

The Sweat Glands and Hair Follicles of Different Species of Bovidae

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Abstract

Measurements were made of hairs and sweat glands in the skins of a number of different Bovidae. The principal differences between the Bovinae and the one member of the Cephalophinae (the duiker) studied were in the dimensions of the skin and its component organs and in hair density; secondary hairs were not present, although in the American bison small primary follicles which appeared to provide a woolly undercoat were seen. In contrast, secondary hair follicles were found in the skins of all the Caprinae, Antilopinae and most of the Hippotraginae studied. The sweat glands of the Bovidae varied in shape from simple sacs as seen in the oryx to the coiled tubes of the wildebeest, and differed markedly in size, the largest being found in the wisent.

Introduction

Jenkinson and Nay (1972, 1973) found that the skin structure of domestic cattle throughout the world was basically similar. The main differences between breeds were in the dimensions of the skin and its component organs. Cattle indigenous to tropical regions had a relatively thin hair follicle depth and very often a simple sac-like sweat gland. Only primary hair follicles are present in the skin and hair grouping such as that described in sheep and goats (Carter 1955; Jenkinson 1965) does not occur in the skin of adult cattle or water buffaloes (*Bubalus bubalis*) (Hafez *et al.* 1955; Nair and Benjamin 1963; Jenkinson and Nay 1972, 1973). Apart from the above species, there is apparently little known about the nature of the skin and sweat glands of Bovidae, although cutaneous moisture loss is of major importance to thermoregulation in species such as the eland and African buffalo (*Syncerus caffer*) (Robertshaw and Taylor 1969; Finch 1972).

The present study was therefore initiated to determine the appearance of the skin of different Bovidae and to compare their skin types with those of domestic cattle, using sweat gland shape and hair follicle depth as the main indices for comparison. Such a study even on small numbers of animals will add to the knowledge concerning the adaptation of Bovidae to their habitats and should also prove of value in the classification of mammalian skins.

Materials and Methods

Duplicate skin samples were obtained from the neck of different Bovidae shortly after death. The animals sampled were feral, except for the water buffaloes. All were sampled in their native habitats with the exception of the gaur, banteng and yak, which were located in Munich Zoo, and the wisent, which was sampled in Poland. The number of animals from each species studied and their classification according to Simpson (1945) are given in Table 1. All skin specimens were taken

with a trephine 1 cm in diameter and were processed as described by Jenkinson and Nay (1968). Measurements were made of hair follicle depth (*FD*), length (*FL*) and diameter (*FDM*) and of sweat gland length (*L*) and diameter (*D*) as defined by Jenkinson and Nay (1968). It was not possible, however, to make these measurements on specimens from all of the animals studied. For example, in some instances the sweat glands were so coiled that intact glands were not obtained for measurements of length and in others the depths of secondary hairs could not be estimated since they were all in telogen. The sexes of the animals from which samples were measured are given in Tables 2 and 3. All were adults over 2 years old unless otherwise stated. Sweat gland shape (*L/D*) and volume (*V*) were calculated from the measurements of sweat gland length and diameter and hair follicle shape (*FL/FDM*) was also determined from hair follicle length and diameter. When material was available hair density was also measured on samples taken with a 1-cm trephine and the data were corrected for shrinkage of the section.

Table 1. Details of the species of Bovidae studied

The number of animals examined is given in parentheses for each species

Subfamily	Latin name	Common name	
Bovinae	<i>Bos taurus</i> ^A	Cattle	
	<i>Bos indicus</i> ^A	Cattle	
	<i>Bos grunniens</i>	Yak	(1)
	<i>Bibos banteng</i>	Banteng	(1)
	<i>Bibos gaurus</i>	Gaur	(1)
	<i>Bubalus bubalis</i>	Water buffalo	(85)
	<i>Bison bonasus</i>	Wisent or European bison	(5)
	<i>Bison bison</i>	American bison or buffalo	(9)
	<i>Taurotragus oryx</i>	Eland	(3)
	<i>Tragelaphus imberbis</i>	Lesser kudu	(10)
	<i>Syncerus caffer</i>	African buffalo	(6)
Cephalophinae	<i>Sylvicapra grimmia</i>	Duiker	(1)
Hippotraginae	<i>Kobus defassa</i>	Waterbuck	(40)
	<i>Oryx beisa</i>	Oryx	(20)
	<i>Connochaetes taurinus</i>	Wildebeest	(12)
	<i>Alcelaphus cokei</i>	Kongoni	(10)
Antilopinae	<i>Aepyceros melampus</i>	Impala	(1)
	<i>Litocranius walleri</i>	Gerenuk	(5)
	<i>Gazella granti</i>	Grant's gazelle	(10)
	<i>Gazella thomsonii</i>	Thomson's gazelle	(13)
Caprinae	<i>Capra hircus</i>	Goat	(4) ^B
	<i>Ovis canadensis</i>	Bighorn (Rocky Mountain) sheep	(1)

^A See Jenkinson and Nay (1972, 1973).

