A HISTOLOGICAL SURVEY OF THE SUDORIFEROUS GLANDS IN INDIGENOUS RODENT FAMILIES.

by

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Submitted in partial fulfilment of the
requirements for the degree of

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ABSTRACT

Skin samples of 26 rodent species representing the nine families indigenous to Southern Africa, were investigated by light microscopy to establish the distribution and structure of the sudoriferous glands. Glandular sites of selected species were studied by TEM and SEM.

Sudoriferous glands occurred only in the palmar and plantar surfaces, and digital pads of all the species, except two. These glands were most abundant in the climbing species of the Muridae, Gliridae, Sciuridae and Petromuridae. The terrestrial Cricetidae, Muridae and Hystricidae had abundant to numerous glands. In the burrowing species of Cricetidae and Pedetidae the sudoriferous glands were few. The semi-amphibious species showed further reduction with Thryonomys swinderianus lacking glands in the feet. The fossorial Bathyergidae totally lacked sudoriferous glands.

Three new sites of sudoriferous glands in rodents were described including the digital ridges, the post-auricular gland in T. swinderianus, and the apocrine glands found in the feet of three species.

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CHAPTER 1

GENERAL INTRODUCTION

Sudoriferous glands, like hair, are a uniquely mammalian characteristic (Stanbury 1972) and are widely distributed over the body skin in many mammalian Orders (Quay 1962; Jenkinson 1970, 1973). It is thus surprising that some zoologists have claimed that - "sweat glands are absent in rodents" (Schmidt-Nielsen 1964, 1972; Rowett 1974; Leake 1975) seeing that the Rodentia is numerically the largest and generically the most diverse of the mammal Orders. Despite this diversity, the differences in the structure of the skin is slight in rodents concluded Sokolov (1982) after having reported on the integument descriptions of over 70 species from 15 Families. Specific skin glands which were mainly specialized sebaceous glands in rodents have been investigated in only a minority of the Rodentia as reviewed by Sokolov (1982), and even fewer comparative studies which included the sudoriferous glands of rodents have been made (Quay 1962, 1965a, 1965b; Kivett, Murie & Steiner 1976). This, together with the fact that most rodents do lack sweat glands in the skin of their bodies (Quay 1962; Jenkinson 1970; Sokolov 1982), has probably contributed to the misconceptions among some authors who report the absence of sudoriferous glands in the Rodentia (Schmidt-Nielsen 1964, 1972; Rowett 1960, 1974; Leake 1975; Van Heerden & Dauth 1987).

The explanations given for their apparent absence vary from - "the hairs in the skin being set too close together" (Rowett 1974), - "in so small an animal (rat) with such a large surface area to volume ratio, makes such a cooling mechanism unnecessary and there are no sweat glands in the skin" (Rowett 1960; 1974) and - "for desert rodents the available water would soon be exhausted if they were to sweat; actually they have no sweat glands" (Schmidt-Nielsen 1972). Even the comparative histologist Leake (1975) concluded that sweat glands are absent in rodents.

However, a survey of the literature revealed ample evidence of sudoriferous glands in rodents with the laboratory species having been the most intensively studied. The presence of sweat

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glands in the soles of the feet in various murids was first reported by Romer (1896 in Quay 1965b) and in other rodents by Schaffer (1940). Rodent sudoriferous glands were similar in structure to the eccrine glands described in man (Montagna & Parakkal 1974) and other animals (Weiner & Hellmann 1960). The most common type described in various rodent species are eccrine sweat glands found in the foot pads. The histology and some physiological aspects of these eccrine glands have been well described in the white rat Rattus norvegicus (Ring & Randall 1947; Wechsler & Fisher 1968), and reported in the white mouse Mus musculus (Ortmann 1956) and the guinea pig Cavia porcellus (Rep 1962). Some cytochemistry work has also been done on these laboratory species including the hamster Cricetus cricetus (Jenkinson 1970).

The histological descriptions of these glands in wild rodents are superficial, with the main emphasis being on where they are found on the animals. They have been reported in the naked foot pads of various wild species (Romer 1896 in Quay 1965b; Schaffer 1940; Sokolov 1962; Quay 1962, 1965; Skurat 1972 in Sokolov 1982; Griffiths & Kendall 1980a; Sokolov 1982; Skurat 1984). Apocrine glands are known to occur in the oral angle, mid-dorsal and anal glands but only in a limited number of species (Quay 1962). Histological descriptions of these specialized apocrine glands have been made in a number of the ground squirrel species (Hatt 1926; Sleggs 1926; Quay 1965b; Kivett et al. 1976; Kivett 1978) while comparative surveys of the oral angle glands of rodents showed sudoriferous glands to be present only in certain Families (Quay 1962; Quay 1965a; Skurat 1972 in Sokolov 1972). The only African species included in these studies was the North African ground squirrel Atlantoxerus getulus where small tubular glands were reported in the hind sole (Skurat 1972 in Sokolov 1982) while Van Heerden & Dauth (1987) found no sweat glands in the indigenous Xerus inauris.

Because the sudoriferous glands of man play such a functional role in thermoregulation, the ultrastucture of sweat glands has been intensively studied (Montagna, Chase & Lobitz 1953; Lee 1960; Munger 1961; Montagna 1962). These findings are well reviewed (Montagna 1962; Montagna & Parakkal 1974) where the

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ultrastructure of the secretory cells in the human eccrine sweat glands revealed two cell types - mucoid or 'dark cells' and 'clear cells'. The dark cells have numerous large apical secretory vacuoles containing acid mucopolysaccharides, apical microvilli and a high ribonucleic acid content. Clear cells lack identifiable secretory granuoles or vacuoles,and are characterized by the prescence of intercellular canaliculi and extensive plications of the plasma membrane (Griffiths & Kendall 1980a). In the rodents, the sudoriferous glands of laboratory rats have been studied primarily as experimental models for "further progress in perspiration physiology, because the rat is more suitable for various experimental procedures than man or other large animals" (Matsuzawa & Kurosumi 1963). These workers found that young rats had two types of secretory cells whereas adult rats had only one type, which shared characteristics of both human secretory cell types. Both Wechler & Fisher (1968) and Munger & Brusilow (1971) studied the ultrastructural changes produced during induced sweating in the plantar sweat glands of the rat. Wechler & Fisher (1968) concluded that - "despite certain differences....the eccrine apparatus of the rat may represent a suitable model for the study of certain parameters of the sweating phenomenon". Munger & Brusilow (1971) again confirming only one atypical type of secretory cell concluded that - "the sweat glands of the rat foot pad are unique as compared with the other cutaneous glands both in their cytologic appearance and in the chemical composition of the sweat they elaborate". Similarly, Quick, Kennedy & Yoon (1984) found that the mouse provides a convenient model for the study of sweat glands and their innervation by the autonomic nervous system, with the practical application that this model system of the mouse would lead to a better understanding of how human sweat glands are affected by diabetic neuropathology.

Electron microscopy studies on the sudoriferous glands of wild rodents are limited to the plantar sweat glands of the bank vole Clethrionomys glareolus (Griffiths & Kendall 1980a) and the apocrine sweat glands in the oral angle of same animals (Griffiths & Kendall 1980b). Among the indigenous rodents the ultrastructure of the sweat glands of Aethomys namaquensis was

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described as part of the present study (Green & Soley 1981). Scanning electron microscopy had been done on the sweat duct openings on various parts of the human body (Johnson, Dawber & Shuster 1970), and the plantar sweat gland openings of the Bank vole Clethrionomys glareolus (Griffiths & Kendall 1980a) while variations in the sweat duct openings on the feet of Aethomys namaquensis, Lemniscomys giselda, and Rhabdomys pumilio were compared by (Green & Soley 1979).

The phylogeny of the sudoriferous glands is poorly understood. Quay (1972) surveyed the various integumentary glands in the vertebrate classes and then attempted to trace the phylogeny of the various glands through from the cyclostomes to the mammals, who have only two main types of skin glands; the sebaceous glands and the sudoriferous glands. He suggested that the holocrine secretory cells of the reptiles, and the sebaceous and the primitive sudoriferous glands of the mammals shared close cytogenetic relations with the lipoidal secretory alveoli of some ancestral reptilian stock. He proposed the generalization that the wider distribution of apocrine sudoriferous glands over the hairy body surface is a primitive mammalian characteristic, and that regional localization and loss are secondary or more advanced (Quay 1965a). From his comparative survey of the sebaceous and sudoriferous glands in rodents, Quay (1965a) concluded that the overall evolutionary pattern of the sudoriferous glands in rodents is one of reduction and loss.

Montagna & Parakkal (1974) however, argued that the phylogenetic history of any organ system cannot be reconstructed by a study of its extant forms. Because eccrine glands in nonhuman primates appear to have evolved gradually over the general body surface and have 'replaced' the apocrine glands normally associated with the hairy skin, one cannot thereby assume that apocrine glands are primitive (Montagna & Parakkal 1974), a view still generally held (Weiner & Hellmann 1960). Furthermore, it is incorrect to assume that the glands in the skin of 'primitive mammals' such as the duck-billed platypus, Ornithorhynchus paradoxus, are necessarily primitive. Poulton 1894 in Montagna & Ellis (1960) stated - "the existence of such typical structures in the most primitive mammal indicates that sweat glands are among the most

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ancestral features of the class." However, the skin of Ornithorhynchus is far from primitve, containing both apocrine and eccrine sweat glands which are highly specialised (Montagna & Ellis 1960). Similarly, systematic studies of the skin of primates have shown that the most primitive primate, the tree shrew Tupaia glis, had eccrine glands in its hairy skin (Montagna, Yun, Silver & Quevedo 1962), a characteristic shared only with the higher primates, the Anthropoidea, while the Cebidae from Central America had only apocrine glands in their hairy skin (Montagna & Parakkal 1974). They concluded that the two types of glands are separate organs with different functions and that both the eccrine and apocrine glands are equally highly specialized and neither is more primitve than the other.

The historical description of the tubular exocrine glands in mammalian skin has been reviewed by Weiner & Hellmann (1960) who accredit the earliest descriptions of the small ('eccrine') glands to Purkinje (1833) and the large ('apocrine') glands to Krause (1844). They also accredit the earliest comparative studies of the skin glands of the human and various domestic animals including the dog, horse, pig and cattle to Gurlt (1835) and Leydig (1859). Romer (1896 in Quay 1965b) first confirmed the presence of sweat glands in the foot pads of the rat.

The still accepted designation of subdividing the merocrine sweat glands into two categories; 'eccrine' and 'apocrine' was done on a histological basis by Schiefferdecker (1917, 1922 in Jenkinson 1967) who distinguished them by "their development", "their position" and "their morphological process of secretion". The following is a summary of the features which characterize these two kinds of glands (Weiner & Hellmann 1960; Jenkinson 1967, 1973; Montagna & Parakkal 1974) and is graphically illustrated in Fig.1:

(i) Embryological development - the anlagen of apocrine glands develop as solid buds from the epithelium of the hair follicles above the sebaceous glands while the anlagen of the eccrine glands develop as cellular buds directly from the basal layer of the epidermis. The buds of both of these glands then grow down

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FIG. 1. A SCHEMATIC DIAGRAM OF THE HUMAN SUDORIFEROUS GLANDS ILLUSTRATING THE DIFFERENCES BETWEEN THE APOCRINE AND ECCRINE GLANDS.

Legend: E - epidermis

c - clear cell

d - dark cell

hf - hair follicle

lb - luminal border

lp - luminal protuberances

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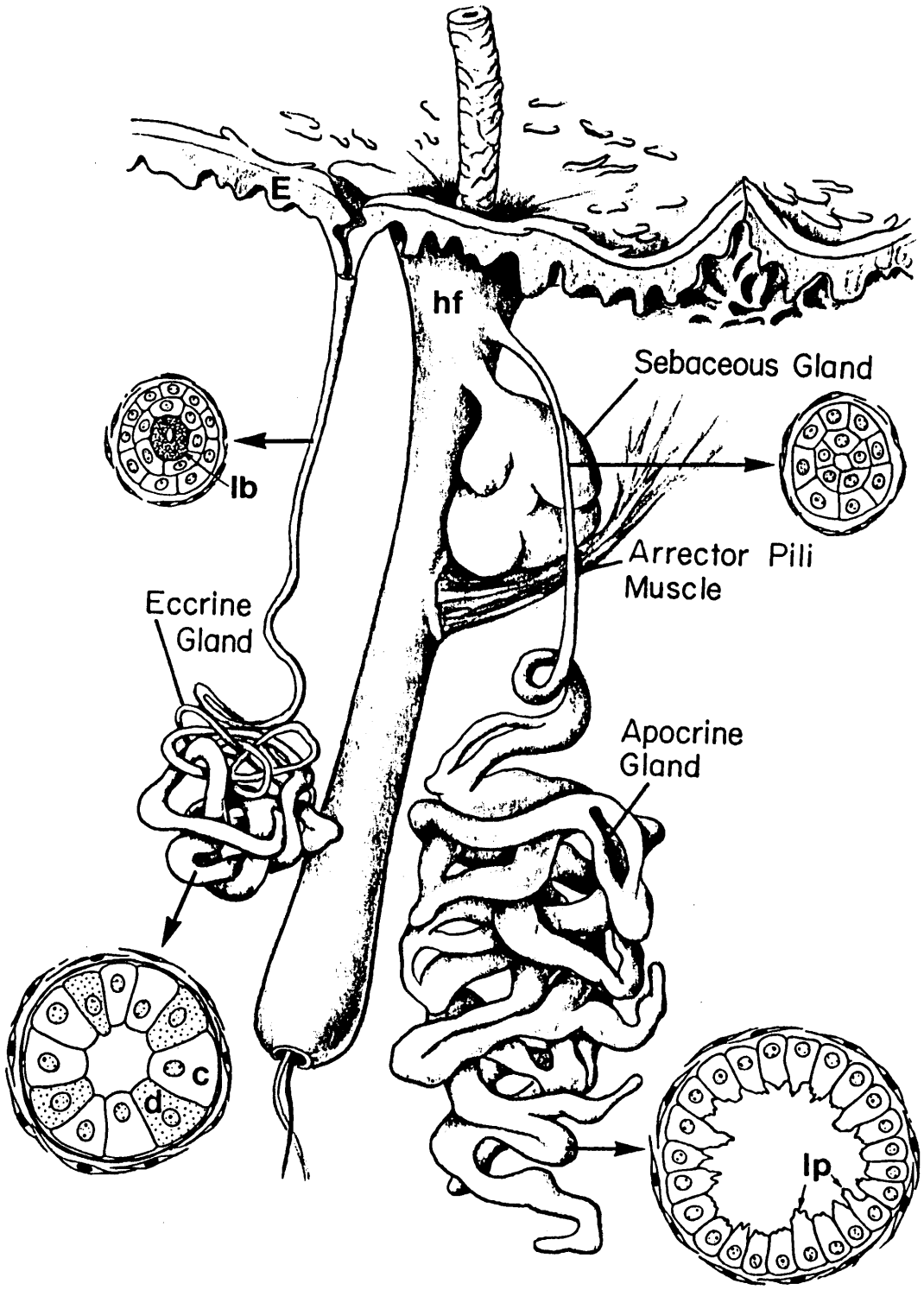

(modified from Weiner & Hellman 1960; Montagna & Parakkal 1974)

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deep into the dermis where they begin to coil at their bases to form what later becomes the secretory tubules.

(ii) Position in relation to hair follicles - the apocrine glands are characteristically associated with hair follicles into which their excretory ducts open. The eccrine glands are not associated with hair follicles and thus often occur in the hairless areas of the skin onto which their excretory ducts open directly, after spiralling through the epidermis (Fig.1). This characteristic has led Jenkinson (1973) to alternatively refer to them as 'epitrichial' and 'atrichial' glands.

(iii) Secretory tubules - the tubules of the apocrine glands vary from simple sac-like structures to loosely coiled tubules which in some species may have diverticula or saccular pouches. The lumens of these tubules are distinctly wide. The eccrine glands have tightly coiled single tubules with narrow lumens (Fig.1).

(iv) Secretory epithelium - single layers of secretory cells line the secretory tubules of the apocrine glands. These cells are only of one type, although they vary in shape from tall columnar to flat cuboidal, depending on their phase of secretion. The actively secreting cells in the 'necrobiotic' stage have 'luminal protuberances which are ruptured or torn off and discharged into the lumen with their protoplasm, globules, granules and even nuclei' (Fig.1). This is followed by a simple fluid secretion or inactive stage during which the flattened cells recommence their regrowth. Jenkins (1967), however, strongly questioned this apocrine secretory process claiming that there was little physiological evidence for a necrobiotic secretory cycle in these glands, and that the 'luminal protuberances' of the secretory cells were artefacts occurring during fixation and dehydration of the tissue.

The secretory epithelium of the eccrine tubules is also a single layer of cuboidal cells but consists of two types of secretory cells, the small mucoid or 'dark cells' and large 'clear cells' (Fig.1). The dark cells have numerous large apical secretory vacuoles containing acid mucopolysaccharides, apical microvilli and a high ribonucleic acid content. Clear cells lack

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identifiable secretory granuoles or vacuoles, and are characterized by the presence of intercellular canaliculi and extensive plications of the plasma membranes.

(v) Excretory ducts - the ducts of both these glands are easily distinguished from the secretory tubules as they consist of double layers of flattened cuboidal epithelial cells surrounding ductal lumens which are far narrower than the lumens of their secretory tubules. The ducts of the apocrine glands begin outside the secretory coils and run straight through the dermis to open into the hair follicles above the sebaceous gland duct opening. The ducts of the eccrine glands usually wind through the dermis before spiralling through the epidermis and its stratum corneum to open onto the skin surface. In cross section the eccrine duct shows a characteristic luminal border which is lacking in the apocrine duct (Fig.1).

The functions of sudoriferous glands have traditionally been accepted as 'thermoregulatory' for the eccrine glands particularly in man, while the apocrine glands being referred to as 'scent glands' (Weiner & Hellmann 1960). However, eccrine glands in the palmar and plantar pads of man and many mammals have many additional functions including that sweating improves the pliability of the upper epidermis and stratum corneum through hydration (Adams 1966; Adams & Hunter 1969). This in turn, increases the resistance of the skin to abrasion and cutting; improves tactile sensitivity; and improves the friction coefficient between the pad surface and the substrate, as has been demonstrated in running and climbing animals such as the cat Felis catus, dog Canis familiaris, rock hyrax Heterohyrax brucei, tenrec Tenrec ecaudatus and laboratory rats (Adams 1966; Adelman, Taylor & Heglund 1975). The effect of the increased sweating when the animals began to run on an angled treadmill was measured, and compared to their performances when sweating was chemically inhibited. The importance of these glands in the foot surfaces of the rat was to prevent these surfaces from drying out, thus maintaining their flexibility (Romer 1896 in Ring & Randall 1947). Similar functions have been suggested for the abundant eccrine glands in the palmar and plantar surfaces of man and the aboreal primates (Weiner & Hellmann 1960;

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Montagna & Parakkal 1974) as well as the climbing rodents (Skurat 1984), where an increased grip and tactile sensitivity would be a great advantage. The function of these plantar glands to produce a scent trail was suggested in the mouse (Ortmann 1956) while Hanney (1975) showed experimentally that the American deermouse Peromyscus maniculatus followed its own scent trail through an adjustable maze. Ropartz (1977) demostrated the 'plantar factor' produced in the sudoriferous secretion on the paws of mice was important in distinguishing between a group or single foreign males.

The functions of apocrine glands, which are the most common sudoriferous glands in furred mammals, also include thermoregulation in the Equidae and some Bovidae (Weiner & Hellmann 1960; Jenkinson 1973); the excretion of waste products in the sweat; the protection of the skin with sweat being an antibacterial secretion and aiding the flow of sebum across the skin surface (Jenkinson 1973). They are further an important source of olfactory communication influencing social and reproductive behaviour (Quay 1972; Ropartz 1977; Sokolov 1982; Brown & Macdonald 1985). It was suggested that the few large apocrine glands occurring amongst the eccrine glands in the foot pads of some canid species are odiferous for leaving a more permanent scent trail (Sands, Coppinger & Phillips 1977).

These functions, together with the ecological behaviour of each species, would form the basis of the functional interpretation of the distribution and abundance of the sudoriferous glands in the rodents investigated in this study.

The main aims of this study include:

(i) to establish the presence of sudoriferous glands in the skin of various wild rodents and so refute those who still hold to the view that 'sweat glands are absent in rodents' (Schmidt-Nielsen 1964, 1972; Rowett 1974; Leake 1975)

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(ii) to investigate the microstructure and ultrastructure of these glands, and compare them with the apocrine and eccrine glands of other species, and particularly in the light of the uniqueness of the sudoriferous glands described in laboratory rodents (Matsuzawa & Kurosumi 1963; Wechler & Fisher 1968; Munger & Brusilow 1971), compared to those in other mammals.

(iii) to establish and compare the distribution patterns of sudoriferous glands in the indigenous rodent families of Southern Africa. Comparative studies on the North American rodents (Quay 1962; Quay 1965a, 1965b; Kivett, et al 1976) and Eurasian rodents (Sokolov 1982; Skurat 1984) have shown that these glands are limited to very specific sites, and may be of taxonomic significance in many families.

(iv) to give a possible interpretation of the functions of these sudoriferous glands, based on the ecological behaviour of the rodents.

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CHAPTER 2

MATERIALS AND METHODS.

The specimens used in this study were live trapped in various habitats of Southern Africa by many individuals and organisations listed in the acknowledgements. A number of species were also obtained as live animals from the South African Medical Research Institute's laboratories. Some of the donated specimens had been preserved in various fixatives and others were even frozen.

These species, listed in Table 1., included specimens of both sexes and various ages from foetal to adult. In the species with a wide distribution, such as Rhabdomys pumilio, specimens were collected from various habitats to show the possible effect of environmental adaptation. Four exotic laboratory species (rat, mouse, guinea pig, and hamster) were also included in the study as reference material to the literature (Ring & Randall 1947; Rep 1962; Jenkinson 1970).

LIGHT MICROSCOPY PREPARATION

A total of 49 specimens of the 26 indigenous species listed in Table 1 were examined. In the laboratory each live animal was euthanased using ether or chloroform. Biopsy plugs were taken from the various areas of the skin as described by Quay (1963, 1965a) and Jenkinson (1970) as shown in Figure 2. These included the following sites: the naked tip of the nose, the oral lips and angle, and the skin around the base of the pinnae. From the body the mid-dorsal, mid-lateral and mid-ventral skin, as well as samples from the axilla, inguinal and perianal regions were taken. From the appendages the digital pads, the palmar and plantar soles, as well as samples half way along the length of the tail were collected. The biopsy plugs (7x7mm) removed from each of these sites was fixed in 10% Baker's formalin (Baker 1958) for a minimum of 24 h. With the small rodents the whole fore and hind feet were removed above the carpal or tarsal joints, and the eviscerated bodies were stored for further reference in 10% formalin. The small feet and tail samples were then decalcified in a formic acid-sodium citrate mixture (Davenport 1969) over a period of

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TABLE 1. CHECKLIST OF THE RODENT SPECIES STUDIED (after De Graaff 1981)

1. Family SCIURIDAE	Xerus inauris (Zimmerman 1780). Cape Ground Squirrel
	Paraxerus cepapi (A. Smith 1836). Bush Squirrel
2. Family PEDETIDAE	Pedetes capensis (Forster 1778). Springhaas
3. Family HYSTRICIDAE	Hystrix africaeaustralis (Peters 1852). Cape Porcupine
4. Family THRYONOMYIDAE	Thryonomys swinderianus (Temminck 1827) Greater Canerat
5. Family PETROMURIDAE	Petromus typicus (A.Smith 1831) Dassie Rat
6. Family BATHYERGIDAE	Cryptomys hottentotus (Lesson 1826) Common Molerat
7. Family CRICETIDAE	Mystromys albicaudatus (A.Smith 1834) White-tailed Rat
	Gerbillurus paeba (A.Smith 1836) Hairy-footed gerbil
	Tatera leucogaster (Peters 1852) Bushveld Gerbil
	Tatera brantsi (A.Smith 1836) Highveld Gerbil
	Desmodillus auricularis (A.Smith 1834) Short-tailed Gerbil
	Saccostomus campestris (Peters 1846) Pouched Mouse
	Otomys irroratus (Brants 1827) Vlei Rat
	Otomys angoniensis (Wroughton 1906) Angoni Vleirat
8. Family MURIDAE	Dasymys incomtus (Sundevall 1847) Water Rat
	Aethomys chrysophilus (De Winton 1897) Red Veld Rat
	Aethomys namaquensis (A.Smith 1834) Namaqua Rock Rat
	Thallomys paedulcus (Sundevall 1846) Tree Rat
	Lemniscomys griselda (Thomas 1904) Single-striped Mouse
	Rhabdomys pumilio (Sparrman 1784) Striped Mouse
	Praomys natalensis (A.Smith 1834) Multimammate Mouse
	Mus minutoides (A.Smith 1834) Pygmy Mouse
	Acomys spinosissimus (Peters 1852) Spiny Mouse
9. Family GLIRIDAE	Graphiurus ocularis (A.Smith 1829) Smith's Dormouse
	Graphiurus murinus (Desmarest 1822) Woodland Dormouse

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Fig. 2. SAMPLE SITES ON THE RODENTS.

Legend: ax - axilla
ff - front foot (incl. digital and palmar pads)
hf - hind foot (incl. digital and plantar pads)
in - inguinal
md - mid-dorsal
ml - mid-lateral
mv - mid-ventral
np - nasal planum
ol - oral angle and lips
pa - peri-anal
pr - peri-auricular
t - tail

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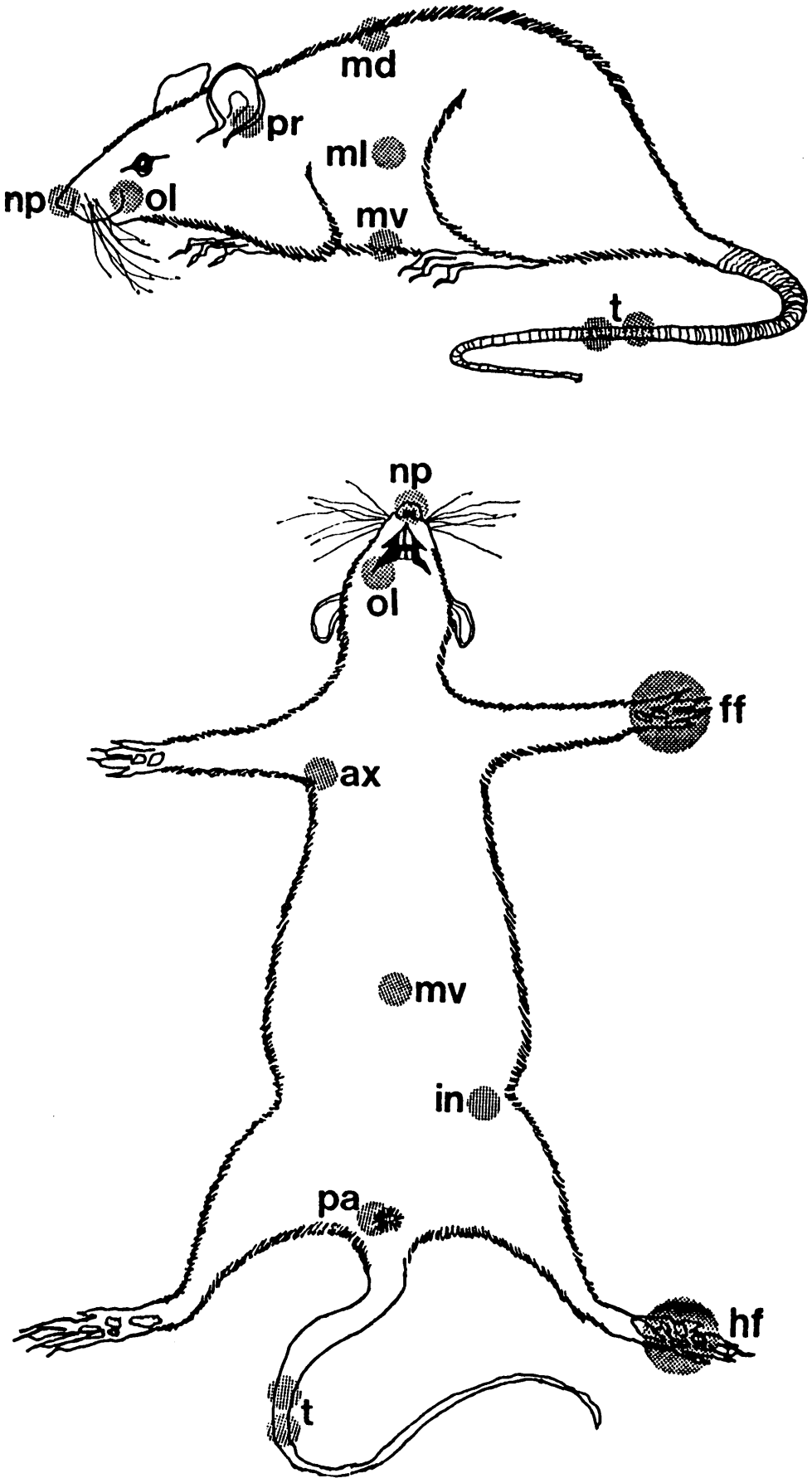

Fig. 2. SAMPLE SITES ON THE RODENTS.

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weeks. Alcoholic nitric acid was also used for the larger feet but this caused destruction of the cytological detail. After decalcification the feet were further dissected longitudinally into two halves and then each half was cut transversely into three parts; namely the distal foot pads and attached digits, the central foot pads, and the proximal foot pads including the sole and heel (Fig.3). This resulted in six sample areas for each foot.

All samples (feet and skin) were washed thoroughly for 4 h in running water before being dehydrated through a series of graded ethyl alcohols, and infiltrated and embedded in Histosec paraffin wax. The tissue blocks were sectioned on a Leitz rotary microtome at 6-10µm as well as 20-25µm thick sections. The body skin was sectioned longitudinally with the body axis, while the tail was sectioned both longitudinally and transversely. Each of the six sample areas per foot was sectioned either longitudinally or transversely. Selected sections were floated out on warm water, and picked up onto slides thinly coated with Mayer's egg albumen. The slides were dried overnight in an oven at 35-40°C. Sections of each tissue block were routinely stained with either Mayer's or Ehrlich's haematoxylin and counter stained with eosin. The sections were then viewed under binocular Nikon or Reichert microscopes. Selected sections where sweat glands occured were then stained with the following stains: toluidine blue to differentiate between possible light and dark secretory cells (Montagna & Parakkal 1974), periodic acid Schiff (PAS) with haematoxylin counter stain for mucopolysaccharides (Wechsler & Fisher 1968) and Verhoeff's elastin stain to differentiate the elastic fibres from the collagen around the glands. The stains were made up according to Humason (1967) and Gurr (1973).

In order to give a comparative indication of the abundance of sudoriferous glands on each site, the following three categories were used:

Abundant glands (+++) - the number of glands was so great that their secretory tubules practically filled the dermis, and lay so compactly spiralled together that the tubules of the glands were not separated enough to be individually identified (Figs.4a & 4b).

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Fig. 3. SEM micrograph of the ventral surface of the front foot of Aethomys namaquensis indicating the relevant foot morphology and how the feet samples were sectioned.

(Bar = 100µm)

Legend: DR - digital ridge
FP - foot pad
TP - distal toe pad
L---L - longitudinal sections
T---T - transverse sections

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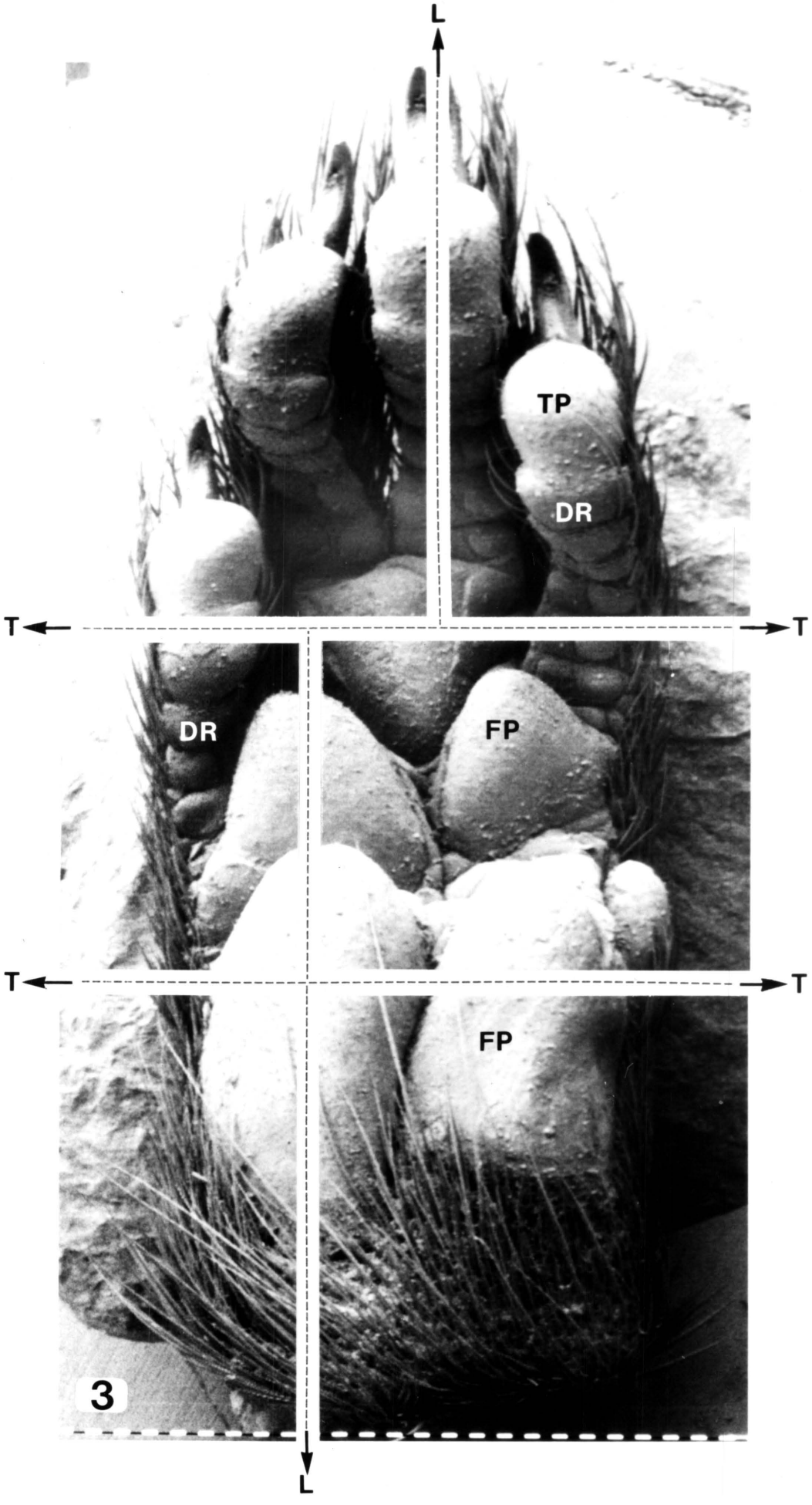

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EXAMPLES OF CATEGORIES OF SUDORIFEROUS GLANDS ABUNDANCE

Fig. 4a. Abundant glands in the L.S. of the hind foot pad of Graphiurus murinus. The secretory tubules (s) practically fill the dermis (D). The abundance of the glands is further reflected by the number of ducts (d) leading up to the many interpapillary pegs of the epidermis (E).

(Bar = 300µm)

Fig. 4b. Abundant glands in the T.S. of the hind foot pad of Acomys spinosissimus. The secretory tubules (s) are so compactly spiralled together in lobules that the tubules of individual glands cannot be easily identified. The number of ducts (d) in T.S. gives an indication of the abundance of the glands. The epidermis (E) is relatively thick compared to the dermis which is almost filled with glands.

(Bar = 50µm)

Fig. 5a. Numerous glands in the L.S. of the hind foot pad of Lemniscomys griselda. The secretory tubules (s) are scattered irregularly deep in the dermis (D) with long ducts (d) running up to the surface of the pad.

(Bar = 200µm)

Fig. 5b. Numerous glands in the T.S. of the hind foot toe of Mystromys albicaudatus showing the digital bone (b) and the claw (cl). The secretory tubules (s) deep in the dermis (D) of the toe pad, are separated from each other by connective tissue septa.

(Bar = 200µm)

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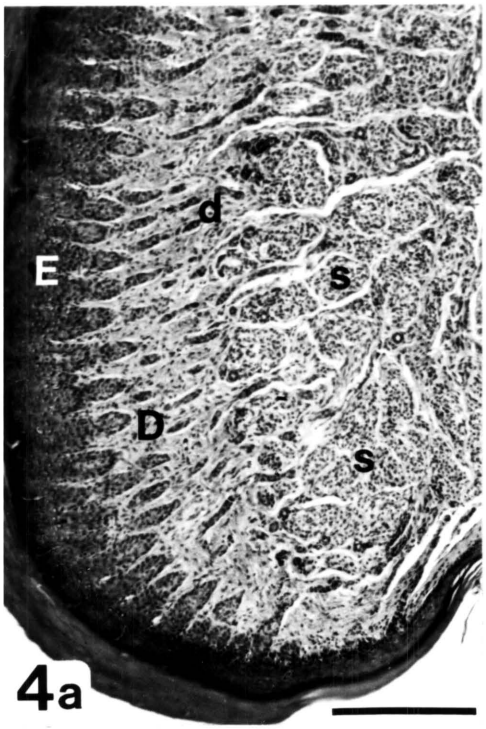
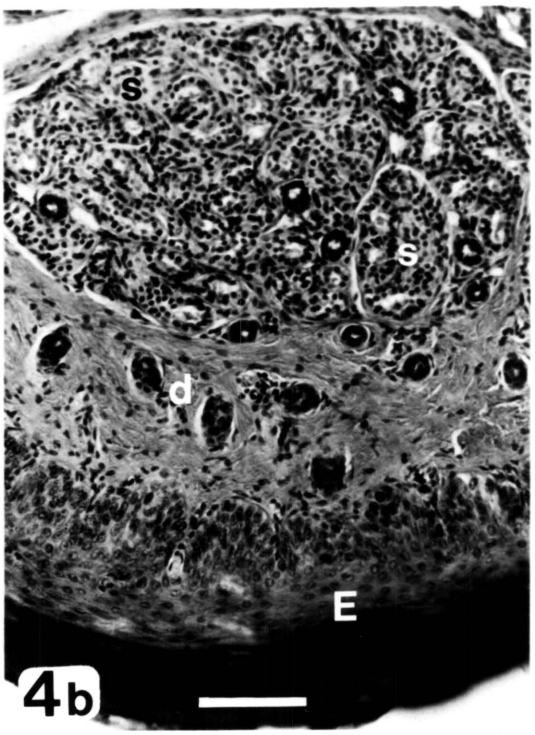
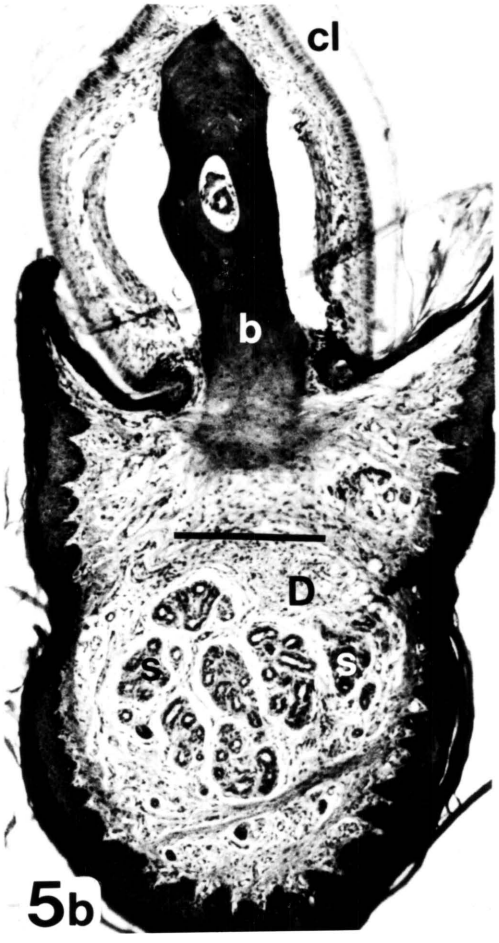


4a



4b

5a



5b

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Numerous glands (++) - numerous glands were scattered throughout the dermis but the secretory tubules were clearly separated by connective tissue septa (Fig.5a & 5b). As a point of reference the eccrine glands in the finger tip (Wheater, Burkitt & Daniels 1979) and sole skin of man (Freeman 1982), and the toe pad of the dog (Adam, Calhoun, Smith & Stinson 1970) would fall into this category.

