AN ATLAS OF HAIR FROM SOUTHERN AFRICAN MAMMAL SPECIES
WITH REFERENCE TO ITS TAXONOMIC AND ECOLOGICAL SIGNIFICANCE

by

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ABSTRACT

This thesis deals with the microstructure of hair of mammal species, in
particular the Carnivora from southern Africa. Various techniques for
investigating the structure of hair, both by transmission and transmission-electro
microscopy are described. A substantial part of the work comprises an
atlas of the hair of thirty-six species of southern African Carnivora
which includes micrographs, coloured plates of typical hairs, locality
data and a descriptive text for each species.

The study is not confined to the Carnivora and the taxonomic importance
of hair is demonstrated with examples drawn from a wider field. The
highly practical relevance of hair identification in epidemiology has
been the source of investigations over the years, and these have been
included to demonstrate the value of hair identification.

In discussing adaptations of hair to ecologically selective pressures,
and the part it plays in the adaption of the mammal to its environment,
the general and detailed structure of hair has been dealt with relative to
the aquatic habitat, thermoregulation and the desert environment.
From considerations of the way in which the mammalian pelt provides a link with the environment there arises a proposition that the microstructure of the hair, and in particular the nature of the medulla, is of significance in the interaction with longwave infrared radiation. This viewpoint, which is backed at this point only by preliminary observations, requires further examination.
Professor J.D. Skinner of the Zoology Department and Director of the Mammal Research Institute (MRI), University of Pretoria, supervised this thesis, and I am indebted to him for invaluable guidance. I sincerely thank him not only for constructive help and critical analysis, but for encouragement when it was most needed. Several members of the MRI have been helpful during the course of this study and I am grateful for their interest and time; in particular, Dr. Reay Smithers generously provided locality data and maps for 29 species of small carnivores. These will not be published prior to publication of his work incorporating these.

This research was carried out at the South African Institute for Medical Research (SAIMR) and funded by a research grant from that organisation. I thank the Director, Professor J. Metz, for the facilities and funds provided, and Professor M. Isaäcson of the Department of Epidemiology, SAIMR, for her co-operation at all times. Colleagues at the SAIMR have readily offered help and kindness in many ways. Mrs. M. Anderson ably assisted in the production of the maps and the coloured plates of the hairs, and Miss P. Hawkins assisted in the arduous task of making hair measurements as well as typing the preliminary drafts. I extend my grateful thanks to them and to Mr. A.R. Sayed for his assistance with statistical analysis. The electron microscope department is thanked for kind co-operation. All the black and white photographs in this study were printed by the photographic department and I am especially grateful for the careful work of the late Mr. M. Ulrich and Mrs. Ulrich. Coloured prints from original drawings were produced by City Lab (Pty) Ltd., Johannesburg.
Thermographs were taken with the assistance of Mr. M.B. Gunn of Stanley Walters Co. (Pty) Ltd., Johannesburg, who lent me the Agavision system, and I am grateful to him for so generously making this facility available. Mr. W. Labauschagne, Curator of the Johannesburg Zoological Gardens, is thanked for co-operation. And the helpful co-operation of Mrs. S.L. Woods, who so kindly typed this manuscript, is greatly appreciated as is that of Mrs. J. Liberati who typed the text of the atlas.

The majority of specimens used in this study were drawn from the mammal collection at the Transvaal Museum, and I acknowledge the steady co-operation and willing assistance of Mr. N.A. Rautenbach, as well as other people who have kindly provided me with study specimens.

During the course of this study I have consulted with experts in fields other than my own, notably in the physical sciences. I take this opportunity of again acknowledging their interest and advice, and stimulating discussion.

Finally, I thank my family for tolerance and forebearance.
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## INTRODUCTION

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INTRODUCTION

The detailed study of hair is an example of a scientific project which has resulted from a synthesis of both purely biological and academic interest, as well as highly practical stimuli. The characters of the pelage as a whole have long been used by mammalogists as taxonomic criteria, and the fur and textile industries, as well as sheep and cattle rearing enterprises, have added great impetus into research on the pelage and hair. Publications on hair are available from the end of the nineteenth century when De Meijere (1894) studied hair morphology, to the present when we have papers dealing with such definitive aspects as the ultrastructure of hair, biochemistry of keratinisation and electrophoretic profiles of fibrous and matrix components of hair.

Biologists have become increasingly appreciative of the way in which hair can be used for identification as well as taxonomy. It has the important advantage of remaining relatively undamaged during digestion and with the passage of time, so that, for example, hairs from stomach and faecal contents of predators can be examined and identified. In this respect hairs are unlike bones which are often fragmented during digestion.

In South Africa the identification of hairs is being used both for law enforcement during antipoaching control and for forensic purposes. Although this region has a rich fauna, relatively little research on hair identification has been published. De Boom and Dreyer (1953), Dreyer (1966) and Stutterheim (1975) have all worked on Bovid hair. More South African research however, is available on the study of the pelt and hair in relation to thermoregulation, vide Bonsma and Pretorius (1943), Riemerschmid (1943 a and b), Riemerschmid and Elder (1945), Bonsma
My own interest in this field arose from the epidemiological implications of taxonomic studies of southern African Muridae (Keogh 1974). Thus, for example, in a plague epizootic, rodent remains or pieces of fur found at burrows can be identified, and could indicate which species has been dying in the greatest numbers. The use of hair identification was then extended in epidemiological surveys involving food and water contamination, and various zoonoses. Running parallel with these practical applications were the interests of taxonomy and ecology, and thus the present study was undertaken with a view to relating the structure and morphology of hair to ecology, as well as to provide an atlas which is a pictorial reference system for identification.

As stated later in the text, the atlas of mammalian carnivore hair to some extent fills a gap in knowledge of hair studies from this region and will form part of a more comprehensive hair atlas which will include other southern African mammals.

Hair identification has been extensively studied. The first significant contribution was made by Hausman (1920, 1924 and 1930) in America. The most important subsequent papers are those of Mathiak (1938 a and b), Williams (1938), Dearborn (1939), Mayer (1952), Benedict (1957), Stains (1958), Spence (1963), Adorjan and Kolenosky (1969), all of America; Lodmuller (1924) of France and Toldt (1935) and Lochte (1938) of Germany; Lyne (1959) and Lyne and McMahon (1951) of Australia. In England, Wildman (1954), Stoves (1957) and Appelyard (1960) worked on hair of commercial furbearers, while Day (1966) and Walker (1972) have published work on hair identification of wild species. More recently research has been carried out in this field by Trevor-Deutsch (1970) in Canada, and probably the most modern reference work on identification
of mammalian hair comes from Australia (Brunner and Coman 1974).

Although in some cases hair characters lend themselves to the formation of a key (such as that constructed for the scale patterns of the southern African Muridae), the photographic reference system adopted by Brunner and Coman (1974) is possibly the most satisfactory approach which minimizes the various problems encountered in hair identification. Thus in the carnivore hair atlas, micrographs of hair structure, together with coloured plates of typical individual hairs, and distribution maps of the various species studied, are all used in conjunction with each other. Even so, variations in hair structure along the length of individual hairs, as well as different hair types on one individual, constitute problems. Further studies using electron microscopy may solve some of these problems, especially where there is a large degree of interspecies overlap. To some extent however, the construction of all identification systems requires experience and familiarity and this is particularly so with the identification of hair. Thus it is necessary to look at a great number of hairs before it is possible to single out the features most suited to diagnosis of any particular species.

All workers classify hair into two main types, the long thick outer hairs and fine short underfur. However, designation of various hair types seems to vary greatly in publications, Hausman (1920), Danforth (1925), Toldt (1935), Lochte (1938), Noback (1951) and Brunner and Coman (1974), to mention but a few. Ryder (1973) classifies the types in the following most comprehensive way (omitting, however, specific classification of vibrissae):

Guard hairs (outer coat) - long and coarse.
1. Spines - very large and often defensive, e.g. quills.
2. Bristles - stiff, heavily pigmented typical protective outer hairs.
3. Awns - hairs with coarse, often flattened tip, but finer base.
Underhair - short, fine and soft (have less pigment).
1. Vellus - shortest and finest hair or 'down'.
2. Fur - thick, fine and relatively short.
3. Wool - longer, soft and usually curly.

Guard hairs and underfur (and mane hairs where present) are described in the atlas of this work.

Hairs are terete structures composed of compactly cemented keratinised cells produced by the sac-like epidermal follicles that grow into the dermis (Montagna 1962). Although much research has been carried out on hair growth the most important references are Lyne and Short (1965), Montagna and Ellis (1958), Montagna and Dobson (1967), who edited books which deal with the biology of hair growth. The structure and the development of the hair follicle have been ably described by Lyne (1966) in a review in which he also describes hair follicle groups. The arrangement of follicle groups is characteristic for a particular species and could be used as a diagnostic feature. However, this aspect of identification has not been dealt with in this study. Hair follicles show intermittent cyclic activity; the stages of activity are described, as anagen, catagen and telogen, being the active, transitional, and resting phase respectively. This aspect of hair growth is not important to this study, but that aspect of growth which is relevant is the sequence in which the hair types appear in the pelage. The guard hairs obviously vary in length as they emerge, and although cuticular scale patterns along the different length hairs also vary, the cross-sectional shape at the widest point is constant. The diagnostic implication of this is evident.
The typical hair consists of the shaft which has a free expelled part and an intrafollicular part, the root, situated below the skin surface. The more superficial part of the root is fully keratinised but the lower part is partially keratinised and merges with the cells of the follicle in the matrix of the hair papilla. The hair consists of the cuticle, the cortex and the medulla, and it is variations of these features which are most commonly used in hair identification.

The Cuticle consists of keratinised overlapping scales, with their free ends aligned towards the hair tip. The keratinised cells are non-nucleated and are filled with hard or α keratin. The pattern made by these scales around the length of the hair, their shapes and sizes and types of margins, have been recognised and used for identification purposes. Thus a scale-index based on scale size was used by Hausman (1930) and Mayer (1952), but has disadvantages in that they disregard scale-shape and variations along the length of the hair. However, many others have used scale shape and patterns for hair identification of various species ranging from monotremes and marsupials (Lyne and McMahon 1951), bats (Benedict 1957) to animal textile fibres (Wildman 1954), and murids (Keogh 1974), to mention but a few.

The Cortex is composed of non-nucleated cells, filled with hard α keratin, which are seen under electron microscopy (Hashimoto and Shibazaki 1975), but cannot be seen by transmission or reflection light microscopy. The spindle-shaped cells are arranged concentrically, and intercellular spaces are filled by electron-dense substances. The colour of the hair is determined by the number of melanin granules in the cortical cells and these can be seen, in some cases, with light microscopy. In this way Dreyer (1966) has in fact classified pigment distribution in cross-sections of hair. The cortex, as such, is not often a diagnostic
character but its size, relative to the medulla, is used in hair
identification.

The Medulla, like both the cuticle and the cortex, is composed
of soft or β keratin in the early stages of their development. The
cuticle and cortex however grow faster than the medulla and this results
(Rhodin 1974)
in airspaces in the medulla/. The dead cells of the cortex are made up of
α, or hard keratin, while those of the medulla of soft or β keratin. The
keratinisation processes of hard and soft keratin are poorly understood
(Rhodin 1974), but hard keratin seems to contain more sulphur than soft
keratin. (The dead cells of the medulla may contain pigment, but more
often they are unpigmented). The air cavities in the medulla appear black
by transmitted light, and this may obscure the actual structure of the
medulla. If, however, the air is expelled, the various arrangements of
the medulla can sometimes more easily be seen. These arrangements have
been classified into types which are described in the text. The significance
of the medullary cavities however may well be related to thermoregulation
(as postulated later in the text), although the various arrangements have
been used as taxonomic criteria by some authors.

In using the findings of the atlas as well as in observations
made during this, and previous studies, I have attempted to relate hair
structure to ecology. Gilbert White's (1771) description of ecology
quoted by Elton (1927) expresses the complexity of this task in a
succinct and picturesque manner. "Faunists (in other words taxonomists)
as you observe, are too apt to aquiesce to bare descriptions and a few
synonyms, the reason for this is plain, because all this may be done at
home in a man's study, but investigation of the life and conversation
of animals is a concern of much more trouble and difficulty ........"
Ecological data for this work has been largely drawn from the following sources: Shortridge (1934), Roberts (1951), Dorst and Dandelot (1970), Smithers (1971, 1978a and b in press), Skinner (1976, 1978 in press) and Cooper and Skinner (1979 in press).

Because of the wide scope of this aspect I have selected for study those cases where ecologically selective pressures have resulted in the more extreme adaptations of the pelage. These are most apparent in aquatic mammals and those mammals on which the environment imposes a particular stress on homeothermy. A great deal of work has been done on the part played by the pelage in thermoregulation but the microstructure of the hair has not been investigated in this connection. Bearing in mind that as much as half of the heat load may be from the far infra-red radiation, the hair was subjected to a search for features which would interact with the wave lengths emitted and received in this region of the spectrum. The size and spacing of the medullary cavities are remarkably constant within this range and have justified a detailed investigation. This has led to an attractive hypothesis that the medullary dislocations act as a selective absorber and wave guide for longwave radiation. Until suitable instruments are available and the relevant measurements can be made, the supposed part played by the medulla in radiation exchange remains speculative.

The size and shape of hairs, especially those of otters and diurnal rodents, have functional adaptations. The latter were investigated as to the manner in which their hairs could nest and the possible function of the deep gutter, which is also found in some species of Bovidae inhabiting drier regions of southern Africa.

Two aspects of mammalian pelage which are common to all
vertebrates are moulting and the power to form melanin, both of which are retained throughout life and obviously must have advantages for survival. The part played by colour is a subject on its own and I have concentrated on colour as a feature of thermoregulation rather than on its cryptic aspect. Pattern in animals seems to be phylogenetically orientated (Portman 1967). Thus in the lower ranking mammalian orders pattern is unrelated to body division, as for example with the stripes of the polecat and in the striped rodents. On the other hand in the higher orders cephalisation becomes apparent, and the head is obviously the leading pole in the pattern arrangement, as for example in the facial colouring of the cats. The neurosensory function of hair has been studied mainly in regard to vibrissae, and Lyne (1959) substantiated the theory that this was its prime function in his findings that more primitive species have larger concentrations of vibrissae, than more advanced mammals. The long guard hairs on mammals, especially burrowing ones, have retained their sensory function (Palmer and Weddel 1964), and a few authors have suggested that guard hairs of various species act as sensory perceptors.

The aim of this present study therefore is two-fold, first to add to our detailed knowledge of hair of mammals from southern Africa, and secondly to point to some of the functions of hair in ecology. Hair has been studied over the years by a great number of workers and from a variety of aspects and its practical applications have been mentioned in regard to taxonomy and various agricultural and industrial facets. It also has applications in the applied science of epidemiology.

Epidemiology may be defined as the study of the distribution and determinants of disease in human populations (Barker 1973). Identification of mammals which may possibly be implicated in the spread of certain diseases, plays an important part in evaluating the cause and
geographical extent of such a disease, and in the implementation of control measures.

As previously mentioned, identification of southern African murids according to the cuticular scale pattern on the hairs, assumed practical application in epidemiological work on plague. Thus rodents can be identified from carcass remains or from hair in stomach contents and scats of carnivores which eat dead rodents in an epizootic (Fourie 1938). This gives a lead as to whether those species which are known to be wild reservoirs of plague, are involved or not.

It is, however, in investigations of virus diseases, such as Lassa Fever, that identification of the rodent reservoir has become of great importance. Mastomys natalensis is the reservoir host of the Lassa type A virus. Recent work in Rhodesia and South Africa (Lyons, Green, Gordon and Walters 1977 a and b; Green, Gordon and Lyons 1978; Hallett 1977), has established that the taxon covers at least two sibling species. The implication of sibling species within the taxon, regarding epidemiological studies, are as yet unknown and of utmost importance to the clarification of the part M. natalensis plays in the epidemiology of virus diseases, as well as Bubonic plague. Preliminary investigations using electron microscopy would seem to indicate that differences in the hair of genetically defined sibling species, can be detected. The use of this method of determining the sibling species need not be underlined and further studies and verifications in this direction are of utmost importance.

Hair identification is used at the South African Institute for Medical Research in routine bacteriological and serological surveillance of zoonoses which involve small mammals. The identifications thus made are important in the delimitation of various species in disease
distribution. Identifying mammal specimens in Leishmaniasis surveillance and ectoparasite surveys often involves the use of hair identification.

It has also proved useful in public health investigations when possible breaches in sanitation and hygiene need to be ascertained; for example, suspected contamination of water sources, or processed and non-processed foodstuffs. In many cases the result of the investigation has depended solely on the identification of hairs in the specimens in question.

This technique of identification of hair is also used in medico-legal and insurance investigation. An example of the latter concerned determination of the type of rodent contamination in a large cargo-load of wheat in a foreign ship docked in a South African port.

Most of the above applications of hair identification concern the small mammals but this work is now being extended to include other mammals. Whilst southern African murid species are relatively easily identified using the variations in the cuticular scale patterns, identification of other families calls for the use of more comprehensive criteria before diagnosis can be made. Cross-sectional appearance as well as gross structure and cuticular scale patterns are used. This method has been employed to identify the contents of vulture pellets from some six localities in southern Africa.

As vultures are implicated in the spread of Anthrax, hairs from these pellets were subjected to bacteriological and biological examination. Bacillus anthracis has not yet been isolated from this source, although Bacillus cereus, a closely related species, has been isolated.

Although rabies in wild carnivores has occurred in epizootics for centuries, more research is needed with information on the epidemiology
of wild-life rabies. In South Africa carnivores implicated in the spread are primarily the mustellids and viverrids, although the felids, canids and Proteles cristatus are also involved.

In rabies surveillance the identification of the species involved is vital, and hair samples may be sent from field stations for identification. Hair in spotted hyaena scats from Namibia were found to contain some weasel hairs. Initially this was somewhat puzzling, as the weasel Poecilogale arbinucha had not previously featured in the diet. However, shortly after this it was reported that weasels had been found to be dying of rabies in this region.
MATERIALS AND METHODS

Hairs from the following 36 species of southern African carnivores were studied both macroscopically and microscopically:

**PROTELIDAE**

Proteles cristatus (Sparman 1783) – Aardwolf

**HYAENIDAE**

Hyaena brunnea Thunberg 1820 – Brown hyena
Crocuta crocuta (Erxleben 1777) – Spotted hyena

**FELIDAE**

Acinonyx jubatus (Schreber 1775) – Cheetah
Panthera pardus (Linnaeus 1758) – Leopard
Panthera leo (Linnaeus 1758) – Lion
Felis caracal Schreber 1776 – Caracal
Felis silvestris (Lybica) Schreber 1777 – Wild cat
Felis nigripes Burchell 1823 – Black footed cat
Felis serval Schreber 1776 – Serval

**CANIDAE**

Otocyon megalotis (Desmarest 1822) – Bat-eared fox
Lycaon pictus (Temminick 1820) – Hunting dog
Vulpes chama (A. Smith 1833) – Cape fox
Canis adustus Sundevall 1846 – Side-striped jackal
Canis mesomelas Schreber 1775 – Black-backed jackal

**MUSTELLIDAE**

Aonyx capensis (Schinz 1821) – Cape clawless otter
Lutra maculicollis Lichtenstein 1835 – Spotted-necked otter
Mellivora capensis (Schreber 1776) – Honey badger
Poecilogale albinucha (Gray 1864) – Weasel
Ictonyx striatus (Perry 1810) – Striped polecat

**VIVERRIDAE**

Nandinia binotata (Gray 1830) – Two-spotted palm civet
Viverra civetta Schreber 1776 – African civet
Genetta genetta (Linnaeus 1758) – Small-spotted genet
VIVERRIDAE (cont.)

