The histology of the pre-natal follicle and hair fibre in four curl types of the Karakul sheep

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In the Karakul sheep of Southern Africa four major pelt types can be identified, namely pipe curl, developed shallow curl, shallow curl and watersilk types. A study of the foetal skin was undertaken to determine whether histological differences do exist between these four types. Skin samples were taken at 10 day intervals from 48 to 138 day-old foetuses. The biopsies were from 11 predetermined sites. In vertical sections skin thickness, follicle lengths and depths, angle of follicles to skin surface and bulb diameter were measured. In horizontal sections counts were made of primary and secondary follicles, as well as anlagen, to determine secondary to primary (S/P) ratios and density, while the long and short axes of fibres were measured to determine mean diameter. Subjective evaluations were carried out on fibre contour, presence or absence of medullae and the nature of the pigmentation. Although differences between lines were established in most of the characteristics it was not possible to relate them to curl pattern.
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By die Karakoelskaap van Suidelike Afrika word vier hoof krullyne onderskei nl. die pypkrul, ontwikkelde vlakkrul, vlakkrul en watersy. 'n Ondersoek van die fetusvel is onderneem om te probeer vasstel of enige histologiese verskille tussen die vier krultipes bestaan. Velmonsters is op elf bepaalde posisies geneem van ouderdomsbepaalde fetusse met tussenpose van 10 dae vanaf die ouderdomme van 48 tot 138 dae. In vertikale sneë is metings uitgevoer op veldikte, follikellengte en -diepte, hoek van follikel teenoor veloppervlakte en follikeldeursneë. In die horisontale sneë is tellings van follikels gemaak vir bepaling van primêre tot sekondêre (S/P) veselverhoudings en follikeldigtheid, terwyl lang en kort asse van vesels vir gemiddelde deursneë gemeet is. Subjektiewe evaluasies van veselkontoer, aan- of afwesigheid van medullas en aard van pigmentasie is gedoen. Alhoewel verskille tussen die lyne ten opsigte van meeste van die eienskappe vasgestel kon word, was dit nie moontlik om dit spesifiek aan krulpatroon te koppel nie.
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Introduction

The Karakul pelt, through its Russian connection, has been an article of high fashion for many centuries. Since this pelt is found in so many variations it was able to maintain its popularity in élite circles. The value of a specific pelt is determined by its particular pattern which will appeal to the selective buyer. Even the smallest deviations in a particular pattern at birth could make the difference between a high and low quality pelt. A few days of post-natal development can bring about major changes to the coat which make the pelt totally unfit for utilization in the trade.

As a continuous carefully-controlled variation in pattern is imperative for survival of the Karakul pelt in the world of fashion, all breeders are naturally alert to the introduction of suitable new types to the market. The shallow curl and watersilk types, developed in South West Africa towards the middle of this century, were products of this search to augment the already existing types.

That prime importance of the pre-natal period of development of the Karakul foetus follows from the fact that the fur qualities exhibited at birth are products of this phase. To investigate this evolvement, the four regionally acknowledged major pelt types i.e. the pipecurl, developed shallow curl, shallow curl and watersilk types were selected for a pre-natal histological study. The rationale was that the differences in pattern between these four types could possibly be traced through a microscopic study of the skin from different parts of the body.

The differences between the four types were based mainly on the amount of curling exhibited by the individual fibres (Nel, 1968). Of the four types the pipe curl type has the tightest curl formation in that the fibre curls upon itself to form a loop. The less the fibre curls upon itself the more open is the pattern, resulting in the shallow-curl or watersilk types.

As the extreme shallowcurl types developed solely in Southern Africa, no relevant literature pertaining to the histology exists on this subject. Parallel studies do, however, exist on the follicle development in the Merino foetus (Duerden & Ritchie, 1924, Carter, 1939, 1943, Carter & Hardy, 1947 and Hardy & Lyne, 1956); on hair development in the Angora goat foetus (Wentzel, 1968);

the foetal skin development in the British breeds of sheep (Wildman, 1932) and the Karakul's pre-natal development (Margolena, 1954). The study by Margolena (1954) was confined to the development of the pipe curl type which is chiefly produced in countries outside Southern Africa.

Procedure

Experimental animals

Forty pure-bred Karakul ewes aged from 4 to 6 years were used as mother-stock. These animals all black, and part of the stud kept on the Experimental Station at Neudam, near Windhoek, South West Africa, were available from the F_2-generation of a curl type experiment where the 4 main types were bred parallel to one another. From each type 10 ewes were selected to serve as experimental animals representing pipe curl, developed shallow curl, shallow curl and watersilk types respectively. The ewes of each type were hand-mated to rams of that particular type and the dates recorded.

Experimental design

The ewes from each curl type were slaughtered according to a specific timetable to obtain a foetus of the appropriate age. The first foetuses were obtained on the 48th day of pregnancy and then consecutively on every tenth day until the 138th day. No foetuses were collected for the 148th day as this was the full-term period. All the specimens were preserved in 10% neutral formalin in large specimen jars. A modification of the system, developed by Carter & Hardy (1947) for skin sampling, was used to take eleven samples on pre-selected sites over the body of the foetus. Principally these covered the dorsal, lateral and ventral aspects of the body (Figure 1).

Laboratory methods

Processing

Skin samples from the various body regions of the older foetuses were cleared of surface hairs. Wherever possible duplicate specimens were prepared for horizontal as well as vertical sectioning. Dehydration, clearing and wax infiltration was carried out in batches through an automatic tissue processor (Shandon Elliot). Ceresine (2½%) was added to the paraffinwax (M.P. 60°C) used for embedding, to ensure adhesion of the ribbon when preparing serial sections. Sectioning was carried out on a rotary (Spencer) microtome and ribbons were floated on a waterbath (40°C) and transferred from there to slides previously prepared with albumen. Horizontal sections were stained with haematoxylin and eosin and the vertical sections with Mallory's collagen stain according to the formula described by Luna (1968).

Measurements

(i) Vertical sections were measured for skin thickness, follicle length and depth, angle of follicle emergence to skin surface and follicle bulb diameter at 50× magnification, according to the chart of Lyne & Heideman (1959). Counts were made of the number of hair germs over one linear mm for foetal ages 88 and 98 days under the projection microscope (Leitz) at 140× magnification. Data were gathered in respect of the initiation of the follicle and its accessory structures. Only intact follicles were considered for measuring.

(ii) From horizontal sections field tracings were prepared for secondary/primary (S/P) follicle ratios, as well as for determinations of relative density by means of a projection microscope at 140× magnification on previously prepared folio pages with a demarcated zone corresponding to one square millimetre on the skin. To facilitate counting this square was quartered. All follicles and follicle anlagen in the area were counted. To maintain a balanced mean, follicles and anlagen overlapping on two sides were included in the count and those on the other two sides were discarded. Duplicate readings were made on slides used for evaluations. S/P ratios were determined for ages where the primary and secondary follicle population, as well as the secondary anlagen were properly discernible. Since material younger than 108 days was still undeveloped, especially as far as secondary follicles were concerned, no comparative evaluations could be undertaken and only subjective assessments could be made.

Follicle and fibre diameters were taken of primary and secondary fibres for ages 128 and 138 days. The long axis and short axis of each were measured and the mean accepted as the diameter. At younger foetal ages, secondary follicles were not developed sufficiently for any measurement.

