turn from an even earlier publication (Von Bergen and Mauersberger(1948) [21]. Ryder wants to insert his Generalised Medium Wool in between primitive two coated sheep and the Merino.

What is important here is that the term "primitive domestic sheep" could mean either Stone Age sheep, which are basically unchanged wild sheep, or Bronze Age sheep, which are still two-coated but the outer coat is less medullated and not as coarse. Both the Stone Age and Bronze Age sheep are shedding sheep. The outer and under coats both shed, but at different times - the undercoat sheds seasonally and all at once, the outer coat fibres shed individually at random times.

So the term "primitive domestic sheep" is ambiguous. It is best considered a broad term encompassing all domestic two-coated sheep from the ancient world.

4

4 The time scale of Merino evolution

From Ryder's diagram (Figure 1) we can put an approximate time scale on the stages of Merino evolution. This is attempted in Table 1

Table 1: Establishing a time scale for the stages of Merino evolution

Stage	Chronology	Years	Generations
Wild	Neolithic (10000-3000BC)	8000	2000
Hairy Medium Wool	Bronze Age (3000 - 1000BC)	4000	1000
Generalised Medium Wool	Iron Age (1000BC - 700 AD)	2100	520

So Ryder is saying that a modern Fine Merino with a 22.5 micron mean diameter, is about 500 sheep generations removed from a Generalised Medium Wool with a 24.4 micron mean diameter.

So how long does it take to change mean diameter of a flock by 2 microns? Well with a heritability of 0.4 and a phenotypic standard deviation of 1.4 microns, if one selected for diameter and nothing else one might achieve a selection differential of about 1.3 standard deviations, so the expected response is

$$
\begin{aligned}
R & = ih^2\sigma \\
& = (1.3)(0.4)(1.4) \\
& = 0.7
\end{aligned}
$$

in one generation, which is about 4 years in sheep. So there is certainly plenty of time in 500 years for this amount of change to have occurred.

However, that is not the whole story. Apart from the change in mean, there are considerable changes in the shape of the distribution between a Generalised Medium Wool and Merino. Also we do not know from Ryder's data, how the diameters of primary and secondary fibres have changed. We look at this from some more extensive data later on. What is clear, from Ryder, is that mean diameter is not the most important part of the story: the fibre population has components which have changed independently during the breeding of wool sheep.

We also need to look at longer term evolution. Lets say we started with wild sheep, and looked just at the outer coat, witha mean diameter of about 140 microns. To change this to the 20 micron mean of all fibres of a Fine Merino would take, on the above calculation $120/0.7 = 170$ sheep generations - easily achieved in the 2000 sheep generations available between Wild sheep and Merinos. However, this also shows that we could reverse the Merino to Wild sheep in a mere 170 generations.

Clearly sheep breeders have taken their time over the years, to the extent of taking 10 times longer to achieve a modern fleece quality than would have been required had they concentrated on nothing else. Clearly our assumed selection differential of 1.3 standard deviations (which comes from a flock with rams replaced annually) is not correct. Ancient flocks probably turned the rams over

much more slowly, so the selection differential would have been smaller and the generation interval longer.

There are also changes in characteristics other than fibre diameter. The seasonally shedding undercoat of Wild sheep and Hairy Medium Wool sheep changed suddenly during the Iron Age to continuous growing fibres. So the secondary follicles all moved into the Anagen phase of the hair growth cycle, and at the same time became slightly coarser. This did not happen to primary follicles. Primary follicles shed asynchronously and aseasonally in all breeds from Wild sheep to Modern Fine Merinos. The only modification to primary fibres has been change from kemp to hair which involves reduction in medullation and reduction in diameter. The continuous growing fibre modification is clearly not systemic. It appears to have happened relatively rapidly somewhere within the 2000 year span of the Iron Age.

The first historical records we have of the Merino breed are around the 12th century AD in Medieval Spain (Massy(2007) [10]. Spanish Merinos were already continuous growing finewool sheep, so we can subtract 1200 years or 300 generations from the timelines in Table 1. The Merino breed also differs from all others in having a higher density of secondary follicles, or a higher S/P ratio, and in having the additional secondary follicles formed by branching from other follicles forming a compound follicle, sometimes with as many as 25 branches. The fibres grown by highly branched follicles appear to differ in internal stucture, being less curved, finer, and longer growing.

5 The Carter(1968) data on diameter of primary and secondary fibres

To do anything more objective, we need measurements. Fortunately, there is a comprehensive set of sheep breed skin data, including Dp and Ds, collected by Dr H. B. Carter (Carter(1968) [3]). We list the breed means here in Table 2

Table 2: Listing of breed means from the Carter(1968) [3] data set

Flock	Breed		Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
1	Early Merino	Fine	NSW	21	11-18	60.2	4.0	14.0	19.2	17.2	17.3	1.1
2	Tas. Merino	Fine	Tas	21	12-14	73.3	3.5	19.6	18.3	17.8	17.9	1.0
3	Tas. Merino	Fine	Scot	11	12-14	62.0	3.0	20.3	21.3	20.9	20.9	1.0
4	Tas. Merino	Fine	Tas	21	12-14	72.8	3.4	20.7	19.2	16.8	16.9	1.2
5	Tas. Merino	Fine	NSW	20	8-9	59.9	2.5	22.8	18.4	19.8	19.7	0.9
6	Tas. Merino	Fine	Vic	21	14-15	79.6	3.6	21.1	19.3	16.7	16.8	1.1
7	Tas. Merino	Fine	NSW	24	36	48.6	2.4	19.4	19.0	18.8	18.8	1.0
8	Tas. Merino	Fine	NSW	16	36	46.6	2.7	16.7	20.6	18.1	18.3	1.1
9	Tas. Merino	Fine	Scot	11	36	54.5	2.6	20.4	21.8	21.7	21.7	1.0
10	Vic. Merino	Fine	Vic	21	14-15	57.2	3.5	15.3	20.2	18.0	18.1	1.1
11	Vic. Merino	Fine	Vic	11	14-15	62.3	3.7	16.0	18.3	15.9	16.1	1.2
12	Vic. Merino	Fine	Vic	13	14-15	76.4	3.8	19.6	15.8	15.7	15.7	1.0

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Table 2 – *Continued from previous page*

Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
13	Vic. Merino Fine	Vic	21	14-15	71.3	3.5	19.8	22.7	19.9	20.0	1.1
14	NSW Merino Fine	NSW	21	10-12	87.4	3.4	24.7	19.0	17.1	17.2	1.1
15	Non-Peppin Fine-Medium Merino	NSW	25	60-72	43.1	2.2	20.7	23.0	22.6	22.6	1.0
16	Non-Peppin Fine-Medium Merino	NSW	22	60-72	50.1	2.3	21.3	22.3	21.0	21.1	1.1
17	Non-Peppin Medium Merino	NSW	22	14-15	55.6	2.4	22.6	26.6	22.3	22.5	1.2
18	Peppin Medium Merino	NSW	30	15-18	57.1	2.8	19.7	29.8	23.7	24.0	1.3
19	Peppin Medium Merino	NSW	20	15-18	63.4	3.1	19.7	25.1	17.8	18.1	1.4
20	Peppin Medium Merino	NSW	20	18-20	63.4	2.8	27.4	28.0	22.8	22.9	1.2
21	Peppin Medium Merino	NSW	20	18-20	58.6	2.4	24.2	25.6	23.2	23.3	1.1

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Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
22	Peppin Medium Merino	Vic	21	14-15	72.9	3.5	20.0	21.6	17.1	17.3	1.3
23	Peppin Medium Merino	Vic	15	12-14	65.7	2.8	22.4	25.5	19.9	20.2	1.3
24	Peppin Medium Merino	Vic	11	14-15	65.2	3.4	18.5	21.1	16.8	17.0	1.3
25	Peppin Medium Merino	Tas	21	12-14	79.8	4.0	19.0	22.5	19.2	19.4	1.2
26	SA Strong Merino	SA	21	12-15	64.8	4.0	15.9	29.7	22.5	22.9	1.3
27	SA Strong Merino	SA	21	12-15	53.5	3.0	16.8	30.8	23.7	24.1	1.3
28	SA Strong Merino	SA	21	12-15	53.1	2.8	18.5	32.6	24.7	25.1	1.3
29	Early Fine Merino (Rambouillet)	France	20	12	50.4	4.1	11.5	24.3	21.1	21.3	1.1
30	Early Fine Merino (Rambouillet)	France	18	14	44.5	2.8	15.4	21.5	19.1	19.2	1.1
31	American Rambouillet	USA	12	18	35.2	2.4	13.9	27.2	23.4	23.7	1.2