^B Feral.

Results

Bovinae

The skins of all the Bovinae studied were basically similar in appearance. Within the dermis were a number of hair follicles of variable size, each accompanied by an arrector pili muscle, a sebaceous gland and a sweat gland, forming typical hair follicle units. Secondary hair follicles (Carter 1955) were not observed. The principal differences between subfamilies were in the dimensions of the skin and the components of the hair follicle unit.

(i) *Yak, gaur, banteng and water buffalo*

The skin of the one yak studied (Fig. 1) resembled that of domestic cattle and the skin measurements (Table 2), including hair density, were within the range of those found in cattle. The hair follicles, which were all primary (Carter 1955), varied in size and did not exhibit any clear pattern of grouping. The sebaceous glands were bilobular and the slightly convoluted sweat glands resembled those in type II skin of cattle (Jenkinson and Nay 1972). The fundus of the sweat gland was lined with two layers of epithelium, an inner secretory epithelium, which unlike that of cattle was generally cuboidal in appearance, and an outer myoepithelium of canoe-shaped cells. The duct of the sweat gland was more proximal to the skin surface than that of the sebaceous gland and, as in cattle, sebum and sweat emerge as a mixture through the same pore.

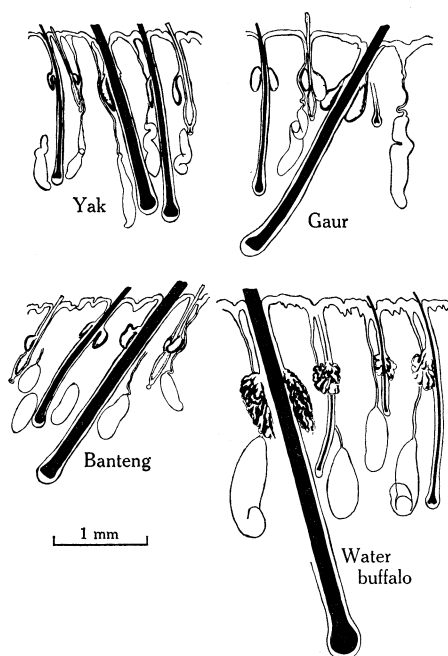


Fig. 1. Tracings of sections through the skins of the yak, gaur, banteng and water buffalo cut perpendicular to the skin surface. The components of the hair follicle unit do not always appear in close association in these and subsequent tracings due to differences in the angles at which the sections have been cut. The presence in some instances of resting hair follicles enables comparison with the measurements in Tables 2 and 3, which were obtained from active follicles.

In the gaur the hair follicles, which were again all primary, formed very distinct groups of three or sometimes two (Fig. 2). In this respect the gaur was unique among the Bovinae. The hair follicle pattern resembled the arrangement in sheep except for the absence of secondary follicles. The sweat glands (Fig. 1) were large and resembled those of cattle.

The skin of the banteng was similar to that of Zebu cattle. The hair follicles (Fig. 1) were short and thick and the sweat glands were simple sacs. Hair density was, however, although still within the range of cattle, lower than that usually found in Zebu breeds.

The water buffalo had a much lower density of hair follicles than cattle. The follicles, which were all of the primary type, showed a much wider range in size than those of cattle and although often randomly distributed were sometimes found in groups of two, three or four. In this respect the buffaloes were intermediate between

Table 2. Mean values of hair follicle and sweat gland measurements for Bovidae that have only primary hairs

Animal	No.	Sex	Hair follicle measurements:				Sweat gland measurements:				
			Depth (mm)	Length (mm)	Diameter (μm)	Shape (FL/FDM)	Density (No./cm ²)	Length (μm)	Diameter (μm)	Shape (L/D)	10 ⁻⁶ × Volume (μm ³)
Bovinae											
Yak	1	F	1.76	2.01	34.0	59.1	990	731	82	8.95	3.82
Banteng	1	F	1.34	1.91	44.1	43.3	709	443	110	4.02	4.20
Gaur	1	F	1.94	2.02	39.4	47.5	596	1230	101	12.20	9.81
Water buffalo	40	33 F, 7 M	2.36	2.84	76.9	36.9	237	1084	135	7.71	17.98
Wisent	1	M	4.48	4.57	75.5	60.5	641	3770	173	21.80	87.59
American bison	1	M	4.31	4.39	83.1	52.8	1616	1767	122	14.48	20.64
Eland	1	Y ^A	1.19	1.48	58.2	25.4	1170	810	90	9.00	5.15
Lesser kudu	10	M	1.51	1.74	53.0	32.8	592	1563	107	14.60	14.28
African buffalo	15	10 F, 5 M	2.21	2.57	71.3	42.1	145	1625	129	12.82	21.82
Cephalophinae											
Duiker	1	M	1.56	1.78	69.0	25.8	— ^B	859	126	6.80	10.71
Hippotraginae											
Oryx	20	10 F, 10 M	2.00	2.40	150.0	16.0	600	738	155	4.80	13.87