Single glands (+) - the number of glands limited to one or occasionally two glands occurring in the dermis of a particular site. (see Chapter 5, Fig.59 & 67-69).

ELECTRON MICROSCOPY PREPARATION

Live specimens of Aethomys namaquensis, Lemniscomys griselda and Praomys natalensis of both sexes, which had been trapped in the same area, were anaethetized and sacrificed in the laboratory using chloroform.

Transmission electron microscopy (TEM)

Samples of skin were removed from the digital, palmar and plantar pads of the feet and divided into small blocks (2x2mm). These specimens were immediately fixed in 4% glutaraldehyde in Millonig's phosphate buffer (pH 7,3) (Millonig 1961) at 4°C for 24 h. They were then thoroughly washed in Millonig's phosphate buffer for 10 min, and post-fixed for one hour in 2% osmium tetroxide in the same buffer. The excess fixative was removed by a further two washes in the same buffer of 10 min each.The tissue blocks were dehydrated through a graded series of ethanol (25%, 50%, 75%, 96% and twice in absolute alcohol), cleared in propylene oxide overnight and embedded in Epon 812 epoxy resin. The blocks were polymerised for 48 h at 60°C.

The Epon blocks were sectioned on a Reichert OM U3 ultramicrotome. For correct orientation, semi-thin sections of 2 µm were first cut and stained with toluidine blue. Thereafter ultra-thin sections were cut from selected areas of the Epon blocks using glass and diamond knives, and mounted on 300 mesh copper grids. These sections were then treated for one hour with a saturated aqueous solution of uranyl acetate (Watson 1958),

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followed by 0,2% lead citrate in 0,1N NaOH (Reynolds 1963) for 4 min. These sections were viewed in a Philips 301 transmission electron microscope operated at 80 kV.

Scanning electron microscopy (SEM)

The remaining fore and hind feet of the animals used for the TEM specimens were amputated above the carpal and tarsal joints. The feet were immediately fixed in the same fixative and buffer described in the TEM preparation except that the fixation time was extended to 48 h due to the large size of the samples. This also necessitated the extension of the washing time in the buffer to 30 min and post-fixation in 2% osmium tetroxide in the same buffer for one hour before being washed twice for 30 min in the buffer to remove the excess fixative.

The feet were dehydrated through a graded series of ethanol but 40 to 60 min was required for each step due to the large size of the specimens. Once dehydrated the ethanol was gradually replaced by amylacetate through a graded series of increasing concentrations ethanol-amylacetate mixture up to pure amylacetate. Specimens were then critical point dried in a Bomar C.P. drying apparatus using liquid CO_2 before being mounted on metal stubs. The mounted specimens were sputter coated with a fine layer of gold and viewed in a Philips 500 SEM.

The feet of the following species which had been fixed in 10% formalin were also removed: Petromus typicus, Thallomys paedulcus, Rhabdomys pumilio, Acomys spinosissimus and Graphiurus murinus. These were washed thoroughly in running water before being dehydrated through a graded series of acetone and water up to two final baths of acetone. These acetone dried specimens were then similarly critical point dried before being mounted on metal stubs and sputter coated with gold for SEM studies.

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CHAPTER 3.

THE MICROSTRUCTURE OF THE RODENT SUDORIFEROUS GLANDS

INTRODUCTION

Rodent sudoriferous glands are similar in structure to the eccrine glands described in man (Montagna & Parakkal 1974) and other animals (Weiner & Hellmann 1960). The most common type described in various rodent species are eccrine sweat glands found in the foot pads. The histology and some physiological aspects of these eccrine glands have been well described in the white rat (Ring & Randall 1947; Wechsler & Fisher 1968), and reported in the white mouse (Ortmann 1956) and the guinea pig (Rep 1962). Some cytochemistry work has also been done on these laboratory species including the hamster (Jenkinson 1970).

The histological descriptions of these glands in wild rodents are superficial, with the main emphasis being on where they are found on the animals. They have been reported in the naked foot pads of various wild species (Romer 1896 *in* Quay 1965b, Schaffer 1940; Quay 1962; Sokolov 1962; Quay 1965b; Skurat 1972 *in* Sokolov 1982, Griffiths & Kendall 1980a; Sokolov 1982, Skurat 1984). Apocrine glands are known to occur in the oral angle, mid-dorsal and anal glands, and only of a few species (Quay 1962; 1965b). Histological descriptions of these specialized apocrine glands have been made in a number of the ground squirrel species (Hatt 1926; Sleggs 1926; Quay 1965b; Kivett *et al*. 1976; Kivett 1978) while comparative surveys of the oral angle glands of rodents showed sudoriferous glands to be present only in certain Families (Quay 1962; Quay 1965a; Skurat 1972 *in* Sokolov 1982). The only African species included in these studies was the North African ground squirrel *Atlantoxerus getulus* where small tubular glands were reported in the hind sole (Skurat 1972 *in* Sokolov 1982) while Van Heerden & Dauth (1987) found no sweat glands in the indigenous *Xerus inauris*.

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RESULTS

The photomicrograph of a longitudinal section through the front foot pad of Praomys natalensis shows the typical structure of the sudoriferous glands in rodents (Fig.6). Each gland consists of a simple tubule which extends as an excretory duct from the epidermis down to the tightly coiled secretory segment in the dermis. Each foot pad may be so filled with these glands that the many coiled secretory tubules are separated by only thin connective tissue septa (Fig.6).

THE SECRETORY SEGMENT

The secretory segments of the rodent sweat gland were tightly coiled tubules which lay, surrounded by adipose and loose fibrous tissue, either in the dermis or, more commonly, in the hypodermis (Fig.7). Each glandular segment was surrounded with bundles of collagenous and elastic fibres which held the tubules together. These fibres blended into the basement membrane on the one side and into the loose, adipose connective tissue on the other (Fig.8). Where many glands were present together as in the foot pads, trabeculae of denser connective tissue formed loose septa around the glands separating them into distinct glandular lobuli (Fig.7). Arterioles were abundantly present in the connective tissue surrounding the glands of certain species, but were relatively sparse in other species. Unmyelinated nerve fibres ramified through the connective tissue surrounding the secretory tubules just outside the basement membrane.

The secretory tubules of these glands were lined by one layer of columnar or pyramidal cells which rested on a prominent basement membrane (Fig.8). These secretory cells of the rodent glands were of one type only, which contained a spherical or ellipsoid nucleus closer to the luminal border than to the base of the cell (Fig.9). The cytoplasm was basophilic and finely granular but no secretory vacuoles could be identified. Faint acidophilic striations were seen in the basal cytoplasm in some species (Fig.9). The luminal edge of these cells often showed a distinct hyalin cuticular border (Fig.9). Squeezed between the secretory cells and the basement membrane were the prominent myoepithelial

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Fig. 6. L.S. through a front foot pad of Praomys natalensis showing the typical arrangement and structure of the sudoriferous glands. Each gland consists of a tightly coiled secretory tubule (s) enclosed in a connective tissue septum (S) to form a secretory lobule. The duct (d) extends almost straight through the dermis (D) to enter the funnel-shaped papillary peg (f) before spiralling (sp) through the epidermis (E) and stratum corneum (Sc) on to the friction surface of the pad. These secretory tubules (s) and their ducts in T.S. (d1) fill much of the dermis (D), extending down to the hypodermis where the adipose tissue (a) and blood vessels (bv) were frequently found.

(Bar = 100µm)

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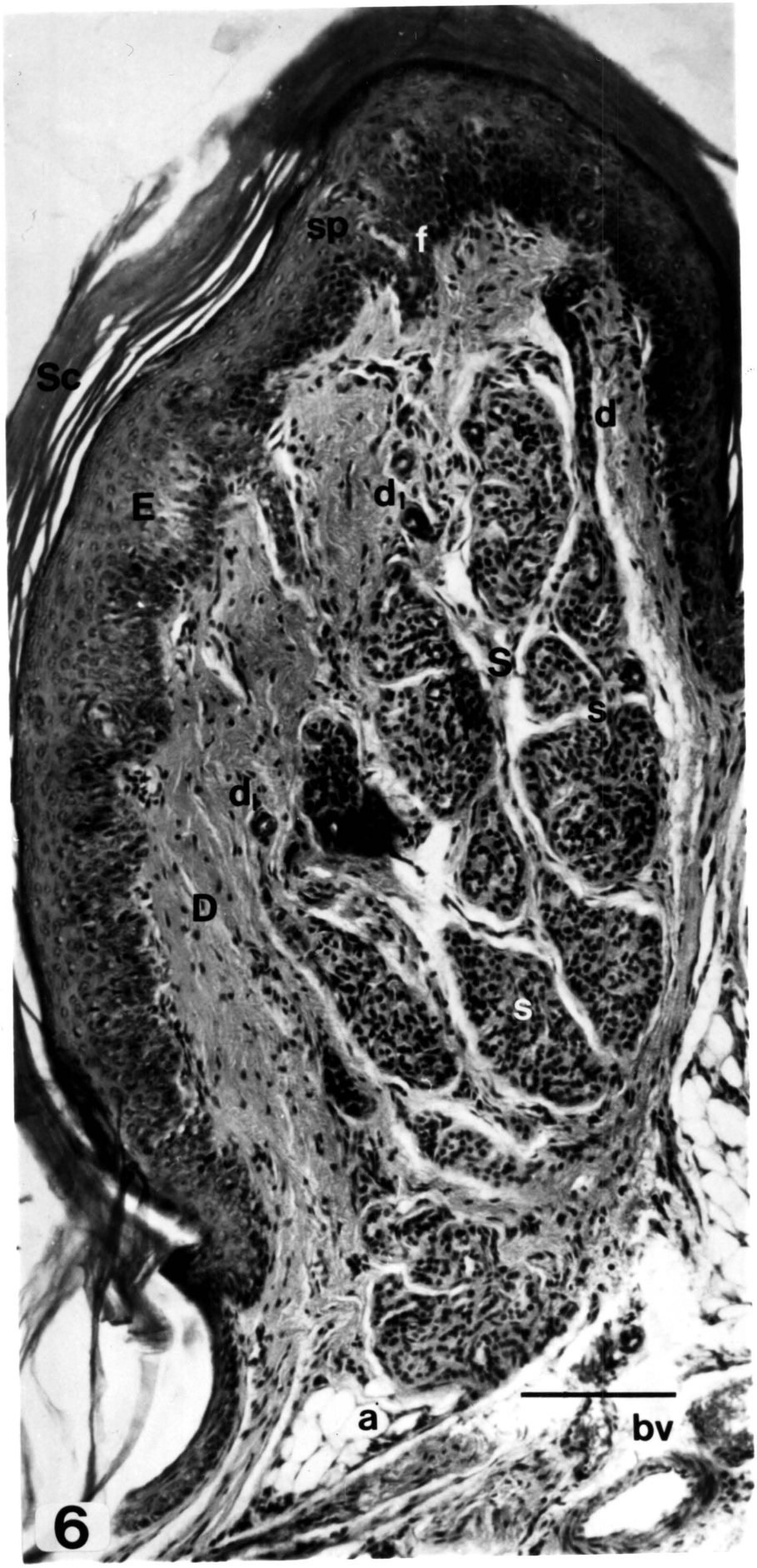

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Fig. 7. L.S. through the hind foot pad of Hystrix africaeaustralis showing the typical arrangement of sudoriferous glands deep in the dermis and hypodermis. The numerous secretory tubules (s) are interspersed by adipose tissue (a) and surrounded by dense connective tissue septa (S) which separate the groups of glands into distinct glandular lobuli. The ducts enter the funnel-shaped papillary pegs (f) which extend deep into the dermis (D) from the thick epidermis (E) through which the ducts spiral to the surface.

(Bar = 0,5mm)

Fig. 8. A high power view of the secretory tubules of the eccrine glands of Hystrix africaeaustralis. The cuboidal secretory cells are only of one type and show a finely granular cytoplasm (c) and large round nuclei. The luminal edge of these cells is lined by a cuticular border (cb). Squeezed between the secretory cells which rest on the basement membrane (bm) are the triangular myoepithelial cells (My). Loose connective tissue supporting the tubules is attached to the basement membranes.

(Bar = 20µm)

Fig. 9. A high power view of the secretory tubules of the eccrine glands of Otomys irroratus. The cuboidal secretory cells show striations in the cytoplasm (c) and large apically placed nuclei. T.S. of the duct (di) shows the double layer of flattened cells surrounding the small ductal lumen compared to the more open lumens of the secretory tubules.

(Bar = 50µm)

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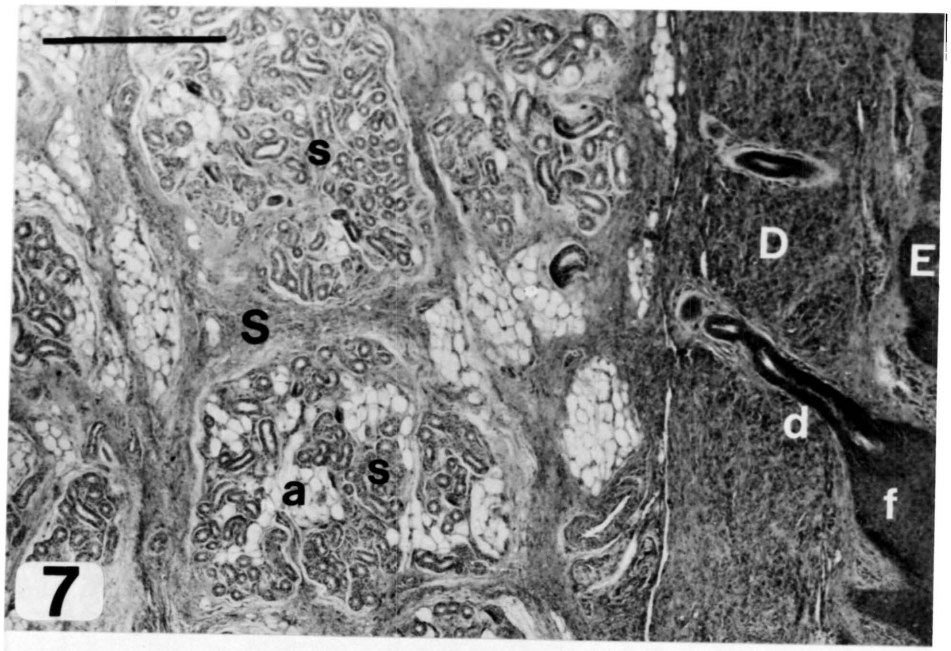

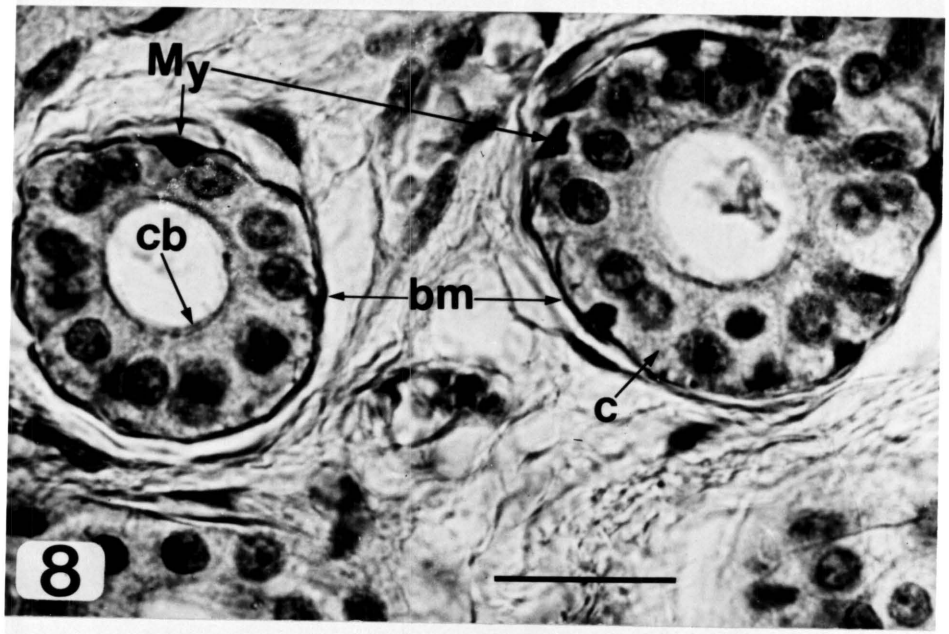

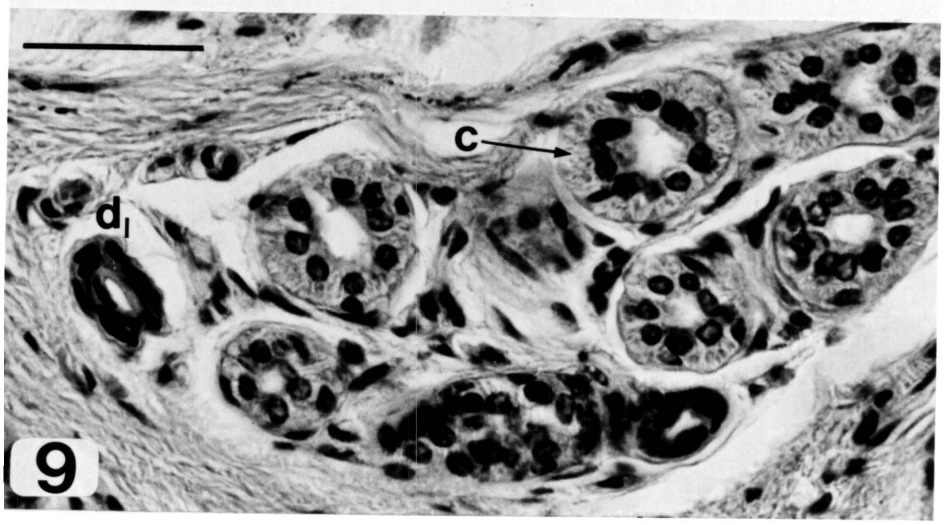

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Fig. 10. Section through the hind foot sole of Xerus inauris showing the sweat duct (d) spiralling through the dermis (D) to the epidermis (E).

(Bar = 100µm)

Fig. 11. T.S. through a toe pad of the front foot of Rhabdomys pumilio showing the duct (d) forming a conical spiral (lower arrow) through the funnel-shaped interpapillary peg of the epidermis (E). The helical spiral of the duct through the stratum corneum (Sc) is indicated by the top arrow. Duct (d) in T.S. is composed of a double layer of flattened cells as indicated by their flattened kidney-shaped nuclei. (Bar = 100µm)

Fig. 12. A high power view of the epidermis (E) of a front foot toe pad of Saccostomus campestris showing how the cells lining the duct lumen (dl) become progressively undifferentiated as the duct spirals through the epidermal interpapillary peg to the stratum corneum(Sc)

(Bar = 10µm)

Fig. 13. A high power view of a T.S. through a sweat duct in an epidermal papillary peg in a hind foot pad of Paraxerus cepapi. The duct lumen (dl) is lined by a single flattened ring-shaped cell (r) which lacks the pigment of the surrounding epidermal cells.

(Bar = 5µm)

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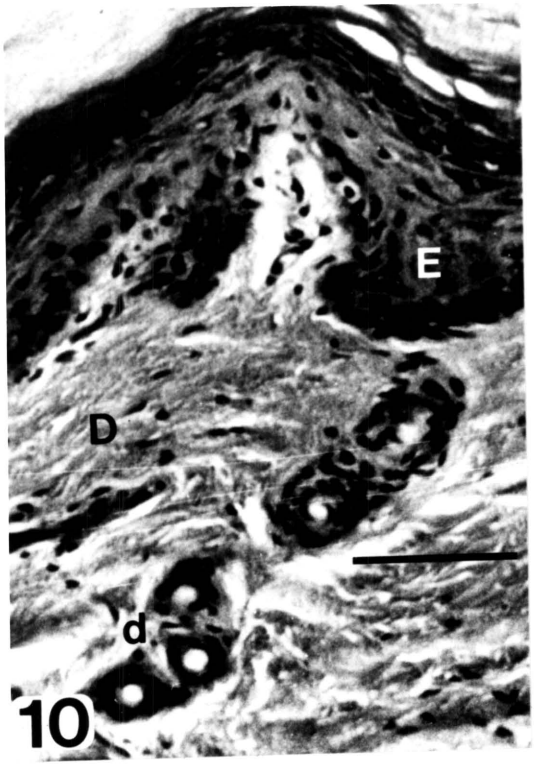

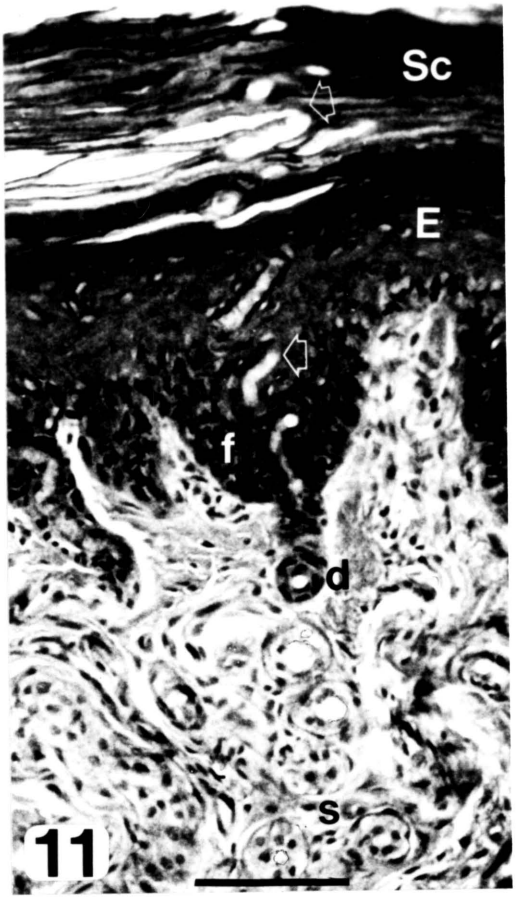

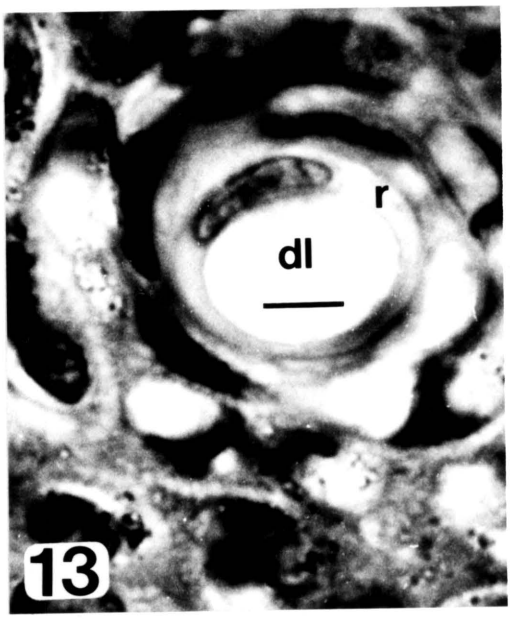

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Fig. 14. A high power view of the epidermis of a hind foot pad of Hystrix africaeaustralis showing how the cells lining the epidermal duct become progressively undifferentiated and keratinized as the duct spirals through the epidermis to the stratum corneum (Sc). The duct lumen size increases during this process as does the characteristic keratinized border.

(Bar = 50µm)

Fig. 15. A high power view of the epidermis of a hind foot pad of Petromus typicus showing the path of the duct (d) which in this species runs almost straight through the epidermis (E). The duct is seen as an opening between the cornified cell spiralling tightly in a narrow helix through the thick stratum corneum (Sc). (Bar = 50µm)

Fig. 16. L.S. through the a hind foot toe pad of Petromus typicus showing the path of the ducts (d) through the funnel-shaped papillary pegs (f) which reach down to the secretory tubules (s). On reaching the stratum corneum (Sc) the ducts (d) are redirected at an angle spiralling (sp) tightly in a narrow helix through the thick stratum corneum (Sc) to open in shallow depressions (de ▶) on the friction surface.

(Bar = 100µm)

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cells. These cells formed a network around the secretory tubule but were attached to the inside of the basement membrane. The dark staining nuclei of these cells seemed flattened against the basement membrane (Fig.8).

THE EXCRETORY DUCT

The transition between the secretory segments with their single-layered secretory epithelium, and the ducts which had a double layer of cells (Fig.9), was abrupt. The excretory ducts began within the secretory lobules where they were found among the secretory tubules. The luminal diameters of these excretory ducts within the secretory lobules, were generally smaller than those of the secretory tubules (Fig.9). However, the lumens of the excretory ducts in the dermis were wider than the ductal lumens within the glandular lobules. Depending on the species, the courses the ducts followed through the dermis to the epidermis were relatively straight as in Mystromys albicaudatus (see Chapter 5; Fig.61) or slightly curved (Fig.6 & 7) or spiralled (Fig.10). The duct was composed of a double layer of darkly staining compactly flattened cells: a basal layer with elongated nuclei rested on the basement membrane, and enclosed the flattened luminal cells with their kidney-shaped nuclei (Fig.11, also see Chapter 5; Fig.85). The cuticular border was clearly seen on the luminal surfaces of the luminal cells in some species. Myoepithelium cells were not seen to extend along the duct outside the secretory lobuli.

The ducts entered the papillary pegs of epidermis which projected down deep into the dermis. Each duct began a cone-shaped spiral as it moved up the funnel-shaped interpapillary peg (Fig.11 & 12) until it reached the stratum corneum through which it made a tight helical spiral to the surface.

As the duct wound through the epidermis the two layers of ductal cells lost their distinctive character and took on the characteristics of the surrounding epidermal cells (Fig.12) until a single cell lined the duct (Fig.13). The cells lining the epidermal ducts lacked pigment making them clearly outlined in the species with well-pigmented feet. Just before entering

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the stratum corneum the epidermal duct lumen became larger with no differentiated lining cells but the cells surrounding the duct underwent keratinization and the lumen itself thus became encircled by a keratinized border (Fig.14). As it spiralled through the stratum corneum the duct was seen as an unlined opening between the cornified cells (Fig.15). In rodents with a thick epidermis the ductal helix curved through the stratum corneum towards the contact or friction surfaces of the foot pads (Fig.16). In the various rodent species the number of rotations in the spiral varied according to the thickness of the stratum corneum (compare Fig.11 & 15).

The ducts of the rodent glands opened directly onto the ventral surfaces of the foot pads where they were regularly spaced. These surfaces were smooth lacking epidermal ridges. In some rodent species such as Petromys typicus and Thallomys paedulcus the duct orifices opened in depressions on the foot pad surface (Fig.16).

DISCUSSION

The sudoriferous glands of the rodent foot pads although basically similar to, are cytologically unique when compared to the descriptions of typical eccrine or apocrine sweat glands in man and other domestic animals. The main distinction between these two types of sudoriferous glands are based on the histological differences of the secretory cells lining the secretory tubules (Weiner & Hellmann 1960; Munger & Brusilow 1971). Only one type of secretory cell could be distinguished by light microscopy. This is in contrast to the eccrine glands of the human (Montagna 1956), other primates (Montagna & Parakkal 1974) and the cat (Munger & Brusilow 1961). In these species two types of secretory cells were described; the dark cells with a basophilic cytoplasm containing secretory vacuoles and the clear cells lacking cytoplasmic basophilia and secretory vacuoles. In the present study, no secretory vacuoles could be identified in the secretory cells as decribed in the dark cells of eccrine glands of the cat (Munger & Brusilow 1961) and various primates (Montagna & Parakkal 1974). The luminal edge of these secretory cells in some species showed a distinct hyalin cuticular border

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characteristic of the eccrine glands of various other animals (Montagna & Parakkal 1974; Munger & Brusilow 1961). These light microscopic findings that the secretory cells of the wild rodent sweat glands are only of one atypical type, is in agreement with those reported in the white rat (Wechsler & Fisher 1968; Munger & Brusilow 1971), the white mouse (Quick, et al. 1984) and the bank vole (Griffiths & Kendall 1980a). However, Matsuzawa & Kurosumi (1963) reported two secretory cell types in 10-day-old rats while only one cell type could be found in the adults.

The sweat ducts followed a relatively straight or slightly curved course through the dermis to the epidermis in most of the wild rodent species. Ring & Randall (1947) described the ducts of the white rat as following a straight or slightly spiralled course as opposed to the undulating or helical (Wells & Landing 1968; Montagna & Parakkal 1974) or spiral course (Ham 1974) describing the human eccrine duct through the dermis.

The cuticular border is clearly seen on the luminal surfaces of the ductal luminal cells, as in other species (Munger & Brusilow 1961, Ham 1974; Montagna & Parakkal 1974). Myoepithelium cells were not seen to extend along the duct outside the secretory lobuli as described in the white rat by Ring & Randall (1947).

In rodents with a thick epidermis the ductal helix curved through the stratum corneum towards the contact or friction surfaces of the foot pads. This was also found in the palms and soles of man by Montagna (1956) who suggested that the thicker epidermis resulted in a longer looser spiral compared to the tighter conical spiral of thinner epidermis. In the various rodent species the number of rotations in the spiral varied according to the thickness of the stratum corneum.

At the junction with the epidermis the two layers of duct cells took on the characteristics of the surrounding epidermal cells so that the duct spiralling through the stratum corneum is unlined by the special duct cells. The origin of the cells lining the intraepidermal duct remains to be answered (Montagna & Parakkal 1974) but because of some cytological differences between these cells and those of the surrounding epidermis, the terminal part of the duct and the immediate adjacent cells have

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been named "the epidermal sweat duct unit" (Lobitz, et al. 1954). These differences were not as apparent in the rodent glands. The cells of the sweat duct lack pigment making the sweat ducts clearly outlined in the well pigmented species. The description of the cells of the "unit" undergoing keratinization and the lumen itself being encircled by a keratinized border (Montagna 1956) is applicable to the sweat ducts of the wild rodents. The ducts of the rodent glands open directly onto the ventral surfaces of the foot pads where they are regularly spaced. These surfaces are smooth lacking the epidermal ridges on which the eccrine gland ducts open in man (Montagna & Parakkal 1974). In some rodent species such as Petromys typicus and Thallomys paedulcus the duct orifices open in depressions on the surface called "beakers" by Montagna (1956). These are similar to those described in the Clethrionomys glareolus (Griffiths & Kendall 1980a).

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CHAPTER 4.

THE ULTRASTRUCTURE OF THE RODENT SUDORIFEROUS GLANDS

INTRODUCTION

Because the sudoriferous glands of man play such a functional role in thermoregulation, the ultrastucture of these glands has been intensively studied (Montagna, et al. 1953; Lee 1960; Munger 1961, Montagna 1962). These findings are well reviewed (Montagna 1962; Montagna & Parakkal 1974) where the ultrastructure of the secretory cells in the human eccrine sweat glands revealed two cell types, mucoid or 'dark cells' and 'clear cells'. The dark cells have numerous large apical sercretory vacuoles containing acid mucopolysaccharides, apical microvilli and a high ribonucleic acid content. Clear cells lack identifiable secretory granuoles or vacuoles,and are characterized by the prescence of intercellular canaliculi and extensive plications of the plasma membrane (Griffiths & Kendall 1980a).

In the rodents, the sudoriferous glands of laboratory rats have been studied primarily as experimental models in perspiration physiology (Matsuzawa & Kurosumi 1963). These workers found that young rats had two cell types whereas adult rats had only one type of secretory cell, which shared characteristics of both human secretory cell types. Both Wechsler & Fisher (1968) and Munger & Brusilow (1971) studied the ultrastructural changes produced during induced sweating in the plantar sweat glands of the rat. Munger & Brusilow (1971) confirming only one atypical type of secretory cell concluded that "the sweat glands of the rat foot pad are unique as compared with the other cutaneous glands both in their cytologic appearance and in the chemical composition of the sweat they elaborate". Similarly, Quick, et at. (1984) found that the mouse provides a convenient model for the study of sweat glands and their innervation by the autonomic nervous system, with the practical application that this model system of the mouse would lead to a better understanding of how human sweat glands are affected by diabetic neuropathology.

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The studies on wild rodents are limited to the plantar sweat glands of the bank vole Clethrionomys glareolus (Griffiths & Kendall 1980a) and the apocrine sweat glands in the oral angle of same animals (Griffiths & Kendall 1980b). Among the indigenous rodents the ultrastructure of the sweat glands of Aethomys namaquensis was described as part of the present study (Green & Soley 1981) which included Praomys natalensis and Lemniscomys griselda by transmission electron microscopy. Scanning electron microscopy was also done on the feet of these species, as well as those of Rhabdomys pumilio, Acomys spinosissimus, Thallomys paedulcus and Petromys typicus.

RESULTS

The sudoriferous glands of the murid rodents consisted of a coiled secretory tubule embedded in connective tissue of the dermis or hypodermis, and a relatively straight duct through the dermis which spiralled through the epidermis opening onto the surface.

THE SECRETORY SEGMENT

The secretory part of the gland consisted of a single layer of secretory epithelium partially covered by myoepithelial cells and enveloped by the basal lamina (basement membrane) and surrounded by connective tissue. Capillaries and unmyelinated nerve fibres coursed through the connective tissue among the secretory tubules.

Secretory Cells

Two types of secretory cells could be distinguished according to their electron opacity. The cuboidal clear cells were larger and more numerous than the more electron opaque darker cells. The cytoplasm of the clear cells was more extensive and their nuclei were ovoid to round and larger compared to the pyramidal shaped darker cells with their electron denser elongated nuclei (Fig.17). The basal borders of the secretory cells mostly rested on a basement membrane except where myoepithelial cells intervened. These secretory cells were characterized by deep infoldings of the basal plasma membranes running perpendicularly from the basement membrane to the perinuclear area (Fig.18). At the junction between the myoepithelial and

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secretory cells these infolds adopted a parallel course above the apical surface of the myoepithelial cells with few interdigitations between them (Fig.18). Most of the infoldings contained a thin slip of cytoplasm which extended to the perinuclear area, and in which large elongated mitochondria lay (Fig.18). The effect of this was to produce a series of parallel sheets of plasma membrane arranged radially in the cytoplasm between the myoepithelial cells (Fig.17 & 18). Because of the elaborate infoldings the lateral boundries and possible intercellular canaliculi between the adjacent cells were difficult to trace except near the luminal border. Here the usual triad junctional complexes present in glandular epithelia, consisting of the zonula occludens, zonula adherens and macula adherens (desmosomes) were seen. Desmosomes were also sparsely present between the adjacent plasma membranes and between the secretory cells and myoepithelial cells. Hemidesmosomes were found where the plasma membranes rested on the basement membrane. These hemidesmosomes were small compared to those of the myoepithelial cells (Fig.18).

Numerous microvilli projected into the gland lumen from the apical plasma membranes of both clear and dark cells. These microvilli were relatively uniform in size and were remniscent of those forming the striated border of the intestinal epithelium (Fawcett 1969; Sandborn 1972). The microvilli could fill the lumen in the inactive secretory tubules while the active glands with large open lumens had microvilli with mushroom-like projections which protruded into the lumen (Fig.19). These 'cytoplasmic blebs' (Griffiths & Kendall 1980a) which seemed to develop as enlarging tips of the microvilli (Fig.20) increased to several microns in size before budding off into the lumen (Fig.20 & 21). The surface membrane covering these blebs was smooth while the cytoplasmic content was organelle free. Collapsed membranous material similar to these blebs could be seen free in the lumen (Fig.21) which may indicate that they contributed to the glandular secretion.

The cytoplasm was somewhat granular in appearance due to the scattered ribosomes, glycogen granules and small vesicles. The large nucleus was generally centrally placed and leptochromatic

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Fig. 17. Electron micrograph of the secretory epithelial cells of the sudoriferous glands in the front foot pad of Lemniscomys griselda. The two types of secretory cells, the 'dark cell' (D) and the 'clear cells' (C), can be distinguished by the electron opacity of their cytoplasm and nuclei (N). Their attachment to the basement membrane is interrupted by the myoepithelial cells (My). The large elongated mitochondria (M) occur mainly in the cytoplasm contained in the plasma membrane infolds between the basement membrane and the nucleus. Arrows indicate the typical end-to-end arrangement of the mitochondria. Numerous small vesicles are seen in the apical cytoplasm.

(Bar = 2,5µm)

Fig. 18. Basal section of a 'clear' secretory cell of the sudoriferous glands in the front foot pad of Aethomys namaquensis showing the deep infoldings of the plasma membranes (p) containing thin slips of cytoplasm and elongated mitochondria (M) which extend up to the perinuclear area. There are few inter- digitations between the plasma membranes of the adjoining myoepithelial cell (My) and the secretory cells except above the apical surface of the myoepithelial cells. Note the difference in size between the hemidesmosomes (h) of the plasma membranes and those of the myoepithelial cell (My) where they rest on the basement membrane (bm).

(Bar = 1.0µm)

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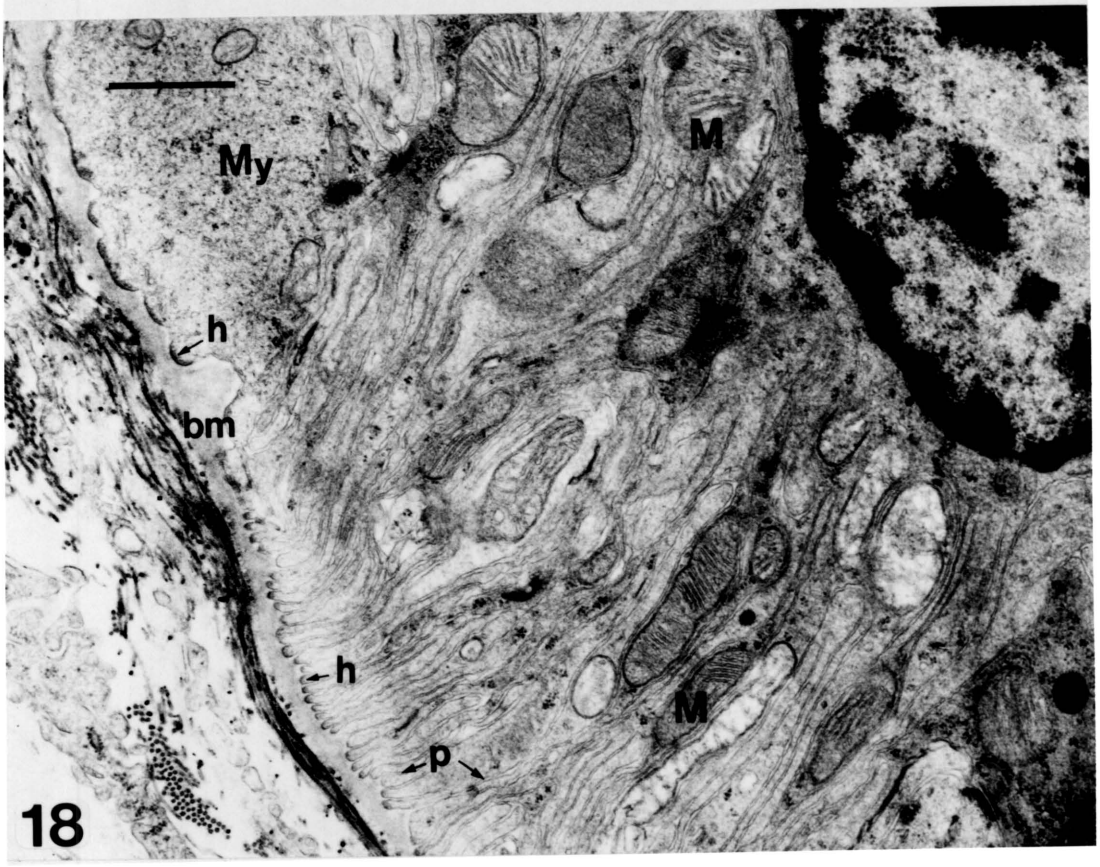

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Fig. 19. The apical surfaces of two secretory cells of Aethomys namaquensis showing the numerous relatively uniform microvilli (mv) projecting into the lumen (L) of the sudoriferous gland. Cytoplasmic blebs (Cb) mushroom from the tips of a number of these microvilli. A junctional complex is seen along the intercellular canaliculi between the adjacent cells. Numerous small vesicles occur in the subluminal cytoplasm.