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Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
32	American Rambouillet	Turkey	21	36	40.8	2.4	16.5	21.6	21.7	21.6	1.0
33	American Merino	USA	12	18	43.0	2.5	16.0	23.3	18.9	19.2	1.2
34	American Merino	Italy	8	24-84	40.3	3.1	12.5	19.3	17.6	17.7	1.1
35	Debouillet	USA	12	12	44.9	3.0	14.3	21.5	16.2	16.6	1.3
36	Merino Tor Mancina	Italy	8	48-84	35.7	2.6	13.0	21.4	19.4	19.5	1.1
37	Improved Apulian	Italy	8	24-84	29.3	2.3	11.8	20.7	20.4	20.4	1.0
38	German Merinofleischaf	Turkey	21	36	30.5	2.1	14.0	20.6	21.3	21.1	0.9
39	German Merinolandschaf	Turkey	19	36	31.5	2.7	10.7	28.5	24.3	26.4	1.1
40	Turkish Merino	Turkey	21	36	27.1	2.4	10.7	23.0	21.6	22.3	1.1
41	Portuguese Merino	Portugal	12	24-84	23.2	3.1	6.7	26.1	23.5	23.9	1.1
42	Polwarth	NSW	21	14-15	52.5	3.8	12.8	23.8	19.2	19.5	1.2
43	Polwarth	NSW	21	14-15	54.0	4.3	11.8	23.6	21.3	21.5	1.1
44	Polwarth	Vic	21	13-14	44.1	2.8	15.0	26.7	23.7	23.9	1.1
45	Polwarth	Vic	11	14-15	46.9	3.2	13.5	21.6	17.4	17.7	1.2
46	Targhee	USA	12	18	27.6	2.0	13.0	28.6	25.4	25.6	1.1
47	Corriedale	NSW	21	11-12	23.1	2.1	10.1	32.8	33.8	33.6	1.0
48	Corriedale	NSW	21	11-12	30.0	2.5	11.0	33.8	31.7	31.9	1.1

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Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
49	Corriedale	NSW	21	7-8	31.1	2.7	10.8	31.4	31.5	31.5	1.0
50	Corriedale	NSW	19	36	19.0	1.8	9.4	37.0	30.4	31.0	1.2
51	Corriedale	Tas	19	36	22.3	2.0	10.5	32.7	33.8	33.7	1.0
52	Corriedale	USA	12	12-72	15.9	1.7	8.4	29.1	26.3	26.7	1.1
53	Columbia	USA	12	18	20.9	1.8	10.6	29.7	28.4	28.8	1.0
54	Sopravissano Rossi	Italy	8	24-84	23.4	2.4	8.6	25.6	22.7	23.0	1.1
55	Ile-de-France	France	14	24-96	20.3	2.5	7.1	33.2	29.3	29.7	1.1
56	Ile-de-France	Italy	8	24-84	12.6	1.7	6.4	27.2	27.4	27.4	1.0
57	Southdown	UK	18	3	31.1	4.8	5.5	27.4	27.5	27.5	1.0
58	Southdown	NSW	21	11-12	27.8	3.9	6.3	26.1	25.2	25.4	1.0
59	Southdown	UK	12	18	16.9	2.7	5.7	34.1	32.9	33.1	1.0
60	Dorset Horn	NSW	19	11-12	18.5	2.9	5.4	33.6	34.6	34.4	1.0
61	Suffolk	Vic	21	11-12	20.4	3.5	4.8	26.0	23.1	23.6	1.1
62	Ryeland	NSW	21	11-12	15.8	2.5	5.5	31.6	31.5	31.5	1.0
63	Ryeland	NSW	16	24	11.2	1.7	5.6	29.5	27.2	27.5	1.1
64	Romney Marsh	NSW	21	11-12	22.0	3.4	5.5	37.2	32.9	33.6	1.1
65	Romney Marsh	NZ	20	18	15.3	2.5	5.1	40.6	32.1	33.4	1.3
66	Border Leicester	NSW	21	11-12	15.8	2.9	4.4	45.6	33.8	36.0	1.4
67	Border Leicester	UK	33	18	15.9	3.1	4.2	41.1	33.1	34.7	1.2
68	English Leicester	Vic	21	11-12	14.4	2.5	4.9	41.8	36.0	36.2	1.2

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Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
69	Lincoln	UK	15	3	18.4	3.3	4.7	48.3	32.0	35.0	1.5
70	Lincoln	Vic	21	10-11	14.6	2.3	5.4	59.0	40.8	44.2	1.4
71	Lincoln	UK	24	18	11.5	2.0	4.7	60.0	39.9	43.5	1.5
72	Cheviot	UK	21	3	19.9	3.8	4.2	36.5	31.4	33.0	1.2
73	Cheviot	UK	18	7-8	14.6	2.7	4.5	25.8	19.9	21.0	1.3
74	Cheviot	UK	40	18	10.2	2.1	3.9	49.8	39.5	41.8	1.2
75	Welsh Mountain	UK	15	3	21.3	4.2	4.2	60.3	28.6	34.9	2.2
76	Welsh Mountain	UK	25	18	13.8	2.8	4.0	55.4	25.2	31.5	2.2
77	Welsh Mountain	UK	40	18	11.9	2.4	4.1	80.5	32.0	41.0	2.5
78	Scottish Blackface	UK	24	3	12.2	2.9	2.2	77.1	32.2	43.0	2.4
79	Scottish Blackface	UK	10	7-8	9.1	2.4	2.9	69.5	21.1	34.2	3.2
80	Scottish Blackface	UK	40	18	7.7	1.7	3.5	109.7	30.0	52.5	3.7
81	Scottish Blackface	UK	18	24	7.0	1.7	3.2	94.5	34.5	48.9	2.7
82	Swaledale	UK	11	4	10.2	2.6	3.1	94.9	29.8	45.9	3.2
83	Swaledale	UK	11	24	8.3	2.0	3.1	70.5	26.5	38.1	2.7
84	Wiltshire Horn	UK	15	5	13.9	2.8	4.1	59.7	34.1	39.3	1.7
85	Wiltshire Horn	UK	18	9-10	11.8	2.6	3.3	58.0	33.7	39.0	1.7
86	Icelandic	Iceland	20	24	12.3	1.5	7.4	65.9	28.0	32.7	2.4

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Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
87	Swedish Landrace (Fine)	Sweden	13	16-17	14.5	1.8	7.1	57.2	36.5	39.0	1.6
88	Swedish Landrace (Carpet)	Sweden	23	16-17	12.8	2.1	5.2	73.2	36.0	42.2	2.0
89	Navajo	USA	12	18	11.3	1.8	5.2	41.9	34.2	35.7	1.2
90	Prealpes du Sud	France	12	18	13.7	2.4	4.9	39.8	33.7	34.9	1.2
91	Limousin	France	12	18	11.0	2.0	4.6	67.8	33.1	39.4	2.0
92	Soay	UK.St.Kilda	8	12-60	18.3	3.6	4.2	42.1	17.2	22.1	2.5
93	Karakul	USA	10	12-24	10.5	2.7	3.0	60.2	29.9	38.0	2.0
94	Karakul	Turkey	17	36	18.8	3.9	3.9	46.1	20.9	32.5	2.2
95	Ivesi	Turkey	19	36	11.6	2.5	3.6	56.8	29.2	43.0	1.9
96	Sakiz	Turkey	17	36	14.5	2.8	4.4	57.5	27.9	42.7	2.1
97	Imroz	Turkey	17	36	16.7	3.2	4.2	60.6	29.4	45.0	2.1
98	Karakaya	Turkey	19	36	10.7	2.1	4.1	66.4	28.0	47.2	2.4
99	Kivircik	Turkey	20	36	11.6	2.5	3.8	47.3	31.6	39.4	1.5
100	Ak-karaman	Turkey	19	36	12.2	1.8	5.7	43.4	20.6	31.9	2.1
101	Daglic	Turkey	19	36	16.4	2.9	4.9	47.9	24.5	36.1	1.9
102	Awassi	Iraq	12	24-48	9.6	1.8	4.2	53.5	28.4	32.4	1.9
103	Awassi	Iraq	12	24	10.4	2.0	4.2	49.7	26.2	31.4	1.9
104	Awassi	Iraq	12	24-96	9.1	1.9	3.9	50.3	26.6	31.5	1.9
105	Awassi	Iraq	12	12-36	7.8	1.9	3.1	57.6	29.2	36.5	2.0
106	Arabi	Iraq	12	12-24	9.1	2.1	3.4	49.8	28.3	33.4	1.8
107	Kerradi	Iraq	12	12-24	6.3	1.5	3.1	61.3	31.9	39.5	1.9
108	Kali	India	8	12-24	11.0	3.1	2.6	45.3	22.5	32.5	2.0
109	Chokla	India	5	12-24	13.3	3.8	2.6	34.5	21.4	27.4	1.6

