THE DISTRIBUTION AND HISTOLOGICAL STRUCTURE OF THE CUTANEOUS GLANDS OF CERTAIN MARSUPIALS. A COMPARATIVE STUDY.

Presented as a thesis

for the degree of Doctor of Philosophy

by

L. M. A. Green, B.A., M.Sc.,

Department of Anatomy

University of Adelaide.

TABLE OF CONTENTS

THE DISTRIBUTION AND HISTOLOGICAL STRUCTURE OF THE CUTANEOUS GLANDS OF CERTAIN MARSUPIALS. A COMPARATIVE STUDY.

GENERAL INTRODUCTION.

"Most cutaneous tubular glands of mammals have their own peculiarities and many of them are vastly different. The glands in the anal sac of the dog, the brown inguinal glands of the rabbit and the glands of the external auditory meatus of the cat, all differ morphologically from either the eccrine or the apocrine glands of man." With these lines from Montagna (1956) in mind, it seemed of interest to discover if any morphological and histological differences were present in the skin glands of certain marsupials.

It is known that in the anal sac of the dog and in the external auditory meatus of the cat, in addition to the tubular glands mentioned above, holocrine cell groups are also present. Glands of this nature are found in some marsupials.

It was decided to investigate several animals, each of which belonged to either one or other of the two dental divisions Diprotodontia and Polyprotodontia (Owen's classification; see Abbie, 1937).

This report presents an account of the normal histology of TRICHOSURUS VULPECULA, DROMICIA CONCINNA, THYLACIS OBESULUS and SMINTHOPSIS CRASSICAUDATA. These animals show

variations in dietary habits : TRICHOSURUS and DROMICIA (diprotodonts) are mostly herbivorous, while of the two polyprotodonts, THYLACIS is insectivorous and SMINTHOPSIS is carnivorous.

MATERIAL AND METHODS.

The material used for this study was taken from several young mature males and females.
Areas of skin, including hypodermis, were excised from the various representative parts of the body and fixed in 10% formalin, or in Zenker's fixative, and finally sectioned in paraffin. These sections were cut at 8 micra and stained with haematoxylin (Harris) and eosin. In some sections phloxin replaced the eosin.

DISTRIBUTION OF GLANDULAR TISSUE.

Areas of skin were removed from the top of the head, axilla, groin, scrotum; sternal and interscapular regions and pinna of the ear. Complete serial sections were cut through the eyeball and its surrounding tissues, as well as through the vestibule of the nose and the cartilaginous portion of the external auditory meatus.

The non-hairy parts of the foot pads and complete serial sections through the middle and tip of the tail were investigated.

The mammary glands, nipples and marsupium of the females of all four marsupials were sectioned and microscopically examined. The anal region was also included

in the survey.

This report has been divided into sections, each with its own short introduction and summary. In these sections similar regions of all four animals have been included, except in those cases where their histological similarity rendered it unnecessary to give a full description of more than one or two of them. Before describing the glands in the areas mentioned above, it was decided, for comparative purposes, to include a general description of the three main types of glands viz: eccrine and apocrine (sudoriferous), and sebaceous.

GENERAL DESCRIPTION OF SUDORIFEROUS AND SEBACEOUS GLANDS.

INTRODUCTION.

Purkinje discovered sweat glands in 1833, but it was Schiefferdecker who in 1922 recognized the two types, viz: eccrine and apocrine.

Eccrine glands appear most extensively in man and rather less frequently in the primates. In some other mammals they are present chiefly on the volar surface of manus and pes and occasionally in a few other localities.

Apocrine glands are usually associated with hairy surfaces as they tend to be appendages of hair follicles although this is not invariably the case.

Montagna (1956) gave the following description of the eccrine variety. "Eccrine glands consist of simple tubes which extend from the epidermis to the lower parts of the

dermis or hypodermis.--- The basal portion of each tubule is irregularly and tightly coiled, while from the coil to the epidermis the tubule is straight or undulating. That part of the duct which runs within the epidermis is again coiled.---- Each tubule consists of a secretory portion and a duct." The secretory portion consists of one layer of pale-staining truncated pyramidal cells which can vary in size. In larger cells the nucleus is usually basal, while in smaller ones its position is nearer to the lumen of the tubule. The luminal margin of the larger cells frequently exhibits a hyaline cuticular border. Acidophilic myoepithelial cells lie between the bases of the secretory ones and both types rest on the basement membrane.

Several authors have given descriptions of myoepithelial cells. Ring and Randall (1947) when referring to these cells in the eccrine sweat glands in the foot pads of the albino rat, remarked that "they appear identical with smooth muscle cells and follow a longitudinal and apparently a spiral course around the sweat gland and its duct."

Sperling and Koppanyi (1946) describe the myoepithelial cells in the paw of the cat, as being as large as $\frac{1}{3}$ the height of the glandular epithelium.

Montagna (1956) in his account of the human eccrine gland says "myoepithelial cells are loosely dove-tailed at the base of the secretory ones and are aligned parallel

to the axis of the tubule. Structurally they are the same as in apocrine glands."

It can usually be noted that the transition from secretory to duct tubule is an abrupt one.

Montagna (1956) divides the duct into three segments: viz: sweat duct unit and its spiral course within the epidermis, a straight or slightly undulating "dermal sweat duct", and within the dermis or hypodermis a third coiled segment. The basal coil of each gland is made up of nearly equal parts of duct and secretory portion.

Several criteria are available to assist the histologist in discriminating between the secretory and duct epithelium in these coils. Ducts have a much smaller diameter and their walls consist of two layers of cuboidal cells (all of similar size), each with a centrally placed nucleus. The duct lumen is usually round and rather larger than that of the secretory tubule, in which it varies in size and is irregular in shape. In addition to being smaller, the duct cells stain more darkly than do the larger, taller, secretory ones.

After the duct leaves the mass of coils it travels through the dermis and frequently enters the epithelium at the apex of an epidermal peg. Once within the Malpighian region two to three coils are again made, followed by a more spiral course through the stratum corneum before reaching the external pore.

It was mentioned above that the duct wall consisted of two layers of cuboidal cells. However, in 1939, Pinkus noted that most authors, who have studied the epidermal part of the sweat duct, have concluded that it loses its own lining epithelium when it enters the epidermis and that the sweat flows through a channel formed by compression of the neighbouring prickle cells.

But Hoepke (1927) had already shown that there is actually a closed tube because the lining cells are fused into a coherent membrane. He insisted however, that the wall is but a functional entity and that its mural cells are those of the prickle cell layer of the epidermis. Also in 1939 Pinkus noted that cells lining the sweat duct are different from and in their behaviour independent of, the rest of the epidermis. He pointed out that this fact can be verified by instances in which the epidermal cells are altered by disease or by experiment. For these reasons he regards the intraepidermal part of the sweat duct as a separate entity of "given length" which adjusts its shape to fit various widths of epidermis. Hence, the differences in kinkings at different levels of the epidermis. For example, when traversing the thick epidermis of palms and soles, the duct takes a steep spiral course, whereas it is much more tortuous in skins with thin epidermal layers.

Lobitz, Holyoke and Montagna (1954) agree with the contention of Pinkus (1939) that the epidermal eccrine sweat

duct is a morphologic and biologic entity, and by this "entity", they mean the "single layer of lining cells." They base these conclusions on the individual staining properties of these cells. They used the Hotchkiss-McManus technique and showed that the free luminal border of the inner layer of duct cells contains Schiff-positive material and that this lining can be traced through the granular zone and stratum corneum to the sweat pore.

In 1956 Winklemann maintained that by using silver preparations, which provide the delicate degree of differentiation, it is possible to distinguish tinctorially between the cells of the duct and those of the epidermis. This investigator also reported that when frozen sections are stained by Sudan black B techniques, the differentiation is such that the eccrine duct unit is revealed. This revelation is due to the differential staining of the lipid in the layer of keratin and to the staining of the kerato-hyalin granules. This effect is not present in the lower $\frac{1}{3}$ of the duct, which of course, does not traverse the epidermis.

THE APOCRINE SWEAT GLANDS.

INTRODUCTION.

These glands according to Rothman (1953) are phylogenetically older than the eccrine type which are distributed over the whole body in the human race.

The apocrine system has become rudimentary in man, in whom it occurs normally, as large glands only in such areas as axilla, around the nipple, mid-line of the abdomen and mons pubis. The perigenital, perianal and perineal regions are also included. The external auditory canal and the nasal vestibule are two other locations in which specialized apocrine glands are found. The mammary gland itself is also regarded as having an apocrine type of secretion.

GENERAL DESCRIPTION OF THE GLANDS.

Montagna, Lobitz Jr. and Chase (1953) described the axillary apocrine glands as simple coiled tubules which lie in the subcutaneous tela.

Sperling and Horn (1935) have shown with wax reconstructions that the dilated secretory portion of the apocrine gland is compactly coiled and that adjacent loops are joined by shunts or may terminate in blind sacs. The normal functioning glands in the adult are lined with an irregularly columnar epithelium, the inner borders of which are often elongated and project into the lumen. The free margins of these cells may have a cuticular border. The segments of the secretory tubules which are in the resting or post-secretory phase are lined with a cuboidal type of cell. The secretory epithelium rests upon a mesh of large myoepithelial cells which lie close to the thick hyaline

basement membrane. Bunting, Wislocki and Dempsey (1948) noted that myoepithelial cells are larger and more numerous in apocrine than in eccrine glands.

According to Hoepke (1927) the secretory cycle in axillary glands begins in cuboidal cells with an accumulation of granules above the nucleus, these granules increase in size and number, the cells lose their cuticular border become cylindrical and protrude as blebs into the lumen. He also believed, as do most other histologists, that the terminal bleb is pinched off as part of the secretion, later the decapitated cells reacquire a cuticular border and the cycle of secretion is renewed.

Montagna, Chase and Lobitz Jr. (1953) reported from their observations that the long apparently detached blebs, when traced in serial sections, are really attached to the subjacent cells. They claimed that the pinched-off appearance of the blebs is brought about by dehydration, since in frozen sections the terminal cytoplasm, however long, is always stout. They also noted that in most apocrine cells, with the exception of the very flat ones, the free border sends out numerous Schiff-reactive delicate projections which terminate in a globule. These authors made the assertion that, in their opinion, the blebs do not break off and become part of the secretion, but probably act as "pseudopodia-like" structures through

which secretion might occur. They cited the resemblance to the "pseudopodia" described and illustrated by Ponse and Altschuler (1940) in thyroid cells.

Bunting, Wislocki and Dempsey (1948) noted that the myoepithelial cells are confined to the secretory portion of the tubule. These elements are spindle-shaped (4-6 micra in diameter and 40-100 micra in length), they are placed with their long axis parallel to that of the tubules and they, themselves, are set in grooves between the bases of the secretory cells - consequently secretory and myoepithelial cells rest alternately upon the basement membrane. The myoepithelial elements are usually strongly acidophilic.

Hurley and Shelley (1954) remarked that myoepithelial cells are conspicuously absent in the duct portion of the human apocrine sweat gland. These authors also mentioned that while these myoid cells stain reasonably well with haematoxylin and eosin, they do so more completely with a phosphotungstic-acid-haematoxylin preparation. Following treatment with this reagent they appear blue in contrast with the brown tubular cells, and under high power magnification faint longitudinal striations, similar to those present in various smooth muscle cells, become visible.

FUNCTIONAL ASPECTS OF APOCRINE GLANDS

Rothman (1953) remarked that while the nature and

function of axillary glands are still under discussion it is known that those in the external auditory meatus of man, dog, and cat are implicated in cerumen production. The nature of the secretion from those apocrine tubules which accompany the large holocrine type of glands around the anal canal has not yet been determined.

Hurley and Shelley (1954) also suggested that the arrangement of the myoepithelial cells has a functional significance, since they run longitudinally with their long axis roughly parallel to that of the tubule. Contraction of these elements would probably cause the secretory cells to express their secretion into the lumen in at least one of the ways mentioned earlier in this review of the literature.

SEBACEOUS GLANDS

INTRODUCTION.

These glands which were first described by Eichorn in 1826 occur everywhere on hairy surfaces, though some of them are free, that is, not associated with hairs. In man these free glands are found chiefly near muco-cutaneous junctions, such as the anal region. They are also present at the edges of the lips, on the prepuce, glans penis and glans clitoridis, labia minora, nipple and areola.

Sebaceous glands may be single such as those attached to hair follicles or multiple as is the Meibomian gland of

the eyelid.

Schaffer (1940) believes that there are primary and secondary free sebaceous glands. The primary are ontogenetically derived from the epidermis or muco-cutaneous junctions, while the secondary type becomes free because of secondary atrophy of the hair follicles (such as in early male baldness in the human species), or because of excessive later development of the sebaceous glands and rudimentary development of the hair follicle.

It is also thought that the cutaneous glands of some reptiles may be the ancestors of the mammalian sebaceous type, for example, the femoral glands of lizards, cloacal glands of crocodiles, and anal glands of turtles and giant serpents. All these organs are sac-like invaginations of the epidermis, the cells of which undergo fatty degeneration before they are shed. The preen gland (glandula uropygialis), the only cutaneous gland of birds, is a bilobular sebaceous gland situated in the coccygeal region at the base of the tail.

In mammals, the sebaceous glands, like some of the coiled apocrine ones, secrete species and sex-specific odorous substances which play a role in sexual attraction and help in recognising the same or foreign species. In man most sebaceous glands develop from the outer root sheath of hair follicles and the earliest anlage consists of a spherical bud of cells. These cells develop into a

multilobulated gland with a short duct which usually passes the glandular secretion into the pilo-sebaceous canal of the hair follicle.

HISTOLOGICAL DESCRIPTION OF SEBACEOUS GLANDS

Its lobules are surrounded by a basement membrane. These lobules consist of two types of cells (Bertalanffy 1957): the first type is basal and usually lies in contact with the reticulum of the basement membrane. It forms a continuous layer at the periphery of the gland and in large structures these basal cells often form a double layer. The basal type cells have a homogeneous basophilic cytoplasm; the nuclei are small, dark and elongated. Basal cells of sebaceous glands are, on the one hand, continuous with the cells of the outer root sheath of the hair, and on the other with the basal stratum of the epidermis. The second type of cell is referred to as the "sebaceous cell" (Montagna, Chase and Lobitz 1952), for the reason that after fatty transformation it forms "the cholesterol containing material (Kandutch, Murphy and Dreisback 1955) called sebum". These "sebaceous" cells comprise the major portion of the gland: they develop from the basal cells and contain, in their cytoplasm, numerous and variable-sized vacuoles. Sebaceous cells also vary much in size and tend to be largest in the central part of the gland: here they usually contain a dark pyknotic nucleus, though some, especially those in which fatty degeneration has taken place, have

entirely lost their nuclei, and the cytoplasm has taken on a reticular appearance. In some glands the central "sebaceous" cells have completely disappeared leaving an empty space surrounded by basal cells. This empty space is doubtless due to the secretion plus cell debris having passed out into the excretory duct to form the complete secretion. After active secretion and expulsion of this product through the short duct into the hair canal of the associated hair, new "sebaceous" cells develop from the basal layer and the gland again passes into the secretory phase.

The large rather more specialized sebaceous glands such as those in the anal sac of the dog, in the human nipple and in the smooth skin of the rabbit's ear, may or may not be associated with one single hair.

DISCUSSION OF FUNCTIONAL ASPECTS OF SEBACEOUS GLANDS.

Those smaller glands which are associated with hairs, produce a fatty secretion which acts as a lubricant for both the hair and the skin surface: it also provides a water-proofing film over the epidermis.

The secretion produced in part by the sebaceous components of glands in the anal sac of the dog is, according to Montagna and Parks (1948) a viscous putrescent fluid, the biological significance of which is unknown.

The sebaceous tissue found in the nipple of human females was examined by Perkins and Miller (1926). They

described the glands as compound and occurring only at the tip of the nipple on to which the ducts emptied. These authors suggested that the function of such glands in the nipple tissue is to keep the skin soft during lactation and also to protect it from the saliva of the nursing infant.

DESCRIPTION OF THE SKIN GLANDS FOUND IN THE FOUR MARSUPIALS.

GLANDS IN THE VENTRAL PADS OF BOTH MANUS AND PES.

INTRODUCTION.

In 1946 Sperling and Koppanyi reported that eccrine were the only type of sweat glands present in the paw of the cat, and in 1947 Ring and Randall made a similar claim for the paw of the albino rat.

The term "paw" in each case referred to the hairless ventral pads of both manus and pes.

Since all four animals investigated for this paper have ventral and interdigital pads, of both manus and pes, completely devoid of hairs, it was decided to discover whether only eccrine glands were present in these regions and, if so, to describe them.

Serial sections, stained with haematoxylin and phloxin were used for microscopic examination, which proved, in all four cases, that eccrine were the only sweat glands present.

In the pads of Trichosurus vulpecula, these glands were situated, surrounded by adipose tissue, at the junction

Fig. 1.- Eccrine sweat glands in the skin of the foot pad of a male Trichosurus vulpecula. Stain H and Phloxin. X60.

A. T.S. of tubules of an eccrine sweat gland.
B. Myoepithelial cells in the secretory tubule.
C. Ducts of the gland.
D. Connective tissue of the dermis.
E. Adipose tissue in the hypodermis.

This section shows in T.S. the large diameter of the secretory tubules compared with that of the ducts.

Fig. 1a.- Shows a higher power picture of the secretory tubules. The lower left hand section of a tubule depicts myoepithelial cells in transverse section, while on the right they are seen in longitudinal view.

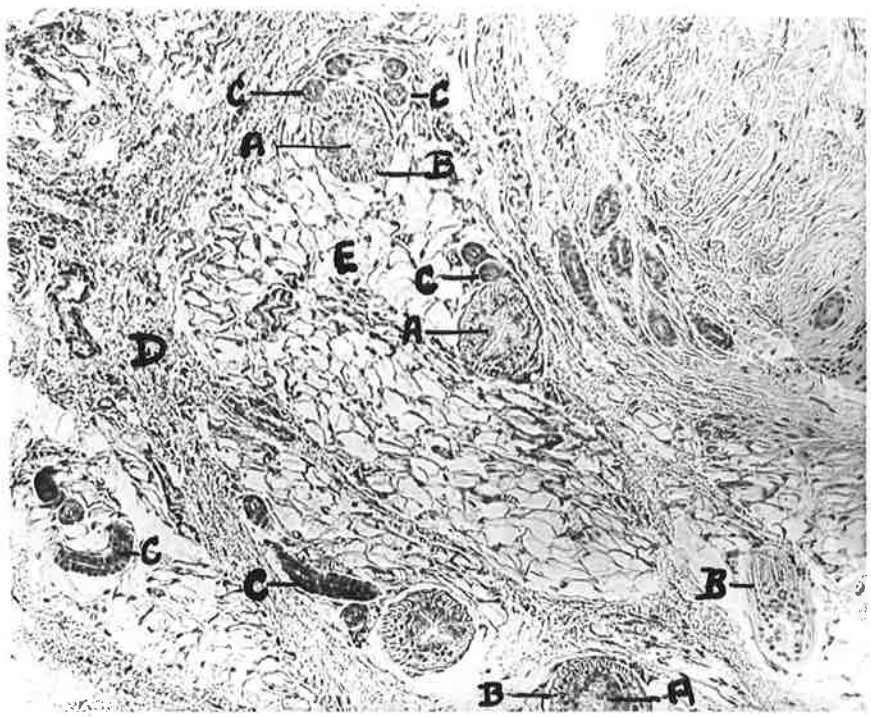

Fig. 1.

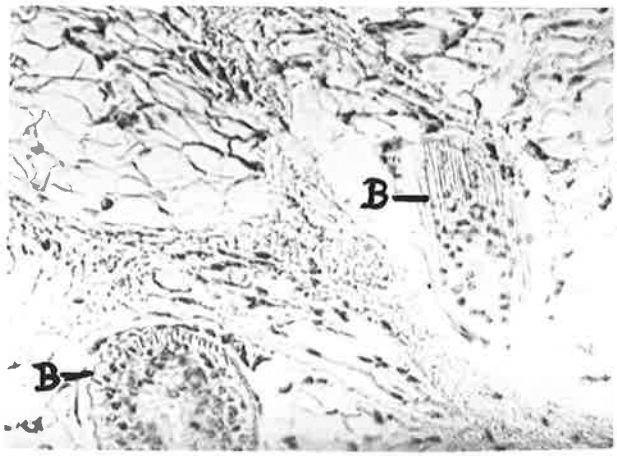

Fig. 1a.

of dermis and hypodermis. The large conspicuous secretory coils were invested with connective tissue, which formed a capsule in which many capillary blood vessels were noted. (Fig. 1.). The large secretory coils consisted of tall, pyramidal cells with pale slightly acidophilic cytoplasm and a circular nucleus. Arranged around the secretory tubule, myopepithelial cells, with their long axis running parallel with the tubule, were made conspicuous by their strongly acidophilic staining reaction and their small dark nucleus. In their contracted state each of these cells appeared to project into an invagination in the base of a superimposed secretory one. Both the secretory and the contractile elements rested on the basement membrane. (Fig. 1a).

It was noted that the secretory coils changed abruptly to become ducts (Fig. 2) which immediately coiled several times and then passed into the dermis through which they travelled in an undulating fashion. The duct wall consisted of two layers of cells; the inner ones were cuboidal, with an acidophilic cuticle facing the small well-defined lumen: while the outer cells tended to be flatter and to have dark nuclei. Following a spiral course through the dermis the ducts were seen to enter the rather infrequent epidermal pegs and then to coil several times. Their passage through the Malpighian layers included several more coils after which they entered the

Fig. 2.- Eccrine sweat glands in the skin of the foot pad of Trichosurus vulpecula. Stain H. and Phloxin. X180.

A. Secretory tubules.
B. Basement membrane.
C. Duct making an abrupt exit from the coiled tubules.
D. Myoepithelial cell.
E. T.S. ducts; the lining cells show a cuticle on the luminal border.
F. Adipose tissue.