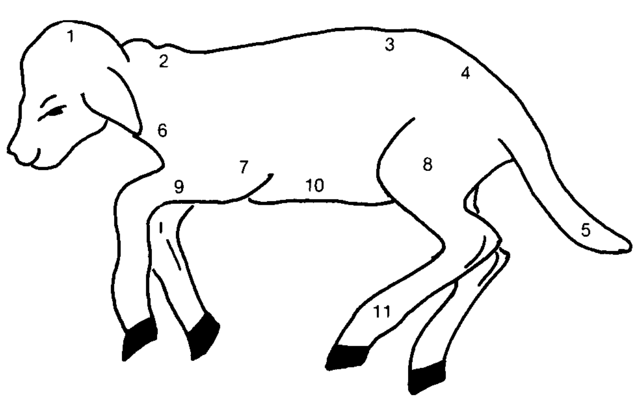

Figure 1 Sampling positions (partly according to Carter & Hardy, 1947).

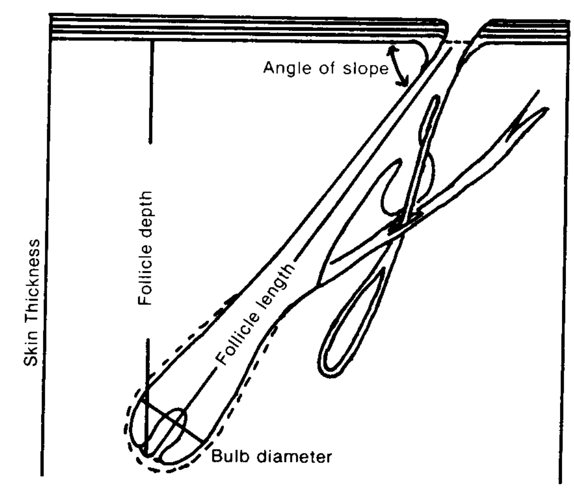

Figure 2 Measuring positions — vertical aspect (adapted from Lyne & Heideman, 1959).

Subjective evaluations

Since comparative microscopic facilities were not obtainable at the time of this study, the only method available for direct comparison of the skin sections of the four curl types was to prepare micrographs. All micrographs were processed at identical magnification at the critical evaluation levels of the three areas representative of the middle of the pelt. These were the mid-neck, mid-back and mid-rump positions, chosen as representing the most valuable parts of the pelt. Preparation of micrographs from all the sites would have been an impossible task.

Differences were sought in follicle grouping, proportion of secondary follicles (including anlagen) per primary follicle, fibre development, follicle and fibre size as well as fibre contour, the presence or absence of medullation on a qualitative basis and the nature of the pigment. Differences could be ascertained by comparing the micrographs in juxtaposition.

Results

Measurements

The skin in vertical aspects

The dermis varies in thickness over the whole body (Sar, Calhoun & Lois, 1966). The thickest skin is encountered over the neck and back of the animal while a thinning takes place towards the belly and extremities. Skin thickness is determined by the quantity of connective tissue present in the dermis, since the epidermis in the mature sheep seldom exceeds three cell layers.

In the 48-day-old foetus the epidermis is very thin, not more than one cell layer thick. This is the germinal layer and a surface layer, the periderm, is also visible (Bell, 1967; Pinkus, 1958). At this stage the first anlagen, or primitive hair germ, starts to develop on the forehead. Margolena (1954) stated that age and sex do not influence the thickness of the germinal layer, which shows a tendency to be thinner on the ventral and dorsal aspects of young lambs and mature sheep.

This survey covered the four chief types which were compared in respect of various measurable and immeasurable attributes. For this purpose the ages most often considered were 108, 118, 128 and 138 days, when follicle grouping was already reasonably advanced.

Due to a lack of measurable attributes, the skin characteristics of the younger foetuses could not be quantitatively evaluated with any real degree of confidence.

Skin thickness

Concomitant with growth, skin thickness gradually increased with age from 108 (approx. 33,26 mm) to 128 days (approx. 71,32 mm), as can be seen in Figure 3. The pipe curl type exhibited a slightly different pattern of skin development from those of the other three types. Skin thickness increased more rapidly between 118 and 128 days in this case than in the other three types, but then inexplicably showed a decrease between 128 and 138 days (Figure 3), although on average it was thickest for all age groups (Figure 4).

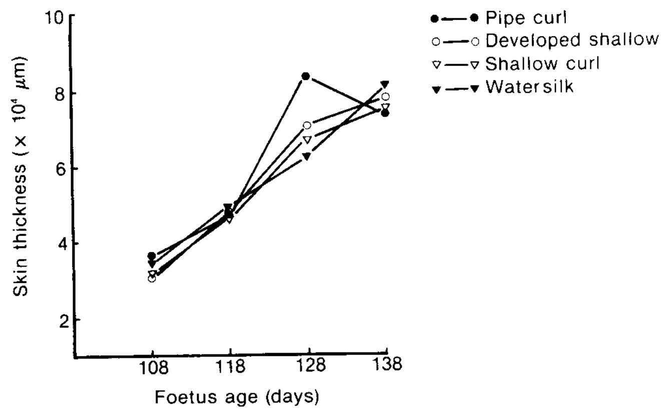

Figure 3 Skin thickness of 4 curl types in Karakul sheep at 4 foetal ages.

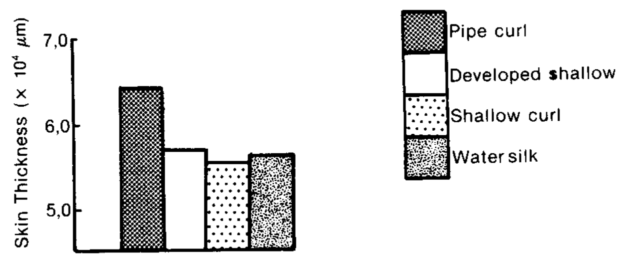

Figure 4 Skin thickness of 4 curl types in Karakul sheep.

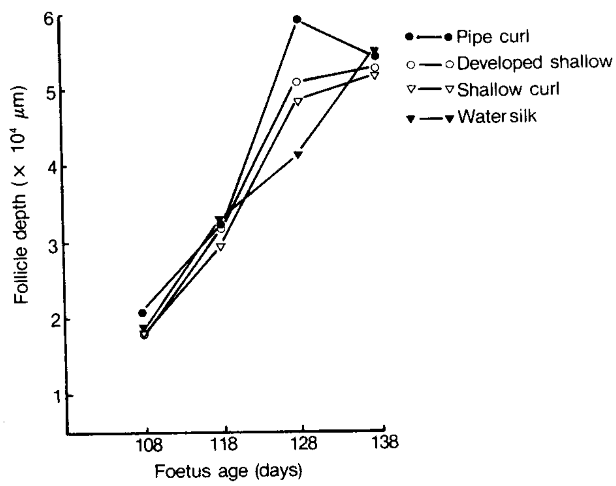

Figure 5 Follicle depth of 4 curl types in Karakul sheep at 4 foetal ages.

Follicle depth

This characteristic showed the expected increase for foetal ages 108 – 128 days in all 4 curl types (Figure 5). A normal increase was noted for shallow and developed curl types from 128 – 138 days but the watersilk type showed a sharper increment and the pipe curl type a lower reading in this respect (Figure 5). On average the pipe curl type showed the highest value for follicle depth (Figure 6). The same trend was encountered in the increase of follicle depth as in the increase of skin thickness over the 4 age groups.

Follicle length

The normal elongation of the shaft of the follicle also took place for the 4 curl types over the 4 successive age periods. Shallow curl types, however, exhibited a decrease in

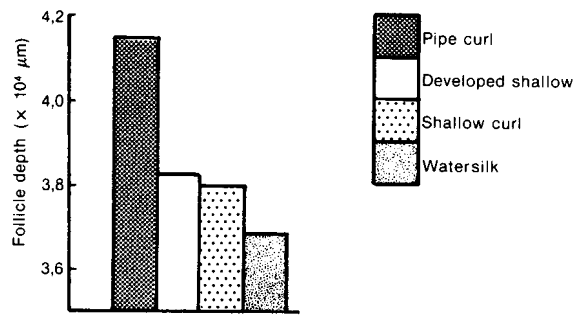

Figure 6 Follicle depth of 4 curl types in Karakul sheep.