(Bar = 0,5µm)

Fig. 20. Numerous uniform microvilli (mv) projecting into the lumen of the sudoriferous gland from the apical surfaces of two secretory cells of Aethomys namaquensis. A cytoplasmic bleb (Cb) is clearly seen forming from the swelling of the tip of the microvillus. A junctional complex, numerous small vesicles and glycogen granules are seen in the the subluminal cytoplasm.

(Bar = 0,5µm)

Fig. 21. Three stages of development of the cytoplasmic blebs on the secretory cells of Aethomys namaquensis are illustrated. A cytoplasmic bleb (Cb_1) forms from the swelling of the tip of the microvillus (mv) which grow out and enlarges being continuously surrounded by the membranes of the microvilli (Cb_2), before budding off to form collapsed membranous debris (Cb_3) which adds to the luminal secretion. These cytoplasmic blebs contain no cytoplasmic organelles.

(Bar = 0,5µm)

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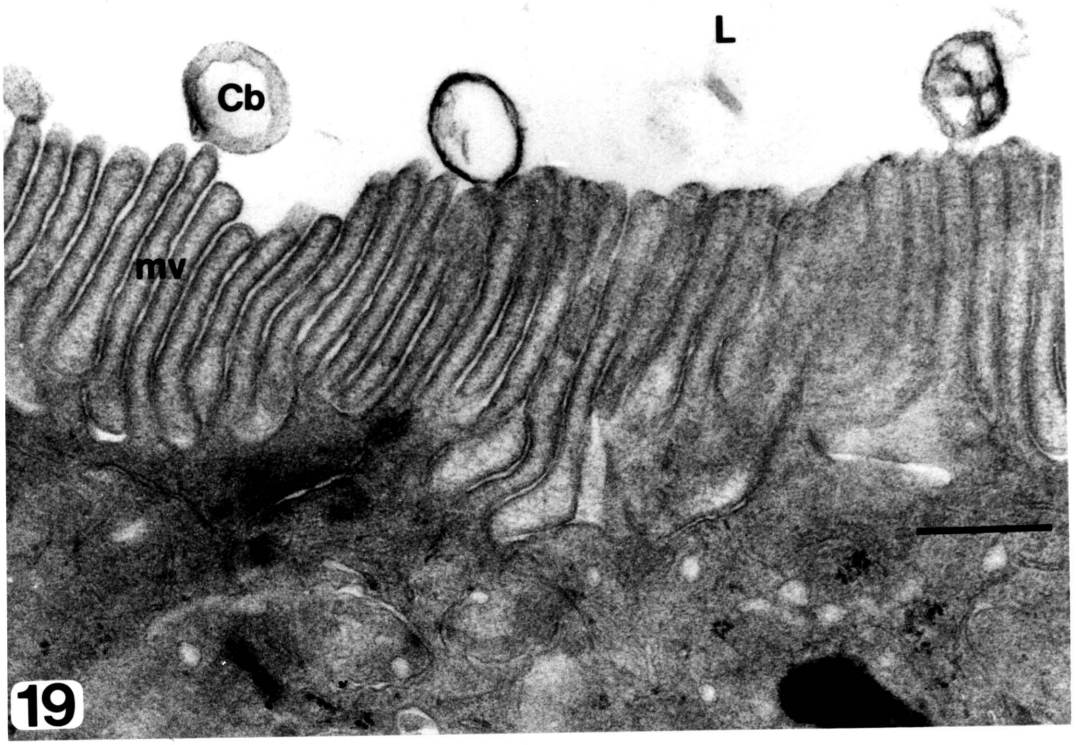

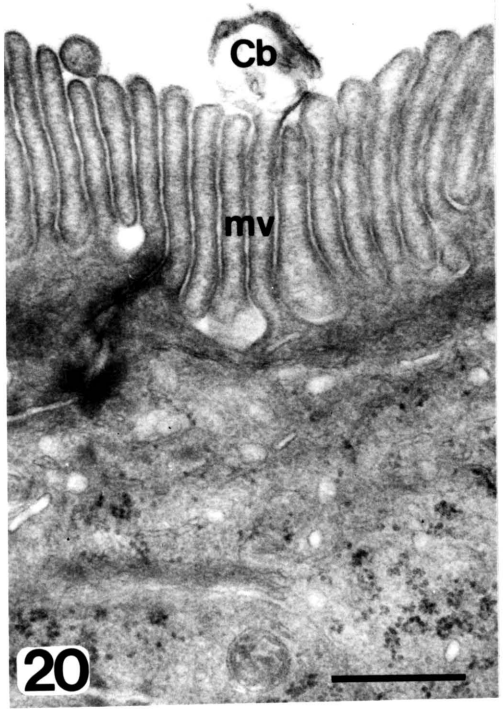

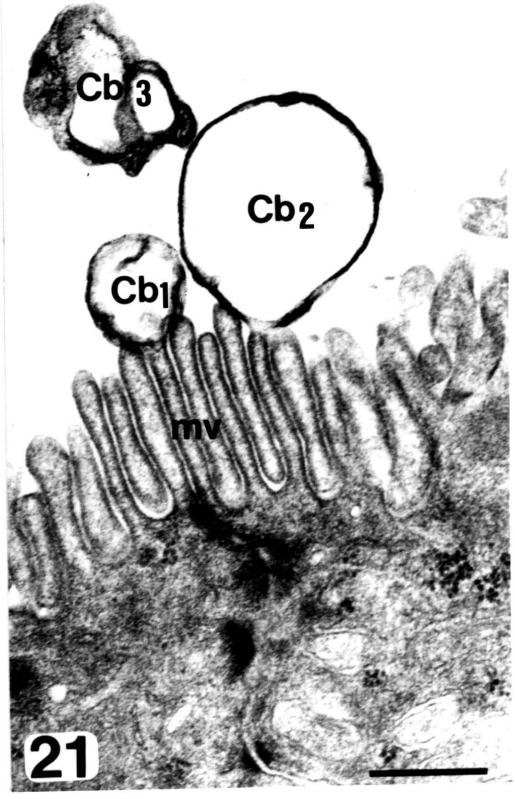

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due to the peripheral location of the heterochromatin. The abundant elongated mitochondria which varied in size and shape were often arranged end to end mainly in the cytoplasm of the plasma membrane infolds between the nucleus and the basement membrane (Fig.17 & 18). No mitochondrial granules were seen. A few scattered mitochondria did occur in the apical part of the cell. Glycogen granules and small vesicles occured throughout the cytoplasm but were more concentrated in the apical part. The golgi apparatus was small and when visible was found below the luminal surface. Some short rough endoplasmic reticulum was scattered through the cytoplasm. Numbers of small electron lucent vesicles and vacuoles were gathered in the apical cytoplasm under the luminal surface (Fig.19 & 20). No distinct differences could be distinguished between the cytoplasmic organelles of the clear and dark cells.

Myoepithelial Cells

These cells formed a net-like layer between the basement membrane and the secretory epithelium. The basement membrane was distinctly thickened and deeply scalloped to interdigitate with the infoldings of the basal plasma membranes of the myoepithelial cells with their well-developed attachment plates (hemidesmosomes) adjacent to the basement membrane (Fig.22). The apical plasma membranes were relatively smooth with few interdigitations and desmosomes attaching to the adjacent secretory cells (Fig.22). The granular cytoplasm was characterized by the abundance of thick myofilaments (Fig.23). The peripheral cytoplasm contained the apical nucleus, endoplasmic reticulum, and small subsurface vesicles, while a few small oval mitochondria and aggregated glycogen granules were also mainly concentrated in this area (Fig.23).

Periglandular Tissue

The connective tissue that entwined between and around the secretory tubules consisted of sheets of collagen fibres interspersed by elongated fibroblasts. Blood capillaries and unmyelinated nerve fibres in the connective tissue were inter-woven in close association but not in direct contact with the

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Fig. 22. A myoepithelial cell (My) in a secretory tubule of Aethomys namaquensis. The thickened basement membrane (bm) is deeply scalloped to accommodate the interdigitation with the infoldings of the basal plasma membranes (p) of the abutting myoepithelial cell with its well-developed hemidesmosomes (h). The lateral plasma membrane surfaces are relatively smooth with few interdigitations or desmosomes (shown by the arrow) attaching to the adjoining secretory cells.

(Bar = 0,3µm)

Fig. 23. A myoepithelial cell (My) in a secretory tubule of Lemniscomys griselda. The granular cytoplasm is filled with only thick myofilaments (mf arrow) in T.S., with no thin myofilaments being present. The leptochromatic nucleus (N) is apically situated while a few small oval mitochondria (M) and aggregated glycogen granules are seen in the peripheral cytoplasm.

(Bar = 0,5µm)

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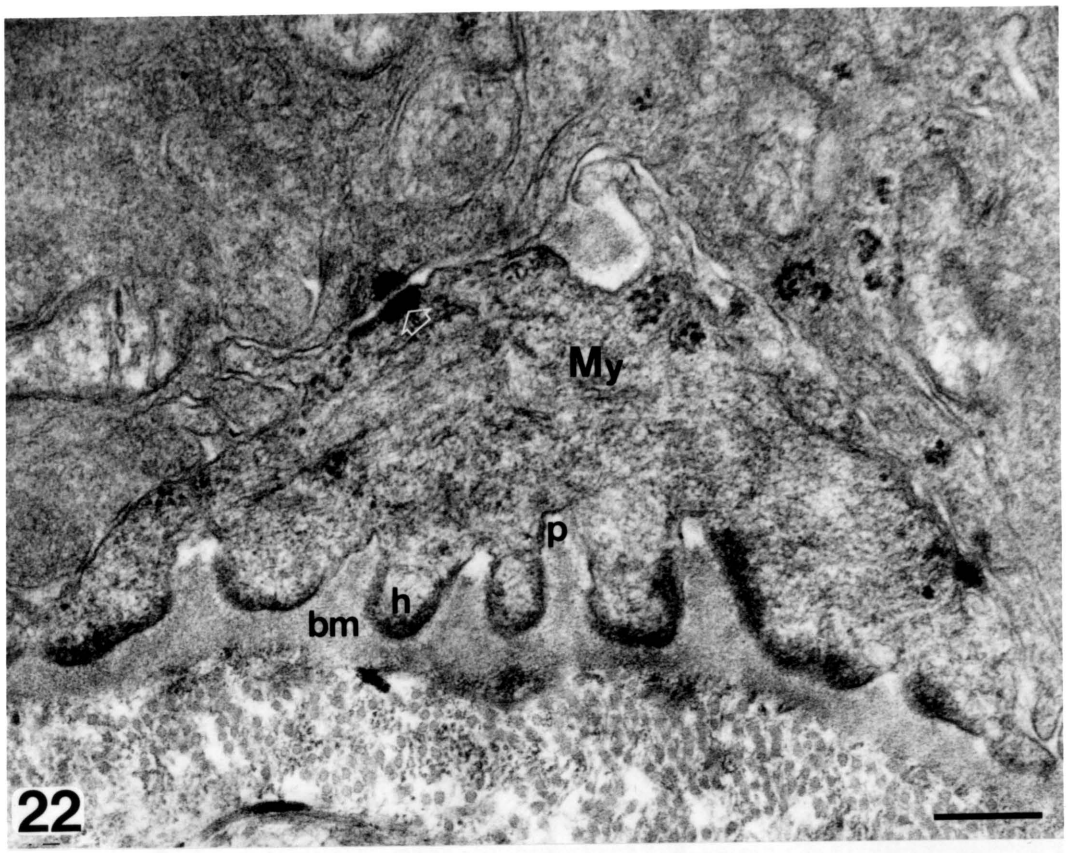

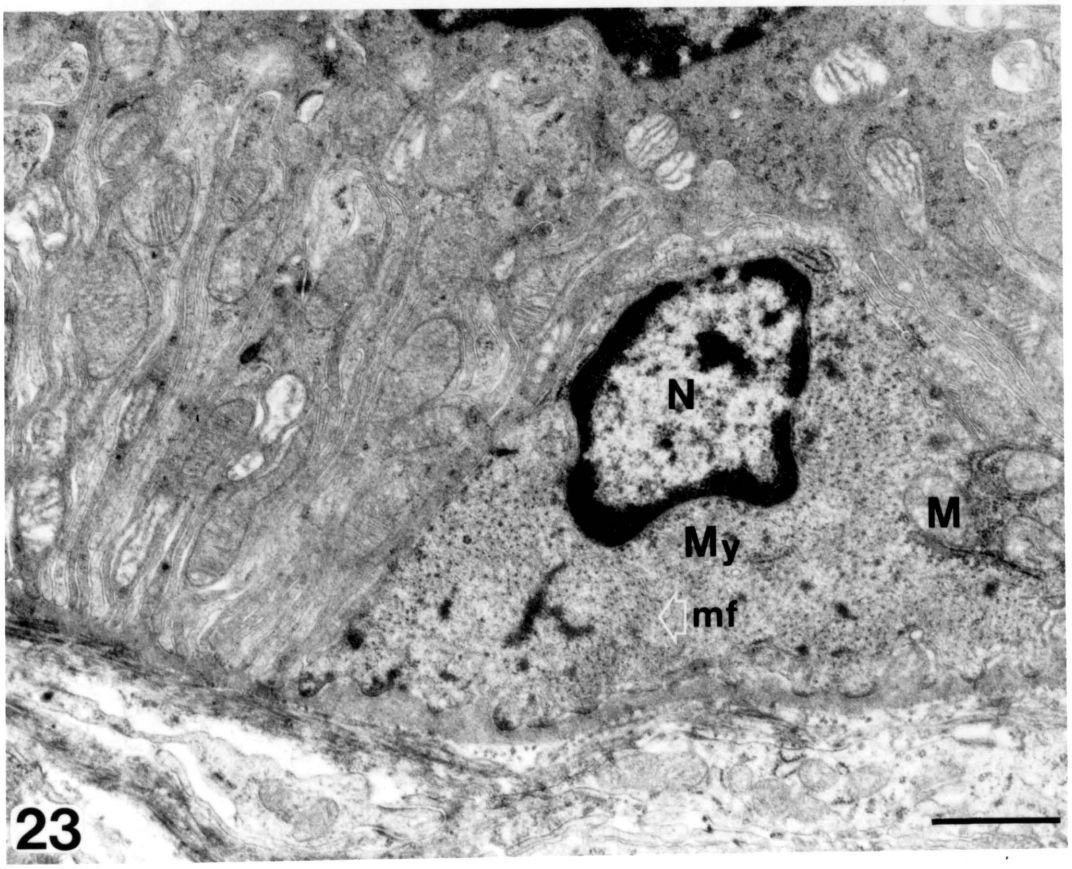

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basement membranes of the glandular cells. The periductal connective tissue was denser with fewer capillaries and nerve fibres compared to the periglandular tissue.

THE EXCRETORY DUCT

The duct was composed of two layers of epithelial cells with the myoepithelium being absent. The basal cells were the most flattened both in their cytoplasm and nuclei, and their almost smooth basal plasma membranes resting loosely with hemidesmosomes on a thin basement membrane. The plasma membranes of these cells interdigitated with the adjacent luminal cells forming uneven wide intercellular channels with irregularly spaced desmosomes (Fig.24 & 25). The flattened cytoplasm of the luminal cells seemed to be spirally connected by interdigitating plasma membranes with many desmosomes and tight junctions particularly around the lumen. The luminal cells had a prominent cuticular border with short microvilli and masses of tonofilaments (terminal web) in the cytoplasm beneath the microvilli (Fig.24 & 25). The lumen of the duct was irregularly star-shaped and narrower than the secretory lumen. The dense cytoplasm of both cells was filled with glycogen granules which were most abundant in the basal cells and became progressively less towards the luminal surface. The oval mitochondria seemed to be evenly distributed in the basal and luminal cells, but far fewer than in the secretory cells. Smaller vesicles and larger vacuoles were more frequent in both cells of the duct. There was a distinct granular luminal content not seen in the secretory lumen (Figs.25).

The duct wound through a conical spiral as it passed through the epidermal interpapillary peg. The duct cells lost their distintive character as they took on the appearance of the surrounding epidermal cells as they spiralled to the surface. In most species the ducts opened directly onto the smooth foot or toe pads as seen on the palmar pad of Aethomys namaquensis (Fig.26). This spiralisation was seen in a number of species where many of the duct openings which were comma-shaped (Fig.27, 28 & 29).

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Fig. 24. T.S. through the duct of a sudoriferous gland of Praomys natalensis. The duct is composed of two layers of flattened epithelial cells which are wound around each other enclosing the irregular star-shaped lumen (L). The basal cells are loosely attached by hemidesmosomes (h) to the thin basement membrane (bm). Myoepithelial cells are absent. The luminal parts of the cells form a dense zone, the cuticular border, with numerous short microvilli and underlying tonofilaments (t). The intercellular channels between adjoining cells are wide with irregularly spaced desmosomes (ds) which become more frequent near the luminal surfaces.

(Bar = 1µm)

Fig. 25. L.S. through the duct of a sudoriferous gland of Praomys natalensis. The flattened luminal cells with their short microvilli (mv) have a cuticular border with tonofilaments (t) and numerous glycogen granules are present in the cytoplasm. Intercellular channels between the adjacent cells are wide with well-developed desmosomes (de) concentrated near the luminal surfaces. The luminal content (lc) is distinctly granular.

(Bar = 1µm)

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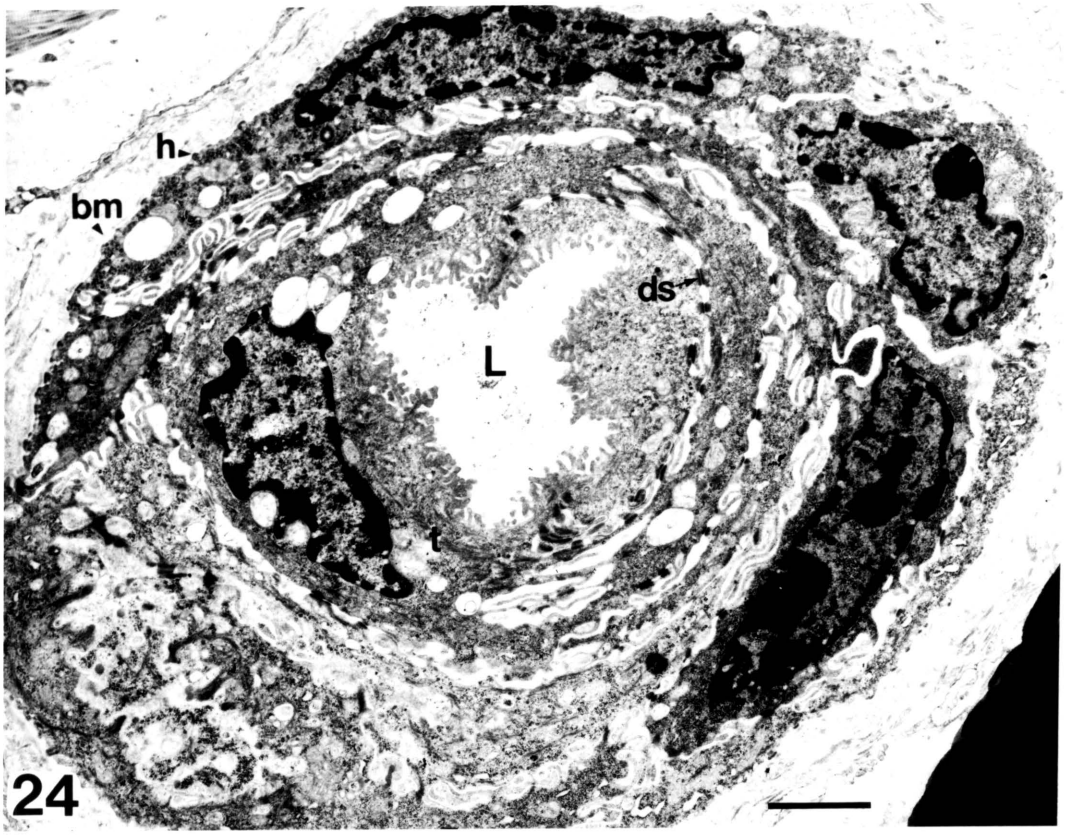

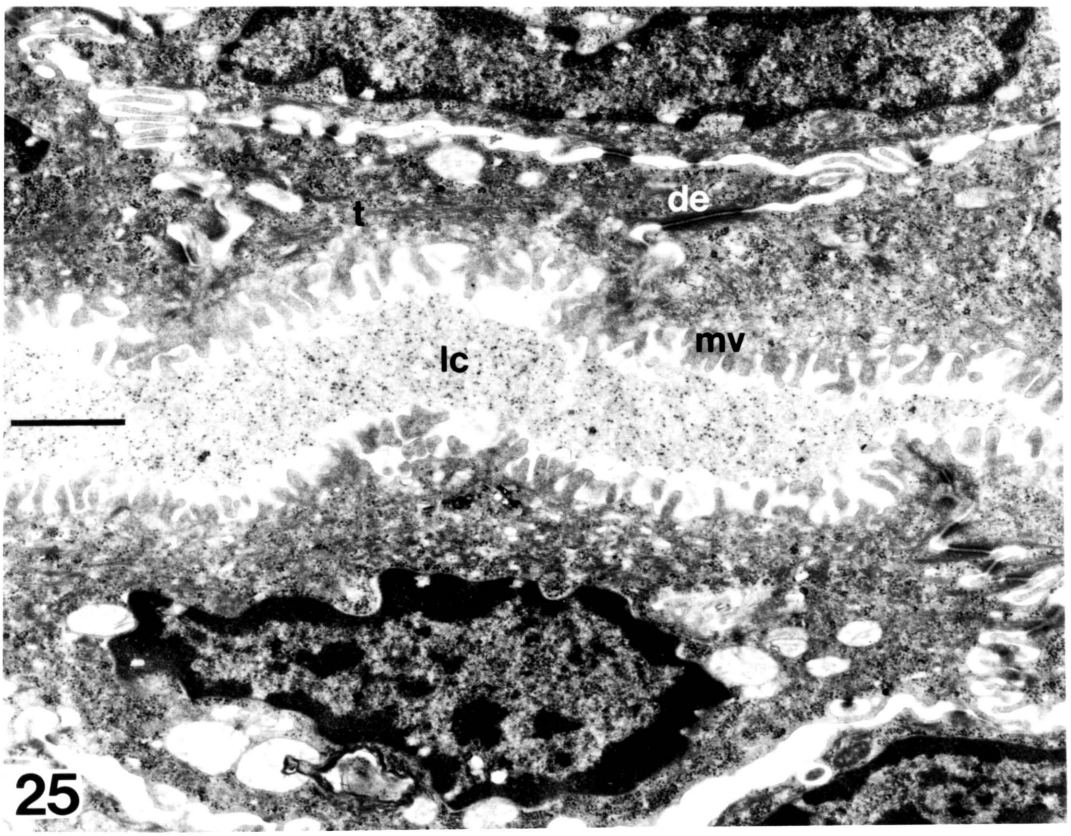

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Fig. 26. Sweat ducts (arrows) opening directly onto the smooth surface of the palmar pad of Aethomys namaquensis. Some of the cornified cells were sloughing off.

(Bar = 100µm)

Fig. 27. Sweat duct opening on the palmar pad of Lemniscomys griselda. The duct lumen (*) is shown with arrows indicating the direction of the duct spiralling through the stratum corneum.

(Bar = 5µm)

Fig. 28. Sweat duct opening directly onto the surface of the plantar pad of Aethomys namaquensis. The duct lumen (*) contains some material. The adjacent cornified cell is lifting.

(Bar = 10µm)

Fig. 29. Sweat duct opening directly onto the surface of the palmar pad of Lemniscomys griselda. The duct lumen (*) contains some keratinous-like material which resembles the lining of the duct. The arrows indicate the direction of the duct spiralling through the stratum corneum. The adjacent cornified cell is lifting.

(Bar = 10µm)

Fig. 30. A sweat duct opening (*) partially concealed in a group of lifted surface cells on a plantar pad of Rhabdomys pumilio. These cornified cells form a tunnel-like canopy (ca) over the duct opening.

(Bar = 10µm)

Fig. 31. A sweat duct opening (*) on a plantar pad of Acomys spinosissimus showing a lifted cornified cell forming a canopy (ca) over the duct opening.

(Bar = 10µm)

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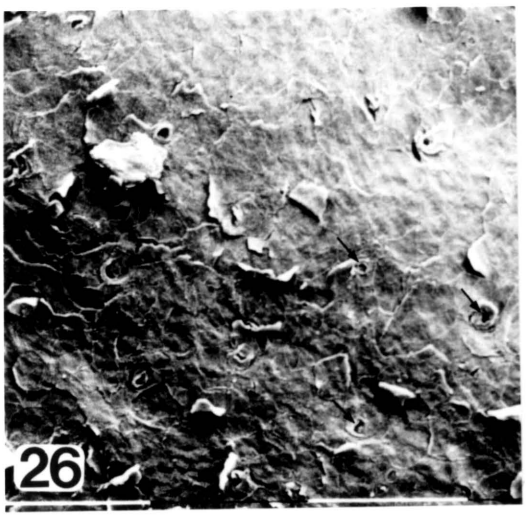

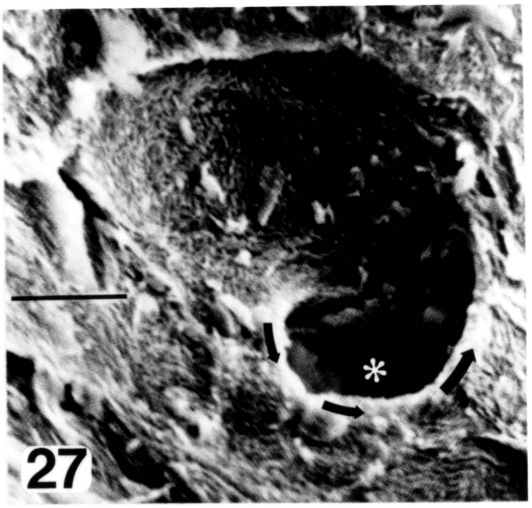

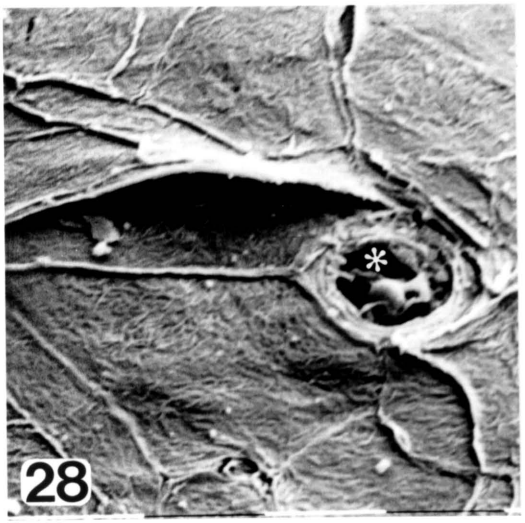

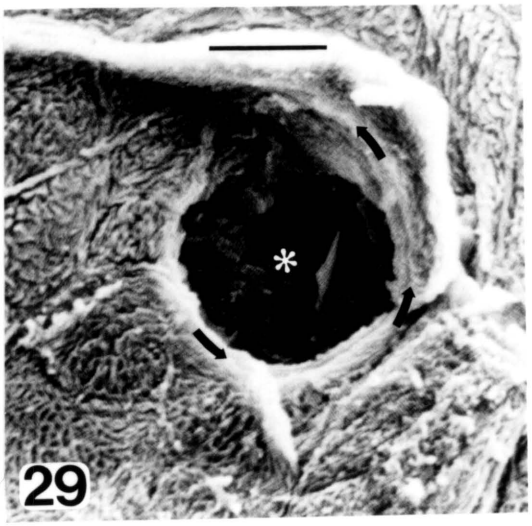

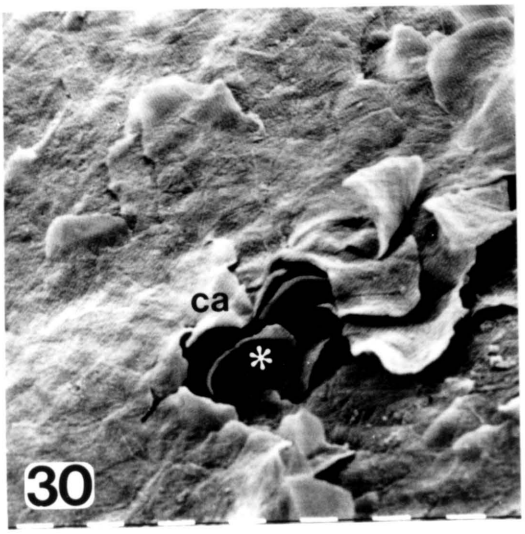

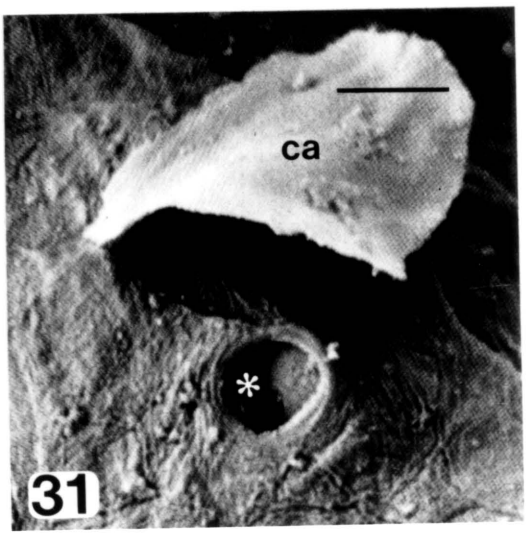

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Fig. 32. A sweat duct opening (do arrow) on a palmar pad of Aethomys namaquensis. The duct lumen contains some material which resembles the keratinous lining of the duct. The surface of the stratum corneum cells surrounding the duct opening are covered with microplicae (Mp) which in this electron micrograph seem coated with an unknown substance.

(Bar = 10µm)

Fig. 33. A sweat duct opening (arrow) on the same palmar pad as Fig. 32. Material which resembles the keratinous lining (De) of the duct, protrudes through the duct opening. The surface of the stratum corneum cells surrounding the duct opening are covered with typical uncoated microplicae(Mp)

(Bar = 10µm)

Fig. 34. Sweat duct openings on the surface of a palmar pad of Petromus typicus. Low epidermal ridges (ER) were found on the pad surfaces with the duct orifices opening in depressions (arrows) scattered at random over these ridges.

(Bar = 10µm)

Fig. 35. Sweat duct openings on the epidermal ridges on a palmar pad of Petromus typicus. The duct orifices open into depressions (arrows) scattered at random over these ridges. Some of these depressions were partly filled (P), leaving only a narrow opening through which the sweat is secreted onto the pad surface.

(Bar = 25µm)

Fig. 36. Sweat duct openings on the surface of a hind foot toe pad of Thallomys paedulcus which had well-developed epidermal ridges (ER) arranged in 'zig-zag' patterns with the ducts opening into shallow cup-shaped depressions (arrows) mainly between the ridges.

(Bar = 20µm)

Fig. 37. A Sweat duct (small arrow) opening acentrically into its large cup-shaped depression (de) on a hind foot toe pad of Thallomys paedulcus.

(Bar = 20µm)

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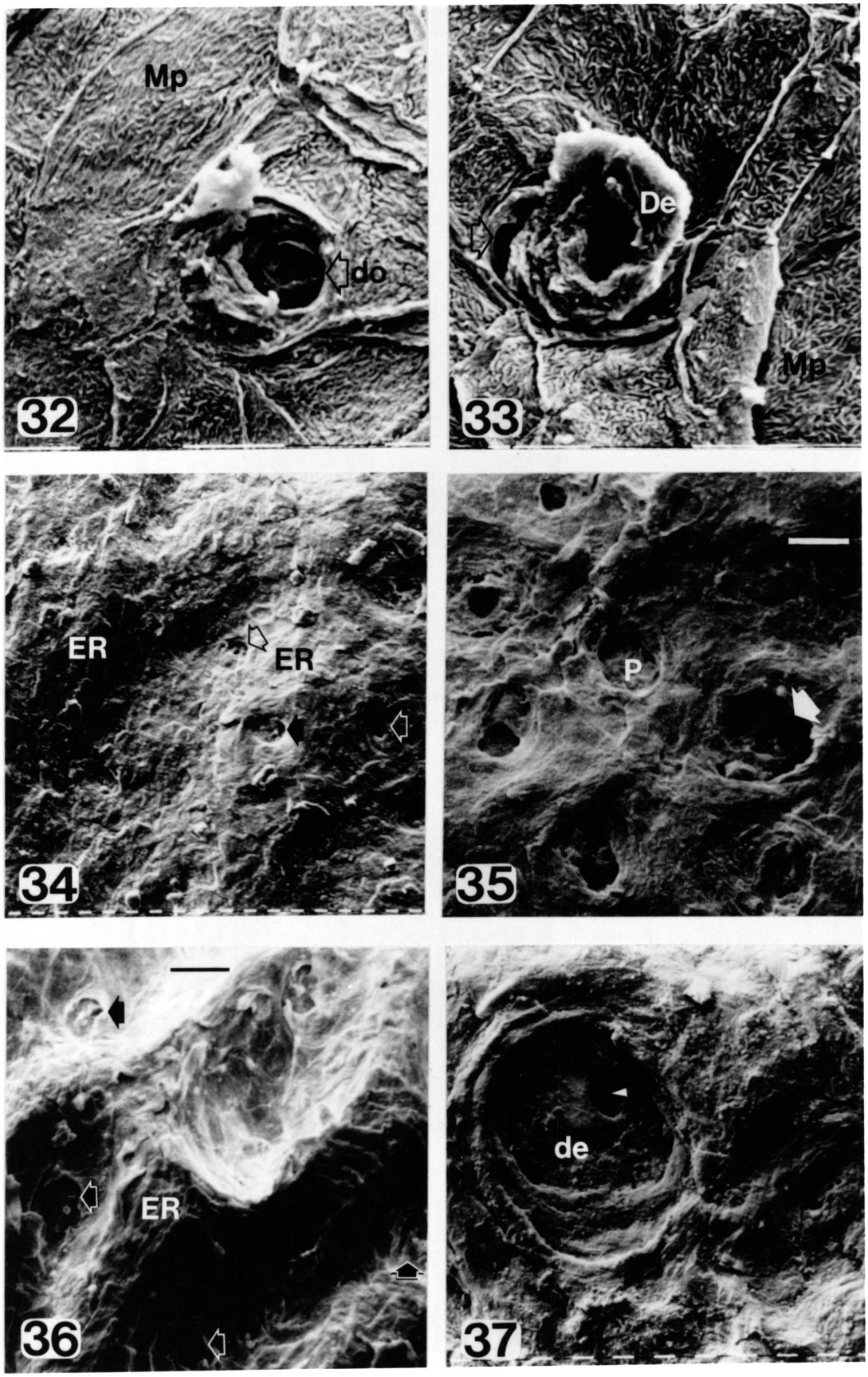

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A number of the surface cells of the stratum corneum were partly lifted (Fig.26, 28 & 29) and these cells formed partial canopies over the openings of some of the sweat ducts (Fig.30 & 31). This was common in Rhabdomys pumilio (Fig.30) and Acomys spinosissimus (Fig.31). The duct orifices showed some variation in shape and structure even on the same site of the same animal (Fig.26). Some openings were round and lined by a distinct border which could be the duct epithelial layer (Fig.32 & 33) while others were simply openings spiralling through the stratum corneum (Fig.27, 29 & 31). The surface of the stratum corneum cells lining and surrounding the duct openings were covered with numerous microplicae (Fig.32 & 33), usually found only on the cell surfaces of epithelium on the inside of the body.

Two climbing species viz. Thallomys paedulcus and Petromus typicus showed further specialisation of the foot pad surfaces. Low epidermal ridges were found on the pad surfaces of P. typicus with the duct orifices opening in depressions scattered at random over these ridges (Fig.34 & 35), while T. paedulcus had more well-developed epidermal ridges arranged in 'zig-zag' patterns (Fig.36) with the ducts opening into shallow cup-shaped depressions (Fig.37) mainly between the ridges.

DISCUSSION

The sudoriferous glands of the three species studied viz. the nocturnal Aethomys namaquensis, Praomys natalensis and the diurnal Lemniscomys griselda, showed no ultrastructural differences. Yet when compared to the descriptions of the glands of the laboratory rat (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968; Munger & Brusilow 1971), mouse (Quick et al. 1984) and wild bank vole (Griffiths & Kendall 1980a) many similarities and a few differences were observed. However, when ultrastructural comparisons were made with the sudoriferous glands of non-rodent species such as man (Ellis 1962; Montagna & Parakkal 1974), the macaque (Ellis & Montagna 1961) and the cat (Munger & Brusilow 1961) very distinct differences were found.

The basic microsructure of the sudoriferous glands of all these species is the same with the main differences being in the secretory cells. The eccrine sweat glands of the non-rodent

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species are very similar containing two distinct types of secretory cells termed the light or clear cells and the dark mucoid cells (Munger & Brusilow 1961; Montagna & Parakkal 1974). The larger clear cells have large centrally placed, round to oval nuclei, an elaborate folding of the basal and lateral plasma membranes forming an intricate system of intercellular canaliculi between adjacent cells. They contain many glycogen rosettes and ovoid mitochondria scattered throughout the electron lucent cytoplasm. The golgi apparatus is small and associated with the small vesicles near the intercellular canaliculi (Montagna & Parakkal 1974). The dark mucoid cells are smaller with dense cytoplasm packed with rough endoplasmic reticulum. The golgi apparatus is large with many membrane-limited vacuoles of various sizes and electron densities which may produce the mucous secretions for these glands. The rod-like mitochondria are few. Both these cells have a luminal border of short microvilli (Montagna & Parakkal 1974).