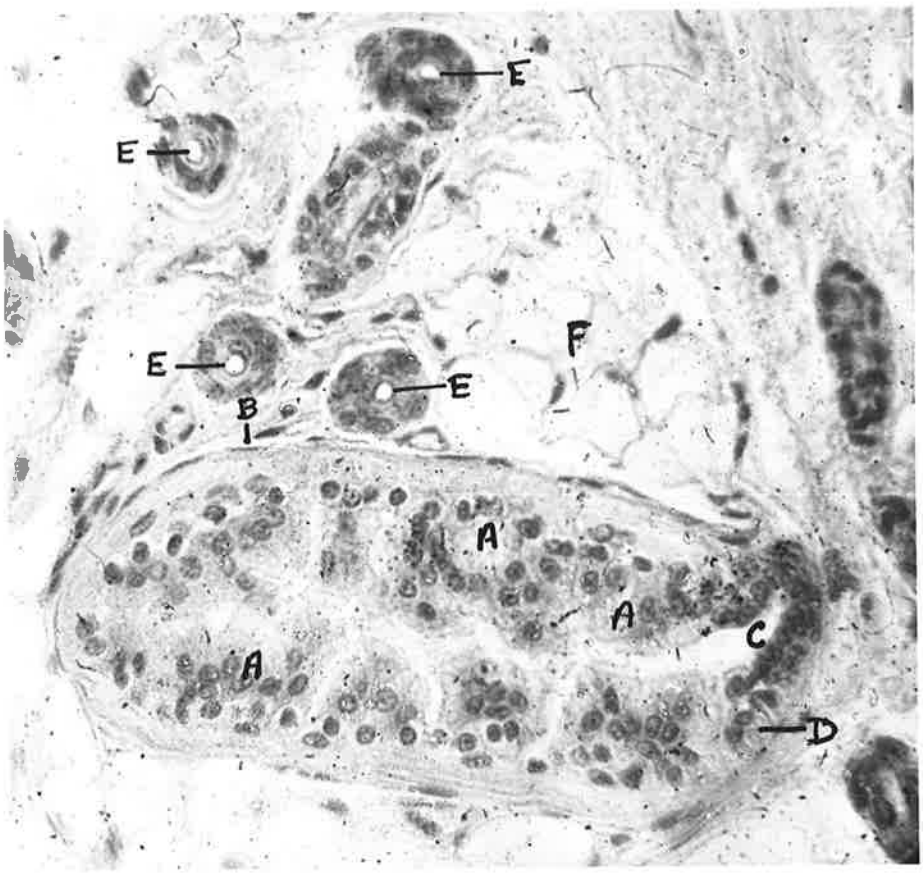

Fig. 2.

stratum corneum where, though the lumen had become flat or slit-like, the acidophilic cuticle could still be traced. The lining cells themselves had, in the external layer of the corneum become reduced to anucleated squames.

In the pads of DROMICIA CONCINNA it was observed that the collagen bundles which formed the hypodermis were practically obliterated by the densely packed coils of eccrine sweat glands. From between the secretory coils the ducts made their way towards the periphery of the glandular mass to reach the dermis, through which they pursued a loose spiral course and finally entered the apices of epidermal pegs. Several spiral turns were made in the stratum spinosum, beyond which an undulating course brought them to the stratum granulosum and finally to the stratum corneum. Throughout its course the lining cells of the duct wall preserved an acidophilic cuticle which, with the duct itself, could be traced only as far as the stratum granulosum. The secretory tubules were similar to those described in Trichosurus.

THYLACIS OBESULUS of this animal, Wood Jones (1924c) states "the manus has naked granular palm and three ill-defined interdigital pads", and the sole conforms to the same pattern.

The animal examined for this investigation was a

mature female, and all the pad regions showed the presence of only eccrine sweat glands which were not so closely aggregated as those in similar situations in Dromica. Also, [redacted] the interdigital pads appeared to possess fewer glands than did the ventral pads of both manus and pes.

The histological structure of these glands showed no variation from that described in the reports on Trichosurus and Dromicia.

Of SMINTHOPSIS CRASSICAUDATA Wood Jones (1923d) noted that the manus had naked granular flesh-coloured palmar areas and only the mid-line region of the pes was devoid of hairs.

For this part of the study mature females were used and again it was found that only eccrine sweat glands are present on non-hairy skin surfaces. These eccrine glands showed the same general structure and characteristics as those given of the other three animals: but since the passage of the ducts through the keratinized layers could not be traced, no details of this part of their course can be given.

GLANDS FOUND IN THE SKIN OF THE TAILS.

INTRODUCTION.

Of the four animals investigated only one, Trichosurus

Fig. 3.- Eccrine sweat glands in the bare ventral surface of the tail of Trichosurus vulpecula.

A. T.S. of the eccrine secretory tubules.
B. Myoepithelial cell.
C. Basement membrane.
D. T.S. of duct from eccrine glands.
E. Cuticle lining the duct of an eccrine gland.
F. L.S. of duct of eccrine gland.
G. Connective tissue.

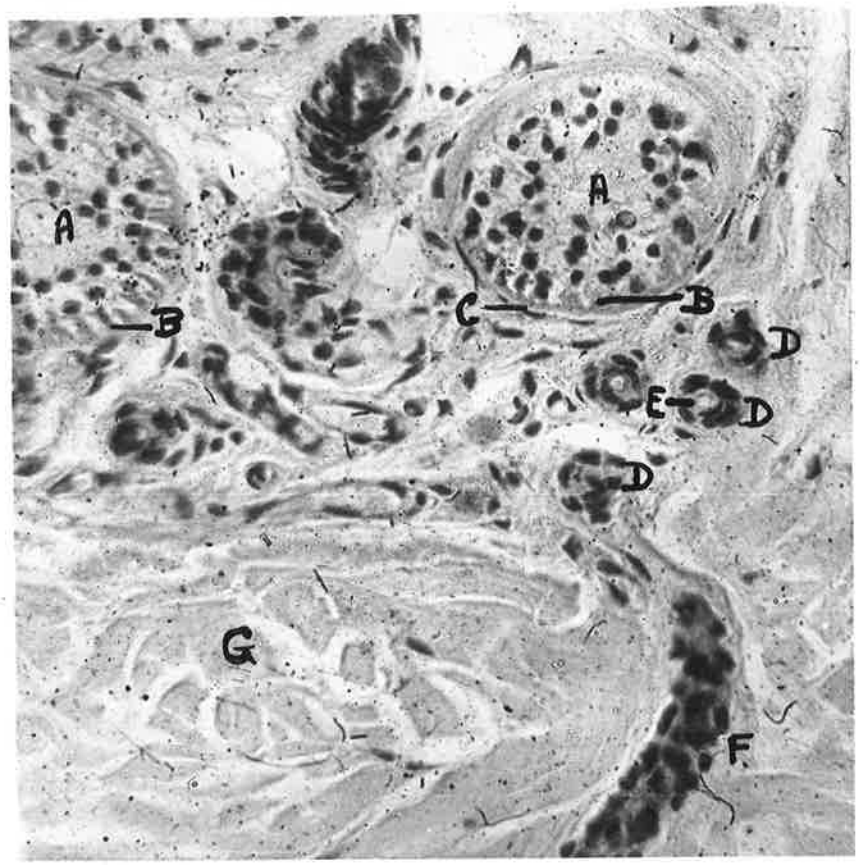

Fig. 3.

vupecula, possessed a tail not completely covered with hair, and so in this case it was decided to examine both the hairy and the naked skin surfaces.

TRICHOSURUS VULPECULA.

Trichosurus means "hairy tailed" since to quote Wood Jones (1924) the caudal appendage "is thick and bushy--- the terminal portion of its ventral surface is naked and prehensile and its skin is finely granular, very much like the skin of the palm and sole."

Serial sections cut through the prehensile part of the tail of a mature male, were stained with haematoxylin and phloxin.

Both naked and hairy parts were examined and a description of glands encountered will be given. Sections of the naked prehensile terminal surface (Fig. 3.) showed transverse cuts through wide coils of eccrine sweat glands. These coils though not numerous, were arranged in groups surrounded by a capsular investment of connective tissue. Their tubular walls consisted of tall pyramidal secretory cells containing a net-like cytoplasm and darkly staining nucleus. Acidophilic myoepithelial cells appeared between the pyramidal ones and the pale-lavender stained basement membrane upon which both types of cell rested.

During the secretory phase of the tubule, the myopepithelial cells which, in the inactive stage were narrow and arranged along the length of the tubule,

appeared to be contracted and thickened. This thickening caused them to project into hollowed-out bases of the overlying secretory ones.

These secretory tubules changed abruptly to form the ducts which had a narrow lumen surrounded by two layers of cells (Fig. 3.).

It was Lever who, in 1949, described the eccrine sweat ducts of man as being lined with a darkly eosinophilic homogeneous membrane or cuticle, which he thought, merely represented the luminal portion of the lining cells. Such a cuticle, perhaps less densely stained, was observed in a similar situation in the eccrine ducts of Trichosurus. (Fig. 3.).

After leaving the secretory tubules the ducts followed a fairly straight course through the dermis, then on entering pegs of the epidermis they were observed to coil several times. Their passage through the stratum granulosum was marked by the acquisition of granules, similar to those in the cells of this stratum, by the outer layer of duct cells. This granulation also appeared to extend back, to the depth of several cells, into the stratum spinosum. A similar observation was made by Ring and Randall (1947) in their report on the sweat glands of the foot pads of the albino rat.

In Trichosurus, in its passage through the stratum corneum, the eccrine duct lumen became flatter and more

irregular and at the same time, the single layer of lining cells retained the acidophilic cuticle.

Lobitz, Holyoke and Montagna (1954) maintain that in human glands the Schiff-positive (acidophilic cuticle in my material) lining of the duct remains intact through the granular zone and the stratum corneum to the sweat pore.

In the Trichosurus material, close to the skin surface, the duct was surrounded by keratinized cells which, on the actual surface, formed a flat depression, rather than a pore, as in human skin. The original lining cells of the duct retained, even in the depressed area, a faint staining of the luminal border.

The above description of eccrine ducts in the prehensile naked portion of this phalanger's tail seems to be in full agreement with the contention of Pinkus (1939) and later of Lobitz, Holyoke and Montagna (1954) that "the epidermal eccrine sweat duct is a morphologic and biologic entity" - the "entity" refers to the single layer of lining cells.

THE HAIRY PORTION OF THE TAIL.

In the more superficial part of the dermis, small hairs, in groups of three to four, were present; most of these groups were accompanied by small sebaceous appendages which displayed the usual holocrine characteristics.

The bulbs of large hairs, in groups of two to four appeared at short intervals in the lower part of the dermis. Deep to these large hair bulbs, at the dermo-

hypodermal border, apocrine tubules with the usual myoepithelial investments were observed.

These apocrine tubules displayed various stages of secretory activity: their ducts possessed the usual two-cell-layered wall, with an acidophilic cuticle present on the luminal surface of the inner cells. These ducts apparently opened into the pilosebaceous invagination of the large hairs situated superficial to their secretory coils.

DROMICIA CONCINNA.

The entire surface of the long slender prehensile tail of these animals is covered with hairs. Two pieces of tail were investigated, one close to the body, the other nearer to the tip. Since no naked skin was present, no eccrine glands were observed.

The very hairy surface which comprised about seven eighths of the tail skin, showed within the dermis, groups (three to four) of small hairs. Each group was supplied with a small sebaceous appendage. The large hair bulbs usually appeared singly and were present, sometimes superficial to, and sometimes deep to the grouped hairs. These large hairs were thought to be associated with the more deeply placed apocrine sweat gland coils which showed both secretory and non-secretory phases. The less hairy ventral surface showed the same characteristics as the very hairy seven eighths, though with fewer hair follicles.

Sections of the small tip of the tail displayed no departure from the general pattern, already outlined, except that there were fewer hair bulbs and rather more apocrine glands present.

THYLACIS OBESULUS.

According to Wood Jones (1924c) the tail of this marsupial is comparatively short and clothed with fine rather stiff hairs, dark coloured dorsally and pale ventrally. Beneath the short bristle hairs is a soft but rather scanty underfur.

The animal investigated for this study was a mature female. On the tail no naked areas were present and no eccrine glands were observed in the microscopical sections examined. As the appearance and description of the apocrine glands given for the hairy surface of both Trichosurus and Dromicia are so similar to that of Thylacis nothing further will be said of the latter animal.

SMINTHOPSIS CRASSICAUDATA.

According to Wood Jones (1923d) the skin covering the tail is scaly. The animal used here was a mature male, the tail was short (3.2 cms.). Small at its base, it increased in girth towards its mid-section and gradually tapered again to its tip. This appendage was uniformly covered with short fine hairs which extended right to the

slightly flattened tip. Microscopical examinations were made of a short length cut from the thick mid-section, as well as some taken from the terminal part.

The tail of Sminthopsis was entirely hairy, no eccrine glands were observed and only the hair-associated apocrine sweat glands, in various stages of secretory activity, were present. These glands appeared, in every way, similar to those of the other animals already described.

SUMMARY OF ALL FOUR ANIMALS.

Of the four marsupials investigated three possessed a tail which was completely clothed with hairs. Trichosurus differed from these three in having a prehensile appendage which was covered with hairs except on the ventral surface of its terminal part.

The hirsute surfaces of all four animals exhibited the presence of apocrine tubules in the border region betwen dermis and hypodermis. These tubules possessed the usual myoepithelial investments and were in various stages of secretory activity. In addition, characteristic sebaceous glands accompanied the groups of small hairs which occupied a mid position in the dermis. No eccrine glands were present in the hairy surfaces, but the naked terminal ventral region of the tail of Trichosurus vulpecula possessed eccrine structures similar to those occurring on the ventral pads of manus and pes of this animal. There

were no apocrine tubules here since the skin surface was devoid of hairs.

GLANDS OF THE CROWN OF THE HEAD, AXILLA, GROIN AND SCROTUM.

INTRODUCTION.

All these areas have hairs which are accompanied by sebaceous glands and in the case of large hairs, by both sebaceous and apocrine.

However, Cooper (1930) in his study of Dasypus novemcinta, notes that the hairs are few in number and that one sudoriferous and one or two sebaceous glands are found in conjunction with each hair follicle.

Duerden (1924) found that in sheep the sweat (apocrine) glands are always associated with hair follicles, but apparently he did not mention the presence or absence of the sebaceous variety.

Carter and Dowling (1954) reported that in cattle each hair follicle is associated with an apocrine as well as a sebaceous gland.

Details of those hairy areas, which in many mammals are more specialised, such as the sternal and the interscapular are reported under separate headings in this paper.

"Mammals are the only class of vertebrates which possess hairs." The hairs of each mammal have peculiarities of their own. Even in the same animal the pelage may be composed of strikingly different hairs. According to their

size and rigidity, hairs are grouped as coarse or fine. Coarse hairs are also known as guard hairs, top hairs or overhairs.... Fine hairs include those of fur, which are the fine and short underhairs." (Montagna 1956).

All four marsupials are included in the following tabulated description of the size and position of hairs and glands present in those areas mentioned in the above heading.

An account of the situation of Hairs, Apocrine and Sebaceous Glands in the regions: CROWN OF THE HEAD, AXILLA, GROIN and SCROTUM.

CROWN OF THE HEAD.

TRICHOSURUS VULPECULA (mature male)

Hairs. Large bulbs associated with apocrine coils appeared at the lower border of the dermis. More superficial bulbs of smaller hairs occurred in groups of three to four, all members of a group emerged through the same pore. Sebaceous appendages were present around the group.

Apocrine glands. Many had a wide lumen, others formed a narrow secretory tubule which ran parallel to the large hair bulb. The ducts opened into the pilo-sebaceous canals of these hairs. Myoepithelial cells were present and many glands were in the secretory phase.

Sebaceous glands. These occurred as small aggregations around groups of smaller hair follicles in the upper part of the dermis.

DROMICIA CONCINNA (mature female).

Hairs. Fine, single or in groups of two to three hairs, occurred at the junction of the dermis and hypodermis.

Apocrine glands occurred at widely separated intervals in the hypodermis. The glands were situated deep to a hair follicle into which the duct opened. Secretory cells showed a wide lumen; the duct a narrow one. Myoepithelial cells were present in the secretory part of the tubule.

Sebaceous glands occurred as small grouped appendages of single hairs or groups of hairs (two to three).

THYLACIS OBESULUS. (mature female)

Hairs occurred as a single large guard hair with smaller hairs in groups (six to eight).

Apocrine glands appeared as a single tubule associated with the guard-hair small-hair grouping.

Sebaceous glands. Very small sebaceous appendages were associated with both small and guard hairs.

SMINTHOPSIS CRASSICAUDATA. (mature male)

Hairs were fine and appeared in groups of three to four, very few single hairs were present.

Apocrine glands. A few tubules appeared at infrequent intervals at the deep dermal level. Their tall pale cells were in the secretory phase and myoepithelial cells were present. No ducts leading to a hair canal were identified.

Sebaceous glands. Very small appendages appeared with small hair groups only and not with single hairs.

AXILLA.

TRICHOSURUS VULPECULA. (mature female)

Hairs larger than those in the groin region were present at mid-dermal level. Several small hairs surrounded each large one.

Apocrine glands. The tubules occurred fairly frequently associated with hair groups at mid-dermal level. The tubules coiled several times and were in the secretory phase. Myoepithelial cells were present.

Sebaceous glands. Large glands were attached to coarse hairs while small hairs had only a small aggregation.

DROMICIA CONCINNA. (young mature female)

Hairs. Bulbs of fine hairs appeared in the hypodermis, the hairs were in separate follicles in groups of two to six. The bulbs of the very few single hairs were situated deep in the dermis. More superficially placed bulbs belonged to very fine hairs which occurred two to three in the same follicle.

Apocrine glands. Myoepithelial cells were present in these tubules from which the ducts opened into the canal of larger deeply placed hairs. Also an occasional apocrine duct opened into the pilo-sebaceous canal of a small superficial hair just below the entrance of a sebaceous duct (Montagna and Harrison 1957).

Sebaceous glands. Small aggregations were packed tightly around the groups of fine hair follicles (two to six). Here only the clusters of fine hairs and not individual hairs possessed sebaceous appendages.

THYLACIS OBESULUS. (mature female)

Hairs. A single large guard hair occurred in a group with six to seven fine hairs.

Apocrine glands. Tubules appeared at frequent intervals in the deepest part of the dermis, but no duct was traced to its destination.

Sebaceous glands were attached to the large hairs, the fine ones possessed only a small sebaceous aggregation.

SMINTHOPSIS CRASSICAUDATA. (mature male).

Hairs. These were small and occurred two to three in a group in the superficial dermal layer but had no sebaceous appendages. Bulbs of single slightly larger hairs were placed either superficial or deep to the bulbs of the small ones.

Apocrine glands. These fairly large tubules frequently in the secretory phase, were situated deep to the hair bulbs. Myoepithelial cells were present.

Sebaceous glands were small and attached to the large hairs.

GROIN.

TRICHOSURUS VULPECULA. (mature female).

Hairs. The deeply situated bulbs tended to occur in

groups (four to six). Very small hairs with bulbs in the superficial dermal layer occurred in groups (three to six).

Apocrine glands. The tubules were widely separated and associated with the deeply situated hair groups. The elongated tubules ran parallel to the hair follicles.

Sebaceous glands. These aggregates accompanied very small superficial hair bulbs. The glands, chiefly in the early secretory phase, formed clusters around groups rather than around individual hairs.

DROMICIA CONCINNA. (young mature female)

Hairs were fine and arranged in irregularly placed groups of three to four, their bulbs appeared in the lower part of the dermis.

Apocrine glands. The single tubules appeared at fairly close intervals in the most superficial layer of the hypodermis, near to bulbs more deeply situated in the dermis.

Sebaceous glands surrounded each hair follicle whether growing singly or in groups of three to four.

THYLACIS OBESULUS. (mature female)

Hairs were generally fine and appeared in groups of

three to four with their bulbs in the upper part of the dermis.

Apocrine glands. With each hair group one apocrine tubule was associated, this opened into the follicle of the group. Myoepithelial cells were present in the tubule.

Sebaceous glands surrounded each fine hair of the group.

SMINTHOPSIS CRASSICAUDATA. (mature male).

Hairs. Small hairs in groups of two to three and widely separated medium-sized hair bulbs appeared in lower part of the dermis.

Apocrine glands. Some apocrine tubules opened into the hair canal of each one of the larger hairs just below the entrance of the sebaceous gland.

Sebaceous glands. Small appendages surrounded the groups of small hairs.

SCROTUM.

TRICHOSURUS VULPECULA. (mature male).

Hairs. Each large single hair follicle, set fairly deep in the dermis was surrounded by three to four smaller grouped follicles.

Anocrina glands appeared frequently with the larger deeper hairs; the slightly coiled tubules were situated at the base of the large hair follicles. The faintly acidophilic cuboidal secretory cells were surrounded with myoepithelial elements. The pale-staining nucleus of the secretory cells displayed numerous small chromatin granules. The ducts were narrow and straight, they usually entered a pilo-sebaceous invagination just below the level of the epidermis.

SMINTHOPSIS CRASSICAUDATA. (mature male).

Hairs. The very small follicles were placed fairly close together.

Anocrina glands. None was observed.

Sebaceous glands were present as small appendages of some of the small hairs.

SUMMARY OF GLANDS OF CROWN OF HEAD, AXILLA, GROIN AND SCROTUM.

1. Hairs varied in size from fine or small to large or coarse, and occurred either singly or in groups.
2. Hair bulbs of large hairs which usually occurred singly were found at the junction of dermis and hypodermis.

3. Smaller hair bulbs were usually present in the upper part of the dermis where they occurred in groups.
4. It was noted that both sebaceous aggregations and apocrine tubules were associated with the deeper coarser hairs, while only the sebaceous aggregations were present with the smaller superficial ones. This finding is in accord with the description given by Bolliger and Hardy (1944) in which they maintain that in the skin of Trichosurus vulpecula, each central follicle has both a sebaceous and a sudoriferous gland associated with it while each lateral cluster has a sebaceous gland only.
5. Myoepithelial cells were more clearly seen when apocrine coils were in the secretory phase; an observation also made by Montagna (1956) who claims that they are more apparent when the epithelium is tall.
6. Phloxine stained sections demonstrated that when apocrine coils were in the secretory phase the basement membrane was wider and more clearly visible. Whereas, when the cells were flat and the lumen wide, the basement membrane was thin and difficult to identify.

STERNAL GLAND

INTRODUCTION

Since Ford (1934) had noted that some sort of sternal or pectoral gland is of frequent occurrence in marsupials, serial sections were made through the skin of this region of the four marsupials used for this investigation.

TRICHOSURUS VULPECULA.

Both male and female specimens were examined, the particular area being the triangular pectoral patch of brownish yellow hairs; this patch is larger in the male than in the female.

The sections of both male and female revealed an epidermis of slightly greater thickness (three to four cells deep) than elsewhere on the body and a dermis many times thicker than the epidermis.

