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*.

Analysis of vulture pellets using hair samples to determine possible differences in the collecting habits of five species of vulture (Aves : Accipitridae): *Gyps copthrotheras* (Forster 1978) Cape vulture (ranching and wilderness areas in South Africa), *Gyps africanus* Salvadori 1865, white-backed vulture, *Torqos tracheliotus* (Forster 1971), lappet faced vulture, *Trigonoceps occipitalis* (Burchell 1824), white headed vulture, *Nectosyrtes morachus* (Temminck 1823), hooded vulture.

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 Soricicinae.

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-

   sectional 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 .... *Otocyon 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 .... *Hyaenna brunnea*

Crocuta crocuta

Lycaon pictus

Canis mesomelas

Mellivora capensis

(The Hyaenas and wild-dog have larger hairs in cross-section and

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*
   Poecilogate albinucha
   Mellivora capensis

   (*Mellivora capensis* distinguished by large cortex. *I. striatus*

   and *P. albinucha* differentiated by typical hair lengths).

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

9. Cuticular scale pattern waved mosaic cross-

   sectional shape varied:- dumbells, 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 dis-
    tinctive 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

Rhynchogale 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 ppposite 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

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
excresences 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
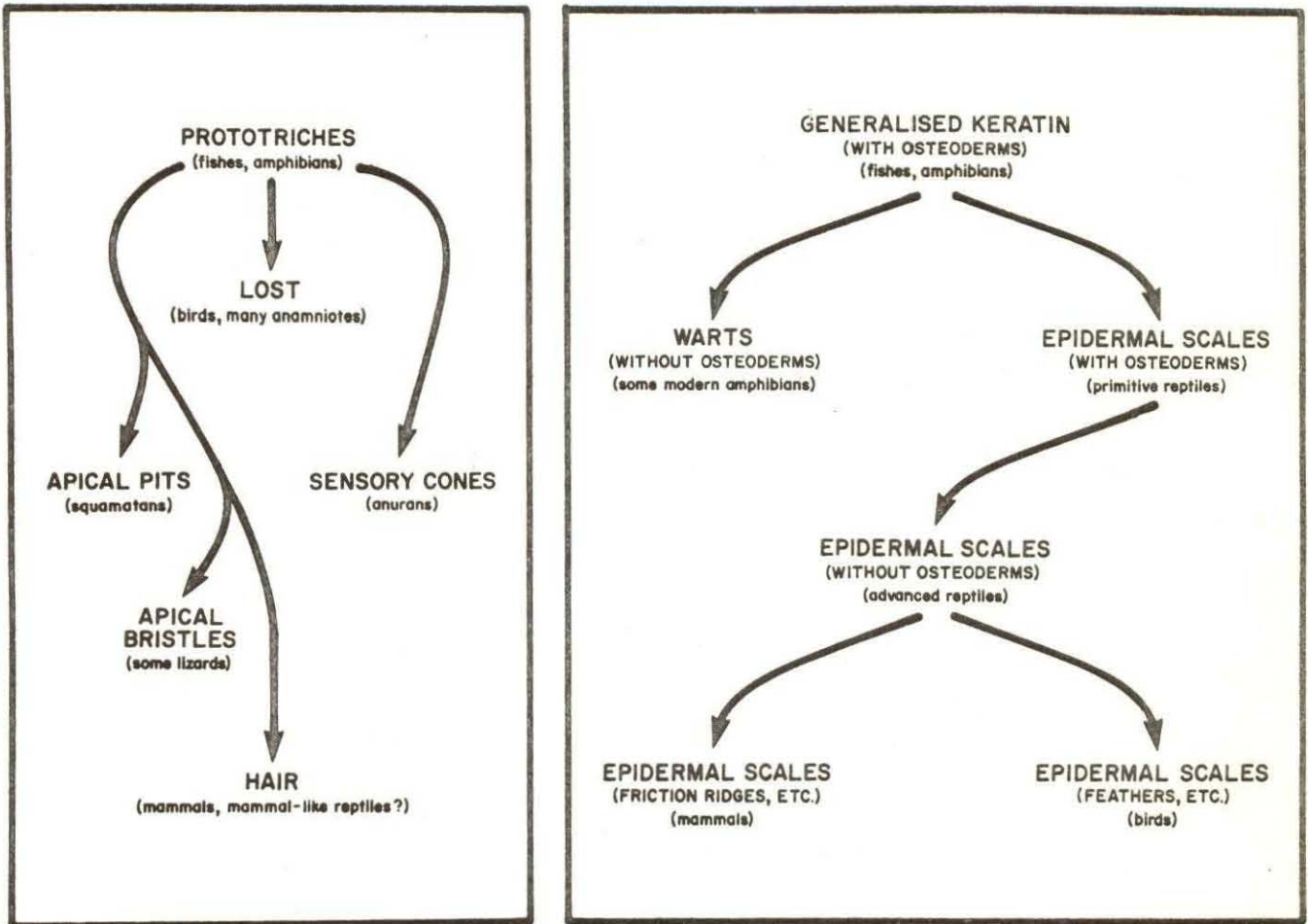metabolic rate. The second enabled them to invade a diurnal niche and

PROTOTRICHES
(fishes, amphibians)

LOST
(birds, many anamniotes)

APICAL PITS
(squamatans)

SENSORY CONES
(anurans)

APICAL BRISTLES
(some lizards)

HAIR
(mammals, mammal-like reptiles?)