^A Young animal (< 2 years old).

^B No data available.

the gaur and domestic cattle. The sebaceous glands in the buffalo (Fig. 1) were large and multilobular. The sweat glands in buffaloes from India-Pakistan (Fig. 1), Turkey, Iraq and Egypt were much less convoluted than those in the skin of S.E. Asian breeds. On the whole, however, the range of variation in sweat gland shape was similar to that in cattle and the glands were much larger. The mean skin thickness found in water buffaloes was 6.32 ± 0.35 mm.

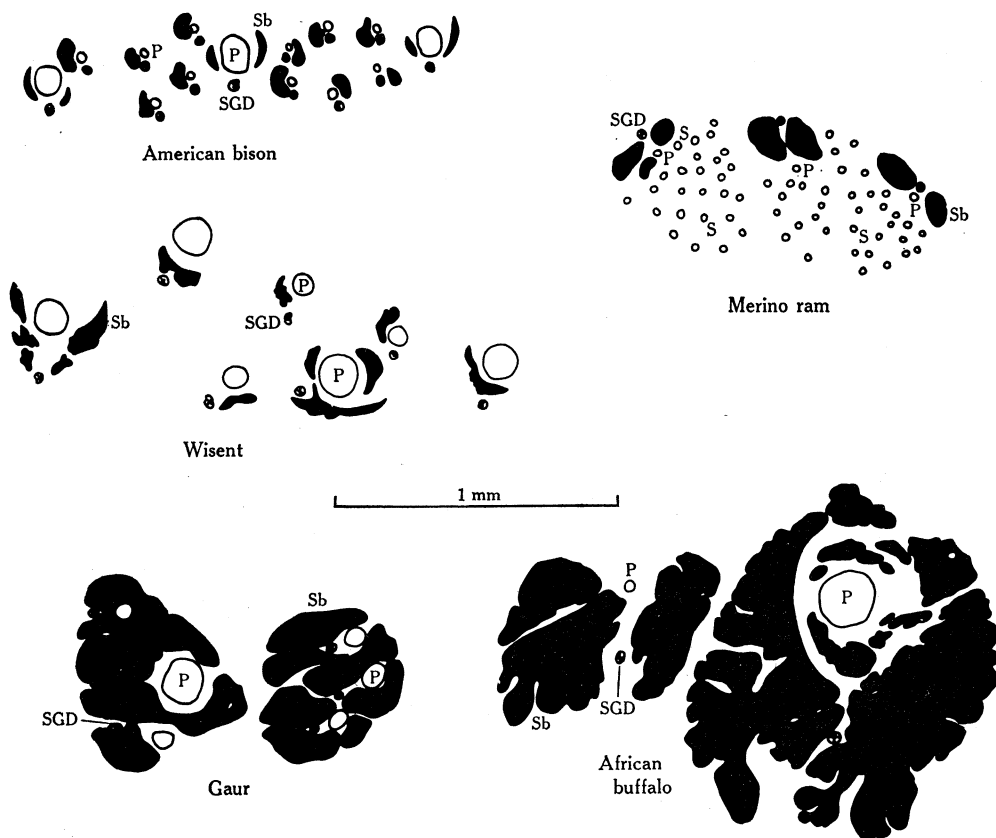


Fig. 2. Tracings of the primary (P) and secondary (S) hair follicles, sebaceous glands (Sb) and sweat gland ducts (SGD) of the American bison, wisent, gaur, Merino ram and African buffalo. These were traced from sections cut parallel to the skin surface and are designed to illustrate the mode of distribution of the hair follicles. Although all the tracings are to the same scale, it should be noted that measurements on these tracings are not comparable since, although the sections are all at the sebaceous gland level, follicle depth is not the same for each species. Only some of the hairs have been labelled. Other primary hairs can be identified by their proximity to sweat gland ducts.