Hairs, both guard and small were present: the small variety occurred in clusters of three to four and were frequently associated with a single discrete guard hair with which a sebaceous appendage was present. At the same level, that is, in the upper part of the dermis sebaceous aggregations surrounded the groups of small hairs, this encirclement appeared to be around the group rather than around individual hairs. The bulbs of some single fairly large hairs appeared in the deepest part of the dermis; these were irregularly grouped.

Apocrine secretory tubules occurred at fairly wide but regular intervals, and did not appear to be associated with hair follicles of any particular size or position. The secretory tubules gave evidence of both secretory and post-secretory phases: the acidophilic myoepithelial cells, as usual, were much more prominent in those tubules which were in the secretory phase.

Skin from mature females, although the yellow-brown patch was well developed, did not exhibit apocrine tubules or sebaceous glands of particularly large size.

Microscopic examination of skin from a similar region in males, revealed that while the arrangement of hairs was similar to that in females, both sebaceous and apocrine tubules were larger and more active in appearance. Those apocrine tubules that were in the secretory phase exhibited cytoplasmic blebs protruding into the lumen, but the crystals mentioned by Bolliger and Hardy (1944) were not observed in my material. The greater size of both apocrine and sebaceous glands in the male Trichosurus suggests a more specialized glandular activity in this region and one that is related to the sexual maturity of the male.

According to Bolliger and Hardy (1944) a sternal region characterised by large and active glands as well as coloured hairs, had so far, been found only in Trichosurus vulpecula, though Beddard (1887) described a glandular

patch in the marsupial banded ant-eater (Myrmecobius fasciata). This animal was again investigated by Ford (1934) who noted an increase in the size of the sebaceous and apocrine glands, but did not agree with Beddard (1887) that a grandular mass under the dermal muscle belonged to the category of sternal glands. By dissection and microscopic examination Ford proved that this glandular substance was an extension of the animal's submandibular salivary gland and in no sense a skin gland.

My examination of both sexes of the other three marsupials, Dromicia concinna, Thylacis obesulus, and Sminthopsis crassicaudata revealed no particular enlargement or specialization of the sebaceous glands of the sternal region, which also did not exhibit any hair coloration - though the epidermis and dermis were somewhat thickened.

However, in Sminthopsis only, serial sections revealed the presence if some gland substance deep to the subcutaneous striated muscle. This gland was somewhat similar to the parotid situated beneath the external auditory canal. The strongly acidophilic cells which formed the wall of the interlobular ducts and the acinar cells filled with conspicuous granules suggested that a salivary rather than a skin gland was present deep to this sternal region. For purposes of comparison and verification sections were also made of the parotid gland of Trichosurus.

INTERSCAPULAR OR HIBERNATING GLAND.

INTRODUCTION.

The interscapular gland is constant in all mammals, and in man is probably the homologue of the so-called "Hibernating gland" of rodents. (Inglis 1927).

Bonnot (1908) described the gland in both human embryo and adult as a paired organ very irregular in shape but definite in outline, situated on the shoulder or on the side of the neck.

SUMMARY.

Examination of the interscapular and lower back regions of all four marsupials failed to disclose, either macroscopically or microscopically any definite "fat glandular" tissue in all but Sminthopsis.

In Trichosurus and Dromicia the hypodermis consisted of a deep layer of adipose tissue and this did not extend beneath the dermal muscle to produce what could be called a "fat gland".

However in Thylacis a fairly thick adipose layer separated the dermis from the underlying striated muscle, but this tissue was not encapsulated and did not present the features of a hibernating gland.

In Sminthopsis between the inner border of the dermis and the striated muscle of the back a mass of fatty tissue appeared. This area was only relatively well vascularized,

the capillary networks being few, the main vessels were some small arteries. This piece of tissue was not observed in either the fresh or the fixed condition and its presence noted only in the serial sections. It was difficult to decide whether this fatty area was ordinary adipose tissue or whether it should be included in the category of "fat glands". An apparent connective tissue capsule separated it from the dermal tissue, but on its deeper aspect it appeared to abut directly on to the striated muscle without the intervention of any connective tissue. Many mast cells were noted, these appeared chiefly in relation to those cells which contained small fatty droplets, the rest being empty cell envelopes, the fat having been removed during the preparation.

According to Shattock (1909) there are two forms of adipose tissue. One of these arises from a deposition of fat in ordinary connective tissue cells, the fat though deposited at first in droplets eventually coalesces into a single sphere. The other is confined to particular areas, the fat being deposited in discrete droplets and remaining so, a form which histologically allies the cell groups to those of a ductless gland. Even this type of fat may eventually be replaced by the ordinary variety.

Following this line of argument, the fatty tissue under consideration in Smithopsis is probably not the ordinary adipose type.

MARSUPIUM, NIPPLES AND MAMMARY GLAND.

INTRODUCTION.

The shape and development of the marsupium or pouch and the number of nipples within it varies from species to species.

In Trichosurus vulpecula the pouch is well developed (Jones 1924b), with the opening directed forwards. This author describes the pouch of Dromicia concinna as being of the shape of a conventional heart, the opening being at the anterior end, while two lateral extensions pass forward to the side of the body in front of the legs. The nipples are six in number.

In Thylacis obesulus the pouch opens downwards and the eight nipples are arranged in an incomplete circle (Jones 1924c).

According to Grasse (1955) the females of Sminthopsis crassicaudata which do not have a marsupium, exhibit around the base of each nipple (they number two to ten) a circular cutaneous fold forming a funnel which encircles the head of the young when attached to the nipple.

Owen (1839-1847) states that the nipple in all marsupialia is imperforate at the centre and the milk exudes from six to ten minute orifices arranged around the apex. The nipple increases in size with the growth of the mammary foetus attached to it.

The marsupial mammary gland is regarded as having the same essential structure as that of ordinary mammals.

The specimens of TRICHOSURUS VULPECULA examined for this paper displayed a true marsupium formed from a fold of the skin approximately five cms. long. It was generally hairy but fairly free of hairs in the immediate vicinity of the nipples and smooth on these projections themselves. Two mammary glands, one on each side of the mid-line, at inguinal level, occurred as elongated structures (4 x 1.5 cms.) just beneath the skin.

Two nipples were attached one on each side.

MARSUPIUM.

Microscopic examination, by serial sections, of areas unrelated to the nipples revealed an epithelium slightly cornified and six to eight layers deep. In the lower two or three layers of the Malpighian region the nuclei were set perpendicular to the basement membrane.

The dermis, six to eight times deeper than the epidermis consisted of, in its upper part, irregularly woven collagen bundles. The lower part, in which the collagen was more loosely arranged, contained the follicles of a few coarse hairs which opened onto the skin surface. At the upper dermal level somewhat small sebaceous glands opened by short ducts into the pilo-sebaceous canal of each coarse hair.

MAMMARY GLAND.

As mentioned in the brief introduction to this section, the mammary gland is similar in structure to those of ordinary mammals, in consequence only the ducts and nipple region which show some differences will be described.

The intralobular ducts had a wide lumen up to five or six times greater than that of the secretory acini. The walls consisted of two to three layers of cells, the innermost tending to have their nuclei elongated and parallel to the luminal surface which appeared to have a thin acidophilic cuticle. The nuclei of the outer layer of cells had their nuclei disposed parallel to the length of the duct. Myoepithelial cells were present outside the secretory ones.

The interlobular ducts which were surrounded with a thick band of connective tissue had a wide irregular lumen. The duct walls consisted of two layers of cells, the inner ones being short columnar. Myoepithelial cells formed an external investment for the duct.

THE NIPPLE was a thin elongated structure, its surface covered with squamous slightly cornified epithelium. The internal stroma consisted of rather fine, fairly densely woven connective tissue in which smooth muscle cells tended to run parallel to the long axis of the nipple. What were probably elongated lactiferous sinuses occupied the length of the slender nipple. The sinus wall consisted

of two to three layers of columnar cells, the innermost formed a scalloped border to the lumen which frequently contained some secretion. Myoepithelial cells were identified in the sinus walls.

Nearer to the glandular end of the nipple other ducts, probably those lactiferous ones which lead from the mammary gland into and through the nipple to reach the lactiferous sinuses, were noted. Tall simple columnar epithelium formed the walls of these ducts. The luminal surface of each cell appeared to be more darkly stained and presented a curved border to the secretion-containing lumen. Strongly acidophilic myoepithelial cells invested the duct walls.

Excretory ducts leading from the lactiferous sinuses to the exits on the nipple surface were lined with stratified epithelium six to eight cells deep, the inner layer became slightly cornified as the duct epithelium met that of the skin at the exit. No myoepithelial cells were present in these ducts.

THYLACIS OBESULUS.

MARSUPIUM.

In this structure the skin was slightly folded and the epithelium moderately keratinized. Very few hairs were present except nearer to the nipple where several large ones, well supplied with sebaceous glands occurred. Deep

to the large hair follicles apocrine tubules were present. Further away from the nipple region the skin lining the marsupium contained, beneath its dermal connective tissue, coils of apocrine glands running parallel to the skin surface.

NIPPLE.

These long slender structures were covered with a somewhat folded, slightly keratinized skin eight to ten cells deep. A few large hairs with sebaceous appendages were arranged around the base of the nipple. A core of dense connective tissue filled the apex of the structure. Smooth muscle cells ran parallel to the excretory ducts which near their exit on to the skin surface were lined with squamous stratified non-cornified epithelium. The actual exit of these excretory ducts on the surface was not observed. Along the length of the nipple, elongated narrow lactiferous sinuses which formed reservoirs connecting the lactiferous ducts with the excretory ducts, appeared. Columnar cells formed the walls of these sinuses which contained secretion in their lumen. No myoepithelial cells were identified in the walls of these structures. Richardson (1949) mentions that in the lactiferous ducts of the goat mammae, myoepithelial cells are present. He, with others, regards these contractile elements as being concerned functionally in the process of the "let-down" of milk.

DROMICIA CONCINNA and THYLACIS OBESULUS.

Owing to a shortage of material it was not possible to make a microscopic examination of the marsupium and nipples of these animals. Details of a macroscopic survey are given in the introduction.

SUMMARY

The marsupia and nipples of Trichosurus vulpecula and Thylacis obesulus have been described both macroscopically and microscopically. These structures present rather similar features in both species.

Owing to shortage of material, it was not possible to examine microscopically the marsupia and nipples of Dromicia concinna and Sminthopsis crassicaudata.

Since it is known that the mammary glands of marsupials resemble closely those of mammals generally, no description of these is given.

GLANDS OF THE NASAL VESTIBULE AND UPPER LIP.

INTRODUCTION.

Hollendorff (1957) in his dealing with the glands in the human nasal vestibule noted that, unlike Schiefferdecker (1900) and Stieda (1902), Alverdes (1932) could find no free sebaceous glands in this region. Those glands that were apparently free more likely belonged to undeveloped hairs.

Fig. 4.- A large apocrine tubule in the upper lip below the nasal aperture of Trichosurus vulpecula. Stained with haematoxylin and eosin. X 450.

A. Apocrine tubules in the secretory phase.
B. Cytoplasmic protrusions into the lumen of the tubule.
C. Secretion in the lumen of the tubule.
D. Nucleus of a myoepithelial cell.
E. Duct showing an abrupt change from a secretory tubule.
F. Hair bulb.
G. Sebaceous gland associated with hair bulb.
H. Connective tissue of the dermis.

This picture provides a striking illustration of the abrupt manner in which a secretory tubule becomes narrowed to meet its excretory duct.

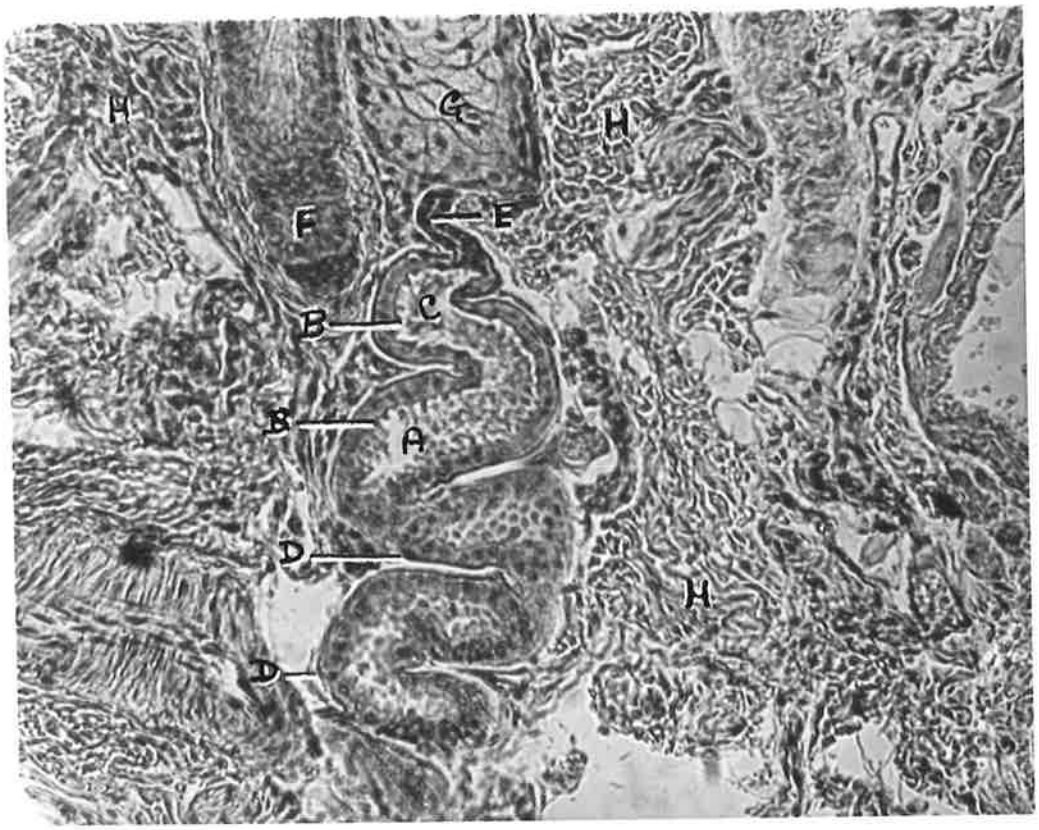

Fig. 4.

Regarding sudoriferous glands in the nasal vestibule, one observer has remarked that according to the statements of Zukerkandl (1893), Schiefferdecker (1900), v. Mihalovics (1900) and Kallius (1905) eccrine sweat glands with wide tubules occurred especially on the septum, though Schumacher (1925) failed to observe them.

However, Alverdes (1932) firmly established the fact that these are not ordinary eccrine sweat glands, but rather tubules with an apocrine mode of secretion, which is emptied into the hair canals of the vibrissae. These coiled tubular glands are smaller than those of Moll in the eyelid and the cerumen tubules of the ear canal. The width of the nasal vestibule tubules measures between 20 and 150 micra, according to whether the cells are secreting or not, and whether the myoepithelial cells are relaxed or contracted.

The secretory parts of the tubules lie in the dermis and frequently spread to the hypodermis; these tubules narrow abruptly to form the ducts, where their epithelium gains an extra layer. (Fig. 4.). After pursuing a steep and almost straight course, the duct opens into the hair follicle belonging to a vibrissa. The range of these glands described by Alverdes (1932) was restricted to a narrow zone along the lower border of the large and small wing cartilages. However, it has

been found that they are numerous in the vestibular fossa, fewer in the roof of the anterior part of the vestibule and on the septum.

Alverdes (1932) stresses that these glands have no relation to the sexual function of their owners and that they occur in all age groups.

If they empty into hair canals their secretion could be similar to that of the sebaceous glands which belong to the hair.

Also whether their secretion is sweat and they themselves, like the axillary glands, could be described as sweat glands is still very doubtful.

Although, so far, a satisfactory answer to this question of function is not forthcoming Alverdes (1932) has made every effort to have these apocrine glands named "Vestibular glands of the nose".

Kato and Nagata (1938) have discussed the apocrine sweat glands in the nasal vestibule of the Chinese and Mogi (1938) has dealt with the development of the apocrine sweat glands in the nasal vestibule of the Japanese foetus.

Maeda (1951) made a comparative study of the number and distribution of the apocrine glands in the nasal vestibule of numerous mammals. He found that the regions in which these glands are most frequently found are the floor, septum and roots of the nasal wings.

Fig. 5.- Apocrine tubules in the upper lip of Trichosurus vulpecula. Stained with haematoxylin and eosin. X 100.

A. Apocrine tubules in the secretory phase.
B. Duct of apocrine tubule.
C. Nucleus of myoepithelial cell.
D. Striated muscle.
E. Connective tissue.

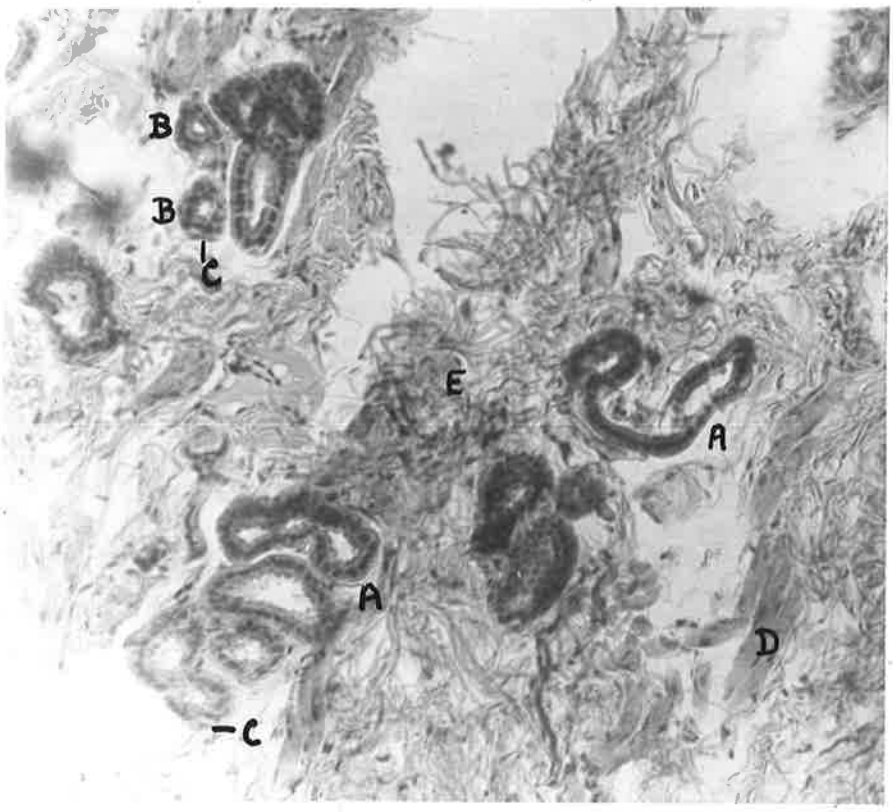

Fig. 5.

TRICHOSURUS VULPECULA.

UPPER LIP, RHINARIUM AND NASAL VESTIBULE.

For the histological description of the glands of the above regions, a mature male animal was used.

THE RHINARIUM was non-hairy and of a fine granulated appearance when examined macroscopically.

Microscopic sections revealed a keratinized squamous stratified epithelium which projected into the dermis in the form of stout pegs. No glands were present in this region.

The external skin around the rhinarium contained large and small hairs, these occurred either singly or in groups of two to three, at the superficial level of the dermis. Most of the hairs had small sebaceous appendages. The large more deeply placed bulbs belonged to hairs which possessed large lobulated sebaceous glands.

The bulbs of large vibrissae were placed in the still deeper tissue, these structures which were provided with the usual blood-filled cavernous sacs, frequently possessed comparatively small sebaceous appendages, just below the level of the epidermis: these glands opened into the hair canals.

Apocrine tubules, large and mostly in cross section, appeared frequently deep to the large hair bulbs but occasionally were superficially placed. (Fig. 5.). Though numerous serial sections were examined it was never possible

actually to follow a duct from one of these tubules to its destination.

THE HAIRY PART OF THE UPPER LIP contained small, medium-sized, and large hairs in addition to many vibrissae. Each small hair was completely encircled with a sebaceous appendage, but no apocrine tubules accompanied it. All hairs possessed sebaceous adjuncts as also did each vibrissa though in this case the holocrine structure was comparatively small. Apocrine tubules of considerable size accompanied the large hairs and vibrissae but it was not possible to trace the destination of their ducts: according to Alverdes (1932) they open into the hair canals of the vibrissae. These apocrine tubules possessed well-marked myoepithelial cells.

THE NASAL VESTIBULE was in its anterior part lined with cornified squamous stratified epithelium in which a well-defined stratum lucidum was noticed. No eccrine glands were present in the dermal region below the lining epithelium. Groups of muco-serous glands occupied the medial aspect of the roof and in the lower part of the lateral wall of the vestibule. Ducts from these glands opened into the vestibular cavity.

No apocrine tubules, large or small, were observed in any of the tissues surrounding the vestibule.

DROMICIA CONCINNA.

RHINARIUM, NASAL VESTIBULE AND UPPER LIP, a male animal was examined.

UPPER LIP.

The smooth part of the lip was covered with a slightly keratinized epidermis which rested on a fairly dense acidophilic dermis. In the hypodermal region of what would correspond to the muco-cutaneous junction, very large compound sebaceous glands occurred, these did not always appear to be associated with hairs. These holocrine glands were lobulated, the lobules being separated by connective tissue in which large coils of apocrine glands were situated. The cells of these tubules were in the secretory phase with blebs of cytoplasm protruded into the lumen. The usual acidophilic myoepithelial cells, not very deeply stained could be recognized outside the tall secretory ones.

THE RHINARIUM.

This region on macroscopic inspection had a non-hairy granular appearance, accounted for in the microscopic sections by the arrangement of epidermal pegs and dermal incursions, these incursions having caused a piling up of the epidermis over their surfaces. The epidermis, about six to eight cells deep in the Malpighian region, had a very thin stratum corneum.

Venous plexuses appeared in the dermis which rested against a strip of hyaline cartilage. Between this cartilage and the epithelial lining of the nasal vestibule, coils of apocrine tubules almost completely obliterated

Fig. 6.- Apocrine-like tubules in the lateral wall of the nasal vestibule and in the terminal part of the conchal process of Dromicia concinna.
Stained with haematoxylin and eosin. X 100.

A. Apocrine-like tubules with a wide lumen in the lateral wall of the vestibule.
B. Apocrine-like tubules in the conchal process.
C. Squamous stratified non-cornified epithelium lining the vestibule and covering the concha.
D. Cartilage.
E. Vestibule.