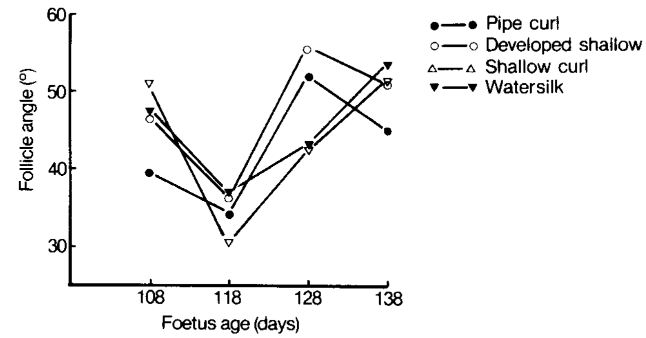

Figure 9 Follicle angle of 4 curl types in Karakul sheep at 4 foetal ages.

length for the period 128–138 days (Figure 7). The pipe curl type exhibited follicles with the greatest length, followed by shallow curl, developed shallow curl and watersilk types. (Figure 8).

Follicle angle

The ectal angle was measured where the follicle formed an acute angle with the skin surface. With pipe curl and developed shallow curl types this angle decreased from 108 to 118 days pre-natal. It increased again at 128 days and then declined again at 138 days. (Figure 9). Shallow curl and watersilk types showed a similar pattern up to 118 days (a decrease) and then an upward trend to 138 days (Figure 9). The developed shallow curl type had on average the largest ectal angles, thus having follicles with the closest approach to the perpendicular (Figure 10).

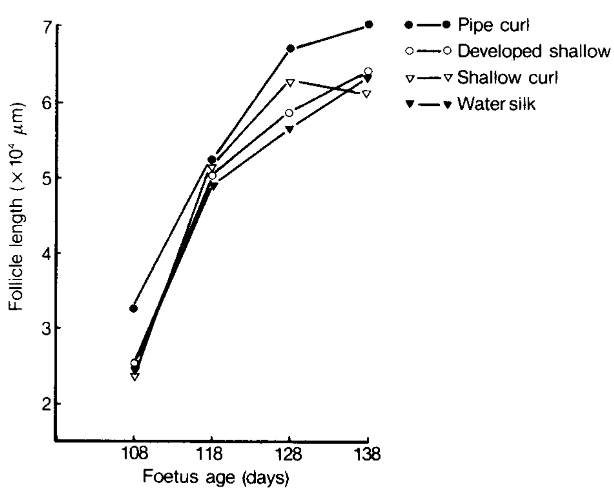

Figure 7 Follicle length of 4 curl types in Karakul sheep at 4 foetal ages.

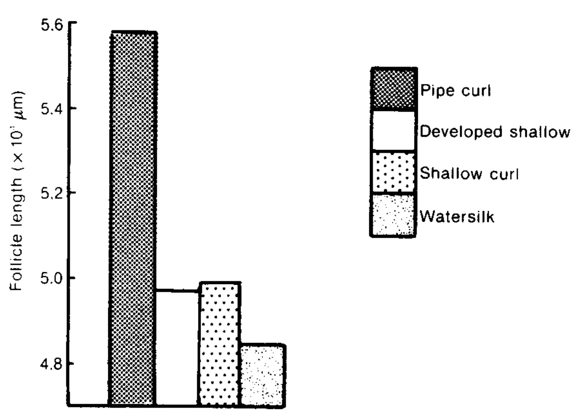

Figure 8 Follicle length of 4 curl types in Karakul sheep.

Follicle bulb diameter

In all four types the diameter of the follicle bulb expanded from 108 to 128 days of foetal development (Figure 11). In the next stage of development only the watersilk type displayed an increase in diameter. On average the shallow curl type had the smallest bulb diameter (Figure 12).

Follicle anlagen

From the counts made of the number of hair germs per linear mm at the foetal ages of 88 and 98 days, the highest numbers of anlagen as well as follicles, in various stages of development, were counted in the pipe curl types (23/mm and 43/mm), an advantage probably already existing at birth (Figure 13). The developed shallow curl type had the second highest count (37/mm) at 98 days, followed

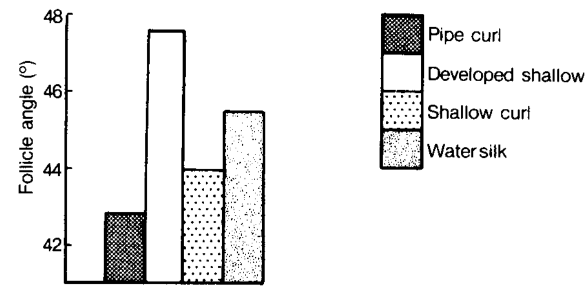

Figure 10 Follicle angle of 4 curl types in Karakul sheep.

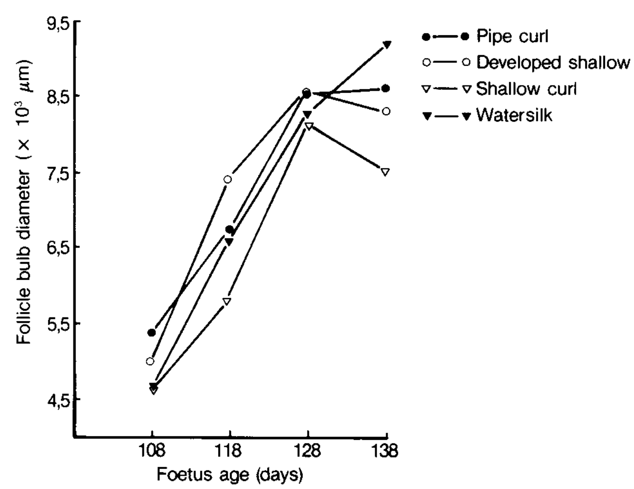

Figure 11 Follicle bulb diameter of 4 curl types in Karakul sheep at 4 foetal ages.

by the watersilk type (28/mm), and shallow curl type (25/mm).

Of the first foetuses collected, the 48-day-old pipe curl type had a developing hair germ on the site of the forehead. At 58 days the anlagen were reasonably abundant in that area (Figure 14a.)

From this age onwards the initiation of further hair germs could be expected at this position for all foetuses concerned. Due to the spacing of these hair germs and the thinness of the sections, it was difficult to demonstrate their presence in every section.

As the newly developing follicles grow down from the epidermis into the dermis, various accessory structures, comprising the sudiferous and sebaceous glands as well as the arrector muscles, also begin to develop. The stages when this occurs and the mechanism whereby it is initiated, have, as mentioned earlier, been thoroughly covered in the literature for a number of important sheep breeds. The developmental stages of the Karakul have been

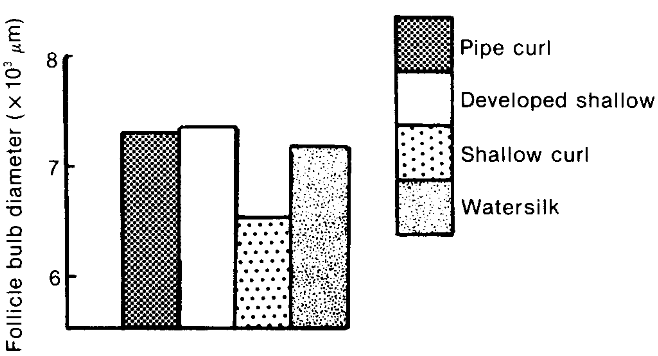

Figure 12 Follicle bulb diameter of 4 curl types in Karakul sheep.