(ii) *American bison and wisent*

The overall appearance of the skins of the American bison and wisent or European bison were similar to those of the Bovinae described above. The hair follicles varied in size, and were all accompanied by a sebaceous gland, an arrector pili muscle and a sweat gland. The hairs showed no clear pattern of emergence (Fig. 2). The bison, however, had much longer and thicker hair follicles (Table 2) which appeared to be situated almost at right angles to the skin surface (Fig. 3). The diameter of the hairs

in the wisent exhibited a normal distribution whereas in the American bison there were relatively few thick hairs, most being of low diameter (Fig. 4). The total skin thickness in the one wisent (14 years old) was 22.0 mm and that in the one American bison (5 years old) was 15.0 mm. Hair follicle depth was similar in the two species and was the greatest found among the Bovidae. The sweat glands of the wisent were also by far the largest examined in Bovidae and probably are among the largest to be found in mammals. The sebaceous glands of the American bison were bilobular and differed from those of the wisent which were multilobular (Fig. 3).

Fig. 3

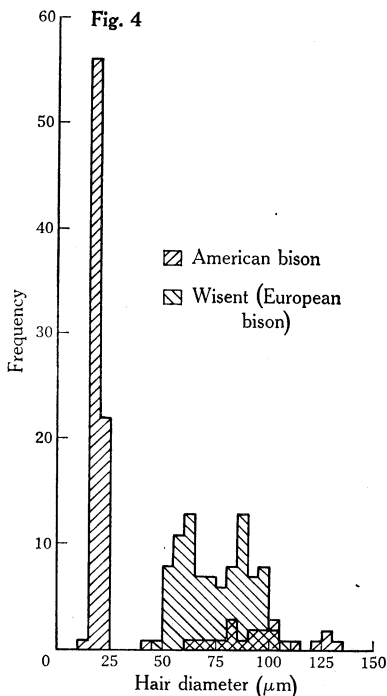
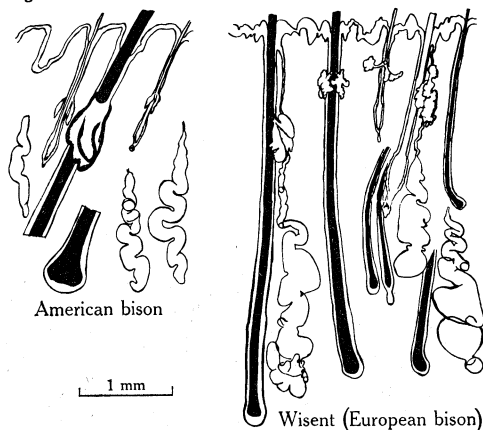


Fig. 3. Tracings of the skins of the American bison and wisent from sections cut perpendicular to the skin surface.

Fig. 4. A histogram illustrating the distributions of hair diameter found in 100 hairs from the American bison and the wisent.

(iii) *African buffalo, lesser kudu and eland*

The appearance of the skin of the African buffalo is illustrated in Fig. 5 and the skin measurements are given in Table 2. The appearance of the skin was essentially similar to that found in the water buffalo. The sweat glands were large and convoluted and the sebaceous glands were multilobular and even larger than those of the water buffalo (Fig. 2). The hair follicles, although comparable in thickness to those of the bison, were similar in length to those of other Bovinae. Apart from the water buffalo, the African buffalo, which has a low hair density, tended also to have a thicker epidermis than other Bovinae.

The skins of the lesser kudu and eland were basically similar to those of the other Bovinae and are illustrated in Fig. 5. Details of the skin measurements are given in Table 2. The eland from which the skin measurements were obtained was a young

animal under 2 years old and the measurements could differ from those of the adult. Hair density per unit area for example may decrease as the animal grows. The sebaceous glands in both species were bilobular but the sweat glands in the eland were less convoluted. Both types of sweat gland were, however, within the range of shapes found in cattle.

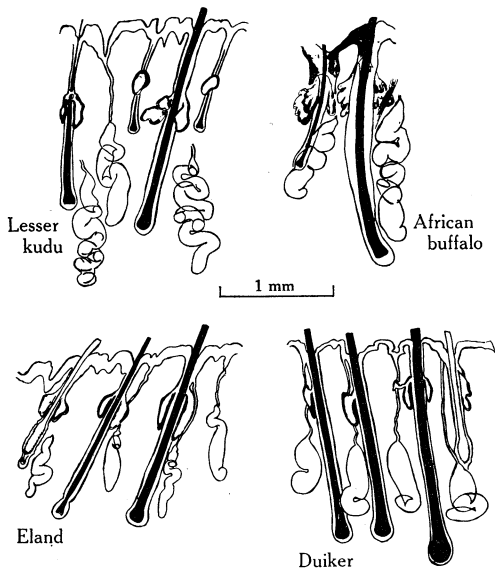


Fig. 5. Tracings of sections through the skins of the lesser kudu, African buffalo, eland and duiker cut perpendicular to the skin surface.