- **Genetta tigrina** (senso lato) (Schreber 1776) Large-spotted genet
- **Suricata suricatta** (Schreber 1776) Suricate
- **Paranectes selousi** (de Winton 1896) Selous' mongoose
- **Cynictis penicillata** (G. Cuvier 1829) Yellow mongoose
- **Galerella angustina** (Rupell 1835) Slender mongoose
- **Herpestes ichneumon** (Linnaeus 1758) Egyptian mongoose
- **Herpestes pulverulentus** Wagner 1839 Cape grey mongoose
- **Ichneumia albicauda** (G. Cuvier 1829) White-tailed mongoose
- **Atilax paludinosus** (G. Cuvier 1829) Marsh mongoose
- **Mungos mungo** (Gmelin 1788) Banded mongoose
- **Helogale parvula** (Sundevall 1846) (Dwarf mongoose)
- **Bdeogale crassicauda** Peters 1852 Bushy-tailed mongoose
- **Rhynochogale melleri** (Gray 1865) Meller's mongoose

I. **SAMPLING**

Hairs can be taken from live or preserved and dried skins. Most workers in this field have used hairs from museum specimens and these have been found to be indistinguishable from fresh material. Trevor-Deutch (1970) reports that there was no deterioration in the hairs of two vole specimens of over a hundred years old. I have had the opportunity of comparing large numbers of hairs from preserved and fresh material, and have not detected any appreciable differences in their microscopic morphology. In particular mammoth hair samples showed no perceptible deterioration.

The only exception is that in older dried specimens the root of the hair is sometimes damaged when it is removed from the pelt. During the course of this study as many hair specimens as possible were examined from live samples from various geographical regions. The main source of specimens, however, was the mammal collection housed at the Transvaal Museum. Specimens from different localities were selected from this
collection and hair was sampled from all available individuals of a species. The hair samples of thirty-six species of southern African carnivora were initially taken from the dorsal region; no less than thirty hairs were examined from each individual, and in most cases many more. Subsequently hairs from the belly, chest and rump were examined from most of the thirty-six species. Although this work is primarily based on the study of southern African carnivore hair, whilst engaged on it, opportunities have arisen to examine hair from many other species: in particular Bovids, such as the bontebok, in detail. In order to clarify certain aspects of the possible role of hair in ecology, gutter hairs prevalent in some diurnal rodents were examined, and for this a technique was evolved which will be referred to later in this section. Samples of these rodent hairs were drawn from museum specimens housed in part of the Medical Ecology collection, and from live rodent colonies at the South African Institute for Medical Research, as well as from field-trapped specimens.

II. MICROSCOPIC WORK

(A) Cuticular scale imprints

With ordinary microscopy cuticular scales cannot be seen on the hair itself, however by using imprints, the scale patterns are revealed and easily studied. Terminology varies but in some instances authors refer to impressions, casts or imprints. The term "impression" has been restricted to cases where the entire circumference of the hair is represented by rolling the hair over a suitable medium, and "cast" refers to the imprint made by placing the hair on the medium and later removing it, leaving the imprint of only that part of the hair which came in contact with the medium. I use the term "imprint" throughout; it refers to the latter method.
Various techniques have been described for cleaning, drying and mounting the hair for examination of cuticular imprints. Practice is important in these techniques and the refinements adopted vary from one worker to another. Thus Trevor-Deutch (1970) washed hairs in carbon tetrachloride, which is possibly a suitable method applicable to cleaning hairs from coprolites which he studied. Brunner and Coman (1974) cleaned hairs in an alcohol-ether mixture and dried them between absorbent paper. I have found the most satisfactory method of cleaning hairs to be that of washing them in a mixture of absolute alcohol and sulphuric ether in equal proportions. The hairs were then washed in distilled water for about three minutes and dried on a clean watch glass. The mounting media used also vary: they include polyvinyl acetate (PVA) (recommended by Brunner and Coman 1974), celluloid, gelatin, and various specialised commercial products such as permount and ethofoil (Wildman 1954). I prefer gelatin, which, although perhaps not so satisfactory for photography as PVA, seems to give more sensitive imprints for microscopic study, especially when the hairs are very fine or very coarse.

Finely granulated gelatin was added to cold distilled water until the solution was saturated. Ten per cent by volume of blue dye (Eosin methyl blue) was added, and the container was heated in a water bath at boiling point. Clean slides were thinly coated with this gelatin solution and the hairs were placed in position. They were removed when the gelatin was dry. In the case of concavo-convex hairs the position of the groove along the length of the hair must be taken into account when making imprints. Similarly care must be taken with twisted hairs, by securing the hair at one end before laying it flat. Positive imprints are obtained by making the imprint on a coverslip and inverting this onto a microscope slide. This method was successfully used by Brunner and Coman (1974). Although a positive imprint prepared in this way may
possibly be easier to interpret, and is protected from dust and damage,
I have consistently used the technique with which I am familiar, of
making negative imprints directly onto the slide.

The nomenclature for scale pattern in this study follows that
of Wildman (1954). As the scale pattern varies along the length of the
hair, it has been described at the base of the hair, the mid-region of
the shaft and the tip region.

Over the years workers in this field have described the
scale pattern of hairs: Hausman (1930), Williams (1938), (Lyne and McMahon 1951)
Mayer (1952), Khemelevskaya (1965) - to mention but a few.

Patterns (see Fig. 1) are described as:

  **Coronal:** Usually a single scale, occasionally two
  scales, across the width of the hair; scales often evenly spaced. The
  margins are transverse and smooth or slightly indented.

  **Chevron:** A waved pattern. In a single chevron either
  the troughs or the crests are narrow 'V' shaped. In a double chevron
  both the troughs and the crests are 'V' shaped.

  **Mosaic:** A pattern composed of a number of units; this
  type is divided into regular, in which the units are approximately the
  same size, and irregular, in which the mosaic has a random mixture of
  different scale sizes.

  **Pectinate:** Comb-like pattern. This type is divided
  into coarse pectinate, in which the "teeth" are wide and large, and
  lanceolate pectinate in which the teeth are long and narrow.

  **Petal:** Patterns in which the scales have the appearance
  of overlapping flower petals and which may also be of a diamond or a
Figure 1. Cuticular scale patterns.
narrow diamond shape.

The distance apart of the scale margins:

This is a distinctive feature of the pattern but cannot easily be quantified. No more than a qualitative measure is justified, and for this purpose the designation used by Wildman (1954) has been followed. Thus distances between margins in the direction of the hair length are described as close, near or distant. See Fig. 2.

The form of scale margin as defined by Brunner and Coman (1974) relates to the free distal edge of an individual scale. This may be smooth, crenate (having shallow but relatively pointed indentations) or rippled (in which the indentations are deeper, but the profile is rounded). (Scalloped and dentate margins have also been described). See Fig. 3.

(B) Cross-sections

(i) Thick sections

(a) Various methods for obtaining cross-sections of hairs have been well described by Brunner and Coman (1974), who used the plate method, with modifications, described by Ford and Simmens (1959). All cross-sections photographed in the Atlas of this work were obtained by the use of this technique, as very thin sections are not necessary for hair identification.

Stainless steel slides approximately 76 x 25 x 0.5 mm with three holes, each 0.8 mm diameter, drilled at equal intervals along the centre line, were used. After drilling, the holes were slightly chamfered to remove sharp cutting edges.

A loop of cotton is threaded through the hole as in Fig. 4. Threads of cellulose acetate yarn are then inserted into the loop,
**Figure 2.** Distance between scale margins.

<table>
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<tr>
<th></th>
<th>Close</th>
<th>Near</th>
<th>Distant</th>
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<tr>
<td>Smooth</td>
<td>Smooth</td>
<td>Crenate</td>
<td>Rippled</td>
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</tbody>
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**Figure 3.** Form of scale margins.
Figure 4. The plate method of cross-sectioning.
and pulled by the cotton thread a short distance down through the hole. The hair tuft is then placed in the centre of the yarn and gently pulled through the hole. I favoured cotton rather than nylon thread as it acted as a better regulator of the amount of hair which could be pulled through the hole. With nylon thread hair can be forced through the hole, resulting in over-packing and hence distortion of the sections. If necessary cellulose acetate solution can be used to dissolve the packing material. The protruding hair bundle is then cut flush with the slide on each side of it. I found a cut-throat razor easier to manipulate than a razor blade, the blade being held at the recommended angle of about $35^\circ$. Immersion oil is placed over the sections, which can then be viewed. I found it useful to cover the slide with a coverslip after having cut the sections, as this protected them when stored (see plate 1, page 24).

Cross-sectional shape, and variations in the relative sizes of the cortex and medulla have been used to describe and assist in identifying hairs. Thus in the Atlas of this work the main types of cross-section shape are described. A schematic representation of the cross-sectional shapes at the widest part of the guard hair most commonly encountered is given in Fig. 5.

(b) A new technique was devised for obtaining cross-sections at known points along the length of the hair. This was used to attempt to evaluate the way in which gutter hairs could nest. The results of this technique are discussed in the Ecology section of the text.

Hair was placed in the middle of a square block of embedding wax, which was cast in two portions. The sides of the blocks were determined by glass sides set in a non-heat-conducting material, and after the first block had set a groove was made, starting at a known distance from the end of the cast. The hair was carefully placed at the end of this groove. The wax was then slightly melted and the second section
Figure 5. Most commonly found cross-sectional shapes.
of the block poured onto this. Four casts were used for the various stages of this procedure. When set and trimmed the blocks were then placed into a square collet in a lathe and trimmed to the exact size of the microtome - (10 mm in diameter). The hair was lying along the axis and the tip was known to be at an exact distance from the end of the block. Coloured lines drawn down the side of the block determined the orientation of the hair. Thus by cutting at 0.2 mm intervals, sections were obtained in sequence along the length of the hair. A small punch fitted onto the nose-piece of the microscope was then used to punch out these sections which were arranged in sequence on a slide, to ensure accuracy of viewing.

(ii) Thin sections

For making thin sections of hair, the following technique was adopted:-

Hairs were fixed in three per cent glutaraldehyde, dehydrated in grades of ethyl alcohol and briefly cleaned in propylene oxide. They were embedded in Spurr's resin (TAAB Laboratories) for 18 hours under light vacuum before orientation in silicone rubber moulds for curing at 70°C for eight hours. Approximately 1.0 μm sections through the shaft medulla, cut with a diamond knife on an LKB Ultrotome, were collected on microslides and dried on a hot-plate at 60°C. The sections were stained in polychrome methylene blue at the same temperature, then washed and mounted in DPX. For examples, see plate 2, page 24, plates 5, 6, 7, page 28.

(C) Whole mounts and the examination of the medulla

(a) For temporary mounts, such as used in identification of unknown hairs, the cleaned hairs can be mounted in paraffin oil and examined under a coverslip.
Plate 1. Thick cross-section of white, red and black hairs of *Dama damaecus.* Medullary structure obscured by reflected light of air spaces. X250.
(b) For permanent mounting, a medium such as DPX can be used. The detailed structure of the medulla is obscured under normal light microscopy because the air cavities appear black due to internal reflection of light at the top surface.

Most authors who have investigated this, describe infiltrating these cavities with the mounting medium, thus facilitating viewing of the internal structure. I obtained the most satisfactory results by heating the hair in a weak acid solution prior to placing it in mounting medium, thus expelling the air by expansion. The cleaned hair was placed in 5.0 per cent acetic acid in a covered petri-dish overnight at 37°C. The hair was then dried and mounted and again incubated for a few hours at 37°C. Once the mounting medium had set the hairs could be examined, and the medulla clearly observed.

Brunner and Coman (1974) have classified the shape and arrangement of the medullary material and its air spaces as: unbroken, broken, ladder and miscellaneous, and have then sub-divided each of these categories, presenting a total of twelve types. On the other hand Ryder (1973) simply classifies medulla types into either latticed or non-latticed. There is considerable variation in the appearance of the medulla, even along the length of a single hair and sometimes between different individuals of the same species, let alone between the species themselves. Moreover, there is often a confusing difference between the structure as seen in the whole mount and that seen in a longitudinal section, and there may be doubt as to whether infiltration has been effective. For these reasons I have felt obliged to discard the use of the medulla as a taxonomic criterion. See plates 3-7, pages 26 and 27.

Nevertheless examination and measurements of medulla have other important uses, particularly in the interpretation of the part played by fur in the thermal exchanges between a mammal and its surroundings, as

Plate 4. Distal part of white hair of *Damaliscus dorcas*. Whole mount showing partial infiltration of medullary cavities. X900.
Plate 5. Oblique thin section of black hair of *Damaliscus dorcas* showing pigmented cortex and complete infiltration of air spaces in medulla. X900.

Plate 6. Longitudinal thin section of red hair of *Damaliscus dorcas* showing cortex relatively narrower than above. Medulla air spaces completely impregnated. X900.
described later in the section on ecology. The relevant lattice and ladder types of medulla are shown in Fig. 6.

III. SURFACE TENSION AND TENACITY OF FIBRES

Critical surface tension and fibre breaking strength, tenacity and breaking extension were measured. These tests were carried out at the South African Wool and Textile Research Institute in Port Elizabeth. The critical surface tension was measured by the method described by Mutchler, Menkart and Schwartz (1969). For the fibre strength tests, the average cross-sectional area of the hair (excluding the area of the medulla) was measured and, assuming a fibre density of 1.31 gm/cm³, the fibre linear density (tex) of the fibres was calculated. The tenacity N/tex was then calculated, this being the unit used in textile technology.

The following species, representative of the nocturnal, diurnal and aquatic carnivora species within the various taxonomic groups, were selected to ascertain possible differences in the surface tension and tenacity: - Lutra maculicollis, Aonyx capensis, Atilax paludinosus, Crocotta crocuta, Hyaena brunnea, Proteles cristatus, Canis mesomelas, Vulpes chama, Paraenictis selousi, Viverra civetta, Acinonyx jubatus, Felis lybica, Lycaon pictus.

IV. ENERGY STUDIES

Measurements on conduction, convection and radiation relating to the mammalian pelage have been described by many authors and these will be referred to later in the text. In order to attempt to ascertain if there was any directional influence on the hairs of a pelt on thermal radiation, measurements were made with a thermopile. These measurements were unsuccessful however, as the equipment was not sensitive enough and
Figure 6. Types of medulla.
the cost of obtaining such instruments to make these measurements with any degree of accuracy proved too great to warrant further pursuit. Thermographic measurements, however, were made on the surface temperatures of the giraffe, the black-backed jackal and the striped polecat. An Agavision System 680 thermal imaging camera was used to measure the surface temperatures of animals in the Johannesburg Zoological Gardens. Filters were incorporated to eliminate errors from solar radiation, thus the longwave radiation was measured. The thermograms presented later in the text (pages 137-139) are in alternate grey tone form. The temperature distribution appears as a gradation of image brightness, the lighter shades representing warmer parts than the darker shades.

V. PHOTOGRAPHY

Photographs were taken with a Univa photomicroscope using Ilford Pan F rated at 50 ASA, developed in Acutol.

All black and white prints in the Atlas are at a magnification of 250X. The coloured prints of hair profiles are at varying magnifications shown by a scale on the print and all other photographs in the text are marked with the magnification.
An Atlas of Hair of Southern African Carnivora
Map 1. Main biotic zones of southern Africa.
Reproduced from Davis (1962), after Moreau (1952) and Keay (1959).
Map 2. Southern Africa: political.

AN ATLAS OF THE HAIR OF SOUTHERN AFRICAN CARNIVORA

WITH DESCRIPTIONS OF THE GROSS AND MICROSCOPIC FEATURES OF

THIRTY-SIX SPECIES

Introduction

The atlas forms the illustrative portion of work on hair studies in relation to ecology, taxonomy and epidemiology. It forms a photographic reference system as an aid to identifying carnivore hairs. This is the first portion of a more comprehensive reference system which will eventually include work on other mammalian families found in southern Africa.

Explanatory notes

1. Sampling: Hair samples were taken from the mid-dorsal and mid-ventral line between the shoulders of at least four representatives of each species. Most of the specimens sampled are housed at the Transvaal Museum. Hair from other body regions, especially that of the underbelly, was subsequently examined and no differences were detected in cross-sectional shape and cuticular scale pattern, although colour differences were marked.

2. Arrangement: The microphotographs of the hairs of each species are accompanied by distribution notes and a map to aid in identification of hair samples. Brief data on habitat and habits are included as having possible relevance to various hair types. A description of the pelage, gross size, and description of various individual hairs is included as well as the descriptions of the microstructure of the hairs.
3. Sources of various data:

a) Black and white illustrations of each species have been derived from plates in Dorst and Dandelot (1970), with the publishers’ permission.

b) The nomenclature used is that used in the Smithsonian Institution publication *The Mammals of Africa: an identification manual.* (1971).

c) Maps are included for clarification of vegetative and locality data mentioned in the text. The vegetation map was compiled from Moreau (1952) and Keay (1959).

d) Distribution data has been drawn from as many sources as possible with special reference to Meester, Davis and Coetzee (1964), Smithers (1971), Skinner (1976), Rautenbach (1978), Pringle (1977), Dorst and Dandelot (1970). A small scale distribution map is included for each species, and the maps of 29 small carnivores are reproduced, with the author’s kind permission, from Smithers (in prep.). Data for the maps of *Proteles cristatus* and *Hyenaena brunnea* were taken from Cooper and Skinner (in press) and Skinner (1976) respectively and are in agreement with Smithers (in prep.). The maps indicate those areas in which the species could occur, and do not always reflect exact collecting localities.

e) Brief habitat and habit notes are in the text as these may be found to have some bearing on various differences in hair structure. The information has been taken from as many literature sources as possible including Roberts (1951), Shortridge (1934), Smithers (1971), Dorst and Dandelot (1972), Rautenbach and Nel (1978) and Skinner (1976 and in press).

f) The hair length refers mainly to guard hairs and never to underfur. It is stated in mm with standard deviation, thus: 78 ± 10 mm.

g) Cross-sectional appearance: The classification of the shapes of hairs in cross-section has been taken from the definitive
types used by Brunner and Coman (1974). The relative size of the medulla in relation to the cortex is described as large, medium and small. This varies according to the species from which the hair was sampled.

h) The pattern of the cuticular scale imprints is described according to the nomenclature used in Keogh (1974). This is based on that of Wildman (1954).
AARDWOLF
**Family:** PROTEIDAE

**Proteles cristatus**
(Sparrman, 1783)

**Aardwolf**

**DISTRIBUTION:**
South African sub-region excluding Namibia coastal strip and south eastern Mozambique.

**HABITAT:**
Open veld and plains. Never in forest areas. Distribution likely to be determined by distribution of termite genus *Trinervitermes*.

