

RELATIONSHIP BETWEEN CYCLIC CHANGES IN THE HAIR FOLLICLE AND SWEAT GLAND SIZE IN CATTLE

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Summary

The morphology of hair follicles has been studied in 23 Africander-Hereford crossbred yearlings. Eleven hair growth phases were recognized as a result of work on two animals. The piloapocrine units representing each phase have been illustrated by tracings. The mean length, diameter, length-diameter ratio, and area of sweat glands corresponding to each phase have been tabulated and illustrated.

Gland size was very significantly influenced by follicle phase. Glands were largest in anagen VI and catagen c and were completely regressed in telogen.

The effect of differences in follicle phases on sweat gland size was studied in all 23 animals. The inherent difference between animals in gland size was determined by a comparison of mean gland size for common phases. Actual mean gland size is also influenced by frequency of the various follicle phases. In the present study the contributions of inherent differences and differences due to phase distribution were in the ratio of 3.2 : 1.

Although doubt is cast on sweat gland morphology as the sole criterion of sweat gland activity, the association between hair growth phase and sweat gland size offers a partial explanation of the association between coat character, sweat gland size, and sweat gland activity. These three are found to vary together when comparisons are made between breeds or strains, between animals within breeds, between different body regions, and between seasons.

I. INTRODUCTION

Carter and Dowling (1954), Nay and Hayman (1956), and others listed by them have found that a hair follicle is invariably accompanied by a sweat gland duct in cattle skin. This was confirmed in the work of Lyne and Heideman (1959) on the prenatal development of skin and hair in cattle. It has been concluded that sweat gland density may be estimated by counting hair follicles at the subepidermal level. Total sweat gland volume or total secretory surface area has been estimated as the product of mean observable sweat gland size and follicle density. This report presents evidence that the sweat gland undergoes cyclic changes in morphology in association with the hair follicle. Among the characteristic phases is a completely regressed state in which the sweat gland size could not be measured by the standard procedure nor could it be in a functional state.

Earlier observations by Dowling (1958) that sleek coats are associated with a higher sweating capacity have been confirmed by Schleger and Turner (1965) who were able to show that this relationship holds between breeds, between animals within breeds, and between seasons. This investigation is an attempt to explain this

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relationship by relating sweat gland size, one of the components of sweating capacity, to growth phase of the follicle which is a determinant of sleekness.

II. MATERIALS AND METHODS

The animals used in this investigation were 23 (16 males and 7 females) Africander-Hereford F₂ crossbreds which formed part of the experimental herd at the National Cattle Breeding Station, "Belmont", Rockhampton (Kennedy and Turner 1959). At date of sampling, November 17, 1961, the animals were approximately 12 months old.

Skin biopsies were taken with a 1-cm trephine from the last intercostal space and fixed in 5% formol saline. The samples were dissected into two halves in the plane of the follicles. For sectioning, the half sample was frozen with its cut face on the surface of the levelled freezing stage. Thus the merit of sections, 100 μ in thickness, largely depended on the accuracy of the initial dissection plane.

Sections were stained with 40% Ehrlich's acid haematoxylin differentiated with 0.125N HCl, washed in 1.0% sodium acetate, and counterstained with 0.2% aqueous eosin.

An essential feature of this investigation was the identification of associated follicles and sweat glands. Confirmation of doubtful cases was achieved by the use of magnifications up to $\times 320$.

All 23 animals were used for counts of phase frequencies and study of gland size in relation to phase groupings, but sweat gland morphology was related in detail to follicle phases in only two animals. In these animals, the hair follicle-sweat gland units were drawn by tracing the image from a projection microscope and adding detail after further examination with a compound microscope. Where possible, 10 units were illustrated for each phase in each animal. One representative drawing for each phase in one of the animals is shown in Figure 1. For each tracing, mean diameter of gland was determined from three measurements, each of which was an estimate of the mean diameter of a one-third segment of the gland. Length was measured from base to duct junction, and in convoluted glands represented the length the gland would have if straightened out. Projected area of the gland was determined by counting the number of squares encompassed on millimetre graph paper and correcting for magnification. The surface area of a gland is approximately π times the projected area, and for sweat gland volume the factor is $\pi d/4$, d being the sweat gland diameter.