Cephalophinae (Duiker)

The appearance of the skin of the duiker sampled is shown in Fig. 5. It resembled the Bovinae in general skin structure although the hair follicles tended to be short and thicker than those of cattle (Table 2). The sebaceous glands were bilobular and the fundus of each sweat gland was a simple sac. No secondary hair follicles were seen and no pattern of hair grouping was detected.

Hippotraginae

(i) *Oryx*

The oryx differed from the remainder of the Hippotraginae studied in having no secondary hair follicles in the skin, which resembled that of the Bovinae (Fig. 6). However, the hair follicles were extremely thick, averaging $150\ \mu\text{m}$ in diameter (Table 2), and the epidermis was thick relative to other members of the subfamily. The sebaceous glands were multilobular and the sweat glands in all the animals examined were simple sacs. No clearly distinguishable pattern of hair grouping (Fig. 7) was discerned.

(ii) *Wildebeest, waterbuck and kongoni*

The skins of the wildebeest, waterbuck and kongoni are illustrated in Fig. 6 and the mean skin measurements are given in Table 3. The sebaceous glands associated with the primary hairs were bilobular in the kongoni and wildebeest. In the waterbuck they were large, unilobular and ovoid in appearance and often formed an almost

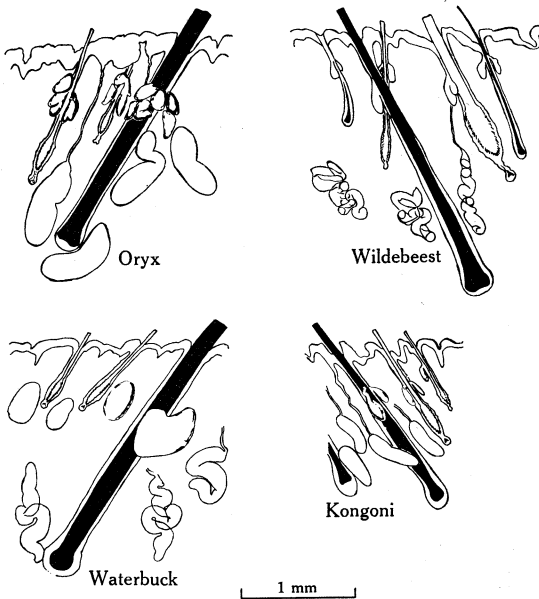


Fig. 6. Tracings of sections through the skins of the oryx, wildebeest, waterbuck and kongoni cut perpendicular to the skin surface.