The secretory epithelium of the sudoriferous glands of the rodents consisted of one type of secretory cells which differs from both the clear and dark cells as described above in the non-rodent species. The infoldings of the basal plasma membranes are far more extensive in the rodent secretory cells, extending up to the perinuclear area and enclosing most of the mitochondria in these thin slips of basal cytoplasm (Munger & Brusilow 1971; Green & Soley 1981). This is the most remarkable feature of these cells and may be indicative of their role to absorb water, electrolytes and some other material for secretion synthesis (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968). Although the lateral plasma membranes of all species have infoldings which interdigitate, the intercellular canaliculi which are characteristic of the clear cells of eccrine glands are lacking in the rodents' secretory cells (Munger & Brusilow 1971). This is unusual as intercellular canaliculi are a distinctive feature of cells engaged in active transport (Munger & Brusilow 1971). The inconspicuous golgi apparatus and small vesicles occur in the sub-luminal cytoplasm instead of their association with the intercellular canaliculi in the non-rodent glands. This contrasts with the well-developed golgi apparatus

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and associated large secretory vesicles and vacuoles which fill as much as two-thirds of the supranuclear cytoplasm of the dark cells in other non-rodent species (Ellis 1962). The mitochondria are similar in structure but fewer, and the rough endoplasmic reticulum is more abundant in the dark cells which also have far less infoldings of the plasma membranes and, like the secretory cells of the rodents, lack intercellular canaliculi. The luminal microvilli of the rodent secretory cells are longer and more regular than those described in the non-rodents, where the formation of cytoplasmic blebs has not been mentioned in the eccrine glands of man (Ellis 1962; Montagna & Parakkal 1974) or the cat (Munger & Brusilow 1961). The secretory cells of the rodent sudoriferous glands may be considered unique both cytologically and physiologically when compared to the accepted eccrine sweat gland models of other species (Munger & Brusilow 1971; Griffiths & Kendall 1980a).

When the ultrastructure of the glands of different rodent species are compared smaller differences are noted. The general structure of the secretory cells fits the decription already given. The wild species and rat (Matsuzawa & Kurosumi 1963; Munger & Brusilow 1971) have irregular oval nuclei while the bank vole (Griffiths & Kendall 1980a) and the mouse (Quick *et al*. 1984) have round nuclei in their secretory cells. This may be due to different fixation techniques. The plasma membrane infoldings, the mitochondrial arrangement in the basal cytoplasm, the intercellular interdigitations and the lack of intercellular canaliculi were consistant in all the rodent species. The dark cells in the young 10-day-old rat lacked these characteristic infoldings of the plasma membranes, while the secretory cells of 21-day-old rats had less developed infoldings than the adults (Matsuzawa & Kurosumi 1963) This may indicate that the dark cells develop into the functional clear cells of the adult rat. The mitochondria which are mainly elongated show considerable variation in form within the secretory cells of a single gland (Matsuzawa & Kurosumi 1963) but the two groups of mitochondria *viz*. the orthodox and the condensed conformation as reported by Munger & Brusilow (1971) in the secretory cells of the rat could not be distinguished in this study. The prominent

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matrical granules reported by Wechsler & Fisher (1968) in the mitochondria of the rat were not seen in any of the wild species. The secretory cells of all three species studied are rich in mitochondria as was the case in the bank vole (Griffiths & Kendall 1980a) and these numerous mitochondria are associated with active transport in these cells (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968; Munger & Brusilow 1971). Glycogen granules had a similar distribution in all species but Wechsler & Fisher (1968) showed experimentally that the glycogen content of the secretory cells varied according to their activity, with cells of salt-overloaded rats showing a high glycogen content.

The luminal microvilli of the three indigenous species were longer, more numerous and more regular (Fig.19 & 20) than the other species. The microvilli of the rats seemed to be irregularly grouped along the luminal surfaces of the secretory cells (Wechsler & Fisher 1968; Munger & Brusilow 1971) while those of the mouse seemed to occur in regular groups (Quick et al. 1984) and those of the bank vole were irregular in both arrangement and length (Griffiths & Kendall 1980a). They also found that the dark cells in the bank vole had short luminal microvilli compared to those of the clear cells. The mushroom-like cytoplasmic projections which seem to develop as the enlarging tips of some of the microvilli as described in the rat (Matsuzawa & Kurosumi 1963), the bank vole (Griffiths & Kendall 1980a) and the Namaqua rock rat (Green & Soley 1981) were also seen frequently in all the wild species. These cytoplasmic blebs seem to swell to a certain size before budding off into the lumen where collapsed membraneous structures are clearly seen (Fig.21). Although these blebs seem to contain no cytoplasmic organelles or secretory granules as in the cytoplasmic protuberances described in apocrine secretory cells (Montagna 1956; Weiner & Hellmann 1960) their content must contribute to the glandular secretion. This may indicate a form of 'micro-apocrine secretion' by these cells as has been proposed by Matsuzawa & Kurosumi (1963) and supported by Green & Soley (1981) who questioned the validity of the term 'eccrine' sweat glands in some rodents (Quay 1965; Wechsler & Fisher 1968).

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The myoepithelial cells of the three wild species showed great uniformity in structure. They differed from the description of the human myoepithelium in that Ellis (1965) could only find thin myofilaments and no thick myofilaments. All three species in this study contained only thick myofilaments similar to those described in the mouse (Quick et al. 1984). In the rat the myofilaments are described only as abundant (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968) and no reference is made to the type of myofilaments. The myoepithelial cells of all the rodents described rest on a distinct basement membrane with hemidesmosomes. Only Wechsler & Fisher (1968) differed in their description of the rat having a thin amorphous basement membrane, where as Munger & Brusilow (1971) refer to the distinct basal membrane. When compared with the micrographs of the basement membranes of the rat (Matsuzawa & Kurosumi 1963; Munger & Brusilow 1971), the wild rodents have greatly thickened basement membranes which scallop deeply to interdigitate particularly with the myoepithelial cells to which they are attached by large hemidesmosomes (Fig.22). This is similar to that described in the mouse (Quick et al. 1984). In the periglandular tissue of the wild species occasional loose fibroblasts were seen in contrast to the fibrocytic sheath that surrounds the secretory coils in the mouse (Quick et al. 1984). Comparing the micrographs of the glands of the various species it seems that in the indigenous species the capillaries and nerve fibres are less numerous.

The ducts of the sudoriferous glands of the wild rodents only revealed the following minor differences when compared to other species. In the wild species the basement membrane is thin but clearly distinct as in the rat (Matsuzawa & Kurosumi 1963) and the cat (Munger & Brusilow 1961), compared to the human (Ellis 1962) and the macaque (Ellis & Montagna 1961) where it is described as indistinct. The ducts were lined by a double layer of epithelial cells in all the rodents whereas those of the human (Ellis 1962) and the macaque (Ellis & Montagna 1961) have two or three epithelial layers lining the ducts. The numerous mitochondria found in the basal cells of the human duct (Montagna & Parakkal 1974) are conspicuously fewer in the wild

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rodents, being more similar to those in the rat (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968) and the cat (Munger & Brusilow 1961). The cuticular border is less conspicuous in the wild rodents, as in the cat (Munger & Brusilow 1961), with less dense tonofilaments found in the apical cytoplasm, compared to the human duct (Montagna & Parakkal 1974). The short microvilli that line the luminal surfaces of the wild rodents are more numerous and regular than those of the human (Ellis 1962; Montagna & Parakkal 1974), the macaque (Ellis & Montagna 1961) and the cat (Munger & Brusilow 1961). These microvilli, together with the greater number of subsurface vesicles and glycogen granules seen in the wild rodents' luminal cells could indicate increased pinocytotic activity and selective reabsorption (Lloyd 1962). Quatrale & Laden (1968) found that sodium and water was reabsorbed during prolonged sweating in the rat, similar to the process in the human (Dobson 1962) but the sweat of the rat contained high concentrations of potassium. This selective reabsorption and the resulting concentration of the luminal secretory product may help to explain the often membranous and distinctly granular luminal content of the ducts of the wild rodents. Less dense filamentous or membranous structures were reported in the lumen of the ducts of the macaque by Ellis & Montagna (1961).

The comma-shaped structure of the duct openings on the smooth foot and toe pads of the wild rodents reflects the direction of spiralization of the ducts through the epidermis (Fig. 27 & 29) as shown by Johnson, et al. (1970) in the human skin. The variation in the duct orifices in shape and structure on different sites in the man was demonstrated by Johnson et al. (1970) while these variations were shown to exist on the same sites of the same rodent by Green & Soley (1979). The partial lifting of some of the surface cells of the stratum corneum is also found in man (Montagna & Parakkal 1974) and in wild rodents (Green & Soley 1979). These cellular canopies partly covering some of the duct openings may partially close the duct orifices enough to prevent foreign material from entering and blocking the terminal ducts, especially as the foot pads are in contact with various substrates. The opening of the ducts into

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cup-shaped depressions in the epidermis in Thallomys paedulcus and Petromys typicus may be an adaptation for better adhesion in these climbing species. These depressions moistened by glandular secretion could increase the traction coefficient between the foot pads and the substrate. Griffiths & Kendall (1980a) suggest that a "discrete drop of secretion" may be released. The numerous microplicae on the surface of the stratum corneum cells lining and surrounding the duct openings may be functionally significant. Nair & Schroeder (1981) suggested that the microplication of the cellular surfaces of the oral mucosa may form channels that aid in the laminar flow distribution of lubricating secretions over the surface. Similarly these microplicae may thus be aiding in the distribution of the sweat from these glands over the surface of the foot pads.

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CHAPTER 5

THE COMPARISON AND DISTRIBUTION OF THE SUDORIFEROUS GLANDS IN THE INDIGENOUS RODENT FAMILIES

INTRODUCTION

Specific skin glands have been investigated in only a minority of the rodent species (Sokolov 1982) and even fewer comparative studies included the sudoriferous glands of these mammals. This has probably contributed to the misconception among zoologists who claim that 'sweat glands are absent in rodents' (Schmidt-Nielsen 1964, 1972; Rowett 1974; Leake 1975). Sudoriferous glands were shown to occur in at least four general sites in North American rodents: (1) perineal area (2) mid-dorsal skin (3) skin of the oral lips and angle, and (4) the pads of the digits and the palmar and plantar sole (Quay 1965b) while Sokolov (1982) reported similar findings in the Eurasian rodents but with fewer species having sudoriferous glands in the former two sites. The results of this study on Southern African rodents are summarized in Table 2, and the findings compared and discussed phylogenetically, and the functional significance of these glands suggested in the light of the behavioural ecology of each species.

RESULTS AND DISCUSSION

1. Family **SCIURIDAE**

Xerus inauris - Cape Ground Squirrel

Paraxerus cepapi - Bush Squirrel

The sweat glands were found on the naked areas of both fore and hind feet of both species, including the plantar, palmar and distal toe pads, where they were most numerous (see Fig.38 - 41 for Xerus inauris and Fig.42 & 43 for Paraxerus cepapi). Glands were also found in the dermis of the naked soles lying parallel to the epidermis (Fig.41). The secretory tubules were situated mainly deep in the dermis where the connective tissue was less dense, lacking the usual adipose tissue except in the hind foot pads of Paraxerus cepapi (Fig.42). The excretory ducts extended straight through the dermis, into the well-pigmented epidermis and extended in a narrow helix through the thick stratum corneum (Fig.40). The ducts which extended to the epidermis on the sides of the pads

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TABLE 2. LOCATIONS OF THE SUDORIFEROUS GLANDS IN THE RODENTS STUDIED

SITES OF THE GLANDS:	FORE FEET			HIND FEET				OTHER
	TP	DR	FFP	TP	DR	HFP	S	AREAS
1. Family **SCIURIDAE**								
Xerus inauris	+++	+	++	+++	+	++	+	o
Paraxerus cepapi	+++	+	++	+++	+	++	+	o
2. Family **PEDETIDAE**								
Pedetes capensis	o	o	+	o	o	o	o	o
3. Family **HYSTRICIDAE**								
Hystrix africaeaustralis	+++A	o	+++A	+++A	o	+++A	+++	o
4. Family **THRYONOMYIDAE**								
Thryonomys swinderianus	o	o	o	o	o	o	o	+(ear)
5. Family **PETROMURIDAE**								
Petromus typicus	+++	o	+++	+++	o	+++	++A	o
6. Family **BATHYERGIDAE**								
Cryptomys hottentotus	o	o	o	o	o	o	o	o
7. Family **CRICETIDAE**								
Otomys irroratus	+++	+	+++	+++	+	+++	o	o
Otomys angoniensis	+++	+	+++	+++	+	+++	o	o
Mystromys albicaudatus	+++	o	+++	+++	o	+++	o	o
Saccostomus campestris	++	+	++	++	+	++	o	o
Tatera leucogaster	++	+	++	++	+	++	o	o
Tatera brantsi	++	+	++	++	+	++	o	o
Gerbillurus paeba	+	o	o	+	o	o	o	o
Desmodillus auricularis	o	o	+	o	o	o	o	o
8. Family **MURIDAE**								
Praomys natalensis	++	+	++	++	+	+++	o	o
Aethomys chrysophilus	+++	+	+++	+++	+	+++	o	o
Aethomys namaquensis	+++	+	+++	+++	+	+++	o	o
Thallomys paedulcus	+++	+	+++A	+++	+	+++	o	o
Dasymys incomtus	o	o	++	o	o	++	o	o
Mus minutoides	++	o	+++	++	o	++	o	o
Acomys spinosissimus	+++	+	+++	+++	+	+++	o	o
Lemniscomys griselda	++	+	++	++	+	+++	o	o
Rhabdomys pumilio	++	+	++	++	+	+++	o	o
9. Family **GLIRIDAE**								
Graphiurus ocularis	+++	+	+++	+++	+	+++	o	o
Graphiurus murinus	+++	+	+++	+++	+	+++	o	o

Legend: TP - distal toe pads
DR - digital ridges
FFP - front foot pads
HFP - hind foot pads
S - hind foot sole

+++ - abundant glands filling the pads
++ - numerous glands scattered through the dermis of the pads
+ - one or two glands in each pad
o - no sudoriferous glands observed
A - apocrine glands

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Fig.38 T.S. of a hind foot pad of Xerus inauris. The tubules of numerous sudoriferous glands (s) lie deep in the dermis (D) where it is less dense. The duct (d) spirals through the well-pigmented epidermis.

(Bar = 150µm)

Fig.39 T.S. of a front foot toe pad of Xerus inauris showing the digital bone (b) and claw (cl). The abundant secretory tubules of the sudoriferous glands (s) almost fill the toe pad dermis. The ducts spiral through the well-pigmented epidermis and its thick stratum corneum (Sc).

(Bar = 0,5mm)

Fig.40 T.S. of a front foot pad of Xerus inauris. The tubules of numerous sudoriferous glands (s) lie deep in the dermis. The ducts spiral (sp) through the well-pigmented stratum corneum (Sc). The duct at the bottom left, is redirected at an angle towards the main friction surface.

(Bar = 150µm)

Fig.41 L.S. of the sole of the hind foot of Xerus inauris. The tubules of the large sudoriferous glands (s) lie deep in the dermis parallel to the epidermis. The duct (d) runs at an angle through the dermis to the tubercle (arrow) on the sole surface.

(Bar = 0,3mm)

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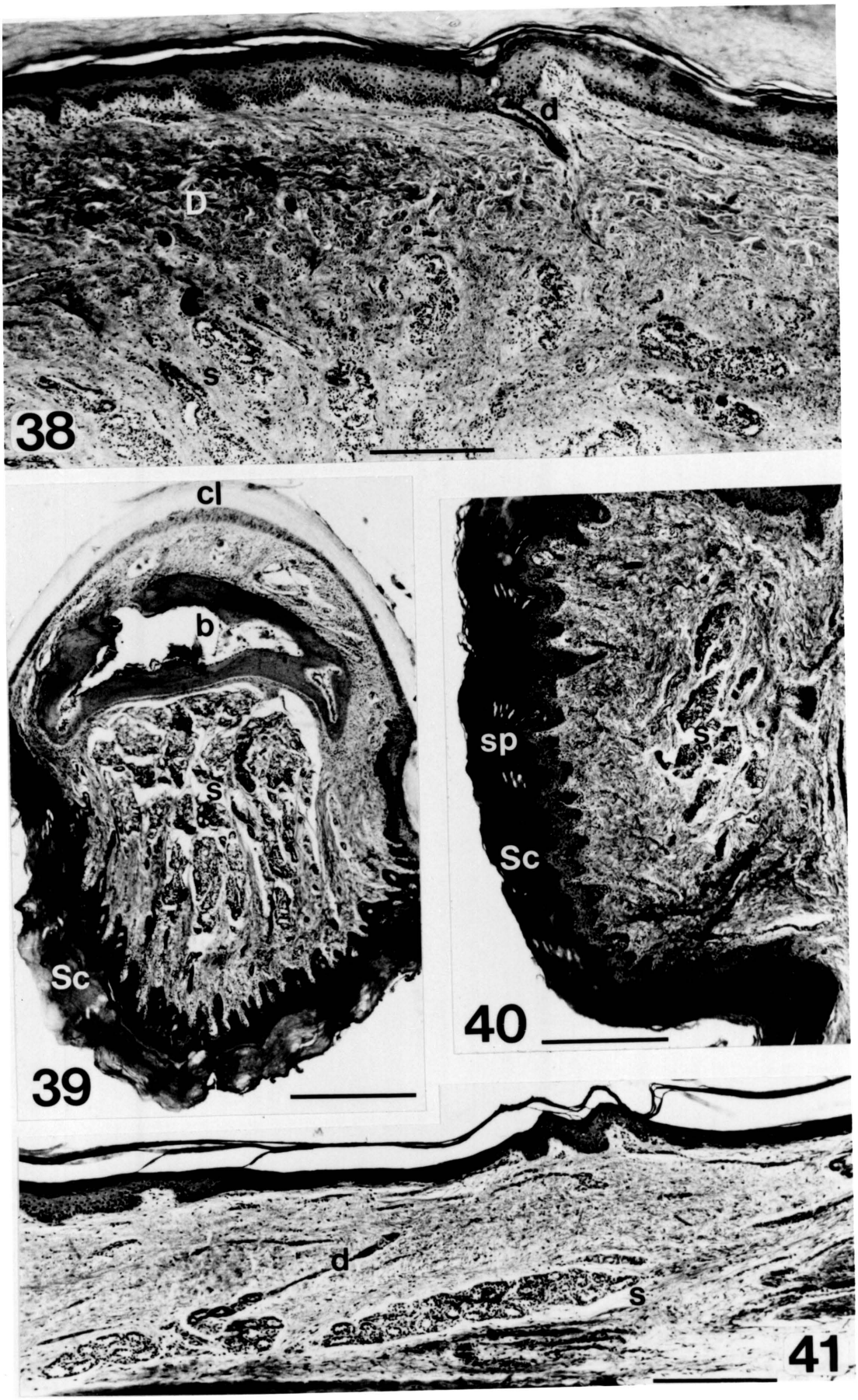

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Fig.42 L.S. of the sole of the hind foot of Paraxerus cepapi. The tubules of the sudoriferous glands (s) lie deep in the dermis which is less dense and interspersed with adipose cells (a). The ducts (d) run straight through the dense upper dermis (D) to the epidermis. (Bar = 150µm)

Fig.43 L.S. of a front foot toe pad of Paraxerus cepapi. The abundant secretory tubules of the sudoriferous glands (s) almost fill the toe pad dermis. The well-pigmented epidermis (E) and its stratum corneum are thick.

(Bar = 0,4mm)

Fig.44 L.S. of the palmar pad of Pedetes capensis showing the single sudoriferous gland tubule (s) and its duct (d) deep in the dermis.

(Bar = 200µm)

Fig.45 A high power view of the duct of the single sudoriferous gland in the palmar pad of Pedetes capensis showing the transition area (tr) between the secretory tubule and the excretory duct (d). The double cell layer of the excretory duct is evident with the luminal cells enclosing the wide lumen, being distinctly columnar and resting at right angles on the flattened basal layer. The duct lumen narrows down and is surrounded by a multi-cell layer which changes from columnar to low cuboidal as the duct moves up the epidermal interpapillary peg.

(Bar = 50µm)

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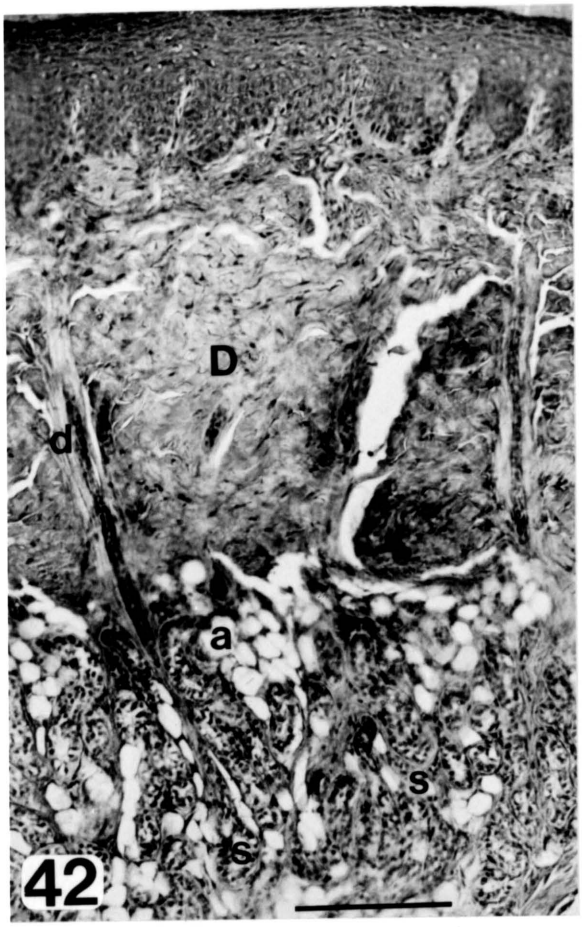

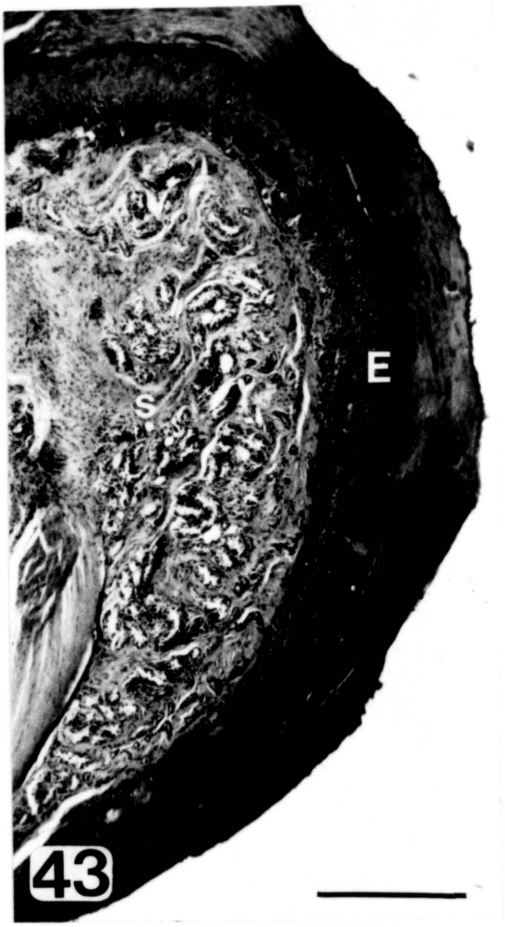

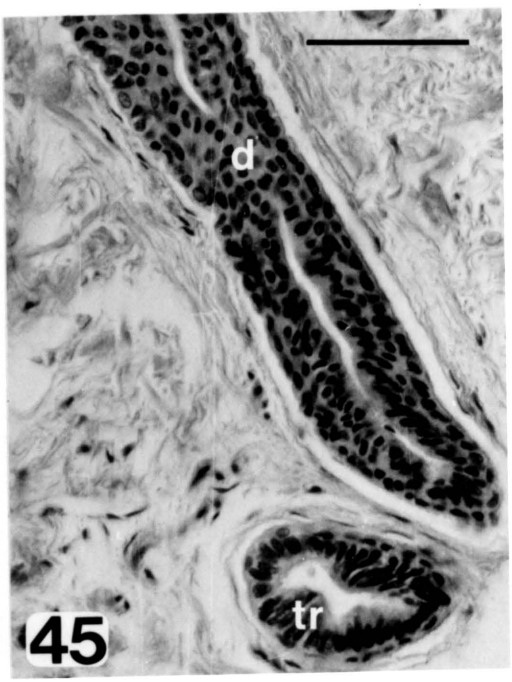

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were redirected at an angle through the stratum corneum to open on the contact friction surfaces of the pads (Fig.40). The ducts of the glands in the naked soles did not open onto the surface of the sole, but ran at an angle anteriorly, almost parallel to the epidermis to the nearest minor plantar pad or tubercle (Fig.41) where it opened onto the friction surface of the epidermis as similarly described for the other glands of the pads. No differences between the glands or their distribution in these two species were noted.

Of all the rodent families the Sciuridae have been most widely investigated generically in terms of specialised skin glands and these studies have shown that the Sciurids, and in particular the ground squirrels have retained well-developed functional sudoriferous glands (Quay 1965b; Kivett et al. 1976; Sokolov 1982). These glands include both eccrine and apocrine glands, and were shown to occur in at least four general sites in the North American sciurids: (1) mid-dorsal skin (2) anal glands (3) skin of the oral angle, and (4) the pads of the digits and the palmar and plantar soles (Quay 1965b).

The mid-dorsal glandular field is composed of many, greatly enlarged individual sudoriferous glands with an apocrine-type secretory process. The secretion is collected in a sinus which opens through a short duct directly onto the surface of the skin (Kivett et al. 1976; Kivett 1978).

The anal glands had three extrusible papillae, one median and two lateral to the anal opening (Kivett et al. 1976). In the North American sciurids Spermophilus(=Citellus) richardsonii (Sleggs 1926) and Spermophilus columbianus (Kivett 1978) each anal gland consisted of enlarged sebaceous glands and apocrine glands which secrete through the common papillae channel.

Sudoriferous glands in both of these sites are known to occur only in some of the ground squirrels including the North American Spermophilus richardsonii (Sleggs 1926) and Spermophilus lateralis (Hatt 1926). Quay (1965b) again reported the occurrance of mid-dorsal apocrine glands in Spermophilus tereticaudalis and Ammospermophilus leucurus supporting the views of these authors that the glands in both these areas may be functionally

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significant in olfactory communication. A comparative study of the scent-gland location and related behaviour in six nearctic ground squirrel species (including Spermophilus columbianus, S.undulatus, S.tridecemlineatus, S.richardsonii, S.franklinii and S.lateralis) showed how the functional structure of the mid-dorsal and anal glands closely reflected the phylogeny of these North American ground squirrel species (Kivett et al. 1976). Yet in the related Citellus(=Spermophilus) undulatus from Asia, Skurat (1972) in Sokolov (1982) found only anal glands but no mid-dorsal glands. As can be seen in Table 3., Sokolov (1962, 1982) could find no other Eurasian sciurid species which had mid-dorsal or anal sudoriferous glands. The African species, Xerus inauris and Paraxerus cepapi from South Africa, and Atlantoxerus getulus from North Africa (Skurat 1972 in Sokolov 1982) follow this pattern of the Old World sciurids.

Greatly enlarged sudoriferous glands in the oral angle and lips have been described by Quay (1965a) as occuring with the sebaceous glands in a number of North American sciurids, including Spermophilus richardsonii, S.armatus and S.lateralis. Similarly, the very large apocrine glands which form the oral glands in Spermophilus undulatus, S.tridecemlineatus, S.richardsonii, S.franklinii, S.lateralis (Kivett et al. 1976) and S.columbianus (Kivett 1978) were described and the functional marking behaviour using these oral glands by these species was discussed by these authors. Quay (1965a) however clearly showed that these sudoriferous glands were not found in many sciurid species (including Tamias striatus, three species of Eutamias and Funambulus palmarum) but all these species had sebaceous glands in their oral angles. As can be seen from Table 3, some of the Eurasian species have oral glands consisting of enlarged sudoriferous and sebaceous glands, but this is not consistent even in the related Citellus species (Skurat 1972 in Sokolov 1982; Sokolov 1982). In the African sciurids included in this study, Xerus inauris and Paraxerus cepapi, only sebaceous glands were found in the oral angle, which was also the case in Atlantoxerus getulus from North Africa (Skurat 1972 in Sokolov 1982). Van Heerden & Dauth (1987) reported the same findings for Southern African Xerus inauris, indicating that sweat glands were absent but that the sebaceous glands in the lips were well developed.

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TABLE 3. COMPARISON OF THE SITES OF SUDORIFEROUS GLANDS IN VARIOUS SCIURID SPECIES.

Sciurid species	Feet			Oral Angle	Perineal area	Mid-dorsal skin
	HFP	FFP	TP			
AFRICAN SPP.						
Xerus inauris	++	++	++	o	o	o
Paraxerus cepapi	++	++	++	o	o	o
EURASIAN SPP.						
Spermophilopsis leptodactylus	++	++	-	++	o	o
Sciurus vulgaris	++	++	-	++	o	o
Citellus undulatus	++	-	-	++	++	o
Citellus pygmaeus	++	++	-	o	o	o
Citellus suslicus	++	++	-	o	o	o
(Sokolov 1962, Skurat 1972 *in* Sokolov 1982, Sokolov 1982)						
N. AMERICAN SPP.						
Spermophilus richardsonii	-	-	-	++	++	++
Spermophilus lateralis	-	-	-	++	++	++
Spermophilus columbianus	++	++	-	++	++	++
Spermophilus tereticaudalis	-	-	-	++	-	++
Ammospermophilus leucurus	++	++	++	+	-	++
(Hatt 1926, Sleggs 1926, Quay 1965a, 1965b, Kivett 1978)						

Legend: HFP - Hind foot pads
FFP - Front foot pads
TP - Distal Toe pads

++ Abundant, well-developed glands
+ Few, atrophic glands
o No sudoriferous glands in histological studies
- Sites not included in studies

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Eccrine sweat glands were found on the fore and hind foot pads as well as the digital pads in each species where these sites were investigated (Table 3), except in Xerus inauris where Van Heerden & Dauth (1987) reported a complete absence of sweat glands. However, in many sciurid species sudoriferous glands were reported to be present only on the naked soles and pads of the feet as shown by Sokolov (1962). He compared skin samples from different parts of the bodies of the Eurasian desert squirrel Spermophilopsis leptodactylus with those of the forest and steppe squirrels, Sciurus vulgaris, Citellus pygmaeus and C.suslicus, and reported that sweat glands were present only in the soles of the paws in all these species. Because of the nature of the concentration of these glands they have been termed 'pedal glands' (Kivett 1978) and 'sole glands' (Sokolov 1982).

The distribution and structure of the tubular glands in Xerus inauris and Paraxerus cepapi were very similar to those described in the North American sciurids Ammospermophilus leucurus (Quay 1965b) and S.columbianus (Kivett 1978). However, they differed somewhat from those glands described in the hind sole of Atlantoxerus getulus from North Africa, as - "small glomeruli of tubular glands surrounded by fat cells, with ducts opening on to the skin surface" (Skurat 1972 in Sokolov 1982). Also in the Eurasian Sciurus persicus the hind soles have tubular glands forming large glomi with secretory ducts opening onto the sole surface (Sokolov 1982). The ducts from the glands in the hind sole of both Xerus and Paraxerus do not open directly onto the sole surface but run parallel to the epidermis to open only on the nearest minor pad or tubercle surface. These tubular glands were not surrounded by fat cells except in the plantar pads of Paraxerus cepapi, and were not considered to be small (Fig.41) when compared to those of the other rodents studied. This may be a relative observation as Sokolov (1962, 1982) clearly showed that the lumen diameter of the secretory tubules varied between the Eurasian species. However, the seasonal differences in lumen diameter between the glands in summer, and the atrophied winter glands in the same species was greater than the interspecific differences, with the lumen diameters increasing by between five and seven times in the active summer glands (Sokolov 1962).

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Only Quay (1965b) noted eccrine sweat glands in the digital pads of Ammospermophilus leucurus and described them as being similar in distribution and structure to the glands in the toe pads of the white rat, which have been well described (Ring & Randall 1947; Munger & Brusilow 1971). The glands in Xerus inauris and Paraxerus cepapi fit this description but the individual glands are more distinctly separated by connective tissue septa in the distal toe pads. Sweat glands in each of the digital ridges as found in the above species were not mentioned by the workers investigating glands in the feet of other sciurids (Sokolov 1962, 1982; Quay 1965b).

Xerus inauris have a characteristic habit, on emerging from their burrows in the morning, of scraping a small shallow hole and urinating in it or pressing the anal region into it which Herzig-Straschil (1978) believes to be a marking behaviour. Probably the perineal sebaceous glands are involved in this behaviour but Kivett (1978) observed vigorous clawing of the substrate prior to scent marking in the North American sciurid Spermophilus columbianus and he suggested that the 'pedal gland' scent produced by the sweat glands on the volar surfaces of the foot pads may also be deposited. This concept is reinforced by Steiner (1974) in his comparisons of scent-related behaviour in ground squirrels, where he further suggests that a mixture of scent from the oral glands and palmar pads may be further spread over the body during allogrooming which often starts by wiping the oral glands with the paws. In view of the similarity of the pedal glands in both of these ground squirrels, it is suggested that Xerus inauris may also use these glands for marking.

Sokolov (1962) on commenting on the large size of the sweat glands in the paws of the Eurasian desert ground squirrel Spermophilopsis leptodactylus, suggested that if these are 'recognitional' glands, they reflect the activity of the animal and the great distance it moves away from its burrow. Similarly Xerus inauris, also being a semi-desert diurnal mammal, must have feet which can tolerate the high temperatures of the hot ground. The position which Xerus inauris takes when feeding during the heat of the day is described by Van Heerden & Dauth (1987) as standing on the toes of the hindlegs, which ensures minimal body contact with the hot

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soil surface. Sand surface temperatures of 56°C were reported by Haacke (1975) in western Botswana, while in the Kalahari up to 70°C was recorded by Bothma (1980). Thus an additional function of these sudoriferous glands may be to keep the surface of the pads, which are in contact with the hot substrate, moist and pliable to minimize abrasion, as well as keeping the pads comfortably cool. This thermoregulation of the feet has been suggested for the Columbian ground squirrel Spermophilus columbianus (Kivett 1978) and proved experimentally in cats where they started sweating on the pads of their paws under extreme temperatures (Sperling & Koppanyi 1949).

Two further forms of marking have been noted in Xerus inauris by Herzig-Straschil (1978) whereby members of a group identify each other by nose touching which is used as a greeting ceremony and secondly, rubbing their snouts on stones near the burrow. Both of these have been functionally described in the North American ground squirrels as marking behaviour, spreading the secretions of the sudoriferous and sebaceous glands of the oral angle (Steiner 1974; Kivett et al. 1976; Kivett 1978). Similarly, 'mouthwiping' as a form of territorial marking has been described in Paraxerus cepapi by Viljoen (1975). Both of these indigenous species have thus retained the typical behaviour patterns but using the large sebaceous glands only, as they lack the sudoriferous glands prominent in the American species.

2. Family **PEDETIDAE**

Pedetes capensis - Springhaas

A single large sudoriferous gland was found in the hairless palmar pad of the fore foot. The remainder of the surfaces of both fore and hind feet were covered with bristly hair (Smithers 1983) and no sudoriferous glands were found, even in the partially hairless plantar pad of the hind foot.

The loosely coiled secretory tubule lay deep in the loose connective tissue of the hypodermis, parallel to the epidermis (Fig.44). The secretory tubule was lined with a single layer of cuboidal cells containing large round to oval, centrally situated nuclei. The lumen of this tubule was large. At the transition between the secretory tubule and the excretory duct, the double

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cell layer became evident with the luminal cells being distinctly columnar and resting at right angles on the flattened basal layer (Fig.45). The lumen was the widest at this point and narrowed down again in the excretory duct. The well-developed interpapillary peg extended way down through the dermis almost to the secretory tubule of the gland. The excretory duct maintained a distinct luminal border within the papillary peg. As it spiralled through the epidermal layers the duct lumen enlarged .

When compared to a similar sized mammal that also lives in burrows such as the rabbit Oryctolagus cuniculus, then the description of the sweat gland distribution is uniquely similar. There are no sweat glands on the general hairy body skin (Jenkinson 1970), except in the specialised inguinal and chin glands (Mykytowycz 1966) which are not found in the Springhaas. The furry paws of the rabbit also lack sudoriferous glands (Jenkinson 1970) but the planum nasolabiale of the rabbit has tubular sudoriferous glands (Sperling & Koppanyi 1949) which is typical of all the domestic mammals (Frandson 1974). In the Springhaas however, there are no sudoriferous glands in the planum nasolabiale which is specialised to form a small rhinarium which allows the nostrils to be closed for burrowing (Smithers 1983). A lack of these glands may be an further specialisation for burrowing to limit the sticking of soil to the rhinarium as is clearly seen on a dog that has buried a bone.

3. Family HYSTRICIDAE

Hystrix africaeaustralis - Cape Porcupine

Large sweat glands were found on the naked areas of both fore- and hind feet, including the whole of the palmar and plantar soles (Fig.46) and the toe pads (Fig.47) where they were most numerous. The secretory tubules had distinctive open lumens and were situated mainly deep in the dermis below the dense connective tissue, where they were arranged in lobules interspersed with adipose tissue and surrounded by thick connective tissue septa (Fig.46). A few large apocrine glands were found deeper in the hypodermis below the normal eccrine glands. These had large open lumens (with diameters of up to 100µm) surrounded by a single layer of cuboidal secretory cells (Fig.47 & 48). In the active apocrine glands cytoplasmic protrusions were seen on the luminal

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Fig.46 L.S. through the hind foot heel of Hystrix africaeaustralis. The secretory tubules (s) of the abundant eccrine glands had distinctive open lumens and are situated mainly deep in the dermis below the dense connective tissue. They are convoluted in lobules, interspersed with adipose tissue (a) and surrounded by thick connective tissue septa (S). A few large apocrine glands (ap) are found deeper in the hypodermis below the normal eccrine glands. The excretory ducts (d) curves through the dermis into the deep funnel-shaped interpapillary pegs (f), in which they spiralize to the surface.

(Bar = 0,5mm)

Fig.47 L.S. through the front foot toe pad of Hystrix africaeaustralis. Even though the secretory tubules (s) of the eccrine gland has distinctly open lumens, these are small when compared to the wide lumens of the adjacent apocrine gland (ap). The arrow in the lumen indicates some of the cytoplasmic protrusions typical of active apocrine secretory cells. (Bar = 50µm)

Fig.48 A high power view of a portion of the secretory tubule of an apocrine gland in the hind foot toe pad of H. africaeaustralis. The flattened cuboidal secretory cells lacking cytoplasmic protrusions are indicative of a 'spent' or inactive portion of the gland. Note the large luminal diameter.

(Bar = 50µm)

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surfaces of the secretory cells (Fig.47). The excretory ducts curved through the dermis into the deep funnel-shaped interpapillary pegs, in which they spiralized tightly through the well-pigmented stratum malpighii (Fig.14) before extending in a narrow helix through the thick stratum corneum. The ducts which extended to the epidermis on the sides of the pads were redirected at an angle through the epidermis to open on the contact friction surfaces.

The feet of H. africaeaustralis are large and glabrous, with the ventral surfaces being made up of folded cushions. This differs sharply from the typical rodent foot structure, lacking the distinct distal digital toe pads, digital ridges and prominent palmar and plantar pads. However, abundant sweat glands occurred throughout these naked cushioned areas of the feet of the Cape porcupine. The distribution is the same as described in the Eurasian porcupine H. leucura by Sokolov (1982) where the sole glands , formed by eccrine sweat glands, are found on both front and hind feet, being most numerous in the skin of the toes. No mention was made of apocrine glands in this species. However, a similar pattern of a few large apocrine glands scattered among the abundant eccrine glands has been decribed in the foot pads of the dog (Adam, et al. 1970) and the coyote (Sands, et al. 1977).