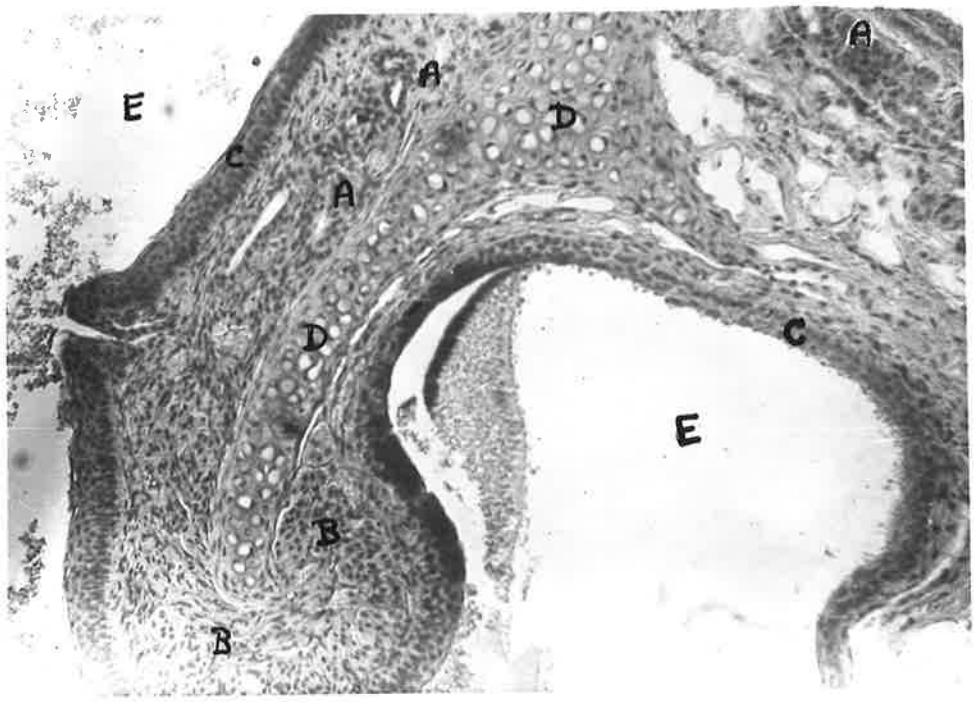

Fig. 6.

the connective tissue. (Fig. 6.). As no hairs were present on this skin, it seemed probable that the ducts from these tubules opened into the nasal vestibule, but this supposition was not verified.

THE NASAL VESTIBULE was lined with squamous stratified (two to three cells deep in the Malpighian region) slightly cornified (in some parts) epithelium. No ducts were actually observed to debouch on to this lining epithelium.

THE LATERAL WALL OF THE NOSE was covered with fine hairs which emerged singly from the surface, each hair possessed a large sebaceous appendage. The bulbs of some larger hairs occurred deep in the dermis or hypodermis. An occasional vibrissa, with its erectile sac was also present at this level. Striated muscle bundles appeared deep to the dermis; medial to this muscle glandular tissue came into view. These glands were of two types, the more cranially situated variety consisted of muco-serous acini, while more ventrally, long apocrine tubules travelled parallel to the surface of the lateral wall of the nose. The ducts from the apocrine glands probably opened into the nasal vestibule: although numerous serial sections were examined no duct outlet was observed.

THYLACIS OBESULUS.

UPPER LIP AND NASAL VESTIBULE.

Sections for this study were taken from the above regions of a mature female.

Previous to cutting the nasal area from the animal, a macroscopic examination showed the rhinarium to be naked and tesselated (Jones 1924). Serial microscopic sections revealed that the skin was squamous stratified and keratinized. A deep acidophilic stratum corneum rested on a three to four cell deep stratum granulosum, but no stratum lucidum was recognized. A deep Malpighian region sent stout pegs at regular intervals into the dermis. This regular arrangement presumably accounted for the tesselated appearance of the surface epithelium. The dermis consisted of fairly thick collagen bundles interwined to form a pale-stained mesh. No eccrine glands were observed in the skin of the rhinarium.

The hairy surface of the external nares when sectioned exhibited an epidermis closely beset with medium-sized hairs, each with its own sebaceous gland, most of these were in the later stages of secretory activity. No apocrine tubules appeared in relation to any of these hairs.

Frontal sections through the nasal vestibule revealed a lining of squamous stratified very slightly cornified epithelium. The conchal process contained hyaline cartilage, except at its ventrally turned extremity where its core was formed by connective tissue in which numerous closely coiled apocrine-like tubules were present. These tubules consisted of columnar secretory cells resting on well-marked myoepithelial units. The duct walls

Fig. 7.- Apocrine tubules in the concha of the nasal vestibule of Thylacis obesulus. Stained H. and E. X 40.

A. Secretory tubule with a wide lumen.
B. Nucleus of a myoepithelial cell.
C. Duct of a tubule.
D. Squamous stratified non-cornified epithelium lining the nasal vestibule and covering the concha.

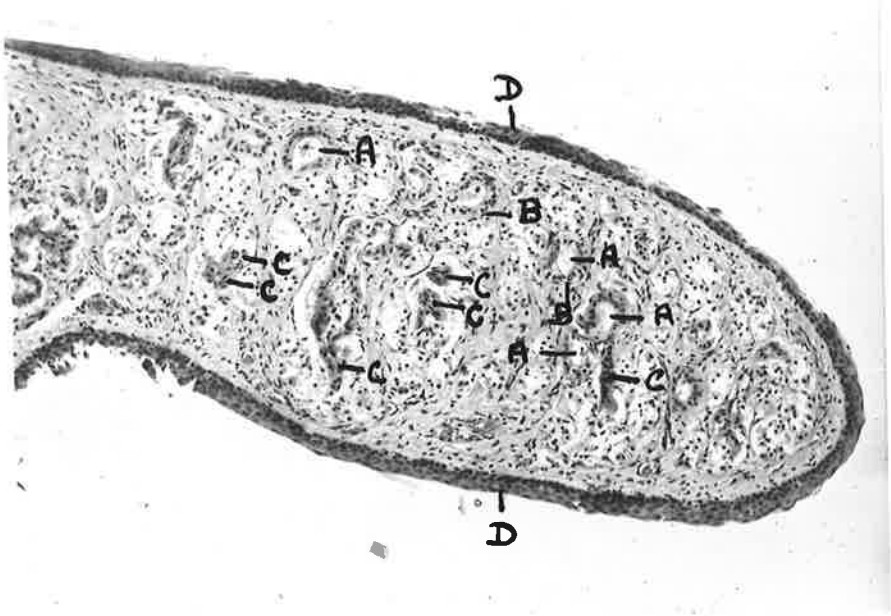

Fig. 7.

comprised two layers of acidophilic cells, no duct exits were observed. (Fig. 7.).

The septum was lined with five to six layers of squamous stratified non-cornified epithelium which with the collagen fibres surrounding the cartilage formed a close association in which no glands were observed.

THE LIP REGION

Just external to the junction between the hirsute and glabrous skin of the lip, there appeared eight to ten large branched sebaceous glands which were apparently not associated with hairs. This observation conforms to the statement made in textbooks (human material) that sebaceous glands, not related to hairs, occur at or near muco-cutaneous junctions. In my sections these sebaceous structures appeared to open by ducts lined with squamous stratified epithelium straight on to the skin surface.

SMINTHOPSIS CRASSICAUDATA.

RHINARIUM AND NASAL VESTIBULE.

Macroscopic inspection of the rhinarium showed it to be deeply grooved in its lower medial part and the epidermal surface to have a granular appearance.

An oblique frontal cut through the right side of the nasal vestibule region of a mature male was used for sectioning.

The subsequent serial microscopic sections revealed superficial epidermal ridges which correspond to narrow

dermal incursions into the epidermis: these ingressions gave rise to wide rounded epidermal pegs. The superficial granular appearance resulted from these arrangements of the underlying tissues.

The epithelium of the rhinarium, squamous stratified slightly cornified, was also fairly thick, the Malpighian layers amounting to six to eight cells in depth. There were no glands, eccrine or apocrine in the tissues of the rhinarium.

The skin covering the nose from the mid-line to the lateral part of the oral cleft, contained, on the nasal part, small hairs, arranged either singly or in groups of two to three. Small sebaceous appendages accompanied some of these hairs. Towards the oral cleft large hairs and vibrissae appeared in addition to the small hairs mentioned above. The vibrissae were accompanied by the usual erectile sacs and deep to the large hairs apocrine tubules were present. There was no evidence of the termination of their ducts.

NASAL VESTIBULE.

Oblique frontal sections cut through the vestibule disclosed that its lining epithelium was squamous stratified noncornified except near the outlet on to the skin surface where a slight cornification was observed.

Long coils of apocrine tubules, frequently in active secretion, occupied the roof region of the vestibule,

into the upper part of which their ducts probably opened. These coils appeared to be in fairly close proximity to the septum.

The nostrils were cleft at their lateral margins and along the upper border of this cleft very closely coiled apocrine tubules displaced the connective tissue of the dermis almost completely. The ducts from these glands probably emptied their contents into the anterior part of the nasal vestibule, though no ducts were observed in the serial sections examined.

There were therefore, as mentioned above, two sets of apocrine tubules related to the vestibular area; those in the vicinity of the roof and septum and those along the upper border of the nasal cleft.

SUMMARY.

RHINARIUM.

ECCRINE GLANDS. No glands of this nature were present in the tissues underlying the non-hairy skin of the rhinarium. This statement applies to all four species examined.

GLANDULAE VESTIBULARES NASI, these are apocrine-like tubules with a wide lumen, which were present in the tissues underlying the squamous stratified non-cornified epithelium in some of the four species of mammals investigated.

TRICHOSURUS VULPECULA. No apocrine tubules present.

DROMICIA CONCINNA. In this animal apocrine tubules appeared to run in the walls of the nasal wings and probably opened by ducts into the nasal vestibule.

THYLACIS OBESULUS. The epithelial lining of the vestibule was slightly cornified. Only in the ventrally turned extremity of the conchal process were apocrine-like tubules found. These were numerous and densely coiled.

SMINTHOPSIS CRASSICAUDATA. In this animal the nasal vestibule epithelium was slightly cornified at the outlet of the external nares. Two sets of apocrine tubules were present in the vestibular area; one set in the roof and the septum, the other set along the upper border of the nasal cleft.

UPPER LIP

TRICHOSURUS VULPECULA. (hairy part) Each small hair was completely encircled with a sebaceous appendage, but possessed no associated apocrine tubule. Large hairs were accompanied by apocrine coils of considerable size: these tubules, which possessed wellmarked myoepithelial cells, appeared also in relation to the vibrissae.

DROMICIA CONCINNA. The smooth part of the upper lip,

at its muco-cutaneous junction, contained many large compound sebaceous glands, not associated with hairs. Large apocrine tubules (in secretory phase) were also present in the same region.

THYLACIS OBESULUS. At the junction between the hirsute and the glabrous skin of the lip, eight to ten large branched sebaceous glands, not apparently associated with hairs, were present. Ducts from these glands opened straight on to the skin surface. No apocrine glands were observed in this region.

SMINTHOPSIS CRASSICAUDATA. No actual lip region was examined but the skin covering the area just above the lateral part of the oral cleft, contained small hairs (with sebaceous appendages), large hairs and vibrissae. It was not possible to determine the presence or otherwise of any accompanying sebaceous glands, but apocrine tubules appeared deep to the large hairs, though no ducts were observed.

GLANDS OF THE OCULAR REGION.

INTRODUCTION.

The glands normally occurring in this region may be divided into three main groups:

1. Sebaceous, e.g.: Meibomian and Zeis (of eyelid), the

Harderian of some mammals, and those sebaceous groups associated with the small hairs on the eyelid.

2. Serous: The Harderian glands of some mammals. (Lacrimal and eccrine types were missing in all four animals examined).

3. Apocrine: Moll (of eyelid) and apocrine tubules associated with the larger hairs of the eyelid.

Some, if not all, of the glands listed above are found in all mammals: for those present in the four marsupials investigated for this study, Fig. 11, may be consulted.

Woronow (1904) made comparative anatomical studies of a large series of mammals and came to the conclusion that there is no recognizable distinction between human and animal lacrimal glands.

In 1694 Harder discovered a gland (later named after him) in the eyelid, and in 1877 Wendt suggested that this Harderian gland was a modified skin appendage and that while it is sebaceous in the lower animals it tends to be more like the lacrimal in the higher mammalian stages.

Jones (1839-1847) noted "that the lacrimal glands exist in man and apes but no glandule of Harder". It was Wolff (1948) who remarked that Harder's gland is found in all vertebrates except the primates and that it is larger in the herbivorous mammals. In the lower apes, it is rudimentary, absent in the anthropoids and in man, in whom however, it is found as a rarity (Giacomini 1887). Whitnall (1921) also mentioned that it has been described in the plica

semilunaris of the human foetus and as persisting in rare cases in the adult.

Wolff (1948) made the comment that where both lacrimal and Harder's gland are present, when one is large, the other is small and vice versa. He also claimed that Harder's gland has a common origin with the lacrimal, in a single gland situated in the lower lid. Growth of the medial portion of this gland produces the Harderian structure, while the lacrimal part migrates towards the outer canthus and then into the upper lid. Thus the rudiment in the lower lid of amphibians is really the rudiment of both the lacrimal and the Harderian gland.

Wolff's claim for the common origin of these two glands coupled with Nemdt's (1877) contention that the Harderian changes from sebaceous in the lower to more like the lacrimal in higher animals, probably accounts for the fact that in some species the Harderian structure belongs to the oily, and in others to the more serous type of secretory tissue. In addition to the above Abbie (1959) made the observation that the conjunctival mucosa may be pluripotential in its ability to produce different types of glandular structure.

It is at this stage that it seems pertinent to discuss the histological detail of the Harderian glands of the four marsupials. That certain differences in cellular detail are present, will be apparent if each case is considered individually.

The histological structure of those glands normally found in the eyelid will then be reported upon.

TRICHOSURUS VULPECULA.

In this animal Harder's gland appeared as an elongated structure lying near the apex of the inferior border of the medial fornix. Its microscopical structure was that of a tubulo-acinar gland, of which the tubular part consisted of pyramidal-shaped cells surrounding a wide lumen. These cells, because of their pale-staining, somewhat foamy cytoplasm, were suggestive of holocrine glands: each basally situated nucleus was darkly stained. Those cells comprising the acinar portion were grouped around a small circular lumen and though similar in shape to those of the tubular portion, were taller, more slender and tapered towards the lumen. In addition, many acini opened into the lumina of the tubules.

Of the acinar cells, some were slightly "bluish pink", and more granular than foamy, probably owing to the state of their secretory activity. This particular type of cell occupied, in some cases, the entire acinus. Another cell, of similar shape, which occurred, either singly or in small numbers in an acinus exhibited cytoplasm of a uniform dark glassy pink which did not appear to contain any granules. Myoepithelial cells, rather faintly stained, were present in both the acinar and tubular components.

The intralobular ducts, which appeared among the

secretory elements were lined with a single layer of cuboidal cells, each with a dark, round, central nucleus. The lumen of the duct was wide and circular.

The interlobular ducts, with walls consisting of a double layer of cuboidal cells, possessed a lumen slightly smaller than that of the excretory ducts. The walls of these latter passages consisted of two to three layers of columnar cells.

An interesting observation was made by Stibbe (1928) in his account of the Harderian gland of the calf. He noted firstly, that its greatest part is a typical alveolar serous gland which would pass for a serous salivary one, and secondly that there is, near its inner or anterior end, a peculiar region which consists of round or oval alveoli lined with cuboidal epithelium. He gave a description of the cells and then acknowledged the uncertainty of his interpretation of their appearance. The secretion of the gland was thick and sticky. The description, to me, suggests a serous gland tending to transform into a sebaceous one, although he referred to a colloid rather than to a fatty change. The calf also had the usual lacrimal serous secreting gland at the outer part of the orbit.

DROMICIA CONCINNA.

This small animal possessed a Harderian gland which

extended from the medial canthus as far temporally as the attachment of the nictitating membrane, which was sickle-shaped. This comparatively large gland was divided by strands of striated muscle into two parts. Serial sections showed that these two parts, upper and lower, gradually coalesced to form a single crescent-shaped structure which lay medial and deep to the conjoined portion of the nictitating membrane into which the gland itself penetrated to some extent.

Structure of the gland.

The secretory part consisted of cells arranged in a tubulo-acinar fashion. In the tubular portion, the cuboidal cells contained a granular cytoplasm and a central, round, dark nucleus. These cells surrounded a wide tubular lumen and myoepithelial cells were present at the base of the secretory cells. In the acinar portion the cells were truncated pyramidal in shape and surrounded a small round lumen. These secretory cells contained a very deeply stained, round, basal nucleus and a coarsely granular fairly darkly-stained cytoplasm. Some of the cells had the appearance of those of a holocrine gland. Myoepithelial elements were present but were much less well defined than those of the tubular portion. The intralobular ducts were lined with a single layer of cuboidal cells, these contained a central round dark nucleus. The duct lumen was fairly wide and myoepithelial cells surrounded the mural ones.

Fig. 8.- Section through the lower eyelid and nictitating membrane of Thylacis obesulus.

A. Harderian gland.
B. Nictitating membrane.
C. Cartilage in nictitating membrane.
D. Cornea.
E. Lower eyelid.
F. Meibomian gland.
G. Cilium.
H. Medial end of the inferior fornix.

N. A single pale-staining acinus of the Harderian gland.
I. Pale round glassy granules.
J. Acidophilic granules in crescent (demilune) cells.
K. Duct with acidophilic staining cells.

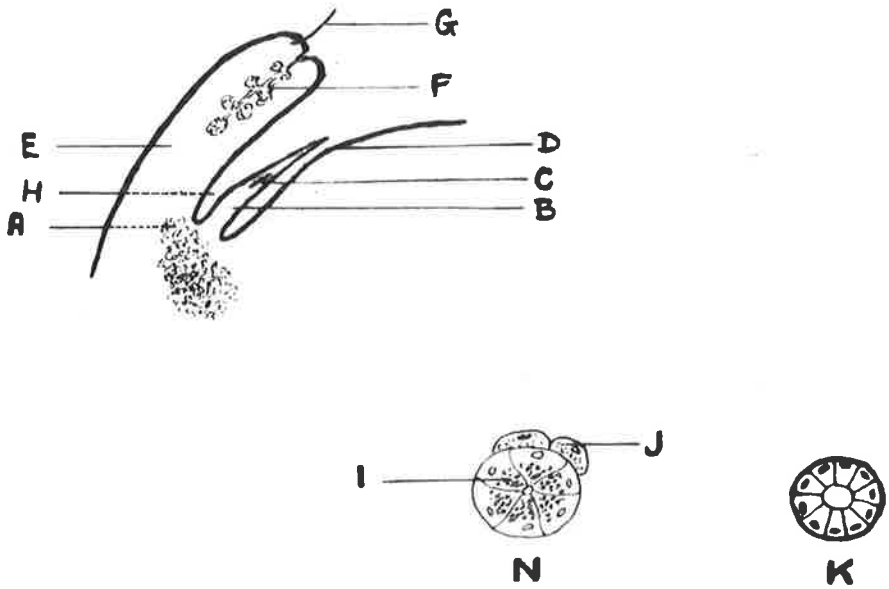

Fig. 8.

Several layers of cells formed the walls of the interlobular excretory passages and again myoepithelial cells were present. No ducts were seen to approach the conjunctival sac but it was assumed that this must be the destination of any secretory product.

Investigation of all the surroundings of the eyeball failed to disclose any lacrimal tissue, supporting Wolff's (1948) suggestion that where the Harderian gland is large, it is quite common for the lacrimal to be missing.

THYLACIS OBESULUS.

In this animal the Harderian gland appeared among the fatty tissues lying between the ocular muscles. (Fig. 8.). Its actual position, at the tip of the inferior medial fornix, set it almost at the entrance to the nictitating membrane. It was of considerable size and probably extended as far laterally as the attachment of the nictitating membrane.

Morphology

The structure appeared to be tubulo-acinar and was sub-divided into lobules by connective tissue in which travelled the interlobular ducts; transverse sections of intralobular ducts were also seen among the secretory components. The lumen of the duct, with its wall consisting of a single layer of cuboidal cells, appeared to be larger than that of the surrounding alveoli. The

Fig. 9.- Section of a Harderian gland of Thylacis obesulus. Stained with haematoxylin and eosin. X 270.

A. Interlobular spaces.
B. Secretory acini. Pale staining cells.
C. Darkly stained cells.
D. Darkly stained cells arranged as demilunes.
E. Intralobular duct.
F. Interlobular duct.

This section shows well the lobulation of the gland. Two types of cells are present, one more darkly stained than the other. The darker cells occur singly, in the form of demilunes outside the acini of the pale cells or in small groups.

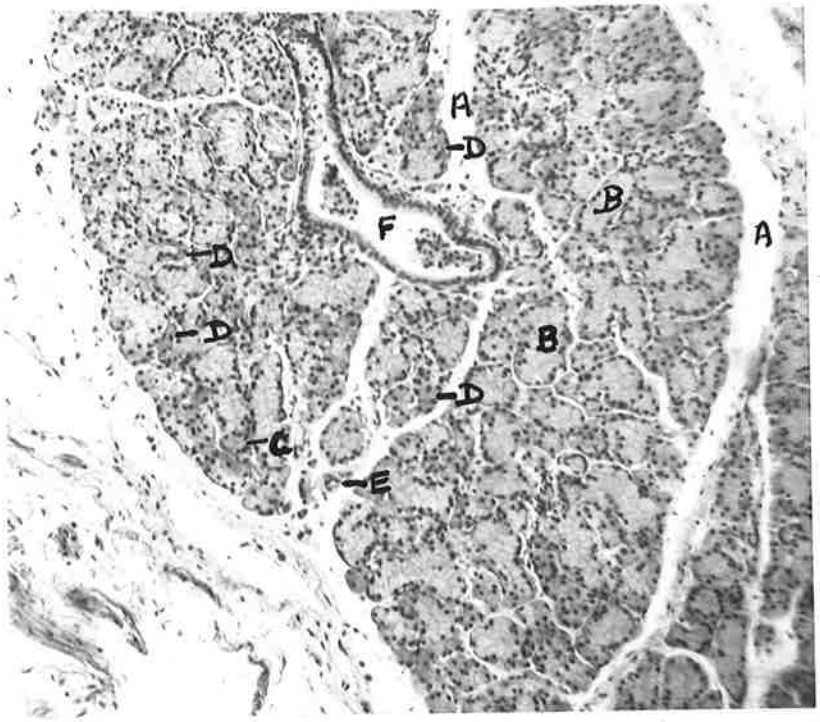

Fig. 9.

interlobular ducts were lined with two layers of columnar cells, their luminal borders displayed an acidophilic reaction. Myoepithelial cells formed an external layer to the duct system; they were identified chiefly by their dark flattened nuclei at the base of the outer duct cells. The large excretory ducts were lined with tall columnar cells (a single layer) with a basal rather pale round nucleus. In some parts the lining cells showed an intact luminal border, in others the free end of the cells was irregular.