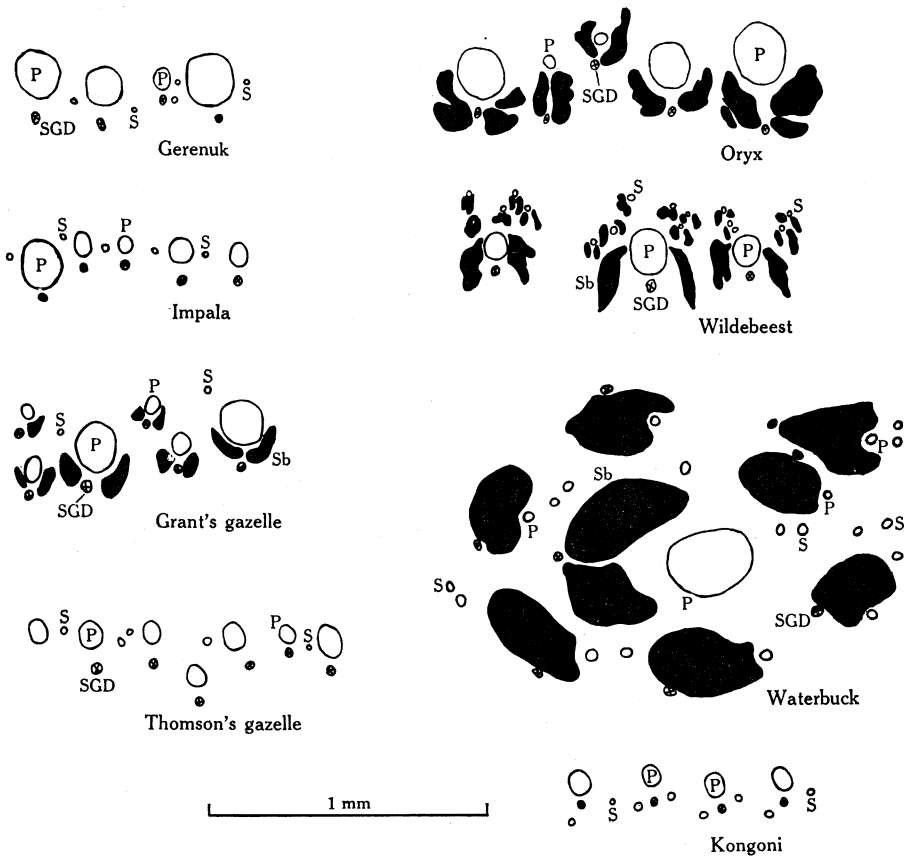


Fig. 7. Tracings from sections through the skins of eight Bovidae cut parallel to the skin surface to illustrate the mode of distribution of the hair follicles. Labelling as for Fig. 2.

continuous layer. Some very large 'giant' primary hairs with a mean diameter of $230\text{ }\mu\text{m}$ (range $180\text{--}300\text{ }\mu\text{m}$), which were also present in the skin of the waterbuck, had bilobular sebaceous glands associated with them. There were approximately 25 of these 'giant' hairs per square centimetre of skin. The primary hair follicles in the waterbuck were arranged in trios (Fig. 7), and there were about 12 secondary follicles associated with each trio giving a secondary : primary (S : P) ratio of approximately 4 : 1. The secondary hairs were unusual in that they were similar in diameter to the primary ones. The S : P ratio in the wildebeest was about 7–8 : 1 and in the kongoni 2–3 : 1. The mode of hair grouping in these species is also shown in Fig. 7. The sweat glands of the kongoni were simple sacs lined with a flat secretory epithelium. Those in the wildebeest, which also had a flat secretory epithelium, and the waterbuck, which had a cuboidal epithelium, were more convoluted with a higher L/D value (Table 3).

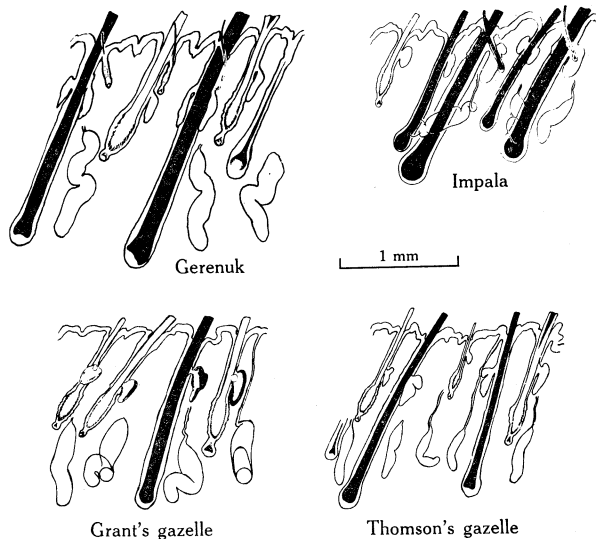


Fig. 8. Tracings of sections through the skins of the gerenuk, impala, Grant's gazelle and Thomson's gazelle cut perpendicular to the skin surface.

Antilopinae

(i) *Impala and gerenuk*

Secondary hair follicles were present in the skin of both the impala and the gerenuk. In both species the ratio of secondary to primary follicles was about 1 : 1; the secondary hairs tended to be interspersed between the primary ones and were very short. Their bulbs did not in general extend below the level of the sebaceous glands associated with the primary follicles (Fig. 8). The sebaceous glands were bilobular in both instances. The sweat glands of the impala were simple sacs (Fig. 8) with a low L/D value (Table 3), whereas those of the gerenuk were convoluted (Fig. 8). Although the gerenuk is a much smaller animal than the oryx or lesser kudu, the sweat glands of all three species were approximately the same size.

(ii) *Grant's gazelle and Thomson's gazelle*

Secondary hair follicles were also present in the skins of the gazelles (Fig. 7). In Thomson's gazelle the bulbs were, as in the gerenuk and impala, generally at or above

Table 3. Mean values of hair follicle and sweat gland measurements for Bovidae that have both primary and secondary hairs

P = primary hairs; S = secondary hairs; R = hairs resting (no measurements possible)