The glands of H. africaeaustralis were the largest in size of all the species studied, having a very active-appearance as indicated by the well-developed secretory cells and the large open lumens of the secretory tubules. The reason for these abundant active sudoriferous glands in the feet may be explained by their almost exclusive nocturnal behaviour (Smithers 1983), when they cover considerable distances of up to 16 km in a night in search of food (Kingdon 1974; De Graaff 1981). Even though they like to follow paths, their normal shuffling plantigrade gait (Kingdon 1974) is well suited for a scent trail to be left by these eccrine glands, but more specifically by the large apocrine glands which are likely to be odoriferous. This would be easy for the porcupine to follow back to its warren with its keen sense of smell (De Graaff 1981).

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4. Family **THRYONOMYIDAE**

Thryonomys swinderianus - Greater Canerat

A few small sweat glands were found only in the relatively hairless areas of skin behind the ears. Each gland was found associated with a group of hair follicles deep in the dermis (Fig.49). The sweat duct narrowly spiralled through the dermis (Fig.50). These post-auricular glands were unique only to T. swinderianus , along with the fact that no other areas of the skin or feet revealed sweat glands.

Although the feet of T. swinderianus are also glabrous and very similar to those already described for the Cape porcupine H. africaeaustralis, the total absence of sweat glands stands in sharp contrast (compare Fig.51 & 46). This observation together with the few individual sudoriferous glands in the hairless skin behind the ear pinnae, make the canerats unique among the rodents studied. The only other species totally lacking sudoriferous glands on the nacked pads of its feet is the mole-rat Cryptomys hottentotus (Fig.52). A possible interpretation for this distribution might be related to the fact that they are limited in the extent of their movements by using distinct runs, which criss-cross their relatively small home ranges in the reedbeds. As much of the surface substrate is wet or moist, a scent trail produced by sweat glands would be diluted and quickly diffused in the moisture, particularly as these animals are fond of swimming and playing in the water (De Graaff 1981). The canerats are likely to know every run throughout their limited home range. This, together with the possible scent marking of the plants which line their runs, with their post-auricular glands as they move through the dense vegetation, may suffice the olfactory communicatory needs of this species. Similar post-auricular glands consisting of simple coiled tubular sweat glands were found to be the main source of musk odour production in the shrew Suncus murinus by Dryden and Conway (1967).

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Fig.49. The tightly spiralled tubule (s) of a sudoriferous gland in the post-auricular skin of Thryonomys swinderianus. Each tubule forms a compact lobule (arrow) associated with a group of hair follicles (h) deep in the dense connective tissue of the dermis.

(Bar = 120µm)

Fig.50. The duct of the tubule (s) of a sudoriferous gland in the post-auricular skin of T. swinderianus, winding through the dermis.

(Bar = 150µm)

Fig.51. L.S. through the hind foot pad of T. swinderianus. Note the complete lack of sudoriferous gland tubules in the dermis (D), or funnel-shaped interpapillary pegs for the ducts in the epidermis (E) and no duct spirals through the thick stratum corneum (Sc).

(Bar = 200µm)

Fig.52. L.S. through the front foot pad of Cryptomys hottentotus. Note the complete lack of sudoriferous gland tubules in the dermis (D), or funnel-shaped interpapillary pegs for the ducts in the epidermis (E) and no duct spirals through the thick stratum corneum (Sc).

(Bar = 150µm)

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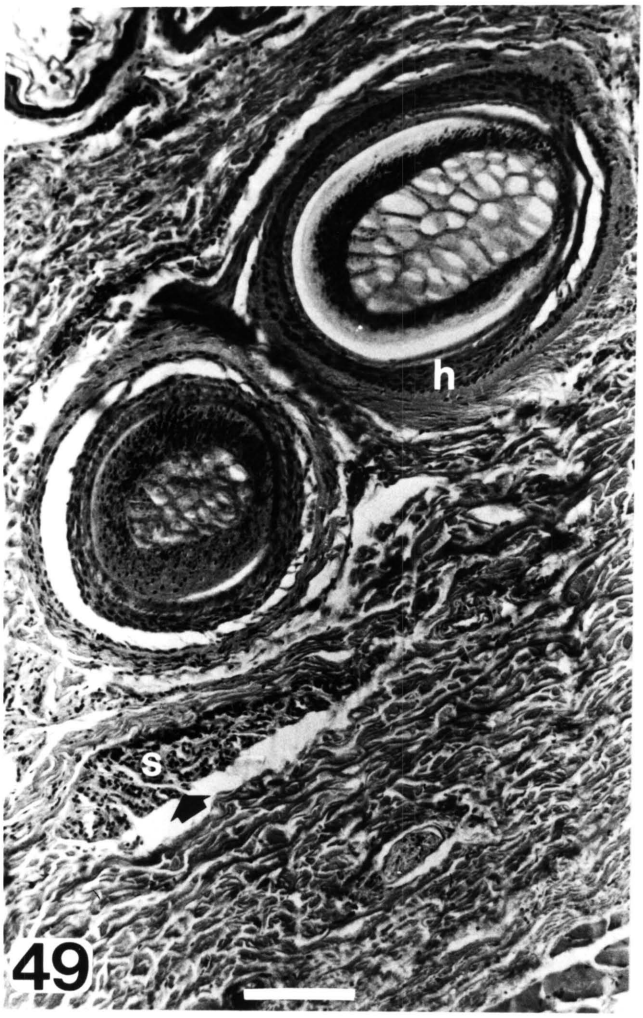

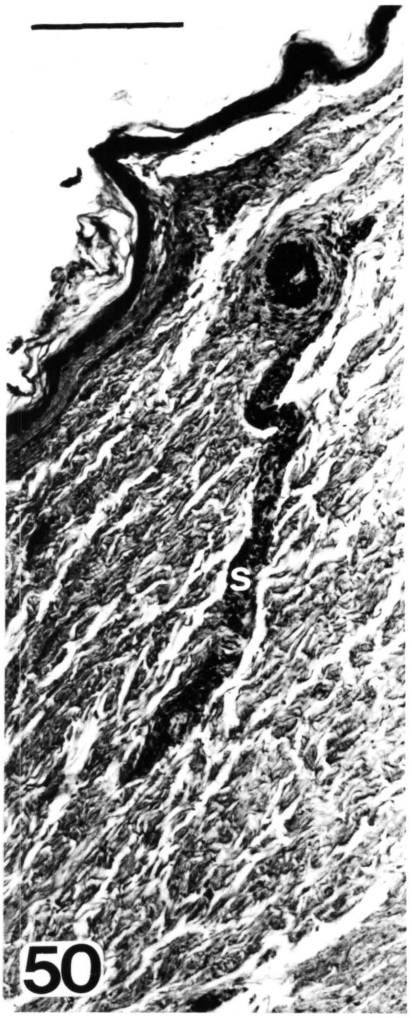

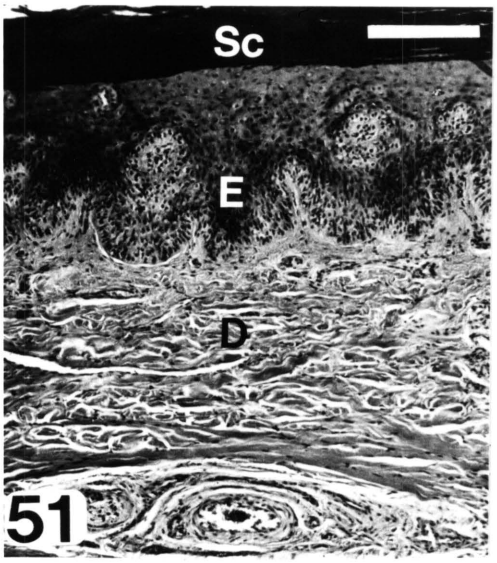

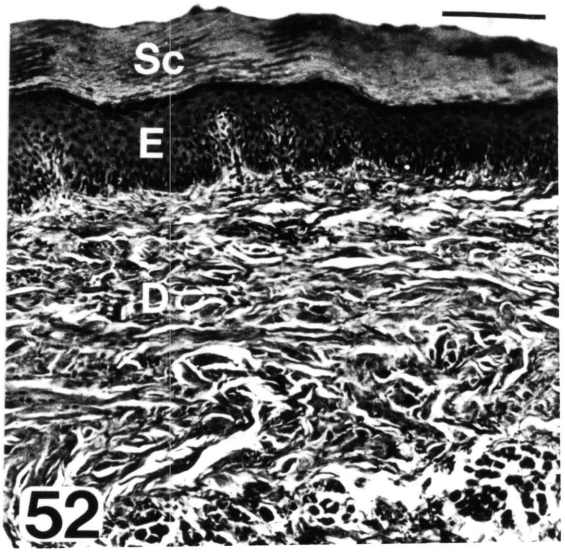

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5. Family **PETROMURIDAE**

Petromus typicus - Dassie Rat

Abundant sudoriferous glands were found on the naked areas of both fore and hind feet, being particularly concentrated in the very well-developed palmar and plantar pads, and glands were also found opening directly onto the naked soles (Fig.53). Eccrine glands were most numerous on the enlarged distal toe pads (Fig.54). No glands were found in the digital ridges. The secretory tubules were situated mainly deep in the dermis where the connective tissue was far more dense, lacking the usual adipose tissue (Fig.53 & 54). Some of the tubules reached into the capillary rich hypodermis. The secretory tubules of the eccrine glands were lined by cuboidal secretory cells which surrounded the open lumens (Fig.54). The intertwined tubules of each gland were separated by dense connective tissue into distinct lobules (Fig.53 & 54).

A number of apocrine glands were found in the soles of the hind feet. These large glands were situated in the hypodermis below the level of most of the eccrine glands (Fig.53). Their secretory cells appeared flattened like those of 'spent' or exhausted apocrine tubules. Their lumens were large (with diameters of up to 60µm) and filled with a dark staining eosinophilic luminal content (Fig.55).

The excretory ducts extended straight through the dermis, and straight through the well-pigmented interpapillary pegs (Fig.16) before following in a narrow spiral through the thick stratum corneum (Fig.56). The ducts which extended to the epidermis on the sides of the pads were redirected at an angle through the epidermis to open on the contact friction surfaces (Fig.56). The secretory ducts opened into shallow cup-like depressions in the epidermis of the ventral surfaces, which were covered with low epidermal ridges (Fig.56, also see Fig.34 & 35).

In P. typicus the macroscopic specialisations of the feet have been noted and described in relation to their function. Smithers (1983) described the under surface of both the fore and hind feet as being naked and having well-developed pads, an adaptation to moving on a rocky substrate. These enlarged digital and foot pads

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Fig.53. L.S. of the hind foot sole of Petromus typicus. The tubules (s) of numerous sudoriferous glands are arranged in lobules, with their ducts (d) running at an angle through the dense dermis into the well-developed funnel-shaped interpapillary pegs of the thick epidermis (E). Large apocrine glands (ap) are seen in the hypodermis.

(Bar = 0,5mm)

Fig.54. T.S. of the hind foot toe pad of P. typicus. Cuboidal secretory cells line the open lumens of the tubules (s) of the abundant sudoriferous glands. These tubules are arranged in lobules which are separated by connective tissue septa.

(Bar = 100µm)

Fig.55. A high power view of a T.S. through an apocrine gland (ap) in the hind foot sole of P. typicus. The wide tubule is lined by flattened secretory cells, and filled with a dark staining eosinophilic luminal content. The tubules are surrounded by a loose connective tissue sheath (sh). The tubules (s) of an adjacent eccrine gland are included for comparison.

(Bar = 40µm)

Fig.56. L.S. of the hind foot toe pad of P. typicus. The ducts (d) spiral only slightly as they pass through the funnel-shaped interpapillary pegs (f) and epidermis. However, they spiral through the thick stratum corneum in narrow helixes (sp) as they are redirected at an angle to the friction surface. Here the ducts open into shallow cup-like depressions (de & arrows) between the low epidermal ridges.

(Bar = 150µm)

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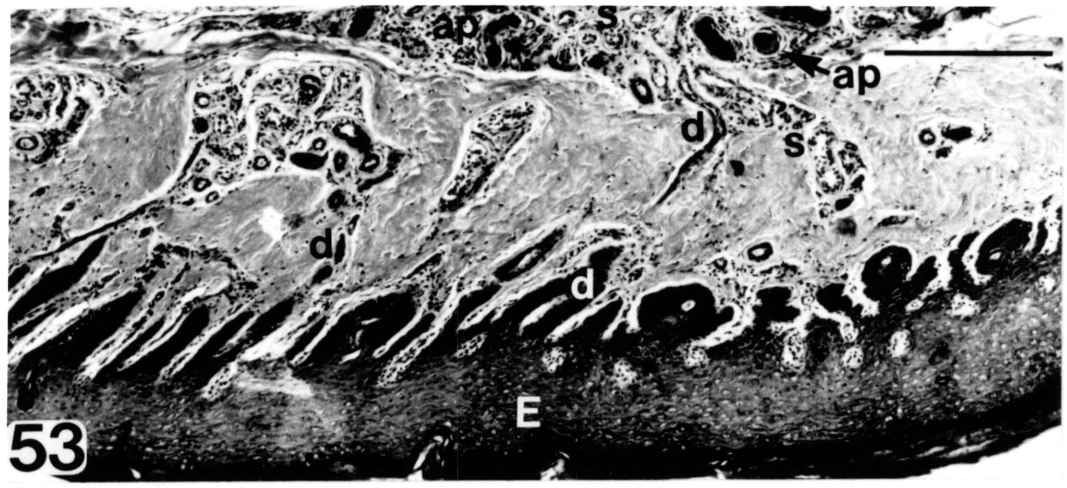

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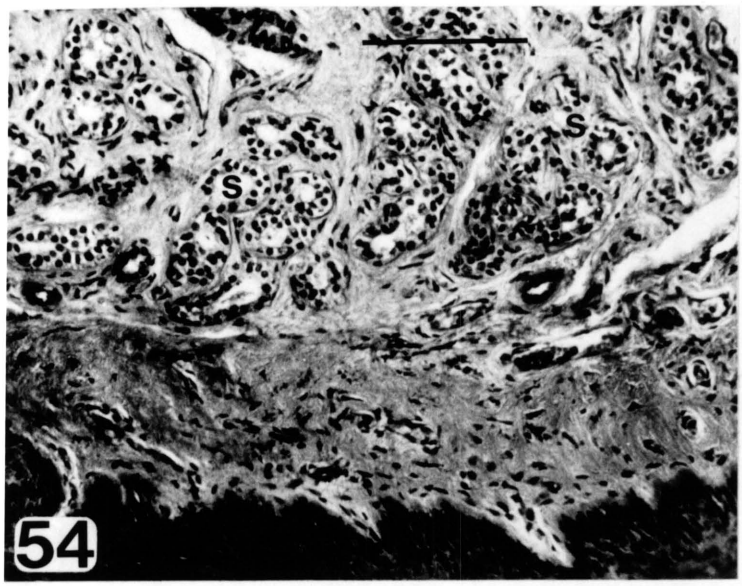

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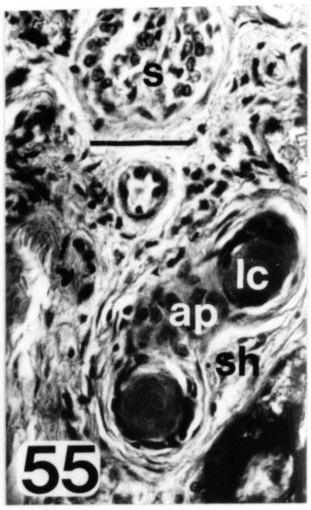

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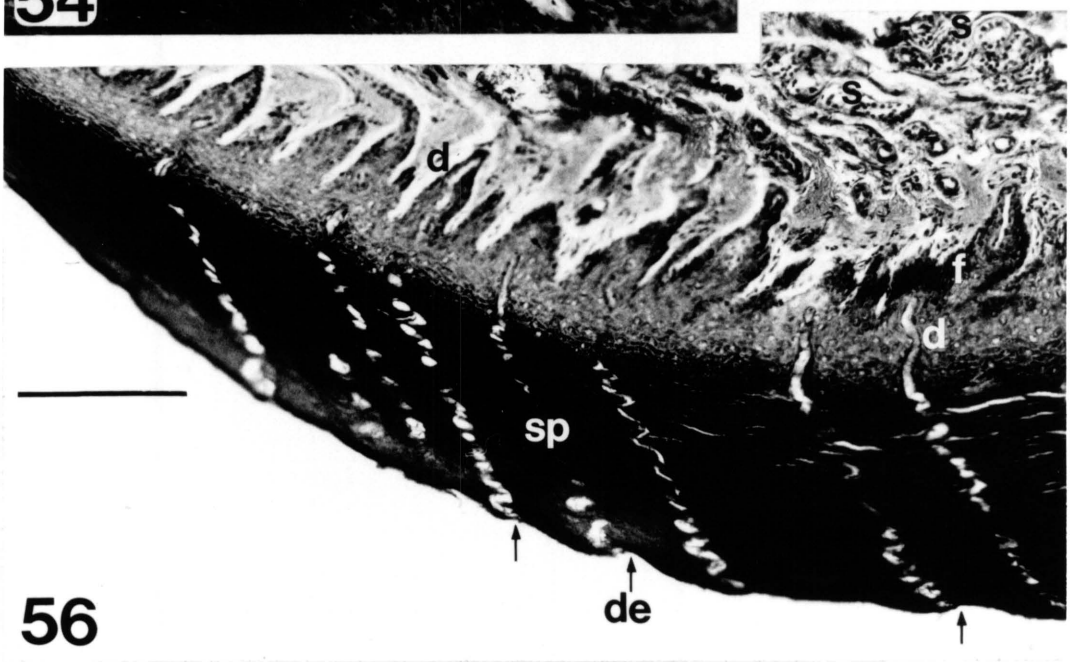

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are filled with large active eccrine glands which may help to enhance this function in three ways. First, the secreted sweat would moisten the frictional surfaces and improve traction for climbing as has been experimentally shown in the dog, tenrec, and particularly in the rat and the hyrax (Adelman, et at. 1975). Secondly, the moisten epidermal layers would help to make the stratum corneum more pliable which improves the contact area of the pads on the substrate (Adams & Hunter 1969), lessens the abrasion factor on the stratum corneum (Adelman, et at. 1975) and increases tactile sensitivity, all of which are important to the animal which moves quickly over uneven rocky surfaces. Because P. typicus is diurnal living in a hot arid habitat which requires moving over hot dry rocks (where the sand surface temperature has been measured up to 70°C by Bothma 1980), a third function of these large glands may be not only to continuously supply the sweat needed for the above functions, but also may help to cool the foot pads or at least to moisten the thick stratum corneum in order to limit the amount of heat penetrating the underlying living tissues. The function of the large apocrine glands may be odoriferous in order to leave a longer lasting scent from the sole glands, as ordinary sudoriferous sweat would evaporate quickly under these hot conditions.

6. Family **BATHYERGIDAE**

Cryptomys hottentotus - Common Molerat

No sudoriferous glands were found on the feet of this species (Fig.52) or any other areas of the skin studied, even though its large naked feet were similar to those of other rodents. In sharp contrast to all the other rodents studied, this was the only species in which sudoriferous glands were found to be totally lacking.

This lack of sudoriferous glands was also reported in the naked mole-rat Heterocephalus glaber (Sokolov 1982) while Quay (1965a) could find no sudoriferous glands in the oral angle or lips of this species. This diminishing of sweat glands particularly on the soles of the feet seems to be a trend amongst fossorial mammals as reflected in some of the true moles. Giacometti & Machida (1965) found that even though simple tubular glands were found over the entire hairy skin of the mole Scapanus townsendii, the palms and

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soles had no glands. Sweat glands are very sparse on the body of the mole Talpa europaea and no glands are found on the sole callosities (Sokolov 1982).

As a fossorial mammal living in a tunnel system which has its own microclimate, the need to have sweat glands is virtually absent. The thermoregulatory function of sweat glands would be limited in the burrows where evaporative cooling and air movement is minimal (McNab 1979). The high relative humidity and relatively cool temperatures , together with the moistness of the soil surface in the closed burrows would probably be sufficient to keep the thick stratum corneum of the naked feet pliable, as digging is mostly a seasonal activity, which is carried out when the soil is relatively soft or moist (Kingdon 1974). A scent trail produced by sudoriferous glands is unnecessary as the rodent-moles are committed to a limited subterranean tunnel existence, and such glands may only have functioned on the rare occasions of them coming onto the surface in helping them to relocate their tunnel entrances. However, their sense of smell seems to be poorly developed (De Graaff 1981; Smithers 1983).

7. Family CRICETIDAE

Although a number of specialised glandular areas have been reported in various species of Cricetidae, they all consist of enlarged or modified sebaceous glands. These sites include 'flank glands', 'rump glands', 'caudal glands' and 'hip glands' in the microtine rodents (Quay 1968; Stoddart 1976; Jannett 1975; Sokolov 1982) and 'ventral/abdominal glands', 'anal glands' and 'costovertebral spot' in the Old World cricetines (Strauss & Ebling 1970; Stewart & Brooks 1975; Sokolov 1982). The present study confirmed such areas of sebaceous gland activity in some African cricetines. However, sudoriferous glands have been reported in only two areas in the cricetines. The first of these are apocrine glands in the oral angle as first shown in the microtines by Quay (1962), and in an extensive survey of 79 species of 10 families Quay (1965a) showed these glands to be present in a number of other rodents. This was also confirmed by Sokolov (1982). Quay (1965a) concluded that within the Cricetidae,

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the presence or absence of these sudoriferous glands in the oral angle or lips appears in a general way to be a subfamily characteristic, with the glands being present in nearly all microtines and New World cricetines, but lacking from the gerbillines and Old World cricetines. The results of the present study confirmed this lack of sudoriferous glands in the oral angle of the African Cricetidae.

The second area is the hairless surfaces of the feet where eccrine sweat glands are usually concentrated in the palmar, plantar and digital pads. The variation in abundance and distribution of sudoriferous glands within the species of this family, is probably a reflection of specialization of the species to extremes of habitat as illustrated by the 'vlei rats' and the semi-desert gerbils. The size or development of the foot pads was indicative of the abundance and development of the sweat glands. The more well-developed the pads, the greater the number of glands which fill each pad.

The sequence in which the species in the family Cricetidae will be described and discussed, will not follow the taxonomically acceptable pattern as set out in Table 1 (after De Graaff 1981), but they have been rearranged according to the abundance and distribution of their sudoriferous glands. Although the latest taxonomic work on Southern African mammals includes the Cricetidae under the Family Muridae (Meester, Rautenbach, Dippenaar & Baker 1986), these two Families have been retained in order to compare the results with the work done on other exotic species that are described under the separate Families Cricetidae and Muridae (Quay 1962, 1965a, 1965b; Sokolov 1982).

Otomys irroratus - Vlei Rat

Otomys angoniensis - Angoni Vleirat

In both these species abundant sweat glands were found on the naked areas of both fore and hind feet, particularly in the large palmar (Fig.57) and plantar pads (Fig.58) and the distal toe pads. In each of the digital ridges, there was a well-developed sweat gland with its sweat duct opening onto the ventral surface of the ridge (Fig.59). Glands were not found on the naked soles. The well-developed secretory tubules were situated mainly deep in the

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Fig.57 L.S. through a front foot pad of Otomys angoniensis. Tubules of the sudoriferous glands (s) lie deep in the dermis in lobules surrounded by connective tissue septa.

(Bar = 150µm)

Fig.58 T.S. through a hind foot pad of Otomys angoniensis. Tubules of the sudoriferous glands (s) lie deep in the dermis in lobules interspersed with adipose tissue (a). The dense connective tissue (Ct) just beneath the epidermis (E) contains many elastic fibers showing up black with Verhoeff's elastin stain.

(Bar = 300µm)

Fig.59 L.S. through a digital ridge (DR) on a front foot toe of Otomys irroratus. Tubules of the single sudoriferous gland (s) lie parallel in the dermis with the straight duct running up to open on the ventral surface through the duct opening (do).

(Bar = 30µm)

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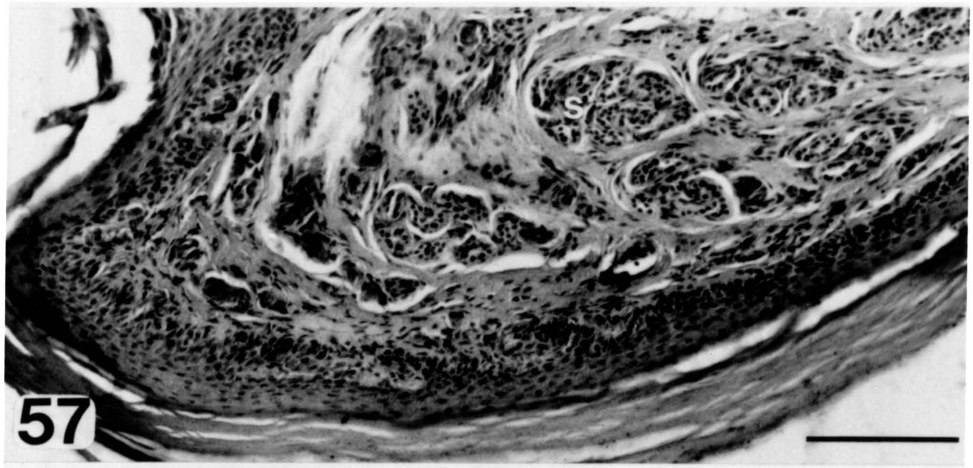

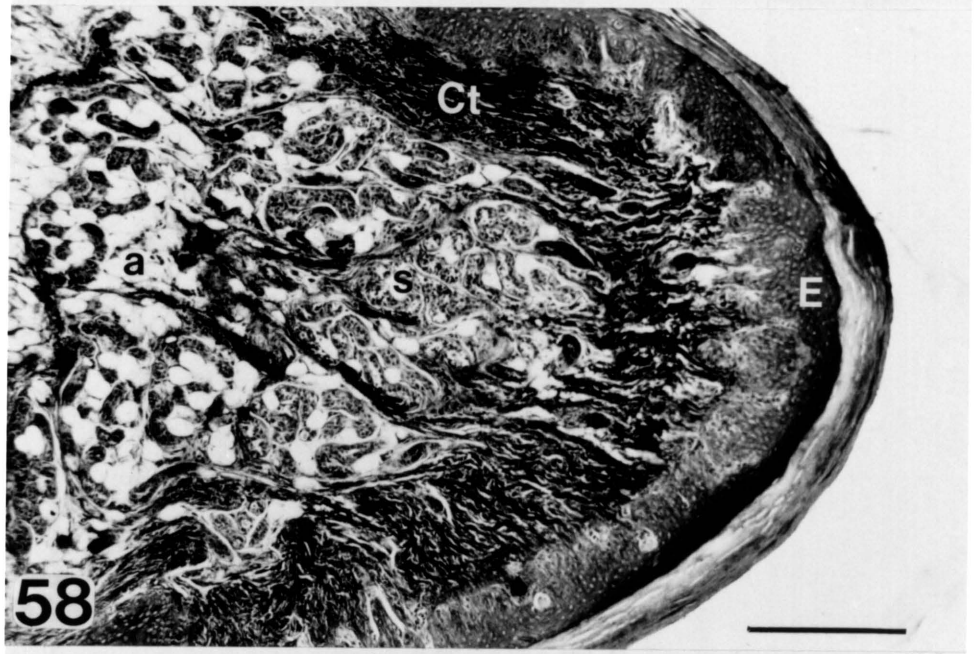

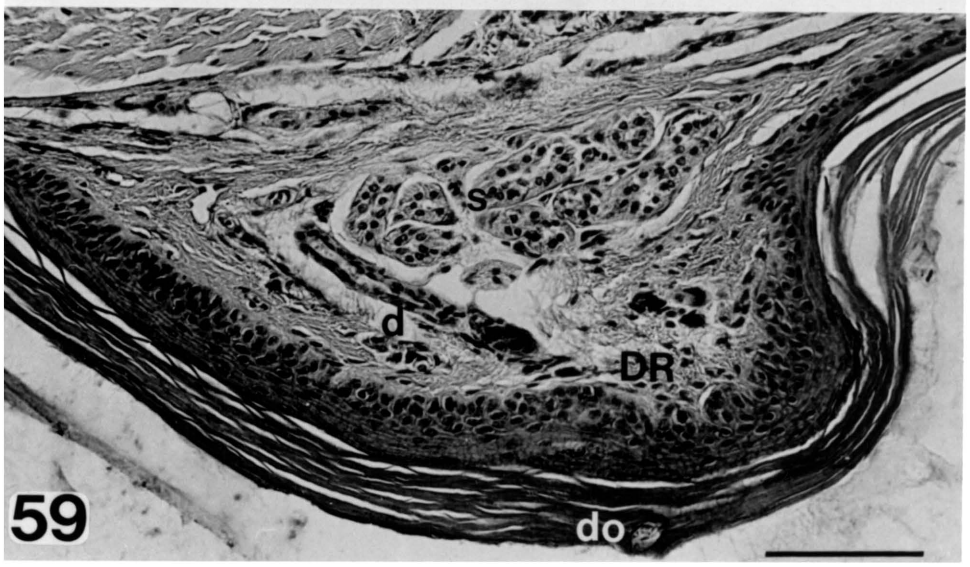

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dermis where the loose connective tissue formed distinct lobules (Fig.57) which contained adipose tissue particularly in the hind foot pads (Fig.58). The secretory cells showed distinct cytoplasmic striations and large apical nuclei (Fig.9). The secretory lumens were characteristically open and large. The excretory ducts extended straight through the dermis (Fig.59), spiralizing tightly through the pigmented epidermis and extended in a narrow helix through the thick stratum corneum. No differences in the glands were noted between these species.

Within this family, the Otomyinae (including Otomys irroratus and O. angoniensis) have the most well-developed and abundant sudoriferous glands, which practically fill the large pads of the feet and digits. The abundance and structure of these glands most closely compares with those described in the bank vole Clethrionomys glareolus by Griffiths & Kendall (1980). Differences which occur include both Otomys species having straight sweat ducts while in C. glareolus the ducts coil through the dermis and open in shallow depressions on the epidermal surface (Griffiths & Kendall 1980). These shallow depressions were not visible on the pads of the two Otomys species. Large eccrine sweat glands formed the 'sole glands' in Clethrionomys rufocanus and C. rutilus (Skurat 1972 in Sokolov 1982) and both of these species also lacked sudoriferous glands in the oral angle. The functional significance of the abundance of these glands is unclear when veiwed against the general trend of a reduction in sudoriferous glands in the other African Cricetidae (Table 2) and their ecological behaviour of being mainly diurnal but with Otomys angoniensis being more nocturnal. Living in wet vleis and river areas as well as using clearly marked runs from their nests to the feeding grounds (De Graaff 1982) their ecological behaviour is very similar to that of the cane rats and the water rats both of which have minimal sudoriferous glands. However, Kingdon (1974) suggests that the exclusively African Otomyinae resemble the Holarctic voles, the Microtinae, due to the convergence of similar forms filling a very similar niche' and possibly sharing an ancient common ancestry. These glands may thus be of phylogenetic importance, and yet may have been retained as 'pedal glands' for scent-marking in these strongly territorial species (Davis 1972)

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as has been suggested for the Microtinae by Quay (1965a) and the ground squirrels (Sokolov 1962; Steiner 1974).

Mystromys albicaudatus - White-tailed Rat

Numerous large sweat glands were found on the naked areas of both fore and hind feet including the palmar and plantar pads, and the distal toe pads (Fig.5b) but none were observed in the digital ridges. The secretory tubules lay deep in the dermis separated by connective tissue septa (Fig.60). They were formed by cuboidal secretory cells which surrounded open lumens. The sweat ducts extended straight through the dermis to the interpapillary peg where they followed a conical spiral through the epidermis (Fig.61).

M. albicaudatus of the Cricetinae also has large abundant sudoriferous glands but they differ in their distribution from the Otomyinae in that these glands are not found on the digital ridges. Also the secretory cells are not as distinctly striated, and the secretory tubules are separated by thick connective tissue septa into distinct lobules. The M. albicaudatus lacks the apocrine glands reported in the oral angle of seven genera of Cricetinae by Quay (1965a) but who also found none of them in Cricetulus barabensis and Mesocricetus auratus. This was similarly confirmed in C. migratorius by Sokolov (1982) who reported that the eccrine sweat glands form large glomeruli (tubules) within the hind foot sole. Although very little is known about the behavioural ecology of this nocturnal species (De Graaff 1981) a suggested function of these glands in the feet is passive scent-marking as the animal wanders out from its burrow in search of food and possibly returns via this scent-trail.

Saccostomus campestris - Pouched Mouse

Sweat glands were found on the naked areas of both fore and hind-feet including the poorly developed palmar and plantar pads, and the distal toe pads where they were numerous (Fig.62). These were small deep tubular glands clearly separated by septa in the dermis (Fig.62), and their ducts ran straight to the epidermis where they followed a helical spiral to the friction surface. The digital ridges were poorly defined, yet contained a single sweat gland

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Fig.60 T.S. through the hindfoot toe pad of Mystromys albicaudatus showing the secretory tubules (s) separated by connective tissue septa deep in dermis. The sudoriferous glands have large tubules with wide lumens.

(Bar = 200µm)

Fig.61 L.S. through the front foot toe pad of M. albicaudatus showing the tightly coiled secretory tubules (s) deep in dermis with a straight duct to the epidermis through which the duct winds in a conical spiral (arrow).

(Bar = 100µm)

Fig.62 L.S. through the front foot toe pad of Saccostomus campestris showing the numerous tightly coiled secretory tubules (s) separated by septa in the dermis. The duct winds through the epidermis in a helical spiral (arrow).

(Bar = 150µm)

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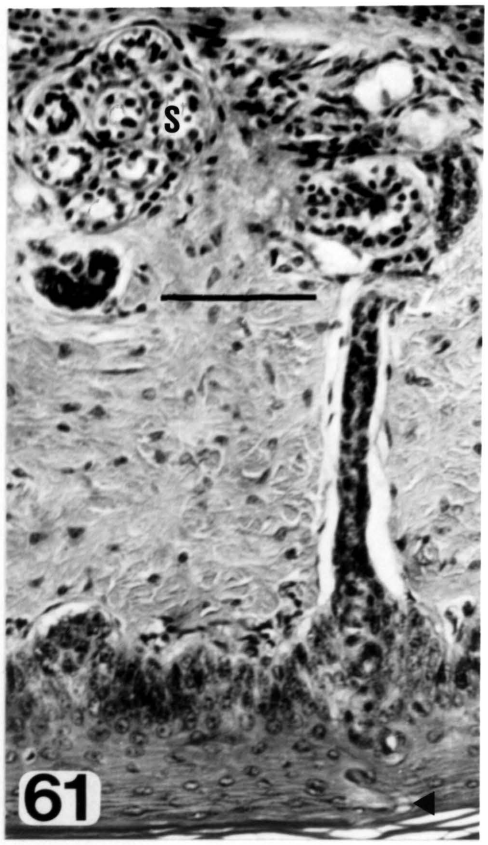

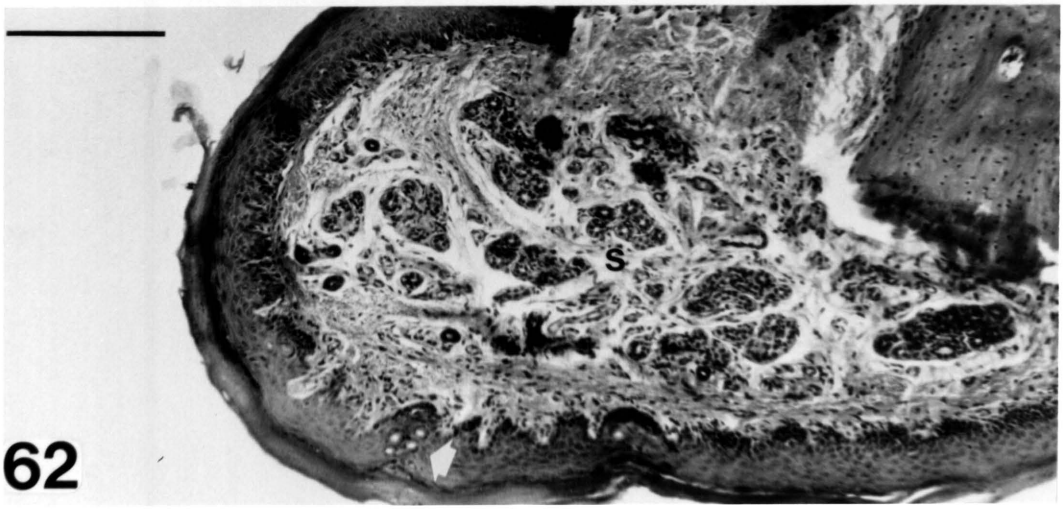

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which lay parallel to the epidermal surface with its sweat duct opening onto the ventral surface of the ridge.

S. campestris of the Cricetomyinae are predominantly solitary and nocturnal rodents which are adept diggers making their own burrows (De Graaff 1981). These are usually in sandy areas in open short grass near pans and river beds where the soil is reasonably soft as their paws are not specialized for burrowing (Kingdon 1974). In the light of the above, the need for functional glands in the feet may be interpreted as three fold. Living with only one animal per hole and with the females aggresive enough to kill males put with them in captivity (Davis 1963), the scent produced by these glands may contribute to indicate the occupancy of a burrow. Secondly, being nocturnal rodents which wander widely from their burrows at night, and have been followed for distances of up to 200m from them on open ground (Smithers 1971), a scent-trail from these glands in the feet may help them to return to their burrows. A third function may be to maintain the thick epidermal layers to minimise the wear-and-tear of the burrowing surfaces of the feet.

In the Gerbillinae there is a further reduction in sudoriferous glands, particularly with the increased hairy ventral surfaces and thus the diminishing naked areas of the feet where these glands usually occur in other species.

Tatera leucogaster - Bushveld Gerbil

Tatera brantsii - Highveld Gerbil

The feet of T. brantsii were more hairy than those of T. leucogaster, and sweat glands were found only on the hairless areas of both fore and hind feet and thus restricted to the small palmar and plantar pads (Fig.63), and the distal toe pads (Fig.64). These were tubular glands which lay deep in the dermis with long almost straight ducts stretching to the epidermis (Fig.63 & 64). Single glands were observed in the digital ridges opening onto the antero-ventral surfaces (Fig.65). The long naked part of the hindfoot soles lacked these glands as well as the thick epidermal layers found on the friction surfaces.

Both species are active burrowers which prefer sandy soils in which they excavate their intercommunicating warrens (De Graaff 1981) which are interchangeably used by various families of the

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Fig.63 L.S. through the hindfoot pad of Tatera brantsii showing the tightly coiled secretory tubules (s) of the sudoriferous glands separated into lobules. The ducts run straight through the dermis to the interpapillary pegs.

(Bar = 150µm)

Fig.64 A high power view through the hindfoot pad of Tatera leucogaster showing the tightly coiled secretory tubules of the sudoriferous glands separated into lobules, with their ducts (d) running directly through the dermis to the interpapillary pegs from where they spiral through the epidermis.

(Bar = 100µm)

Fig.65 L.S. through two digital ridges of the hindfoot toe of T. leucogaster. Each digital ridge (DR) contains the small secretory tubules (s) of a single sudoriferous gland. The duct (d) runs at an angle directly through the dermis to the interpapillary peg from where it spirals through the epidermis to open onto the antero-ventral surface of the digital ridge (arrow).

(Bar = 100µm)

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colonies (Kingdon 1974). The main function of these sudoriferous glands in the feet of these nocturnal social species may be primarily for maintenance of the epidermal friction surfaces, particularly in the elongated hindfeet with their saltatorial locomotion (De Graaff 1981), and their short clawed forelegs which allow them to dig proficiently. Scent-trails would be of little value once out of their burrows in view of their kangaroo-like leaping movement and their large eyes which appear to be their main sense for orientation. Quay (1965a) could also find no traces of sudoriferous glands in the oral angle or lips of T. indica.