Cytological details. (Fig. 9.)

In the acinar portion the cells, prismatic in shape, surrounded a not always identifiable lumen. The tubular components were columnar and both types of cells contained dark round basal nuclei. The acinar secretory elements appeared to be of two different types, or at least in two different phases of secretory activity. The majority of these cells presented a light granular appearance, these granules were pale round and rather glassy. The other type, contained small dark, punctate, acidophilic granules. These dark cells occurred either as crescents of two or three cells outside a pale-staining acinus or singly among pale-staining acini. Occasionally they appeared in groups of three or four, no lumen was seen here therefore they were thought not to form an acinus. In the crescent-cell formation, some of these dark cells appeared to send a cytoplasmic projection between the pale cells to reach

the acinar lumen.

The general appearance of this gland was similar to that of a serous salivary gland in which dark crescent cells were a prominent feature. Myoepithelial cells were not identified with certainty. No lacrimal tissue was observed.

SMINTHOPSIS CRASSICAUDATA.

Harder's gland was present in the usual position - at the root of the nictitating membrane and was not extensive. The secretory portion was tubulo-acinar with intralobular ducts present among the acini. These ducts had the usual wall, a single layer of cuboidal cells which surrounded a round fairly large lumen. A few myoepithelial cells were probably present outside the single layer of mural ones. A double layer of cells formed the walls of the interlobular ducts. Of these cells the inner ones were cuboidal, the outer being rather flatter, and all showed a darker staining reaction than those of the glandular portion. No large excretory ducts were observed. Cytoplasmic details of acini and tubules included the fact that in the acinar portion, the secretory cells were tall and pyramidal, and surrounded a very small lumen. These secretory elements with their dark basal nuclei contained a coarsely granular cytoplasm that was slightly acidophilic. Myoepithelial cells were not observed. The tubular portion consisted of short pyramidal cells set around a circular

Fig. 10.- Eyelid of Trichosurus vulpecula.
Stained with haematoxylin and eosin. X 40.

A. Meibomian gland showing lobulation.
B. Duct of the above gland opening on to the surface of the eyelid.
C. Gland of Moll.
D. Small hairs with sebaceous appendages.
E. Eyelash.
F. Skin of the outer surface of the eyelid.
G. Conjunctiva.
H. Striated muscle of the eyelid.

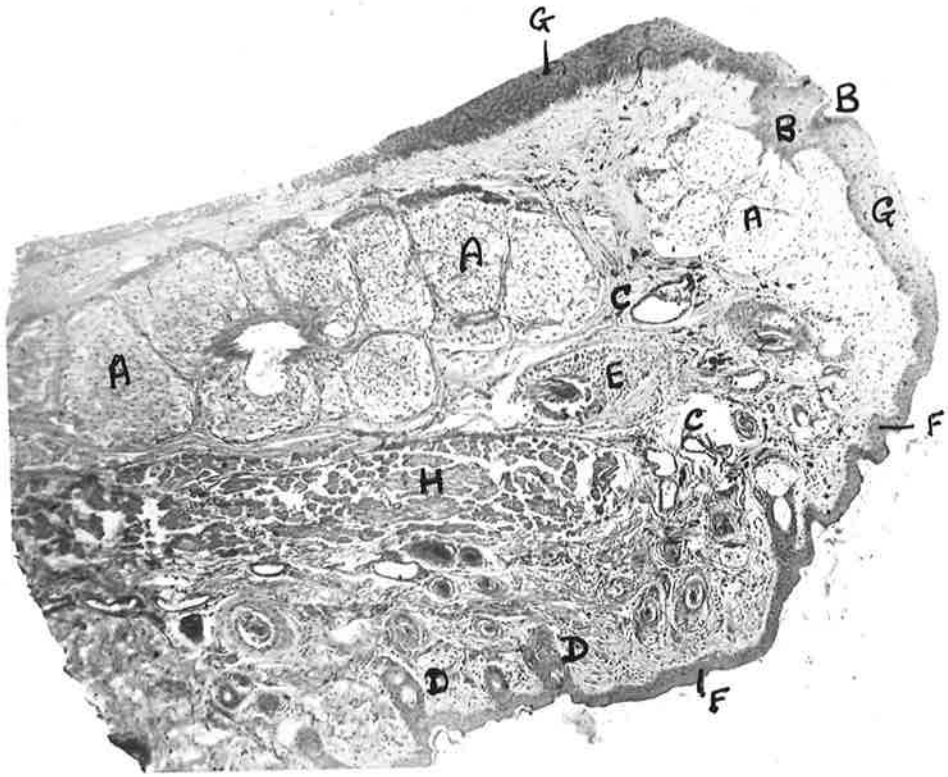

Fig. 10.

well-defined lumen. Since these cells were rather flat the large dark nucleus occupied the greater part of the cell of which the cytoplasm was coarsely granular. Myoepithelial cells could definitely be identified. Very little connective tissue was present between the secretory elements. No lacrimal tissue was identified.

GLANDS OF THE EYELID.

TRICHOSURUS VULPECULA (Fig. 10.)

Meibomian. These well-defined glands extended about one third of the depth of the eyelids. Each had an excretory duct lined at its exit by several layers of squamous stratified cells. The duct opened on to the free palpebral margin where its superficial lining cells became keratinized as they met the skin of the lid margin. The gland, a typical compound sebaceous one, had a single main duct into which the secretory acini emptied through its short branches. These acinar cells were obviously of holocrine type and presented various phases of fatty secretion.

Zeis gland (Oily type).

Two of these were present, one on each side of the hair follicle of the cilium.

Sebaceous appendages of the smaller hairs on the eyelid.

The hairs occurred in groups of two to five, and each group was supplied by a collection of holocrine cells forming a small gland.

Glands of Moll (apocrine type).

These consisted apparently of a very loose spiral as only one or two transverse sections of coils were seen in relation to the cilia. The wide lumen of the tubules was lined with flat or cuboidal cells, probably in the post-secretory phase. The presence of myoepithelial cells at the base of the secretory cells was fairly well demonstrated.

DROMICIA CONCINNA.

Glands of the eyelid.

Meibomian gland, this multilobulated structure extended more than halfway up each lid. Its structure was typically that of a holocrine sebaceous gland similar to that of Trichosurus which has already been described.

Gland of Zeis (Oily).

A pair of these appeared one on each side of the cilium hair follicle. No ducts from these structures were identified.

Small hairs, supplied with sebaceous appendages, were present on each eyelid.

Apocrine Glands of the Eyelid included:

(a) Glands of Moll noted in relation to only a few of the cilia; the lower lid appeared to be the more frequent site.

(b) Apocrine tubules situated deep to the hair bulbs of the larger hairs and occurring at widely separated intervals.

THYLACIS OBESULUS.

Glands of the eyelid.

Meibomian, these large well-developed holocrine glands, not associated with hairs, possessed a long main duct set perpendicular to the free palpebral border. This duct exit was placed external to the muco-cutaneous junction.

Wolff (1948) remarked that these modified sebaceous glands of the skin, while well developed in man, are much less so in other mammals; and that they represent a row of lashes which, in man, have disappeared but may reappear in the rare cases when Meibomian glands are absent.

In Thylacis the Meibomian duct system was similar to that described in the notes on Trichosurus.

The secretory part consisted of acini which appeared at the end of each small side duct. The large flat cells comprising these acini showed the various stages of breakdown into fatty sebaceous secretion - only the basal cells, that is those resting on the basement membrane, exhibited a round fairly pale nucleus rather than the dark uneven pyknotic one characteristic of degenerating cells.

The Glands of Zeis.

These oily sebaceous appendages were noted in association with the cilia of both lids: they were typical holocrine glands of only medium size.

The Glands of Moll, no representatives of this group were noted in either lid.

Sebaceous and Apocrine Glands.

The small hairs covering the external surface of the eyelids appeared to be of two sizes. The smaller which occurred in groups of four to six were usually surrounded, as a group, with a small investment of sebaceous tissue.

Somewhat larger hairs which occurred sometimes more superficially and sometimes at a deeper level, did not show any associated holocrine type cell groups.

Still larger hairs, which were not cilia, possessed bulbs situated in the deep fat-filled region just superficial to the striated muscle (levator palpabrae superioris) of the upper lid. With these hair bulbs were thought to be associated some apocrine coils which were in active secretion: the myoepithelial cells were very evident. Some of these glands, especially those in the deepest part were very large and consisted of several coils from which a long duct led towards the pilo-sebaceous canal of the coarser hairs which also possessed a sebaceous appendage.

Well developed myoepithelial cells occurred between the basement membrane and the secretory cells; these were tall columnar in shape.

SMINTHOPSIS CRASSICAUDATA

Glands of the eyelid.

The Meibomian glands occupied nearly the whole depth of both lids.

Their structure conformed generally to that described of the other marsupials considered in this paper. Some of the secretory acini appeared to be in an early stage of the secretory process whereas others showed the central portion of the acinus to be empty of both cells and secretion - the remaining peripheral cells three to four layers deep, constituted a residuum from which new secretory elements would develop.

Zeis Glands could not be found in either lid.

Gland of Moll

This gland was situated near to a cilium and consisted of several apocrine coils composed of rather tall pyramidal cells with elongated nuclei perpendicular to the basement membrane. Acidophilic myoepithelial cells were situated at the base of the secretory cells. No duct was observed.

Hairs, most of those covering the lids were fine and appeared in the dermis in groups of three to four, with each group a sebaceous appendage was present.

SUMMARY OF THE OCULAR GLANDS

1. No lacrimal glands were found in any of the four species investigated.
2. Harder's gland was present in all and was of considerable size; tubulo-acinar in form, it showed variations in the secretory cells in each of the animals examined.
   (a) TRICHOSURUS: Three types of secretory cells:-
      i. Non-granular, bright, pink, glassy cells:

they occurred singly or in small numbers in an acinus.

ii. Intermediate stained cells, pink with a bluish tinge: these were granular and occupied a whole acinus or were present in an acinus which contained other, much more lightly stained components.

iii. Paler stained cells which formed the major part of the secretory tissue. The cytoplasm was pale to colourless with a cell content more like that of a sebaceous cell at middle stage of secretion.

Ducts

Intralobular: wall, single layer of cuboidal cells. Interlobular: wall, double layer of cuboidal cells. Excretory duct: larger than the interlobular, with a very wide lumen and two or three layers of mural cells which tended to be columnar.

(b) DROMICIA CONCINNA

Harder's gland a tubulo-acinar one. Tubular portion: two cells which had a granular content were cuboidal and surrounded a fairly wide tubular lumen. Myoepithelial cells were also present. Acinar portion: the cells were truncated pyramids which surrounded a small round

lumen. Their cell content was coarsely granular and fairly darkly stained, an appearance similar to those of a darkly stained holocrine sebaceous gland.

Ducts.

Intralobular. Wall with a single layer of cuboidal cells: also myoepithelial cells present.

Interlobular: Larger lumen and increased number of layers of mural cells - myoepithelial cells still present.

No excretory ducts of larger size observed.

(c) THYLACIS OBESULUS.

Tubular part: the cells tended to be columnar.

Acinar part: the cells were prismatic and appeared to be of two different types. The majority were light staining and contained coarse granules of pale round rather glassy appearance. The remainder contained dark punctate acidophilic granules. These dark cells occurred either as crescents of two or three cells outside a pale-staining acinus or occasionally in groups of three or four which, since a lumen was lacking

did not form an acinus. General appearance of gland was that of a serous salivary one in which darkly stained serous cells were a prominent feature. Myoepithelial cells were difficult to define.

Ducts.

Intralobular: one layer of caboidal cells as a wall.

Interlobular: Wall: tall columnar cells in two layers. The cytoplasm of their luminal border showed an acidophilic reaction.

Larger excretory ducts were lined with a single layer of tall columnar cells.

(d) SMINTHOPSIS CRASSICAUDATA.

Harder's gland again a tubulo-acinar structure, pyramidal cells formed both parts. Cells were of only one type and contained a coarsely granular cytoplasm slightly more acidophilic than neutral.

Ducts

Intralobular wall one layer of cuboidal cells.

Interlobular duct, lumen wide and round: inner mural cells cuboidal, outer ones slightly flatter.

4. Zeis gland present in all but Sminthopsis crassicaudata.
5. Moll gland present in all but Thylacis obesulus.
6. Meibomian gland present in all four species.

TABLE OF GLANDS OF OCULAR REGION. (Fig. 11.).

Animal	Glands of eyelid	Harderian gland
Trichosurus vulpecula. (Diprotodont)	Meibomian gland well developed and extended for ⅓ depth of both lids. Zeis) both glands Moll) present in association with each cilium.	Gland was present and was somewhat extensive. Its strucure tubulo-acinar and its secretory cells showed certain cytoplasmic differences. Three types of cells were identified.
Dromicia concinna.	Meibomian gland well developed in both lids. Zeis: One pair present with each cilium Moll: One apocrine tubule with each cilium	Gland appeared outside medial angle between nictitating membrane and cornea, was of considerable size, compared with that of animal. Its structure was tubulo-acinar with cells which did not appear to be mixed in type - though some showed a more definite holocrine appearance.
Thylacis obesulus. (Polyprotodont)	Meibomian gland well formed and present in both lids. Zeis: One pair present with each cilium. Moll: None present.	Gland present at entrance to nictitating membrane. A mixed tubulo-acinar structure of considerable size and extending laterally from inner canthus along lower lid. Two types of cells: pale acinar and dark acidophilic crescent ones.

Sminthopsis crassicaudata. (Polyprotodont)	Meibomian glands were extensive and occupied nearly the full depth of both lids. Zeis: None present. Moll: Several apocrine tubules associated with each cilium.	Gland not very extensive. Its structure was tubulo-acinar. Cell cytoplasm of both parts was coarsely granular and slightly acidophilic. Only one type of cell was identified.

GLANDS OF THE EXTERNAL AUDITORY MEATUS.

INTRODUCTION.

In his work on the skin gland organs of mammals Schaffer (1940) stated that those located in the aural appendages of vertebrates needed further investigation.

This statement followed that of Zawisch, who in 1933, had pointed out how little is known concerning these structures in many of the mammals.

Later, in 1951, Eberl-Rothe published a paper dealing with variations in the glands in the external auditory meatus in the various classes of mammals. In this survey she noted that both the structure and distribution of the apocrine tubules and the sebaceous glands in the cartilaginous or in the bony parts of the meatus seemed to be related to the habits of the animal. For this reason these organs tend to show some protective functions: animals living in water, or on, or under the ground develop some accessory structures. The valve-like closing mechanism in the armadillo and the venous plexuses or cavernous tissues of some cheiroptera and carnivores are examples. This author also observed that the external meatus of rodents is entirely devoid of specialized apocrine glands.

It was Horstmann (1957) who described the human cerumen glands as very wide apocrine ones, the diameter of their lumen being from 50-150 micra. The secretory portions

of these glands are coiled whereas their ducts run a fairly straight course and open directly into the external auditory meatus or into the duct of a sebaceous gland (Simonetta and Magnoni 1937). Although Horstmann (1957) has remarked on their wide luminal diameter, Shelly and Perry (1958) have noted how small are the apocrine ceruminous glands compared with those in the axilla of the human subject.

In his description of the cerumen gland ducts Horstmann (1957) refers to their inclination, as they grow older, to produce ampullary enlargements, situated near to the passage through the epidermis and frequently filled with concentrically arranged epithelial masses. This author also maintains that cerumen is a mixture of the secretion of the ceruminous and the sebaceous glands with some desquamated epithelium. The milky apocrine product tends to soften the rather hard waxy secretion of the sebaceous glands.

The biological significance of this secretion is unknown; though several writers have suggested that the presence of a bitter substance may serve to prevent any unwelcome invasion of the external auditory canal.

Following his studies of these animals, Horstmann (1957) concluded that the cerumen glands of pig, monkey, cow, goat, horse, dog, cat and mole are histologically comparable.

It now remains to append a report on the histological structure of these glands in the four marsupials under investigation.

TRICHOSURUS VULPECULA. (a mature female).

This study includes the pinna of the ear, the skin covering the four cartilaginous processes (tragus, antitragus, antihelix and processus antihelicis) which guard the entrance to the distal portion of the external ear canal, as well as the canal itself.

The pinna presented an external hairy surface and an internal almost naked one: between these two, a cartilaginous core was interposed.

In the hairy surface, near each group (two to five) of deeply placed hair bulbs, apocrine glands were present: their secretory cells contained a granular cytoplasm which gave a neutrophilic staining reaction. Most tubules appeared to be in the post-secretory phase since their luminal surface was flat and intact. Acidophilic myoepithelial cells formed an incomplete layer outside the secretory ones.

The ducts leaving the apocrine tubules opened into the superficial part of the pilo-sebaceous canals of the larger hairs. Most of the hairs were endowed with a sebaceous appendage which conformed to the usual description of this type of gland in a similar situation.

The almost naked skin lining the inside of the pinna contained a few apocrine tubules, not apparently associated with hairs. The secretory cells of these tubules contained a granular cytoplasm from which blebs protruded into the lumen where a somewhat granular secretion was

present. Their round nucleus exhibited, as well as the nucleolus, some darkly stained chromatin granules. The strikingly acidophilic myoepithelial elements which surrounded the secretory cells, appeared to be contracted and tended to push up into the basal part of the superimposed secretory ones for each of which, at least, one contractile element was present. These apocrine coils occurred at wide intervals on the inner side of the cartilaginous core from which they were separated by the thick longitudinally running collagenous bundles of the perichondrium: no excretory ducts were identified.

The skin covering the tragus, antitragus etc., contained small hairs and numerous large apocrine glands which consisted of many coiled tubules with a wide lumen. Each tubule was lined with rather short, pale-staining secretory cells each of which contained a pale nucleus with a well-defined nucleolus. Both secretory and resting stages were represented in these tubules which were surrounded by acidophilic myoepithelial elements. Only a few ducts from these apocrine glands could be followed, they appeared to empty into the invaginated canal of an adjacent hair, and not independently on to the skin surface. The duct walls possessed the usual two layers of cells: inner cuboidal and outer flatter, each with a dark round nucleus. The inner cells exhibited the usual acidophilic

Fig. 12.- Apocrine cerumen glands in the roof of the external auditory meatus of Trichosurus vulpecula. Stained with haematoxylin and eosin. X 100.

A. Apocrine (cerumen) tubules.
B. Tubules have a wide lumen.
C. Myoepithelial cells (with nucleus) in surface view.
D Connective tissue.

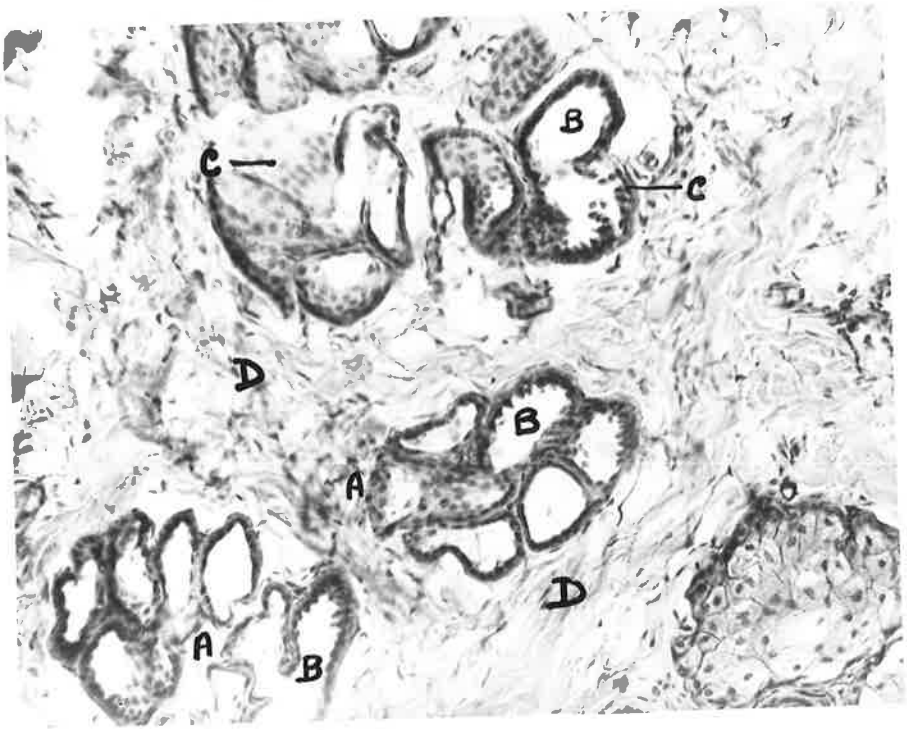

Fig. 12.

cuticle on their luminal border. The small hairs in the skin covering the cartilaginous tragus etc., occurred at fairly wide intervals: each hair was surrounded by a large accumulation of sebaceous gland cells grouped in the accustomed saccular formation. Peripherally in each sac, there appeared small cells, often two layers, with normal nuclei; nearer to the centre of the sac, the cells became hypertrophic and their nucleus pyknotic: more centrally still, the nuclei had disappeared leaving cells filled with a network from which fat droplets had been removed during the preparation of the sections. In some gland groups, empty spaces in their central areas, showed that the total secretion had passed, by means of the short duct, into the pilo-sebaceous canal of the accompanying hair.

The external ear canal was lined with squamous stratified epithelium, five to six cells deep, which displayed some cornification and a slight scaling. Dense acidophilic connective tissue formed the thick underlying dermis. In the distal cartilaginous part of the canal the dermis contained numerous branched apocrine tubules which displayed both secretory and post-secretory phases. Acidophilic myoepithelial cells were a prominent feature in these tubules from which no ducts were seen to emerge.

It was noted also that in the roof region of the canal the apocrine structures reached their highest peak of concentration. (Fig. 12.).

The bulbs of some small hairs, each with a moderate-sized sebaceous appendage, took up a position between the epithelial lining and the cartilaginous core of the wall.

In the proximal cartilaginous end of the ear canal there appeared, at fairly wide intervals, small hairs, each encircled with a small sebaceous appendage. Deep to the hair bulbs several apocrine coils, all possessing a wide lumen, were located. Ducts from these tubules opened into the pilo-sebaceous canals of the accompanying hairs.