GENERALISED KERATIN
(WITH OSTEODERMS)
(fishes, amphibians)

WARTS
(WITHOUT OSTEODERMS)
(some modern amphibians)

EPIDERMAL SCALES
(WITH OSTEODERMS)
(primitive reptiles)

EPIDERMAL SCALES
(WITHOUT OSTEODERMS)
(advanced reptiles)

EPIDERMAL SCALES
(FRICTION RIDGES, ETC.)
(mammals)

EPIDERMAL SCALES
(FEATHERS, ETC.)
(birds)

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
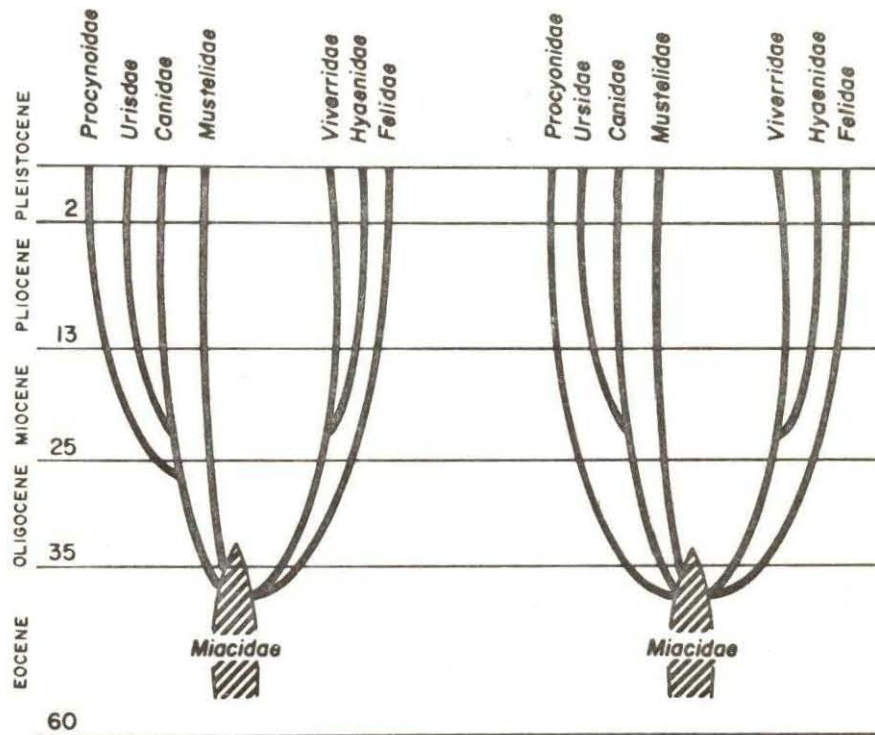
Figure 8.   Two possible interpretations of the families of Carnivores.
(a)   The Procyonidae arising as an offshoot from the Canidae or
(b)   originating independently from the Niacidae.
Figures on the left are millions of years ago.   From Ewer
(1974).

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 bouyancy 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 ($\pm 30^{\circ}$) 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
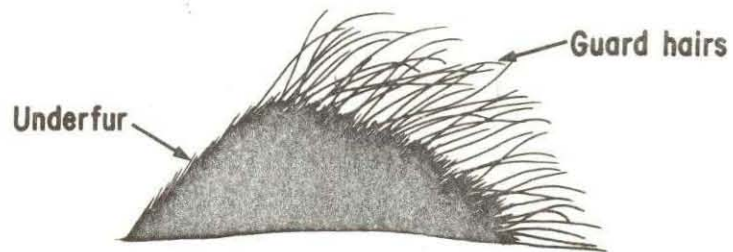
Figure 9.   Guard hairs and underfur of *Lutra maculicollis.*

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
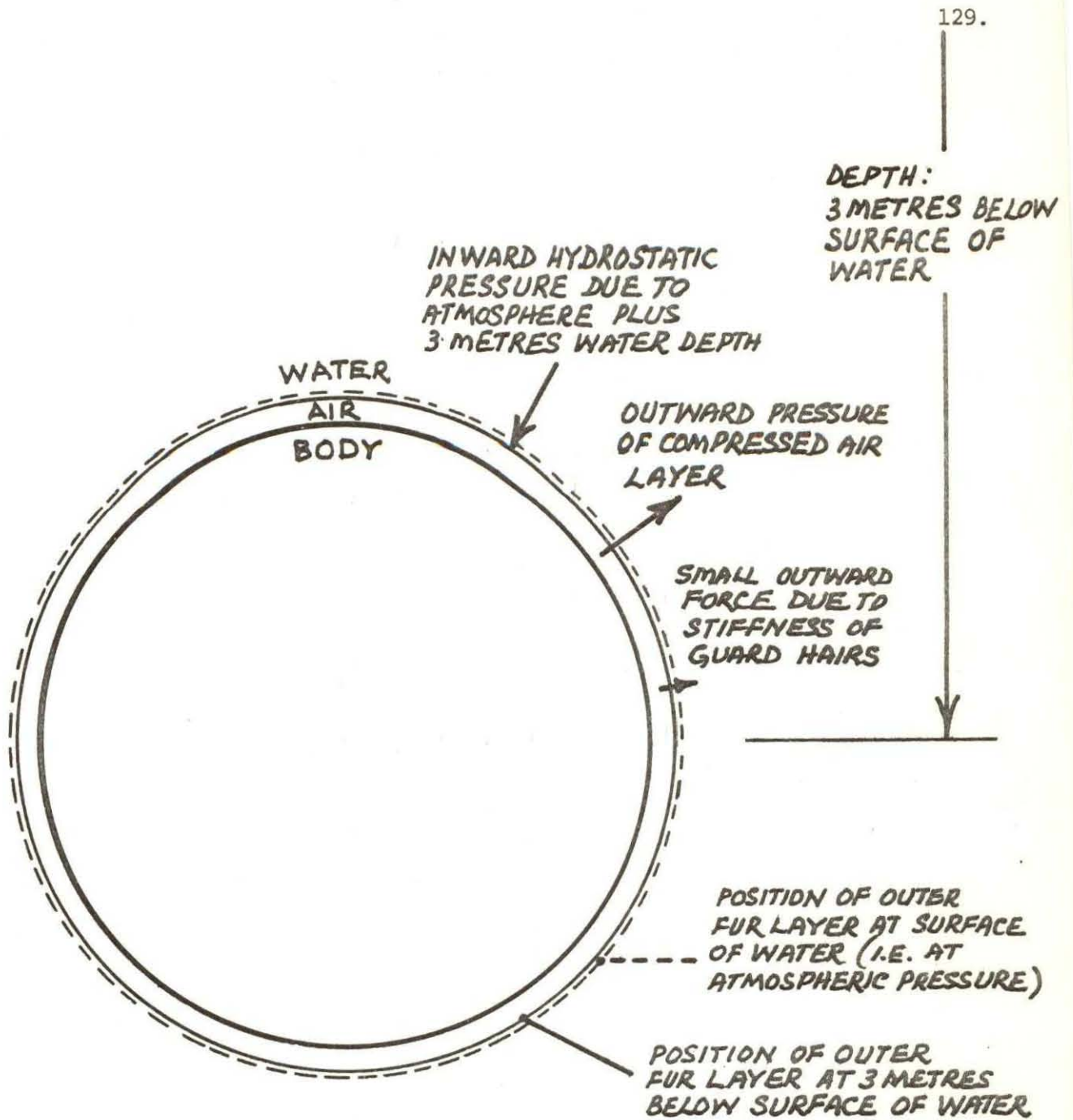
DEPTH:
3 METRES BELOW
SURFACE OF
WATER