Gerbillurus paeba - Hairy-footed gerbil

As the common name indicates this species has hairy feet, with hairs even on the ventral sole surfaces 'with only a narrow central line naked' (De Graaff 1981). No glands were found in these areas. The distal toe pads on both fore and hind foot were however naked, and it is here that the only sweat glands were found (Fig.66). The tubular glands were compactly spiralled and deliniated into lobules by thin connective tissue septa. These lobules lay at different depths in the dermis with their ducts leading straight to the friction surface where the epidermis was thickest. The secretory cells were large, with the clear cytoplasm containing large vacuole-like structures and large oval nuclei.

Even though a lot of auto- and allogrooming is practised (Smithers 1983), sudoriferous glands were not present in the oral angle of G. paeba. No traces of sudoriferous glands could be found in the oral angle or lips of G. gerbillus either by Quay (1965a). Similar to other nocturnal burrowing rodents in semi-arid areas (Quay 1965a), these gerbils have hairy feet which is an adaptation to life on the preferred sandy soils (Smithers 1983). The absence of sweat glands on the furred surfaces of the feet was similarly reported in North American desert rodents such as Dipodomys deserti and a Microdipodops species which have furred plantar surfaces that lack sudoriferous glands (Quay 1965b). He also found traces of glands in the terminal pads of the digits in Microdipodops. Haired feet would be more functional on loose sand than the improved traction caused by sweat on the frictional pads of the feet on a solid substrate as shown for the dog, hyrax, tenrec and rat (Adelman, et. al. 1975). The function of these

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Fig.66 L.S. through the distal toe pad of the front foot of Gerbillurus paeba showing the claw (cl) and the digital bone (b). Compact secretory tubules (s) of numerous sudoriferous glands almost fill the dermis. The ducts (d) run directly through the dermis to the deep funnel-shaped interpapillary pegs (f) from where they spiral through the epidermis onto the frictional surface.

(Bar = 150µm)

Fig.67 - 69 Serial sections through the hairless pad of the front foot of Desmodillus auricularis showing the small compactly spiralled secretory tubule (s) of the single sudoriferous gland which lies deep in the dermis (Fig.67 & 68). With the transition to the duct (d) which gently winds to the epidermis (E) (Fig.69).

(Bar = 100µm)

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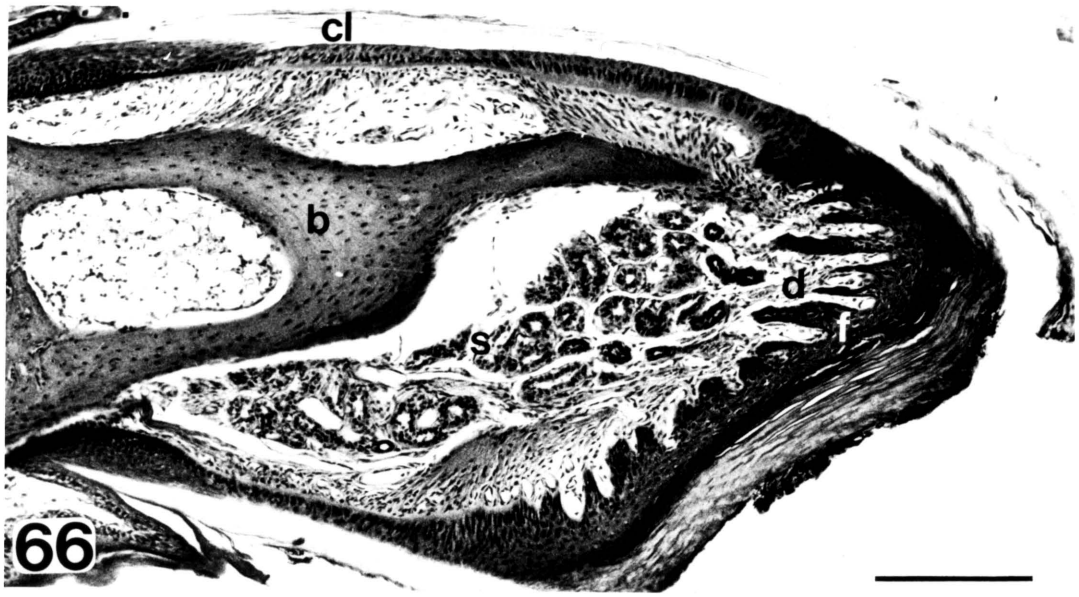

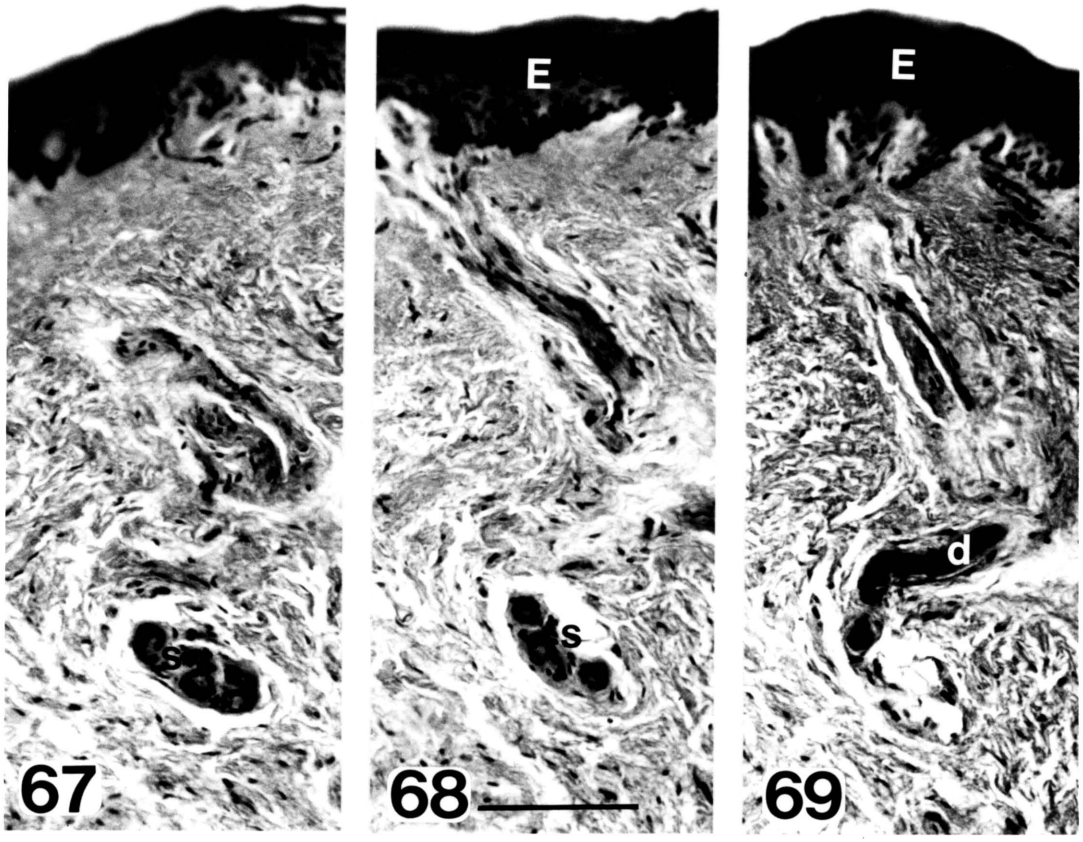

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active glands in the terminal digital pads of G. paeba may be the same as previously suggested for the Tatera species.

Desmodillus auricularis - Short-tailed Gerbil

In this species, the palms and approximately half of the soles were naked, but the distal half of the soles and undersides of the toes were closely haired as described by De Graaff (1981). Sudoriferous glands were found only on the hairless pads of the front feet where they occurred usually as a small single tubular gland deep in the dermis of each pad (Fig.67 - 69). In one pad two glands were noted. No glands were found on the hairy hind feet or on the naked toe pads of either feet.

Although D. auricularis overlaps in distribution with Gerbillurus paeba, it prefers hard open ground with grass cover particularly around dry pans (Smithers 1971, 1983). They excavate extensive burrows which may be up to 2m deep (De Graaff 1981) where their hairy feet, like those of Pedetes capensis, must be useful for digging loose soil. Like G. paeba the hairy feet are probably an advantage in the drier western areas including the Kalahari and Namib deserts when moving about on loose sand. The burrows may be short distances from each other but do not form warrens (Smithers 1971) as they are asocial (Nel 1975) showing a strong animosity between the sexes in captivity (Nel & Stutterheim 1973). Being nocturnal, these single glands in the palmar pads may form a scent-trail when the animal moves out in search of food along the well defined pathways beween the burrows. The similarity in behavioural ecology, hairy feet and sudoriferous gland abundance and distribution between Pedetes capensis and Gerbillurus paeba is striking. However, this pattern extends to other desert rodents as Quay (1965b) showed that active-appearing eccrine glands occurred only in the palmar tubercles of Dipodomys deserti and D. merriami which have furred feet.

8. Family **MURIDAE**

Compared to the Cricetidae, the Muridae have relatively few specialized glandular areas in their skin. These include the oral angle and lips ('mouth glands') (Quay 1965a; Sokolov 1982) and the perineal area ('anal glands') which are composed of large multilobal sebaceous glands and were found in almost all of the

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investigated species (Quay 1965a; Skurat 1972 in Sokolov 1982). There is a conspicuous difference in the oral angle glands between the Cricetidae where many of the species have mixed sebaceous and apocrine glands, whereas in the Muridae no traces of sudoriferous glands could be found in oral angle or lips (Quay 1965a; Sokolov 1982). The third common site is the hairless ventral surfaces of the feet where concentrations of eccrine sweat glands occur in most species (Quay 1965b; Skurat 1972 in Sokolov 1982; Sokolov 1982).

Other specialized sites include the 'midventral gland' described in thirteen Asian Rattus and Chiropodomys species (Quay & Tomich 1963; Rudd 1966), while 'caudal glands' were described in Apodemus sylvaticus and A. flavicollis on the lower surface of the tail (Skurat 1972 in Sokolov 1982).

Kingdon (1974) suggested that the African Muridae can be grouped into two divisions according to ancestral entrance into Africa. The larger Rattus-like murids seem to be related to Parapodemus, a fossil murid from Europe, and probably moved into Africa before the smaller Mus-like murids whose ancestral line seemed to have migrated from Eurasia independently at a later date (De Graaff 1981). Praomys(Mastomys), Aethomys, Thallomys and Dasymys are genera grouped under the Rattus-like murids (Kingdon 1974; Ellerman 1941 in De Graaff 1981) while the Mus-like murids include Mus, Lemniscomys, Rhabdomys and Acomys. For the purpose of this study this grouping should suffice as Kingdon (1974) concludes that 'mice are miniature rats, retaining the generalized body plan, locomotory versatility and omnivorous diet of their larger cousins'.

Praomys(Mastomys) natalensis - Multimammate Mouse

Abundant sweat glands were found in the naked areas of both fore and hind feet of both these species, particularly in the well-developed palmar (Fig.70) and plantar pads, and the distal toe pads (Fig.71). In each digital ridge there is a single sweat gland with its duct opening onto the antero-ventral epidermal surface (Fig.72). The secretory tubules were distinctly lobular, being surrounded by loose connective tissue, and lay fairly deep in the dermis (Fig.6 & 71).

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Fig.70. L.S. through a front foot pad (FFP) and digital ridge (DR) of Praomys natalensis. Tightly coiled secretory tubules (s) of the sudoriferous glands lie deep in the dermis, reaching almost to the hypodermis. The secretory tubule (arrow) and duct of the single sudoriferous gland is seen in the digital ridge (DR).

(Bar = 200µm)

Fig.71. L.S. through a front foot toe pad of P. natalensis. Lobules of tightly coiled secretory tubules of the sudoriferous glands almost fill the dermis. The ducts wind gently up to the deep funnel-shaped interpapillary pegs before spiralling (sp) through the epidermis to the friction surface.

(Bar = 150µm)

Fig.72. L.S. through a digital ridge of a hind foot toe of P. natalensis. Note the faint cytoplasmic striations (arrow) in the secretory cells lining the tightly coiled tubule (s) of the single sudoriferous gland. The interpapillary peg extends down to the secretory lobule and the duct follows a conical spiral (sp) through the epidermis to open onto the antero-ventral surface of the digital ridge.

(Bar = 50µm)

Fig.73. The typical structure of a single sudoriferous gland in a palmar pad of P. natalensis showing the lobular structure of the tightly coiled secretory tubule (s) and the course of the duct (d) through the dermis, and spiralling into the epidermis.

(Bar = 50µm)

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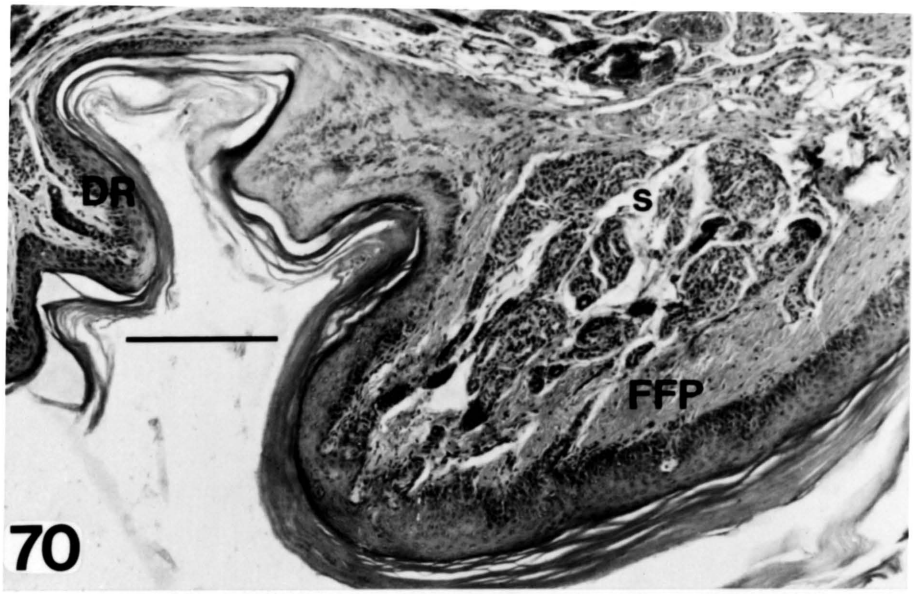

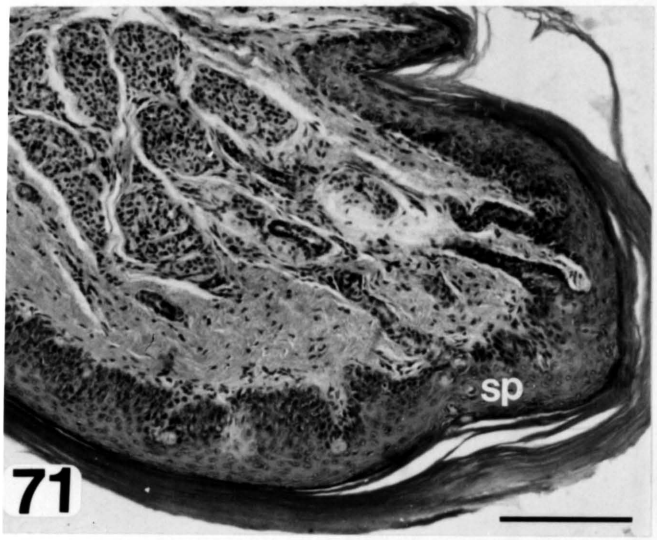

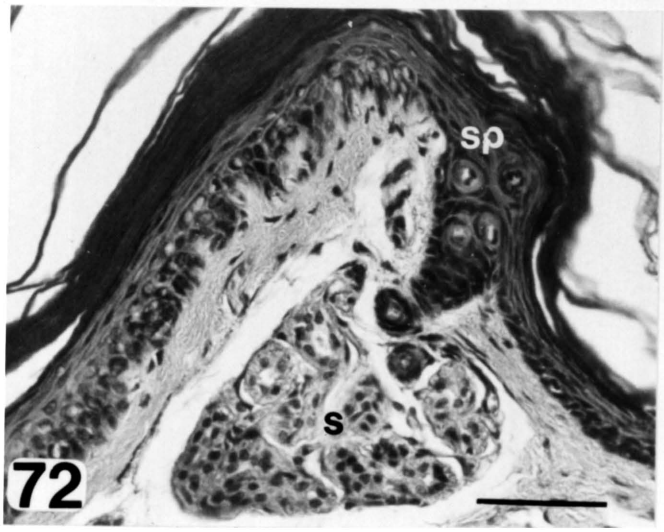

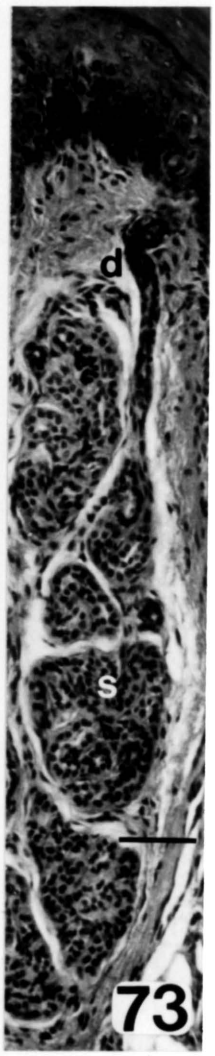

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The secretory cells were finely striated. The sweat ducts extended almost directly through the dermis towards the frictional surfaces where the epidermis was thickest (Fig.73). The papillary pegs were very well developed and the ducts followed a conical spiral through the thick epidermis (Fig.71).

P. natalensis has been previously treated as an African branch of the genus Rattus with anatomical similarity and being a typical omnivorous generalist or unspecialized rat closely associated with human activity (Kingdon 1974). It is nocturnal and communal (De Graaff 1981) with several families living together in burrows often under the floors and walls in dwellings of local people, where it is traditionally the dominant domestic African rat (Kingdon 1974). It has generalized ecological requirements inhabiting a wide range of habitats. Meester, Lloyd & Rowe-Rowe (1979) decribe it as a 'pioneer species' as it is one of the first rodent species to become established in an area which is recovering from some form of habitat destruction. Like Rattus rattus, P. natalensis has retained the generalized foot structure which allows it to be a terrestrial burrower as well as a fairly competent climber (De Graaff 1981) with the hind feet having high and sharply pointed pads, and with the distal toe-pads being pronounced and pointed, being adapted for climbing (Earl & Nel 1976). The numerous sudoriferous glands in the feet are also similar to those found in Rattus (Ring & Randall 1947) and could fulfill similar functions to those later described for Aethomys namaquensis and the more aboreal Thallomys paedulcus. Although the vertical utilization of the habitat by African murids is largely unknown, Earl & Nel (1976) suggested that P. natalensis could be an important user of this component, particularly when faced by competition from the more specialist species on the ground (De Graaff 1981). In captivity, Earl & Nel (1976) reported that Praomys had a higher climbing frequency than even the arboreal Thallomys paedulcus.

Aethomys chrysophilus - Red Veld Rat

Aethomys namaquensis - Namaqua Rock Rat

Numerous sweat glands were found in the naked areas of the fore and hind feet of both these species, but were limited to the large well-developed palmar and plantar pads (Fig.74), and the distal

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Fig.74. L.S. through a hind foot pad of Aethomys chrysophilus. Lobules of tightly coiled secretory tubules (s) of the sudoriferous glands almost fill the dermis. The ducts (d) run straight through the dermis into the well-developed interpapillary pegs (f). Arrows indicate the compressed spirals of the ducts winding through the thick stratum corneum (Sc) to the friction surface.

(Bar = 300µm)

Fig.75. L.S. through a hind foot toe pad of A. chrysophilus. Lobules of tightly coiled secretory tubules (s) of the sudoriferous glands almost fill the dermis. The duct (d) runs directly up to the deep funnel-shaped interpapillary pegs (f) before winding through the stratum corneum in helical spiral (arrow).

(Bar = 150µm)

Fig.76. L.S. through a hind foot toe pad of A. namaquensis. Lobules of tightly coiled secretory tubules (s) of the sudoriferous glands almost fill the dermis. The ducts run straight through the dermis to the funnel-shaped interpapillary pegs (f) before winding through the stratum corneum in helical spirals (sp) to the friction surface.

(Bar = 200µm)

Fig.77. L.S. through a front foot toe pad of Thallomys paedulcus . Lobules of secretory tubules (s) of the sudoriferous glands almost fill the dermis. The ducts (d) wind up to the deep funnel-shaped interpapillary pegs before spiralling through the epidermis to open in shallow cup-shaped depressions (de & arrows) on the friction surface.

(Toluidine blue stain) (Bar = 200µm)

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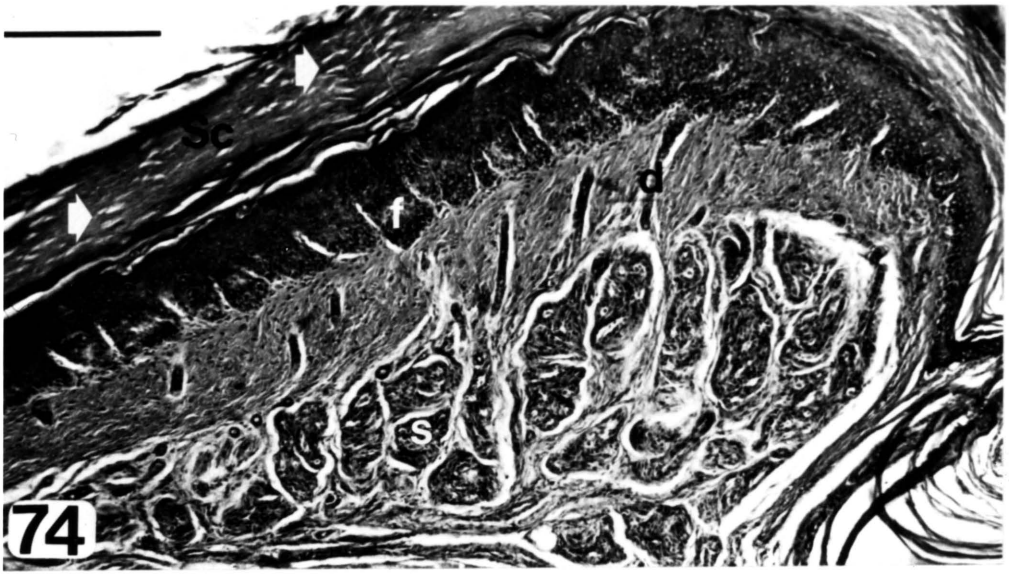

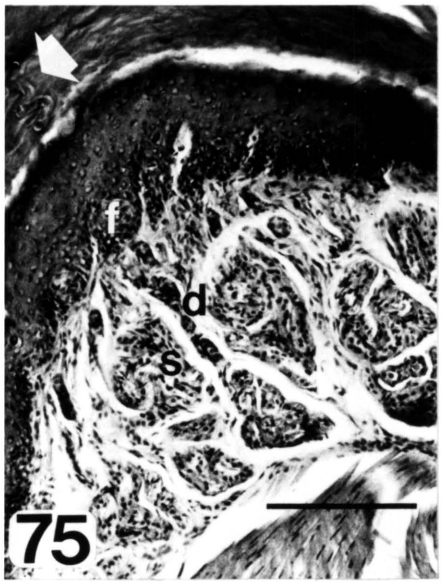

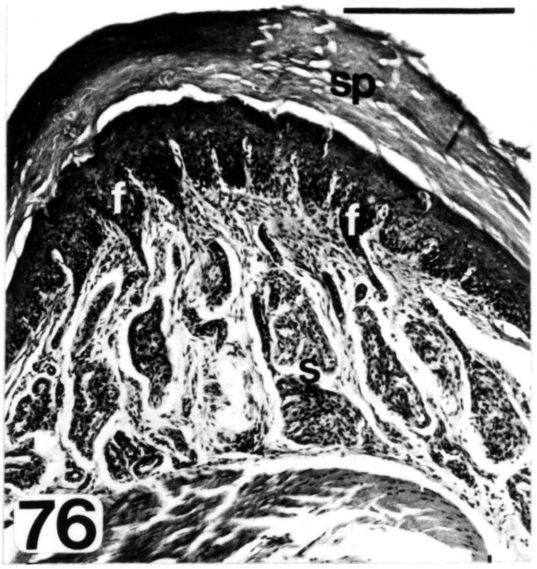

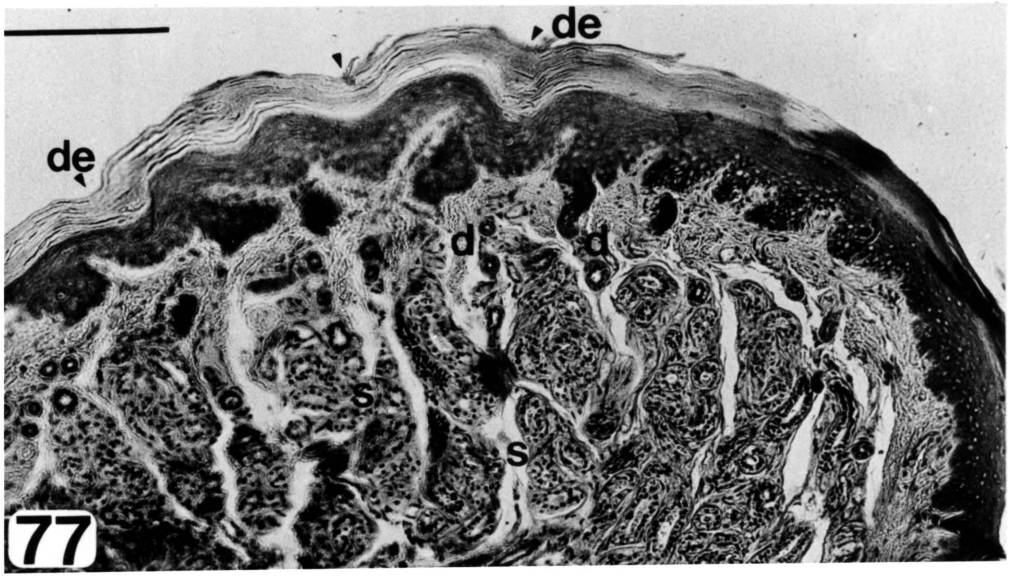

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toe pads (Fig.75 & 76). In each of the digital ridges there was at least a single sweat gland with its duct opening onto the ventral epidermal surface. The secretory tubules with their relatively wide lumens lay compactly spiralled in lobules fairly deep in the dermis. The sweat ducts extended almost directly through the dermis to where the epidermis was thickest (Fig.74). The papillary pegs were very well-developed, and the ducts followed a regular helical spiral through the thick stratum corneum of the epidermis (Fig.76 & 77). No differences were observed between the sudoriferous glands of these two species.

Both Aethomys species are nocturnal and overlap in their distribution range. They are exclusive with the more aggressive, non-gregarious A. chrysophilus found on the well-grassed plains or in dry acacia scrub where they excavate burrows under the vegetation (De Graaff 1981). They also build nests in termitaria and rocky sites on slopes where it is usually associated with Acomys species (Kingdon 1974). The abundant sudoriferous glands may function to keep the particularly thick stratum corneum moist and pliable especially during burrowing, but being non-gregarious and showing interspecific aggression to the extent that they kill each other in captivity, a 'scent-trail' from these glands may warn intruders and thus help to avoid conflict situations. A. namaquensis is a more communal species with a number of family parties occupying the same rocky crevice (De Graaff 1981). They are semi-arboreal living on rocky outcrops where grass-nests are built in crevices or in holes in trees (Smithers 1983; De Graaff 1981). The pads on their feet are more well-developed than those of A. chrysophilus and thus contain proportionately more sweat glands for improved traction as shown in the rat by Adelman, et al. (1975). This is an adaptation already described in other 'rock climbers' such as Petromus typicus. Being a communal species a 'scent-trail' left by these glands may indicate some form of recognition to other members of the group as shown for Mus musculus (Brown 1985).

Thallomys paedulcus - Tree Rat

Abundant sudoriferous glands were found in the naked areas of both fore and hind feet, particularly in the distal toe pads (Fig.77), and in the well-developed plantar and palmar pads (Fig.78). In

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each digital ridge there were two sweat glands with their ducts opening onto the ventral epidermal surface (Fig.79). The numerous secretory tubules lay superficially almost filling the dermis, while the sweat ducts wound through the dermis via the inter-papillary pegs which often extended down to the secretory tubules (Fig.77). The ducts followed a regular spiral through the thick epidermis to open into cup-shaped depressions between the epidermal ridges on the friction surfaces (Fig.77, 36 & 37). A few apocrine glands with wide lumens lay with their tubules deep in the dermis of the front foot pads, surrounded by the smaller eccrine glands (Fig.78). Their wide secretory lumens (of up to 50µm in diameter) were lined by low cuboidal cells surrounded by many myoepithelial cells and a distinct connective tissue sheath (Fig.80). The tubules of the apocrine glands were filled with a luminal content which stained with Toluidine blue.

T. paedulcus is nocturnal and arboreal living in Acacia woodland (Smithers 1983) where they are described as very adept at running among the thickest parts of the thorny canopy of Acacia trees (Kingdon 1974). They live in family groups building grass and twig nests in the branches and also burrow holes for nests between roots of trees. They have become specialists in occupying this arboreal niche' and yet without any great modification of form, remaining a typical rat and certainly very close to the root stock of all African murids (Kingdon 1974). This common ancestry may further be reflected in the similarity with Rattus rattus which is also nocturnal and predominantly an accomplished climbing species whose agility among the murids is only matched by Thallomys paedulcus (De Graaff 1981).

The pads of the feet of the tree rat seem to be comparatively larger than R. rattus and more similar to those of the genus Graphiurus. Layne (1970) states that the number and development of the plantar tubercles (plantar pads) in rodents are structural adaptations for climbing, with the higher more sharply pointed and enlarged pads being best adapted for clutching slender branches and twigs. Earl & Nel (1976) described Thallomys as having large round pads on the hind-feet with pronounced pointed toe pads making its feet well adapted for climbing. The abundant sweat glands in these pads are very similar in structure and

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Fig.78. L.S. through a front foot pad of Thallomys paedulcus. The secretory tubules (s) of the abundant eccrine glands which almost fill the dermis, surround the large centrally placed apocrine gland (ap). The ducts (d) wind up to the deep funnel-shaped interpapillary pegs (f) before spiralling through the epidermis.
(Toluidine blue stain) (Bar = 150µm)

Fig.79. A high power view of a L.S. through digital ridge of a hind foot toe of T. paedulcus, showing the secretory tubules (s) of the two sudoriferous glands and their ducts (d) which wind up to the funnel-shaped interpapillary pegs before spiralling (sp) through the epidermis to open on the ventral surface.
(Bar = 100µm)

Fig.80. A high power view of a T.S. through the apocrine gland in the front foot pad of T. paedulcus. A single layer of low cuboidal secretory cells lined the wide lumen containing the stained luminal content (lc). Many myoepithelial cells (My) were seen between the basement membrane and the secretory cells while a connective tissue sheath (sh) surrounded the tubule, separating it from the adjacent eccrine tubules.
(Toluidine blue stain) (Bar = 40µm)

Fig.81. L.S. through a hind foot pad of Dasymys incomtus. The tightly coiled secretory tubules (s) of the scattered sudoriferous glands are arranged in large compact lobules. The straight ducts (d) run directly to the well-pigmented interpapillary pegs before spiralling through the epidermis.
(Bar = 200µm)

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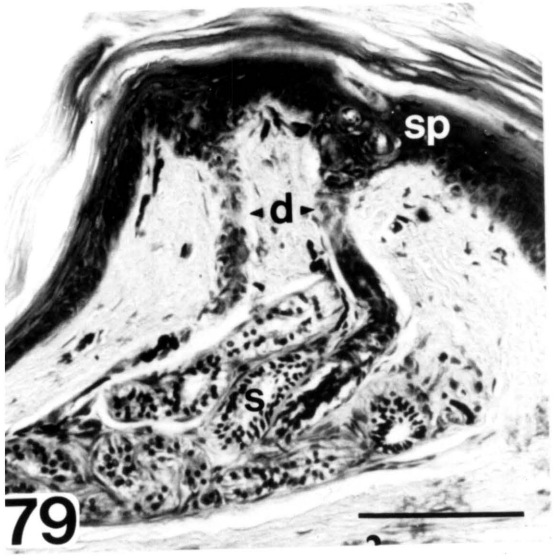

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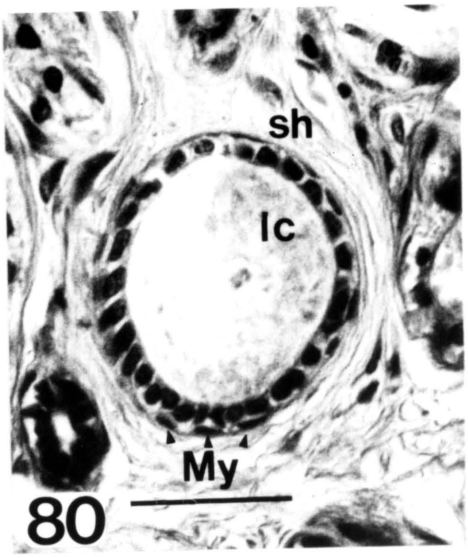

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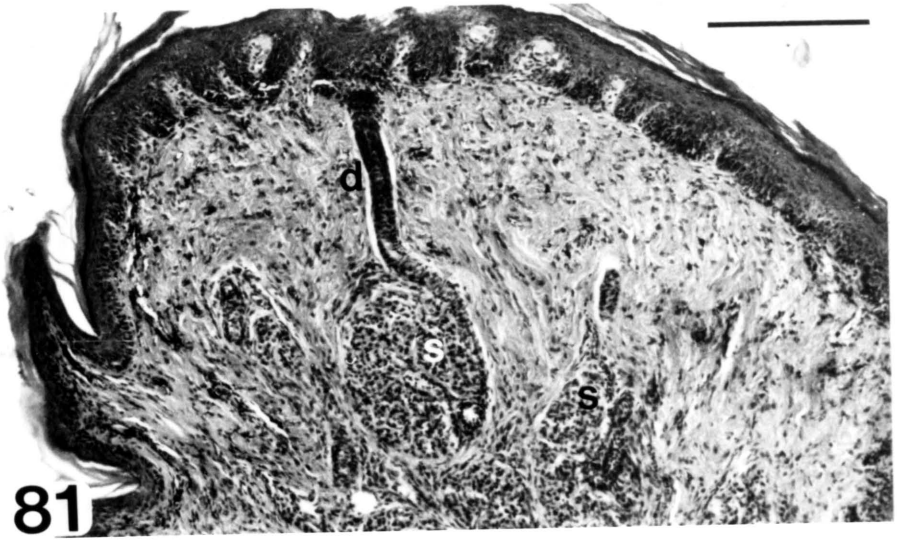

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distribution when compared to those in the white rat (Ring & Randall 1947) and it can be assumed that they are fulfilling similar functions. Adelman, et. al. (1975) showed experimentally that sweating increased immediately with the onset of running on the feet of the rat, tenrec, rock hyrax and dog, increasing with increased running speed and reaching a constant rate within the first minute. When sweating from the paws was blocked by injecting with atropine sulphate, the percentage decrease of the coefficient of static friction between the foot pads and the substrate was 16% in the rat, and 42% in the rock hyrax. The more terrestrial laboratory white rat was used in these experiments and it may be assumed that the sudoriferous glands may be of even greater functional significance in the more arboreal species. The regular runs of R. rattus are marked by smears where difficult obstacles have been negotiated and caused by the repeated contact with their greasy fur or feet (Smithers 1983). Sweating also improves the tactile sensitivity of the paws (Wechsler & Fisher 1968; Adelman, et. al 1975) which would be an added benefit to a 'climber'. Cheek-marking and perineal dragging against the branches was observed by Earl & Nel (1976) who suggested that this marking behaviour would facilitate T. paedulcus finding its way along branches during darkness by means of scent. A 'scent-trail' left by the numerous sudoriferous glands and particularly the large apocrine glands (which may be odoriferous) in the feet, may be expected to fulfill this function even more proficiently.

Dasymys incomtus - Water Rat

The sweat glands were found restricted to the more prominent palmar and plantar pads (Fig.81), and absent from the minor foot pads and poorly developed distal toe pads of both fore and hind feet. Although the digital ridges were well developed no sweat glands were present. The tubular glands were well developed, with the tightly coiled secretory tubules forming large compact lobules which lay fairly deep in the dermis (Fig.81). The sweat ducts were wide and extended as straight ducts through the dermis to the papillary pegs which were very well-pigmented (Fig.81), and through which the ducts followed a narrow spiral to the friction surfaces of the epidermis.

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The crepuscular to diurnal D. incomtus inhabits wet swampy areas, and as its common name implies is semi-aquatic and able to swim well (Smithers 1983). They make use of well defined runs which form tunnels among the lush vegetation (De Graaff 1981) from excavated burrows or grass-nests (Kingdon 1974). The relative absence of sudoriferous glands particularly on the toe pads and digital ridges, and being limited to only certain of the foot pads seems to be a feature shared with other semi-aquatic rodents. Although belonging to different families, no glands were found on the soles of the Muskrat Ondatra zibethica by Sokolov (1982) while in Myocastor coypus, only a few tubular glands which formed small glomeruli (lobules) were found in the hind foot sole callosities of one specimen only (Sokolov 1982). Though limited in number, the sudoriferous glands in D. incomtus form large glomeruli (lobules) which are distinctly oval in shape.

The possible functions of these glands are not clear, but the tendency towards the reduction in sudoriferous glands may be the same as those suggested for the cane-rat. These would include the fact that particularly the digital pads are in contact with wet soil which would keep the epidermis moist and pliable. This wet substrate together with their use of runs, would make a 'scent-trail' superfluous in those animals living in true swamp habitat. However, these palmar and plantar pad glands may have been retained for those members that are forced to inhabit the drier marginal areas of their range (as shown by Hanney (1975) who trapped specimens among the rocks up to one km from open water).

Mus minutoides - Pygmy Mouse

This, the smallest of the rodents studied, had well-developed sudoriferous glands which practically filled the pads of the feet (Fig.82) and digits (Fig.83). The palmar pads are taller and more pointed (Fig.82 & 84) than the smaller flatter plantar pads but the number of glands was similarly abundant on the well-developed pads of both feet (Fig.84). However, the small plantar and digital pads had relatively few glands (Fig.82 & 83) which were in turn similar to those found in the white mouse. No sudoriferous glands were found in the digital ridges or the naked hind foot sole of M. minutoides. The secretory cells and their oval nuclei were large, and enclosed a relatively small lumen (Fig. 85) which is

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Fig.82 L.S. through the front foot of Mus minutoides. The secretory tubules (s) of the sudoriferous glands are mainly concentrated in the large foot pad (fp), with fewer glands occuring in the minor foot pads and distal toe pad (tp).

(Bar = 0,5mm)

Fig.83 L.S. through the front foot toe of Mus minutoides. The few secretory tubules (s) of the sudoriferous glands are concentrated in the limited distal toe pad (tp) beneath the claw (cl).

(Bar = 200µm)

Fig.84 L.S. through a major front foot pad of Mus minutoides. The lobules of secretory tubules (s) of the sudoriferous glands almost fill the dermis and extend to the blood vessels (bv) in the hypodermis. Deep funnel-shaped interpapillary pegs (f) extend through the dermis almost to the lobules.

(Bar = 150µm)

Fig.85 A high power view of the sudoriferous glands in the hind foot foot pad of Mus minutoides. The secretory tubules (s) are lined by a single layer of tall cuboidal secretory cells with large apical nuclei surrounding narrow lumens. Prominent myoepithelial cells (My) rest on the basement membranes. The duct (d) consists of two layers of flattened epithelial cells enclosing a very narrow lumen.