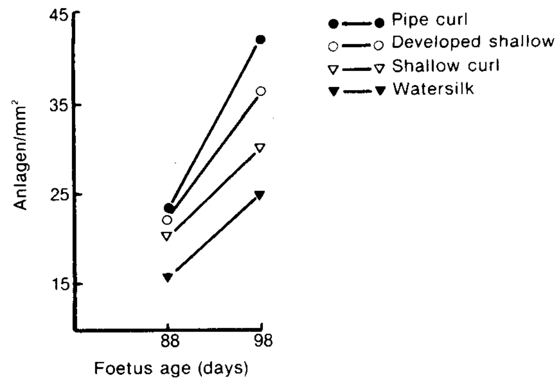

Figure 13 Follicle anlagen total in Karakul sheep at 2 foetal ages.

described in detail by Margolena (1954) and show no important deviations from those catalogued for other breeds.

By employing Mallory's collagen stain it was possible to demonstrate a qualitative difference in the collagen structure at various levels in the skin as could be seen from the dermis proper and the underlying hypodermis. In some of the preparations from 128- and 138-day-old foetuses it was observed that when follicles penetrate into the dermis and reach the hypodermal layer, usually at an angle, no further follicle descent seems to occur. The impression gained was that owing to the vigour of the follicle bulb, the constituent collagen fibres of the hypodermis were displaced in some cases but no real piercing of that tissue took place. In other cases it would appear that the follicle bulb and the papilla were undergoing some degree of flattening (Figure 14b) due to growth pressure on the barrier layer. Artefact formation was suggested, but appeared not to be involved since this phenomenon was

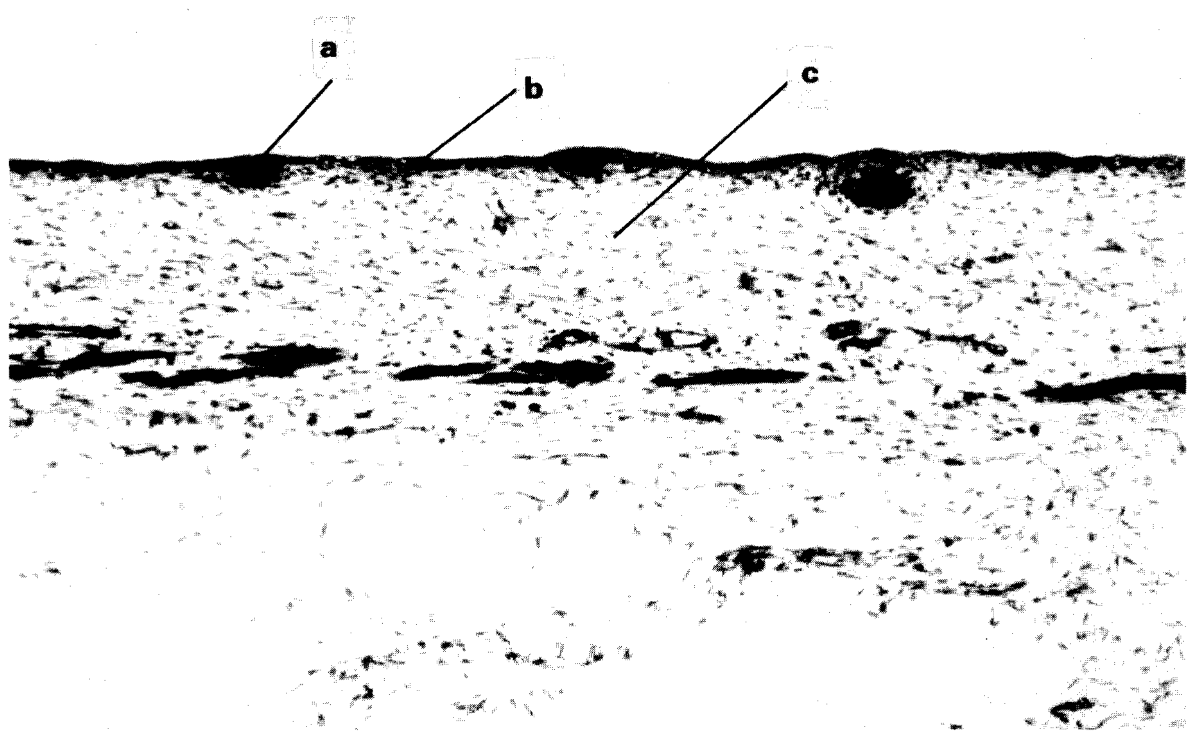

Figure 14a Anlagen. Pipe curl. Vertical section. Forehead. 58 days pre-natal. Magn. 114×. a. Anlagen. b. Periderm. c. Mesenchyme.

seen in different sections and from various positions. This barrier effect could also explain the deflection of the bulb to any side as it reacts to the force exerted by downward growth.

The pigment in the hair fibre was usually gathered into granular bead-shaped clumps in the shaft of the hair fibre. Pigment formation seems to begin at the same time as follicle development. Two types of pigment were observed: tyrosine-melanin of the brown-black type and pheomelanin of the red-yellow type occurring along the length of the fibre shaft according to the classification of Fitzpatrick, Brunet & Kukita, (1958).

Horizontal aspects of the skin

Whereas the vertical section gives the thickness of the layers of the skin and the orientation of the epidermal derivatives in the dermis in profile, the horizontal section provides a picture of the grouping and the relationship of the follicles and their accessories within the compass of the spread-out skin (Figure 14c).

In the horizontally-orientated foetal skin, the initiation of the earliest of primary follicles and the later formation of the secondary follicles in relation to the primaries, can be more fully traced through the developmental stages. This development is of such a nature that only in the foetal skin over 115 days of age, can the grouping of the follicles be traced with reasonable accuracy. Of necessity this type of evaluation could only be directed at the 118 to 138 day age groups.

At 108 days the primary follicle grouping was discernible, while secondary follicles were still mostly in the hair germ state. The means of the duplicate readings are summarised in Table 1.

Table 1 Mean St/Pt of 11 sampling sites

Curltype	Age (days) 108	118	128	138	$\bar{x}$
1. Pipe curl	1,14	2,60	3,00	3,16	2,48
2. Developed shallow	0,59	2,26	1,55	2,32	1,68
3. Shallow curl	0,94	1,54	1,90	2,82	1,80
4. Water Silk	0,70	2,10	2,49	2,49	1,95
$\bar{x}$	0,84	2,13	2,24	2,69	1,98

Secondary/primary follicle ratio (S/P ratio)

The number of secondary and primary follicles expressed as S/P ratios were calculated for the 4 curl types at the 4 age groups concerned, the original 11 sampling sites on each foetus being regarded as replicates for the calculations (Table 1).

From Table 1 it can be inferred that the S/P ratio increases with age, the reason being that the primary follicle population becomes stabilized at approximately 100 days in contrast to the still developing secondary follicle population which can even continue to develop post-natally. Pre-natally, however, the trend is not absolutely consistent.

Over all 4 ages the pipe curl type had a higher S/P ratio (2,48) than any of the other types. In the developed shallow curl type the S/P ratio diminished between the ages of 118 to 128 days (2,26 – 1,55) and the watersilk type

Figure 14b Deflected follicle bulbs on hypodermal layer. Pipe curl. Vertical section. Tail position. 128 days pre-natal. Magn. 114×. a. Follicle bulb. b. Hypodermis.