INWARD HYDROSTATIC
PRESSURE DUE TO
ATMOSPHERE PLUS
3 METRES WATER DEPTH

OUTWARD PRESSURE
OF COMPRESSED AIR
LAYER

WATER
AIR
BODY

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

Figure 10.   Diagrammatic representation of pelt of *Lutra maculicollis*.

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 irroratus* and *O. angoniensis* and *Dasymys incomtus*. 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. maculicollis*, 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

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 μm) and the longwave region (wavelength greater than 2-3 μm). 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

8

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.

9

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.
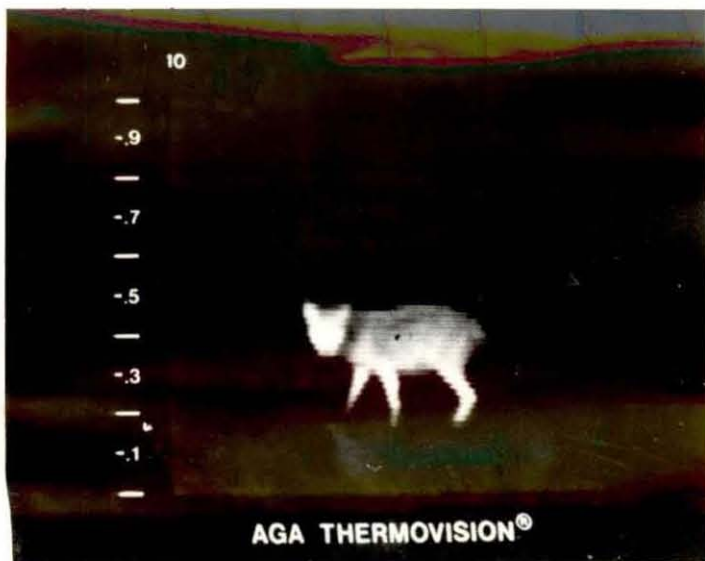
11

12

13

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.
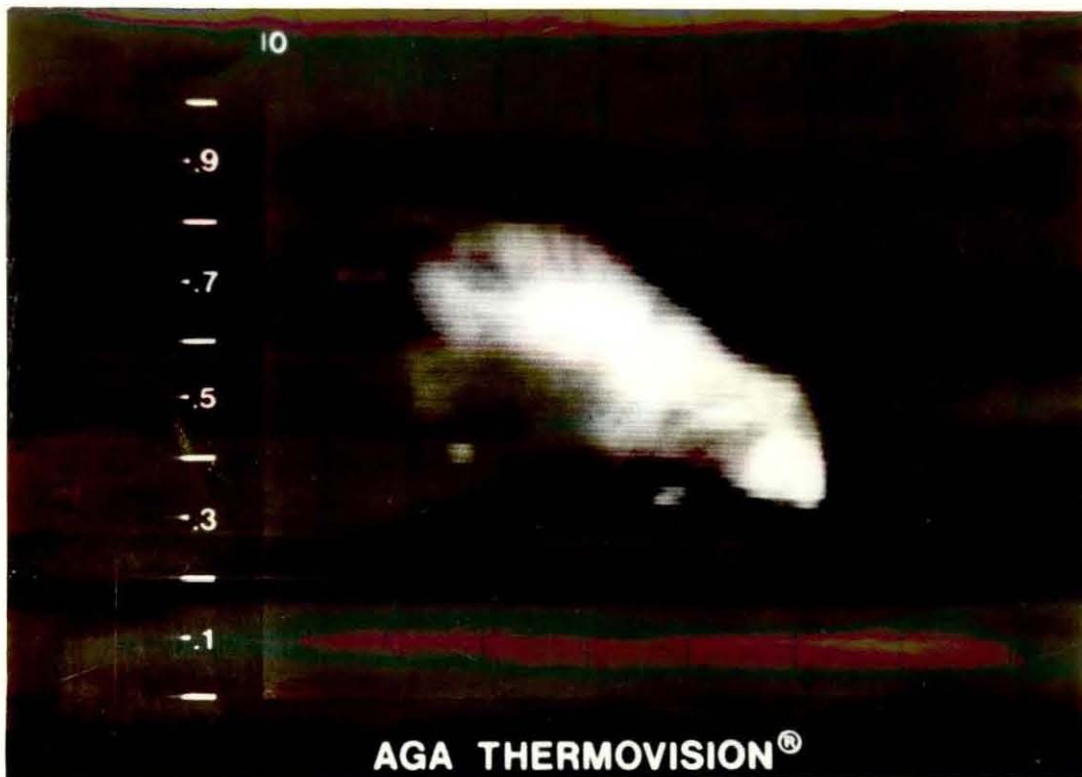
Plate 14.   Thermogram of a striped pole-cat in sunshine.
            The pattern reveals a differential solar heat
            gain which is not wholly associated with the
            visible pattern of the coat. Variations in
            thickness of coat cause differences in local
            energy 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, *Gerbillarus 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