Although giant follicles showed striking cyclic changes in sweat gland morphology, their number was too small to provide a separate set of data, and they were excluded from the population of glands examined in detail in order that they should not bias estimates of mean gland size. Glands near the edge of sections were also excluded because of the distorting effect of biopsy.

Definition of Follicle Phases

The classification of hair follicles is based on that of Chase, Rauch, and Smith (1951) and Straile, Chase, and Arsenault (1961) for the mouse. Eleven phases have been recognized, comprising six in anagen, four in catagen, and telogen. The six in anagen correspond to those of Chase, Rauch, and Smith except that their anagen I has

been divided into Ia and Ib, and their anagen IV and anagen V have been treated as one phase. New definitions have been adopted for catagen phases. A typical example of each phase is shown in Figure 1. The following definitions for cattle supplement published descriptions of phases in the mouse.

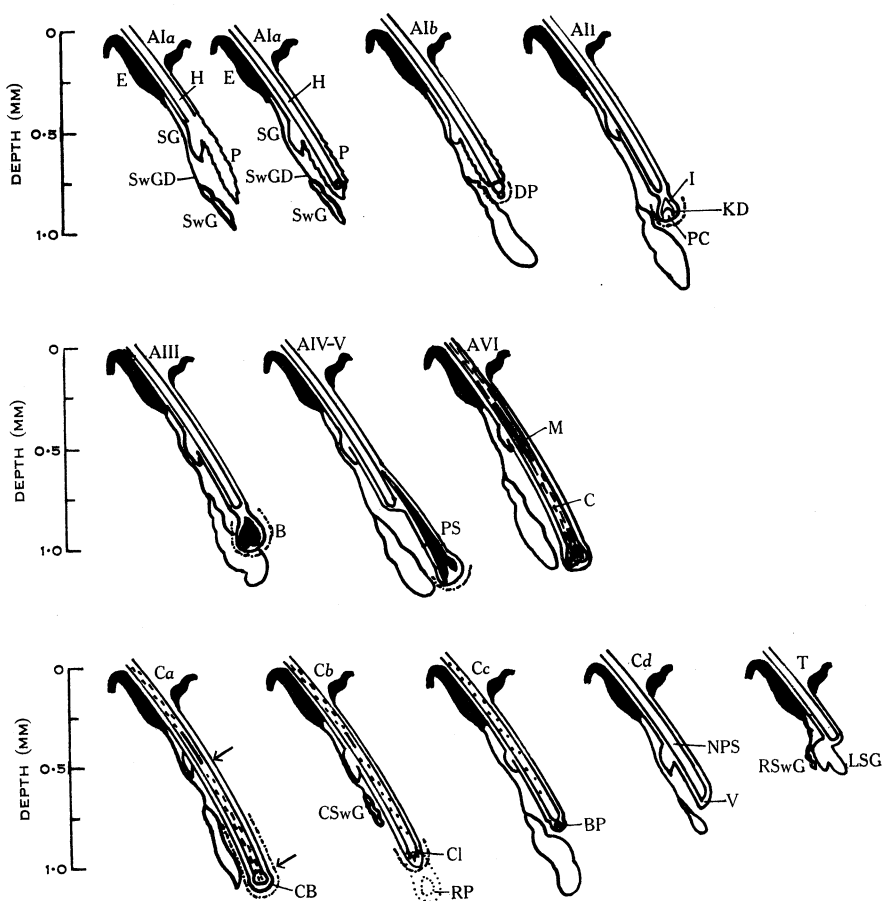


Fig. 1.—Tracings of hair follicle-sweat gland units corresponding to each phase of the hair growth cycle in animal 0-211. The scale (in millimetres) indicates the corresponding depth in the skin.

AIa (anagen Ia): *E*, epidermis; *P*, proliferated outer root sheath; *SG*, sebaceous gland; *SwG*, sweat gland; *SwGD*, sweat gland duct; *H*, non-pigmented hair shaft. *AIb* (anagen Ib): *DP*, dermal papilla staining bright pink with haematoxylin-eosin, as indicated by broken line.