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Table 2 – *Continued from previous page*

Flock	Breed	Country	NoSamp	Age	Npsua	Npua	NsovNp	Dp	Ds	Dps	DpovDs
110	Jaisalmeri	India	7	12-24	10.9	3.2	2.5	40.9	23.3	29.2	1.8
111	Magra	India	8	12-24	11.1	3.6	2.2	40.6	21.8	27.8	1.9
112	Marwari	India	9	12-24	10.2	3.4	2.1	38.2	21.5	32.4	1.8
113	Malpura	India	8	12-24	8.7	3.1	1.9	48.5	24.0	34.7	2.0
114	Sonadi	India	8	12-24	5.7	2.8	1.1	50.3	23.1	43.3	2.2
115	Nilgiri	India	20	12	17.9	4.1	3.5	31.3	25.9	27.2	1.2
116	Bikaneri	India	10	12	18.5	6.6	1.8	37.7	25.5	29.9	1.5
117	Black Kurumbai Adu	India	20	12	7.8	3.6	1.2	62.0	32.0	47.2	2.0
118	Mandya	India	10	12	11.1	4.7	1.3	95.5	28.3	58.7	3.4
119	Bellari White	India	10	12	7.1	3.0	1.4	94.3	28.5	56.3	3.4
120	Nellore	India	8	12	6.0	2.3	1.7	117.1	22.3	59.1	5.3
121	Ossimi	Egypt	11	6	31.0	3.0	3.1	47.0	26.0	30.5	1.8
122	Rahmani	Egypt	11	6	31.0	3.0	3.1	42.0	25.0	29.4	1.7
123	Blackhead Persian	Tanganyika	6	18	19.9	3.7	4.6	80.5	14.0	25.9	5.8
124	Tanganyika Long-tailed	Tanganyika	6	18	10.7	3.3	2.1	74.6	13.1	32.8	5.7
125	Yankasa	Nigeria	5	12	16.1	3.4	3.9	93.8	17.6	34.2	5.7
126	Ouda	Nigeria	5	12	13.2	3.2	3.3	85.2	15.6	31.9	5.5

We will use these data combined with the evolutionary history of breeds developed by Ryder, to investigate ways of determining whether a particular sheep, or group of sheep, show signs of regression towards its ancestor breeds.

6 Using skin data to measure distance between breeds

What we are going to do here is look for a *data driven* answer to the question posed in the title of this document - how to define a primitive sheep relative to a modern Merino sheep. We start by looking at the Carter(1968) [3] data. Figure 3 shows a plot of all of Carter's breed mean data for Ds and Dp.

The use of the ratio D_p/D_s was introduced by Dr Carter. We can see that it clearly separates the hairy African and Indian breeds, and that it also has high values for carpetwool breeds. Then there are a number of intermediate breeds with D_p/D_s at about 2, including the Soay. The Soay sheep sampled by Dr Carter were of the Wooly Soay type. Finally there are the various strains of Merino, the Merino derived breeds, and the British Longwools and Downswools with D_p/D_s between about 1.0 and 1.3.

The ratio D_p/D_s is not a complete descriptor of fleece diameter, it measures the tendency toward two-coatedness. There is also the average diameter of all the fibres D_{p+s}. If we plot these two we get Figure 4.

We see that the Merino lies in the lower left corner of Figure 4 - neither two-coated nor coarse, relative to other breeds.

An alternative way of parameterizing two-coatedness and coarsness is to use rotation of axes in the graph og D_p against D_s. If we rotate axes 45 degrees in Figure 3 we get one axis running along the line $D_p/D_s = 1$, and the second axis at right angles to this. We call the first axis *L-axis* (for large fibres), and the second axis *W-axis* (for wild two-coated type. A plot of W-axis aginst L-axis is given in Figure 5

We see the Merino still in the lower left corner, but the other breeds spaced in a manner indicating a positive correlation of large fibres with a wild type two-coated fleece. The closest thing to a primitive domestic sheep in these data are the hair sheep from Africa and India, and they have W values of around 50-60 microns. The wooly Soay has a W value of only 20 microns, but its L value is only 40 microns, compared to 70-100 microns for the hair breeds. Merinos are distinguished from British Longwools and Downswools by a lower L value, Their W values are similar. On this criterion, Merinos are no further separated from two-coatedness than are modern British breeds - all 3 have similar W values (and similar D_p/D_s.