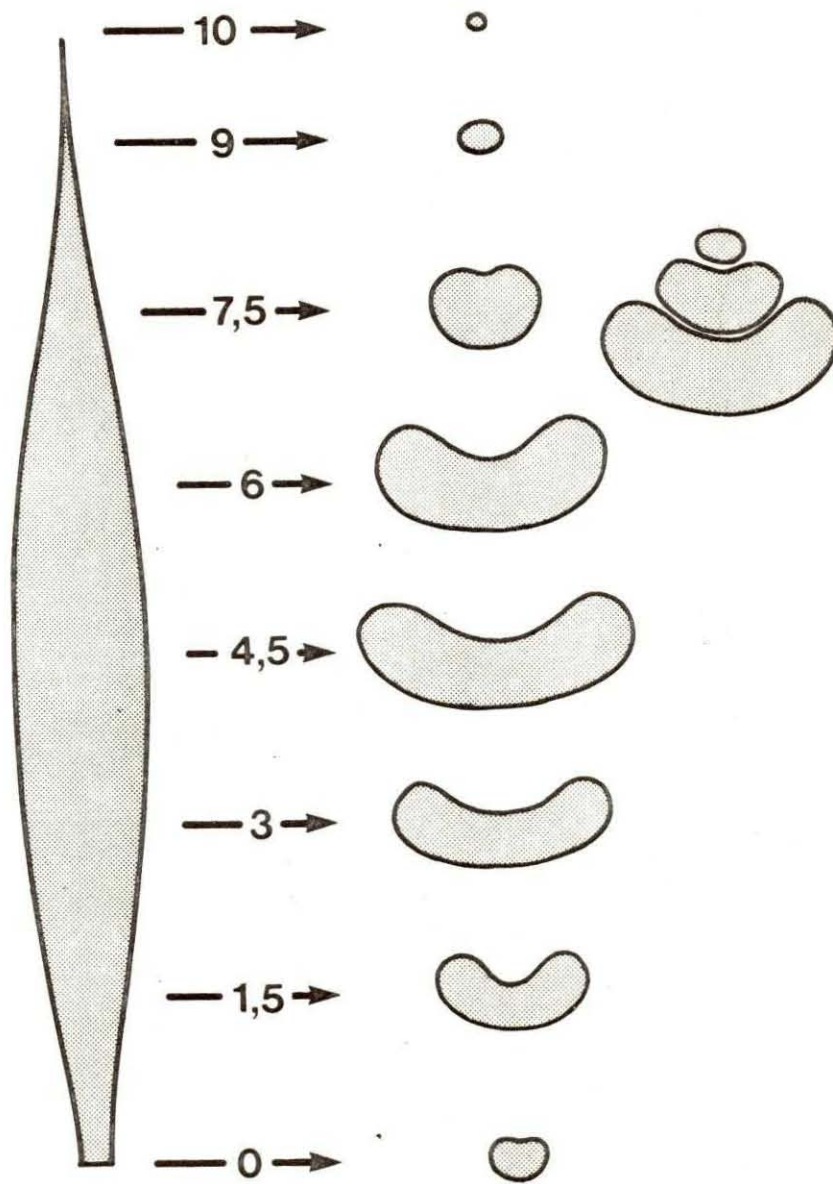found in some species of American desert rodents that the guard hairs

Figure 11. Cross-section at defined points along the guard hair of *Rhabdomys 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.