**HABITS:**
Nocturnal. Solitary or in pairs or small family groups. Shy and elusive. When attacked secretes musky smell. Not well equipped for defence, except loud vocal roar. Well developed canine teeth. Rests in holes in the ground.

**Diet:** Almost entirely termites and larvae.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Well developed mane along dorsal spine from neck to tail, erected when alarmed. Buffish yellow to reddish brown coat, paler and darker stripes running vertically on shoulders, flanks and thighs.

**INDIVIDUAL HAIRS:**

**Length:** $32.59 \pm 9.12$ mm

**Colour:** Tawny banded white. Sepia banded white. Beige, sepia tipped. Grey. Brown. (9)

**Cross-sections:**

**Guard hairs** -
Mane hairs: Circular and dumb-bell, medium medulla (1) and (2).
Body hairs: Reniform (3a) and (b), (6). Dumb-bell (4c) and (5).
Oval, medium medulla (3b).

**Underfur** -
Oval, medium medulla. Oval, large medulla.

**Cuticular scale patterns:**
Waved mosaic, but waves in definite peaks (7) and, enlarged x 5, (8). One or two scales across width. Scale margins: crenate. Distance apart of scales: near.
Family: **HYAENIDAE**

**HYAENA BUNNEA**

**Thunberg, 1820**

**DISTRIBUTION:**
Eastern Cape Province, Orange Free State, Transvaal, Mozambique, Rhodesia, Botswana and Namibia.

**HABITAT:**
Dry savannah and desert

**HABITS:**

**Diet:** Omnivorous. Scavenger.

---

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Coarse, shaggy, blackish brown. Neck, shoulder and upper back have long lighter hairs forming a mantel. Tail bushy, long.

**INDIVIDUAL HAIRS:**

**Length:** $112 \pm 60$ mm

**Colour:** Dark brown. Dark brown merging tawny into white. Tawny banded white. (5)

**Cross-sections:**

- **Guard hairs** -
  Circles with small medulla ($1d$) and ($2$). Few circles and ovals with large medulla ($1b$), ($1e$).
  Colours: browns and whites.

- **Underfur** -
  Round or oval, medium medulla.

**Cuticular scale patterns:**
Waved mosaic with one, or two, scales across width of hair. Scale margins: crenate. Distance apart of scales: near (3) and, enlarged $x$ 5, (4).
SPOTTED HYAENA
Family: HYAENIDAE

Crocuta crocuta
Erxleben, 1777

DISTRIBUTION:
Lesotho, northern Transvaal, Mozambique, Rhodesia, Botswana and Namibia.

HABITAT:
All types of savannah.

HAIR

GENERAL DESCRIPTION OF FUR:
Coat short and coarse. Ground colour, buffy to dull grey. Irregularly marked with blackish round spots. Throat light coloured, unspotted. Face, muzzle and lower limbs dark brown. Young, blackish. Tail short with bushy tip.

INDIVIDUAL HAIRS:
Length: 33.54 ± 10.37 mm

Colour:

Cross-sections:
Guard hairs -
Ovals and circles with small medulla. Cortex large (1f). Cortex white, orangy or light brown. Some ovals with large medulla (1g) or medium medulla (2).

Underfur -
Circles with small medulla. Circles and ovals with medium medulla.

Cuticular scale patterns:
Irregular waved mosaic, one or two scales across width (3) and, enlarged x 5 (4). Scale margins: Smooth or slightly crenate. Distance apart of scales: near. Overall appearance as wind-swept sand.
Cheetah
Family: FELIDAE
Acinonyx jubatus
(Schreber, 1775)

DISTRIBUTION:
Northern Cape Province, northern Transvaal, Rhodesia, Botswana (except eastern part) and Namibia, game reserves of Kruger National Park and Hluluwe (Map adapted from Wrogeman, 1975).

HABITAT:
Open and semi-arid savannah; never forested country.

HABITS:
Diurnal. Solitary or in pairs but may be found hunting larger prey in troops.
Diet: Small antelope, warthog, hares and birds.

HAIR

GENERAL DESCRIPTION OF FUR:
Coat roughish, entirely covered with small round black spots. General colour tawny to pale buffy; lighter, almost white on belly. Black stripe from eye to mouth.

INDIVIDUAL HAIRS:

Length: 20.35 ± 7.67 mm


Cross-sections:

Guard hairs –
Circles with medium medulla (1h), or large medulla (2). Ovals with medium medulla (1i).

Underfur –
Circles and ovals with medium medulla. Few with large medulla.

Cuticular scale patterns:
Mosaic, one or two scales across width (3), and (4). Waved mosaic towards tip (cf leopard, no petal pattern). Scale margins: smooth except in waved mosaic, when rippled. Distance apart of scales: Near.
**Family:** Felidae

**DISTRIBUTION:**
Northern Cape Province. Mozambique, Transvaal, Rhodesia, Botswana and Namibia. May be found in very mountainous regions elsewhere (not shown on map).

**HABITAT:**
Varied. From dense forests to open dry country. Frequently in fairly dense bush in rocky surroundings.

**HABITS:**
Nocturnal, solitary except in mating season when lives in pairs. Sometimes small groups up to six. Climbs trees.

**Diet:** wide range of birds and mammals.

---

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Coat dense and soft, rather short, marked with numerous spots arranged in rosettes. Broken bands across chest. Underparts and inner sides of limbs pure white. Tail long, spotted, with terminal tuft.

**INDIVIDUAL HAIR:**

<table>
<thead>
<tr>
<th><strong>Length</strong></th>
<th>19.20 ± 6.59 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Colour</strong></td>
<td>Sepia or black. White or white tipped tawny or tawny to black. White (6).</td>
</tr>
</tbody>
</table>

**Cross-sections:**

- **Guard hairs**
  Mostly circles medium medulla (1j). Some ovals with medium medulla (2k). Colours reds, blacks and yellows.

- **Underfur**
  Predominantly circles (2L) with small and large medulla.

**Cuticular scale patterns:**
Petal at base (3). Mosaic along shaft, one or two scales across width (4), distal part waved mosaic (5). Scale margins: crenate in waved mosaic, smooth in petal. Distance apart of scales: near in waved mosaic, distant in mosaic and petal.
LION

10 cm
Family: FELIDAE

Panthera leo (Linnaeus, 1758)

DISTRIBUTION:

HABITAT:
Open and lightly wooded grassland: even mountain grassland up to 10,000 feet. Sometimes semi-desert country.

HABITS:
Diurnal, although they will hunt and move at night. Rarely seen alone, very sociable. Prey on herbivores from small antelope to elephant.

HAIR

GENERAL DESCRIPTION OF FUR:
Coat coarse, short, of uniform colour varying from ochraceous silver grey to dark ochre brown. Head darker, underparts lighter. Mane on neck and shoulders varies from silver blond to rufous to black. Long tufts on elbows. Tail long with black tuft.

INDIVIDUAL HaIRS:
Length: (not mane) 9.21 ± 2.17 mm

Colour: White. White tipped tawny marging sepia. Tawny tipped black or white (4).

Cross-sections:
Guard hairs –
Mane hair: ovals with medium medulla (2).
Body hair: mainly circles with medium medulla (1m).

Underfur –
Ovals and circles – with medium medulla.

Cuticular scale patterns:
Irregular waved mosaic (3). Scale margins: rippled crenate.
Distance apart of scales: near.
Family: FELIDAE

DISTRIBUTION:
Throughout the southern African sub-region except Namibia coastal strip and parts of Natal.

HABITAT:
All types of savannah and semi-desert. Never in dense forest.

HABITS:
Mainly nocturnal. Takes refuge among boulders or in thick underbush in daytime. Good climber. Little known of habits. Diet: various mammals from young antelope to rodents, birds, hares, dassies. (Jumps for birds).

HAIR

GENERAL DESCRIPTION OF FUR:
Coat thick and soft, uniform reddish fawn to brick-red brown. Sometimes darker, can be entirely blackish. Long tassel of hairs on ears. Underparts lighter, whitish with faint indication of spots. Tail shorter than other African cats.

INDIVIDUAL HAIRS:

Length: 21.68 ± 9.97 mm

Colour: White darkening to yellow brown, black tipped. Entirely buffy white, or white tipped beige (3).

Cross-sections:

Guard hairs –
Circles and ovals with medium medulla (1n). Some with large medulla. Occasional true oval shape (lo).

Underfur –

Cuticular scale patterns:
Pectinate flattened scales along shaft (2). Tip, waved mosaic, basal part coronal. Scale margins: smooth except towards tip. Distance apart of scales: near in mosaic, distant in other patterns.
AFRICAN WILD CAT
Family: **FELIDAE**

**Felis libyca** Schreber, 1777

**African Wild Cat**

**DISTRIBUTION:**
Throughout southern African sub-region except Namibia coastal strip.

**HABITAT:**
All types of savannah.

**HABITS:**
Nocturnal. Remains hidden in thick bush during the day. Diet: birds, (particularly guinea fowl and francolins), rodents, snakes, lizards, insects and fruits.

---

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
General colour from greyish to buffish or ochraceous with rather indistinct "tabby-cat" vertical stripes.

**INDIVIDUAL HAIRS:**

**Length:** 38.79 ± 7.47 mm

**Colour:** Black. Black banded white, some merging grey. Grey (4).

**Cross-sections:**

**Guard hairs** -
Circles or roundish ovals with medium medulla (lp). Large medulla in some cases.

**Underfur** -
Present in large amounts. Circles with medium medulla.

**Cuticular scale patterns:**
Large guard hairs, diamond petal (2). Smaller hairs mosaic or coronal (3). Scale margins: smooth except near tip when waved mosaic becomes crenated. Distance apart of scales: distinct in petal, near in mosaic.
BLACK-FOOTED CAT
Family: **FELIDAE**

**FELIS MIGREPS**
Burchell, 1823

**DISTRIBUTION:**
Eastern and northern Cape Province, Orange Free State, southern Transvaal, Botswana and Namibia.

**HABITAT:**
Dry open country.

**HABITS:**
A rare cat of little known habits.
Diet: probably ground squirrels, small rodents, birds.

---

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Tawny, lighter on underparts. Profusely marked with large black spots. These are rather long, not in rings or ocellated, and elongated into transverse stripes on shoulder. Tail short, bushy, with spotted tip.

**INDIVIDUAL HAIRS:**

- **Length:** 16.72 ± 4.73 mm
- **Colour:** Entirely black or black banded yellow-brown. Yellow-brown dark tipped. Dark grey, tipped black (3).

**Cross-sections:**
- **Guard hairs**
  - Circles, large medulla, (lt) circles medium medulla (lu).
  - Colour: black and tawny.
- **Underfur**
  - Present in large amounts. Circles, medium medulla. Circles, large medulla.

**Cuticular scale patterns:**
Mosaic (2). Tip, waved mosaic, base coronal. Scale margins: crenate in waved mosaic, otherwise smooth. Distance apart of scales: near.
SERVAL
Family: **FELIDAE**

**Distribution:**
South-eastern Cape Province, Natal, Swaziland, Transvaal, Mozambique, Rhodesia, northern Botswana and northern Namibia.

**Habitat:**
Open savannah from slightly bushed country to forests, especially near marshy places or rivers. Also high mountain moorlands.

**Habits:**
Nocturnal, sometimes partly diurnal, although terrestrial can climb trees. Long legs good for running and seeing prey. Diet: small animals, lizards, rodents, birds. Reputed to eat fish and vegetable matter.

---

**Hair**

**General description of fur:**
Yellowish buffy, heavily marked with black spots, bands and stripes. Underparts whitish or buffy.

**Individual hairs:**

- **Length:** $30.93 \pm 3.15$ mm
- **Colour:** Tawny, black tipped, or entirely tawny or black or buff (6).

**Cross-sections:**
- **Guard hairs**
  - Shape: circles with medium medulla (lr). Some with large medulla as in (3). Some ovals with medium medulla (ls). Colour of cross section distinctive yellows and blacks.
- **Underfur**
  - Much underfur. Circles with medium medulla (2).

**Cuticular scale patterns:**
Broad scales in mosaic pattern (4). Tip waved mosaic (5), base coronal. Scale margins: smooth except towards tip when crenate. Distance apart of scales: near except in waved mosaic when close.
BAT-EARED FOX
Family: Canidae

Otocyon megalotis

(Desmarest, 1822)

**Distribution:**
Cape Province, Orange Free State, western Transvaal, southern and western Rhodesia, Botswana and Namibia, except Namib coastal strip.

**Habitat:**
All types of savannah and semi-desert specially associated with dry open plains.

**Habits:**
Mostly nocturnal. Spends days in burrows or at entrance to den. Lives in groups up to ten, sometimes in pairs. Diet: insects, mice and wild fruit, birds and lizards. Digs out prey with long claws of front feet. Predominantly insectivorous.

---

**Hair**

**General Description of Fur:**
Face blackish, upper parts grizzled silvery buff. Flanks lighter, underparts buffish. Limbs black at extremities. Tail bushy, blackish above and at tip.

**Individual hairs:**

<table>
<thead>
<tr>
<th>Length</th>
<th>22.08 ± 8.08 mm</th>
</tr>
</thead>
</table>


**Cross-sections:**

- **Guard hairs**
  - Distinctly oval with large or medium medulla (lv).
  - Colour: red, yellow and black.

- **Under-fur**
  - Ovals and circles with medium medulla.

**Cuticular scale patterns:**
Petal pattern, even at base (2). Waved mosaic towards tip (4). Scale margins: smooth except in mosaic. Distance apart of scales: distant in petal, near in mosaic.
HUNTING DOG
**Family:** CANIDAE  
**Vulpes chama (A. Smith, 1833)**

**DISTRIBUTION:**
Cape Province, Orange Free State, Natal, western Transvaal, Botswana, Namibia except Namib coastal strip.

**HABITAT:**
Dry country, mainly open plains and Karroo veld, also Kalahari savannah.

**HABITS:**
Nocturnal. Hides in rocky crevices or sandy burrows in daytime. Solitary or in pairs. Diet: insects, birds, small mammals and vegetable matter.

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**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Head and upper parts silvery grey, dark grey with white or black tips. Roots of hairs grey, buffish. Underparts pale buffish.

**INDIVIDUAL HAIRS:**
- **Length:** $18.82 \pm 7.43$ mm
- **Colour:** Black. Sepia banded white. Grey or grey merging with white, black tipped (5).

**Cross-sections:**
- **Guard hairs**
  - Circles and oblongs with medium medullas (1x). Some dumb-bells and some concavo-convex with medium medullas (2z).
  - Colour: red, yellow, black and beige.
- **Underfur**
  - Circles and oblongs with medium medulla. Oblongs with large medulla.

**Cuticular scale patterns:**
Coronal at base (3), petal along shaft (4), waved mosaic towards tip. Scale margins: smooth, except in mosaic. Distance apart of scales: distant in petal, near in mosaic.
CAPE FOX

10 cm
**Family:** CANIDAE

**Vulpes chama** (A. Smith, 1833)

**DISTRIBUTION:**
Cape Province, Orange Free State, Natal, western Transvaal, Botswana, Namibia except Namib coastal strip.

**HABITAT:**
Dry country, mainly open plains and Karroo veld, also Kalahari savannah.

**HABITS:**
Nocturnal. Hides in rocky crevices or sandy burrows in daytime. Solitary or in pairs.
Diet: insects, birds, small mammals and vegetable matter.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Head and upper parts silvery grey. Roots of hairs grey, buffish
dark grey with white or black tips. Underparts pale buffish.

**INDIVIDUAL HAIRS:**

**Length:** 18.82 ± 7.43 mm

**Colour:** Black. Sepia banded white. Grey or grey merging white, black tipped (5).

**Cross-sections:**

**Guard hairs**
Circles and oblongs with medium medullas (1x). Some dumb-bells and some concavo-convex with medium medullas (2z).
Colour: red, yellow, black and beige.

**Underfur**
Circles and oblongs with medium medulla. Oblongs with large medulla.

**Cuticular scale patterns:**
Coronal at base (3), petal along shaft (4), waved mosaic towards tip. Scale margins: smooth, except in mosaic. Distance apart of scales: distant in petal, near in mosaic.
SIDE-STRIPED JACKAL
**Family:** CANIDAE

**Canis adustus** Sundevall, 1846

**DISTRIBUTION:**
Northern Natal, eastern and northern Transvaal, Mozambique, Rhodesia and northern Botswana, and north-eastern Namibia.

**HABITAT:**
Open savannah and even mountains.

**HABITS:**

Diet: essentially a scavenger where carrion available, but also feeds on birds, insects and vegetable matter.

---

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Greyish brown, darker on upper parts, lighter on sides. Whitish line along flanks from shoulder to tail bordered by black on lower line. Underparts whitish/grey. Tail bushy, blackish white-tipped.

**INDIVIDUAL HAIRS:**

**Length:** 35.11 ± 4.72 mm

**Colour:** White tipped black. Black banded white. Black. Beige (5).

**Cross-sections:**

**Guard hairs**
Circles and ovals, medium medulla (1a), large medulla (2b). Colour: black and white.

**Underfur**
Circles, large and medium medulla.

**Cuticular scale patterns:**
Petal, (3) waved mosaic at tip (4). Scale margins: smooth in petal, rippled in waved mosaic. Distance apart of scales: distant in petal, near in waved mosaic.
BLACK-BACKED JACKAL
Family: CANIDA

Canis mesomelas
Schreber, 1775

Black-backed Jackal

DISTRIBUTION:
Throughout southern African sub-region.

HABITAT:
Open savannah and light woodland.

HABITS:
Mainly nocturnal but often seen in daylight. Solitary but aggregations at killings.
Diet: hares, rodents, birds eggs, reptiles, insects; but it is also a scavenger attracted to other carnivore kills.

HAIR

GENERAL DESCRIPTION OF FUR:
Head, greyish, sandy coloured on muzzle and cheek. Broad conspicuous dark mantel on upperparts from neck to tail, black and white, sharply contrasted to rufous colour on flanks. Tail bushy, black and white.

INDIVIDUAL HAIRS:
Length: 36,41 ± 9,16 mm

Cross-sections:
Guard hairs –
Cortex thick and distinctive (not as wide as in wild dog). Circles medium medulla (1c) concavo-convex (2d) and also 'Dumb-bell' shapes (2e). Medium medulla.

Underfur –
Circles, distinctive cortex (1f).