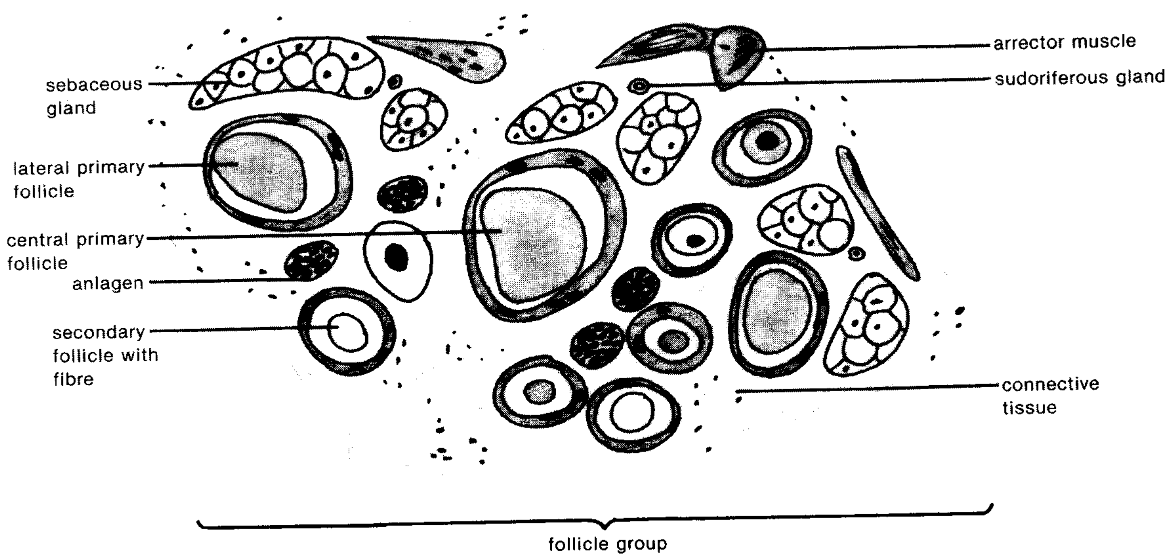

Figure 14c Diagrammatic representation of follicle group.

showed no increase in this ratio from 128 to 138 days (Table 1).

At the age periods of 128 and 138 days the S/P ratio of the pipe curl (S/P 3,00 and 3,16) related quite well to that of two mature Karakuls (S/P 3,33 and 3,45) which were available for comparison.

Density

Density, designated as the number of follicles per unit area, could only be determined in a relative way since numerous factors such as shrinkage and body position influence this reading. The pipe curl type showed more follicles per mm^2 for all the sites ($167/mm^2$) examined than the other three types (Figure 15) and the higher number of secondary hair germs may be indicative of a higher density figure ($396/mm^2$) for the pipe curl type than the shallow curl type ($330/mm^2$).

Carter (1943) in the woolled sheep and Margolena (1954) in the Karakul also found the density to be the highest on the neck, shoulder and back regions of the animal and decreasing towards the belly and extremities.

Follicle and fibre sizes

Follicle shaft and fibre diameters were found to be proportionate at the level of the sebaceous gland at 138 days of foetal age, in that the diameter of the follicle shaft was approximately twice that of the fibre (Table 2). This observation is not valid for positions above or below the level of the sebaceous gland. Fibre structure regularity depends on follicle structure regularity which will ultimately be reflected in the pattern of the skin covering. A variation was noticed in the different curl types between follicle shaft diameter and fibre diameter with the watersilk having the largest primary follicles. A large variation in follicle diameter was noticeable between primaries and secondaries and to some extent between central primary and lateral primary follicles.

The diversity in follicle diameter, referred to previously, was also evident as regards fibre diameter. A large variation was found in all foetuses especially at 128 and 138 days. Considerable variation in fibre diameter was observed on the same site and between sites (Figures 16a–d). Those sites situated anteriorly had larger fibres than those situated posteriorly. Variation in diameter was not confined to differences between primary and secondary fibres but was found between the primary fibres themselves. Central primary fibres were usually larger than lateral primaries. First-formed seondaries were also larger than ones formed

Table 2 Mean fibre and follicle diameter of four curl types at 138 days

	Fibre $\bar{x}$		Outer of follicle $\bar{x}$	
Curl types	Prim.	Sec.	Prim.	Sec.
1. Pipe curl	49,70	20,70	93,90	49,00
2. Developed shallow	54,20	20,65	101,20	49,95
3. Shallow curl	42,60	21,50	81,00	49,20
4. Watersilk	60,40	19,50	99,50	49,30

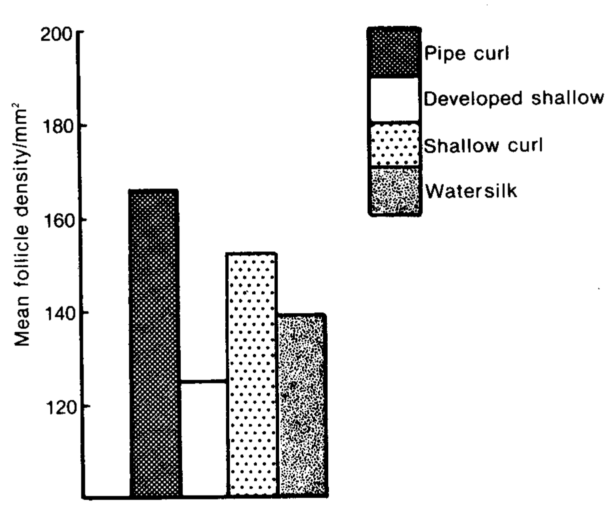

Figure 15 Mean follicle density/mm^2 for 4 curl types and 11 positions at 108, 118, 128 & 138 days.

later. The watersilk type in addition to having the largest primary fibres, also had the most uniform spread of fibre diameter, taking into account the differences between fibre types.

Observations

Trio-grouping

The most clearly defined trio-grouping, which relates to the 3 primaries with their complementary secondaries, was observed in the watersilk type (Figure 16d). Trio-grouping was at times highly disorganized and irregular in respect of the arrangement of the primary groups, mostly due to a disorderly pattern of skin growth resulting in poorly defined follicle groups. Therefore it was also difficult to identify proper trio-groups within the other 3 lines studied.