AII (anagen II): *I*, inverted cone of epidermal cells; *PC*, papilla cavity; *KD*, keratinized dome. *AIII* (anagen III): *B*, large pigmented hair bulb. *AIV-V* (anagen IV-V): *PS*, pigmented hair shaft. *AVI* (anagen VI, with the new emergent hairs in active growth): *M*, medulla; *C*, cortex—the stippling indicating decreased pigmentation.

Ca (catagen a): *CB*, contracted, rounded bulb. The arrows indicate extent of hollow between the inner and outer root sheath and the broken lines the extent of pink staining of the inner root sheath.

Cb (catagen b): *RP*, detached papilla almost completely regressed; *Cl*, newly formed club; *CSwG*, contracted sweat gland. *Cc* (catagen c): *BP*, ball of papilla cells which may contain pigment granules. *Cd* (catagen d): *V*, vestige of papillary cells; *NPS*, non-pigmented hair shaft. *T* (telogen): *LSG*, large sebaceous gland; *RSwG*, completely regressed sweat gland.

Anagen Ia.—The outer root sheath surrounding the lower portion of the club hair shows considerable thickening through cellular proliferation, but no activity is apparent in the papilla. This phase occurs in two forms (Fig. 1) which means that the telogen phase is sometimes by-passed.

Anagen Ib.—The dermal papilla stains a characteristic bright pink colour (shown by broken line in Fig. 1), but no structural differentiation is apparent.

Catagen a.—As described by Straile, Chase, and Arsenault (1961), the beginning of catagen is morphologically similar to anagen VI. Distinguishing features are a regression of bulb structure, decreased pigmentation in the hair, pink staining of

TABLE 1

CHANGES IN SWEAT GLAND MORPHOLOGY WITH VARIATION IN HAIR GROWTH PHASE FOR TWO AFRICANDER × HEREFORD CROSSBREDS OF THE 1960 DROP SAMPLED NOVEMBER 1961

Hair Growth Phase	Crossbred No. 0-211				Crossbred No. 0-158			
	No. of Hair Follicles	Sweat Gland Length (mm)	Sweat Gland Diam. (mm)	Projected Area (mm ²)	No. of Hair Follicles	Sweat Gland Length (mm)	Sweat Gland Diam. (mm)	Projected Area (mm ²)
Anagen Ia	9	0.196	0.0396	0.0092	10	0.098	0.0292	0.0043
Ib	10	0.435	0.0750	0.0288	10	0.346	0.0625	0.0190
II	10	0.473	0.0875	0.0344	10	0.442	0.0958	0.0345
III	5	0.456	0.0833	0.0372	7	0.433	0.0923	0.0353
IV-V	8	0.467	0.0875	0.0327	10	0.469	0.0896	0.0398
VI	10	0.456	0.0875	0.0365	10	0.488	0.0854	0.0401
Catagen a	10	0.350	0.0625	0.0210	10	0.319	0.0563	0.0195
b	10	0.246	0.0417	0.0134	10	0.223	0.0417	0.0097
c	10	0.469	0.0896	0.0369	10	0.446	0.0938	0.0376
d	10	0.142	0.0313	0.0053	10	0.177	0.0292	0.0066
Telogen	10	0	0	0	10	0	0	0
Total	102				107			

the inner root sheath at the bulb level and for varying distances within the keratogenous zone, and the development of a space between the inner and outer root sheath, the length of which is shown by arrows in Figure 1. This phase seems to include the catagen I, II, and III phases of Straile, Chase, and Arsenault (1961).

Catagen b (detached papilla).—The characteristic features of this stage are detachment of the papilla except for a connecting bridge of epithelial cells, presence of pigment throughout a large proportion of the shaft, though of less intensity than in the previous stage, and, in the earlier stages, a residual pink staining round the base of the developing club.

Catagen c (attached papilla).—This phase represents the major difference between cattle and mice. In cattle a proportion of follicles appear to regress as for mice, so that relatively shallow, lightly pigmented yet papilla-free shafts are visible. Otherwise, the transition from the earlier stage with detached papilla to the later stage where the regressed papilla is firmly attached as a nipple-like projection seems

to take place without any great decrease in follicle depth (Fig. 1). Catagen *c* is characterized by an almost complete absence of pigment except for a diffuse stippling. The small contracted dermal papilla may be dark, may contain a few pigmented cells, or may be pigment-free.

