

# **Past and present climates: owl pellet composition as an indicator of local climatic change**

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## **DECLARATION**

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.



## ABSTRACT

During Holocene times a considerable deposit of barn owl pellet material accumulated in the Hot Pot Cave at De Hoop Nature Reserve on the southern coast of the Western Cape Province, South Africa. An excavation of this accumulation has yielded information on barn owl prey species over the past some two millennia.

Four distinct layers were excavated and radiocarbon-dated to AD 381, AD 615, AD 991 and AD 1417. The micromammalian cranial contents of these layers were compared to material from two pellet collections that represent modern barn owl predation at De Hoop (AD 2000). Comparisons were made from three perspectives: (1) physical size measurements of certain cranial parameters, (2) micromammal community species composition and (3) community structure indices, such as the Shannon-Wiener diversity index, Simpson's diversity index and the species equitability index.

By extrapolating from known ecological distribution information of the relevant prey species, these data were used to recreate the local climate at the time of the accumulation of the layers. The results were compared to other palaeoclimate models for the region as a test of validity.

It was found that the lower two layers of the sequence represented mild conditions with possibly more grass than in recent times, while the upper layers represented cool weather with a possible increase in scrub. AD 381 was found to be somewhat dry and mild, AD 615 to be the wettest level and possibly milder than AD 381, AD 991 to be the coolest of all the levels and driest of the ancient levels, AD 1417 to be somewhat cool and probably drier than AD 615, but wetter than AD 381, and AD 2000 to be the mildest and driest of all levels, with the artificial influence of nearby agricultural activities evident.

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## SAMEVATTING

Tydens die Holoseen tydperk het 'n relatief groot hoeveelheid nonnietjie-uil bolusmateriaal versamel in Hot Pot Grot in die De Hoop Natuurreservaat aan die Wes-Kaapse suidkus, Suid-Afrika. Opgrawings van hierdie bolusversameling het waardevolle en insiggewende inligting aandie lig gebring rakende nonnietjie-uil prooi tydens ongeveer die afgelope tweeduisend jaar.

Vier definitiewe lae is opgegrawe en deur radiodatering is die lae se datums vasgestel op 381, 615, 991 en 1417 n.C. Deur gebruik te maak van kraniale kriteria, is die mikrosoogdier inhoud van die opgrawings vergelyk met dié van twee bolusversamelings wat die huidige uilprooi (2000 n.C.) in De Hoop verteenwoordig. Die vergelykings is op drie maniere getref: (1) fisiese groottemates van sekere kraniale parameters, (2) species-samestelling van die mikrosoogdiergemeenskap en (3) gemeenskap-struktuur indekse nl. die Shannon-Wiener diversiteitsindeks, Simpson se diversiteitsindeks en die species-gelykheid indeks.

Deur ekstrapolasie vanaf bekende ekologiese verspreidingsinligting rakende die betrokke species, is hierdie data gebruik om die klimaat van daardie tydperke te herskep op 'n streeksbasis en vergelyk met ander paleoklimaat-modelle om die geldigheid daarvan te beproef.

Die resultate het getoon dat die onderste (oudste) twee lae warmer toestande met moontlik meer gras verteenwoordig, terwyl die boonste twee lae koeler weer met moontlik meer bosse verteenwoordig. Daar is verder gevind dat 381 n.C. redelik droog en warm was, 615 n.C. die natste laag en moontlik warmer as 381 n.C., 991 n.C. die koudste van al die lae en droogste van die grot-lae, 1417 n.C. redelik koel en moontlik droër as 615 n.C., maar natter as 381 n.C., en 2000 n.C. die warmste en droogste van al die lae, met kunsmatige invloed van nabygeleë landbou aktiwiteite.

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## 1. INTRODUCTION

### 1.1 Background

This thesis is a study in local palaeoclimatic reconstruction using an indirect climatic indicator, subfossil micromammal remains accumulated by owls in a cave, Hot Pot Cave in De Hoop Nature Reserve. The owl species identified as the collecting agent is the African barn owl *Tyto alba affinis* (Blyth). The 'micromammals' as here defined, are members of the orders Rodentia, Macroscelidea and Insectivora weighing less than 100 g. The more restricting term 'micromammals' is used here rather than the more general term 'small mammals' which also include slightly larger members of the above mentioned orders, as well as members of the orders Marsupialia, Chiroptera and Lagomorpha (Fleming, 1975).

Palaeoclimatic reconstruction depends on the principle that micromammal community composition correlates with a definable set of habitat characteristics of vegetation and climate. The possibility of correlating micromammal community composition with certain habitat characteristics is suggested by studies such as, e.g. that of Nel & Rautenbach (1975). As they can reflect more subtle environmental changes than can larger mammals, micromammal species are particularly suited as environmental indicators (Avery, 1982a; Deacon *et al.*, 1984). Mares & Willig (1994) found particular micromammal species of rodents and insectivores to generally occur in fewer biomes than larger mammal species, and thus to be more specific in their habitat preferences. These authors consequently make the point that small mammal data from fossil sites are more likely to provide an accurate determination of the palaeoenvironment at a site than would an equivalent amount of data from larger animals.