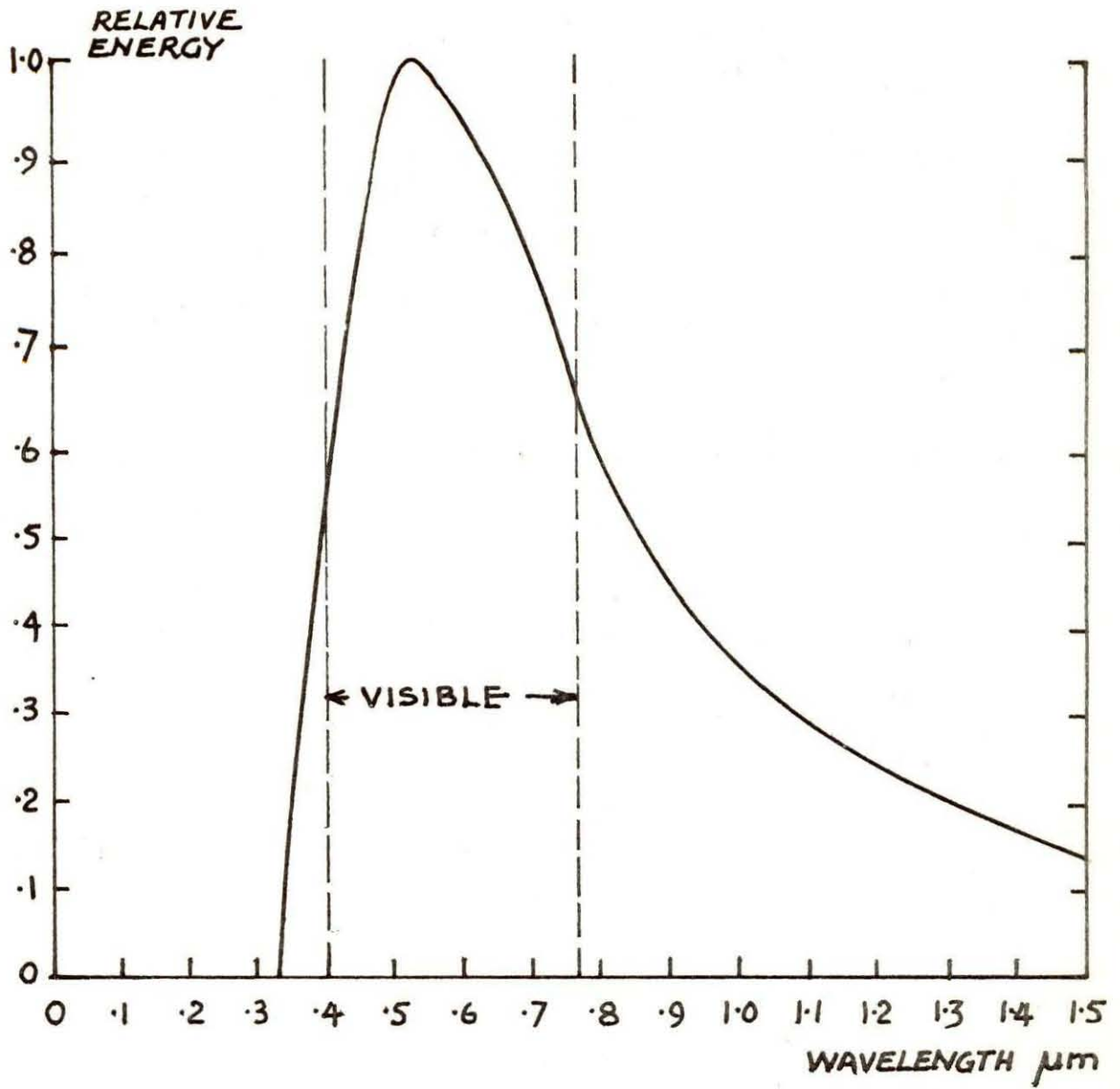The absorption of sunlight in animal coats of different colours

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

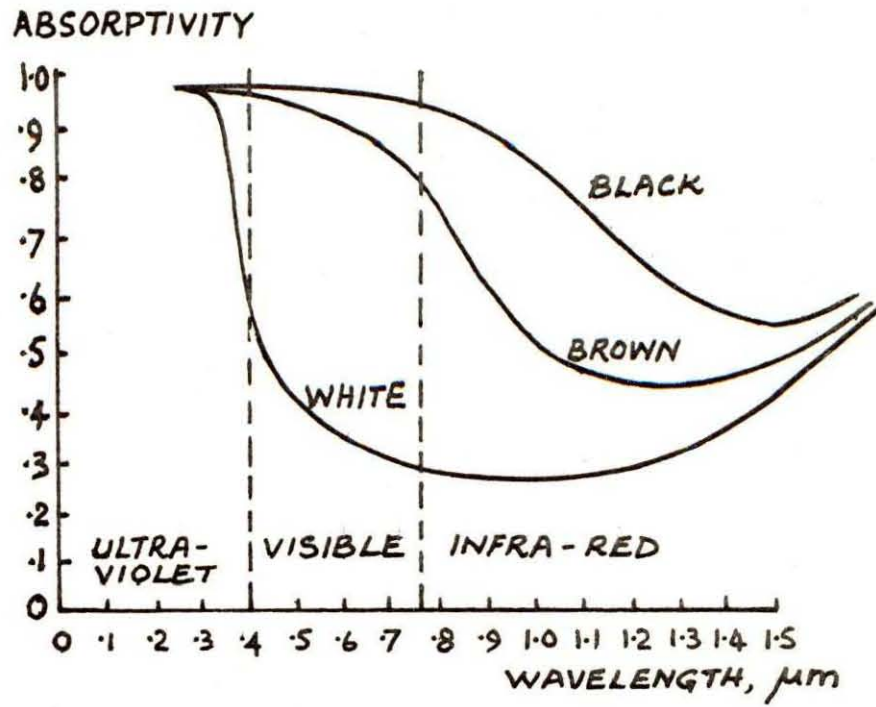region of the solar spectrum is of no great importance, because it