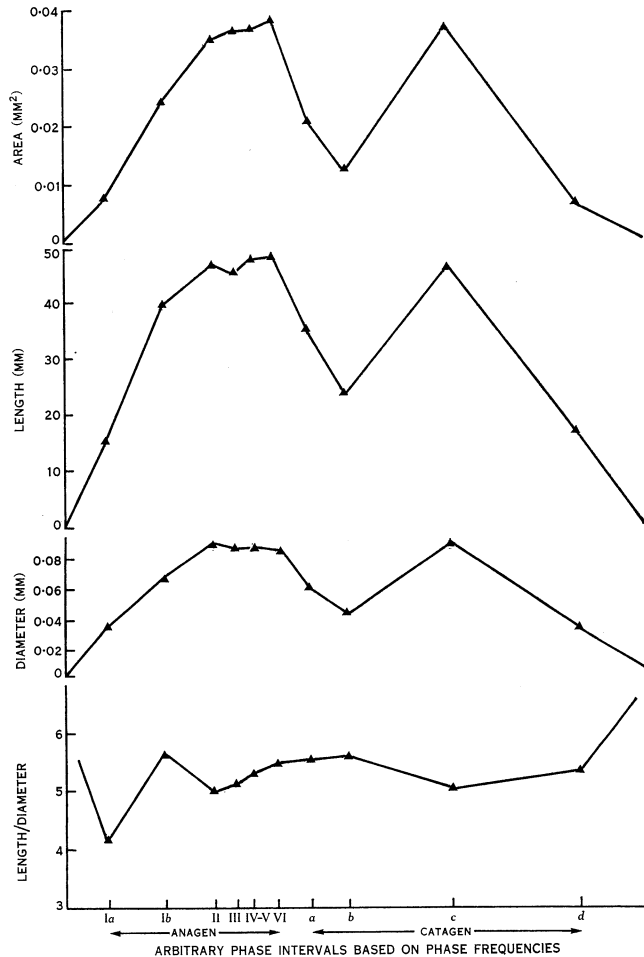


Fig. 2.—Variation in mean gland size throughout the hair growth cycle for two Africander-Hereford crossbred animals. The number of glands represented by each point, as well as gland sizes, are as given in Table 1. The phase intervals are arbitrary, being based on phase frequencies in Table 3.

Catagen d.—This is a transitional phase such as anagen Ia. The papilla is in various stages of regression so that the club may assume a blunt finger-like appearance. Follicle depth is intermediate between that of catagen *c* and telogen. The chief difference between this stage and anagen Ia is the non-proliferative appearance of the connective tissue sheath with its much more limited basophilic cytoplasm.

Telogen.—An obvious feature of this phase is the distended sebaceous gland and the colourless shaft extending no deeper than the sebaceous gland. On many occasions the shaft has completely regressed above the sebaceous gland or is absent.

III. RESULTS

(a) Sources of Variation in Sweat Gland Size

Mean gland dimensions for each follicle phase in two animals are shown in Table 1 and Figure 2. In Figure 2 phases are spaced on the abscissa to represent an approximate time scale. It is assumed that the duration of any phase, as a percentage of the total cycle length, is equal to the percentage of total follicles which are in that phase. The phase frequencies used for this purpose are those given in Table 3.

With 10 glands (in most cases) representing each phase in each animal, significant differences in sweat gland size between phases are demonstrated. Projected areas vary from essentially zero in telogen to 0.006 mm^2 in anagen Ia and 0.038 mm^2 in anagen VI and catagen c. There is strong agreement between the two animals ($r = 0.960$, d.f. = 9, $P < 0.01$).