Cuticular scale patterns:
Waved mosaic (3). Scale margins: rippled-crenate. Distance apart of scales: near.
CAPE CLAWLESS OTTER
Family: VIVERRIDAE

Viverra civetta
Schreber, 1776

DISTRIBUTION:
Northern Natal, Swaziland, Transvaal, Mozambique, Rhodesia, eastern and northern Botswana, north-eastern Namibia.

HABITAT:
All types of savannah, sometimes dense forest.

HABITS:
Diet: carrion and a variety of prey including rodents, birds, eggs, small game, lizards and frogs and insects.

HAIR

GENERAL DESCRIPTION OF FUR:
Long, coarse bristly hairs, light-grey forehead and white muzzle. From neck to tail, line of shaggy black hairs. Ground colour - grey buffish with black spots in rows along body and across tail.

INDIVIDUAL HAIRS:

Length: 72.0 ± 2.79 mm

Colour: Entirely black. Black banded off-white, or off-white base. Entirely sepia or sepia tipped light brown (4).

Cross-sections:
Guard hairs -
Large circles, medium medulla (1t). Some large circles with clearly pigmented cortex (1u).

Under-fur -
Small circles some with small medulla, and some with large medulla.

Cuticular scale patterns:
Petal, almost diamond petal along shaft (2) changing to fairly regular waved mosaic towards tip (3). Scale margins: smooth in petal, slightly rippled in mosaic. Distance apart of scales: distant in petal, near in waved mosaic.
SPOTTED-NECKED OTTER
Family: MUSTELLIDAE

Lutra maculicollis
Lichtenstein, 1835

**DISTRIBUTION:**
Eastern Cape Province, Natal, Orange Free State, Lesotho, Swaziland, Mozambique, northern Botswana and Namibia. Also found along parts of Orange river (not shown on map).

**HABITAT:**
Larger streams, rivers, and lakes and mountain streams with rapid flow.

**HABITS:**
Mainly nocturnal. Shy and seldom seen. Solitary or in small groups. More aquatic than *Aonyx capensis*.

Diet: fish, amphibians and fresh water animals.

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**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Upper parts dark brown/chestnut, conspicuously mottled with brown spots. Underparts paler.

**INDIVIDUAL HAIRS:**

- **Length:** $13.63 \pm 2.86$ mm
- **Colour:** Sepia (7).

**Cross-sections:**

- **Guard hairs** -
  Oblong with large medulla (11) and (3) or medium medulla (1j) and (4).

- **Underfur** -
  Sparse: round or oblong with medium size medulla.

**Cuticular scale patterns:**
Lanceolate pectinate along entire length of hair (5) and (6), except at extreme tip when waved mosaic. Scale margins, smooth. Distance apart of scales: distant except in mosaic when near/close.
HONEY BADGER
Family: MUSTELLIDAE  Mellivora capensis  (Schreber, 1776)

DISTRIBUTION:
Throughout southern African sub-region except Namib coastal strip.

HABITAT:
Diverse, varying from open dry savannah to dense forest.

HABITS:
Nocturnal. Solitary or in pairs. Digs burrows.
Diet: omnivorous, feeds on small rodents or shrews, snakes, insects even young antelope but also roots, bulbs, fruit and honey and pupae of wild bees.

HAIR

GENERAL DESCRIPTION OF FUR:
Upperparts from crown of head to tail whitish, grey. Tail, sides and underparts black.

INDIVIDUAL HAIRS:
Length: 31.78 ± 4.51 mm

Colour: Entirely black or yellowish white (4).

Cross-sections:
Guard hairs —
Oblong medium medulla (1k) darkly pigmented cortex in some hairs (1l).

Underfur —
Oblong medium and large medulla.

Cuticular scale patterns:
Irregular waved mosaic along length (2) and (3). One or two scales across width (2). Scale margins: rippled-crenate. Distance apart of scales: near.
WHITE-NAPED WEASEL
Family: MUSTELLIDAE

DISTRIBUTION:
Eastern and northern Cape Province, Natal, Orange Free State, Transvaal, western Mozambique, Botswana and Rhodesia.

HABITAT:
Savannah and open country.

HABITS:
Diurnal as well as nocturnal. Terrestrial. Lives singly or in pairs or small groups. Scent-gland well developed. Enters burrows in search of food. Runs alongside prey then rolls itself round it.
Diet: mostly rodents, birds, reptiles and insects.

HAIR

GENERAL DESCRIPTION OF FUR:
White top of head, divides to form four white stripes down length of body. Rest of body blackish or yellowish.

INDIVIDUAL HAIRS:
Length: 7.44 ± 0.35 mm
Colour: Entirely black or yellowish-white (5).

Cross-sections:
Guard hairs -
Distinctly oblong, medium medulla (lm) or large medulla (ln).

Under-fur -
Oblong, medium and large medulla.

Cuticular scale patterns:
Base, waved mosaic, one or two scales across width of hair (2). From third of hair to tip, irregular waved mosaic (3) and (4). Scale margins: rippled-crenate. Distance apart of scales: near/close.
STRIPED POLECAT
**Family:** MUSTELLIDAE

**Ictonyx striatus** (Perry, 1810)

**DISTRIBUTION:**
Throughout southern African sub-region.

**HABITAT:**
Diverse, from savannah open country to high mountains.

**HABITS:**

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Soft coat. Strikingly contrasted black and white stripes on upper parts. Four conspicuous white stripes run length of back. Underparts black.

**INDIVIDUAL HAIRS:**

- **Length:** 30.33 ± 11.05 mm
- **Colour:** Entirely black or yellowish-white. Dark grey. Yellowish-white banded. Black (3).
- **Cross-sections:**
  - **Guard hairs**
    - Oblong, medium medulla (10). Oblong large medulla (1p).
  - **Underfur**
    - Oblong medium medulla, oblong large medulla.
- **Cuticular scale patterns:**
  Irregular waved mosaic with slight chevron peak to the scales (2). Scale margins: distinctly rippled. Distance apart of scales: near.
TWO-SPOTTED PALM CIVET

10 cm
Family: VIVERRIDAE

Nandinia binotota (Gray, 1830)

Two-spotted Palm Civet

DISTRIBUTION:
Eastern Rhodesia and parts of Mozambique.

HABITAT:
Forests and forested savannah.

HABITS:
Nocturnal. Arboreal. Spends day hidden among trees or vines.
Diet: diversified, feeds on vegetable matter—particularly fruit, arboreal rodents, birds and birds eggs.

HAIR

GENERAL DESCRIPTION OF FUR: Coarse coat of dense hairs.
General colour buffish grey tinged with chestnut and marked with numerous indistinct black spots in rows on upper parts. Two creamy spots on shoulders. Underparts light-grey, tinged yellowish. Tail long, dark with +12 narrowish rings.

INDIVIDUAL HAIRS:
Length: 18.1 ± 4.5 mm

Colour: Entirely sepia, or sepia tipped grey. Sepia banded paler, tipped black (4).

Cross-sections:
Guard hairs—
Circles medium medulla (lq). Ovals medium medulla (lr).
Ovals large medulla (ls).

Underfur—
Circles and ovals (numerous) medium and large medulla.

Cuticular scale patterns:
Distinct diamond petal. 4 scales across width (2) and (3). Waved mosaic towards tip. Scale margins: smooth in petal, rippled-crenate in mosaic. Distance apart of scales: distant in petal, near in waved mosaic.
CIVET
**Family:** VIVERRIDAE

**Viverra civetta**
Schreber, 1776

**DISTRIBUTION:**
Northern Natal, Swaziland, Transvaal, Mozambique, Rhodesia, eastern and northern Botswana, north-eastern Namibia.

**HABITAT:**
All types of savannah, sometimes dense forest.

**HABITS:**
Diet: carrion and a variety of prey including rodents, birds, eggs, small game, lizards and frogs and insects.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Long, coarse bristly hairs, light-grey forehead and white muzzle. From neck to tail, line of shaggy black hairs. Ground colour - grey buffish with black spots in rows along body and across tail.

**INDIVIDUAL HAIRS:**

- **Length:** 72.0 ± 2.79 mm
- **Colour:** Entirely black. Black banded off-white, or off-white base. Entirely sepia or sepia tipped light brown (4).

**Cross-sections:**

- **Guard hairs**
  - Large circles, medium medulla (lt). Some large circles with clearly pigmented cortex (lu).

- **Underfur**
  - Small circles some with small medulla, and some with large medulla.

**Cuticular scale patterns:**
Petal, almost diamond petal along shaft (2) changing to fairly regular waved mosaic towards tip (3). Scale margins: smooth in petal, slightly rippled in mosaic. Distance apart of scales: distant in petal, near in waved mosaic.
SMALL-SPOTTED GENET
Family: VIVERRIDAE

Genetta genetta (Linnaeus, 1758)

DISTRIBUTION:
Throughout southern African sub-region except part of south coast and eastern regions as shown, and Namib coastal strip.

HABITAT:
Dry savannah and open country. The only genet found in open dry savannah.

HABITS:

HAIR

GENERAL DESCRIPTION OF FUR:
Coat long and soft with well developed crest along spine. Ground colour greyish to fawn with dark line along back. Dark brown and blackish spots arranged more or less in rows. Tail 9-10 dark rings, white tipped.

INDIVIDUAL HAIRS:
Length: 32.90 ± 11.40 mm.

Colour: Black, white base, or banded white. Dark Grey (4).

Cross-sections:
Guard hairs –
Circles medium and large medulla (lv) and (lw). Fewer ovals with large and medium medullas (lx). Colours black and white.

Underfur –
Ovals and circles with medium medullas.

Cuticular scale patterns:
Clearly marked diamond petal (3). Base coronal (2), mosaic at tip. Scale margins: smooth, slightly crenate in mosaic. Distance apart of scales: distant in petal, near in mosaic.
LARGE-SPOTTED GENET
Family: **VIVERRIDAE**

**Genetta tigrina**
(Schreber, 1776) (sensa lato)

**DISTRIBUTION:**
Western and eastern Cape Province, Natal, Transvaal, Mozambique, Rhodesia, northern Botswana, and north-eastern Namibia.

**HABITAT:**
Bush, woodland, savannah but not high forest.

**HABITS:**
Nocturnal. Terrestrial and arboreal.
Diet: birds, lizards, insects and vegetable matter.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Coat soft, short with distinct dorsal line. Ground colour, brownish grey to pale yellowish or buffish white with dark spots which are more or less arranged in longitudinal lines. Tail with eight or nine dark rings and wide dark tip.

**INDIVIDUAL HAIRS:**

**Length:** \[24.0 \pm 3.25 \text{ mm}\]

**Colour:** Brown or sepia banded yellow-white or light brown. Entirely sepia. Entirely grey. Light brown, tipped sepia.

**Cross-sections:**

**Guard hairs** —
Ovals, large medulla (not clear in photograph).
Ovals, medium medulla (ly).

**Underfur** —
Circles and ovals, large medulla. Circles medium medulla.

**Cuticular scale patterns:**
Petal (3), waved mosaic towards tip. Scale margins: smooth in petal, crenate in mosaic. Distance apart of Scales: distant in petal, near in mosaic.
SURICATE
Family: VIVERRIDAE

Suricata suricatta
(Schreber, 1776)

**DISTRIBUTION:**
Cape Province, Orange Free State, Lesotho, southern Transvaal, Botswana, Namibia except Namib coastal strip.

**HABITAT:**
Dry plains.

**HABITS:**
Diurnal. Highly sociable. Digs own burrows but usually uses excavated burrows of ground squirrel. Vision well developed. Sits up on haunches.

Diet: mainly insects, spiders, millipedes, also bulbs.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**

**INDIVIDUAL HAIRS:**

- **Length:** 26.32 ± 3.22 mm
- **Colour:** Yellow white banded, or tipped black. Grey, or grey tipped white (3).

**Cross-sections:**

- **Guard hairs**
  Ovals medium medulla (la). Some ovals/oblongs with irregular medulla (lb).

- **Underfur**
  In profusion mainly ovals, medium medulla.

**Cuticular scale patterns:**
Petal on shaft (2) mosaic towards tip. Scale margins: smooth, slightly rippled in mosaic. Distance apart of scales: near.
SELOUS' MONGOOSE
Family: VIVERRIDAE

Paracynictis selousi
(d de Winton, 1896)

DISTRIBUTION:
Northern Natal, eastern Transvaal, western Mozambique, Rhodesia, northern Botswana, and north-eastern Namibia.

HABITAT:
Open country and light woodland.

HABITS:

HAIR

GENERAL DESCRIPTION OF FUR:

INDIVIDUAL HAIRS:

Length: 12.6 ± 4.8 mm

Colour: Black. Black banded white. Grey tipped or banded white, or grey banded white.

Cross-sections:

Guard hairs –
Ovals (1c), and oblongs with medium medulla (1d). Some concavo-convex as in (2).

Underfur –
Ovals or oblongs with medium medulla.

Cuticular scale patterns:
Irregular waved mosaic (3) and (4). Scale margins: rippled crenate. Distance apart of scales: near/close.
YELLOW MONGOOSE
**Family:** VIVERRIDAE

**Cynictis penicillata**

(G. Cuvier, 1829)

**DISTRIBUTION:**
Cape Province, Orange Free State, western Lesotho and Swaziland, north-western Natal, Transvaal, Botswana, Namibia except Namib coastal strip.

**HABITAT:**
Open savannah and Karroo country.

**HABITS:**

**HAIR**

**GENERAL DESCRIPTION OF FUR:**

**INDIVIDUAL HAIRS:**

- **Length:** $17.98 \pm 4.72 \text{ mm}$
- **Colour:** Yellow brown banded black or grey based (3).

**Cross-sections:**

- **Guard hairs** - Concavo-convex with medium medulla (l), ovals medium and large medulla (lf) and (lg).
- **Underfur** - Circles with large and medium medulla. Ovals medium medulla.

**Cuticular scale patterns:**
Neat waved mosaic pattern, one or two scales across width (2). Scale margins: smooth. Distance apart of scales: near.
SLENDER MONGOOSE
Family: VIVERRIDAE

Galerella sanguinea
(Rüppell, 1835)

Slender Mongoose

DISTRIBUTION:
Throughout southern African sub-region except Namib coastal strip and parts of Cape Province.

HABITAT:
Diverse from desert country to dense forest.

HABITS:
Diurnal. Terrestrial but can climb trees. (Genus as a whole has all-purpose dentition).
Diet: rodents, birds eggs, reptiles and insects and vegetable matter and fruits. Good killers.

HAIR

GENERAL DESCRIPTION OF FUR:

INDIVIDUAL HAIRS:
Length: 20.29 ± 4.55 mm

Colour: Yellow brown banded sepia, merging grey (3).

Cross-sections:
Guard hairs —
Ovals medium and large medulla (lh) and (li). Reddish colour under microscope, distinctive.

Underfur —
Circles large and medium medulla.
Concavo-convex medium medulla.

Cuticular scale patterns:
Regular waved mosaic. One or two scales across width (2). Scale margins: smooth/slightly crenate becoming more so towards tip. Distance apart of scale margins: near.
EGYPTIAN MONGOOSE
**Family:** VIVERRIDAE

**Herpestes ichneumon**
(Linnaeus, 1758)

**DISTRIBUTION:**
Natal, Swaziland, parts of Cape Province, Mozambique, northern Rhodesia, Botswana and Namibia.

**HABITAT:**
Savannah, chiefly well wooded and near water.

**HABITS:**
Diurnal. Lives singly or in pairs or family groups. Terrestrial. Lives in burrows or crevices between rocks. Diet: diverse, but mainly rodents, game birds, reptiles, crabs and fish.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Uniform grizzly coat of fairly long and coarse hair. Upperparts speckled black and white, woolly underfur, yellowish buffy. Slides lighter. Underparts partly bare. Tail long and slender with black tassel at tip.

**INDIVIDUAL HAIRS:**

- **Length:** 21.08 ± 2.4 mm

- **Colour:** Black or grey, banded white. Black or black tipped white (3).

- **Cross-sections:**

  - **Guard hairs**
    Large oval hairs with medium and large medulla (lj) and (lk).

  - **Underfur**
    Ovals and circles.

**Cuticular scale patterns:**
Irregular waved mosaic (2). Scale margins: rippled crenate. Distance apart of scales: near.
**Family:** VIVERRIDAE

**Herpestes pulverulentus** Wagner, 1839.

**DISTRIBUTION:**
Namibia, except Namib coastal strip, Cape Province, southern Orange Free State.

**HABITAT:**
Savannah, and mediterranean evergreen trees and shrub.

**HABITS:**
Diurnal. Lives singly or in pairs, terrestrial but may climb trees. Diet: rodents, ground squirrels, juvenile hares, snakes, birds, eggs and insects.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Rather long loose coat, general colour speckled grey. Face darker, underparts lighter, and less speckled than above. Feet uniform dark brown. Tail long, bushy and speckled.

**INDIVIDUAL HAIRS:**
- **Length:** 22.1 ± 3.25 mm
- **Colour:** Black banded white or grey banded white (5).

**Cross-sections:**
- **Guard hairs** —
  Ovals, medium and large medulla (1%) and (1m). Black and white colour distinctive (cf. *Mungos mungo*).

- **Underfur** —
  Ovals, medium and large medulla. Circles, large medulla.

**Cuticular scale patterns:**
Base, diamond petal almost pectinate (2). Shaft typical petal (3), tip waved mosaic (4). Scale margin smooth slightly crenate in waved mosaic. Distance apart of scales: distant in petal, near in waved mosaic (cf. *Mungos mungo*).
WHITE-TAILED MONGOOSE

10 cm
Family: VIVERRIDAE

Ichneumia albicauda (G. Cuvier, 1829)

White-tailed Mongoose

DISTRIBUTION:
Cape Province, Orange Free State, Lesotho, Swaziland, Transvaal, Mozambique, Rhodesia, northern Botswana and Namibia.

HABITAT:
Savannah dense bush, particularly near water.

HABITS:
Nocturnal, partly diurnal, usually solitary. Terrestrial, partly arboreal.
Diet: frogs, rodents, reptiles, insects, grubs, eggs.

HAI R

GENERAL DESCRIPTION OF FUR:
Coarse shaggy coat, general colour grizzled grey or brownish grey with long black hairs in varying amounts but especially on the hind parts. Underparts and limbs usually dark black or brown. Tail bushy but tapering, dark at base then white or bushy white.

INDIVIDUAL HAIRS:
Length: \( 41.1 \, \pm \, 3.1 \, \text{mm} \)


Cross-sections:

Guard hairs –
Large ovals with reddish pigment in cortex (ln). Some with white cortex (lo), medium medulla. (Some black hairs large medulla).

Underfur –
Ovals, not much underfur.

Cuticular scale patterns:
Waved mosaic along entire length (2). Scale margins: crenated. Distance apart of scales: near.
WATER MONGOOSE

[Diagram of a water mongoose with a scale of 10 cm]
Family: **VIVERRIDAE**

**Atilax paludinosus**
(G. Cuvier, 1829)

**DISTRIBUTION:**
Cape Province, Orange Free State, Lesotho, Natal, Swaziland, Mozambique, Transvaal, Rhodesia, northern Botswana and north-eastern Namibia.