The use of owl pellet content to determine owl diet is an old and established method, used by Errington (1930) and others since. Micromammalian bone material from South African hominid sites has been studied as an indicator of past environmental conditions from as early as 1960 (De Graaff, 1960). In the 1970s Brain (1974) used micromammal remains from the Mirabib rock shelter in the central Namib plains as a test of whether the Namib



sand sea had extended further north in the terminal Pleistocene and Holocene. It had not - species specific to the sand habitat were absent. In a further study on the same material Brain & Brain (1977) inferred oscillating periods of wetter and drier conditions over the last 6000 years in the Namib, mainly from the relative frequencies of *Eremitalpa granti namibensis* and *Malacothrix typica* remains. Also in the 1970s Avery (1982a) conducted a study similar to this one on samples from a number of archaeological sites in the Western and Eastern Cape provinces, although on a larger scale. She was able to identify a wide range of micromammal species in samples of different periods of time, ranging from 110 000 BP at Klasies River Main Site and 80 000 BP from Boomplaas A to very recent (within the last 2000 years - see below) and also modern samples. Further research on micromammal remains in owl pellets relating to studies of Late Quaternary climates in South Africa, includes that of Thackeray (1987 - material collected by D.M.Avery) and further studies of Avery (1982b; 1992; 1997) (Figure 1).

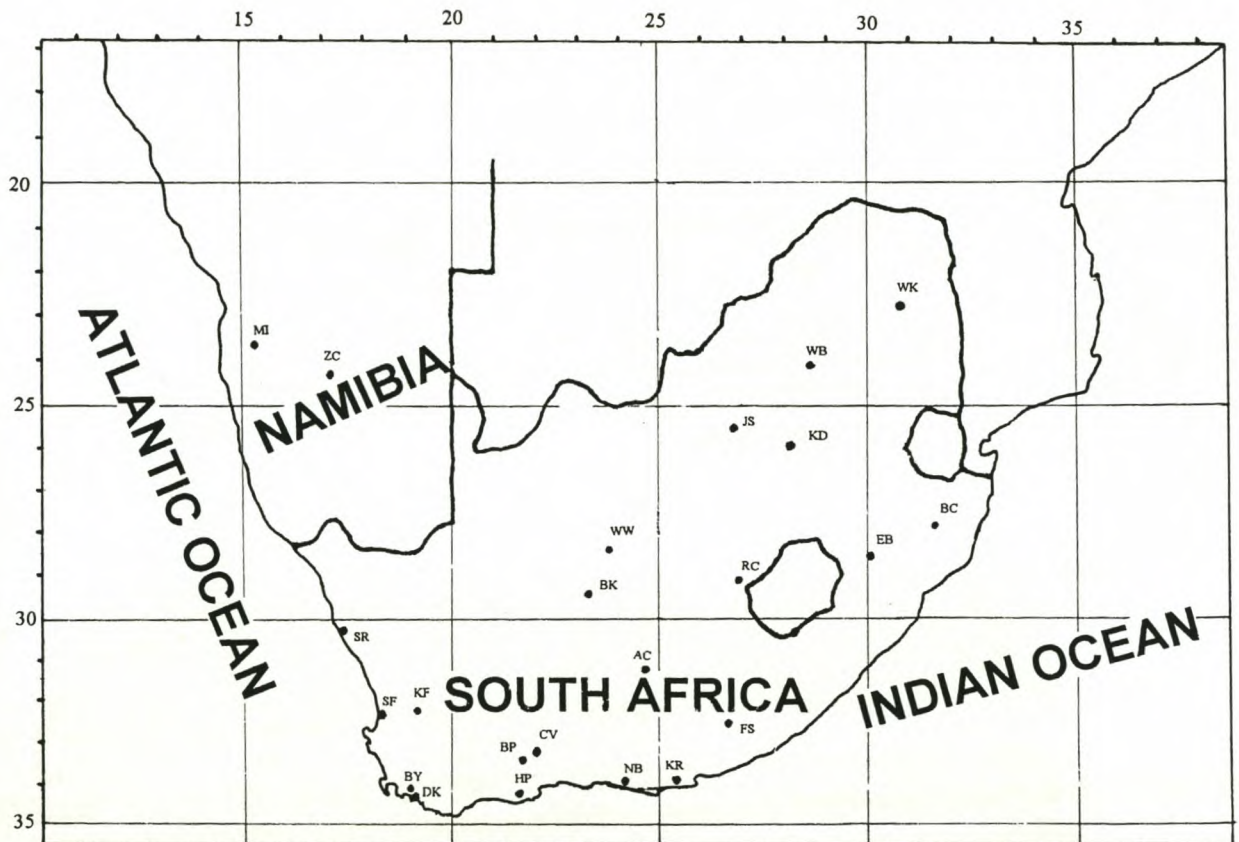
In 1978 C.E.Gow excavated and analysed the micromammal remains contained in about 3 litres of deposit (Gow, 1980) from two locations in Hot Pot Cave. Although these samples were not dated, Gow made a valuable contribution by describing the accumulation and suggesting the site was worthy of further research. Figure 1 gives the research locations.