As can be seen from the tracings in Figure 1 and the photomicrographs in Plate 1, the gland is always completely contracted in telogen, often in catagen b or catagen a, and partly contracted in anagen Ia, catagen a, and catagen d. That is, the curve of gland size is biphasic (Fig. 2) but, whereas the trough at telogen is absolute and invariable, the trough in early catagen, though unmistakable, is less consistent. With certain types of follicles, particularly those with lightly pigmented non-medullated hairs, only limited contraction of the gland appears to take place in early catagen, and this phenomenon appears to be related to the type of changes in the hair club. In catagen c the glands are of the same mean size as in anagen VI (Fig. 2) and invariably appear fully distended (Plate 1). Because of the varying degree of gland contraction in catagen b it is possible that a more precise definition of follicle status at this stage would identify a phase containing completely collapsed glands.

For the whole group of 23 animals, 50 randomly selected complete piloapocrine units per animal were identified and measured. For this purpose only five phase groupings were used—early anagen (I-II), mid-anagen (III-V), late anagen (VI), early catagen (a and b), and late catagen (c and d). Telogen phase was not included so the actual phase difference overall would be greater than that estimated in this sample. Table 2 is an analysis of variance of mean gland sizes of the various phases in these animals. There is no sex difference in gland size. A large proportion of the variation is accounted for by differences between phases, but there is still a highly significant animal difference. The agreement between the two animals in Table 1 is fortuitous.

Because of the large differences in gland size associated with follicle phases, any heterogeneity between animals in frequency distribution of phases could have a strong effect on mean gland size. One-hundred randomly selected follicles from each of 21 animals (two of the 23 slides had been damaged at this stage) were classified into the 11 defined phases. The mean frequency of each phase and the contributions to

χ^2 are shown in Table 3. The value of $\chi^2 = 1064$ (d.f. = 200, $P < 0.01$) shows a marked heterogeneity between animals in phase distribution.

Thus animal differences in mean gland size may arise both from inherent differences which exist independent of phase (Table 2) and from effects of different patterns of phase frequencies. The relative contribution of these components has

TABLE 2

ANALYSIS OF VARIANCE OF SWEAT GLAND SURFACE AREA BASED ON MEAN PHASE SIZE FOR THE 23 AFRICANDER CROSS ANIMALS UNDER INVESTIGATION

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Sexes	1	50,062	50,062	
Animals within sexes	21	196,443	56,973	8.43
Phases	4	378,888	344,722	51.02
Phases \times sex	4	56,232	14,058	
Phases \times animals within sexes	84	567,500	6,756	

been assessed in the following way. Relative inherent gland size, I_c , was obtained by expressing the mean size of 10 glands in catagen c in each animal as a percentage of the mean for catagen c in the two reference animals (Fig. 2). A similar estimate (I_a) was made for anagen III-V, although 10 glands were not available for all animals in this phase grouping. The correlation between I_c and I_a was 0.808

TABLE 3

DISTRIBUTION OF FOLLICLES BETWEEN PHASES FOR 100 RANDOMLY SELECTED FOLLICLES FROM EACH OF 21 ANIMALS

	Anagen Phase						Catagen Phase				Telo-gen	Total
	I_a	I_b	II	III	IV-V	VI	a	b	c	d		
No. of glands	176	252	101	61	55	121	119	125	631	306	153	2100
Expected distribution	8.4	12.0	4.8	2.9	2.6	5.8	5.7	6.0	30.0	14.5	7.3	100
$\Sigma(d^2/E)^*$	132	210	76	70	45	48	85	116	126	112	44	1064†

* d , deviation of individual from expected frequency; E , expected frequency.

† $\chi^2 = 1064$, d.f. = 200, $P < 0.01$.

(d.f. = 19, $P < 0.01$) and the mean, I , of the two values was used in subsequent analyses. The contribution of heterogeneity of phase frequencies was obtained by applying the observed frequency distribution for each animal to the mean gland size of each phase in the two reference animals, giving an estimate of mean gland size (E) as influenced by phase frequency. Then actual mean gland size (A) is estimated as $A = EI$. Thence

$$\log A = \log E + \log I,$$

and

$$\text{var. log } A = \text{var. log } E + \text{var. log } I + 2 \text{ cov. log } E \text{ log } I.$$

From the data described:

$$\begin{aligned}\text{var. log } E &= 2834, \\ \text{var. log } I &= 9142 \\ \text{cov. log } E \text{ log } I &= -1196\end{aligned}$$

The covariance is not significant ($r = -0.235$). Contributions to mean gland size of differences in frequency of follicle phases and of differences in inherent gland size are in the ratio of 1 : 3.2.