DROMICIA CONCINNA (a mature male and female)

Since the description already given of the glands found in the skin covering the external and internal surfaces of the pinna of Trichosurus vulpecula applies equally well to those of Dromicia it will not be repeated.

However the hairless integument covering the inner surface of the tragus etc., exhibited some variations from the Trichosurus pattern. This skin contained large compound sebaceous glands, many of them opening on to the skin surface by very short ducts. The duct walls consisted to three to four layers of squamous cells. These glands were typical sebaceous ones which presented all the well known characteristics.

Deep to the sebaceous structures, and surrounded by adipose tissue, the secretory coils of numerous apocrine glands were grouped adjacent to the connective tissue of the perichondrium which enclosed the cartilaginous core

Fig. 13.- Section through the inner region of the external auditory meatus of Dromicia concinna. Stained with haematoxylin and eosin. X 100.

A. Sebaceous glands.
B. Space left in the gland substance after the secretion has passed into the duct.
C. Duct of a gland opening into the auditory canal.
D. Squamous stratified non-cornified epithelium lining the auditory canal (inner part).
E. Inner part of the external auditory canal.
F. Cartilage.
G. Striated muscle.

This section shows the massive accumulation of sebaceous glands which surround the inner portion of the external auditory canal. The glands depicted are in the active stage of secretion.

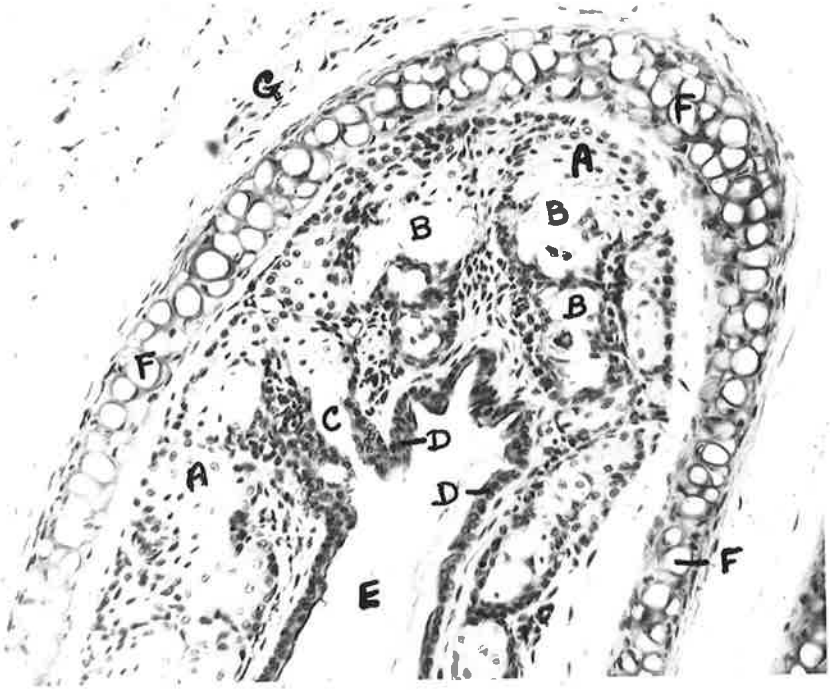

Fig. 13.

of the tragus, etc. Ducts with a wide lumen took an abrupt rise from the secretory coils and followed a straight course towards the skin surface upon which they debouched directly. The duct walls were characteristically two cells thick and the lining ones exhibited, on their free surface, the usual acidophilic cuticle.

The proximal end of the external auditory canal was lined with hairless squamous stratified non-cornified epithelium. Between the skin and the cartilaginous wall of the canal, compound sebaceous glands formed an almost complete investment of the tube. (Fig. 13). These glands opened directly, by ducts lined with three layers of squamous stratified epithelium, on to the skin surface.

No apocrine tubules were present in this region.

Conclusion.

It was assumed that the cerumen secreting elements were composed of the sebaceous and apocrine glands found in the skin covering the tragus, etc. and the sebaceous ones lining the wall of the external auditory canal. The fact that the ducts of both types of glands debouched directly on to the skin surface, as is common in the external auditory meatus of the cat, (Montagna 1949), strengthened this assumption.

THYLACIS OBESULUS. (a mature female).

The similarity of the skin appendages of the pinna in Thylacis obesulus, Trichosurus vulpecula, and Dromicia

Fig. 14.- Sebaceous glands in the distal part of the external auditory canal of Thylacis obesulus.
Stained with haematoxylin and eosin. X 100.

A. Large compound sebaceous glands.
B. Several compound glands share the same duct.
C. Opening of the main duct on to the skin lining the external auditory canal.

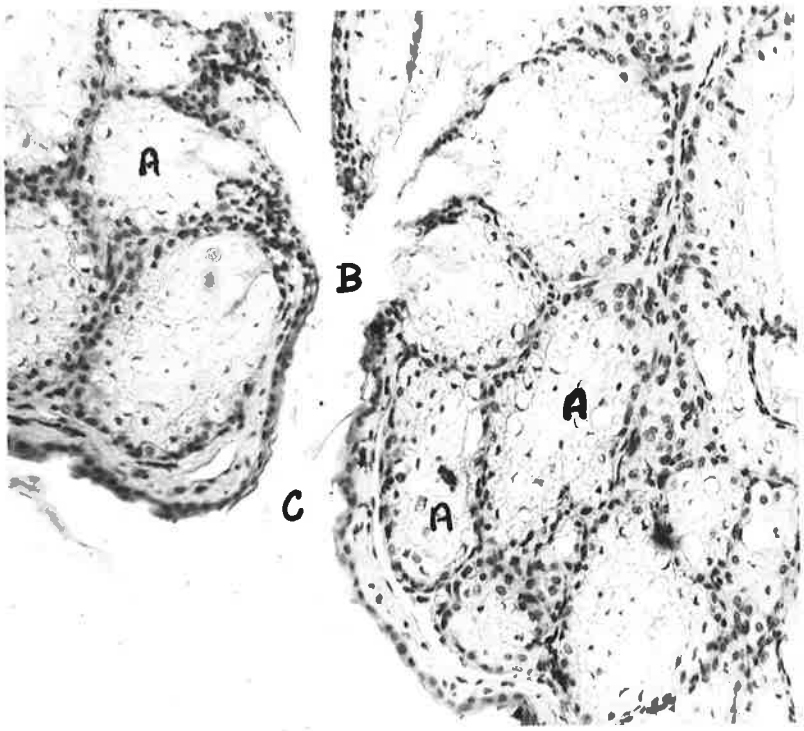

Fig. 14.

concinna renders it unnecessary to repeat the description, already given, of these species. However, certain differences did appear in the skin covering the tragus etc., and in that lining the wall of the ear canal itself. In these regions the thin two-cell-layered slightly keratinized epidermis rested upon a wide collagenous dermis within which numerous large, much-branched sebaceous glands were aligned adjacent to the cartilaginous framework.

Occasionally, some of these glands were associated with fairly small hairs into the pilo-sebaceous canals of which their ducts presumably opened. However, many of these large glands did not appear to be adjuncts of hairs; in these cases a very short wide duct, at the neck of the gland, opened on to the surface of the skin. The wall of this tube consisted of squamous stratified epithelium (six to eight cells deep), the number becoming reduced to three to four as the duct reached the epidermis.

Frequently a common duct opening served several large glands. (Fig. 14.).

Connective tissue septa divided the compound sebaceous glands into lobules which took the form of sacs with their peripheral cells resting on an indefinite basement membrane. These wide cylindrical or polyhedral cells contained a slightly granular cytoplasm which enclosed a round or oval pale nucleus. The peripherally arranged cells exhibited clear outlines, but those towards the centre of the sac,

while still retaining a cell membrane had become hypertrophied, their cytoplasm net-like and the nuclei pyknotic. The empty central space within the lobular sacs was probably due to the final disintegration and disappearance of those cells which had formed the glandular secretion.

Only an occasional apocrine tubule was noted in association with the compound holocrine glands described above.

Conclusion.

In this animal, judging by the number and position of the sebaceous glands and the scarcity of the apocrine type, it seemed justifiable to conclude that the sebaceous elements contributed almost exclusively to the production of an oily secretion, which, as one of its functions, acted as a lubricant for the skin of the ear canal.

The fossorial food-hunting habits of Thylacis would probably cause dust or sand to become lodged in the auditory canal, in spite of the protection afforded by the tragus etc. In these circumstances, the production of an oily secretion by the sebaceous glands, could conceivably have an additional protective function.

SMINTHOPSIS CRASSICAUDATA.

The description of the external hairy surface of the

the pinna of the ear of this animal, conformed too closely to that already given of the other three species, to warrant a repitition.

The epidermal lining of its inner surface contained fine hairs to which were attached large sebaceous cell groups, these were in the advanced stage of secretion, which frequently exhibited an empty sac, surrounded by two to three layers of basal cells.

The fine hairs possessed an acidophilic hyalinized inner root sheath encircled by a three to four cell wide outer sheath.

A few larger hairs appeared at wide intervals, but no apocrine glands were noticed in association with them. The bulbs of these large hairs were situated in the adipose hypodermis which intervened between the skin and the underlying cartilage.

The epidermis itself was very thin, only two to three cells deep, and became even thinner as it covered the tragus etc., where it was also hairless and devoid of apocrine elements.

The external auditory canal was lined with squamous stratified non-cornified epithelium, five to six cells deep in places.

Between the epithelium and the cartilaginous framework around the inner part of the canal numerous sebaceous glands occurred, these were in the later stages of secretory

activity and exhibited the changes in appearance common to their functional state. The ducts from these glands opened into the pilo-sebaceous canals of the small hairs with which they were associated.

In some regions, especially those not immediately supported by cartilage and deep to the sebaceous accumulations, voluminous coils of apocrine tubules in active secretory phase were present. The tall cylindrical secretory cells contained a nucleus in the lower $\frac{1}{3}$ which was darkly stained compared with the pale granular upper $\frac{2}{3}$. Secretory blebs protruded into the lumen. These apocrine tubules all possessed myoepithelial cells.

Ducts from the tubules made the customary abrupt emergence: their walls consisted of an outer and an inner layer of cells, the latter having an acidophilic cuticle on their luminal surface. In the most superficial strata of the dermis the excretory tubes made several open spiral turns before opening into the pilo-sebaceous canals of the small hairs just at the junction of the dermis and the epidermis.

External to the cartilage mentioned above, extremely massive accumulations of compound sebaceous glands were present. These were much lobulated with only a small amount of connective tissue separating the lobules. The component cells displayed all stages of the secretory process.

A central duct, lined with two layers of flat cells supported by acidophilic connective tissue, presented an uneven outline probably due to the openings into it of the smaller ducts emanating from the component lobules.

It was not possible to observe the actual exit of the main duct on to the surface of the lining epithelium.

Conclusion.

Since in the external ear canal of this animal both apocrine and sebaceous glands occurred in considerable excess over the number normally present in skin, it was concluded that both types contributed to the production of a secretion which could be called ceruminous.

SUMMARY

The cerumen glands of the four marsupials examined.

TRICHOSURUS VULPECULA — Two types of glands, sebaceous and apocrine, present in sufficient numbers to warrant the assumption that they were cerumen producing.

DROMICIA CONCINNA — Sebaceous and apocrine glands present, but on a smaller scale: may produce cerumen.

THYLACIS OBESULUS — Very large much branched sebaceous glands present - some were associated with very small hairs, while others which opened by a very short duct on to the skin surface, were not related to hairs. The few apocrine tubules present could make no significant

contribution to the cerumen which must therefore be oily in character.

SMINTHOPSIS CRASSICAUDATA. Apocrine and sebaceous glands occurred in masses sufficient to suggest that both combined to form a ceruminous type of secretion.

CLOACAL GLANDS.

INTRODUCTION.

In all those marsupials that have been investigated, anal, rectal or paraproctal glands have been found. They number one, or more often, two pairs and are present in the slides of the orifice, or between it and the striated muscle forming the cloacal sphincter.

Usually they are oval in shape, exceed one centimeter in length and resemble large sized sebaceous glands which by a holocrine type of secretion produce odorous substances.

These glands are not associated with hairs, but are surrounded with an investment of ramifying tubular sudoriferous type glands. These apocrine tubules open by ducts into the commencement of the excretory outlets of the holocrine (paraproctal) glands. In some cases these tubules form an almost complete ring around the rectum. Their function is not known.

According to van den Broek (1905) there are usually, in adult marsupials, only two pairs of cloacal glands, of

which the more ventral is often much better developed than the dorsal.

Schaffer (1924) says that these large holocrine glands are typical paraproctal ones and correspond to the anal sac of higher mammals.

Fraser (1919) describes a dissection by Mr. K. S. Tan, of the cloacal region of an adult male Trichosurus vulpecula. This description mentions two pairs of large cloacal glands, the more dorsal pair communicating with the cloaca by a long narrow duct on each side, while the ducts of the more ventral and slightly larger pair are very short.

TRICHOSURUS VULPECULA.

The cloacal regions from two mature animals, one male and one female were sectioned for this examination in which two young immature females were included.

Haematoxylin and eosin stained serial sections were cut both longitudinally and transversely and it is on the former that the following description is based.

Longitudinal sections cut through the cloacal canal disclosed the presence, just outside the external aperture, of large Meibomian-like sebaceous glands. These were apparently not associated with hairs, and passed their secretion into ducts, lined with squamous stratified non-keratinized epithelium, which opened on to the surface of the skin.

Fig. 15.- Plan of a transverse section through the cloacal glands and showing the probable arrangement of the accompanying apocrine-like tubules in the cloacal region of Trichosurus vulpecula.

A. Rectum at its entrance into the cloaca.
B. Apocrine tubule surrounding a cloacal gland.
C. Cloacal gland.
D. Duct of cloacal gland.
E. Apocrine tubule opening into the cloaca.
F. Septum of cloacal gland.
G. Apocrine tubule opening into the duct of a cloacal gland.
H. Urogenital sinus at its entrance into the cloaca.

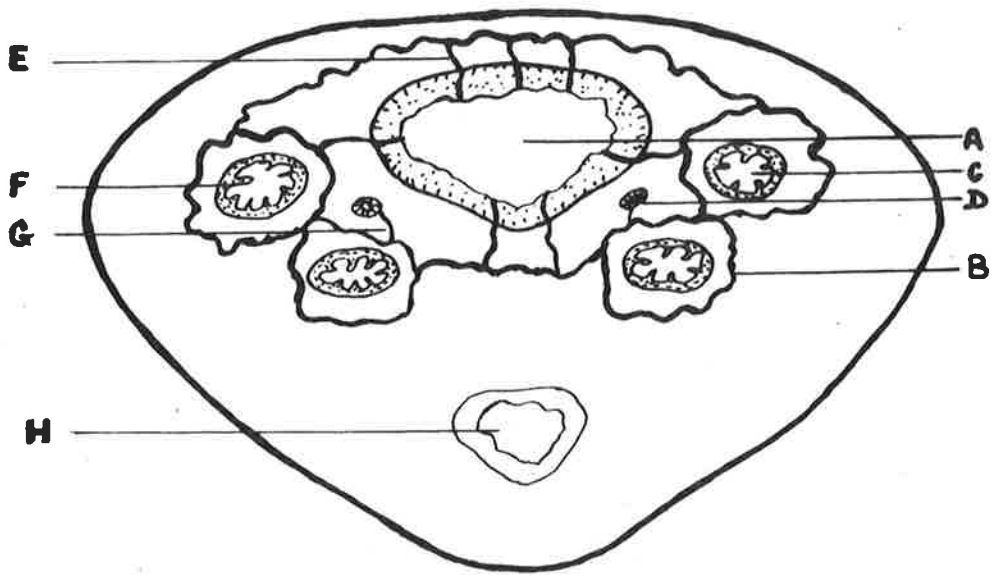

Fig. 15.

More laterally were several compound sebaceous structures. These were associated with fairly large hairs, into the pilo-sebaceous canals of which the sebaceous ducts probably emptied.

In a still more lateral position, smaller hairs with sebaceous appendages made their exits from the skin surface.

Examination of the lateral walls of the canal disclosed a heavy lymphocyte infiltration which surrounded glands of apocrine type (in secretory phase with myoepithelial cells present). These glands coursed parallel to the epithelial lining of the canal into which their ducts (two cells deep) opened. Bundles of striated muscle cells which formed the cloacal sphincter were evident around and in between the apocrine coils.

The transverse sections disclosed two pairs of a holocrine type of gland, one pair in each lateral wall of cloacal canal. These structures were fairly large, oval to round in shape, and apparently lobulated. Encircling each gland, in company with circularly disposed striated muscle bundles, apocrine tubules formed a capsular arrangement. These tubules appeared to open individually by their own ducts into those of the holocrine glands. (Fig. 15.).

Coils of apocrine tubules passed posterior to the cloacal canal, these coils joined on each side with those surrounding the posterior member of each pair of holocrine glands. Most of these tubules were in the secretory phase,

with the tall secretory cells resting on the myoepithelial units. The coils opened into ducts of somewhat similar calibre: the duct walls were doubled layered, their inner cells being short columnar and the outer ones rather flattened. As they approached the surface of the cloacal lining, these ducts appeared to become narrower and in the last part of their course took four or five spiral turns before making their exits on to the cloacal lining surface.

Other apocrine coils ran anterior to and between the two sets of cloacal glands. These coils also opened by ducts into the cloaca in a similar manner.

At this stage of the description it is of interest to note the structure of the cloacal lining epithelium. No basement membrane was identified, the basal cells, cuboidal to low columnar in shape, appeared to rest on the surrounding connective tissue. Several layers of polygonal cells, separated by intercellular spaces crossed by intercellular bridges, occupied the middle section of the Malpighian strata, the more superficial layers consisted of rather flattened cells with a flat dark nucleus. Of the outermost layer some cells were more fleshy in appearance and some still retained a nucleus.

A small duct with a wall of three to four layers of flattened cells emerged from each lobule of the holocrine glands. These ducts appeared to join a long main duct which eventually opened into the cloacal canal. The walls of this

main tube consisted of six to eight layers of squamous type cells.

The whole gland apparently comprised a basal stratum of cuboidal acidophilic cells (with a round nucleus) which rested on an encircling capsular arrangement of connective tissue. No basement membrane was identified. From the capsule, septa consisting of two layers of connective tissue cells projected into the lumen of the gland. A layer of cuboidal cells continuous with the basal stratum already mentioned, rested upon the connective tissue core of the septa. On each side of the septa and resting upon the cuboidal layer, several additional rows of cells were present. These large cells were polygonal in shape and their cytoplasm exhibited fine dark granules. The cytoplasm of the most superficial of the polygonal cells was filled with large pale fatty-looking granules, a nucleus was present in a few of them. Some of these outermost cells became free in the lumen where presumably they broke down to form a fatty granular secretion.

In many of the sections the gland appeared to be filled with interlacing septa, which in transverse sections gave the appearance of tubular structures cut transversely. Each pseudo-tubule appeared to be lined with such cells as are described as being attached to each side of a septum; the largest palest cells facing towards the pseudo-lumen, which was usually small. Presumably at the height of its activity

the lumen of the gland becomes completely obliterated by the interlacing septa with their attached layers of cells, all in process of becoming at least a part of the final product - a fatty secretion.

A yellow coloured cloacal gland measuring 1.2 cms. x 0.8 cms. was removed by dissection from a mature male Trichosurus.

This structure was opened with a scalpel whereupon a thick yellow greasy substance was released. After the interior of the cyst-like gland was cleared of secretion, macroscopic inspection revealed the internal lining to have a yellow interlacing pattern on a greyish brown background. The very thin cyst wall was then prepared for sectioning. The haematoxylin and eosin stained sections exhibited numerous interlacings of connective tissue septa, bearing upon their surfaces layers of cells similar to those already mentioned in the description of the female cloacal glands which were sectioned, in situ, with the whole cloacal region. These holocrine cells after becoming detached from the septa began a progressive degeneration into small granular masses without any cell outlines, though the nucleus and the nucleolus remained intact at this stage. Finally the nucleus became dark shrunken and irregular in shape prior to disappearing completely leaving an amorphous fatty granular secretion to occupy the now almost empty lumen.

Fig. 16.- Glands of the cloaca of Trichosurus vulpecula. Stained with haematoxylin and eosin. X 100.

A. Holocrine type of gland.
B. Secretory cells of the holocrine gland.
C. Connective tissue septa containing capillary blood vessels.
D. Secretory cells undergoing disintegration.
E. Apocrine type tubules.
F. Secretion in the lumen of an apocrine tubule.

Two types of gland are present here: one holocrine and one apocrine. The holocrine cells are produced on the connective tissue septa which grow in from the capsule. The apocrine tubules are lined with cuboidal cells which are in the post-secretory phase. Secretion is seen in the lumen.

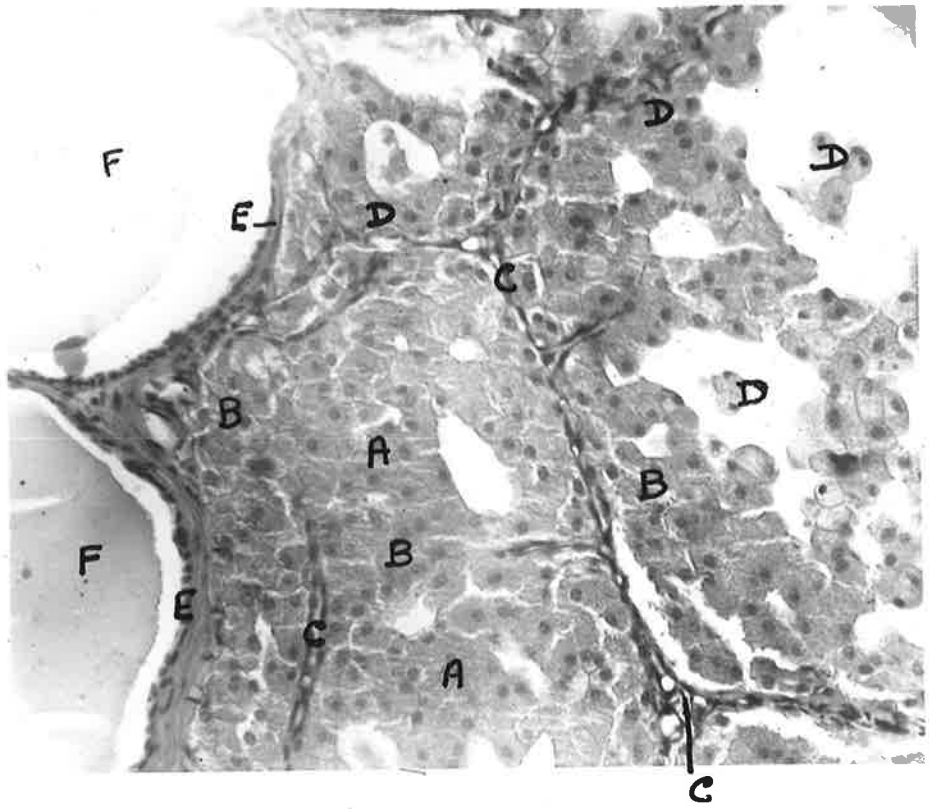

Fig. 16.