Figure 3 is not the full story. Dr Carter also introduced another ratio N_s/N_p or the ratio of number of secondary follicles per unit area to number of primary follicles per unit area. If we look first at N_s and N_p (Figure 6) we see that the Merino (and Merino derived breeds) is substantially different from all other breeds in N_s, and apart from a couple of Indian breeds with a high N_p, that is
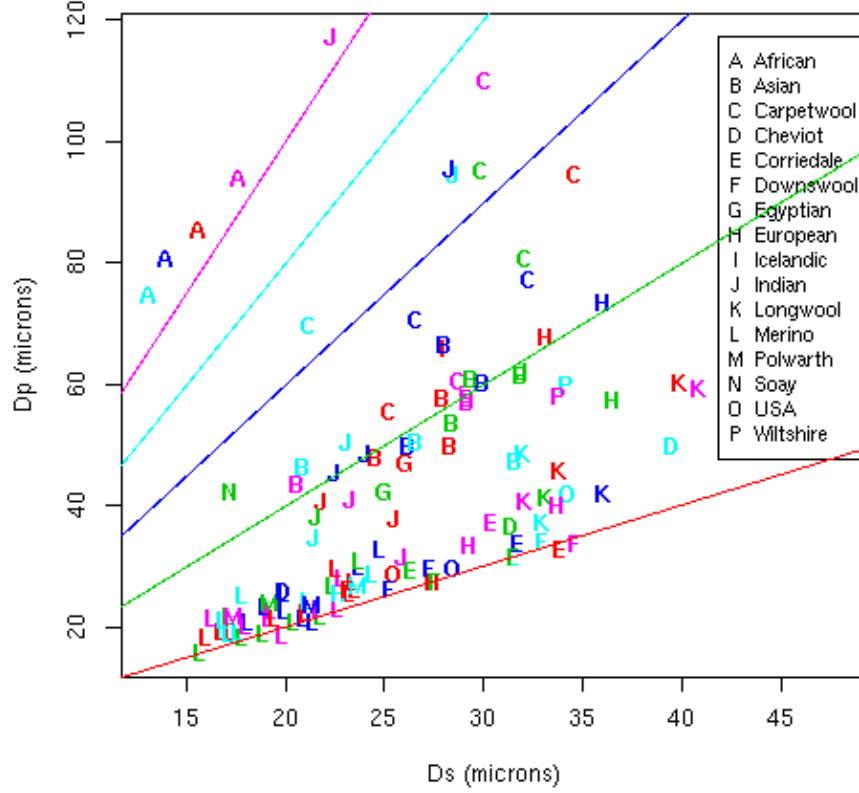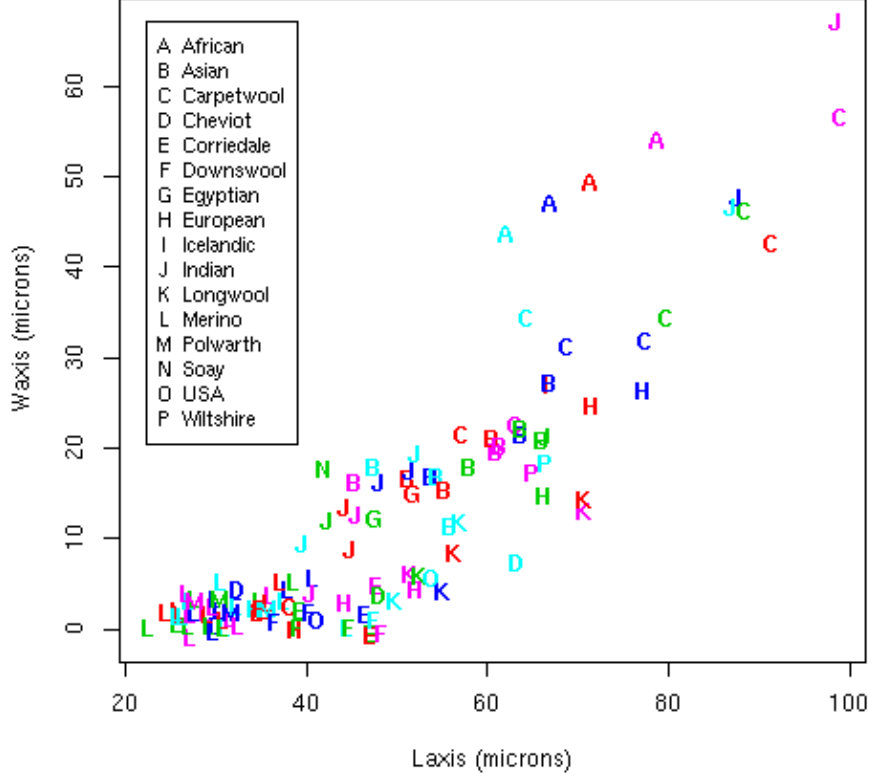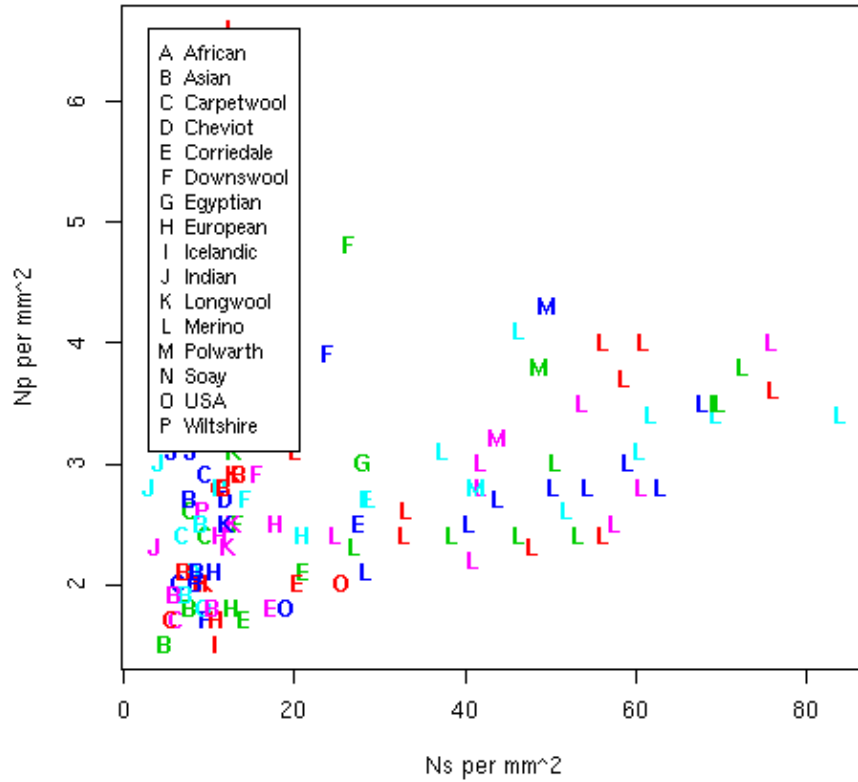
Figure 3: Plot of breed means of secondary fibre diameter D_s and primary fibre diameter D_p for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin. The coloured lines represent various values of the ratio D_p/D_s. Red is $D_p/D_s = 1$, green is $D_p/D_s = 2$, blue is $D_p/D_s = 3$, cyan is $D_{pi}/D_s = 4$, and magenta is $D_p/D_s = 5$.

about the only significant difference. Most non-Merino breeds have N_p between 1 and 3, and N_s less than 20.

We mostly see data on N_s presented as the ratio N_s/N_p rather than as the straight density. This is supposed to avoid some of the errors involved in density measurement. It also reduces the presentation to one trait, because N_p variation is small and probably reflects variations in body growth.

We can put the information from Carter's two ratios together, as in Figure 7 where we see the Merino distinguished mainly by a high N_s/N_p ratio, but also
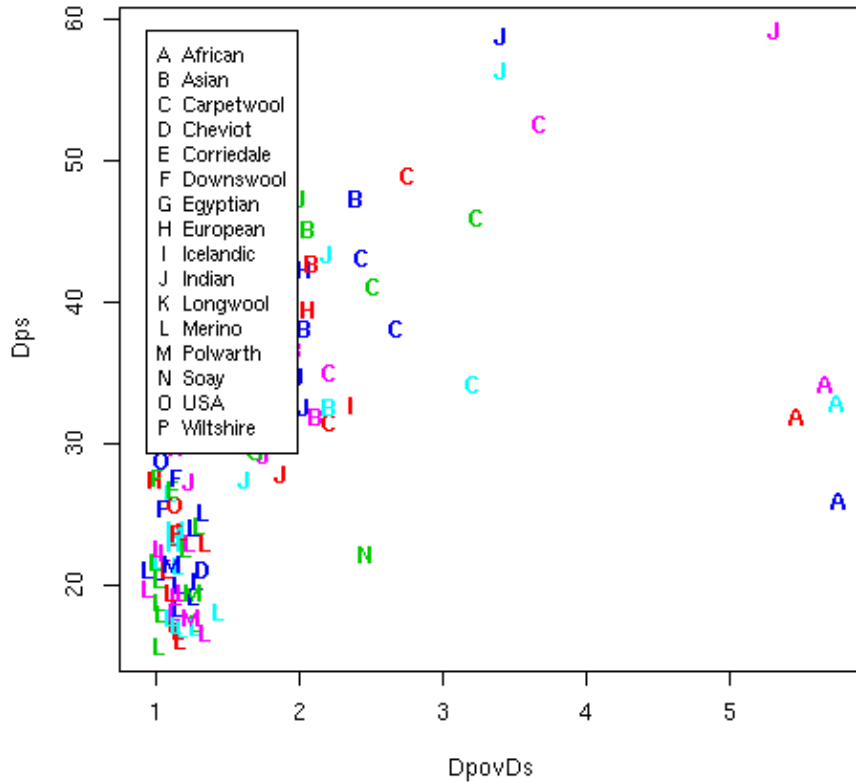
Figure 4: Plot of breed means of D_p/D_s and mean fibre diameter D_{ps} for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin.

by a low D_p/D_s ratio. Figure 7 condenses everything that the Carter(1968) [3] data have to say about breed differences in skin characteristics.

But Figure 7 is Carter's approach. For reasons that will become more apparent later, we prefer D_p to D_p/D_s ratio. So we repeat Figure 7 using D_p instead of D_p/D_s ratio in Figure 8

The relationship is still nonlinear, but less so, and the spread of points vertically is more uniform.