This estimate, A , of actual mean gland size and its components E and I were correlated with the observed mean size of 50 unselected glands as follows:

$$A, r = 0.661 (P < 0.01); I, r = 0.832 (P < 0.01); E, r = -0.329.$$

It appears that the normal system of measuring glands accounts for differences in inherent gland size but not for differences in mean size arising from frequencies of follicle phases. In other contexts, e.g. between seasons, the discrepancy between actual and measured mean gland size may be even greater.

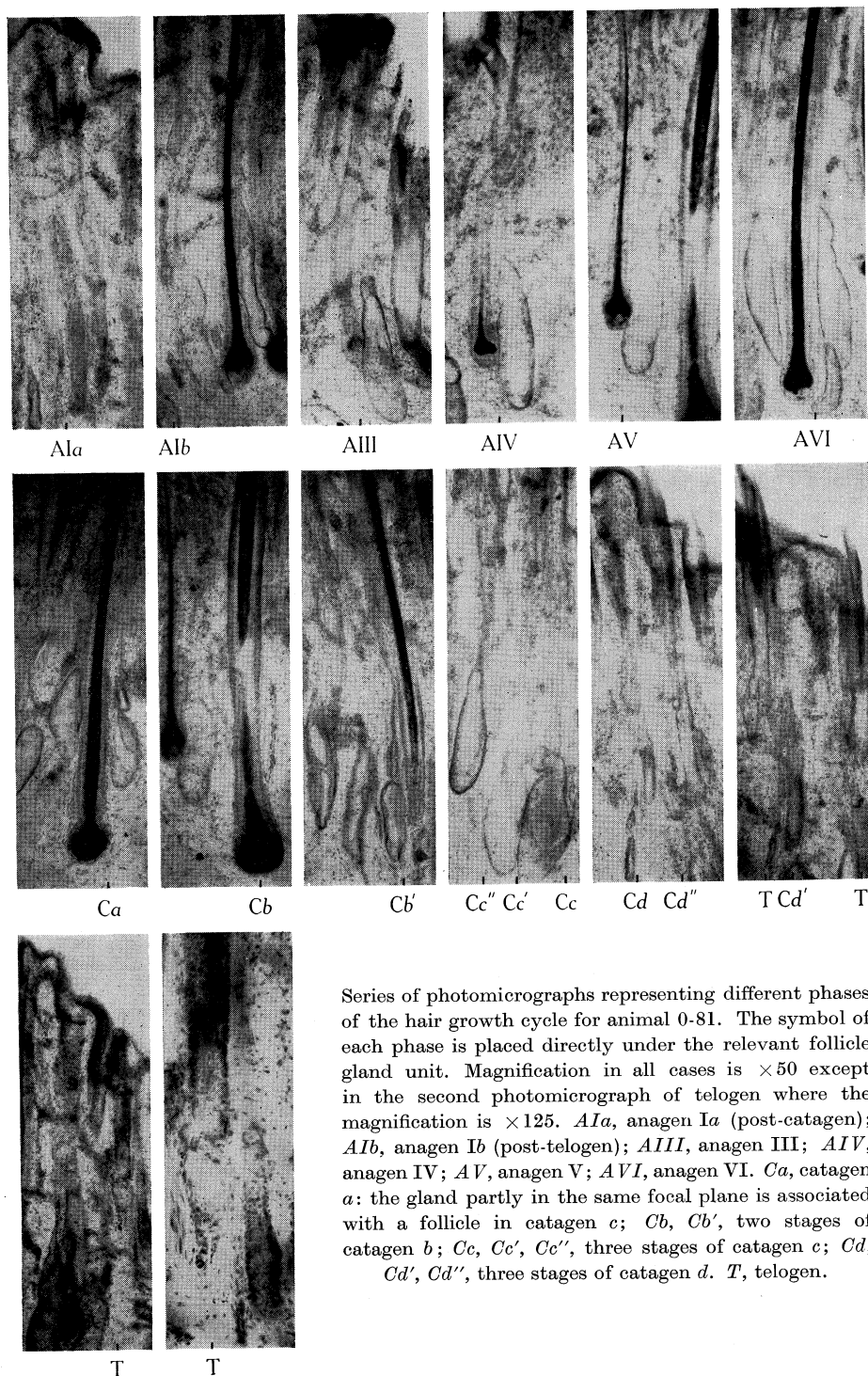
It has been assumed in the foregoing treatment of data that follicles of different size are similarly distributed between the various follicle phases. When giant follicles are brought into consideration, it is found that this is not so. Table 4 shows frequencies of phase groups for 4600 follicles of all types (200 in each of 23 animals) and for 684 giant follicles (a mean of 30 per animal). The frequencies are significantly different, the giant follicles showing a higher proportion in anagen and fewer in the resting phases. This relative advancement of giant follicles into the growing phase in spring is in accord with the observation that giant hairs are the first to be shed in spring (Schleger and Turner 1960). Giant follicles have been excluded from the data used to determine effects of follicle phase on gland size, so the phenomenon here described has not biased the curves of Figure 2. They have been included at their normal incidence in frequency counts but proportions of giant follicles are small and fairly constant between animals.