Figure 13. Absorbtivity 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 $(0^{\circ}C)$ and at typical body temperature $(37^{\circ}C)$ 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
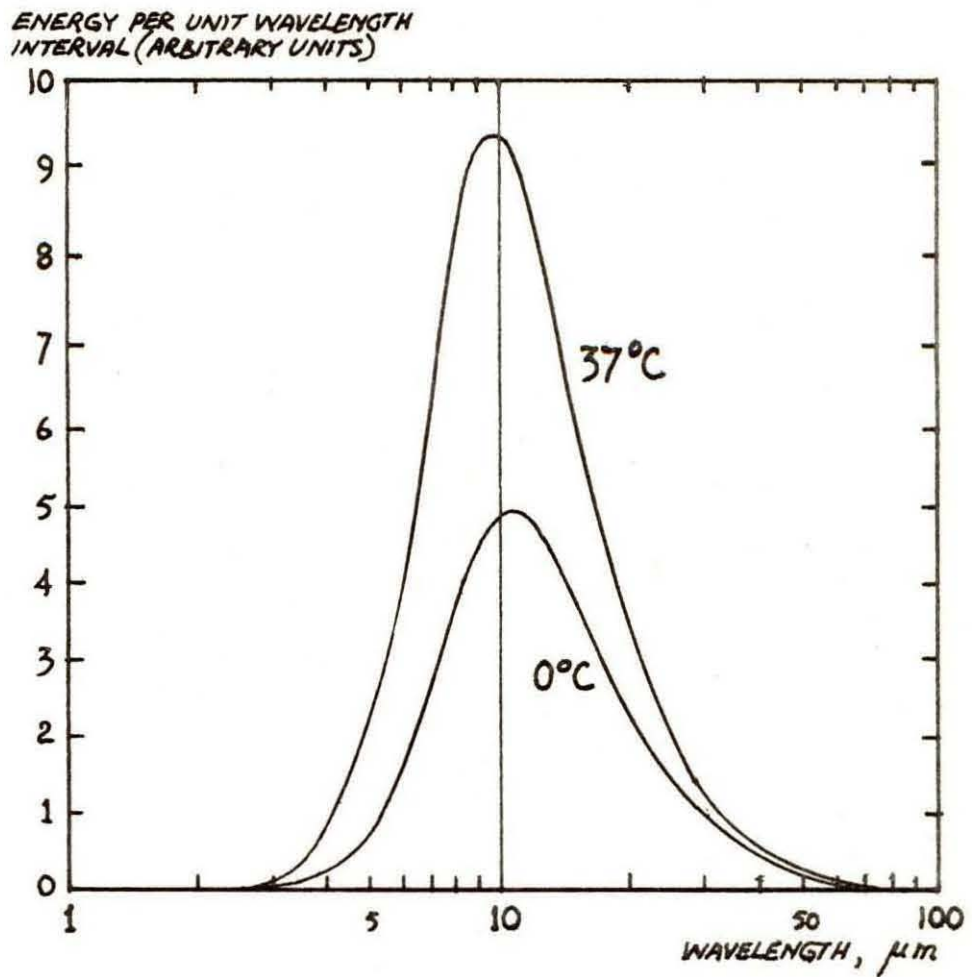
Figure 14. Thermal radiation emission.

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 betweeen 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 cm^2, whereas the densities quoted for certain mammals (Cena and Monteith 1975) range from about 100 per cm^2 (goat) to about 4000 per cm^2 (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

Table I: Wavelength of maximum energy radiation
as a function of temperature

Temperature, °C	Wavelength of maximum energy, μm
-30	11,92
-20	11,45
-10	11,02
0	10,61
10	10,24
20	9,89
30	9,56
40	9,26
50	8,97
60	8,70
70	8,45
80	8,21