(Bar = 10µm)

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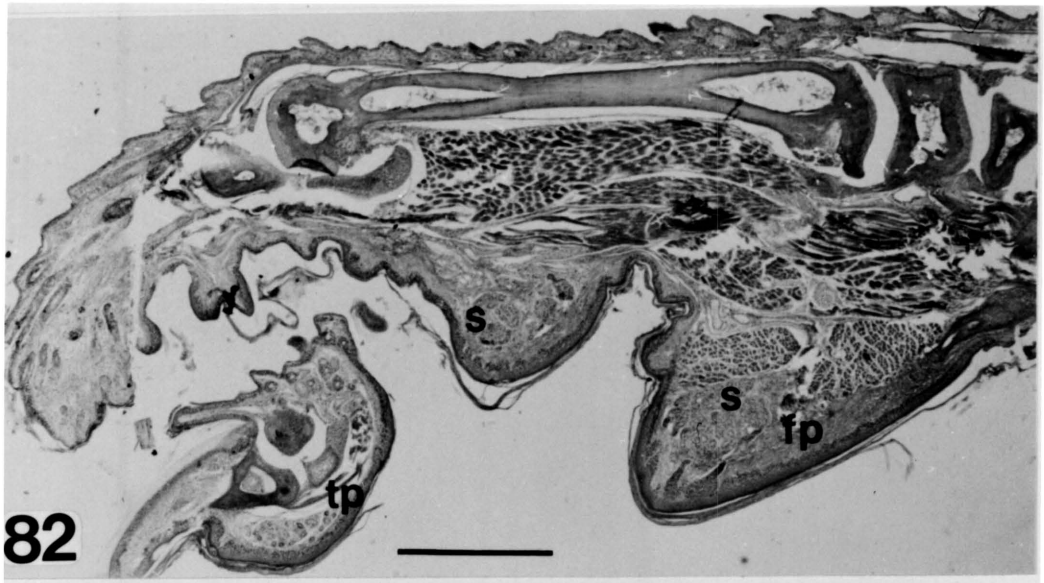

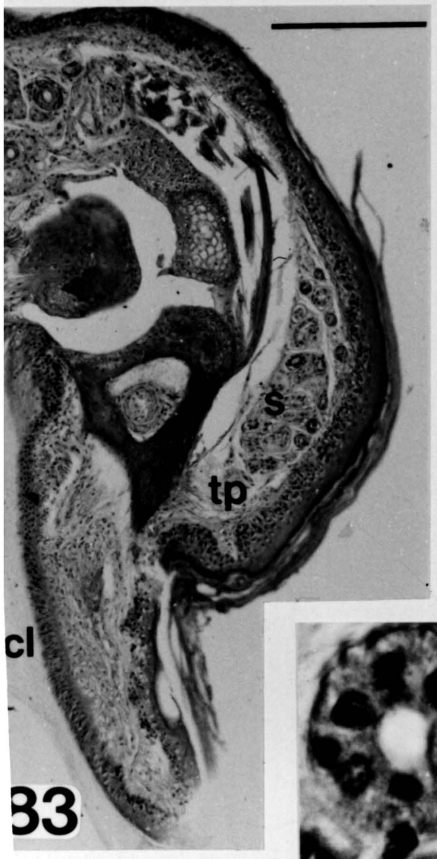

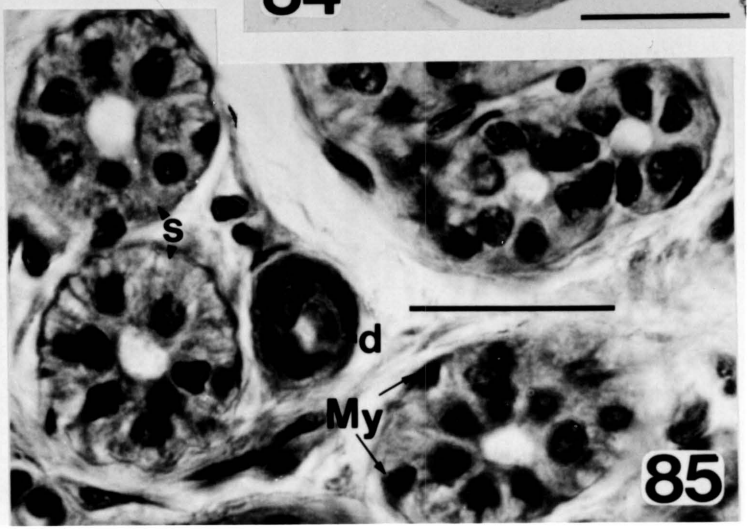

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indicative of active glands. The tightly coiled secretory tubules formed irregular compressed lobules in the dermis. The ducts followed a straight course through the dermis whereas in M. musculus the ducts were irregularly spiralled (Fig.84).

M. minutoides are almost exclusively nocturnal and terrestrial (Kingdon 1974) and are found over a wide range of habitat that includes forest and semi-arid bush. They are not communal but normally a pair or a family use shallow burrows or natural holes or shelters from which they move out to forage singly (Smithers 1983). The well-developed palmar pads and long tail may at first suggest adaptations for climbing (Earl & Nel 1976), but the small planter and digital pads or tubercles with their few sudoriferous glands, along with the lack of glands in the interdigital ridges refutes this particularly when compared to competent climbing species such as Praomys natalensis (Earl & Nel 1976). In the Eurasian Micromys minutus eccrine sweat glands were found in the thickenings of the hind foot (Sokolov 1982). The glands may be leaving a 'scent-trail' as Mus minutoides moves out to forage at night as suggested for Mus musculus by Ortmann (1956). He showed that both the direction and type of locomotion was indicated by the physical scent pattern left by the palmar and plantar glands of M. musculus on the substrate. The well-developed palmar glands may help in gripping the seeds and live insects with the paws when feeding. Females in captivity show aggressive territoriality (Smithers 1983) and a 'scent-trail' may help to warn intruders and thus limit physical confrontation. Ropartz (1977) described a 'plantar factor' odour produced by the sudoriferous secretion in the paws of male M. musculus which allowed recognition of the 'scent-trail' of foreign males as being from a single male or a group of strange males.

Acomys spinosissimus - Spiny Mouse

Abundant sweat glands were found only in the naked areas of both fore and hind feet. The well-developed palmar (Fig. 86) and plantar pads (Fig.87), and the distal toe pads, were filled with numerous secretory tubules which lay deep in the dermis. In each digital ridge there was a single sweat gland with its duct opening onto the anterio-ventral epidermal surface. The secretory cells

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Fig.86 L.S. through a major front foot pad of Acomys spinosissimus. The lobules of secretory tubules of the sudoriferous glands almost fill the dermis. The ducts form within the secretory lobules and run directly into the deep funnel-shaped interpapillary pegs (f) which extend down from the thick epidermis under the friction surface.

(Bar = 90µm)

Fig.87 T.S. through a hind foot pad of A. spinosissimus. The tightly coiled secretory tubules of the sudoriferous glands are bound together by thin connective tissue septa into a large oval lobule which almost filled the dermis. The ducts (d) within the secretory lobules and the interpapillary pegs in the dermis (seen in T.S.) give an indication of the large number of glands comprising the lobule.

(Bar = 100µm)

Fig.88 L.S. through a pointed minor front foot pad of A. spinosissimus. The tightly coiled secretory tubules of the sudoriferous glands are here also bound together by thin connective tissue septa into an oval lobule which almost filled the dermis. The ducts from within the secretory lobules run directly into the funnel-shaped interpapillary pegs before spiralling through the thick epidermis (arrow).

(Bar = 100µm)

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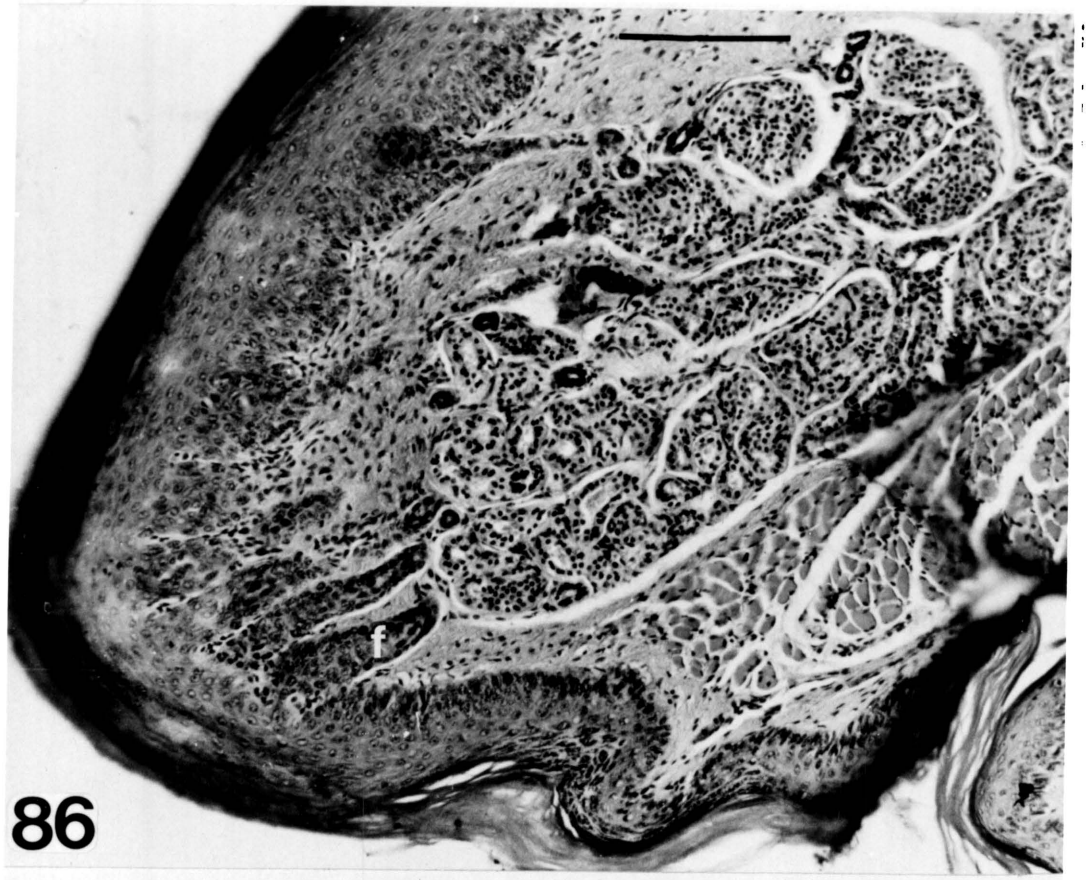

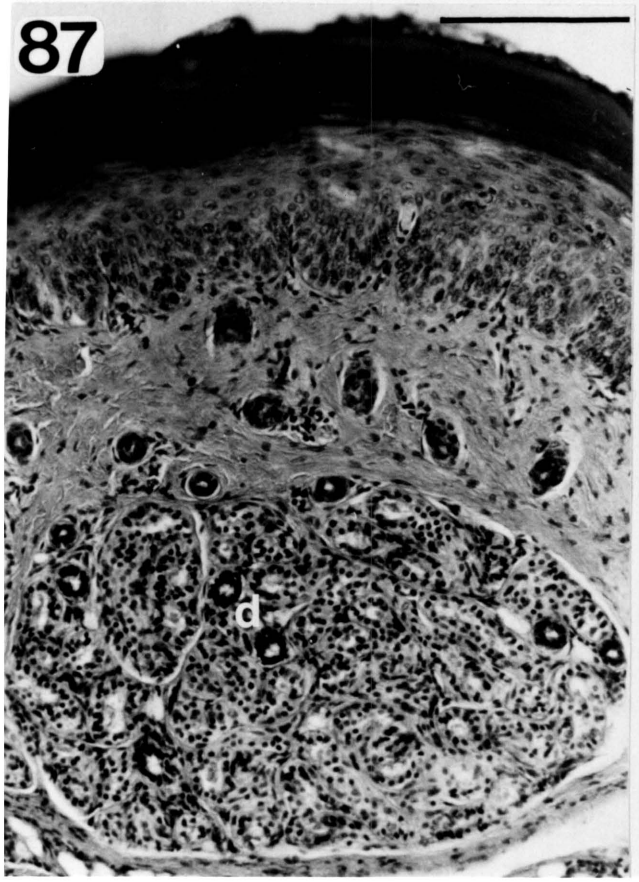

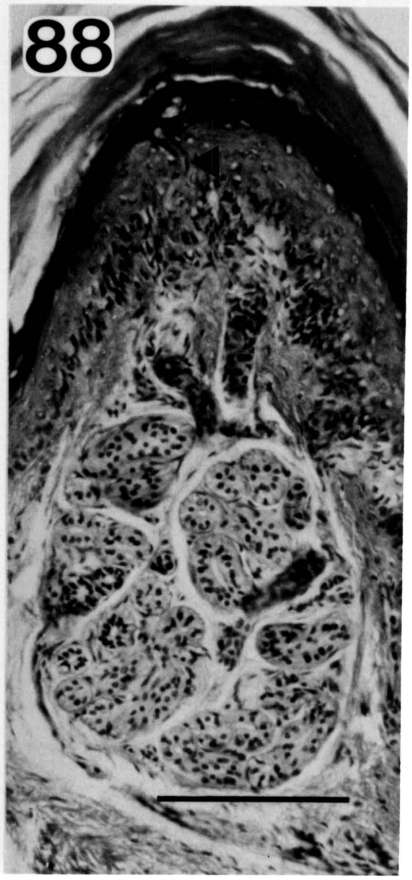

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were cuboidal with large apical nuclei. The lumens of the secretory tubules and ducts were distinctly large and open. The secretory tubules were very tightly coiled in compact lobules, being held together by thin connective tissue septa (Fig.87). The sweat ducts extended almost directly through the dermis to the frictional surfaces via the interpapillary pegs which extend down to the lobules (Fig.86). The ducts followed a regular spiral through the thick epidermis (Fig.88).

A. spinosissimus are nocturnal terrestrial mice which inhabit dry woodland rocky sites (Kingdon 1974 ; De Graaff 1981). They are gregarious with up to nine being collected from a single rock crevice (Smithers 1983). The feet of these animals is adapted for climbing with both the palmar and plantar pads being well-developed and pointed (Layne 1970; Earl & Nel 1976) and filled with sudoriferous glands (Fig.86 & 88), as are the enlarged distal digital pads. These glands should improve the traction of the pads as they climb over the rocks (Adelman, et al. 1975) and also leave a possible 'scent-trail', that would be functionally advantageous to this nocturnal rodent. These advantages are not only limited to rock-climbing, as A. spinosissimus has been trapped up trees (Kingdon 1974).

Lemniscomys griselda - Single-striped Mouse

Rhabdomys pumilio - Striped Mouse

The sweat glands of these two species were very similar with numerous sweat glands found in the naked areas of both fore and hind feet of both these species, but limited to the palmar and plantar pads (Fig.89), and the distal toe pads (Fig.90). In each digital ridge there is one large sweat gland whose duct opened onto the anterior epidermal surface in L. griselda (Fig.91) but on to the ventral surface in R. pumilio (compare Fig.92 & 93). The secretory tubules which appeared to be relatively fewer than many other murids, lay compactly spiralled in distinct lobules in the dermis. The sweat ducts wound through the dermis to where the epidermis was thickest (Fig.89). The ducts followed a conical spiral through the very well-developed interpapillary pegs and epidermis, followed by a regular spiral through the thick stratum corneum of the epidermis (Fig.90). The only differences observed between the sudoriferous gland structure of these two species were

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Fig.89 T.S. through a hind foot pad of Lemniscomys griselda. The tightly coiled secretory tubules (s) of the sudoriferous glands are arranged in separate lobules throughout the dermis. The duct (d) winds through the dermis, in which scattered adipose cells (a) occur, to the funnel-shaped interpapillary peg through which the duct follows a conical spiral (arrow). (Bar = 100µm)

Fig.90 L.S. through the front foot toe pad of Rhabdomys pumilio. The secretory tubules (s) of the sudoriferous glands almost fill the dermis of the distal toe pad. The duct follows a conical spiral (arrow) through the funnel-shaped inter- papillary peg and epidermis, and then a regular spiral through the thick stratum corneum.

(Bar = 150µm)

Fig.91. A high power view of a L.S. the through digital ridge of a hind foot toe of L. griselda, showing tightly coiled secretory tubule (s) of the single sudoriferous gland. The duct (d) follows a conical spiral (sp) through the funnel-shaped interpapillary peg (f) of the epidermis to open on the anterior surface of the digital ridge.

(Bar = 50µm)

Fig.92. L.S. through three digital ridges of a front foot toe of L. griselda, showing the secretory tubule (s) of the single sudoriferous gland in each. The anterior position of the duct opening on the digital ridge is indicated by the arrow.

(Bar = 200µm)

Fig.93. L.S. through a digital ridge of a front foot toe of R. pumilio, showing the secretory tubule (s) of the single sudoriferous gland, and the ventral position of the duct opening on the digital ridge as indicated by the arrow.

(Bar = 100µm)

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the positions that the ducts opened onto the digital ridges (Fig. 92 & 93).

These species may occur sympatrically as shown by De Witt (1972) with a very similar behavioural ecology which includes being mainly diurnal, non-gregarious, and requiring a habitat with good grass cover (Kingdon 1974; De Graaff 1981). Both species will burrow and build grass nests but with L. griselda using terrestrial nests while R. pumilio usually nests in its burrow (De Graaff 1981). Both make use of well-defined runways through the grass in their home ranges. De Wit (1972) found L. griselda to have a home range that is more than twice the size of the 1200m^2 mean seasonal home range of R. pumilio. Kingdon (1974) however reported that R. pumilio can range over about 20 ha and is able to climb trees and into birds nests.

Both of these species had very well-developed digital ridges on the toes of both feet in which large sudoriferous glands occurred (Fig.91 - 93). The pads of the feet are moderately developed and in R. pumilio distinctly anteriorly pointed which Layne (1970) suggested is an adaptation for climbing. Being a diurnal species, the abundant sudoriferous glands may help with local thermoregulation of the surface of the feet in contact with the hot substrate, especially with sand surface temperatures of up to 70^{o}C recorded in the Kalahari (Bothma 1980). The use of the sudoriferous glands to produce a 'scent-trail' would be an advantage in ranging over the large areas such as 20 ha (Kingdon 1974), but again, large sweat glands would be required to produce enough liquid to be effective with the fast rate of evaporation on the hot substrates moved across by these diurnal murids.

9. Family GLIRIDAE

Graphiurus ocularis - Smith's Dormouse

Graphiurus murinus - Woodland Dormouse

Abundant sweat glands were found on the naked areas of both fore and hind feet, particularly in the enlarged palmar and plantar pads (Fig.94) and the bulbous distal toe pads (Fig.95 & 96). Glands were not found opening onto the naked soles of the hind feet. The tightly coiled secretory tubules literally filled the

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Fig.94 L.S. through a large hind foot pad of Graphiurus murinus. The tightly coiled secretory tubules (s) of the abundant sudoriferous glands are so compactly arranged that the lobules almost fill the dermis. The ducts (d) wind gently between the lobules and through the dermis to the many funnel-shaped interpapillary pegs (f), which are an indication of the great number of glands in the pad.

(Bar = 0,3mm)

Fig.95 L.S. through a front foot toe pad of G. murinus. The tightly coiled secretory tubules (s) of the abundant sudoriferous glands are so compactly arranged that they almost fill the dermis. The ducts (d) wind gently between the lobules and through the dermis to the many funnel-shaped interpapillary pegs (f) which reach almost to the secretory lobules. The ducts run an almost straight course through the epidermis (arrow) to the thick stratum corneum where they follow helical spirals (arrows) to the friction surface.

(Bar = 150µm)

Fig.96 L.S. through a front foot toe pad of G. oculariis. The tightly coiled secretory tubules (s) of the abundant sudoriferous glands almost fill the dermis. Numerous ducts (d) are seen running at angles through the dermis towards the friction surface on which they will open, after they have followed helical spirals (arrows) through the thick stratum corneum.

(Bar = 150µm)

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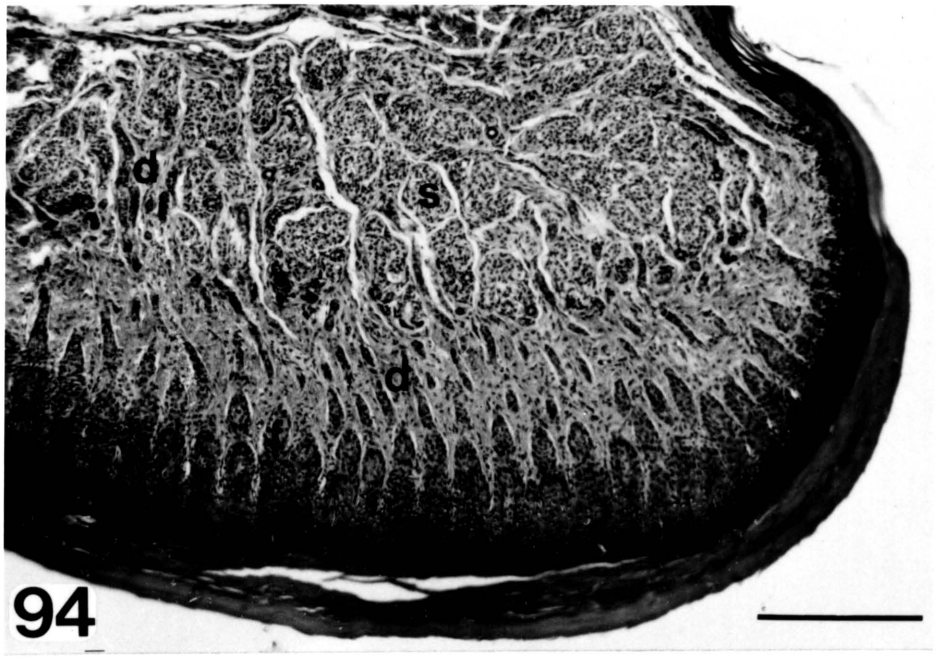

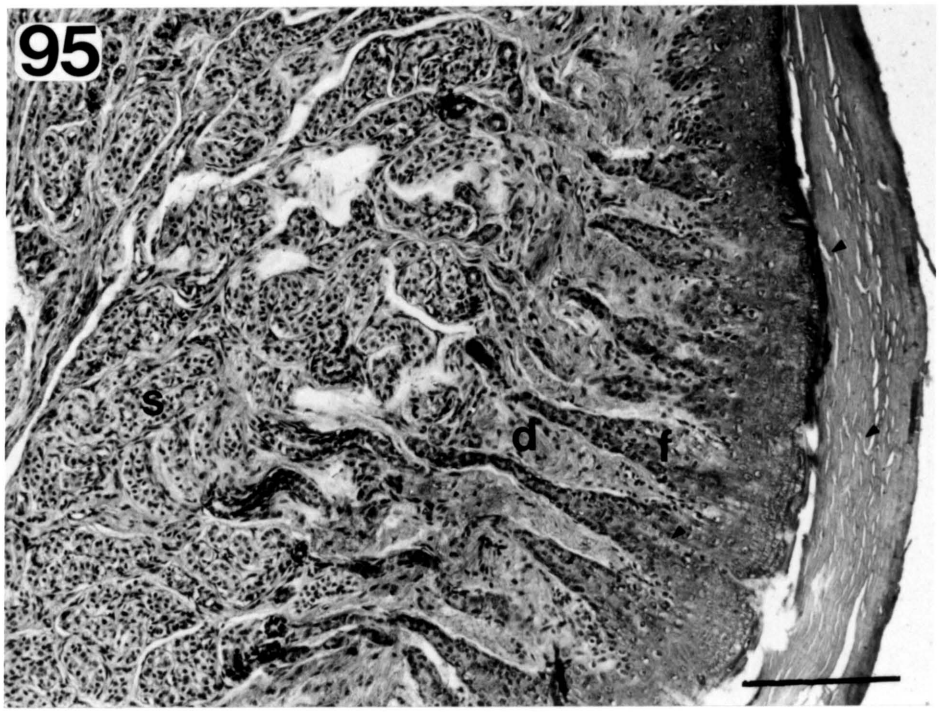

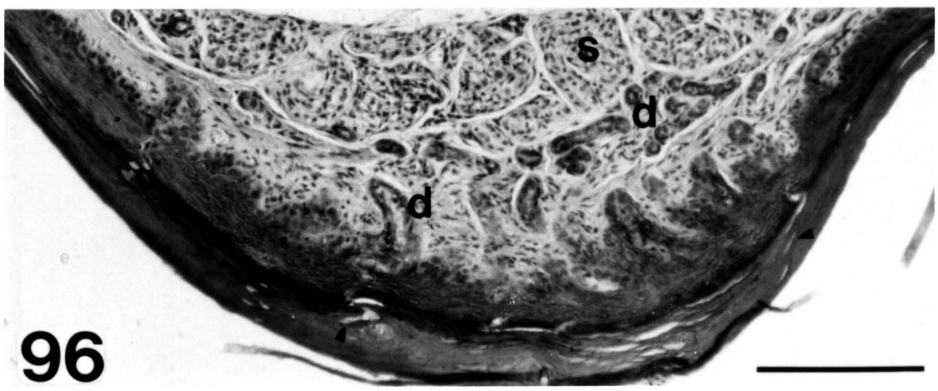

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available dermis in each pad, with little connective tissue separating the lobules which also lacked the usual surrounding adipose tissue (Fig.94). The lumens of both the secretory tubules and their ducts were small. The abundant excretory ducts wound loosely through the dermis, but extended almost straight through the papillary pegs (Fig.95). Each duct extended in a narrow helix through the thick stratum corneum (Fig.96). The ducts which extended to the epidermis on the sides of the pads were redirected at an angle through the epidermis to open on the ventral friction surfaces of the pads (Fig.95). No differences between the glands of these two species were observed.

These are allopatric species with G. ocularis frequenting trees and crevices on rocky outcrops mainly in the more arid western regions of southern Africa, while G. murinus inhabits holes in large trees as well as rocky terrain in the higher rainfall areas (De Graaff 1981). Both species are considered arboreal and also partly terrestrial being swift and agile climbers both and on rocky surfaces and in trees (De Graaff 1981). Dormice can move with incredible speed and agility in the branches of trees and are extremely agile climbers, running up and down stems with equal ease. They can balance on very thin branches or run down upside-down (Kingdon 1974). Their feet have well-developed pads adapted for climbing and also sharp little claws (Kingdon 1974), and like the other arboreal rodents such as Thallomys paedulcus these pads are packed with sudoriferous glands as are the bulbous toe pads and well-developed digital ridges. Other species of the Gliroidea show similar glands, including Glis glis which has very large eccrine sweat glands in the hind sole callosities, and in Eliomys quercinus where huge eccrine sweat glands surrounded by fat cells occur in the hind sole callosities (Sokolov 1982). The palmar and digital skin was not investigated in these studies which is unfortunate for comparative purposes.

The distribution and functions of sweat glands in the palmar and plantar soles and toe pads of the Primates have been well-documented (Montagna & Parakkal 1974) as well as other arboreal mammals such as the tree shrew Tupaia glis (Montagna, et at. 1962). As the digital and foot pad sufaces of the dormice are smooth, lacking the dermal ridges characteristic of the

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Primates (Weiner & Hellmann 1960; Montagna & Parakkal 1974), the well-developed digital ridges (each with a sweat gland opening onto its surface) of the 'climbing' rodents like Graphiurus, are reminiscent of the glands opening on to the dermal ridges of the digits of man (Misumi & Akiyoshi 1984) and other Primates (Montagna & Parakkal 1974). The function of these glands is to - "enhance the prehensibility of the Primates and presumably the glands of the pad are of utility to other species for analogous reasons" (Weiner & Hellmann 1960). Similarly these glands in the Graphiurus species should be secreting a constant supply of sweat to keep the thick epidermis moist and pliable (Ring & Randall 1947; Jenkinson 1973) and so improve the traction of the friction surfaces of these pads with the substrate being climbed (Ring & Randall 1947; Adams 1966; Adelman, et al. 1975). In a similar way to the Primates that do not use their flat nails but rather their glabrous feet for climbing (Montagna & Parakkal 1974), dormice can climb on twigs even after amputation of the claws, using only their pads for a firm grip (Eibl-Eibesfeldt 1958 in Kingdon 1974).

As Earl & Nel (1976) suggested that Thallomys paedulcus scent-marks branches to find its way through the tree tops during darkness, so too may a 'scent-trail' left by the abundant sudoriferous glands in the feet of these Graphiurus species be expected to fulfill this function. In captivity, Graphiurus murinus shows signs of strong territoriality with captive males having been known to kill and eat one another (Kingdon 1974). A 'scent-trail' left by these 'pedal glands' may, as a secondary function, help in individual and group recognition and thus limiting territorial conflict, as is the function of the 'plantar factor' odour from the sudoriferous glands in the feet of male Mus musculus (Ropartz 1977).

In the more common species (Thryonomys swinderianus, Xerus inauris, Hystrix africaeaustralis, Aethomys namaquensis, Rhabdomys pumilio, Praomys natalensis) where specimens from both sexes, and various ages and habitats were compared, no histological differences in the sudoriferous glands of each

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species were found. The exceptions being in the species with altricial neonates where these glands only developed within the first ten days after birth. Similarly, studies on the sudoriferous glands of young rats showed that the gland lumens had not yet developed, and that the secretory cells and myoepithelium were also undifferentiated in the three-day-olds, but were functionally differentiated in the ten-day-old rats (Matsuzawa & Kurosumi 1963). In the precocial young such as Petromus typicus, these glands were well-developed even before birth. In nine-month-old human foetuses, the eccrine glands are morphologically similar to those of adults and can be stimulated to function with sudorific drugs (Montagna & Parakkal 1974). Apocrine glands developed during the last twenty five days of gestation in the pig foetus and were also functional at birth (Meyer & Gorgen 1986).

THE PHYLOGENETIC AND TAXONOMIC IMPLICATIONS OF THE SUDORIFEROUS GLANDS IN THE INDIGENOUS RODENT FAMILIES.

There is strong phylogenetic support for the distinctness of the abundance and distribution patterns of sudoriferous glands in the feet of indigenous rodents at Family level (Table 4). The following sudoriferous gland patterns may be considered to be of taxonomic importance as they fit the accepted classification of the southern African rodents (De Graaff 1981; Smithers 1983) which include the Cricetidae and Muridae as separate Families (Table 2). The more recent classification combines the rodents of these two Families under the Muridae (Meester, et al. 1986) (Table 4). Evidence based on the sudoriferous gland patterns would seem to indicate that the Family Cricetidae with its great diversity of sudoriferous gland abundance be taxonomically retained when compared to the almost homogenous sudoriferous gland pattern of the Family Muridae (Table 4). Within the limitations of the numbers of species investigated, the sudoriferous gland patterns would also seem to extend to the Subfamilies of the combined Muridae (Meester, et al. 1986) (Table 4).

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TABLE 4. PHYLOGENY OF THE SUDORIFEROUS GLANDS IN THE RODENT FAMILIES

SITES OF THE GLANDS:	FORE FEET			HIND FEET				OTHER
	TP	DR	FFP	TP	DR	HFP	S	AREAS
1. Family **SCIURIDAE**								
Xerus inauris	+++	+	++	+++	+	++	+	o
Paraxerus cepapi	+++	+	++	+++	+	++	+	o
2. Family **PEDETIDAE**								
Pedetes capensis	o	o	+	o	o	o	o	o
3. Family **HYSTRICIDAE**								
Hystrix africaeaustralis	+++A	o	+++A	+++A	o	+++A	+++	o
4. Family **THRYONOMYIDAE**								
Thryonomys swinderianus	o	o	o	o	o	o	o	+(ear)
5. Family **PETROMURIDAE**								
Petromus typicus	+++	o	+++	+++	o	+++	++A	o
6. Family **BATHYERGIDAE**								
Cryptomys hottentotus	o	o	o	o	o	o	o	o
7. Family **MURIDAE**								
OTOMYINAE								
Otomys irroratus	+++	+	+++	+++	+	+++	o	o
Otomys angoniensis	+++	+	+++	+++	+	+++	o	o
GERBILLINAE								
Desmodillus auricularis	o	o	+	o	o	o	o	o
Gerbillurus paeba	+	o	o	+	o	o	o	o
Tatera leucogaster	++	+	++	++	+	++	o	o
Tatera brantsi	++	+	++	++	+	++	o	o
CRICETINAE								
Mystromys albicaudatus	+++	o	+++	+++	o	+++	o	o
CRICETOMYINAE								
Saccostomus campestris	++	+	++	++	+	++	o	o
MURINAE								
Acomys spinosissimus	+++	+	+++	+++	+	+++	o	o
Lemniscomys griselda	++	+	++	++	+	+++	o	o
Rhabdomys pumilio	++	+	++	++	+	+++	o	o
Dasymys incomtus	o	o	++	o	o	++	o	o
Mus minutoides	++	o	+++	++	o	++	o	o
Praomys(Mastomys)natalensis	+++	+	+++	+++	+	+++	o	o
Thallomys paedulcus	+++	+	+++A	+++	+	+++	o	o
Aethomys chrysophilus	+++	+	+++	+++	+	+++	o	o
Aethomys namaquensis	+++	+	+++	+++	+	+++	o	o
8. Family **GLIRIDAE**								
Graphiurus ocularis	+++	+	+++	+++	+	+++	o	o
Graphiurus murinus	+++	+	+++	+++	+	+++	o	o

(classification after Meester, *et al*. 1986)

Legend: TP - distal toe pads
DR - digital ridges
FFP - front foot pads
HFP - hind foot pads
S - hind foot sole

+++ - abundant glands filling the pads
++ - numerous glands scattered through the dermis of the pads
+ - one or two glands in each pad
o - no sudoriferous glands observed
A - apocrine glands

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A Taxonomic Application of the Sudoriferous Gland Patterns to the Indigenous Rodent Families.

Family **SCIURIDAE**

Abundant sudoriferous glands in the enlarged toe pads, glands in the digital ridges and numerous glands in the palmar and plantar pads, with the characteristic single glands lying parallel in the soles of the hind feet which only secrete through small tubercles onto the soles' surface.

Family **PEDETIDAE**

An absence of sudoriferous glands except a single large gland opening onto the hairless palmar pad.

Family **HYSTRICIDAE**

Abundant large eccrine-type sudoriferous glands are arranged in large lobules deep in the dermis of the toe pads, palmar and plantar pads and hind foot soles and heels. Large apocrine glands which lie in the hypodermis secrete onto the ventral surfaces of all these sites. The feet lack the typical digital ridges and their associated glands found in the smaller rodents.

Family **THRYONOMYIDAE**

Sudoriferous glands are uniquely absent in the feet, but form the characteristic post-auricular glands behind the pinnae.

Family **PETROMURIDAE**

Abundant large eccrine-type sudoriferous glands are arranged in large lobules deep in the dermis of the toe pads and palmar and plantar pads. A number of large apocrine glands lie in the hypodermis below the numerous eccrine glands, and secrete onto the hind foot soles. No glands occur on the digital ridges.

Family **BATHYERGIDAE**

Sudoriferous glands have been characteristically absent in the skin of those species so far investigated.

Family **GLIRIDAE**

Abundant sudoriferous glands practically filling the dermis in the large palmar and plantar pads and distal toe pads. These pads are greatly enlarged and proportionately comparable in size only to those of Thallomys paedulcus but from which they are distinguishable by the absence of large apocrine glands in the palmar pads. Well-developed sudoriferous glands also occur in the digital ridges.

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Family **MURIDAE (CRICETIDAE & MURIDAE)**

The sudoriferous gland patterns are so diverse that they cannot be used as taxonomic characteristics, except possibly at the Subfamily level.

Within a rodent Family of many species, the whole spectrum of abundance and distribution of sudoriferous glands may be found. This can be clearly seen in the combined Family Muridae, where the extremes of the Otomyinae having abundant glands compared to Desmodillus auricularis of the Gerbillinae where one or two glands occur only in some palmar pads. However, the abundance and distribution of sudoriferous glands is reasonably constant within the subfamilies (Table 4). In the Gerbillinae there is a strong tendency to a reduction of sudoriferous glands particularly in those species with haired feet such as Gerbillurus paeba and Desmodillus auricularis (Table 4). On the other hand, subfamily Murinae have mainly retained the typical well-developed glands in their feet, with the exception of Dasymys incomtus where the glands are limited to certain of the palmar and plantar pads only. These extremes may be viewed as ecological behavioural adaptations which are discussed later.

At generic levels the sudoriferous glands' distribution and structure are indistingtuishable as shown in Tatera leucogaster and T. brantsi; Otomys irroratus and O. angoniensis; Aethomys chrysophilus and A. namaquensis. A similar situation is found even in more distantly related Xerus inauris and Paraxerus cepapi which are very different in their ecological behaviour.

DISTRIBUTION PATTERNS OF RODENT SUDORIFEROUS GLANDS INTERPRETED ACCORDING TO THEIR ECOLOGICAL BEHAVIOUR.

An attempt to group the Rodents studied according to their general ecological behaviour and to relate their patterns of sudoriferous gland distribution to this is made in Table 5. It is accepted that certain genera such as Otomys, Praomys and Tatera may be alternatively placed, but for the majority of species this grouping holds and forms the basis of the functional interpretation of the sudoriferous gland distribution in indigenous rodents which follows.

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TABLE 5. DISTRIBUTION OF THE SUDORIFEROUS GLANDS IN THE RODENTS ACCORDING TO THEIR ECOLOGICAL BEHAVIOUR.

SITES OF THE GLANDS:	FORE FEET			HIND FEET				OTHER
	TP	DR	FFP	TP	DR	HFP	S	AREAS
1. ROCK OR TREE CLIMBERS:								
Nocturnal:								
Graphiurus ocularis	+++	+	+++	+++	+	+++	o	o
Graphiurus murinus	+++	+	+++	+++	+	+++	o	o
Thallomys paedulcus	+++	+	+++A	+++	+	+++	o	o
Aethomys chrysophilus	+++	+	+++	+++	+	+++	o	o
Aethomys namaquensis	+++	+	+++	+++	+	+++	o	o
Acomys spinosissimus	+++	+	+++	+++	+	+++	o	o
Praomys natalensis	++	+	++	++	+	+++	o	o
Diurnal:								
Petromus typicus	+++	o	+++	+++	o	+++	++A	o
Paraxerus cepapi	+++	+	++	+++	+	++	+	o
2. TERRESTRIAL USING RUNS:								
Nocturnal:								
Otomys angoniensis	+++	+	+++	+++	+	+++	o	o
Diurnal:								
Otomys irroratus	+++	+	+++	+++	+	+++	o	o
Lemniscomys griselda	++	+	++	++	+	+++	o	o
Rhabdomys pumilio	++	+	++	++	+	+++	o	o
3. NOCTURNAL TERRESTRIAL WANDERERS:								
Hystrix africaeaustralis	+++A	o	+++A	+++A	o	+++A	+++	o
Mystromys albicaudatus	+++	o	+++	+++	o	+++	o	o
Saccostomus campestris	++	+	++	++	+	++	o	o
Mus minutoides	++	o	+++	++	o	++	o	o
4. SEMI-ARID BURROWERS:								
Nocturnal:								
Pedetes capensis	o	o	+	o	o	o	o	o
Gerbillurus paeba	++	o	o	o	o	o	o	o
Desmodillus auricularis	o	o	+	o	o	o	o	o
Tatera leucogaster	++	+	++	++	+	++	o	o
Tatera brantsi	++	+	++	++	+	++	o	o
Diurnal:								
Xerus inauris	+++	+	++	+++	+	++	+	o
5. FOSSORIAL:								
Cryptomys hottentotus	o	o	o	o	o	o	o	o
6. SEMI-AMPHIBIOUS RIVERINE DWELLERS:								
Dasymys incomtus	o	o	++	o	o	++	o	o
Thryonomys swinderianus	o	o	o	o	o	o	o	+(ear)

Legend: TP - distal toe pads
DR - digital ridges
FFP - front foot pads
HFP - hind foot pads
S - hind foot sole

+++ - abundant glands filling the pads
++ - numerous glands scattered through the dermis of the pads
+ - one or two glands in each pad
o - no sudoriferous glands observed
A - apocrine glands

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Diurnal versus nocturnal species:

Even though these glands are very similar to the eccrine glands in man which are mainly responsible for his thermoregulation, the very limited distribution of these glands in the rodents would make their functional contribution to thermoregulation minimal or at the most, localized. Thus no difference in gland distribution between nocturnal and diurnal species is expected. This is well illustrated in the indistinguishable sudoriferous glands of the mainly nocturnal Otomys angoniensis and the diurnal Otomys irroratus, which are so sympatric that they have been caught in the same runs (De Graaff 1981). However, the diurnal rodents whose feet are exposed to very hot surfaces (up to 70°C in the Kalahari - Bothma 1980) may well need plenty of sweat glands to keep their foot pad surfaces moist and cool. This may apply to Xerus inauris, Petromus typicus and Rhabdomys pumilio.