But this is not all that we know. We need to overlay these data with Ryder's summary of the stages in evolution of sheep breeds. We attermpt this in the next section

17

Figure 5: Plot of breed means of secondary fibre diameter (Ds) and primary fibre diameter (Dp) for 126 flocks sampled by Carter(1968) [3]. The axes have been rotated 45 degrees so that L-axis represents projections onto the line $D_p/D_s = 1$, and W-axis represents projections onto a line at right angles to the L-axis. The W-axis is interpreted a two-coatedness, and the L-axis is interpreted a large fibres. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin.

7 Combining skin data with knowledge of breed evolution

From Ryder's presentation of fibre data, and from various sources as indicated, we were able to put together some approximate measurements of sheep representing Ryder's stages of evolution of wool sheep. We have also added SRS Merino data, because this modern development of the Australian Merino is

18

Figure 6: Plot of breed means of secondary fibre density (Ns) and primary fibre density (Np) for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin.

becoming a significanltly different flece type. These are given in Table 3

It is clear that there has been more than one significant change during evolution of the Merino.

- reduction in diameter of primary fibres

- loss of medullation in primary fibres in Bronze Age sheep

- change from seasonal shedding to continuous growth of secondary fibres in Iron Age sheep
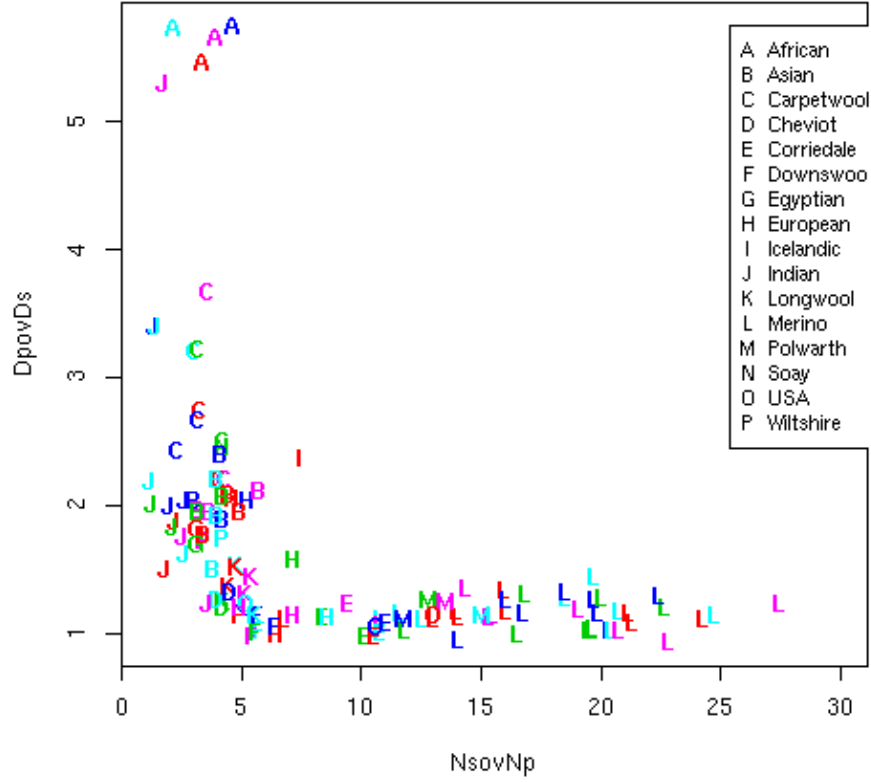
Figure 7: Plot of breed means of N_s/N_p and D_p/D_s for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin.

- large increase in S/P ratio at the Finewool Merino step. Probably a mutation at this point.

- further reduction of primary fibre diameter and further increase in S/P ratio at the SRS Merino step

There are some aspects of these changes which are not fully understood at the skin biology level. We do understand how the reduced Dp in SRS Merino sheep leads to increased S/P Ratio - it is explained by the pre-papila cell theory of Moore et al (1998) [12]. However the pre-papilla cell theory does not obviously explain the change from Wild to Hairy Medium Wool sheep - here we have a substantial reduction in Dp, but Ds increased and S/P was unaffected. Clearly
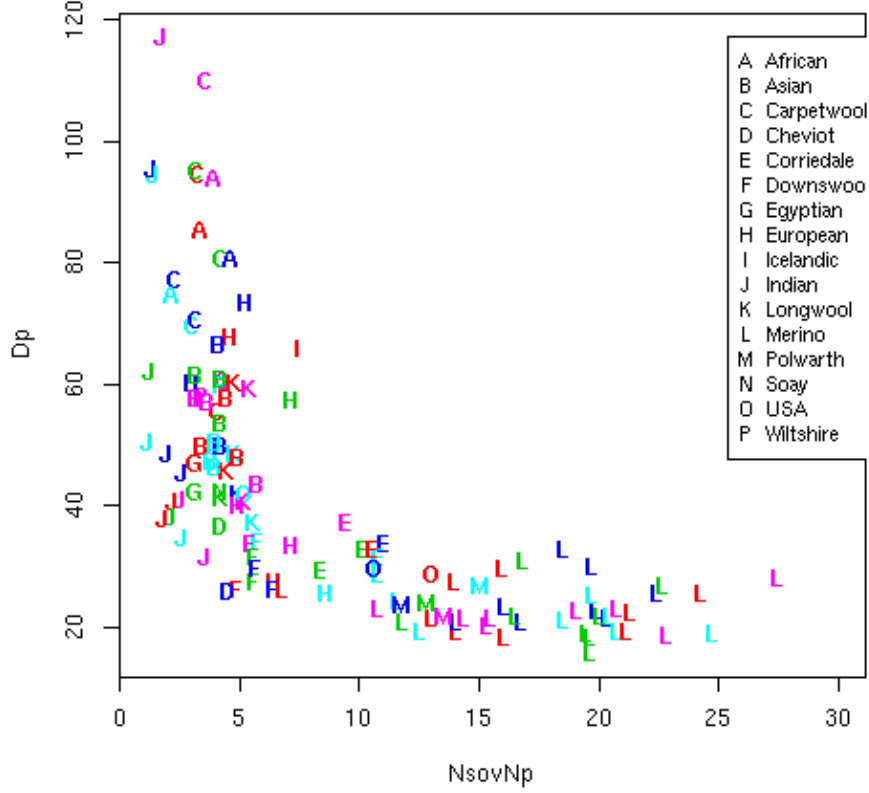
Figure 8: Plot of breed means of N_s/N_p and D_p for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin.

changing Dp by removing the medulla does somethin different from reducing Dp in a non-medullated fibre. The relationship between Dp and number of papilla cells in the follicle may not be the same for medullated fibres.

Then we have another substantial reduction in Dp between Hairy Medium Wool and Generalised Medium Wool, and Ds actually increased further but S/P was probably unchanged. It would seem that to become continuous growing secondary fibres became coarser.

Then there is the substantial jump in S/P Ratio at the Finewool Merino stage. This almost has to have been a single gene effect when it originally occurred. When Finewool Merino's are crossed with other breeds today we do not see single gene segregation with respect to S/P Ratio. This is because there

21

Table 3: Approximate measurements for sheep representing Ryder's 4 stages of Merino evolution, extended to the modern SRS Merino. Sources lines 1 to 3 Ryder(1992) [18], line 4 Carter(1968) [3], line 5 Watts(2017) [22].

Stage	Chronology	Dp	Ds	S/P ratio	Medullation	Shedding
Wild	Neolithic (10000-3000BC)	80-200	14-16	3-5	Outercoat kemp	Undercoat sheds
Hairy Medium Wool	Bronze Age (3000 - 1000BC)	40-140	18-28	4-5	Outercoat hair	Undercoat sheds
Generalised Medium Wool	Iron Age (1000BC - 700 AD)	20-50	18-35	5-7	No outer-coat?	Secondaries continuous
Finewool Merino	(1200AD - present)	18-20	17-19	15-25	No outer-coat	Secondaries continuous
SRS Fine Merino	(1990AD - present)	14-17	17-19	25-40	No outer-coat	Secondaries continuous

has been many years of selection of modifying genes from 1200AD to present. The original mutant was probably the Rex gene. If you look at the effects of Rex gene on the coat of cats (Fraser(1953) [4]) you see a substantial increase in S/P ratio and an increase in crimp in the fibres. Rex cats and rabbits have a *wavy* coat - Merino sheep have a more *wavy* coat than any other sheep breed. We can best explain the increased S/P Ratio of Modern Finewool Merinos compared to their ancestors, the Generalised Medium Wool, by postulating a Rex mutation, because this explains the concurrent change in crimp. In the SRS Merino the further increased S/P Ratio is associated with a reduced crimp frequency, so that is best explained by reference to the reduced Dp which according to the pre-papilla cell theory will lead to increased S/P ratio and reduced fibre curvature.