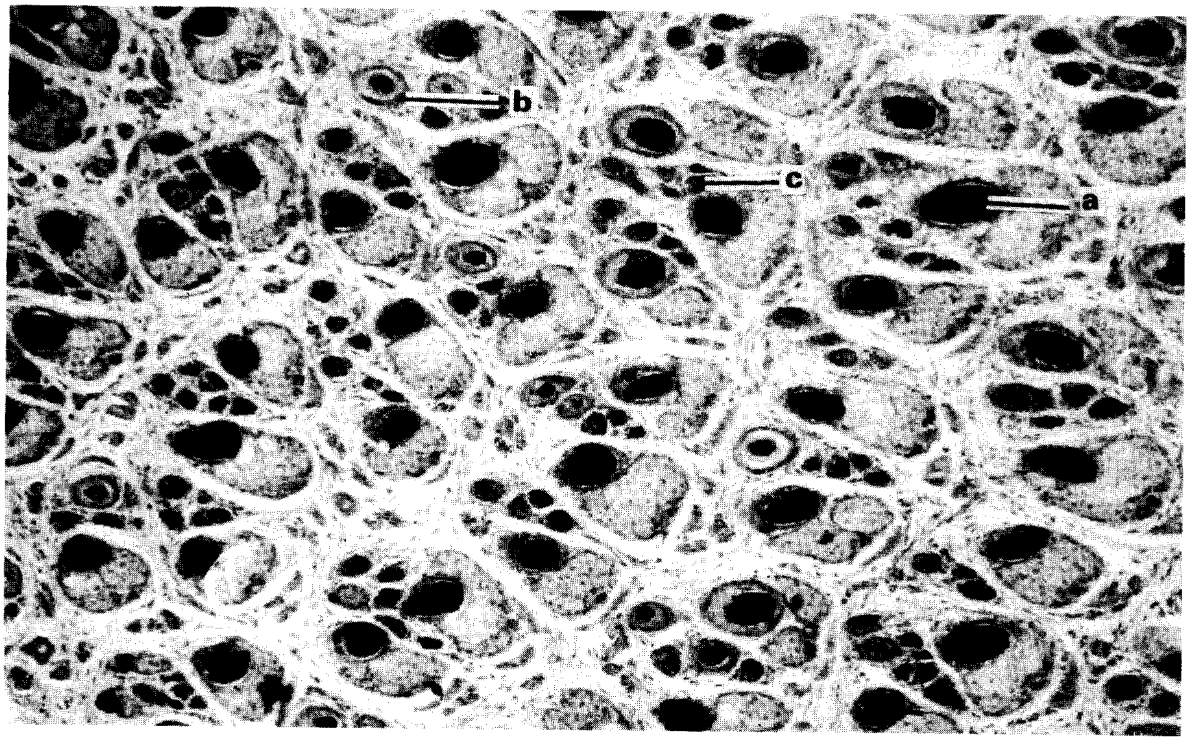

Figure 16a Follicle grouping. Pipe curl. Horizontal section at sebaceous gland level. Midrib position. 138 days pre-natal. Magn. 114×. a. Primary follicle. b. Secondary follicle. c. Anlagen.

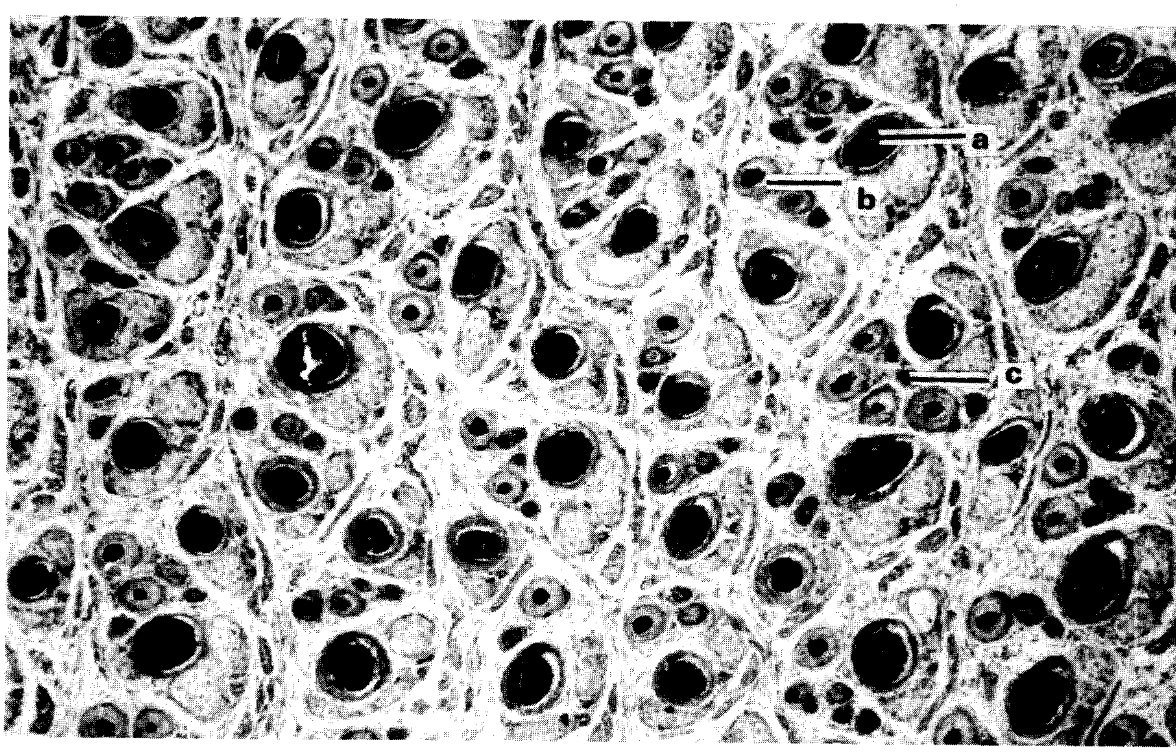

Figure 16b Follicle grouping. Developed shallow curl. Horizontal section at sebaceous gland level. Midrib position. 138 days pre-natal. Magn. 114×. a. Primary follicle. b. Secondary follicle. c. Anlagen.

Fibre contour

A circular shape being accepted as the theoretical norm, many deviations in shape from that norm were encountered, especially among the primary fibres. Most often the outline of the primary fibres was a modified ovoid shape. This ranged from a crescent shape to a crenated outline resembling the contour of blood cells in a drying phase (Figure 17). Secondary fibres did not exhibit any appreciable variation in fibre shape and most often approximated the circular outline.

Medullation

The presence of a medulla was difficult to demonstrate in a highly pigmented fibre and while a large number of medullae were present in the primary fibres of the 128 and 138 day stages of the developed shallow curl type, medul-

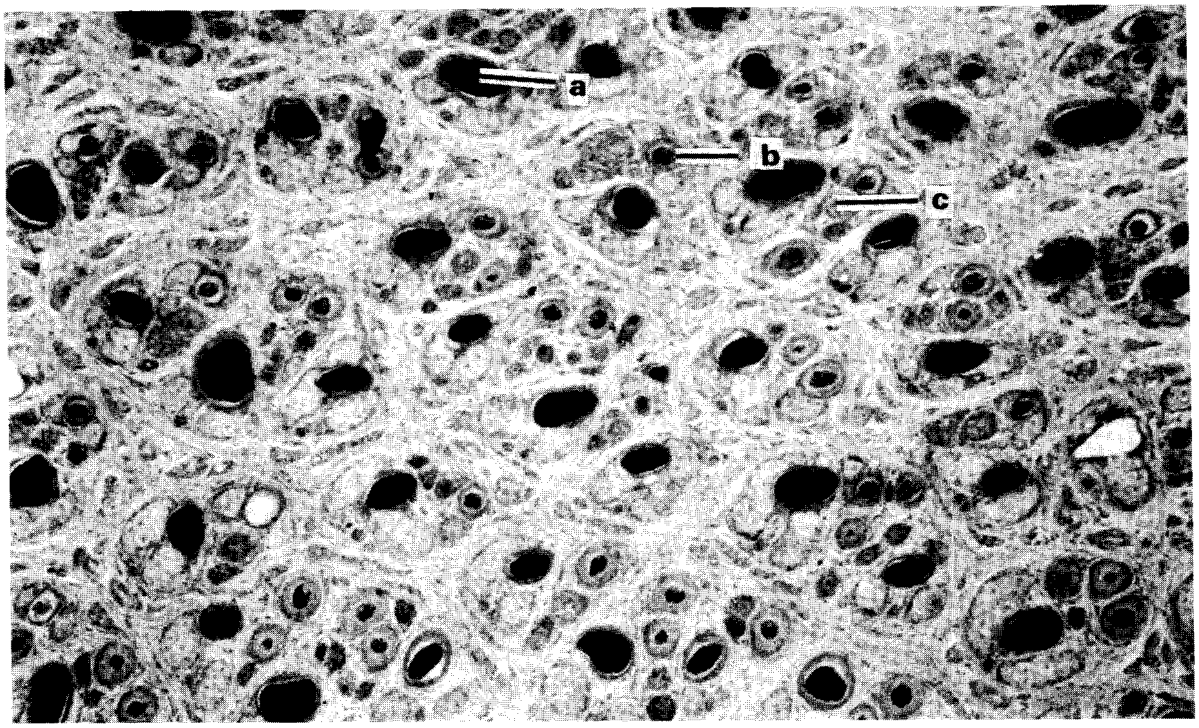

Figure 16c Follicle grouping. Shallow curl. Horizontal section at gland level. Midrib position. 138 days pre-natal. Magn. 114×. a. Primary follicle. b. Secondary follicle. c. Anlagen.