(b) *Sweat Gland Morphology*

Lengths and diameters of glands tend to vary together through the various phases. In anagen III there is a slight recession in length but the two animals (Fig. 2) show a consistent change in length-diameter ratio for only a limited portion of the growth cycle.

Some characteristic changes in gland shape have been observed. From the contracted state of telogen the gland first expands distally into a small loop. In anagen Ib there is a moderate expansion throughout most of the gland length so that a slender gland with high length-diameter ratio results. In anagen II the increase in diameter is relatively greater than the increase in length so that the length-diameter ratio falls. In large glands, contraction at the end of anagen appears to take place proximally and then distally so that the gland consists of only one or two median loops before complete constriction takes place. Expansion in early catagen appears to take place distally first so that glands with thick contracted proximal walls and thin expanded distal walls are apparent (Plate 1).

HAIR FOLLICLES AND SWEAT GLANDS IN CATTLE



Series of photomicrographs representing different phases of the hair growth cycle for animal 0-81. The symbol of each phase is placed directly under the relevant follicle gland unit. Magnification in all cases is $\times 50$ except in the second photomicrograph of telogen where the magnification is $\times 125$. *AIa*, anagen Ia (post-catagen); *AIb*, anagen Ib (post-telogen); *AIll*, anagen III; *AIV*, anagen IV; *AV*, anagen V; *AVI*, anagen VI. *Ca*, catagen a: the gland partly in the same focal plane is associated with a follicle in catagen c; *Cb*, *Cb'*, two stages of catagen b; *Cc*, *Cc'*, *Cc''*, three stages of catagen c; *Cd*, *Cd'*, *Cd''*, three stages of catagen d. *T*, telogen.

IV. DISCUSSION

The foregoing results demonstrate a relationship between phase of the hair growth cycle and morphology of the sweat glands in cattle. This relationship is analogous to that between sebaceous gland and hair growth in the mouse (Montagna 1962). Although the variation in sebaceous gland structure throughout the hair growth cycle has not been studied in this investigation, considerable changes in this gland have also been observed in bovine samples.

In the mouse, where hair growth phases move across the skin in bands involving all follicles, it has been made clear that the skin is an integrated organ system (Montagna 1956). Anagen skin is an actively proliferating tissue while telogen skin is more mature and refractory (Rothman 1954). Davis (1962) claims some

TABLE 4
COMPARISON BETWEEN GIANT FOLLICLES AND ALL FOLLICLES IN FREQUENCIES
OF FOLLICLE PHASES

Phase Group	Giant Follicles		All Follicles	
	No.	%	No.	%
Anagen I-V	223	32.6	1022	22.2
Anagen VI, catagen <i>a</i>	192	28.1	876	19.1
Catagen <i>b, c, d</i> , telogen	269	39.3	2702	58.7
Total*	684	100	4600	100