There is also a possibility thet the Finewool Merino may not have evolved from the Generalised Medium Wool as Ryder proposed. There is no direct historical account of Merino origins. It suddenly appeared in Spain in about the 12th century and there is the possibility that it came from North Africa into Spain (Massy(2007) [10]. There is therefore the possibility that it came directly from Hairy Medium Wool sheep, perhaps by a mutation, as suggested above. The Rex mutation in cats and rabbits turns a double coat into a fine single coat with crimped fibres, but it does not lead to continuous growing fibres. That would have to come from some other genetic change. Exactly what the lines of descent were does not matter here - we are looking at recurrence of ancestral characteristics not at how they were transmitted.

So we say that there are a number of issues to consider in Merino evolution. In spite of that we will attempt to reduce the comparisions to a couple of graphs

in which we attempt to superimpose Ryder's long term picture on the available data.

We start with the plot of D_s against D_p. Figure 9 is a repeat of Figure 3 with the approximate measurements of D_s and D_p representing Ryder's 4 stages of Merino evolution from Table 3 superimposed as coloured rectangles representing the approximate ranges of measurements.

The first thing to note is that the superimposed rectangles seem to locate sensibly in relation to the Carter(1968) [3] data. The African hair sheep are just at the lower tip of the Wild sheep rectangle. The green Hairy Medium Wool rectangle contains some carpet wool breeds and Asian (ie Middle Eastern) and Indian breeds. The Soay, which was a Wooly Soay, is just to the left of the blue Generalised Medium Wool rectangle, which also embraces some of the British and European breeds and the Merino derived breeds.

We now have an approximate criterion for judging whether a sheep is primitive. Figure 9 indicates that D_p alone is the prime criterion. The entire evolutionary history of the Merino has been a story of decreasing D_p at all stages, right down to the modern SRS Fine Merino with its D_p less than D_s. If we want to show that a particular Merino sample is showing signs of primitive characteristics, the first thing we should look at is D_p .

The story of how D_s changes during Merino evolution is more complicated. It increased between Wild sheep and Hairy Medium Wool sheep, increased slightly more in Generalised Medium Wool, then decreased again in Finewool Merino, and did not change going from there to SRS Fine Merino. We have to look at further data to understand this. There is a suggestion that the change to a continuous growth on secondary fibres from the undercoat led to an increase in secondary fibre diameter. There is also a suggestion that the large increase in S/P ratio in Finewool Merino compared to previous stages led to finer secondary fibres. Again we have to look at further data.

The use of D_p/D_s is problematic. Over a broad range it is essentially the same as using D_p - it clearly separates Wild from Hairy Medium Wool from Generalised Medium Wool, but it does not separate Generalised Medium Wool from Fine Merino or any of the other modern breeds..

If we move to the rotated version of the D_s versus D_p graph (Figure 5) and superimpose the data of Table 3 we get Figure 10.

We see that the direction of evolution has been a reduction in both W-axis and L-axis. So neither of these alone is sufficient to describe observed evolutionary changes.

We need to look at N_s/N_p ratio as well as D_p, so we redo Figure 8 with the approximate measurements representing Ryder's 4 evolutionary stages from Table 3 superimposed. This is shown in Figure 11

It is now clear that evolution of the Fine Merino has involved reduction of D_p and increase in N_s/N_p at all stages. The dramatic increase in N_s/N_p between Generalised Medium Wool and Fine Merino is the only *jump* in the evolutionary progression and suggests the possibility of a mutation, although there are breeds located in-between these two in Figure 11. The other obvious point is that the SRS Merino is a continuation and extension of the same evolutionary process.
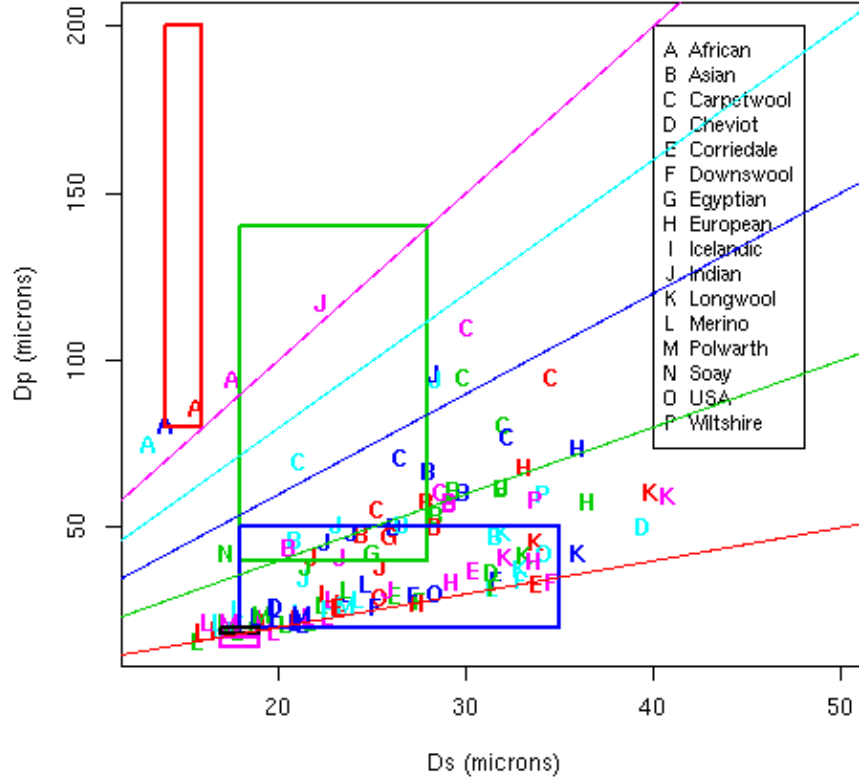
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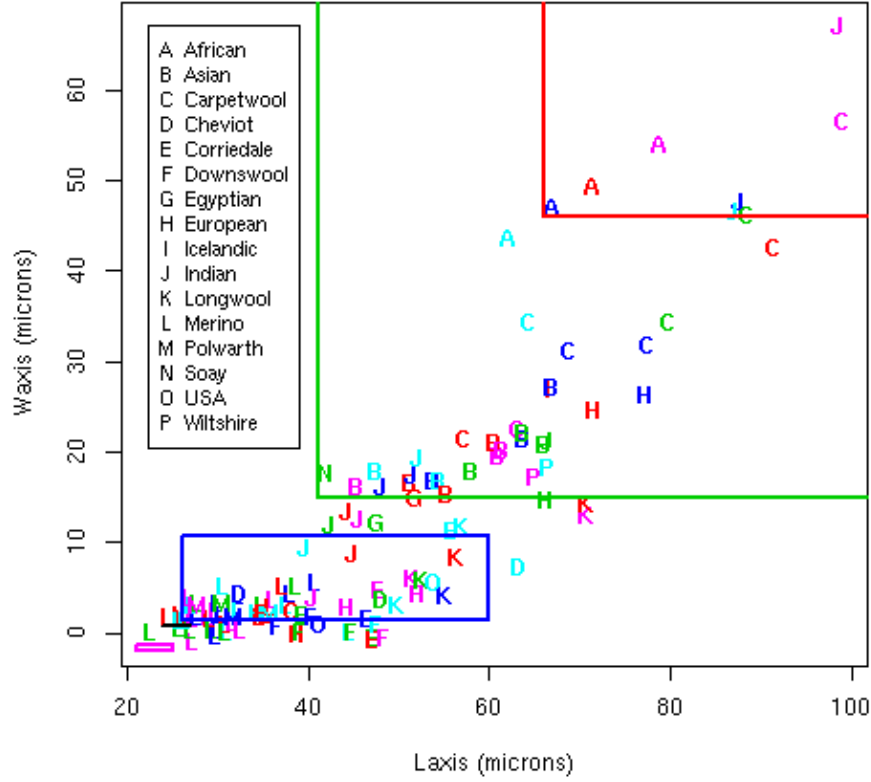Figure 9: Plot of breed means of secondary fibre diameter D_s and primary fibre diameter D_p for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin. The coloured lines represent various values of the ratio D_p/D_s. Red is $D_p/D_s = 1$, green is $D_p/D_s = 2$, blue is $D_p/D_s = 3$, cyan is $D_p/D_s = 4$, and magenta is $D_p/D_s = 5$. The coloured rectangles represent the approximate ranges of measurements for sheep representing Ryderś 4 stages of Merino evolution, plus the modern SRS Fine Merino. Red rectangle is Wild stage, green is Hairy Medium Wool, blue is Generalised Medium Wool, black is Finewool Merino, and magenta is SRS Fine Merino.