**HABITAT:**
Savannah and forest. Dense bush and marsh vegetation, usually near water.

**HABITS:**

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Coat coarse, shaggy, dark brown sometimes almost blackish, but grizzled appearance of brownish-black and ochraceous at close view. Underparts lighter. Limbs darker. Tail, short thick bushy at base tapering, same colour as body.

**INDIVIDUAL HAIRS:**

- **Length:** 11.6 ± 3.6 mm
- **Colour:** Sepia or brown, sparsely banded buff. Dark or light tipped (3).

**Cross-sections:**

- **Guard hairs**
  Colour in cross-section 'oranges', 'yellows', 'whites'.
  The 'orange sections have small medulla. Ovals and oblongs with large (lp) or medium (lq) medulla.

- **Underfur**
  Oval, large and medium medulla.

**Cuticular scale patterns:**
Irregular waved mosaic (2), pectinate towards base, 2 or 3 scales across width of hair. Scale margins: rippled crenate, or rippled or just crenate. Distance apart of scales: near.
BANDED MONGOOSE
Family: VIVERRIDAE

Mungos mungo (Gmelin, 1788)

**DISTRIBUTION:**
Natal, Transvaal, Mozambique, parts of Rhodesia, Botswana and Namibia.

**HABITAT:**
Dry savannah and woodlands, never dense forest. Usually not far from water.

**HABITS:**
Mostly diurnal. Very sociable, lives in packs, makes warrens. Diet: insects, grubs and larvae, also frogs, reptiles, birds, eggs, rodents, molluscs, fruit and bulbs.

**HAIR**

**GENERAL DESCRIPTION OF FUR:**
Coarse wiry coat, continuous striped pattern. Ground colour brownish grey covered with conspicuous transverse dark brown bands alternating with light bands of same width. Tail bushy at base, tapering to blackish tip.

**INDIVIDUAL HAIRS:**

**Length:** 17.94 ± 1.47 mm

**Colour:** Sepia banded tawny to buff, or tawny to buff and white. Sepia banded rufous, some with white base (3).

**Cross-sections:**

**Guard hairs:**
Black and white strongly contrasted. Ovals, medium and large medulla (1h). (cf Herpestes pulverulentus).

**Underfur:**
Circles, medium and large medulla.

**Cuticular scale patterns:**
Coronal at base, petal along shaft (2), waved mosaic towards tip. Scale margins: smooth but rippled in waved mosaic. Distance apart of scales: distant in petal, near in waved mosaic.
DWARF MONGOOSE

10 cm
**Family:** **VIVERRIDAE**

**Helogale parvula**
(Sundevall, 1846)

**DISTRIBUTION:**
Northern Natal and Swaziland, Mozambique, Transvaal, Rhodesia, northern Botswana and Namibia.

**Habitat:**
Dry savannah and woodland.

**HABITS:**
Diurnal (not especially shy). Gregarious, living in small colonies. Takes refuge in hollow trees or rock crevices or anthills. Nomadic, young born in holes. Diet: mainly insects, larvae, spiders but also small rodents, lizards, and eggs and young birds.

**Hair**

**GENERAL DESCRIPTION OF FUR:**
Uniform speckled brown or reddish hairs ringed brownish, whitish, appearing dark brown. Underparts lighter. Feet dark brown. Tail short, tapering, not bushy.

**INDIVIDUAL HAIRS:**

**Length:** $11.74 \pm 2.79$ mm

**Colour:** Black banded buffy white. Brown, tipped buff (3).

**Cross-sections:**

**Guard hairs**
A lot of black seen in section, but whites and yellows as well. Ovals medium medulla (1r).

**Underfur**
Oval with medium and large medulla.

**Cuticular scale patterns:**
Waved mosaic (2) (coronal in base) one or two scales across width of hair. Scale margins: rippled. Distance apart of scales: near.
BUSHY-TAILED MONGOOSE
Family: VIVERRIDAE

Bdeoga e crassicauda
Peters, 1852

DISTRIBUTION:
Mozambique, north-eastern Rhodesia.

HABITAT:
Associated with rocky outcrops.

HABITS:
Rare. Little known of habits. Reputed to take refuge in hollow trees.
Diet: insects (termites), and rodents and possibly aquatic animals (crabs), and fruit.

HAIR

GENERAL DESCRIPTION OF FUR:
Long coarse coat, upper parts very dark, blackish and dull underfur obscured by numerous black and white banded hairs. Underparts lighter. Limbs black. Very bushy black tail.

INDIVIDUAL HAIERS:

Length: 20,1 ± 3,8 mm

Colour: Sepia banded white. Sepia banded white and grey. Grey, beige tipped (3).

Cross-sections:

Guard hairs -
Oval large and medium medulla (Ie)
Dumb-bell, medium medulla (Ilt)

Underfur -
Numerous oblong hairs in tufts small medulla or oval with medium medulla.

Cuticular scale patterns:
Waved mosaic on shaft and tip (2). Coronal at base. Scale margins: smooth in basal part, rippled crenate in waved mosaic. Distance apart of scales: near.
MELLER'S MONGOOSE
Family: VIVERRIDAE  
Rhynchogale melleri  
(Gray, 1865)

Meller's Mongoose

DISTRIBUTION:
Parts of Transvaal, Swaziland, Mozambique and Rhodesia.

HABITAT:
Savannah

HABITS:
Nocturnal and solitary. Terrestrial. Young born in holes in ground. 
Diet: Predominantly and nearly exclusively a termite eater.

HAIR

GENERAL DESCRIPTION OF FUR:
Long, coarse fur. Crest formed by hairs growing forward below ear to lower shoulder. Grizzled brown, darker on back, greyer and lighter on head and underparts. Legs darker. Tail bushy long, black at tip.

INDIVIDUAL HAIR:
Length: 12.1 ± 3.2 mm

Colour: Sepia banded rufous or white. Brown-grey (3).

Cross-sections:

Guard hairs –
Ovals and circles with large medulla (lu). A lot of black seen in cross-section.

Underfur –
Circles and ovals medium medulla.

Cuticular scale patterns:
Waved mosaic (2). Scale margins: rippled crenate. Distance apart of scales: near.
RESULTS AND DISCUSSION

PART 1. TAXONOMY

Identification of mammals according to morphological characters of hair has many practical and empirical applications which have been discussed in the introduction to this study. However, apart from identification morphological studies on a few species of ungulates (De Boom and Dreyer 1953; Dreyer 1966; Stutterheim 1975) and southern African Muridae (Keogh 1974) little has been published on the hair of South African mammals. The atlas of the hair from southern African carnivora partially bridges this gap. It is intended for use as a photographic reference system in which the various hair characters presented, together with distribution data, form an aid to identification of southern African carnivora. The value of such a reference system will be enhanced when other mammal species from this region have been included. When this is achieved the value of a key will be realised.

Although the findings of the atlas do not lend themselves to the formation of a dichotomous key, I have nevertheless attempted to make a key, but stress that identification should be based on the use of the micrographs in conjunction with the other data presented. It is perhaps worth noting that in the case of the Muridae, the characters of the cuticular scale patterns and hair shape were such, that it was possible to key individuals to species level in all cases studied and to sub-specific level, in many instances.

Applications

1. Identification

During the course of compilation the atlas has been used,
in conjunction with the photographic section of the work on other mammalian orders, in several projects involving hair identification. One such project - the identification of hair from vulture pellets, is still in progress. Others have involved analysis of hairs from stomach contents and faecal remains of predators, in particular of *Hyaena brunnea* and *Crocuta crocuta*.


Pellets were sent to The South African Institute for Medical Research by Mundy* for analysis. Animal remains from the abovementioned five vulture species, as well as Ruppel's Griffon were examined by Plug (1978) to determine collection habits of vultures, and when the hair analysis is complete, these projects, together with descriptions of nesting sites and discussion for sampling biases for bones and hair will be detailed in a comprehensive paper (Keogh, Mundy and Plug in prep.).

Sampling of the pellets was carried out in the following way:- The pellet was halved, one half being retained for cross-reference purposes, the other half was completely teased out. Hairs were separated on gross examination and then studied macroscopically and microscopically. Results have not as yet, been subjected to statistical analysis, but do reveal differences between collections made in wilderness areas and ranching.

*Mr. P. Mundy, Vulture Study Group, Zoology Department, University of the Witwatersrand.*
areas. Thus pellets collected from ranching areas contain a preponderance of domestic animal hair, as well as hairs from Bovids, while those collected from wilderness areas have a preponderance of impala hair, as well as hairs from a variety of wild species.

Hairs were subjected to culture and biological tests for *Bacillus anthracis* with negative results, although organisms resembling *Bacillus anthracis* - *Bacillus cereus* were isolated. All the biological tests were negative.

2. Systematics

The use of hair characters as a tool in solving taxonomy problems has been demonstrated when hair morphology has taxonomic value at the sub-family level. Thus in Switzerland, Vogel and Besancon (1978), using hair characters examined by scanning electron microscopy, have been able to confirm designation of two species of Insectivora to the sub-family Soriciciniae.

However, in a study on the sub-species of the springbok *Antidorcas marsupialis*, Stutterheim (1975) found that scanning electron microscopy failed to reveal significant differences in cuticular structure of the hairs, confirming Robinson's (1975) conclusion that there are probably no valid grounds for subspeciation in *marsupialis*. Nevertheless, the use of hair characters in solving taxonomic problems may vary with different genera, and these differences may indicate differing systematic relationships or convergent adaptations.

In the study of hair of southern African Muridae (Keogh 1974) several instances where hair characters demonstrated taxonomic value were found. Mammalogists find the taxonomy of the genus *Acomys* (Muridae) unsatisfactory. However, based on hair characters, especially the type
of cuticular scale pattern in the deep gutter of these hairs, it has been possible to distinguish between the species *A. subspinosus*, *A. spinossissimus* and *A. cahirus*, (Keogh 1974). Similar clarification was possible in the genus *Aethomys*. The described forms of *A. nyikae* and *A. chrysophilus dollmani* were found to be conspecific and quite distinct from *chrysophilus* group. Electron microscopy of cuticular scales of hair is being used to assist in the clarification of the distribution of two sympatric species of the genus *Tatera* from the Vryburg area in the northern Cape Province.

Hair studies on the fairly recently described *Lemniscomys bellieri* (Van der Straten 1975) show it to have clearly defined hair characters, in particular the cuticular scale pattern, when compared to *Lemniscomys striatus striatus* from the same area.

In any event such findings, where present, should be supported by electrophoresis. Only when these have been used to establish the taxonomic status, can hair analysis then be used on museum specimens that may be in need of reassessment. The species complex *Mastomys natalensis* is one such species at present being defined by the use of electrophoresis. The two species within this complex species A and species B (as yet unnamed) will then be subjected to hair analysis and if possible, a reclassification of museum specimens could then be undertaken. This work has been mentioned in the introduction.

Variations in texture, colour and appearance of the pelage of mammals has long been used as one of the taxonomic criteria both for identification and systematic studies. The published work on the use of hair morphology has been reviewed in the introduction to this study, and more recent research has demonstrated the value, in some cases, of scanning electron microscopy of hairs and these and future studies, when supported by electrophoresis, will be of value to mammalian taxonomy.
Key for the Identification of hair of southern African Carnivora
based on scale patterns and cross-sectional shapes of the guard hairs

1. Cuticular scales lanceolate-pectinate
   2/3rds of length of hair .................. Lutra maculicollis
       Aonyx capensis
   Cuticular scales other than in 1 .................. 2.

2. Cuticular scales lanceolate-pectinate
   in lower 3rd of hair .................. Atilax paludinosus
   Cuticular scales other than in 2 .................. 3.

3. Cuticular scales petal-patterned
   Near 2/3rds of length of hair .................. 4.
   Cuticular scales mosaic or waved mosaic
   in 2/3rds of length of hair .................. 7.

4. Cuticular scales petal-patterned in near
   2/3rds of length of hair. Cross-sectional
   shape of hairs predominantly oval. Cross-
   sectioned appearance strongly contrasted
   black and white .................. Herpestes pulverulentus
       Mungos mungo
   (Distribution maps useful in distinguishing the above two species).
   Not as above in cross-section .................. 5.

5. Cuticular scale pattern clearly
   diamond petal in near half of hair ...... Nandinia binotata
       Viverra civetta
       Genetta genetta
   V. civetta characterised by clearly pigmented cortex.
   G. genetta - colour not sepia.
N. binotata - distribution map critical.

Cuticular scale pattern not clearly diamond petal ........................................ 6.

6. Cuticular scale pattern petal in near 2/3rds of length of hair.

Cross-sections mainly circles, (with ovals as well) .............................. Felis caracal

Felis lybica

Canis adustus

Vulpes chama

Hair colour and distribution maps used as further criteria for differentiation.

Petal cuticular scale pattern in near 2/3rds of hair. Cross-sectional shapes mainly ovals,

with circles ............................ Otoyoon megalotis

Genetta tigrina

Suricata suricatta

Hair colour and distribution maps used to distinguish the above.

7. Cuticular scale pattern waved mosaic.

Cortex noticeably large in cross-section, medulla small ......................... Hyaenama brunnea

Crocuta crocuta

Lycaon pictus

Canis mesomelas

Mellivora capensis

(The Hyaenas and wild-dog have larger hairs in cross-section and the cortex is relatively wider than that of Canis mesomelas. Hair colour to be used in distinguishing these hairs. The cross-sectional shape of Mellivora capensis is **oblong** or oval).

Cortex not noticeably wide ................................. 8.
8. Cuticular scale pattern waved mosaic.

Cross-sectional shape distinctly oblong ........................................... *Ictonyx striatus*  

*Poecilotruga albinuaha*  

*Mellivora capensis*  

(*Mellivora capensis* distinguished by large cortex. *I. striatus* and *P. albinuaha* differentiated by typical hair lengths).

Cross-sectional shape other than oblong ........................................... 9.

9. Cuticular scale pattern waved mosaic cross-sectional shape varied: - dumbbells, concave convex, reniform ........................................... *Proteles cristatus*  

Cross-sectional shape not varied as above ........................................... 10.

10. Cuticular scale pattern mosaic or waved mosaic, cross-section concavo-convex with ovals ........................................... *Cynictis penicillata*  

*Paracynictis selousi*  

Cross-sectional shapes mainly ovals or circles ........................................... 11.

Cuticular scale pattern mosaic or waved mosaic cross-sectional shape mainly circles ........................................... *Panthera leo*  

*Panthera pardus* - (petal scale pattern at base of hair).  

*Acinonyx jubatus*  

*Felis serval* - (colour of cross-section distinctive yellows and blacks).  

*Felis nigripes*
11. Cross-sectional shapes mainly ovals.

Distinctive red colour in cross-section .................................. Galerella sanguinea

Colour not as above in cross-section ...................................... Ichneumia albicauda

Herpestes ichneumon
Helogale parvula
Bdeogale crassicauda
Rhynohogale melleri

Hair colour and distribution maps to be used to differentiate the above from each other.
PART II. HAIR IN RELATION TO ECOLOGY

Hair provides one of the principal links between a mammal and its environment and its function is concerned with maintenance of homeothermy. Heat is transferred from the body to the environment by radiation, convection and conduction, and by the evaporation of water. Heat transfer by radiation, convection and conduction can operate in the opposite direction. In the solar radiation energy exchange, hair colour is important, whilst the insulative properties of fur play their part in the convective and conductive heat exchange, and the function of evaporative water loss is effected by the density of the pelage. Hair is also the first point of mechanical contact between the body and the environment; and in a changing environment, survival may depend upon the degree to which the homeotherm responds to environmental cues, and the degree to which the effectiveness of the coupling through the hair can be maintained. Understandably therefore one would expect hair to be related to ecological variations. However, adaptive characteristics of hair are not always simple to define, for there is great taxonomic variation both in the hair itself and in follicular arrangement, as well as in the hair growth cycle, although the medullary spacings seem remarkably constant. The part played by hair can therefore be most clearly defined if the separate components that make it up are treated as if they were largely independent. In discussing the part that hair plays in mammalian ecology I shall therefore refer separately to hair types such as guard hairs, underfur and vibrissae; their cuticular scales, cortex, medulla, shape, size, colour and density; mechanical and surface properties and moulting. Follicular arrangements have not been studied in detail.

Evolution and Phylogeny

Smith (1960) summarised the evolutionary story of the
chordate integument in which the development of keratin was a major contribution to the vertebrate conquest of land, and Spearman (1964) has reviewed keratinisation well. Danforth (1925) rejected the hypothesis which is now current - that the forerunners of hair follicles were depressed epidermal thickenings arranged in patterns on warty excrescences of amphibians, and which often contained a spine-like or hair-like appendage. These thickenings, called prototriches, performed a mechanicosensory function. Later they gave rise to sensory pits between the imbricated scales of ancestral mammals. Hair follicles evolved from these pits in contrast to the direct evolution of feathers in birds from reptile-like scales. Primitive prototriches may still be seen as epidermal thickenings on fish, wart-like elevations on amphibians and sensory bristles on reptiles. The "basic trio" group is still to be seen behind the epidermal scales in rodents and certain marsupials and reptiles. Like vibrissae, which maintain their sensory function, primitive hairs probably had a sensory function and with the advent of thermoregulation they assumed other functions. Hair became more abundant, by follicular branching and through the development of the "basic trio" group to which almost all follicle groupings in modern mammals may be related (Lyne 1966). See Fig. 7.

Mammals first appeared some 180 000 000 years ago, and the characteristics they evolved such as homeothermy and viviparity, as well as the development of fur contributed to their success. Recently however, Crompton, Taylor and Jagger (1978) have offered the following hypothesis on the evolution of homeothermy in mammals: the one ecological niche that reptiles were not able to invade was the nocturnal one and mammalian homeothermy was acquired in two steps. The first enabled mammals to invade the nocturnal niche without an increase in resting metabolic rate. The second enabled them to invade a diurnal niche and
Figure 7. Gross evolution of epidermal scales. From Smith (1958).
involved the acquisition of higher body temperature. This is supported by the fossil record which indicates that during Jurassic and Cretaceous times most mammals remained in the nocturnal insectivorous niche.

The first hairs were probably sensory. Loss of visual information in a nocturnal niche was compensated for by better developed senses of hearing and smell (and a larger brain for processing this additional information). Is it possible that these sensory hairs were also more exercised in the nocturnal niche, and that natural selection in the colder nocturnal environments would have favoured a more densely covered skin, thus establishing fur? Later in the text I will discuss the hypothesis that the medulla of the hair acts as a receiver of longwave radiation. As such radiation would have been the only source of external energy, in the absence of direct solar energy, it is not unreasonable to postulate that if the medulla acts in this way, the development of fur would have been even more stimulated.