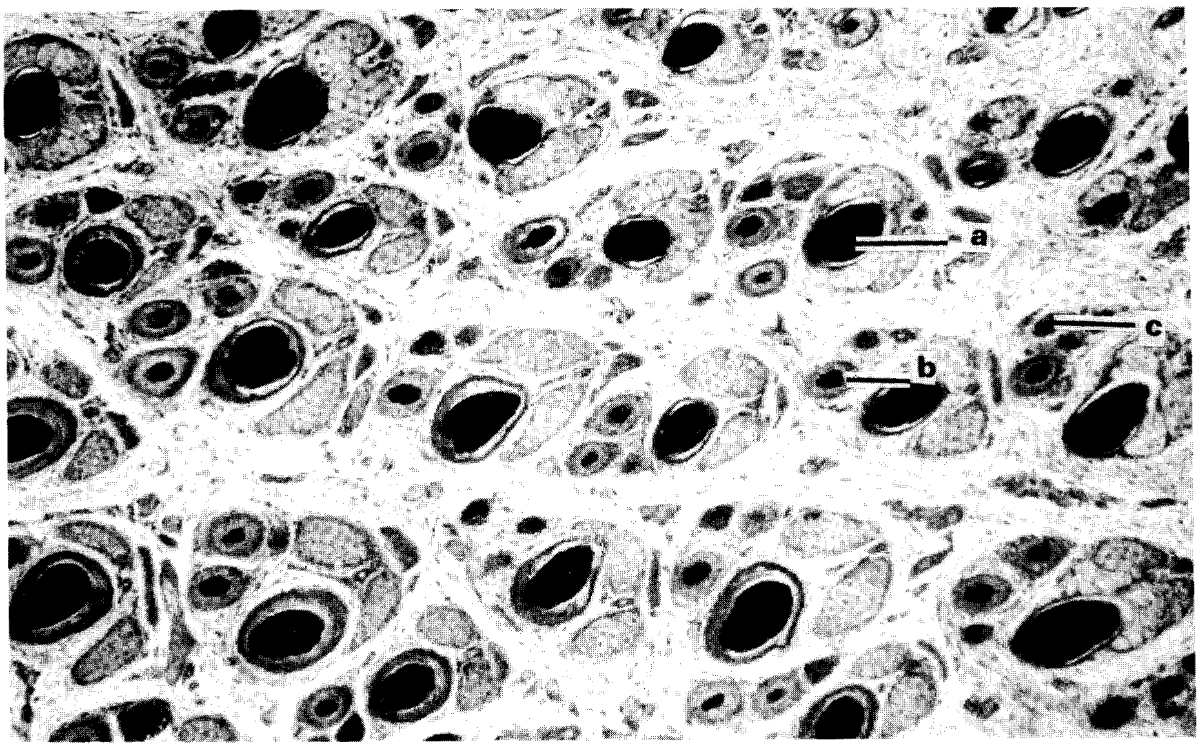

Figure 16d Follicle grouping. Watersilk. Horizontal section at sebaceous gland level. Midrib position. 138 days pre-natal. Magn. 114×.

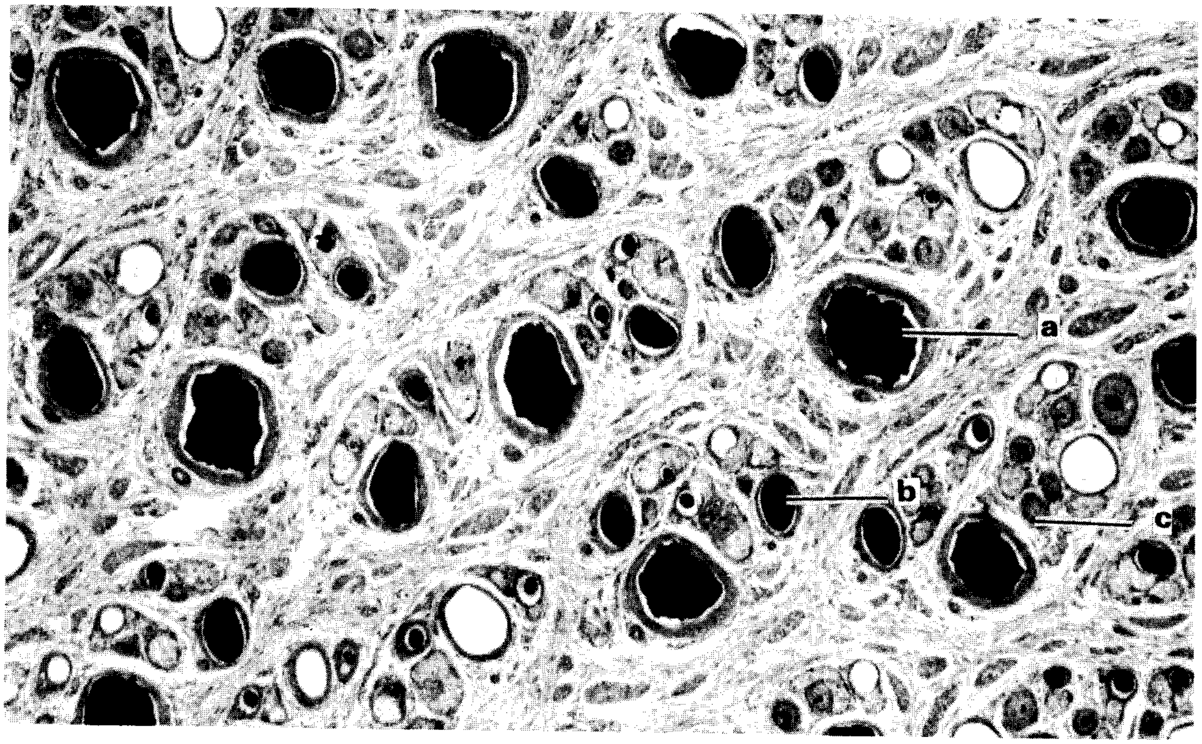

Figure 17 Crenated fibre type. Pipe curl. Horizontal section. Tail position. 138 days pre-natal. Magn. 114×. a. Primary follicle. b. Secondary follicle. c. Anlagen.

lation could also have occurred in the other types. An interrupted medulla (Wildman, 1954) is very difficult to demonstrate in all cross-sections. The presence of a continuous medulla can more frequently be recognized in cross-section or in a perfect vertical bisection.

Pigment

The presence of various shades of black as well as brown and yellow in the present study, strengthens the finding that all types of pigment can occur within the same fibre. Pigment granules were mainly round and arranged in beads comparable to a straightened necklace or otherwise gathered into clumps.

Discussion

The dermis serves as the matrix for follicle and fibre development and its thickness has a bearing on the ultimate hair pattern of the pelt. An increase in skin thickness will accommodate longer and more deeply situated follicles of which the ectal angle can be considered as indicative of a particular pattern. A thinner dermis, however, would place a limitation on follicle length development and perhaps thereby also limit the expression of the final pelt pattern.