If we refer back to Figure 10 we see that the L-axis and W-axis transform is just a linear version of Figure 11. It uses D_s instead of N_s/N_p, but they are nearly the same thing. Figure 10 also shows an evolutionary progression involving both L-axis and W-axis. Figure 11 is preferred, because of the conceptual

Figure 10: Plot of breed means of secondary fibre diameter (Ds) and primary fibre diameter (Dp) for 126 flocks sampled by Carter(1968) [3]. The axes have been rotated 45 degrees so that L-axis represents projections onto the line $D_p/D_s = 1$, and W-axis represents projections onto a line at right angles to the L-axis. The W-axis is interpreted as two-coatedness, and the L-axis is interpreted as large fibres. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin. The coloured rectangles represent the approximate ranges of L-axis and W-axis values for sheep representing Ryders̀ 4 stages of Merino evolution, plus the modern SRS Fine Merino. Red rectangle is Wild stage, green is Hairy Medium Wool, blue is Generalised Medium Wool, black is Finewool Merino, and magenta is SRS Fine Merino.

difficulty of the L-axis and W-axis presentation.
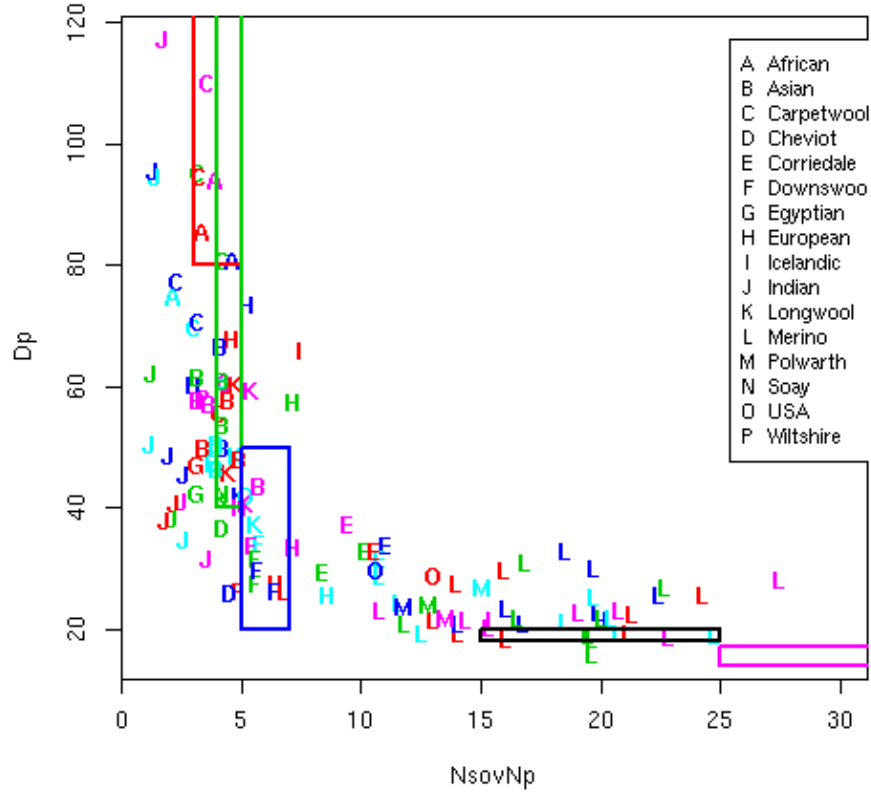
Figure 11: Plot of breed means of N_s/N_p and D_p for 126 flocks sampled by Carter(1968) [3]. The breeds have been grouped into a *breed type* which in some cases is an individual breed and in other cases is a country of origin. The coloured rectangles represent the approximate ranges of measurements for sheep representing Ryder's 4 stages of Merino Evolution, plus the Modern SRS Fine Merino. Red rectangle is Wild stage, green is Hairy Medium Wool, blue is Generalised Medium Wool, black is Finewool Merino, and magenta is SRS Fine Merino.

8 Discussion

We have reached a conclusion. If one wishes to decide whether a sheep or a flock shows primitive characteristics, one looks at the three things that have changed most during evolution of the Fine Merino

- diameter of primary fibres. The association of this with medullation and kemp formation can be noted.

- N_s/N_p ratio

- lack of continuous growth of secondary fibres - ie shedding of secondaries. Data on this are not often available.

There are sound biological reasons behind this choice. The pre-papilla cell theory of Moore et al (1998) [12] shows that if follicles formed at primary sites use only a small number if pre-papilla cells in their development, then the remaining undifferentiated population of pre-papilla cells will be larger and will multiply to more cells by the time secondary follicles start to form. If there are more pre-papilla cells than are required by the secondary sites, then the remaining cells will form branching follicles, leading to a large N_s/N_p ratio and fine secondary fibres. This theory cleary fits with what has happened in going from Generalised Medium Wool to Fine Merino to SRS Merino. In the two earlier steps, which involve reduction of medullation of primary fibres, we can not be sure how D_p would be related to the number of pre-papilla cells used by primary follicles. Between Wild sheep and Hairy Medium Wools, D_p has reduced enormously, but D_s has increased and N_s/N_p has not changed much. It may be that reducing D_p by reducing medullation is not accompanied by use of fewer pre-papilla cells. We simply have no data on this.

Why use two criteria (D_p and N_s/N_p) that are highly related? Well there is a temptation to look at the distribution of D_p from fibre to fibre on one animal, and to note presence of some very coarse primary fibres which may not impact greatly on the mean diameter of primaries. What is the significance of a proportion of coarse primary fibres? Well it says that some primary follicles have followed a more ancient development path, while others have not. So there should be some impact on the mean D_p and on N_s/N_p. Without going into distributions one can not quantify the impact. We should note that Ryder(1992) [18] emphasized the skewed shape of the diameter distribution of his Generalised Medium Wool sheep, and of the earlier stages.

We can combine D_p and N_s/N_p into one numerical criterion. If we look at Figure 11 we see that the relationship between D_p and N_s/N_p is hyperbolic (that is like the graph of Y against $1/X$). What we want to do is measure the position of a point along this hyperbolic curve. A convenient way of doing this is to use the ratio

$$\frac{D_p}{N_s/N_p} = \frac{D_p N_p}{N_s}$$

which varies from zero (at the extreme right of the graph) to infinity (at the extreme top of the graph), and is in units of microns. We can have a look at