Animal	No.	Sex	Hair follicle measurements:					Sweat gland measurements:					
			Depth (mm)	Length (mm)	Diameter (μ m)	Shape (FL/FDM)	Density of P (No./cm ²)	Ratio S : P	Length (μ m)	Diameter (μ m)	Shape (L/D)	10 ⁻⁶ \times Volume (μ m ³)	
Hippotraginae													
Waterbuck	28	M	P (R) S (R)	(R) (R)	(R) (R)	(R) (R)	619 730	4.00 7.70	1220 1635	103 81	11.80 19.10	10.09 9.38	
Wildebeest	12	F	P 1.82 S (R)	2.22 (R)	119.0 14.6	18.6 (R)	730 1170	7.70 2.20	1635 609	81 96	19.10 6.30	9.38 4.40	
Kongoni	10	F	P 1.29 S (R)	1.94 (R)	77.6 15.2	25.0 (R)	1170	2.20	609	96	6.30	4.40	
Antilopinae													
Gerenuk	5	M	P 1.38 S (R)	1.85 (R)	120.0 22.0	15.4 (R)	400	0.95	1027	123	8.30	12.20	
Grant's gazelle	10	F	P 1.35 S (R)	1.66 (R)	74.4 15.4	13.8 (R)	1420	0.26	960	95	10.10	6.77	
Thomson's gazelle	13	F	P 1.32 S (R)	1.68 (R)	59.4 14.0	28.2 (R)	1340	0.83	424	58	7.30	1.19	
Impala	2	M	P 1.24 S (R)	1.44 (R)	68.2 16.7	21.1 (R)	— ^A	1.00	619	102	6.41	5.23	

^A No data available.

the level of the sebaceous glands associated with primary hairs. They were relatively longer in Grant's gazelle. The mean S : P ratio was 0.26 : 1 and 0.83 : 1 respectively for Grant's and Thomson's gazelle and was particularly low in the former. The spatial distributions of the primary and secondary hairs in the gazelles are given in Fig. 7. The primary hairs were medullated and were thicker in Grant's gazelle. The sebaceous glands of both gazelles were bilobular but the sweat glands were much larger in Grant's than in Thomson's gazelle (Table 3). The sweat glands were slightly convoluted in the former but were simple sacs in the latter (Fig. 8).

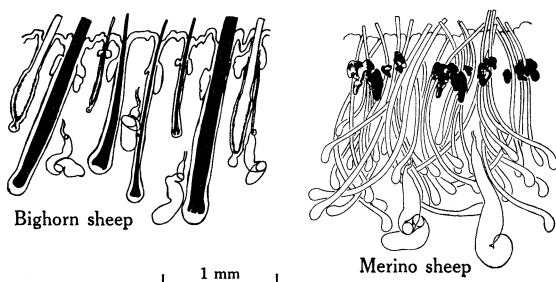


Fig. 9. Tracings of sections through the skin of the bighorn (Rocky Mountain) and Merino sheep cut perpendicular to the skin surface.

Caprinae

The structure of the skin of sheep and goats has been well described (Carter 1955; Jenkinson 1965) and the S : P ratios range from about 30 : 1 in the 'woolly' breeds of sheep such as the Merino (Figs 2 and 9) to about 2 : 1 in 'haired' breeds. The skins of the feral goats and domestic sheep studied were basically similar to those previously described. Unlike the Merino, in which the fibres in the primary follicles were similar in thickness to those in the secondaries, those of the bighorn or Rocky Mountain sheep (Fig. 9) had relatively larger primary hair follicles containing fibres which ranged from about 190 to 250 μm in diameter compared with 10–14 μm for the fibres in the secondary follicles.

Discussion

It seems reasonable to conclude from the present evidence and that obtained with domestic cattle (Jenkinson and Nay 1972, 1973) that the skin structure is basically the same throughout the Bovinae. Secondary hair follicles were not found in any member of this subfamily and the principal differences between members lay (1) in the dimensions of the skin and the components of the hair follicle unit and (2) in the density of hair follicles. With the exception of the gaur, in which the primary hairs were grouped in trios, the hair follicles although variable in size were apparently randomly distributed throughout the skin. In the American bison some of the primary hairs had apparently assumed the role of secondary ones in the sense that they produced small fibres which could be classed as woolly. This pattern was not found in the wisent and may indicate an adaptation to different habitats. The American bison, which is mainly a grazing animal dwelling in prairies and subject to intense cold, may have developed a thick woolly undercoat. This may not have been required by the wisent which largely lived as a browser in dense forests within the temperate zone of Europe. On the other hand, the differences found may simply be a reflection of individual animal variation within the two types of bison. Sokolov

(1962) gives a description of the skin of what he terms aurochs (*Bison bonasus* L.) which, although in broad agreement with the present findings, indicates that wool hairs are present in the European bison. He suggests that the density of hairs, especially wool hairs, in aurochs changes with the season. His conclusion, however, requires further investigation since he apparently used only two animals for his comparison and was unable to study the same animal in different seasons. The appearance of the skin of the water buffalo was similar to that found by Nair and Benjamin (1963). All the hairs were primary ones although there was in some instances evidence of hair grouping. The measurements obtained in the present study were, however, in general greater than those found by Nair and Benjamin (1963). This is most likely due to differences in technique as these authors used routine histological methods in comparison to the thick-section mounts prepared in the present investigation.