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

RELATIVE ENERGY AT 37℃

SCALE SIZES

HAIR DIAMETERS

HAIR SEPARATIONS

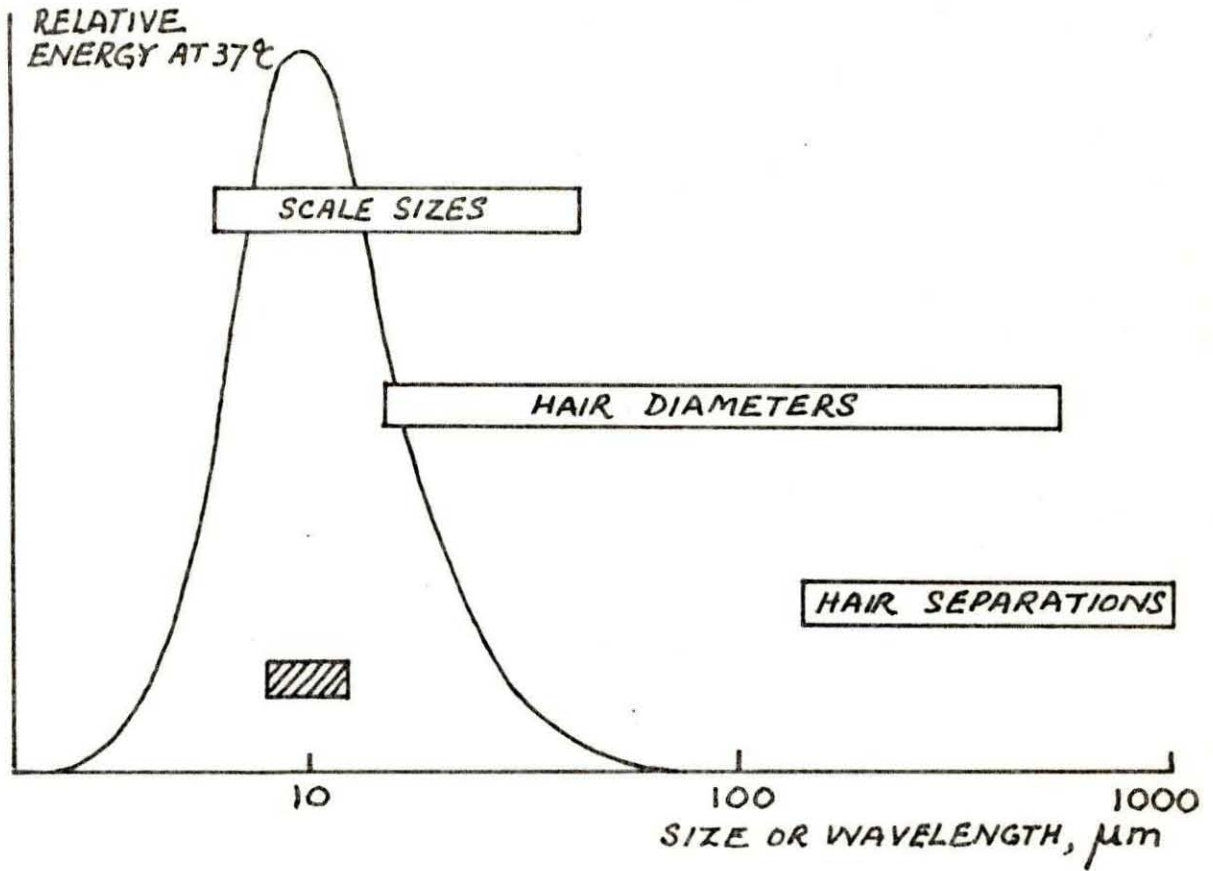10   100   1000

SIZE OR WAVELENGTH, μm

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 μm. The histogram in Fig. 16 shows the result. The mean spacing is 9,7 μm, with a standard deviation ± 1,59 μm and a 95 per cent confidence interval between 9,44 and 9,96 μm (corresponding to peak wavelengths for temperatures between 18°C and 34°C). Note particularly that 80 per cent of the spacings lie within the predicted range 8 to 12 μm.

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 μm):-

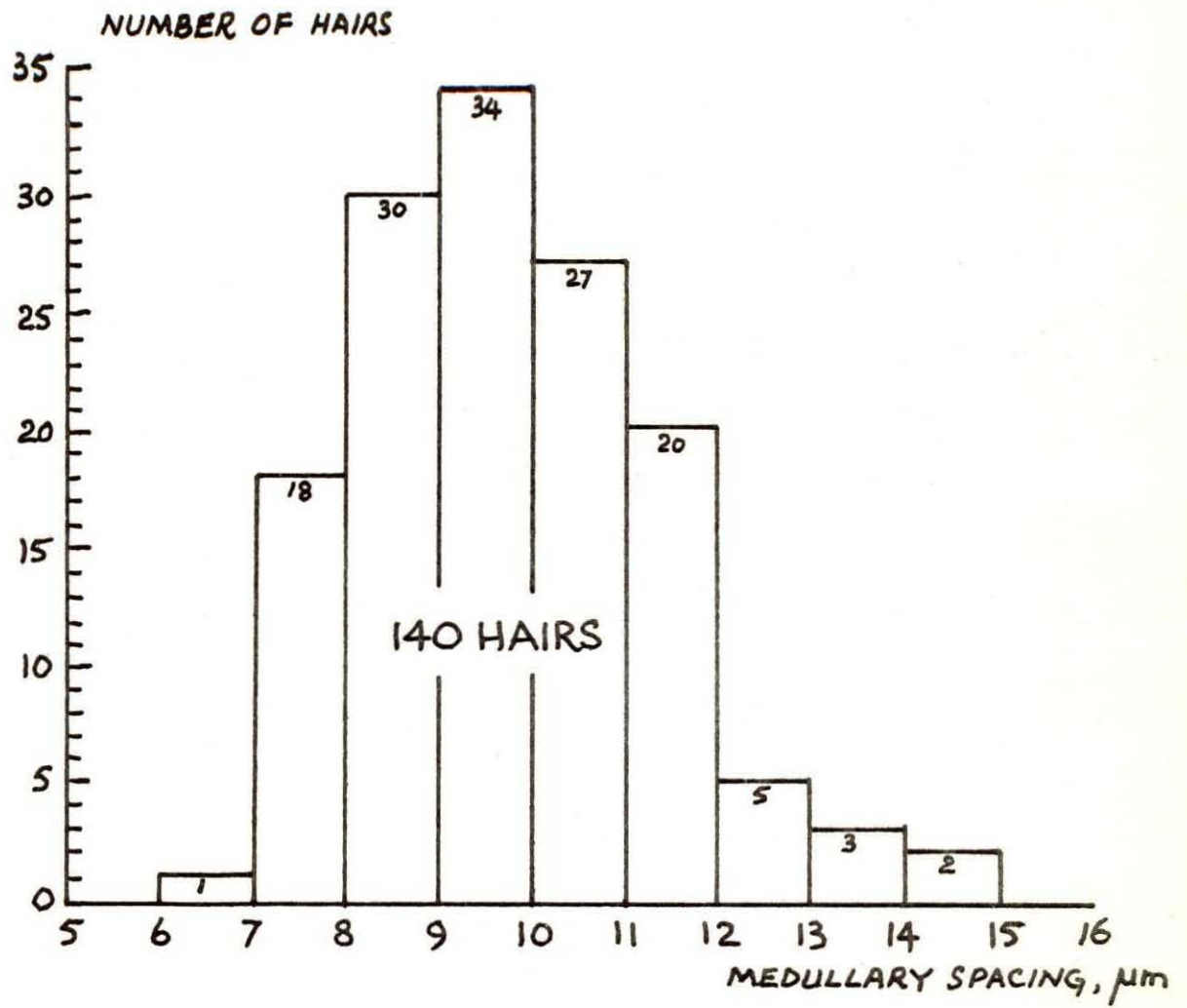Figure 16. Distribution of medullary spaces,