how this ratio varies from sheep to sheep within a Merino flock using data from Jackson(2015) [7] by graphing the histogram of ratio values for 813 sheep. This is shown in Figure 12.
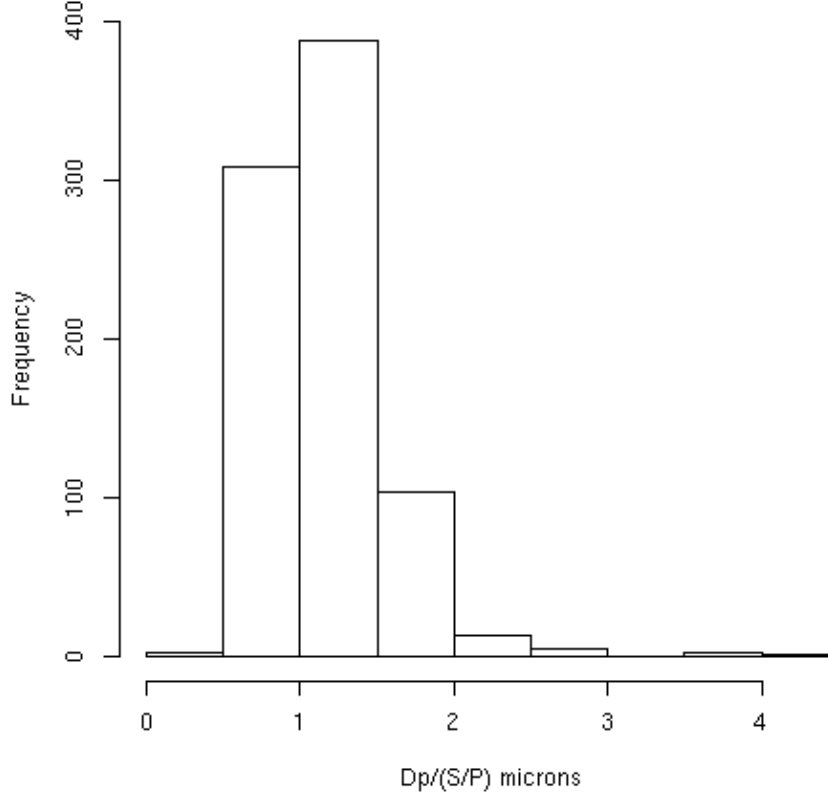

Figure 12: Histogram of values of the ratio $D_p/[N_s/N_p]$ for 813 sheep in a flock of medium to fine wool Merino ewes described by Jackson(2015) [7]

We see that this ratio has a substantial skew to the right in its histogram. There are small numbers of sheep with quite high ratios. How do we judge what is high. Well, let us calculate the $\frac{D_p}{N_s/N_p}$ ratio for each of Ryder's stages of evolution listed in Table 3. We get Wild sheep 26-40, Hairy Medium Wool 10-28, Generalised Medium Wool 4-7, Finewool Merino 1.2-0.8, SRS Merino 0.5-0.4. So those sheep with a ratio of 4 or greater are in the Generalised Medium Wool range, and way outside of the Finewool Merino range. So these individuals with a $\frac{D_p}{N_s/N_p}$ ratio of about 4 are abot 2000 years or 500 sheep generations of breeding away from an average Fine Wool Merino. One might argue about

whether one should call them *primitive* but they are extremes in the direction of the primitive ancestors of the Merino.

We can look to see if the extreme sheep are coming from D_p or N_s/N_p by examining their histograms separately. These are shown in Figures 13 and 14
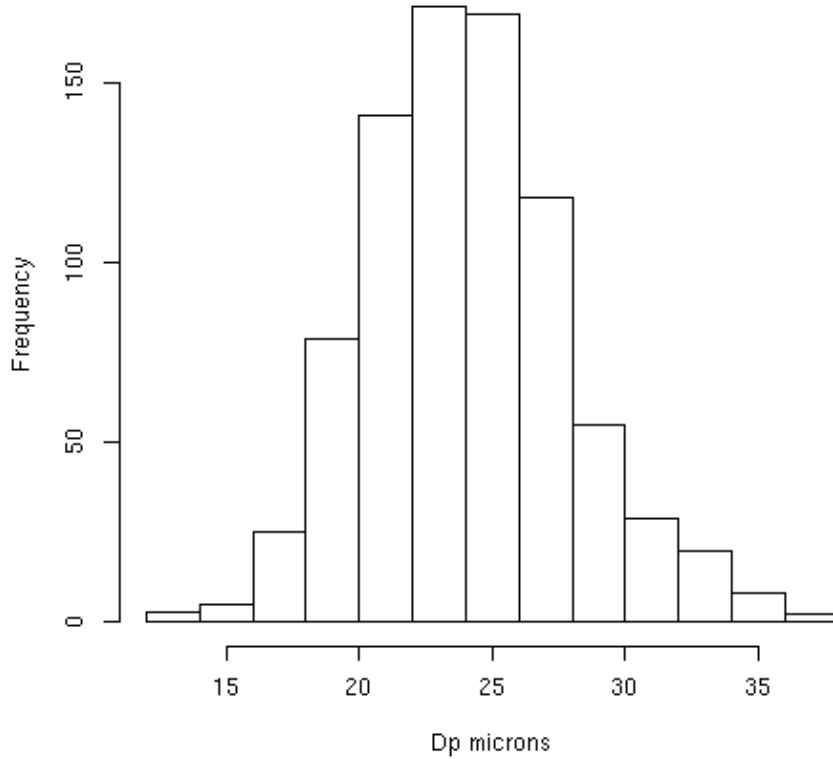

Figure 13: Histogram of values of D_p for 813 sheep in a flock of medium to fine wool Merino ewes described by Jackson(2015) [7]

and we see that D_p has a slight skew to the right while N_s/N_p has a slight skew to the left. Neither is as extreme in skew as the ratio. So combining the two criteria by computing position along the hyperbolic curve is a better detector of primitive characteristics than either trait alone. That is not surprising.

We have said nothing about why individual sheep or flocks might exhibit ancestral or primitive characteristics. The genetics of atavism is another whole topic. The first step is to demonstrate that atavistic sheep actually occur and in which characteristics, and which flocks, is the phenomenon most obvious. That
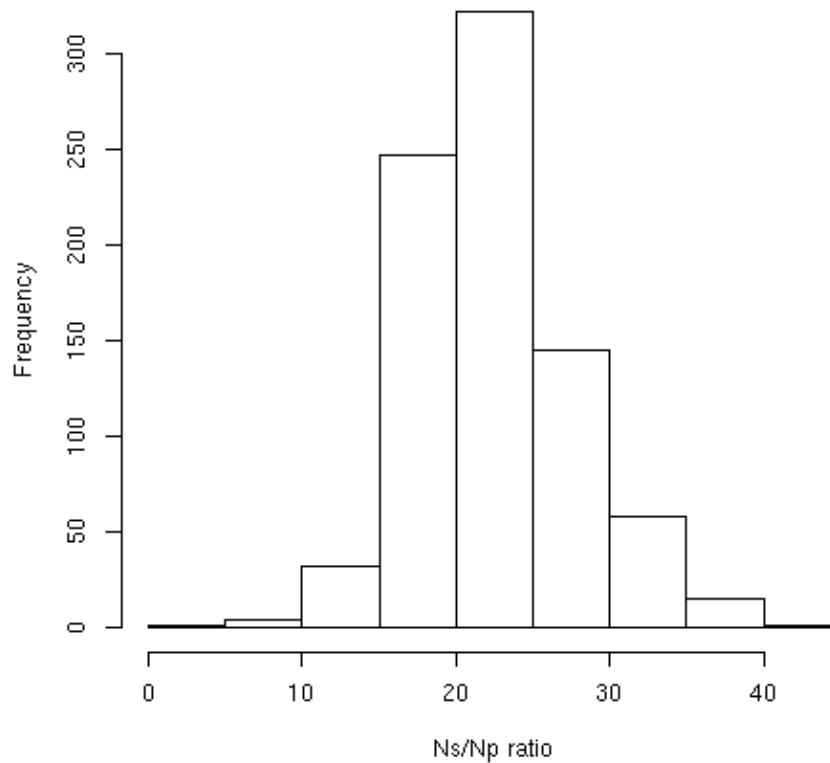
Figure 14: Histogram of values of N_s/N_p for 813 sheep in a flock of medium to fine wool Merino ewes described by Jackson(2015) [7]

is the task of the current rewrite of Jackson et al (1990) [9].

We shall end with a little mystery (courtesy of Louis Robinson [16]). Why do most breeds of domestic sheep have long tails? They are supposedly evolved from Wild sheep. All Wild sheep breeds have short tails. When did the change occur, and why? One struggles to think of any reason why early sheep breeders would have deliberately selected for long tails. After all, shepherds have spent the last several thousand years cutting them off. Perhaps long tail is genetically linked to something else, perhaps continuous growing secondary fibres. We simply do not know.

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