The skin of the one member of the subfamily Cephalophinae studied (the duiker) was basically similar in appearance to those of the Bovinae. In contrast, secondary hairs were found in all the Caprinae, confirming previous findings (Carter 1955), and all the Antilopinae examined. In the Caprinae hair grouping was easily distinguished and in some species such as the Merino sheep there was a very high S : P ratio. In contrast, the S : P ratio in the Antilopinae examined was in every instance low and only in Grant's gazelle was there a clear pattern of hair grouping. The low S : P ratio in Antilopinae may be an adaptation to their tropical environment, since a woolly coat with a high proportion of secondary hairs is likely to be disadvantageous in the heat (Bianca 1966).

Secondary hair follicles and hair grouping were found in most of the Hippotraginae examined, the exception being the oryx in which neither was found. Whereas in Bovidae in general the primary follicles tended to contain hairs of wide diameter compared with secondary follicles, those in the waterbuck were relatively thin and of the same order of magnitude as the secondary hairs. In this respect the waterbuck resembled the Merino sheep. The waterbuck, however, had a number (about 25 per cm²) of giant hair follicles which produced fibres about five times thicker than other primary follicles. One unique feature of the waterbuck was the large ovoid unilobular sebaceous glands which formed an almost complete layer in the skin. This system may well provide the animal with a well-protected skin surface when browsing in swamps. If it is an adaptive feature it would be of interest to investigate if a similar development of the sebaceous glands has evolved in other animals with aquatic habits such as the South American swamp deer or the African water chevrotain.

The primary fibres in the Bovidae were in the main medullated and apart from those in the yak they tended to be thicker than those of domestic cattle. The hairs of the oryx, wildebeest and gerenuk were the thickest found in the Bovidae. The presence or absence of secondary hairs or of hair grouping did not appear to be related to the body size of the animal. Hair grouping was found, for example, in the wildebeest and Grant's gazelle and no secondary hairs were present in the skin of the small duiker or in the buffalo or bison.

The sweat glands of the wisent were the largest observed among the Bovidae and probably rank among the largest in mammals. In most of the species investigated in the present study the secretory cells were cuboidal. Notable exceptions were those of the kongoni and wildebeest, which were flat and indistinguishable from the secretory

cells in cattle (Jenkinson 1965). The overall range of sweat gland shape in Bovidae was within that found in domestic cattle (Jenkinson and Nay 1972, 1973). The glands varied in appearance from simple sacs such as those of the oryx to the convoluted or coiled tubes seen in the wildebeest. Consequently, the present evidence indicates that as in cattle (Jenkinson and Nay 1973) no one sweat gland shape is specifically found in warm climates.

Robertshaw and Taylor (1969) found different patterns of sweating in East African Bovidae and concluded that the magnitude of sweating was better correlated with the size of an animal than with its phylogenetic position. The differences in the magnitude and pattern of sweat output cannot be explained solely in terms of sweat gland size or shape. This is not altogether surprising since the skin measurements, unlike sweat output, were not related to body size. The Grant's gazelle for example has a higher sweat output than the duiker and Thomson's gazelle but has an intermediate sweat gland volume. The waterbuck and duiker, which have sweat glands of a similar size, exhibit different patterns of sweating (Robertshaw and Taylor 1969). The L/D value of the glands in the African buffalo is of a similar order of magnitude to that of the waterbuck and Grant's gazelle, yet these three species exhibit different patterns of sweating. Animals that have secondary follicles in the skin and exhibit hair grouping do not show one type of sweating pattern; the discrete and stepwise patterns described by Robertshaw and Taylor (1969) are not limited to breeds that exhibit hair grouping. It would seem, therefore, that the differences in the magnitude and patterns of sweating are in general mainly due to differences in the physiology of the sweat glands. Glandular size and number may, however, in some instances contribute to the differences in sweat output observed. Robertshaw and Taylor (1969) for example concluded that, since the oryx has a similar cutaneous moisture loss to the waterbuck yet exhibits a different pattern of sweating, the oryx would require to have either a more complete myoepithelial contraction or a larger sweat gland lumen, because the frequency of sweat bursts in this species was approximately the same as the frequency of oscillations in cattle. It would seem that sweat gland width could be a contributory factor since the glands in the oryx were considerably wider than those in cattle.

Acknowledgments

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