Apocrine tubules with a wide lumen, containing secretion, surrounded the holocrine gland. These tubules were lined with the flattened epithelium characteristic of the post-secretory phase. External to the apocrine secretory cells, myoepithelial units could be observed in some of the tubules. (Fig. 16).

Apparently there is no sex specialization so far as the structure of these cloacal glands is concerned.

DROMICIA CONCINNA.

Several animals were used for this investigation - all of them females.

Prior to removing the cloacal region for sectioning, it was noted that one pair of cloacal glami was yellow in colour, oval in shape, and measured 2.5 mm. in length, and 1.5 mm. in width.

As several animals were available, it was possible to cut some of the material in transverse section and some longitudinally.

Longitudinal sections revealed that the cloacal canal was lined with squamous stratified non-keratinised epithelium, three to four cells deep. This epithelium also covered the anal folds where its thickness increased to the depth of six to seven cells. The muco-cutaneous junction was sharply defined, its location being practically at the external os of the canal. Just outside the entrance of the os, on the skin side, appeared several coarse hairs, each accompanied by a large compound sebaceous gland from

from which ducts opened into the pilo-sebaceous canal of associated hair follicles.

Medial to these sebaceous glands and parallel to the mucous lining of the canal, coiled apocrine type tubules lined with tall columnar cells, each with a round basal nucleus, were noted. Some of these cells were in the secretory phase, myoepithelial cells were present at their bases and both types rested on the basement membrane. A few ducts were noticed to open into the hair canals of nearby large hairs which emerged from the skin surface just external to the canal opening. The walls of these ducts consisted of two layers of cells, the outer ones rested on a brightly stained basement membrane.

Transverse sections of the cloacal canal, just outside the os region, exhibited large compound sebaceous glands which consisted of typical holocrine cells arranged in lobular sacs separated by connective tissue. Each gland opened by a wide main duct into the pilo-sebaceous canal of its fairly large associated hair. These hairs surrounded the cloacal aperture. A single small apocrine tubule also appeared to be connected with each of these pilo-sebaceous groups.

Smaller sebaceous glands, slightly more deeply placed, appeared to belong to hairs of intermediate size. The striated muscle bundles of the cloacal sphincter surrounded

Fig. 17.- Two holocrine glands and three large apocrine-like tubules in the lateral wall of the cloaca of a female Dromicia concinna. Stained H. and E. X 40.

A. Holocrine gland almost at the close of a secretory phase.
B. Fatty globules of secretion in the lumen of the above holocrine gland.
C. Basal layer from which new secretory cells will develop.
D. Holocrine gland showing septa on which secretory cells develop.
E. Septa and secretory cells.
F. Fatty secretion in the lumen of the above holocrine gland.
G. Apocrine-like tubules with a very wide lumen.
H Striated muscle forming a capsular arrangement around the two holocrine glands.

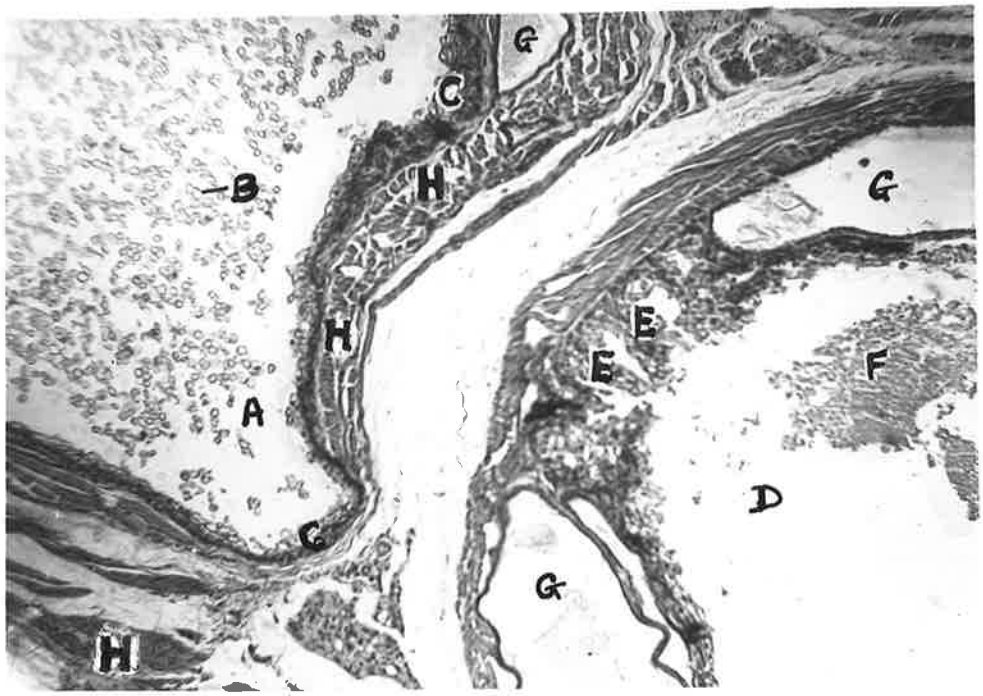

Fig. 17.

the deeper aspects of these glands.

Higher up in the cloacal wall coils of apocrine tubules opened by ducts into the cloacal canal. The walls of these ducts consisted of outer circularly arranged cells while the inner ones ran in a longitudinal direction. The tall slender pyramidal cells of the apocrine tubules were in the secretory phase since each showed a bleb of cytoplasm protruding into the lumen. These secretory cells rested on a layer of well defined acidophilic myoepithelial elements which were wedged in between the bases of the secretory elements.

Just below the level of the anal folds a pair of cloacal glands (yellow in fresh state) were present. These glands, which were enclosed in the striated muscle bundles of the sphincter cloacae and situated one on each side of the cloacal canal, appeared to be of holocrine type. Fig. 17.). They consisted of polygonal fat-filled cells arranged (two to three cells deep) on irregular strands of connective tissue which formed short septa extending from a peripheral connective tissue investment towards the centre of the gland sac. The middle of the sac was filled with cells, similar to those on the septa, but in various stages of breakdown. This latter process appeared to follow a pattern of nuclear degeneration then nuclear loss, the anucleated cells finally becoming fat-filled envelopes which presumably underwent further breakdown to form the secretion,

or at least, a part thereof. This secretion appeared in some of the gland sacs as a fatty granular material. This pair of holocrine-type glands exhibited a similarity to sebaceous glands, since the more superficial cells of each lobule tended to be flattened while the central ones were polygonal and contained a central round nucleus. The cytoplasm also showed the usual reactions of fatty materials to preparation reagents. The glandular sacs formed a compact body of lobules separated from each other by connective tissue which also surrounded it to form a capsule.

Outside this capsule and completely encircling it were coils of apocrine glands. These tubules consisted of, either flat cuboidal cells surrounding a wide lumen which contained some coagulated secretion, or their lining cells were tall and in the secretory phase.

The striated muscle of the cloacal region encircled the whole holocrine-apocrine complex.

Further examination of serial sections revealed the fact that Dromicia possessed two pairs of holocrine type glands, i.e. two situated on each side of the cloacal canal. The more ventral pair were the larger and have already been described. However, the members of the pair were fairly close together and each had an investment of apocrine type tubules and a small amount of striated muscle appeared between the two glands.

The second more dorsally placed pair differed from the first both as regards the secretory cells and the type of secretion present in the lumen. The cells of this second pair were arranged in sacs which were separated by connective tissue. In these sacs the superficial cells tended to be wide columnar, with a pale elongated nucleus, this contained a definite nucleolus. The basement membrane was difficult to identify. The more centrally situated cells became polyhedral and granular in appearance and then vacuolated, though less so than those of the ventral glands. This granular appearance rapidly gave way to fatty globules and the nucleus changed to a more circular form and became paler though the nucleolus still remained prominent. Then as further degenerative changes took place, both nucleus and cytoplasm lost colour and the latter infiltrated with fatty globules which became free in the lumen to form the secretion. It was noted that the nucleus appeared to degenerate without the preliminary pyknosis seen in those of the ventral glands. The combined ducts from the two larger holocrine type glands probably opened into the cloacal canal fairly near to its os. The actual exit was not observed but the ducts appeared to travel in that direction.

THYLACIS OBESULUS.

The cloacal region of a mature female was removed for

sectioning; after fixation, the material, which was limited to that of a single animal, was serially sectioned. The cranial end of the region was cut transversely in order to obtain a horizontal view of the cloacal glands: the lower portion was cut longitudinally and used to show the caudal part of the cloacal canal and the arrangement of glands and hairs around the cloacal aperture.

The squamous stratified non-keratinized epithelium lining the canal was folded owing to contraction of the sphincter muscle. The dense underlying (dermal) connective tissue appeared to be very wide and contained some longitudinal strands of striated muscle.

In the lateral walls of the cloacal canal many apocrine-like coiled tubules coursed parallel to the epithelial lining. The majority of these were lined with cuboidal cells which surrounded a wide lumen, while some tubules contained tall cells (in the secretory phase) with blebs of cytoplasm protruding into the lumen. The myoepithelial cells were more easily identified in those tubules which showed the secretory phase. These apocrine coils were separated into parallel columns by longitudinally running striated muscle.

Another layer of striated muscle, this time circularly arranged, appeared betwen the outer coils of apocrine tubules and several groups of large compound glands, some of these were associated with large hairs

Fig. 18.- Lateral wall and canal of the cloaca of a female Thylacis obesulus. Stained with haematoxylin and eosin. X 40.

A. Epithelial lining of the cloacal canal.
B. Apocrine tubules in transverse section.
C. Large Meibomian-like sebaceous gland in the lateral wall.
D. Main central duct of the above gland.
E. Exit region of the main duct of the above gland.
F. Duct of ? apocrine tubule.
G. Circularly arranged striated muscle.
H. Canal of the cloaca.

The excretory duct of the sebaceous gland opens on to the surface of the skin just lateral to the cloacal aperture.

Of the ducts marked F, the two cut in cross section probably empty into the cloacal canal; while that cut longitudinally appears to join the excretory duct of the sebaceous gland almost at its exit on to the surface of the skin.

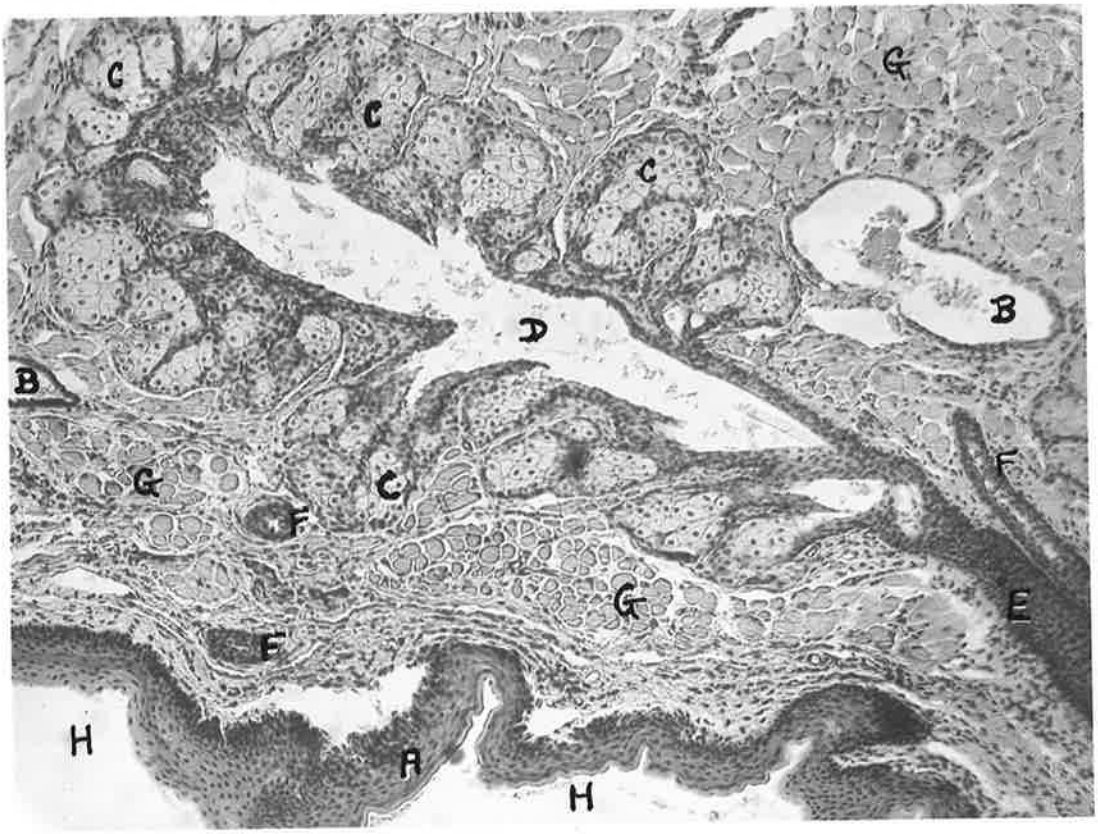

Fig. 18.

into the pilo-sebaceous canals of which their ducts opened.

Nearer to the hairy surface, there appeared smaller sebaceous structures (many of them compound) which were invariably associated with hairs.

Between these sebaceous structures and the hairy skin surface a few coiled apocrine tubules became evident, these were chiefly in the secretory phase but with lining cells of different heights, thus providing the tubal lumen with an irregular border. Myoepithelial cells though present were not strikingly apparent. From each of these tubules a coiled duct opened into a hair canal. These apocrine glands were much smaller than those, already described, which were surrounded by the sphincter muscle.

Lateral to the cloacal aperture, a very large compound sebaceous gland, similar to the Meibomian unit of the eyelid, opened via the pilo-sebaceous canal of a large hair, on to the outside skin surface. (Fig. 18). This sebaceous appendage was composed of lobules consisting of closely packed sacs with scant connective tissue intervening between them. The small intralobular ducts with their single layer of mural cells drained the fatty secretion into the interlobular outlets, the walls of which consisted of two layers of somewhat flattened cells. The largest excretory passage which had a thick wall (six to eight cells deep) opened into the superficial part

Fig. 19.- Holocrine and apocrine glands in the wall of the cloaca of Thylacis obesulus. Stain H. and E. X 40.

A. Epithelial lining of the cloaca.
B. Lumen of the cloaca.
C. Holocrine glands.
D. Secretion material of the holocrine glands.
E. Apocrine tubules.
F. Secretion in the lumen of the apocrine tubules which surround the holocrine gland.
G. Spaces left by degenerating holocrine cells.
H Circularly arranged striated muscle.

The section shows the lobulation of the holocrine glands as well as the cell changes which take place from the periphery to the centre of the lobule during the production of the secretion.

No ducts of either type of gland are present in this illustration.

Fig. 19.

of the pilo-sebaceous canal of its associated large hair.

Just below the point where the lowest secretory lobules debouched on to the main duct, another duct joined it. This thin-walled (three cells thick) outlet appeared to belong to a set of fairly densely coiled apocrine tubules which showed a post-secretory phase and consisted of cuboidal cells which surrounded a wide lumen: this frequently contained coagulated secretion. This set of apocrine tubules, densely coiled above the summit of the sebaceous structure, extended in much looser coils below and parallel to the posterior border of the sebaceous gland: their combined ducts finally, as mentioned above, opened into the main excretory duct of the sebaceous gland.

The transverse sections taken through higher levels of the cloacal canal revealed the presence of three pairs of modified sebaceous type glands two large and one small in each lateral wall of the canal. (Fig. 19).

The glands all appeared close together on each side, and all were similar in appearance except for their size. All were encircled with striated circular sphincter muscle bundles, among these bundles coils of apocrine tubules were present. The tubules, most of which were in secretory phase, consisted of tall columnar and myoepithelial cells resting on a well stained basement membrane. Secretion in the form of discrete acidophilic globules frequently appeared in the lumen.

The paired holocrine glands, apparently the cloacal, were arranged antero-posteriorly around the lateral walls of the canal. On each side, the smallest was the most anteriorly placed and with the middle gland appeared to have a less dense encirclement of apocrine tubules. The encircling coils in each lateral wall were connected anteriorly with tubules which ran deep and parallel to the skin surface.

Transverse sections of the cloacal glands showed them to be subdivided into lobules by connective tissue and, in some places, by a little striated muscle. The lobules consisted of secretory acini which contained typical holocrine sebaceous cells. The peripheral layer tended to be cuboidal with a pale round nucleus. Towards the centre of the acinus the cells became hypertrophied, the cytoplasm reticular and filled with fatty globules. Further degenerative changes resulted in the nuclear pyknosis giving rise to discrete dark granules, cell membranes disappeared leaving a coarse reticulum which contained fat droplets varying from small to very large. Later the nuclear particles also disappeared leaving a space filled with granular secretion and some clumps of apparently anucleated degenerated secretory cells. The presence of some peculiar irregularly shaped structures which contained a bright pink substance surrounded by fairly large discrete granules, was also noted.

Fig. 20.- Holocrine cloacal gland of Thylacis obesulus. Stained with haematoxylin and eosin. X 20.

A. Lobulated holocrine gland of the cloaca.
B. Secretory products in the lumen of the main duct.
C. Colloid-like material in the lumen of the duct.
D. Shows the disintegration of the cells to form the secretion.

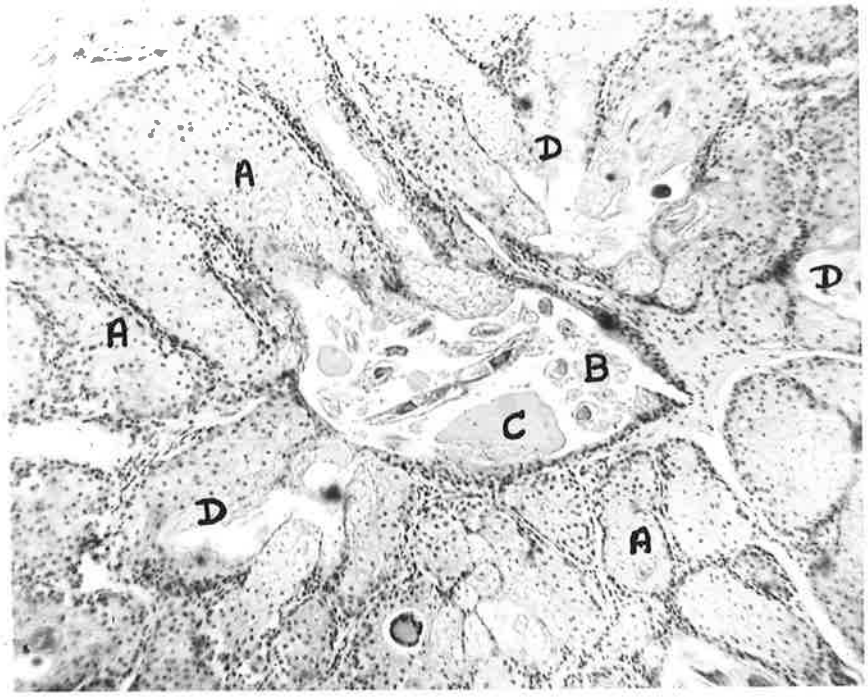

Fig. 20.

Also occasionally, a large pink colloid mass was present among the elements already described. (Fig. 20.).

Ducts from these cloacal glands opened by fairly short tubes into the cloacal canal. The several layers of squamous type cells comprising the walls of the ducts became continuous with those lining the cloacal canal.

The cloacal glands of Thylacis obesulus differed from those of the other three marsupials in conforming much more closely to the structural pattern of a sebaceous gland of the surface skin and to that of a Meibomian gland of the eyelid.

SMINTHOPSIS CRASSICAUDATA.

The animals available for the investigation of the cloacal region of this species were a mature female and a young mature male.

The cloacal region was excised and, after fixation, serially sectioned both in longitudinal and in transverse directions.

Though the longitudinal sections, stained with haematoxylin and eosin, provided the greatest amount of information regarding the general plan of the region, the description is actually based on both series.

The sections indicated that very large compound sebaceous type glands, with a long central duct, occupied the lateral walls of the cloacal canal. Each gland

consisted of secretory holocrine lobules which opened straight into the long central duct (similar to that of the Meibomian gland of the eyelid). This duct was formed throughout its length by several layers of squameus stratified epithelium. This epithelium increased in depth as the duct opened on to the skin surface just lateral to the cloacal canal aperture. A fatty secretion which contained some cell debris occupied a portion of the duct lumen.

As in the other animals investigated, the above mentioned glands were probably associated with hairs.

Further examination of the serial sections disclosed that deeper within the lateral walls of the cloacal canal, two pairs of holocrine type cloacal glands were present. These occurred two on each side surrounded by a layer of striated muscle which with the underlying connective tissue formed a capsule around each of them. The muscle cells appeared to run parallel to the long axis of the canal and perpendicular to the transverse section of the gland lumen.

Spanning the interval separating the capsules around the two large cloacal glands there appeared coils of apocrine tubules which were located between the striated muscle bundles of the sphincter cloacae. Their tall glandular cells contained within their cytoplasm, in addition to the pale round nucleus, fairly large translucent granules; these were probably the precursors

Fig. 21.- Two holocrine glands and several apocrine-like tubules in the lateral wall of the cloaca of a male Sminthopsis crassicaudata. Stained with H. and E. X 40.

A. Two holocrine glands with secretion in the lumen.
B. Septa bearing secretory cells.
C. Connective tissue capsule surrounding the gland.
D. Striated muscle surrounding capsule of the gland.
E. Apocrine-like tubules associated with the holocrine gland.
F. Apocrine tubules in cross section.
G. Myoepithelial cells in apocrine tubules.
H. Striated muscle separating the apocrine tubules.

This section shows two holocrine glands with their secretory cells arranged on septa which project inwards from the connective tissue capsule. Large apocrine-like tubules surround the holocrine gland on the right.