The Carnivora of southern Africa have formed the basis of this particular study on hair, and it is mainly to this group of mammals that I will refer in this discussion. The Carnivora are traditionally placed in two groups: the Feloidae comprising the Felidae, Viverridae and Hyaenidae: and the Canoidae comprising the Canidae and Mustellidae (Ewer 1974). See Fig. 8.

The most modified of the Carnivores are in the Feloidae, the civets and mongooses showing many characters possessed by this type in the oligocene (Young 1962). The hair types of this group are varied and diverse. See for example the brown hyaena hair which is long, coarse and shaggy, and has a comparatively small medulla in cross-section, page 40 in atlas, and the lion which has a short-haired coat with the medulla of medium size, page 48 in atlas, and the yellow mongoose with its long
Figure 8. Two possible interpretations of the families of Carnivores.

(a) The Procyonidae arising as an offshoot from the Canidae or
(b) originating independently from the Niacidae.

Figures on the left are millions of years ago. From Ewer (1974).
coat and thick underfur and concavo-convex shaped hairs in cross-section, page 90 in atlas. The Canoidae appeared very early and have changed very little, the modern Canis being practically a survivor of the Eocene stage of Carnivore evolution. The hairs of this group are not as diverse in shape, or as varied as those in the Feloidae, being mostly, although not always, oval or oblong in cross-section, for example the hair of the bat-eared fox and the Cape fox, pages 58 - 62 in atlas. It is of interest, however, to note that the Canoidae are typically plain coloured and the Feloidae are typically marked with blotches, spots or stripes. This difference suggests a basic divergence in early phylogeny into forest or woodland ancestral feloids and open country ancestral canoids.

The evolution and adaptive function of vertebrate moulting is another aspect to be considered in this section. Epidermal cycles appear to be a basic vertebrate characteristic (Ling 1972), and these cycles, giving rise to outer generations of epidermis and its derivatives, need only to be synchronised to environmental conditions for the integument to achieve great survival value. Although hairs in the pelage function collectively, it is essential that they act individually if seasonal needs are to be met. It is the response of individual follicles to the mechanisms which stimulate moulting which determine the moult. Ling (1972) points out that the cyclical nature of moulting and the regulatory systems which govern it are alike in all five vertebrate classes.

The development and structure of hair follicles has been thoroughly reviewed by Lyne (1966) who notes that, on the whole, the arrangement of follicle groups seems to be phylogenetically related, and who poses some fascinating questions for future research on hair
follicles. The answers to some of these questions could perhaps throw more light on the part that ecological pressures play on the mammalian pelt. There are great gaps in our knowledge of the evolution of hair partly due to the lack of fossil records. The earliest hairs I have examined are those from a mammoth found in the ice at the mouth of the Lena River in Siberia. They have many features in common with elephant hair from the Kruger National Park: for one example, the medulla, if present at all, is very small. In hair structure, taxonomic affinities, however, are often masked by ecologically selective pressures. This is most marked in specialised environments such as the aquatic habitat.

Aquatic Habitat

Many workers have studied adaptations of the mammalian skin to the aquatic mode of life. Most of those have dealt with the Pinnepedia. Among the foremost in this field is Ling (1965a, 1965b, 1968, 1969 and 1970) and Ling and Thomas (1967). Bartholomew and Wilke (1956), Gentry (1972), Scheffer and Johnson (1963), Irving and Hart (1957), Irving, Peyton, Bahn and Peterson (1962), Ray and Fay (1968), Oritsland (1971) and Ohata and Miller (1977) have all dealt with the pelage of Pinnepedia. While Soholov (1960 and 1962) has written more generally on hair of aquatic species and Johansen (1962) studied buoyancy and insulation in the muskrat.

As the thermal conductivity of water is some twenty-five times greater than that of air, and as heat will be removed rapidly by forced convection in the water, aquatic mammals require particularly effective thermal insulation. Air trapped within the underfur, which insulates the bodies of most land mammals, can serve also for insulation in the water, but only so long as it is sealed with a water-tight layer of guard hairs. Mechanical disturbance of the fur necessitates a return to dry land to restore it, so that in mammals, an insulating air layer is found
only in those that are not exclusively aquatic.

The entirely aquatic mammals, on the other hand, do not rely on fur for insulation, but rather on subcutaneous fatty tissue. This difference has thus determined one trend in the evolutionary process, for survival in the aquatic habitat favours a non-furry pelage. Thus with increasing attachment to the aquatic environment, hair covering is reduced, the role of hair in thermoregulation is lost, and insulation is provided in the form of blubber (Soholov 1962). Otters found in southern Africa, however, are very much semi-aquatic and the hair of both Lutra maculicollis and Aonyx capensis is adapted to this environment. They have both guard hairs and underfur, the former being much longer than the latter, especially in the case of Lutra maculicollis, see Fig. 9. In fact the average ratio of the length of the guard hairs to that of the underfur is 3:1 in the otters and 2:1 in the terrestrial Mustellids. This is in agreement with the findings of Sokolov (1962) regarding hair lengths of semi-aquatic species.

The guard hairs are flattened dorso-ventrally, producing an oblong shape in cross-section, see pages 68 and 70 in atlas. They have no piloerector muscles and the follicles are so arranged that these hairs emerge at an acute angle (± 30°) to the skin. All these factors ensure that they lie flat to form a covering for the underfur. The medulla of the guard hairs is small and often discontinuous towards the tip and this gives some stiffness to an otherwise very flexible structure. The underfur is short and dense, often crinkled towards the base providing cavities for trapped hair. It is denser on the belly of both otters studied, and this protects the soft underparts from cooling. The above characters (dense fur, broad and flattened guard hairs, slight development of the medullary layer) all favour the retention of an air
Figure 9. Guard hairs and underfur of Lutra maculicollis.
layer while swimming. The hair of the water mongoose, *Atilax paludinosis*, also exhibits some of these features, but as it is not semi-aquatic to the same extent as the otters, one would not expect to find so many adaptive features.

This discussion leads naturally to the consideration of surface tension. Surface properties have been measured on hairs, but mostly in relation to textile fibres, where such matters as the take-up of dyes and waterproofing properties of fabrics are important. This type of test has been applied to hairs of thirteen species of Southern African Carnivora and the results are included in Appendix I. They tend to show very little difference between the animal hairs selected. The tests were made on hairs from museum specimens, and as surface tension depends on surface oils, this could point to a defect in the tests. At first sight it may seem unlikely that unwoven or unfelted fibres can provide a covering layer which is impervious to deep water, or, to put it the other way, that it should prevent the escape of air. However, consideration of the various forces which act on the layer of guard hairs shows, if only qualitatively, that this impermeability can readily be achieved.

The forces concerned arise from surface tension, hydrostatic pressure and compression of trapped air. Surface tension in the boundary between water and air cause the hairs to adhere strongly together. Such forces are apparent whenever wet fur is left to dry in the surrounding air, but they are no less strong if, as in the case of a swimming animal, the air is within, encased by water. The surface tension forces between the hairs are greatly increased if the surfaces conform closely to one another, as can be seen with a film of liquid between two microscope slides, and the guard hairs of a semi-aquatic animal are therefore broad and flat, and relatively flexible.
Notwithstanding this close contact between the guard hairs, there must be narrow channels between them. Whether or not water will penetrate these interstices depends partly on the nature of the hair surface. Where the boundary between water and air abuts a solid, the surface is distorted by adhesive forces into a meniscus which meets the solid at the "angle of contact". If the angle of contact is smaller than 90°, the water will spread over the hair surface, wetting it, and will therefore seep through into the air layer in the underfur beneath. However, if the angle of contact is greater than 90°, as with a waxed surface, water will not spread and the solid is considered "unwettable". (The sebaceous glands in the skin probably provide such a coating for the hairs). This is the term commonly used for the hairs of some semi-aquatic mammals.

Nevertheless water under pressure may flow through apertures in an unwettable material. Whether or not it will in fact penetrate the guard hair layer therefore depends also on the pressure difference across this layer and the sizes of the interstices between the hairs. These two are linked and can be calculated. Thus when the pressure difference is equivalent to a water depth of say three meters, the water can penetrate interstices which are wider than about five microns. Note, however, that the pressure difference across the guard hair layer will in fact never be so great as the hydrostatic pressure. For the guard hair layer is compliant, and the air trapped within can be compressed. It is therefore inevitable that as the animal dives the guard hair layer will be moved inwards, raising the pressure of the trapped air within until the forces are balanced. The air pressure will remain just less than the water pressure because of the bending of the guard hairs, and the 'springiness' of the underfur. These mechanical forces are however small, probably contributing the equivalent of no more than about 10 cm
water pressure, which is therefore the remnant force available to drive water through the interstices. At this small pressure the critical width of the interstices would be no less than about 150 microns, comparable with the cross-sectional sizes of the hairs themselves. It can therefore be seen that barring accidental or mechanical disturbance the guard hair layer has the capacity to function as an impermeable layer.

The dimensions of the pelt of a semi-aquatic mammal are such that the actual movements necessary for adjustments of pressures are relatively small. Fig. 10 shows schematically a cross-section through the trunk of the spotted-necked otter.

On surface, at atmospheric pressure, the underfur thickness is about 5.0 mm. At a depth of three meters, it would be compressed to about 4.0 mm, an inward movement of only 1.0 mm to achieve the requisite increase in pressure.

Compression of the guard hair layer requires a small sliding movement between flat surfaces of the guard hairs. The strong surface tension forces binding them together do not greatly impede this sliding motion, as can be seen in the analogy, already cited, of glass microscope slides with a water film between. Using the same example of the spotted-necked otter, diving from the surface to a depth of three meters, the change in circumference will only be five per cent. The follicles of the guard hairs which lie side by side in the same layer are spaced about 125 μm apart and the maximum width of the flat shield of each hair is about 110 μm, see page 69 and 70 in atlas. These dimensions are in conformity with the need for small sliding movements.

The cuticular scale pattern of the guard hairs of both *L. muculicollis* and *A. capensis* is lanceolate-pectinate, see page 70 and 68.
Figure 10. Diagrammatic representation of pelt of *Lutra maculicollis*. 

- Inward hydrostatic pressure due to atmosphere plus 3 metres water depth.
- Outward pressure of compressed air layer.
- Small outward force due to stiffness of guard hairs.
- Position of outer fur layer at surface of water (i.e. at atmospheric pressure).
- Position of outer fur layer at 3 metres below surface of water.
in atlas, although in the water mongoose this pattern occurs only on the base of the hair. This type of scale pattern is found in seal hairs and it is of interest to note that it is also found in the rodents which inhabit vlei areas such as *Otomys irroration* and *O. angoniensis* and *Dasymys incomitus*. Hausman (1930) showed that the cuticular scale types are related to the size of the hair shaft, and at first this may seem relevant as broad flat guard hairs are found in semi-aquatic species. There are however broader hairs of other species which do not exhibit this lanceolate pectinate type of scale pattern. For example the broad hairs of the brown hyaena which have a waved mosaic cuticular scale pattern, page 40 in atlas. Whether or not this scale pattern has advantages, perhaps in providing an efficient water-tight cuticular covering, is not known.

The well-developed vibrissae of semi-aquatic mammals probably act as sensory detectors to obstacles in murky water, or to changes in currents produced by moving fish.

Although Maxwell (1961) and Harris (1968) have given a comprehensive account of otters in general, and Mortimer (1963) has studied *L. maculicolis*, little seems to be known of the swimming habits of young otters. However it is generally held that they are unwilling to enter the water when young (Rosevear 1974). Seal pups do not convert from land to the aquatic life until they have acquired "unwettable" adult body fur, at the age of 3-4 months (Irving et al. 1962). It would be of interest to know whether juvenile otters swim before they have developed the adult pelage.

A high degree of adaptation exists in the mammalian pelage in aquatic and semi-aquatic species, and this functions in the pelage as a whole as well as in the structure and characters of individual hairs.
In sharp contrast to the above habitat is the desert environment.

The Desert Environment, Colouration and Thermoregulation

All the factors of the environment (including both macro- and micro-climates), if summarised, are expressed as biotic zones. Thus the desert and semi-desert regions are biotic zones to which certain species are adapted, and mammals living in these regions have differentiated functionally as far as possible from aquatic forms. Many of their morphological adaptations to these regions concern the pelt and more specifically, the hair. As the climatic factors of a given biotic zone influence the organism through the flow of energy to or from that organism, it is the physical properties of the coat (as well as various other factors such as metabolism) which will assist in bringing the animal into harmony with its surroundings.

Consider the colour factor first: heat exchange to and from an animal occurs through conductive heat transfer, radiant heat transfer and convective heat transfer, and in discussing the influence of colour on energy flow, it is the solar or shortwave radiation which is referred to. There is much published work on this subject, some of which has been stimulated by economic reasons, those of coping with the adverse effects of heat stress in domestic animals, which mostly affect metabolism and reproduction. Variations in coat colour were found to be directly related to response to heat stress by Bonsma and Pretorius (1943), Bonsma (1949), Bonsma and Louw (1963), Riemerschmidt (1943 a and b) and Riemerschmidt and Elder (1945). Finch and Western (1977) substantiates this. Bonsma and Pretorius (1943) in a highly practical study in which large numbers of observations were made on live animals, discussed the influence of coat cover on the adaptability of cattle to tropical and subtropical environments. They concluded that animals with light coats are better
adapted to these conditions than animals with dark coloured coats, provided that the skin is dark; and that smooth coated cattle are better adapted to these climates. However, Schleger (1962) found that in Queensland, Australia, there was no indication of a higher heat load on darker animals as evidenced by body temperatures. Hammel (1956) showed that colouration had no effect on heat loss although he does not confirm his results. Hutchinson and Brown (1969) following on the work of Kovarik (1964) point out that "since heat load at skin level depends upon the site of absorption, as well as the amount of radiation absorbed, the superiority of light over dark coloured coats would be less than has formerly been believed". Kovarik concluded on mathematical grounds, that the heat load would be less with coats of absorptance intermediate between that of black and white coats. Interestingly Bonsma and Pretorius (1943) observed that the cream coloured Africander ox reflected more solar radiation than the white Zulu ox.

Most of the above examples of studies on radiative heat exchange refer to experimental measurements made on livestock, which are probably more effective than those made in the wild, as trends can be traced more readily. It is likewise obvious that many theories advanced on the subject of heat exchange would be greatly enhanced if they were confirmed by using live animals, and that those results where live animals have been used have particular value.

Three papers by Cena and Monteith (1975) have added much to the knowledge of transfer processes in animal coats. In measuring the transmission and reflection of both shortwave and longwave radiation through coats of sheep, cattle and other animals, they conclude that hair length and density, and not colour, are the properties mainly affecting solar radiation. Solar radiation must be a critical factor in
the thermoregulation of desert animals as they have complex shade-seeking
behaviour, Dawson (1972) and Nel and Rautenbach (1977). And yet there
is a large variety of coat colours in desert-living animals. Amongst the
southern African Carnivora this is particularly so, with variations
ranging, for example, from the dull buffy colour of the brown hyaena to the
highly defined colours of the small-spotted genet and the variations of
colouring between the black-backed jackal, bat-eared fox and the Cape
fox, all of which inhabit desert and semi-desert areas.

Colouration in the mammalian pelage as a cryptic device is
convincingly justified. Thus the function of colouration has been
described by Ewer (1974) as concealment which may be defensive, offensive
or both at once. In addition, facial markings, tail colouration and
various warning or recognition colouration patterns can act as signalling
devices for mate-recognition and interspecific recognitions and other
behavioural responses. It is however, the nocturnal species which exhibit
marked colouration which have stimulated my interest. In this realm there
are many unanswered questions. To what extent, for instance, does the
function of colouration in the dark, or at best partial light for only
some nights, act as a character for survival? Certainly to human eyes
the colours of nocturnal carnivores blend in with their environment,
when these animals are photographed using a flash-light. But this
degree of light is not available naturally in the wild at night. In any
event reddish pigmented hairs would appear black at night, so the advantage
of this colour as a cryptic device is lost. The cryptic significance of
colouration of nocturnal carnivores applies, therefore, to their ability
to blend in with their surroundings and remain obscure during their less
active (and less alert) daylight hours, and colouration of this kind
would hence be highly selected for survival. Another possible explanation
could be the following one:- I have mentioned the hypothesis that the
first mammalian niche was probably a nocturnal one (Crompton et al. 1978) and that in the course of evolution mammals occupied the diurnal niche. The colours, important in the solar radiation wavelengths, evolved under various selective pressures. Could these variously patterned nocturnal species - such as for example the small-spotted genet, and the leopard, have returned to the nocturnal niche? If this were so, then the importance of colourations and patterns in high contrast would have been heightened at dawn and dusk, and as the transition to the nocturnal niche would presumably have been a very slow one over a great time span, survival in the twilight hours may have depended on accentuation of their colour patterns. Once fully in the nocturnal niche, this colouration would not be of any great functional value, but for the same reason, there would be no pressures demanding the selection of colour changes. At most the low solar illumination of moonlight would favour black and white contrast, and such highly cryptically coloured mammals are in fact found in the nocturnal niche. Rautenbach and Nel (1978) in their study of co-existence in Transvaal carnivora found that there are no extremely nocturnal/gregarious species amongst the species studied and that there is a definite trend ranging from nocturnal/solitary mode of life, to an entirely diurnal/gregarious existence. As a possible explanation for this they offer the suggestion that there is a difficulty in maintaining group structure in the dark.

The fur operates as a thermoregulatory device in various ways and it is of interest to note that where solar radiation does not affect the animal, that is, on its under-belly, there is no need for colour - hence the white under-belly of many mammals.

The physical and ecological implications of mammalian colouring are, however, far from being fully understood. For instance, Hutchinson,
Brown and Allen (1973), Cena and Monteith (1975) and Kovarik (1964), all confirm that black is a far more favourable colour, regarding heat stress, than some of the intermediate colours between black and white, as black coats trap thermal radiation near the outer surface. Thus the black tipped hairs of many of the carnivora inhabiting the desert regions, could perhaps have been selected for this reason.

The distribution of various species of wild rodents throughout southern Africa shows a definite trend for lighter-coloured forms of species to be found in progressively more desert-like environments. It is known that mammalian species which inhabit warm and humid regions have more melanin pigmentation than the same species in cooler drier regions, and some mammals in arid regions are characterized by an accumulation of yellow and reddish-brown phaeomelanin pigmentation. Colour variations are genetically controlled and result from qualitative modifications of pigmentation. Guiler (1953) and Guiler and Banks (1958) showed that the distribution of the brush possum and the black rabbit, both follow Gloger's Rule, that more melanic phases of a species are encountered in more humid regions. In preliminary studies of the distribution of Desmodillus auricularis in southern Africa, I have found this same trend. More work needs to be done in this direction however, to establish what part, if any, lighter colouring plays in thermoregulation of desert rodents. Many desert rodents have a white under-belly, as do numerous other mammals, as previously mentioned.