Rock and tree climbers:

These climbing species share the typical characteristics of large foot pads and bulbous toe pads (Layne 1970) filled with abundant sudoriferous glands. The more arboreal the species, the greater the development of these pads (Earl & Nel 1976) and their associated glands as seen in the genera Graphiurus and Thallomys. In Paraxerus cepapi, the palmar and plantar pads and their associated glands are less developed than expected for a semi-arboreal species, being similar to the ground squirrel Xerus inauris. This may however, be a reflection of their phylogeny as Kingdon (1974) suggests that the Ethiopian tree squirrels evolved from the ground squirrels which now survive in the Xerini. The enormous foot pad development and their abundant glands in diurnal Petromus typicus are probably adaptations to climbing the hot rocks of the arid western regions as previously suggested.

Terrestrial using runs:

For terrestrial rodents, the Otomys species had well-developed foot and digital pads, which were filled with sudoriferous glands which seemed to be superfluously developed, for, if they had to be judged micro-anatomically would lead to the conclusion that these feet belonged to climbing species. Alternative

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functions have been previously discussed under the Otomys species.

The digital and foot pads and their associated glands are comparatively more moderately developed in Lemniscomys griselda and Rhabdomys pumilio (Table 5) and are more in line with those of terrestrial rodents. The use of runs through the grass cover would limit their exposure to hot surfaces, except in the arid regions where vegetation cover is sparse. Here the larger plantar pads with their abundant glands may help to keep the contact surfaces of the hindfeet moist and cool when the animals are sitting on their haunches and eating food held in their paws.

Nocturnal terrestrial wanderers:

Being nocturnal, these species do not face the problems of walking on hot surfaces. However, not being limited to runs like the previous group, they move over wide areas on comparatively rough terrain at night. The functions of their sudoriferous glands in their less prominent foot and toe pads may be to limit the abbrasion of the epidermal friction surfaces by keeping them moist and pliable while at the same time to leave a 'scent-trail' which might be followed over this new terrain on returning to their burrows or nest.

Hystrix africaeaustralis which had the largest and most abundant sudoriferous glands in pads of its glabrous feet, is known to cover distances of up to 16 km per night in search of food (Kingdon 1974, De Graaff 1981). Similarly, on commenting on the large size of the sweat glands in the paws of Spermophilopsis leptodactylus, Sokolov (1962) suggested that if these are 'recognitional' glands they reflect the activity of the animal and the great distance it moves away from its burrow. In addition to the abundant eccrine sweat glands H. africaeaustralis also had a few large apocrine glands scattered through the pads of its feet.These are likely to be odiferous leaving a longer lasting 'scent-trail' similar to the glands in the foot pads of the coyote (Sands, et al. 1977) which also ranges over wide areas.

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A further observation is the apparent loss of sudoriferous glands in the digital ridges in most of the species in this group (Table 4). These glands would not be as functionally important to strictly terrestrial rodents as to the 'climbers' where they increase the adhesion of these friction surfaces (Ring & Randall 1947; Adel, et al.) , which is very important in maintaining a good grip particularly with the toes. Earl & Nel (1976) showed Saccostomus campestris to be the least efficient climber when compared to the semi-arboreal Praomys natalensis and the arboreal Thallomys paedulcus who had two sudoriferous glands in each digital ridge. The less developed pads and fewer glands found in S. campestris would confirm it as being a terrestrial rodent. It is also interesting to note that Mus minutoides lacks these digital ridge glands which are present in Mus musculus which is a fair climber (De Graaff 1981).

Semi-arid burrowers:

Except for Xerus inauris whose well-developed sudoriferous glands have already been discussed as a 'diurnal species', all the other species in this group are nocturnal and had limited sudoriferous glands (Table 5). The ecological behavioural reasons for this is given by Schmidt-Nielsen (1972) who states: "For desert rodents the available water would soon be exhausted if they were to sweat; actually, they have no sweat glands and avoid the need to sweat by staying in their relatively cool burrows during the hot desert day, restricting their active life to the cooler nights." His eco-physiological reasoning may be sound when relating the main function of sweat glands to thermoregulation, but it does not lead to the incorrect statement that desert rodents 'have no sweat glands'. Prior studies on Asian desert rodents by Sokolov (1962) and North American rodents by Quay (1965b) both showed that desert rodents do have substantial sudoriferous glands but limited to specific areas. The decrease in the distribution of these glands is largely proportional to the increase in hairiness of the ventral surfaces of the feet and toes, a characteristic of animals burrowing in sandy habitat. Pedetes capensis, Gerbillurus paeba, and Desmodillus auricularis had distinctly hairy feet with limited naked digital and palmar pads in which the few sudoriferous glands were found (Table 5), whereas the feet of

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the Tatera species were only partly furred and even with the reduced size of the pads, numbers of sudoriferous glands were present. The decrease in the sudoriferous glands is thus due to an alternative adaptation to effectively moving over a sandy surface by increasing the hairy surface of the feet, and to quote Quay (1965b) - "the apparent lack of eccrine sweat glands here may be only indirectly, if at all, related to problems of water concentration (conservation) in the desert environment". Due to the saltatorial locomotion used by a number of these species, the functional significance of these limited glands on the front paws may be related to the burrowing behaviour of these rodents.

Fossorial/Subterranean:

The total absence of sudoriferous glands on the furred skin and more particularly on the large naked surfaces of the feet of Cryptomys hottentotus made this animal the exception in this study. However, this may be seen as a continuation of the trend of a sharp reduction in sudoriferous glands in the 'semi-arid burrowers' through to these subterranean rodents who seldom leave their tunnels. As a fossorial mammal living in a tunnel system which has its own microclimate, the need to have sweat glands is virtually absent as shown by a similar lack of sudoriferous glands in the naked mole-rat Heterocephalus glaber (Sokolov 1982). These naked mole-rats, like the other Bathyergidae, have a low body temperature and are virtually incapable of thermoregulation (Lovegrove 1986). Similarly another subterranean rodent Spalax microphthalmus, also totally lacks sudoriferous glands, including on its front and hind feet (Sokolov 1982). Furthermore, the thermoregulatory function of sweat glands would be limited in the burrows where evaporative cooling and air movement is minimal (McNab 1979). The high relative humidity and relatively cool temperatures, together with the moistness of the soil surface in the closed burrows would probably be sufficient to keep the thick stratum corneum of the naked feet pliable as digging is mostly a seasonal activity, which is carried out when the soil is relatively soft or moist (Genelly 1965; Kingdon 1974). A possible 'scent-trail' produced by sudoriferous glands is unnecessary as the rodent-moles are commited to a limited subterranean tunnel

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existence, and such glands may only have been important to help them relocate their tunnel entrances on those rare occasions of them coming onto the surface. However, this would be further complicated as their sense of smell is poorly developed (De Graaff 1981; Smithers 1983).

Semi-amphibious riverine dwellers:

The tendency in the semi-aquatic rodent species to have a reduction in sudoriferous glands on the naked appendages (Table 5), is also seen in other rodents living in a wet habitat like Myocastor coypus where only in one specimen, a few tubular glands were found in the hind foot sole callosities, while in the Muskrat Ondatra zibethica no glands could be found on the soles (Sokolov 1982). Even in an amphibious mammal like the duck-billed platypus, Ornithorhynchus paradoxus, the palms and soles, the volar surface of the digits, and the web between the digits are all glabrous and yet completely free of sweat glands (Montagna & Ellis 1960). They conclude that these surfaces are kept moist and pliable by being in contact with water, moist earth or mud and therefore have no eccrine glands. The same may hold for Dasymys incomtus and Thryonomys swinderianus.

A possible second function of scent-marking as raised for some other rodents might not be relevant due to the fact that they both make use of distinct runs which criss-cross their relatively small home ranges in the reedbeds. As much of the surface substrate is wet or moist a 'scent-trail' produced by sweat glands would be diluted and quickly diffused in the moisture, particularly as these animals are fond of swimming and playing in the water (Kingdon 1974; De Graaff 1981). They are also likely to know every run throughout their limited home ranges. The cane-rats may be using their post-auricular glands for scent-marking the plants as they move along their runs which become tunnels through the dense vegetation. This may suffice the olfactory communicatory needs of this species.

There is thus some evidence for sudoriferous gland uniformity in abundance and distribution when species are compared on an ecological behavioural basis. This is to be expected as a result of similar functional demands being met by the convergent adaptation of these glands in different species.

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CHAPTER 6.

CONCLUSIONS

The presence of sudoriferous glands was conclusively established in the integument of 25 of the 26 species of wild rodents representing the nine families indigenous to Southern Africa (Table 2). This has confirmed the author's hypothesis - "that the Rodentia have retained the typical mammalian characteristic of sweat glands", which is in sharp contrast to those who still hold to the view that 'sweat glands are absent in rodents' (Schmidt-Nielsen 1964, 1972; Rowett 1974; Leake 1975).

Sudoriferous glands were found only in the hairless skin of the feet of all the species, with the exception of the greater cane-rat Thryonomys swinderianus and the common mole-rat Cryptomys hottentotus (Table 2). This is in agreement with the findings of Quay (1962) who concluded that although sweat or sudoriferous glands are widely distributed over the body in many mammalian Orders, in the Rodentia they are nearly restricted to the digital, plantar and palmar pads. Indeed this was confirmed in this study, where these tubular glands were so abundant in many of the African species, that their secretory tubules practically filled the dermis in the palmar and plantar pads, and distal toe pads.

Although the microstructure of the sudoriferous glands of the rodent foot pads were basically similar to eccrine glands, they were cytologically however unique when compared to the descriptions of typical eccrine or apocrine sweat glands in man and other domestic animals. The main distinction between these two types of sudoriferous glands is based on the histological differences of the secretory cells lining the secretory tubules (Weiner & Hellmann 1960; Munger & Brusilow 1971). Only one type of secretory cell could be distinguished by light microscopy in the sudoriferous glands of the wild rodents. This is in contrast to the eccrine glands of the human (Montagna 1956), other primates (Montagna & Parakkal 1974) and the cat (Munger & Brusilow 1961). In the above species two types of secretory cells were described; the dark cells with a basophilic cytoplasm containing secretory vacuoles and the clear cells lacking

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cytoplasmic basophilia and secretory vacuoles. In the present study, no secretory vacuoles could be identified in the secretory cells as decribed in the dark cells of eccrine glands of the cat (Munger & Brusilow 1961) and various primates (Montagna & Parakkal 1974). These light microscopic findings that the secretory cells of the wild rodent sweat glands are only of one atypical type, are in agreement with those reported in the white rat (Wechsler & Fisher 1968; Munger & Brusilow 1971), the white mouse (Quick, et al. 1984) and the bank vole (Griffiths & Kendall 1980a).

Apocrine glands were described for the first time in the feet of three rodent species. Previous descriptions indicated that they were limited to dorsal and anal glands of certain sciurids (Quay 1965b; Kivett 1978; Sokolov 1982) and the oral angle of various sciurids and many Cricetidae (Quay 1962, 1965a; Sokolov 1982). The apocrine glands occurred in combination with the more numerous eccrine type glands and their ducts also atypically opened directly onto the hairless skin of the foot pads. This combination of eccrine and apocrine glands together has also been described in foot pads various canids (Sands, et al. 1977). It is suggested that the apocrine glands are odiferous leaving a longer lasting 'scent-trail'.

The ultrastructure of the sudoriferous glands of the three species studied showed no interspecific ultrastructural differences. However, when ultrastructural comparisons were made with the sudoriferous glands of non-rodent species such as man (Ellis 1962; Montagna & Parakkal 1974), the macaque (Ellis & Montagna 1961) and the cat (Munger & Brusilow 1961) very distinct differences were found. The eccrine sweat glands of the non-rodent species are ultrastructurally very similar, containing two distinct types of secretory cells termed the light or clear cells and the dark mucoid cells (Munger & Brusilow 1961; Montagna & Parakkal 1974). The secretory epithelium of the sudoriferous glands of the rodents in this study consisted of only one type of secretory cells which differed from both the clear and dark cells as described above in the non-rodent species in the following ways. First, the infoldings of the basal plasma membranes are far more extensive

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in the rodent secretory cells extending up to the perinuclear area and enclosing most of the mitochondria in these thin slips of basal cytoplasm (Fig.18) indicative great secretory activity. This is the most remarkable feature of these cells. Secondly, the luminal microvilli of the three indigenous species were longer, more numerous and more regular (Fig.19 & 20) than those described in the other rodent species. In the non-rodents, the formation of cytoplasmic blebs has not been mentioned in the eccrine glands of man (Ellis 1962; Montagna & Parakkal 1974) or the cat (Munger & Brusilow 1961). The mushroom-like cytoplasmic projections which seem to develop as the enlarging tips of some of the microvilli as described in the rat (Matsuzawa & Kurosumi 1963), the bank vole (Griffiths & Kendall 1980a) and the Namaqua rock rat (Green & Soley 1981) were also seen frequently in all the wild rodent species. These cytoplasmic blebs seem to swell to a certain size before budding off into the lumen where collapsed membraneous structures are clearly seen. Although these blebs seem to contain no cytoplasmic organelles or secretory granules as in the cytoplasmic protuberances described in apocrine secretory cells (Montagna 1956; Weiner & Hellmann 1960), their content must contribute to the glandular secretion. This may indicate a form of 'micro-apocrine secretion' by these cells as has been proposed by Matsuzawa & Kurosumi (1963) and supported by Green & Soley (1981) who questioned the validity of the term 'eccrine' sweat glands as applied to some rodents (Quay 1965b; Wechsler & Fisher 1968).

The myoepithelial cells studied in the three wild species showed great uniformity in structure and contained only thick myofilaments, as in the mouse (Quick, et al. 1984). When compared with the electron micrographs of the glands of the laboratory rat (Matsuzawa & Kurosumi 1963; Munger & Brusilow 1971), the wild rodents have greatly thickened basement membranes which scallop deeply to interdigitate particularly with the myoepithelial cells to which they are attached by large hemidesmosomes. This may indicate an increased contraction function for a faster secretion.

As these SEM studies on the ventral surfaces of the feet of various species were unique, literary comparisons were limited

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as similar studies have only been done on man (Johnson, et al. 1970) and the bank vole (Griffiths & Kendall 1980a). Variations of the duct orifices in shape and structure were shown not only between species, but also on the same sites of the same rodent (Green & Soley 1979), unlike those of man which differed only on different parts of the body (Johnson, et al. 1970). The hoped for interspecific differences were limited. The use of the SEM to determine the number of sweat duct openings per area was also not successful as the stratum corneum cells were partly lifted in most species which obscured the duct openings, making counting difficult.

The SEM studies were however, useful in observing the micro-structural adaptations of the traction surfaces of the feet such as the digital ridges and the opening of the ducts into cup-shaped depressions in the epidermis of the feet of Thallomys paedulcus and Petromys typicus. These may be adaptations for better adhesion in these climbing species. Similarly, the numerous microplicae on the surface of the stratum corneum cells lining and surrounding the duct openings may aid in the distribution of the sweat from these glands over the surface of the foot pads. Thus the SEM can be a useful tool to study the foot morphology and micro-structural adaptations of the traction surfaces of the small rodents as related to locomotory behaviour, and even as a taxonomic aid.

Significant differences in the abundance and distribution of sudoriferous glands were found between the species of the different families investigated. There is strong phylogenetic support for the distinctness of the distribution of these glands in rodents particularly at Family and Subfamily levels (Table 4). These sudoriferous gland patterns may be of taxonomic importance as they fit the recent classification of southern African rodents well (De Graaff 1981; Smithers 1983), but adding evidence for the retention of the Cricetidae and Muridae as separate Families. This is in contrast to the combined single Family Muridae according to Meester, et al. (1986) but even here the glandular distribution supports the Subfamilies classification.

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There is also some evidence for sudoriferous gland uniformity in abundance and distribution when species are compared on an ecological behavioural basis. This is as a result of similar functional demands being met by the convergent adaptation of these glands in different species. The number of glands were most abundant in the climbing species of the Muridae and Gliridae, along with the diurnal Sciuridae and Petromuridae which also have additional sudoriferous glands in their plantar soles. The terrestrial Cricetidae, Muridae and Hystricidae had abundant to numerous glands. In the burrowing species from semi-arid habitats such as Pedetidae and some of the Cricetidae which have partly furred feet, the sudoriferous glands were limited to a few small glands or a single large gland in the small hairless pads of the feet or toes. Similarly, the semi-amphibious species showed a further reduction in glands with the water rat Dasymys incomtus only having a few sudoriferous glands in only certain of the foot pads, while no glands were found in the feet of Thryonomys swinderianus. The fossorial Bathyergidae represented by Cryptomys hottentotus, totally lacked sudoriferous glands.

Three new sites for sudoriferous glands in rodents were described for the first time. In most species with digital ridges, a single eccrine gland opened onto the ventral or antero-ventral surface of each ridge. In Thallomys paedulcus two glands occured in each ridge. Apocrine glands were described for the first time in the feet of rodents, where they occurred together with the eccrine glands in the palmar and plantar pads of Hystrix africaeaustralis, the plantar soles of Petromus typicus and in the palmar pads of T. paedulcus. The only other site besides the feet where sudoriferous glands were found, was the tubular glands forming the post-auricular gland behind the ear in Thryonomys swinderianus.

"There are numerous published reports of the lack of sudoriferous glands at certain sites in certain species, but no systematic survey of rodent sudoriferous glands has been made" - wrote Quay (1962). Since then single comparative surveys on the North American rodents (Quay 1965a, 1965b; Kivett 1978) and the Eurasian rodents (Sokolov 1962; Skurat (1972) in Sokolov 1982;

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Sokolov 1982) have been published. This, the first comparative survey of the sudoriferous glands in African rodents should make a significant contribution to fill the gap in glandular biology in the Ethiopian rodents. This may be useful in following certain intercontinental patterns in the universal rodent Families as shown in the Sciuridae (Table 3).

With the surge of interest in olfactory communication in mammals (Stoddart 1976; Albone 1984; Macdonald & Brown 1985), and particularly in the rodents that are convenient experimental models for determining the importance of social odours and pheromones (Ropartz 1976; Stoddart 1976; Brown 1985a; Halpin 1985), there is a renewed interest in glandular biology. The structure and function of the glands, and particularly the specialized integumental glands, as the source from these social odours and pheromones are produced (Mykytowycz & Goodrich 1974; Sokolov 1982; Brown 1985b), is of great importance to the behaviourists who have shown up the limited research on the glands of particularly the wild mammals (Sokolov 1982; Brown 1985b). It is hoped that this study will provide some of the necessary reference material of the sudoriferous glands to those behavioural ecologists working on our indigenous rodents. It is also hoped that some young mammalogists may be inspired into seeing the importance of this type of glandular research and take up the challenge of this open field in our mammals. Finally, as the medical researchers have already found that the laboratory rat (Matsuzawa & Kurosumi 1963; Wechsler & Fisher 1968), and the white mouse (Quick, et al. 1984) are suitable models for experimentation in the physiology of sweating, it may be that some of these wild species may be found to be even more suitable, especially with their sudoriferous glands being larger and far more abundant.

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SUMMARY

Skin samples were taken from 11 sites on the body, feet and tail of each of 26 species of wild rodents representing the nine families indigenous to Southern Africa. These were then investigated by means of light microscopy to establish the distribution of the sudoriferous glands and to compare them histologically. Glandular sites of selected species were studied by transmission electron microscopy while the duct openings on the feet were compared by scanning electron microscopy.

Sudoriferous glands were found only in the hairless skin of the feet of all the species, with the exception of the greater cane-rat Thryonomys swinderianus and the common mole-rat Cryptomys hottentotus. The eccrine type sudoriferous glands of the wild rodent foot pads were histologically similar to those decribed in other non-rodent species. The great abundance of secretory tubules were so compactly coiled in the dermis that individual glands were often difficult to distinguish, and often occurring in far greater concentrations than in the foot pads of man, monkey, dog or cat. The secretory cells of the rodent sudoriferous glands are cytologically unique, with only one type being distinguished by light microscopy, compared to the two cell types distinguished in the above non-rodent species. The few apocrine glands were characterized by darkly staining luminal content, and their ducts atypically opened directly onto the hairless skin of the foot pads in certain species. Although myoepithelium cells were well-developed in the secretory tubules they were not seen to extend along the ducts outside the secretory lobuli.

The sweat ducts followed a relatively straight or slightly curved course through the dermis to the well-developed epidermal interpapillary pegs through which they followed a tight spiral in most of the wild rodent species. In rodents with a thick epidermis the ductal helix curved through the stratum corneum towards the contact or friction surfaces of the foot pads. The ducts of the rodent glands opened directly onto the ventral surfaces of the foot pads which are smooth lacking the epidermal ridges on which the eccrine gland ducts open in the primates.

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The ultrastructure of these glands in the three wild species studied, was similar to those described in laboratory rodents. Although two secretory cell types could be distinguished according to their cytoplasmic electron density, their ultrastructure showed them to be only one type. The luminal microvilli of the secretory cells were longer, more numerous and more regularly spaced than in the other rodent species. The mushroom-like cytoplasmic projections which developed as the enlarging tips of some of the microvilli, were also seen frequently in all the wild species. These cytoplasmic blebs seem to swell to a certain size before budding off into the lumen where collapsed membraneous structures were clearly seen. This may indicate a form of 'micro-apocrine secretion' by these cells as has been proposed by Matsuzawa & Kurosumi (1963) who questioned the validity of the term 'eccrine' sweat glands in some rodents .

The myoepithelial cells studied in the three wild species showed, as in the mouse, great uniformity in structure and contained only thick myofilaments. When compared with the electron micrographs of the glands of the laboratory rat, the wild rodents have greatly thickened basement membranes which scallop deeply to interdigitate particularly with the myoepithelial cells to which they are attached by large hemidesmosomes. This is similar to that described in the mouse.

The ducts of the sudoriferous glands of the wild rodents, were lined by a double layer of epithelial cells which contained relatively few mitochondria and a less conspicuous cuticular border with few tonofilaments. The short microvilli that line the luminal surfaces of the wild rodents were more numerous and more regularly spaced than those of the non-rodent species. The luminal content of the ducts of the wild rodents was often membranous and distinctly granular.

Variations of the duct orifices in shape and structure were shown not only between species, but also on the same sites of the same rodent. The comma-shaped structure of the duct openings on the smooth foot and toe pads of the wild rodents reflected the direction of spiralization of the ducts through the epidermis. The lifting of some of the surface cells of the

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stratum corneum formed cellular canopies partly covering some of the duct openings. In some rodent species such as Petromys typicus and Thallomys paedulcus the duct orifices open into cup-shaped depressions on the foot surface. Numerous microplicae covered the surface of the stratum corneum cells lining and surrounding the duct openings.

These tubular eccrine type glands were so abundant in many species that their secretory tubules practically filled the dermis in the palmar and plantar pads, and distal toe pads. The differences in the abundance and distribution of sudoriferous glands found between the species of the different Families investigated, were phylogenetically significant. However, species from different families who shared a similar behavioural ecology also had a similar distribution of sudoriferous glands. The number of glands were most abundant in the climbing species of the Muridae and Gliridae, as well as the diurnal Sciuridae and Petromuridae which also had additional sudoriferous glands in their plantar soles. The terrestrial Cricetidae, Muridae and Hystricidae had abundant to numerous glands. In the burrowing species from semi-arid habitats such as Pedetidae and some of the Cricetidae which have partly furred feet, the sudoriferous glands were limited to a few small glands or a single large gland in the small hairless pads of the feet or toes. Similarly, the semi-amphibious species showed a further reduction in glands with the water rat Dasymys incomtus only having a few sudoriferous glands in only certain of the foot pads, while no glands were found in the feet of Thryonomys swinderianus. The fossorial Bathyergidae represented by Cryptomys hottentotus, totally lacked sudoriferous glands.

Three new sites for sudoriferous glands in rodents were described. In most species with digital ridges, a single eccrine gland opened onto the ventral or antero-ventral surface of each ridge. Apocrine glands were found together with the eccrine glands in the feet of three species, including the palmar and plantar pads of Hystrix africaeaustralis, the plantar soles of Petromus typicus and in the palmar pads of T. paedulcus. The only other site besides the feet where sudoriferous glands were found, was the tubular glands forming the post-auricular gland behind the ear in Thryonomys swinderianus.

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OPSOMMING

Velmonsters is van 11 areas op die liggaam, pote en stert van elk van 26 spesies van wilde knaagdiere geneem. Hierdie spesies is verteenwoordigend van die nege families wat endemies in Suid Afrika is. Monsters is deur middel van die ligmikroskoop ondersoek om die verspreiding van die sweetkliere aan te toon en histologies te ondersoek. Klierstreke van geselekteerde spesies was met behulp van die deurstraal-elektronmikroskoop bestudeer terwyl die buisopeninge op die pote deur middel van die aftaselektronmikroskoop vergelyk was.

Sweetkliere was uitsluitlik in die haarlose velgedeeltes van die pote by al die spesies gevind, met uitsondering van die grootrietrot Thryonomys swinderianus en die knaagdiermol Cryptomys hottentotus. Die ekkrienagtige sweetkliere wat aangetref word in die voetkussings van die wilde knaagdiere was histologies soortgelyk aan daardie wat in die nie-knaagdierspesies beskryf is. Die groot aantal sekreterende buisies was so dig opgekrul in die dermis dat indiwiduele kliere dikwels moeilik onderskei was. Genoemde buisies kom in veel groter aantalle by knaagdiere voor as in die voetsole van die mens, aap, hond of kat. Die sekreterende selle van knaagdiere is sitologies uniek deurdat slegs een tipe onder die ligmikroskoop herkenbaar was in teenstelling met die twee seltipes wat in bogenoemde nie-knaagdier spesies voorkom. Die enkele apokriene kliere wat voorgekom het was gekenmerk deur 'n donker kleurende luminale inhoud en hulle afvoerbuisies wat atipies direk op die haarlose vel oppervlakte van die voetkussings by sekere spesies geopen het. Alhoewel mio-epiteel selle by die sekreterende buisies goed ontwikkel is, was hulle nie aanwesig by die afvoerbuisies aan die buitekant van die sekreterende lobbetjies nie.

Die afvoerbuise van sweetkliere volg 'n relatiewe reguit of effens gebuigde verloop deur die dermis na die goed ontwikkelde epidermale interpapillere papillae waarin hulle 'n stywe spiraal by die meeste wilde knaagdierspesies volg. In die knaagdiere met 'n dik epidermis kronkel die heliksvormig-gekrulde afvoerbuisies deur die stratum corneum in die rigting van die kontak- of

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wrywingsoppervlakte van die pote. Die afvoerbuise van die sweetkliere by knaagdiere open direk op die ventrale oppervlak van die voetkussings wat glad en sonder epidermale riwwe is. By primate open die ekkriene buise op hierdie riwwe.

Die ultrastruktuur van die sweetkliere by die drie wilde spesies wat bestudeer was, is soortgelyk aan die' van laboratorium-knaagdiere. Op grond van die elektrondigtheid van die sitoplasma kon twee tipes sekreterende selle onderskei word, maar hul ultrastruktuur het getoon dat hulle net een tipe is. Die luminale mikrovilli van die sekreterende selle was langer, meer talryk en meer eweredig gespasieer as by die ander voorheen bestudeerde knaagdiere. Die paddastoelvormige sitoplasmiese uitstulpings wat ontstaan as gevolg van die vergroting van die eindpunte van sommige van die mikrovilli het meer geredelik by al die wilde spesies voorgekom. Dit wil voorkom asof die sitoplasmiese knobbels opswel tot op 'n sekere grootte voordat dit afknop in die lumen in, waar ook afgebreekte membraanagtige strukture te bespeur was. Die verskynsel mag dui op 'n soort "mikro-apokrien afskeiding" deur die selle soos voorgestel deur Matsuzawa & Kurosumi (1963). Laasgenoemde outeurs bevraagteken ook die geldigheid van die term "ekkriene sweetkliere" by sekere knaagdiere.

Die mio-epiteelselle van die drie bestudeerde wilde spesies toon, soos by die muis, groot eenvormigheid in struktuur en bevat slegs dik miofilamente teenoor ander spesies wat beide dik en dun miofilamente besit. By wyse van vergelyking tussen die elektron-fotomikrograwe van die rot en wilde knaagdiere het laasgenoemde aansienlik verdikte basaalmembrane wat diep golf om in te voeg met die mio-epiteelselle waaraan hulle deur middel van groot hemidesmosome vasheg. Dit stem ooreen met die toestand wat in muise beskryf is.

Die afvoerbuise van die sweetkliere van wilde knaagdiere word uitgevoer deur 'n dubbele laag epiteelselle wat relatief min mitochondria bevat en 'n minder opvallend kutikulere voering met min tonofilamente het. Die kort mikrovilli wat die lumen se oppervlakte by wilde knaagdiere uitvoer is meer talryk en eweredig versprei as daardie by nie-knaagdierspesies. Die inhoud

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van die lumen van die afvoerbuise by wilde knaagdiere was dikwels membraanagtig en opvallend korrelrig.

Die verskille in vorm en struktuur van die afvoerbuise se openinge was nie slegs gevind tussen die verskillende spesies nie, maar ook in dieselfde area in dieselfde knaagdier. Die kommavormige struktuur van die afvoerbuise se openinge by die gladde poot- en toonkussings van die wilde knaagdiere weerspieel die rigting van spiralisering van die buise deur die epidermis. Sommige van die oppervlakkige selle van die stratum corneum lig op om sellulere koepels te vorm wat die openinge van sommige afvoerbuise gedeeltelik bedek. By sekere knaagdierspesies soos Petromys typicus en Thallomys paedulcus open die afvoerbuise direk in koppievormige induikings op die poot se oppervlak. Veelvoudige mikroplicae bedek die oppervlak van die stratum corneum selle wat die openinge van die afvoerbuise se openinge uitvoer en omgeef.

By baie van die spesies was hierdie buisvormige ekkrienagtige kliere so talryk dat hulle sekreterende buisies byna die totale dermis van die palmare- en plantare kussings, sowel as die distale toonkussings gevul het. Die verskille is in die hoeveelhede en verspreiding van sweetkliere gevind tussen die spesies van die verskillende families wat bestudeer is, is filogeneties betekenisvol. In die families waar die spesies die dieselfde gedragsekologie gehad het, was die verspreiding van sweetkliere soortgelyk. Die aantal kliere was die hoogste in die klouterende spesies binne die Muridae en Gliridae terwyl die daglewende Sciuridae en Petromuridae ook bykomstige kliere in hulle plantare sole gehad het. Die grondlewende Cricetidae, Muridae and Hystricidae het volop tot menigte kliere gehad. By die grawende spesies wat in semi-dorre omgewings voorkom, soos die Pedetidae en sekere Cricetidae, wie se pote gedeeltelik met hare bedek is, was sweetkliere beperk tot 'n paar klein kliertjies of 'n enkele groot klier in die klein haarlose kussings van die pote of tone. By die semi-amfibiese spesies was daar 'n verdere afname van kliere. Die waterrot Dasymys incomtus het slegs 'n paar sweetkliere in sekere voetkussings gehad terwyl Thryonomys swinderianus geen kliere in sy pote het nie.

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Die fossoriale Bathyergidae verteenwoordig deur Cryptomys hottentotus het glad nie sweetkliere nie.

Drie nuwe lokaliteite van sweetkliere was in knaagdiere beskryf. By die meeste spesies met digitale riwwe open 'n enkele ekkriene klier op die ventrale of antero-ventrale oppervlak van elke rif. Apokriene kliere sowel as ekkriene kliere was tesame op die pote van drie spesies aangetref, insluitend die palmare en plantare kussings van Hystrix africaeaustralis, die plantare sole van Petromys typicus en die palmare kussings van Thallomys paedulcus. Sweetkliere was slegs op een ander lokaliteit behalwe die pote aangetref, naamlik die die post-aurikulere buisvormige kliere agter die oor by Thryonomys swinderianus.

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Elektronmikroskopievereniging van Suidelike Afrika DURBAN (1981)

ULTRASTRUCTURE OF THE SWEAT GLANDS OF THE RODENT Aethomys namaquensis

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Studies on the sweat glands of laboratory rats[1,2] have shown that the cytology and physiology of the rodent sweat gland is unique[3]. This study of the sweat glands of a nocturnal indigenous rodent, Aethomys namaquensis, presents complementary information which may help clarify some of contradictions regarding the cellular structure of such glands.

Foot pads were removed from specimens sacrificed in the laboratory, immediately fixed in 4% glutaraldehyde in phosphate buffer, post-fixed in 2% osmium tetroxide in the same buffer, and then processed for TEM using standard techniques.

The sweat glands of the foot pads of Aethomys are similar to those of the white rat[1,2,3] and the bank vole[4]. They consist of a coiled secretory tubule and a straight duct to the epidermis which then spirals upwards through the stratum corneum to the surface.

The secretory tubule is lined by a single layer of columnar epithelium which is partially covered by myoepithelial cells and surrounded by a distinct basal lamina. The two types of secretory cell distinguished by some authors[1,4] were not observed in the material studied, all cells being characterized by an extensive cytoplasm containing a large leptochromatic nucleus. In the epithelial cells the basal plasma membrane has numerous infolds which extend perpendicularly from the basal lamina to a point close to the nucleus. Most of the folds contain a thin slip of cytoplasm and large elongated mitochondria which are arranged end to end and extend to the perinuclear area. Where the plasma membrane abuts the basal lamina hemidesmosomes occur. The infoldings of the lateral plasma membranes form such elaborate interdigitations that the boundaries between adjacent cells are difficult to trace. At the junction between myoepithelial and secretory cells the infolded membranes of the latter adopt a parallel course above the surface of the myoepithelial cells. The basal lamina thickens and scallops distally towards the broad attachment plates (hemidesmosomes) which are present at intervals along the basal plasma membrane of the myoepithelial cells (Fig. 1).

Long microvilli extend into the lumen from the apical plasma membrane. Mushroom-like cytoplasmic projections, which seem to develop as enlarged tips of the microvilli, erupt from the luminal surface. As in the rat[1] and bank vole[4], these cytoplasmic blebs contain no organelles and similar membrane-bound bodies are seen lying free in the lumen (Fig. 2). This may indicate a micro-apocrine secretion by these cells as has been proposed by some authors[1,4], an interpretation which questions the validity of the term "eccrine" sweat glands in rodents[2].

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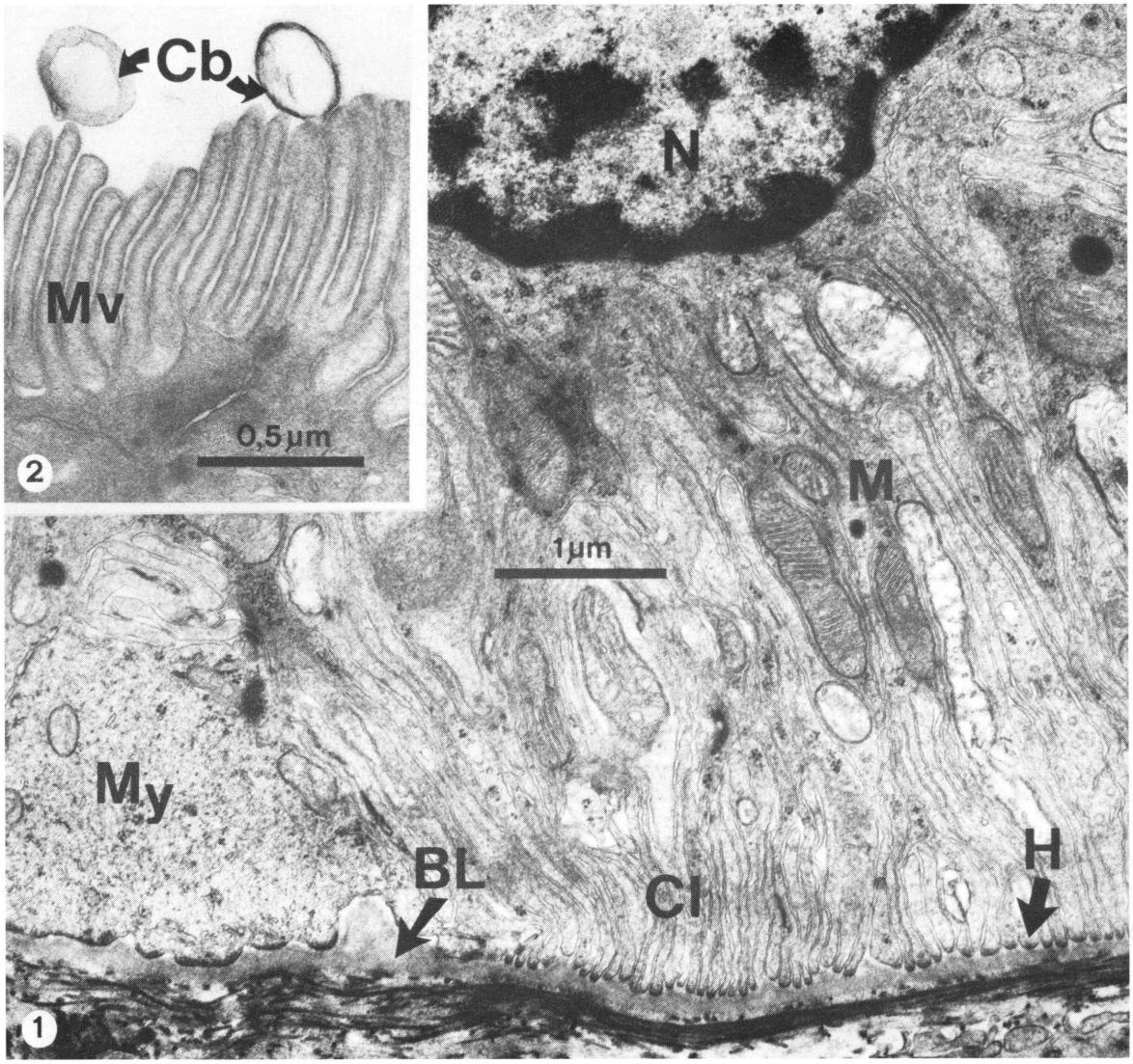

Fig. 1. The proximal region of a secretory cell from the sweat gland of Aethomys namaquensis. Note the nucleus (N), mitochondria (M) extensive cytoplasmic infoldings (CI), a portion of a myoepithelial cell (My), hemidesmosomes (H) and the basal lamina (BL).

Fig. 2. Microvilli (Mv) extending into the lumen of a secretory tubule. Cytoplasmic blebs (Cb), one of which appears to project from a microvillus, may indicate a micro-apocrine secretion by these cells.

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