The apocrine tubules in the top right segment of the picture contain myoepithelial cells and are separated from each other by the striated muscle of the cloacal sphincter.

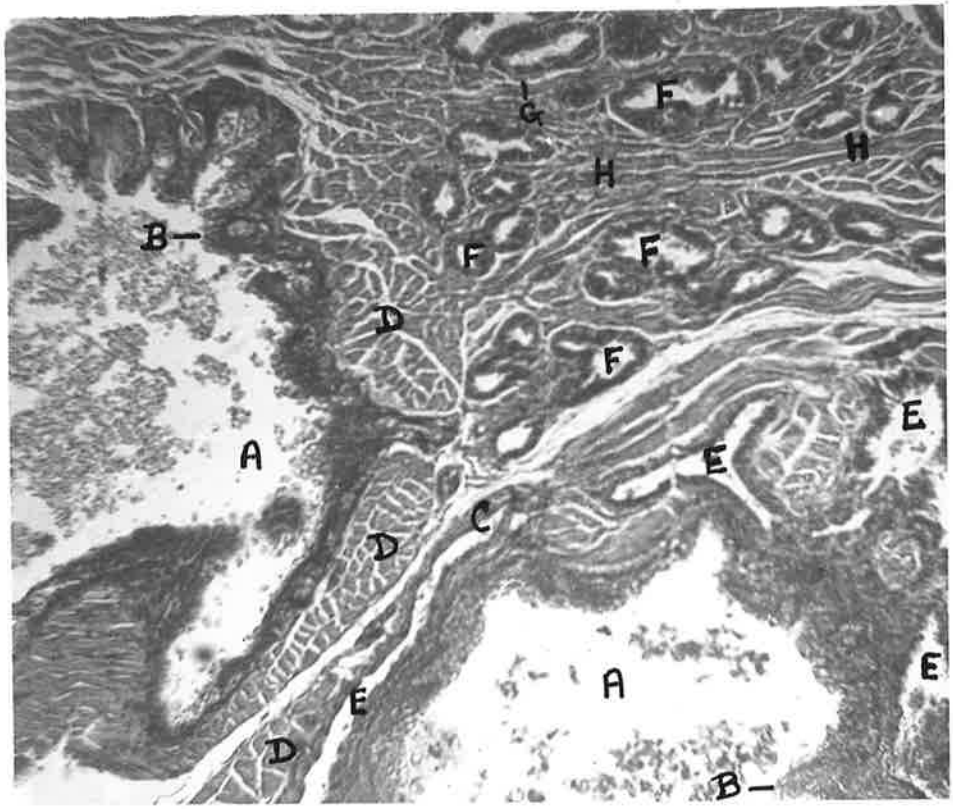

Fig. 21.

of the secretion. Myoepithelial cells were present in their typical position.

Of the two cloacal glands one was larger than the other and appeared to be placed slightly postero-medial to it. The larger gland was holocrine in type with its secretory cells very pale-staining and angular in shape. These cells appeared to be attached (several layers deep) to connective tissue septa which extended in from the surrounding capsule. The pale cells contained a reticular cytoplasm which enclosed fat vacuoles as well as a round pale centrally placed nucleus with a well marked nucleolus. (Fig. 21.).

Those cells nearest to the centre of the glandular mass contained in their reticular cytoplasm fatty globules which tended to break down to form the fatty granular secretion present in the central lumen of the glandular mass. This lumen was probably formed when the secretory cells, which constituted the original fairly compact non-lobulated sebaceous type gland, broke away from their septal position and underwent a transformation into the secretion.

The second type of gland, situated antero-lateral to the larger one, occupied a position not very deep to the skin covering the lateral surface of the cloacal protuberance. Apocrine tubules surrounded it, so separating it from the skin laterally and the larger gland

Fig. 22.- The lateral wall of the cloaca of a male Sminthopsis crassicaudata showing coils of apocrine glands arranged around the two holocrine glands and also running parallel to the lumen of the cloaca.

Striated muscle of the cloacal sphincter appears between the apocrine tubules.

A. Holocrine gland with secretory cells attached to the basal layers.
B. Holocrine gland with secretory cells attached to the septa.
C. Apocrine tubules with a wide lumen.
D. Nucleus of a myoepithelial cell.
E. Basement membrane.
F. Striated muscle.

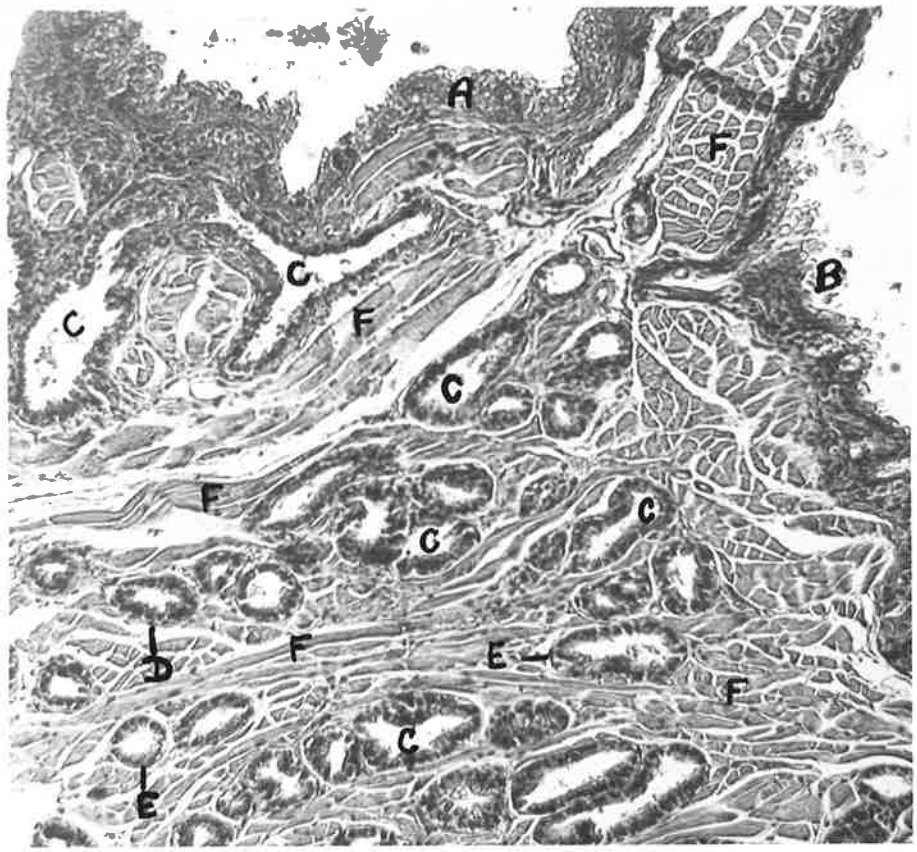

Fig. 22.

medially. Connective tissue formed a capsule for this structure which consisted of lobules with much folded walls. From each lobule a duct emerged which joined with others to form a main duct which opened on to the side of the cloacal canal.

The lateral gland lobules consisted of secretory cells lining a large open lumen which contained secretion. The two outermost layers, resting on the basement membrane, consisted of cuboidal cells (with a dark nucleus); these two layers gave way immediately to several rows of a larger and paler sebaceous type of cell, each with a reticular cytoplasm and a central, much lighter nucleus. This innermost layer apparently provided the major part of the secretion which, at this stage, took the form of fatty globules. A few cells, containing a pyknotic nucleus, were present among the fatty globules, in the lumen of the lobule.

On each side of the cloacal canal, two ducts emerged, one from each of the two glands just described. These two ducts were separated throughout their length by coils of apocrine tubules; (Fig. 22) similar tubules also bounded these ducts laterally and medially. The medial coils were interposed between the medial duct and the lining epithelium of the anal canal. The lateral set of coils separated the large superficial sebaceous glands (with hairs) from the lateral duct.

The destination of the apocrine system of ducts could not be ascertained: it was assumed that, as in the other species discussed, they joined the main excretory ducts of the holocrine cloacal glands.

SUMMARY OF CLOACAL GLANDS.

Haematoxylin and eosin stained serial sections through the cloacal region of three of the marsupials revealed a similarity in histological structure. Thylacis obesulus differed somewhat.

Surrounding the cloacal aperture, very large compound holocrine glands, similar in appearance to the Meibomian structures in the eyelid were noted. Some of these were associated with large hairs, while others opened by short ducts directly on to the skin surface.

Deeper in the tissue of the cloacal protuberance two or three pairs of holocrine-type gland were observed, these were situated, two or three on each side, in an antero-posterior position in the lateral walls of the cloacal canal. There appeared to be only a slight difference in their respective sizes.

These holocrine glands were surrounded by connective tissue forming a capsule from which septa passed into the gland substance. These septa carried several rows of cells; the basal ones being cuboidal and fairly small with a dark nucleus, while the more superficial ones were polygonal in shape, larger and paler in colour

and contained a round pale nucleus. The cytoplasm of these polygonal cells contained coarse refractile granules, which apparently eventually become part of the secretion. Some of the cells lost their nuclei and appeared as anucleated spheres filled with fat. Thus the lumen became filled with fatty granules and fat-filled spheres which took the place of the original cell-covered septa. Ducts from these glands opened into the cloacal canal.

Surrounding each holocrine gland there appeared, between striated muscle bundles, coils of apocrine-like tubules. These consisted of tall columnar cells (in the secretory phase) which rested on myoepithelial elements.

It was judged that ducts from these coils opened into the main ducts of the holocrine glands.

In addition to the encircling ring of apocrine tubules two other sets were observed, those on the medial side ran parallel to the lining surface of the cloacal canal into which their ducts opened, while the lateral set travelled parallel to the external skin surface. The destination of the ducts from the latter could not be determined though it was assumed that either they made connections with the tubules surrounding the holocrine glands, or that the tubules themselves became continuous and opened by the ducts already described into the cloacal canal.

The type of secretion produced by these apocrine tubules has not yet been determined.

It is proposed later to subject the glands of this region to cytochemical examination, the results of which may shed some light on the type of substance secreted.

In their paper entitled "A Histochemical Study of the Glands of the Anal Sacs of the Dog", Montagna and Parks (1948) state that "the combined secretion of the tubules of the anal sac and the sebaceous glands associated with its excretory duct forms a viscous putrescent fluid. The biological significance of this secretion in the dog is unknown." The cloacal glands of Thylacis obesulus numbered six: three pairs on each side of the cloacal canal. Two pairs on each side were large and of similar size and appearance, while the third member of each pair was smaller. The general structure of all three pairs of glands was similar to that of a modified much-lobulated sebaceous structure. Their final secretory product consisted of cell debris, possible colloid masses and fatty granules.

The glands were not related to hairs.

GENERAL SUMMARY

A comparative histological investigation of all those glands regarded as being "cutaneous", has been made on four marsupials namely: TRICHOSURUS VULPECULA, DROMICIA CONCINNA, THYLACIS OBESULUS and SMINTHOPSIS CRASSICAUDATA.

These "cutaneous" glands are described under various headings.

"Glands of the general skin" include the sebaceous and apocrine types of the hairy surface as well as the eccrine glands present on the foot pads of all four species. The skin of the naked, ventral terminal portion of the tail of TRICHOSURUS also contained eccrine sweat glands.

The ocular region included those glands associated with the eyelid and the Harderian structure, this latter though present in all four, varied as regards its secretory cells, from species to species.

The specialized cerumen producing glands of the external ear canal also exhibited species variation. Included in this report are the apocrine and sebaceous appendages of hairs on the pinna of the ear.

Those peculiar apocrine and sebaceous type glands associated with the anal canal and frequently regarded as corresponding to the so-called anal sac of the dog, displayed certain species differences.

Of the mammary structures the nipples and marsupia of

all four species are described and compared. The large apocrine tubules present in the nasal vestibue are discussed as well as other glandular structures belonging to this region.

The so-called sternal and suprascapular glands were investigated and a report on the findings is given.

Several fairly recent theories concerning the gland structures have been mentioned: frequently the marsupial material bore out the accuracy of these hypotheses. For example, it has long been believed that the wall of an eccrine duct, as it passes through the Malpighian layers, consists simply of the epidermal cells which surround it. Pinkus (1939) and more recently, Lobitz, Holyoke and Montagna (1954) maintain that the epidermal eccrine sweat duct is a morphologic and biologic entity, i.e.; the duct lining cells are similar throughout its length.

In the four marsupials investigated, the sweat ducts of the skin on the paws, appeared to support the accuracy of the above theory.

References.

Abbie, A. A. 1937. Some Observations on the Major Subdivisions of the Marsupialia. Journ. of Anat. 71: 429.

Abbie, A. A. 1959. "Hinc Illae Lacrimae", Trans. Ophth. Soc. Aust., (in press)

Alverdes, K. 1932. Die Apokrinen Drüsen im Vestibulum Nasi des Menschen. Z.f. Mikrosk. Anat. *

* Indicates additional references at the end of this list.

* Bertalanffy, F. D. 1957. Mitotic activity and renewal rate of the sebaceous gland cells in the rat. Anat. Record 129: 231-239

Bolliger, A. (2) and Hardy, N. H. 1944. The sternal integument of Trichosurus vulpecula. P. Royal Soc. N. So. Wales. Vol. 78: 122-133.

Bonnot, E. 1908. The Interscapular Gland. Journ. of Anat. and Physiol. Vol. 43: 43.

Broek van den, A. J. R. 1905. Untersuchungen uber die weiblichen Geschlechtsorgane der Beuteltiere. Petrus. Camper. Dl. III. 1905.

Bunting, H., Wislocki, G. B. and Dempsey, E. W. 1948. The Chemical Histology of Human Eccrine and Apocrine Sweat Glands. Anat. Rec. 100: 61.

Carter, H. B. and Dowling, D. F. 1954. Hair follicle and apocrine gland occurrence in cattle skin. Aust. J. Agric. Res. 5: 745-754.

Cooper, Z. K. 1930. A histological study of the integument of the Armadillo, Tatusia novemcincta. Am. J. Anat. 45: I.

Eberl- Rothe, G. 195I. Über das Gehorgangsorgan von Saugetieren. Acta. Anat. Vol. 11: 616-644.

Ford, E. 1934. Note on the sternal gland of Myrmecobius. J. of Anat. Vol. 68: 346-349.

Fraser, E. A. 1919. The development of the urogenital system in the Marsupialia (Trichosurus vulpecula) Journ. of Anat. 53: 124-127.

Giacomini, C. 1887. Giorn. del l'Accad. Ed. di Torino.

Grasse, P. P. 1955. Marsupiaux. Traité de Zoologie. XVII. Prem. Fascic. Masson, Paris.

Hoepke, H. 1927. Die Haut. V. die Drüsen der Haut. Möllendorff Handb. d. Mikroskop. Anat. d. Menschen. III, I: 55-66.

Horn, G. 1935. Formentwicklung und Gestalt der Schweissdrüsen der Fussohle des Menschen. Zeitschr. f. mikroskop.- Anat. Forsch. 38: 318-329.

Horstmann, E. 1957. Die Ceruminaldrusen und andere a-Drusen. Handbuch der Mikroskopischen Anatomie des Menschen. T.3/3 v. Möllendorff 1957.

Hurley, H. J. Jr. and Shelly, W. B. 1954. The Role of the Myoepithelium of the Human Apocrine

Sweat Gland. Journ. Invest. Derm.
V. 22 : 143-156.

Inglis, K. 1927. The So-called Interscapular Gland and Tumours arising therein. Journ. of Anat. 61: Pt. IV. 452.

Jones, F. W. 1924.a. Dromicia concinna in The Mammals of South Australia. Pt. II: 190. S.A. Government Printer. 1924.

Jones, F. W. 1924.b. Trichosurus vulpecula in The Mammals of South Australia. Pt. II: 196. S.A. Govt. Printer.

Jones, F. W. 1923.d. Sminthopsis crassicaudata in The Mammals of South Australia. Pt. I: 111. S.A. Government Printer. 1923.

Jones, F. W. 1924.c. Thylacis obesulus in The Mammals of South Australia. Pt. II: 138. S. A. Govt. Printer. 1924.

Jones, T. W. 1839-1847. "Lacrymal Organs" in the Encyclopaedia of Anatomy and Physiology. ed. R. B. Todd. V. 3: 78, 96, 98 (1839-1847). Longman. London.

Kato, Sh. 1936a. Über das Vorkommen apokriner Drüsen in der Aussenhaut des nasenflügels bei den Japanern. Fol. Anat. Jap. 14: 97-100. (1936a).

*
*
Kandutch, A. A., Murphy, E. D. and Dreisbach, M. E. 1955.

Provitamin D in certain sebaceous tissues of mouse and guinea pig. Arch. Biochem. Biophys. 61: 450-455.

Lauber, H. 1936. Lacrimal gland and Gland of Harder in Handb. der Mikroskopisch. Anatomie des Menschen III/2 592. (1936) v.Mollendorff

Lever, W. 1949. Histopathology of the Skin. 10-12. J. W. Lippincott Co. Philadelphia. U.S.A. (1949)

Lobitz, W. C. Jr., Holyoke, J. B., and Montagna, W. 1954. Response of the human eccrine sweat duct to controlled injury. "Growth centres of the epidermal sweat duct unit". Journ. Invest. Derm. 23: 329-344.

Maeda, M. 1951. Die vergleichend-histologische Untersuchung der sog. Glandulae vestibulares nasi bei den Säugetieren 1. Mitteilung. Fol. Anat. Jap. 25: 229-233 (1951).

* Mogi, E. 1938. Beiträge zur Entwicklung der apokrinen Schweissdrüsen im Vestibulum Nasi bei den japanischen Feten. Folia. Anat. Jap. 16: 147-182. (1938).

Möllendorff v, W. 1957. "Glandulae vestibulares nasi". Handbuch der Mikroskopischen Anatomie des Menschen. T.3/3 [redacted].

Montagna, W. 1949. The Glands of the External Auditory Meatus of the Cat. J. Morphol. 85: 423-442.

Montagna, W. 1956. Apocrine glands. 129-169. The Structure and Function of Skin. Academic Press Inc. New York.

Montagna, W., Chase, H.B., and Lobitz Jr. W. C. 1952. Histology and cytochemistry of human skin. II. The distribution of glycogen in the epidermis, hair follicles, sebaceous glands and eccrine sweat glands. Anat. Rec. 114: 231-248 (1952).

Montagna, W., Chase, H. B. and Lobitz Jr. W. C. 1953. Histology and Cytology of human skin. V. Axillary apocrine sweat glands. Am. J. Anat. 92 : 451-470. (1953).

Montagna, W. and Harrison, R. J. 1957. Specialization in the skin of the seal. (Phoca vitulina). Am. J. Anat. 100: 81.

Montagna, W. and Parks, H.F. 1948. A Histochemical study of The Glands of the Anal Sac of the Dog. Anat. Rec. 100: 297-315.

Owen, R. "Marsupialia". Encyclopaedia of Anatomy and Physiology ed. R. B. Todd. V.3: 327. 1839-1847.

Pinkus, H. 1939. I. The Wall of the Intraepidermal Part of the Sweat Duct. Journ. Invest. Derm. 2: 175-186.

Perkins, O. C. and Miller, A. M. 1926. Sebaceous Glands in the Human Nipple. Am. J. of Obstret. & Gynecol. II. 789

Richardson, K. C. 1949. Contractile tissues in the mammary gland, with special reference to myoepithelium in the goat. Proc. Royal Soc. of London. V. 136: Ser. B. 1949. p.30

Ring, J. R. and Randall, W. C. 1947. Distribution and histological structure of sweat glands in the albino rat and their response to prolonged nervous stimulation. Anat. Rec. 99: 7-16. (1947).

Rothman, S. 1953. Biochemistry and Physiology of Skin. 154-193. University of Chicago Press. (1953).

Schaffer, J. 1940. Die Hautdrüsen organe der Säugetiere. Urban u.Schwarzenberg, Wien. Berlin.

Schaffer, J. 1924. Über Anal-und Circumanaldrüsen. I. Z. Zoology. 122: 79-96.

*Schiefferdecker, P. 1922. Die Hautdrüsen des Menschen und des Säugetieres ihre Beteuerung sowie die Muscularis sexualis. Zoologica 72: 1-154.

*Shattock, S. G. 1909. Proc. Royal Soc. of Medicine. Vol. 2. Pt. 3. Path. section. p. 208.

Shelley, W. B. and Perry, E. T. 1958. The Human Ear Canal. A. M. A. Arch. Dermat. Vol. 78: 254-263.

Simonetta, B. and Magnoni, A. 1937. Lo sviluppo delle ghiandole ceruminose del condotto auditivo esterno nell uomo. Arch. ital. Anat. e Embriol. 39: 245-261.

Sperling, G. 1935. Die Form der apokrinen Haardrüsen des Menschen. Zeitschr. f. mikroskop. anat. Forsch. 38: 318-329.

Sperling, F. and Koppanyi, T. 1946. Pharmacology of sweat glands in the paw of the cat. Anat. Rec. 96: 1946. Suppl. 54, p. 550.

Stibbe, E. P. 1928. A Comparative Study of the Nictitating Membrane of Birds and Mammals. Journ. of Anat. 62: 159.

* Wendt, E.C., 1887. Inaug-Dissert., Strassburg. Reference from The Anat.of the Eye and Orbit. E. Wolff.Lewis & Co. London. 1948.

Whitnall, S. E. 1921. The Anatomy of the Human Orbit and Accessory Organs. H. Frowde. Hodder & Stoughton.

Winklemann, R. K. 1956. The Epidermal Eccrine Duct. (short report). Journ. Invest. Derm. Vol. 26: 169-171.

Wolff, E. 1948. The Anatomy of the Eye and Orbit. 3rd. ed. H. K. Lewis & Co. 1948.

* Zawisch, 1933. Das Talgdrüsenorgan des Gehörganges von Nagern Insectivoren. Quoted only from a note by another author. Zawisch-Ossenitz, C. v: Z. f. mikr. anat. Forsch. 33: 625. (1933).

Acknowledgements

I wish to thank Professor A. A. Abbie for his advice and helpful criticism during the preparation of this thesis.

To Miss Pilton of the Department of Zoology who provided me with the greater part of the material used, I am deeply grateful.

Mr. P. Kempster was responsible for the preparation of the microscopic sections used and Mr. B. Selge made the photographic illustrations, to both these members of this department, I am much in debt.

STATEMENT CONCERNING MATERIAL USED IN THIS THESIS.

I hereby make the following statement.

"This thesis contains no material previously submitted for a degree in any University either by me or by any other person, except when due reference is made in the text of the thesis".

Department of Anatomy,
University of Adelaide.

4th December 1959.