In the physiological approach to thermoregulation the radiant heat which takes part in the energy exchange of animals is divided into the shortwave or optical region (wavelength less than 2-3 \( \mu m \)) and the longwave region (wavelength greater than 2-3 \( \mu m \)). This division is based
purely on a difference in the optical properties of animal coats in the two regions (Mitchell 1974). And as Mitchell (1977) states, what appears white to human eyes may well appear otherwise to the eyes of animals more sensitive to the ultraviolet. In any event it has been established by Finch (1972) that longwave radiation may impose a greater heat load than shortwave radiation does and this will be referred to later in this section.

I have made measurements of surface temperatures of animals, i.e. the longwave radiation, in the open. An Agavision system 680 thermal imaging camera was employed and filters on the system eliminated errors from solar radiation. Temperatures were measured using the isotherm system and the thermograms appeared in alternative grey form, the temperature distribution appearing as a gradation of image brightness. The pictures were taken on 26th June 1978 at the Johannesburg Zoological Gardens between 09h00 to 13h00. The air temperature was 17°C, there was no wind and the sky was cloudless. Measurements were taken between three and about 20 meters.

Although these readings are somewhat difficult to explain, I have included them, if for no other reason, to point to the need for further investigation into the part colour plays in the radiant heat exchange. See plates 8-14, pages 137-139.

The type of hair in the pelt in desert mammals varies enormously. Virtually no information exists about wild desert carnivores (Schmidt-Nielson 1964), but most of those animals pant and heat loss by evaporative cooling is one of the most efficient methods of coping with thermoregulation in a hot environment. The evaporation of one gram of water reduces body heat by 580 cal. Species of Bovidae, however, have glossy coats and no underfur and evaporative cooling
Plate 8. Giraffe flank. Confirming earlier work by Clark (1974), the temperature distribution caused by differential heat gain between visible dark and light areas of the coat pattern is shown. Warmest areas of the coat are shown as light areas on the thermogram print.

Plates 9 and 10. Giraffe neck. Temperature distribution according to visible coat pattern similarly defined. Nominal temperature span (0-1.0) of grey tone scale alongside thermogram is 10°C.
Plates 11, 12 and 13 of the Black backed jackal showing variations in radiation absorption remain constant with the recorded changes of posture. The darker region of the visible black coat appears cooler on the thermogram, possibly due to insulation of this thicker part of the coat. The head and extremities appear warmer.
Plate 14. Thermogram of a striped pole-cat in sunshine. The pattern reveals a differential solar heat gain which is not wholly associated with the visible pattern of the coat. Variations in thickness of coat cause differences in local energy balance as well as the effects of posture of the area exposed. Cena and Clark (1973) note that postural control of basking heat gain is more important for species of small size. The darker facial markings appear decidedly warmer than the rest of the visible lighter pigmented head.
occurs from the skin in those species which sweat, as the spacing of
the hair allows air currents to reach the skin. Some Bovids do not
sweat however, and a detailed examination was made of hairs from
species of these two categories. No marked difference in morphological
characters of these hairs was noted. This evaporative heat loss is
acceptable if the accompanying loss of water can be replaced,
but in desert areas the body is often insulated by thick underfur.
The role the fur plays in this environment is usually insulatory. The
amount of heat that reaches the body in a hot environment depends on
the amount of insulation covering the surface (Schmidt-Nielson 1964).
Convective and conductive heat transfer through fur have been calculated
(Cena and Monteith 1975) and temperature gradients between the outer
pelt and the skin of various species have been reported. There is no
doubt that desert animals are protected from heat stress by a thick
underfur, which seems to be an advantage for diverse distribution. Take
for example the striped pole-cat, with its long dorsal pelage as
correlated with its even distribution throughout southern Africa. There
is a tendency for fine hair in desert living rodents such as Desmodillus
auricularis, Gerbillurus paeba and G. vallinus. In captivity the
pelage of these animals becomes oily if they are deprived of sand for
sand bathing. The active sebaceous secretion in the fine hair probably
forms a protection against water loss. Diurnal rodent species in
southern Africa have a noticeably large gutter in the guard hairs
(referred to by Rosevear (1974) as gutter hairs). Studies have been made
on these hairs and the way in which they nest. The follicular arrangement
allows them to lie over each other (with fluff hairs in between) in such
a way that they fit into the gutter of the hair beneath them, the tips
always protruding by the same length. See Fig. 11. Quay (1965) has
found in some species of American desert rodents that the guard hairs
Figure 11. Cross-section at defined points along the guard hair of Rhabdomyx pumilio.
are affixed to one another by a lipid film. I have not fully investigated this in *Rhabdomys pumilio* - but have postulated that, the arrangement of these gutter hairs, if some liquid film were involved, would facilitate surface tension forces between the hairs and these would then form a protective covering against excess evaporative water loss. This is an important factor to guard against in an animal of this size, as with a low mass-to-surface ratio it is at a disadvantage as the ratio between its thermal inertia and its exposed areas is low. Another speculation as to the mechanical advantage of these deeply guttered hairs, is that they assist reflection of solar radiation. It is interesting to note that the klipspringer and the steenbok are amongst the Bovidae which inhabit more arid regions that have hairs which are markedly grooved. It must not be overlooked that many of the carnivores and rodents which live in desert or semi-desert areas, are nocturnal and the thick insulating underfur must act as protection against drop in temperature at night.

Certainly the deeply guttered hair seems to have some adaptive significance for the protection from solar radiation and evaporative water loss in rodents.

Cuticular scale patterns of the hairs of the different rodent species are distorted by the deep gutter in the waved mosaic type. The fine hairs of nocturnal desert rodents have coronal or chevron-type scale patterns which have been referred to in a previous study (Keogh 1974). A petal type scale pattern is the predominant one found in carnivore species inhabiting the desert and semi-desert areas of southern Africa. Thus *Proteles cristatus*, *Felis caracal*, *Felis lybica*, *Otocyon megalotis*, *Genetta genetta*, *Suricata suricatta*, *Vulpes chama* and *Herpestes pulverulentus*, all have this type of scale pattern. But then
so do the civet cat, the two-spotted palm civet and the large-spotted genet, not found in these areas. There is probably no significance in this correlation as various other species inhabit these areas, to a lesser degree however. The structure of the cortex, with its various pigmentations, serves as a support for the hair and varies only in diameter, amongst all these species. It is however in the structure of the medulla that interesting facts emerge which could have significance in the transmittance of longwave radiation.

Absorption of radiation

Colouration in the pelt is the result of selective absorption of visible radiation, coupled with the capacity of the eye to discriminate in some way between wavelengths. If the eye is not sensitive to wavelength, as for example with a dark-adapted human eye in low levels of illumination, or as may be presumed for some animals at all levels of illumination, then the pattern rather than the colouration will be seen by virtue of the different intensities of the reflected light.

About half of the solar energy reaching the earth is in the form of visible light. The remainder is mainly infra-red radiation, and there is a relatively small amount of ultra-violet. An indication of the distribution of energy (which depends to some degree on latitude, climate, weather, and other influences) is given in Fig. 12.

The effect of absorption of any part of this total radiation is to transform a fraction (termed the 'absorptivity') of the incident radiant energy into heat energy in the absorbing fur or skin, with a consequent rise in temperature. The unabsorbed portion is reflected, to be absorbed in the surroundings.

The absorption of sunlight in animal coats of different colours
Figure 12. Distribution of solar energy at ground level.
has been measured, particularly in relation to the important practical issue of the heat load on livestock. For example by adapting data from measurements by Hutchinson and Brown (1969) I indicate the absorptivity of the coats of black, brown and white cattle by the shapes of the curves in Fig. 13.

We can distinguish three regions: in order of increasing wavelength they are the near ultra-violet, the visible, and the near infra-red. In the near ultra-violet the absorptivity is almost 1.0 for all the coats: that is to say the radiation will be mostly absorbed and very little will be reflected. Such a coat is therefore termed 'black' to ultra-violet light, whatever its visible colour may be.

The colours of the three coats could be foreseen from the shapes of the absorptivity curves in the visible region. Thus as expected the black coat has a high absorptivity, and the white coat a relatively low absorptivity, throughout all wavelengths from violet to red. The brown coat, on the other hand, absorbs strongly at the blue end of the visible spectrum, but less so towards the red: thus although the coat is predictably a dark one because of the generally high level of absorption, there will be an enhanced proportion of red in the reflected light.

In the near infra-red the absorptivities converge to a value of about 0.5 at a wavelength of 1.5 μm, and thereafter they rise together. Beyond about 2 μm, at which the absorptivity may be about 0.7, the shape of the absorptivity curve for an animal's coat becomes erratic due to the effect of moisture, which absorbs heavily just beyond this wavelength. But for a study of the heating effects in animals the absorptivity in this region of the solar spectrum is of no great importance, because it
Figure 13. Absorptivity of cattle coats.
contains only a negligible amount of the total incident energy.

The shape of the absorptivity curve again becomes important at longer wavelengths associated with ambient and body temperatures. The long-wave radiation in question is due entirely to the temperature of the surface which emits it, and is therefore termed 'thermal' radiation to distinguish it from the short wave solar radiation (which may be reflected or scattered simultaneously from the same surface). The thermal radiation wavelengths range from about 3 μm to about 50 μm, although the longer waves are quickly attenuated and in practice the upper limit of wavelengths incident on an animal's coat will be about 30 μm. The distributions of energy emitted by surfaces at the ice-point (0°C) and at typical body temperature (37°C) are shown, plotted on a logarithmic scale of wavelength, in Fig. 14.

The total radiation energy emitted by unit area of a hot surface depends on the fourth power of its absolute temperature: this accounts for the different areas under these two curves. By the same token the curve for radiant emission from the sun, even at these extreme wavelengths, would be vastly greater. Nevertheless the sun is also at a vastly greater distance, and the importance of ambient thermal radiation lies in the proximity of the sources. Finch (1972) demonstrated that in the equatorial sunshine about half of the heat load on an animal's coat was due to such thermal radiation. Clearly at night it will become the dominant, if not the only, source of radiant energy received by an animal, and also emitted by an animal.

The absorption of radiant energy in fur at these wavelengths is not easy to measure. Nevertheless it has been taken as axiomatic by most authors that the absorptivity of fur, as also of skin, is very close to unity. Such high absorptivity is readily understandable, for it is of great importance for the nocturnal heat balance of any diurnal
Figure 14. Thermal radiation emission.
mammal, particularly the small ones, and it is not inconsistent with the proposition that mammals evolved first as nocturnal creatures.

This acceptable finding, that the absorptivity of fur to thermal radiation is near unity, does not appear to have been followed by any reported discovery of the underlying cause. It therefore seemed a matter of importance to investigate more closely the nature of the interaction between far infra-red radiation and the pelt.

Radiation waves are absorbed when they transfer their energy to material objects, setting them in vibration. The extent of the absorption therefore depends partly on the amount of matter which stands in the way, and partly on the ease with which the matter can be set into vibration. If the material contains objects which can oscillate freely at or near the frequency of the wave they will be set into large amplitude vibrations, and will rob the wave of its energy. For example in the visible region of the spectrum it is vibrations due to the forces between atoms in a molecule which give rise to this resonant absorption of light waves, and which therefore account for the different colours of chemical compounds.

This same principle applies to absorption of the far infra-red radiation emitted by warm objects. Here, however, we are no longer dealing with the vibration of sub-microscopic particles such as atoms and molecules, and the conditions for far infra-red resonance are similar to those in the adjoining radio micro-wave region of the spectrum. Such micro-waves can be trapped in cavities which have linear dimensions near to the wavelength, and the effect can be increased in a regularly spaced array of these cavities. The interaction between the shortest radio micro-waves and structures of various shapes and sizes is thoroughly well known, and by reducing the scale it is possible to predict the
dimensions of similar structures which will be effective in the absorption and conduction of far infra-red radiation.

The wavelengths in question can be seen from Fig. 15 to be in the region of 10 μm. At 0°C the peak of radiant energy is at a wavelength slightly greater than 10 μm, and at 37°C it is slightly less. The wavelength of the peak energy radiation can be calculated as a function of the temperature, and for the range of temperatures with which we are concerned, see Table I.

By reference to the behaviour of radio-waves we can expect that a mammal's interaction with thermal radiation will be most effective when its pelt has arrays of components with linear dimensions concentrated in the above relatively narrow range, between about 8 and 12 μm.

Neither the gross dimensions of hairs, nor the distances between them, match the requirement well. Although the fluff hairs of many smaller mammals, and the guard hairs of a few (for example some bats) have diameters as small as about 12 μm, the variations along the length of a single hair, between hairs of the same pelt, and between different species, are nevertheless considerable. Indeed the guard hairs of different species have diameters measured throughout a range up to more than 500 μm. As to the spacing between hairs, this also has great variation, and moreover appears to be of the wrong order of magnitude. Thus an average separation of 10 μm would require a density of one million hairs per cm², whereas the densities quoted for certain mammals (Cena and Monteith 1975) range from about 100 per cm² (goat) to about 4000 per cm² (rabbit), giving average separations between hairs of 1000 μm and about 160 μm respectively. Notwithstanding the follicular grouping of the hairs, they will not be sufficiently close to match the peak wavelength of thermal radiation.
Table I: Wavelength of maximum energy radiation as a function of temperature

<table>
<thead>
<tr>
<th>Temperature, °C</th>
<th>Wavelength of maximum energy, μm</th>
</tr>
</thead>
<tbody>
<tr>
<td>-30</td>
<td>11.92</td>
</tr>
<tr>
<td>-20</td>
<td>11.45</td>
</tr>
<tr>
<td>-10</td>
<td>11.02</td>
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<tr>
<td>0</td>
<td>10.61</td>
</tr>
<tr>
<td>10</td>
<td>10.24</td>
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<tr>
<td>20</td>
<td>9.89</td>
</tr>
<tr>
<td>30</td>
<td>9.56</td>
</tr>
<tr>
<td>40</td>
<td>9.26</td>
</tr>
<tr>
<td>50</td>
<td>8.97</td>
</tr>
<tr>
<td>60</td>
<td>8.70</td>
</tr>
<tr>
<td>70</td>
<td>8.45</td>
</tr>
<tr>
<td>80</td>
<td>8.21</td>
</tr>
</tbody>
</table>
We are therefore obliged to turn to the microscopic structure of the hair. The most obvious repetitive feature is the cuticular scale pattern. The shapes and sizes of the scales, and the spacing of the scale margins, are however sufficiently variable for them to be used as an aid to identification. The dimensions, with a lower limit of about 6 μm, cover the range occupied by the radiation wavelengths with which we are concerned, and in certain mammals, notably bats, the scales are uniformly spaced at about 10 μm. The upper limit is however relatively large, about 40 μm, and in view of the considerable variability there is no strong evidence that in most pelts the cuticular scale pattern could play a significant part in absorption of thermal radiation.

The ranges covered by the features already referred to are illustrated in Fig. 15, where they have been superimposed on the energy curve for 37°C radiation, extracted from the earlier Fig. 14. There is no clear relationship with the required range of dimensions, shown as a hatched band at the base of the radiation curve.

An examination of the internal structure of the hair, however, shows much greater uniformity of dimensions. In whole mounts of the hairs of many mammals the medulla is seen by transmitted light to have regularly spaced dark interruptions, caused by internal reflection of the light at the upper surface of air cavities. These are better demonstrated in longitudinal sections. Examples of such medullary patterns, which are spaced with relative precision, are shown in Plate No. 15.

The exact pattern of the medulla differs between species, and has been used by Brunner and Coman (1974) as one of their aids to hair identification. The one feature which differs...
Figure 15. Comparison of hair dimensions with thermal radiation wavelengths. The hatched band indicates the required range of dimensions.
Plate 15. Thin longitudinal section of hair of the domestic cat showing medullary spacings. X900.
species, however, is the distance between air cavities. To demonstrate this I take as an example my measurements on the series of very clear whole mount photomicrographs published in the above work by Brunner and Coman. They illustrate the hairs of 75 mammals, of which 48 have hairs with medullae in which the air cavities can be sufficiently well seen for measurement.

There are 140 photographs of such hairs, in which it was possible to measure the average distance between cavities to within 0.1 \( \mu \text{m} \). The histogram in Fig. 16 shows the result. The mean spacing is 9.7 \( \mu \text{m} \), with a standard deviation \( \pm 1.59 \) \( \mu \text{m} \) and a 95 per cent confidence interval between 9.44 and 9.96 \( \mu \text{m} \) (corresponding to peak wavelengths for temperatures between 18\(^\circ\)C and 34\(^\circ\)C). Note particularly that 80 per cent of the spacings lie within the predicted range 8 to 12 \( \mu \text{m} \).

This analysis has several defects. Thus certain of the species were represented by more whole mount photographs than others. Other species, in which the medullary spacing was not discernable, were excluded. Moreover only a relatively small number (17) of fluff hair photographs were available for measurement. Nevertheless it is clearly indicated that for a wide variety of mammals the medullary cavities, if present, are spaced at uniform intervals within a narrow range corresponding to the peak wavelengths in ambient thermal radiation.

Another finding is that within the pelt of any one of these mammals there are hairs with different medullary spacings spread over the same range. Thus to take as examples three species in which several different hair photographs from each were available for measurement, we have the following spacings (in \( \mu \text{m} \)):
Figure 16. Distribution of medullary spaces.
Eastern pygmy possum: 7.0 7.0 8.1 8.2 9.2 10.0
Greater glider: 7.0 8.0 9.0 9.0 10.2 10.5
Common marsupial mouse: 7.5 8.0 9.0 11.0 11.0

Without a great many more measurements on hair samples from a single pelt it is not possible to say whether the distribution of spacings bears any relation to the radiation curve. It does however seem a reasonable supposition that fur is "black" to thermal radiation because the medullae constitute absorbers which are tuned to wavelengths with overlapping bands within this range.

This notion is consistent with at least some of the measurements which have been made of the transmission of long wave radiation through fur. If the absorption is independent of wavelength, the energy transmitted will decrease logarithmically with penetration, so that a graph in which the logarithm of the fraction transmitted is plotted against depth of penetration will be a straight line. On the other hand, if the absorption depends on wavelength the graph will be a curve.

Measurements by Cena and Monteith (1975) on nine different coats show evidence of this selective absorption. Their measurements were made for the purpose of comparison with a calculated straight line representing their "interception function" based only on the dimensions and numbers of hairs in the coat. It seems likely however that their observations could be matched better by calculations based on selective absorption, for example, in the medulla. See addendum, page 187.

Thus using a typical energy curve for radiation such as the one shown in Fig. 15, and assuming that the distribution of medullary spacings within the fur is similar to the distribution shown in Fig. 16, then it is possible to derive a transmission curve which fits the measurements reasonably
well, as for the sheep used for the data in Fig. 17. The closeness of the fit should not however be taken as strong evidence of selective absorption in the medulla, for it rests at present on untested assumptions.

It can be expected that not only the medullary spacing, but the air cavities themselves, will be implicated in the exchange of radiation. However the size and shape of the cavities cannot readily be seen in a whole mount, whether or not the trapped air has been replaced with a liquid of suitable refractive index. The information must be looked for in cross-sections.