* $\chi^2 = 92$, d.f. = 2, $P < 0.01$.

characteristic metabolic activity of telogen as a phase of recovery but this phase in cattle is clearly one of complete inactivity in regard to the sweat gland. Montagna and Ellis (1958) described catagen as a retrograde morphogenetic transformation and not a degenerative process. These descriptions fit the relationships observed between follicles and sweat glands in cattle, where the unity is found in individual piloapocrine units rather than in whole areas of skin. Large, distended glands are found in association with the presumably more metabolically active phases of anagen and catagen, whereas the glands are deflated to some extent in the hiatus between these phases and completely during the resting phase of telogen.

It is perhaps surprising that the curve showing the size of the gland is biphasic within the duration of a follicle cycle. It has not been clearly established whether the reduction in size is a structural involution, or a simple deflation. The sweat gland has a high turnover rate, and deflation could result from a reduction in secretion rate relative to the rate of expulsion of sweat (Hayman and Nay 1958). The transient and variable reduction in size in early catagen might arise in this manner, but the complete collapse in telogen probably represents a thorough involution. The question is being investigated.

The association between follicle phase and gland size which has been described offers a partial explanation for the association of coat characters with differences in sweat gland size and activity between breeds, between strains, between animals within breeds, between different body regions, and between seasons (Dowling 1958; McLean 1963; Schleger and Turner 1965). The fuller explanation almost certainly lies in a more general association between follicle activity and gland activity, of which this morphological association is one facet. Gland size is probably not the only determinant of sweating capacity. It remains to be investigated, for instance, whether a gland associated with a follicle in catagen has the same functional capacity as one of equal size associated with a follicle in anagen. This seems unlikely in view of the vascular supply to the papilla in the two phases as demonstrated in rat skin by Montagna and Ellis (1958) and in cattle skin by Schleger (unpublished data).

In regard to seasonal differences in sweating capacity, Dowling and Nay (1960) and Hayman and Nay (1961) showed that the winter coat contains a higher proportion of club hairs, representing catagen and telogen phases, than the summer coat. The high proportion of club hairs in winter would mean a high proportion of glands in proximity to the regressed catagen *a* and telogen phases and this would cause a reduced sweating capacity, such as has been observed.

The number of functional glands in the skin is usually less, and under some circumstances can be considerably less, than the number of hair follicles. The proportion of regressed, and therefore virtually invisible, glands must be taken into account, together with the mean size of visible glands, in assessing mean gland size. In the results presented, heterogeneity of phase distribution between animals sampled at the one date accounted for about one-quarter of the variance in overall mean gland size. This fraction of between-animal variance is likely to vary with season, nutritional status, breed, and age. The fraction may be much larger when variation between seasons, between breeds, etc. is considered.

The manner in which the sweat glands undergo change in size leads to characteristic changes in gland shape so that hair growth phase and gland shape are fairly well correlated. Differences in hair growth pattern may partly explain differences in morphology existing between animals (Nay 1959) and between body regions (Pan 1963).

A highly characteristic pink acidic response to haematoxylin-eosin by the inner root sheath is found particularly in anagen *Ib*, anagen *II*, catagen *a*, and around the developing club of catagen *b*. This is taken as a valuable aid to identification of follicle phases. The occurrence is presumably associated with other chemical changes, in sulphhydryl groups, phospholipids, and acid phosphatases, known to occur in these same phases (Montagna and Ellis 1958).

Implications of an integral, labile, piloapocrine unit may be relevant in various situations. Berman (1957) reported an increase in sweating rate associated with clipping, and Ishii (1964) stated that daily grooming of cattle increased sweating rate by 8.33%. An accepted essential part of the routine in the training of thoroughbred horses is clipping and regular grooming. Whereas there is no basis to the belief that cutting of hair *per se* accelerates growth, Rothman (1954) concluded that treatment promoting hyperaemia could cause an increased rate of hair growth and thickening

of the hair shaft. A logical deduction is that mechanical stimulation promotes follicle activity and produces a higher proportion of hairs in the actively growing phase, and a higher proportion of sweat glands in the functional state.

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