Of the 4 types the pipe curl type showed the thickest dermis taken over the 4 pre-natal ages considered, although the oldest specimen of the pipe curl type at 138 days of pre-natal age, had a thinner skin than the other 3 types of the same age. Attributes of a thick skin are subject to individual variation and not confined to individuals of any particular type.

Follicle depth is dependent on the thickness of the skin, but independent of follicle length, since follicles in some cases grow almost parallel to the skin surface. Depth increases with age in accordance with the increase of skin thickness.

Follicle length, on the otherhand, is not necessarily correlated with skin thickness, since the angle at which the follicle penetrates the dermis determines the ultimate length of the follicle. The pipe curl type with its advantage in skin thickness in this case also had the longer follicles when taken over the 4 age periods. It is generally accepted that the follicle length, rather than the number of follicles, contribute to an increase in keratin production. Thus a denser and longer coat can be expected under these circumstances which is not necessarily an advantage.

Follicle angle is closely associated with follicle length. A more acute angle of the follicle to the skin surface and increasing skin thickness are conducive to maximal fibre length. Usually, but not inevitably, the longer follicles in the Karakul will produce a finer type of hair and a longer fibre than the shorter follicles (Nel, 1968). The shorter follicles, as in the watersilk type, have a greater uniformity in fibre size than the skins of types with longer follicles, especially where a larger variation in fibre size was encountered.

Follicle bulb diameter, as a linear measurement, can only serve as an indication of fibre size in that a large follicle usually has a larger papilla and grows a large fibre (Rudall, 1955). According to Rudall (1955) there is a high correlation (r = 0,84) between fibre cross-sectional area and papilla volume. In the Karakul, the bulb and dermal papilla show no appreciable difference in shape and size from those of other sheep breeds and in this respect there were also discernible differences between the 4 types (Dreyer, 1980 unpublished). The advantage of an early development of follicles, as is the case in the pipe curl type, lies in a higher density count with possibly smaller follicle diameters and longer fibres (Nel, 1968). These features enable the hairs of the pipe curl type to display all the possible variations of pattern of that particular type. With the watersilk type there is a more flattened pattern.

The limitation of follicle depth by the hypodermis cannot be accepted as a generalization, however, since specimens were also observed in which this phenomenon could not be demonstrated. Where present, it may be that the differing inherent properties of the two layers, cause a deflection of the bulb in an effort to preserve the dermal integrity of the papilla itself. The arrangement of the follicle bulbs in the dermis must almost certainly also have a bearing on pattern formation. The arrangement of the follicles in the skin, however, would have a definite influence on the formation of the pelt (Hornitchek, 1938, 1941 as cited by Nel 1950) as can be seen on a closer inspection of the skin itself.

As was mentioned before, the colour of the hair of the Karakul is a combination of two types of pigment — the black-brown or tyrosine-melanin and the yellow-red or pheomelanin (Fitzpatric *et al.*, 1958). Combinations of the two types, grouping in the hair and concentration also play a major role in the final colouring of the pelt. In this study all the pelts would have been black had they gone full-term. The sheen imparted by the pigment combined with other hair characteristics, determines the ultimate quality of the pelt (Nel, 1950).

The number and grouping of the primary and secondary follicles, as seen horizontally, determine the final coat pattern of the lamb. In the Merino it is common practice to express the number of secondary to primary follicles as a ratio (S/P ratio) and this usage has been carried over to other sheep breeds as well. The pipe curl type had the highest S/P ratio compared to the other types studied. The S/P ratio in itself is not necessarily correlated with density, as the groups themselves could be thickly populated with follicles, but the intergroup connective tissue could be formed in such wide trabeculae that real density would be decreased. The organisation of the follicle group and the ratio of secondary to primary follicles therefore plays a definite role in the formation of birthcoat pattern.

The orderly or haphazard appearance of the follicle trio-grouping is mainly due to skin expansion and all its inconsistencies. If orderly growth occurs, the harmonious whole of the group would be maintained. Should differential growth occur the groups would be subjected to strains and stresses, thus losing their initial regular appearance and resulting in disarrayed groupings. All this will have an influence on the way in which the pelt develops.

Fibre density is subject to large variation between animals and over the skin of the same animal. It is interesting to note that the areas with the thickest skin, such as neck and back, have a higher density than areas with thin skin e.g. the belly. The pipe curl type had the highest density, which due to the crowding of the fibres, may influence expression of birthcoat pattern but may also bestow on it an added advantage in countries where the wool from the mature animal is prized as a textile fibre (Margolena, 1954). However, a high secondary fibre density is not desirable for good quality Karakul pelts according to Frölich & Hornitchek (1931) — cited by Scheepers, (1963) — since it can adversely influence curl formation and have an unfavourable effect on the elasticity of the pelt, thus preventing it from retaining its curl pattern during processing.

Fibre outline or contour, can be considered as the final shape of the fibre in cross-section, after keratinization has occurred and desiccation has set in following the eruption of the fibre above the skin surface. But even in the skin itself, above the level of keratinization, a very close approximation of the ultimate fibre shape can be observed. A certain amount of stress and strain is probably introduced into the cortical cells formed from the matrix of the bulb, resulting in fibre shapes not conforming to the circular. These varying shapes must also have, to a greater or lesser degree a bearing on pattern-formation since the primary hairs are considered to play a major part in establishing the coat pattern.

From a commercial point of view the presence or absence of a medulla in the fibres of an animal coat can be viewed differently. In the pelts of other furred animals used for expensive furs, medullation does not seem to adversely affect the quality and, on the contrary, may even enhance it. In the fibre of the woolled sheep however, it seems that a medulla weakens the fibre strength, thereby negatively affecting fibre elasticity. The medulla cannot be implicated in every case where quality is not up to standard, since the structure of the cortical cells also has a bearing on hair quality (Rolfes, 1958).

Pigmentation, even as an adaptational characteristic, lends the particular sheen to the pelt. All 4 curl types showed the same type of pigment and no doubt at birth, under other circumstances all the pelts would have been black.

In conclusion it must be stressed that the differences between the 4 curl types studied, seemed to be associated with the amount of curl exhibited by the individual fibres forming the pelt pattern. Of the 4 types, the pipe curl type has the closest curl formation, resulting in that particular type of pattern and then the watersilk type, in which the more open curl arrangement is typical. The total effect of this type of fibre response, following foetal hair development, results in the particular classification system used in Southern Africa. It seems possible that the pelt of the Karakul stemmed originally from a single basic pattern. All the differences noted are variations from this common pattern and subject to genetic control.

It could be postulated that these differences in pelt types may be related to certain developmental variations. In some cases a certain degree of retarded follicle development may have taken place, resulting in the more open curl patterns such as in the shallow curl and watersilk types. The pipe curl type had a greater number of developing follicles and hair germs at the critical stages of development than the other three types. Assuming that histologically the pipe curl is the most advanced of all the pattern types, early development is necessary to ensure the closing of the curl to give shape to this pattern. Should pre-natal development be checked, (Dry, 1935) this could interfere with the closure of the curl as found in the shallow curl patterns. A physiologically induced inertia in the mitoses of cells in the bulb matrix may also result in retarded growth prohibiting the complete closure of the curl in the final pattern. It must also be emphasised that the ultimate expression of pelt pattern can probably be attributed to many largely unknown, intrinsic factors of skin, follicle and fibre which interact to give the particular pattern of any one pelt. In addition individual variation must be taken into account in any hypothesis concerning aspects of follicular growth and development. Unfortunately the number of individuals studied did not comply with the statistically acceptable minimum required to allow for wide variation but studying the required number would have meant an unrealistic drain on the numbers of any stud as well as being prohibitive in cost. The significance of the differences discussed cannot therefore be vouched for statistically.

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