Any transverse cross-section greater than about 10 μm thick will also show the medulla as a black area due to reflection of the substage light, as can be seen in all such photographs in the atlas. For interpretation of shape of the cavities the section must be very thin, and preferably cut longitudinally at a small angle to the axis of the hair so that it intercepts each successive cavity at a different depth. Examples of sections prepared in this way are shown in Plate No. 15.

The cavities are seen to be separated by partitions formed from closely packed granules* of diameter less than 1 μm. These walls between the cavities are thin, possibly no more than 2 μm, but are broader where they join the cortex, frequently giving the cavities the form of a flattened sphere. The granular walls may be very strongly cohesive, for medullary "cells" separated from rabbit hairs by Matoltsy (1953) remained virtually intact after vigorous chemical and mechanical treatment.

The axial length of the cavities is determined by the spacing between them, and the thickness of the separating walls. In a typical

* Although it is unlikely that they are formed entirely by these granules (Lyne pers. comm.).
Figure 17. Transmission of radiation through coat of Clun Forrest sheep.
hair with medullary spacing of 9 \( \mu m \), the length of the cavity is about 7 \( \mu m \). The diameter of the cavities is determined by the inner diameter of the cortex, the number of parallel strings of cavities contained within it, and the thickness of the separating walls. In whole mounts of hairs, which have clearly distinguishable medullary cavities, the diameter of the cavities can be seen to increase as the diameter of the hair, or the inner diameter of the cortex, increases, but only up to a certain limit. Beyond this limit a single row of cavities gives way to a double row, or double to triple, and so on. The transition commonly takes place over a relatively short length of the hair, as can be seen clearly in the rabbit hair photographed in Plate Nos. 16 and 17.

In the microscopic view of a whole mount, two or more cavities placed side by side across the medulla are likely to overlap partially, and it is not possible to obtain a precise measure of their diameters or of the wall thickness between them. The diameter of the cavity can however be estimated by measuring the inside diameter of the cortex, dividing by the number of cavities which span this distance, and subtracting the estimated wall thickness associated with each. In Table II, I give the measurements made on a single guard hair of Otomys unisulcatus - where the number of cavities spanning the medulla ranged from one near the tip and at the root to at least six in the widest part of the shield region.

From Table II it can be seen that in the case of this mammal there appears to be a constraint on the growth of the cavities which limits their diameter to a range between 5 \( \mu m \) and 12,5 \( \mu m \). This range is consistent with the dimensions of a cavity which would resonate to thermal radiation. For example a cylindrical cavity resonates to radiation of a wavelength \( \lambda \) when it has a diameter 0,77 \( \lambda \). Thus a wavelength of 9,3 \( \mu m \), corresponding to the peak energy of thermal radiation from a surface at
Plates 16, 17 and 18. Whole mounts of rabbit hair showing consistency in size of medullary cavities along hair length.
Table II: Diameters of medullary cavities of *Otomya uniautacae*

<table>
<thead>
<tr>
<th>Width of medulla at transition (μm)</th>
<th>Number of cavities across medulla</th>
<th>Estimated diameter of each cavity (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
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<tr>
<td>12.5</td>
<td>1</td>
<td>12.5</td>
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<tr>
<td>12.5</td>
<td>2</td>
<td>5.25</td>
</tr>
<tr>
<td>25.0</td>
<td>2</td>
<td>11.5</td>
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<tr>
<td>25.0</td>
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</tr>
<tr>
<td>35.0</td>
<td>3</td>
<td>10.3</td>
</tr>
<tr>
<td>35.0</td>
<td>4</td>
<td>7.25</td>
</tr>
<tr>
<td>47.0</td>
<td>4</td>
<td>10.25</td>
</tr>
<tr>
<td>47.0</td>
<td>5</td>
<td>7.8</td>
</tr>
<tr>
<td>60.0</td>
<td>5</td>
<td>10.4</td>
</tr>
<tr>
<td>60.0</td>
<td>6</td>
<td>8.3</td>
</tr>
</tbody>
</table>
37°C, would require a cavity with diameter approximately 7 μm.

The present literature relating to heat transfer in animal coats appears to contain only one direct reference to the possible interaction of the medulla with longwave radiation. On the basis of his measurements on various live cattle coats throughout a cycle of seasons in Queensland, Dowling (1959) cited the "degree of medullation" of the hair as the one factor which had a close correlation with heat tolerance.

The foregoing describes the early stage of a research investigation with hypothesis and initial measurements only. It is included to support the thesis that the microscopic study of hair has ecological relevance and implications.
CONCLUSION

Many workers who have studied the part played by hair in relation to the environment have taken the gross structure of the fur into account. Particular attention has been paid to its contribution to thermoregulation, and the way in which it provides the mammal with mechanical or visual protection. In contrast, the emphasis of the studies described in the foregoing thesis has been on the microstructure of single hairs, with results which supplement or explain observations made on the entire pelt.

An important example is the exchange of radiant energy between the mammal and its surroundings. Whereas investigations of colouration and other outward features of the pelt, which have significance in the visible region of the spectrum, may not gain much from the study of individual hairs, the reverse is true in the far infra-red. The microstructure of the medulla is such that it warrants consideration as a means by which thermal radiation is absorbed and emitted. Other examples are given by the mechanical and surface properties of individual hairs, which differ greatly and show clear means of adaptation. In many cases comparison and discrimination between these features provide a practical basis for identification, with uses in several fields.

Thorough investigation of individual hairs calls for patient application of techniques, some of which have been developed during the course of this work. Some of these techniques have been previously applied to surveys of hair characters of a few groups of southern African mammals, notably some of the bovids and the murids. They have now been applied in a comprehensive survey of carnivore hair from this region, which had not previously been studied. The thirty-six species show considerable diversity in their distribution, habitat and habits, yet
using the criterion of hair morphology, there is a considerable degree of interspecies overlap, with the exception of the otters. As taxonomic criteria, however, and as a tool for identification, microscopic evidence should be supported by other relevant data such as colouration and locality. For this purpose micrographs of the hairs have been combined with a full description of each species. The resulting atlas will serve for identification of carnivore hair from southern Africa and for reference by those who are studying the relevance of microscopic features. A key has been constructed to assist in the use of this photographic reference system.

The protective role of the pelage has often been stressed. This emphasis can however obscure the fact that hair is equally the principal link between a mammal and its environment: it is the interface at which mechanical or radiation influences are received, so that in the sense in which the word is used by engineers, it serves to couple the animal to its environment. Study of the fine structure of hair leads to the conclusion that the microstructure of hair plays an important part in the efficiency of this coupling.
SUMMARY

This thesis is a study of the microstructure of hair of southern African mammals, in particular of the Carnivora. It serves to fill a gap in knowledge of hair studies from this region, and points to the use of these studies in various fields.

A major portion of the work is a hair atlas of southern African Carnivora, in which micrographs and coloured plates of hairs are presented with locality data and a descriptive text for each species. Although the findings of the atlas do not lend themselves to the formation of dichotomous key, it serves as a reference system and has proved useful in the identification of hairs from selected study areas where species distribution is defined. This is intended to form part of a comprehensive atlas which will include examples of all southern African mammal species.

Techniques for studying hair structure are discussed and the micrographs of both thin and thick cross-sections are included to demonstrate the results of different methods used.

The taxonomic importance of hair identification is well known and examples of this are discussed, mainly in regard to the smaller mammals, such as the Muridae. The extent to which hair morphology can be used as a taxonomic criterion varies with various groups however, but more often than not, by using a combination of parameters it is possible to differentiate many species.

The identification of unknown hair samples has been discussed, with special reference to the highly practical field of epidemiology. Examples of both laboratory investigations, as well as field surveillance,
in which hair identification is used have been cited as an important aspect of hair studies.

The extent to which hair is related to ecology forms a broad field of study, and for this reason those situations where ecologically selective pressures are more clearly defined have been chosen for particular mention. Thus the aquatic habitat and the desert environment are discussed with reference to the hair types such as guard hairs, underfur, and the microstructure of hair as well as its mechanical and surface properties. Thermoregulation is referred to and arising out of this aspect a hypothesis is presented in which the part played by the medulla in the absorption of longwave infrared radiation is discussed.
Hierdie proefskrif handel oor 'n studie van die mikrostruktuur van die hare van soogdiere van suidelike Afrika en in besonder die van karnivore. Dit vul 'n leemte aan in ons kennis oor haarstudies in hierdie gebied en dui op die gebruik van hierdie studies op verskillende terreine.

'N Groot deel van die werkstuk word beslaan deur 'n haaratlas van die karnivore van suidelike Afrika waarin mikrofotos en kleurplate van hare tesame met lokaliteitsdata en beskrywende teks vir elke spesie aangebied word. Alhoewel die bevindinge aangebied in die atlas hulle nie leen tot die opstelling van 'n tweedelige identifikasiesleutel nie, dien die atlas wel as 'n nuttige hulpmiddel vir die identifikasie van hare in sekere areas waar spesieverspreiding bekend is. Hierdie resultate sal uiteindelik deel uitmaak van 'n omvattende atlas oor die hare van soogdierspesies in suidelike Afrika.

Tegnieke vir die studie van haarstruktuur word bespreek en mikrofotos van beide dun en dik dwarsnitte word ingesluit om die resultate wat met die verskillende metodes verkry is, te demonstrer.

Die taksonomiese belang van haaridentifikasie is welbekend en voorbeeldle hiervan word bespreek, veral wat die kleiner soogdier betref soos die Muridae. Die mate waartoe haarmorfologie as taksonomiese maatstaf gebruik kan word, varieer egter in die verskillende groepe maar gewoonlik, deur die gebruik van verskillende parameters, is dit moontlik om tussen baie spesies te onderskei.

Identifikasie van haarmonsters van onbekende oorsprong word bespreek met spesiale verwysing na die hoogs praktiese veld van epidemiologie. Voorbeeldle van laboratoriumondersoeke sowel as veldopnames
waar haaridentifikasie gebruik is, word aangehaal as 'n belangrike faset van haarstudies.

Die verband tussen hare en ekologie behels 'n breë studieveld en om dié rede is toestande waar ekologiese selektiewe druk meer duidelik gedefineer is spesiaal vermeld. Die akwatische habitat en woestynomgewing word dus bespreek met verwysing na haartipes soos beskermhare, onderpels en die mikrostruktuur van hare sowel as die mekaniese en oppervlakte-eienskappe van hare. Daar word natermoregulering verwys en voortspruitend daaruit word 'n hipotese voorgestel waarin die bydrae van die medulla in die absorpsie van lang infra-rooi-radiasie bespreek word.
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APPENDIX

Some tests on textile properties of wild animal fibres

The results of tests carried out at the South African Wool and Textile Research Institute have been included, although after careful analysis they appear inconclusive.

The techniques used are outlined in the Material and Methods section of this work. Samples were selected from species which exhibited different hair shapes, and differences in the relative size of the cortex to the medulla, as well as exhibiting examples of various scale patterns.

Fibre breaking strength, fibre tenacity and breaking extension of hairs from thirteen species of Carnivores were tested.

The results are listed in Table III.

There appears to be no relation between these physical properties and the size and shape of the hairs submitted. The relatively large cortex found in the hair of *Hyaena brunnea* may be a contributory factor to the high breaking strength and breaking extension of hairs of this species, as shown in Table III. Other parameters used for analysis all produced inconclusive results. The Table however is included in support of this, and for possible future interest to other workers.

Critical surface tension

The methods for this test are outlined in the Material and Methods section, and the results are referred to in the Discussion. Table IV is included to demonstrate that the tests used produced results showing
Table III. Textile properties of guard hairs of thirteen species of Carnivores

<table>
<thead>
<tr>
<th>Species</th>
<th>FIBRE BREAKING STRENGTH (cN)</th>
<th>CV(%)</th>
<th>FIBRE TENACITY (cN/tex)</th>
<th>CV(%)</th>
<th>INITIAL MODULUS (cN/tex)</th>
<th>CV(%)</th>
<th>BREAKING EXTENSION (%)</th>
<th>CV(%)</th>
<th>DIAMETER OF FIBRE (μm)</th>
<th>DIAMETER OF MEDULLA (μm)</th>
<th>NO. OF FIBRES TESTED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proteles cristatus</td>
<td>65,1</td>
<td>35,5</td>
<td>6,87</td>
<td>66,7</td>
<td>81</td>
<td>54,6</td>
<td>33,9</td>
<td>28,3</td>
<td>167</td>
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<td>10</td>
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<tr>
<td>Hyaena brunnea</td>
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<td>39,3</td>
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<td>54,7</td>
<td>19,9</td>
<td>132</td>
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<td>10</td>
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<td>7,8</td>
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<td>9,2</td>
<td>62</td>
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</tr>
<tr>
<td>Lutra maclellis*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Viverra civetta</td>
<td>38,5</td>
<td>26,0</td>
<td>6,05</td>
<td>47,0</td>
<td>79</td>
<td>49,1</td>
<td>43,4</td>
<td>11,2</td>
<td>135</td>
<td>107</td>
<td>10</td>
</tr>
<tr>
<td>Paraconyctis selousi</td>
<td>46,9</td>
<td>24,1</td>
<td>8,38</td>
<td>46,1</td>
<td>132</td>
<td>39,2</td>
<td>37,4</td>
<td>15,7</td>
<td>105</td>
<td>89</td>
<td>10</td>
</tr>
<tr>
<td>Attilax paludinosus</td>
<td>134,9</td>
<td>17,9</td>
<td>23,4</td>
<td>39,1</td>
<td>267</td>
<td>36,2</td>
<td>44,8</td>
<td>13,5</td>
<td>111</td>
<td>79</td>
<td>10</td>
</tr>
</tbody>
</table>

Gauge length: 10 mm
Rate of extension: 10/min
Time of break: 25s
Pretension: 1% of breaking strength

*Fibres too short
very little difference in the critical surface tension of the hairs investigated, although there appears to be a large range in critical surface tension values. Variations in hair diameter within and between hairs from a particular species could account for this. The critical surface tension is generally dependent upon the solvent in which it is measured. In this particular case only non-polar solvents were used. Some preliminary tests on fibres, probably located closer to the skin of the animal, had a lower critical surface tension than the coarser fibres which had probably had a greater exposure to weathering. For wool it is known that the critical surface tension near the fibre tips is slightly higher than that measured near to the fibre root.
### Table IV. Critical surface tension of guard hairs from thirteen species of Carnivores

<table>
<thead>
<tr>
<th>Sample</th>
<th>Critical Surface Tension</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lutra maculicollis</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Aonyx capensis</em></td>
<td>25-36</td>
</tr>
<tr>
<td><em>Atilax paludinosis</em></td>
<td>24-33</td>
</tr>
<tr>
<td><em>Crocuta crocuta</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Hyaena brunnea</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Proteles cristatus</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Canis mesomelas</em></td>
<td>25-36</td>
</tr>
<tr>
<td><em>Vulpes chama</em></td>
<td>28-33</td>
</tr>
<tr>
<td><em>Paracynictis selousi</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Viverra civetta</em></td>
<td>24-33</td>
</tr>
<tr>
<td><em>Acinonyx jubatus</em></td>
<td>28-36</td>
</tr>
<tr>
<td><em>Felis lybica</em></td>
<td>25-36</td>
</tr>
<tr>
<td><em>Lycaon pictus</em></td>
<td>28-36</td>
</tr>
</tbody>
</table>
The statement on page 157 that when transmission (or absorption) depends on wave-length, the energy transmitted can be represented graphically as a function of penetration by a curved line, can most easily be seen by taking the example of radiation consisting of two approximately equal components which are absorbed at a different extent. The curve drawn on the co-ordinates shown in Fig. 17 (page 159) will always have a slope which becomes less negative with penetration, i.e. the curve will be convex downwards. All furs reported by Cena and Monteith in the paper under reference show this trend. In no cases are the points representing their measurements a satisfactory fit to a straight line. Those on the Clun Forest sheep appear to lie on a well defined curve which is a clear departure from a straight line. This has been chosen by way of example only for comparison with the results of a calculation based on the assumption that the incident radiation on a coat has a wavelength distribution \( F_1(\lambda) \) and that the properties of the coat are such that the absorption of radiation is a function of wavelength \( F_2(\lambda) \).

Whilst the distribution of energy in the incident radiation can be assumed with reasonable confidence to follow some such curve as indicated in Fig. 15 (page 153) (that is, the customary distribution curve for a full radiator) there is at present no evidence as to the way in which absorption depends on wavelength. There is, in fact, great difficulty in making such measurements in the range of long wavelengths with which we are particularly
concerned here. It is therefore necessary to make an assumption as to the wavelength dependence of absorption.

The assumption made here for reasons which will have become obvious on reading the relevant portions of this work, is that longwave radiation is trapped and therefore abstracted as heat from the incident beam by the structure of the hair, and in particular the medullary cavities of some other repetitive pattern such as cuticular scales on the hair. [In the case of wool hairs on the sheep the spacing of the cuticular scales is regular and spreads over a relatively small range similar to that covered by the medullary spacings of the hairs of many mammals.] There is only scant data on the frequency distribution of medullary spacings, and this is related to a survey of many different mammals. A few examples of hairs from a single animal serves to show that medullary spacings vary to some degree within the coat. It can be assumed that if radiation absorption by single hairs depends on wavelength in some such manner then the passage of radiation through a coat will be selective and the quality of the radiation will be altered.

For the purpose of comparison with the measurements by Cena and Monteith (1975) of the Clun Forest sheep, the coarse assumption was made that radiation within a narrow band of wavelengths 10 m wide is totally absorbed by a hair standing in its way and which has a medulla (or other structural spacing within the same wave-band). The frequency distribution of medullary spacing illustrated in Fig. 16 (page 156) was used for this purpose. A combination of energy distribution in the radiation and frequency distribution of the absorbing elements in the fur permits the construction of a
curve showing the way in which the energy of the total radiation beam decreases with the depth of penetration. The distribution of energy bands in the incident radiation gives the starting points of the components of the radiation transmission curves, each of which will be a straight line equivalent to that representing the interception function which would be calculated by Cena and Monteith (1975) using monochromatic radiation. The population density of the relevant absorbing element in the fur dictates the slope of the line representing the decrease in energy transmitted with penetration. The total beam decreases in energy with penetration in accordance with a curve which is obtained by the summation of the numerous straight lines. There is no formula which can readily be derived to describe this curve, which is derived graphically. The shape of the curve is affected by the total population density of the hairs (just as the slope of the single straight line used by Cena and Monteith (1975) is dependant on the density of hairs in the coat). The density of the notional coat represented by the curve in Fig. 17 (page 159) has been chosen in order to demonstrate the strong possibility that absorption in fur is selective, rather than independent of wavelength.

There is no formula which fits this curve because although energy distribution in the incident radiation $F_f(\lambda)$ may approximate to Planck's radiation law, there is no such formula which can at present be expected to fit the frequency distribution of hair structural patterns in fur, and $F_2$ must be based upon the best available data.