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

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* Although it is unlikely that they are formed entirely by these granules (Lyne pers. comm.).
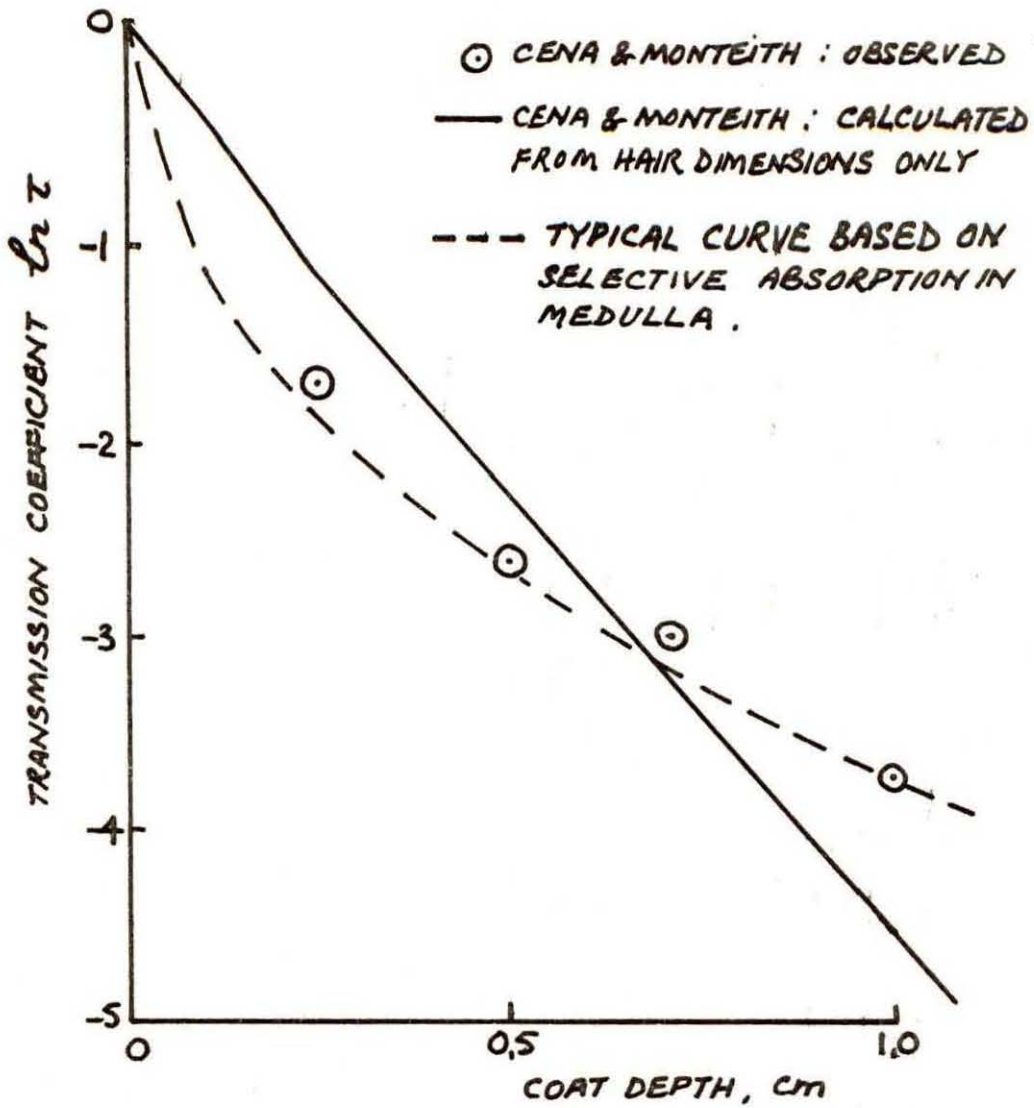
Figure 17. Transmission of radiation through coat of Clun Forst sheep.

hair with medullary spacing of 9 µm, the length of the cavity is about
7 µm. 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 µm and 12,5 µm. 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 λ when it has a diameter 0,77 λ. Thus a wavelength of 9,3 µm,
corresponding to the peak energy of thermal radiation from a surface at

16

17

18

Plates 16, 17 and 18.   Whole mounts of rabbit hair showing
consistency in size of medullary cavities

Table II: Diameters of medullary cavities of
Otomys unisulcatus

Width of medulla at transition (µm)	Number of cavities across medulla	Estimated diameter of each cavity (µm)
5	0	-
5	1	5
12,5	1	12,5
12,5	2	5,25
25,0	2	11,5
25,0	3	7,0
35,0	3	10,3
35,0	4	7,25
47,0	4	10,25
47,0	5	7,8
60,0	5	10,4
60,0	6	8,3

$37^{\circ}C$, 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 aforegoing 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 aforegoing 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

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.

OPSOMMING.

Hierdie proefskrif handel oor 'n studie van die mikrostruktuur van die hare van soogdiere van suidelike Afrika en in besonder dié van karnivore. Dit vul 'n leemte aan in ons kennis oor haarstudies in hierdie gebied en dui op die gebruike 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 demonstreer.

Die taksonomiese belang van haaridentifikasie is welbekend en voorbeelde 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. Voorbeelde 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 akwatiese habitat en woestynomgewing
word dus bespreek met verwysing na haartipes soos beskermhare, onderpels
en die mikrostruktuur van hare sowel as die meganiese en oppervlakte-
eienskappe van hare. Daar word na termoregulering verwys en voortspruitend
daaruit word 'n hipotese voorgestel waarin die bydrae van die medulla in
die absorpsie van lang infra-rooi-radiasie bespreek word.