*Tyto alba* has been proven to be a very effective sampler of micromammals in the sense that it samples a high proportion of the species present in a given area (Vernon, 1972; Dean, 1977) - more so than in the case of trapping or other methods (Goetze *et.al.*, 1991) (also see results below). A further benefit of using prey remains of barn owls, is the low degree of breakage in and damage to the bones found in the pellets (Dodson & Wexlar, 1979), due to the low pH of the barn owl's stomach (Smith & Richmond, 1972).

Climate is the main variable to be correlated with occurrence of micromammal species in this study. However, climate can influence the occurrence of micromammals in indirect ways, such as the effect of climate on vegetation, which is, according to the Clementian school, mainly controlled by climate (Krebs, 1978). The structure and composition of vegetation plays an important role in the distribution of micromammals and, consequently,



has to be taken into account in the interpretation of micromammal data. The relationships between climate, vegetation and the biota are illustrated in figure 2.



**Figure 1:** Map indicating locations, researchers and publication dates of other palaeoenvironmental studies done in South Africa, using owl pellets. KD = Krugersdorp deposits (De Graaff, 1960); MI = Mirabib (Brain, 1974); BY = Byneskranskop (Avery, 1977); BP = Boomplaas (Avery, 1977); DK = De Kelders (Avery, 1977); CV = Cango Valley (Avery, 1979); NB = Nelson Bay Cave (Avery, 1979); KR = Klasies River Mouth (Avery, 1979); BK = Blinkklipkop (Avery, 1981); WW = Wonderwerk (Avery, 1981); BC = Border Cave (Avery, 1982b); FS = Fairview Shelter (Avery, 1984a); ZC = Zebrariver Cave (Avery, 1984b); JS = Jubilee Shelter (Avery, 1987); WB = Wolkberg (Thackeray, 1987 - excavations by D.M. Avery); WK = Wonderkrater (Thackeray, 1987 - excavations by D.M. Avery); EB = Eastern Biggarsberg (Avery, 1988); AC = Abbots Cave (Avery, 1991); SR = Spoeg River (Avery, 1992); KF = Klipfonteinrand (Avery, 1993); RC = Rose Cottage Cave (Avery, 1997); SF = Steenbokfontein (Avery, 1999).



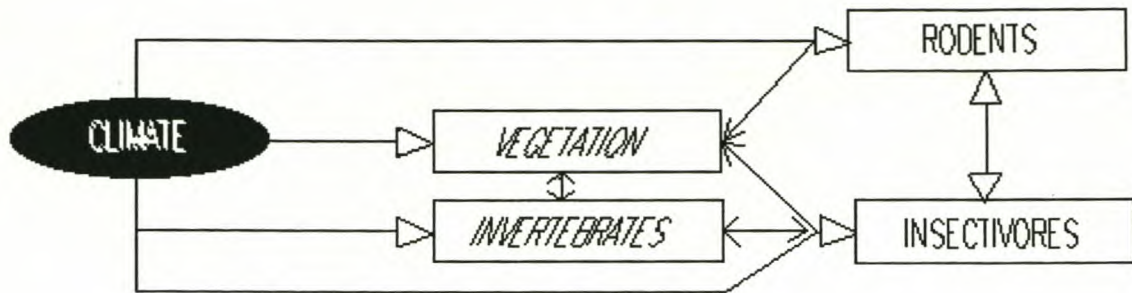


Figure 2: Climatic influence on certain biotic components and the direction of main interactions among the biotic components.

Of course, the main controlling factor for micromammals is not in all cases vegetation. For moles (both rodent and insectivore) it may be the nature of the substrate (Bigalke, 1978) although the presence of geophyte bulbs may also be a major factor. Not all inter-community interactions are shown in Figure 2. As the emphasis in this study is on relatively short-term *change*, possible edaphic changes are irrelevant. Changes due to biotic interactions (animal-animal; animal-plants) are assumed to have resulted from climatic fluctuations.

Changes on (1) individual level i.e. physical size measurements and (2) community level i.e. proportional importance of species within different communities and species diversity and equitability, were studied and used to interpret habitat and local climatic fluctuations (ecosystem level), which, in turn, were compared with existing local climate change models, as well as, to global climate change models (biosphere level). Comparison of ancient pellet data with those from modern pellet data is emphasized, and for this reason a considerable modern pellet collection was incorporated into the study.

The results listed in this study have a direct bearing on the southern coastal region of the Western Cape Province, South Africa, but the correlation with climatic trends on a broader scale is equally important. Coastal fynbos (Acocks, 1988) comprises most of the De Hoop Nature Reserve's vegetation. Fynbos is a very diverse biological system (Kruger & Taylor, 1980) and should, as a result of this wide array of vegetational indicators, be perfectly suited for studying indications of climate change. Furthermore, Taylor (1994) specifically mentions the Western Cape Province as an area where barn owl diets tend to be very species-rich. This high degree of species richness provides us with a fine-grain tool for



detecting environmental changes. Therefore, as far as resolution is concerned, not only is the method applied here relatively sensitive to climatic change, but the area in which the research was conducted, the Cape Ecozone coastal region, also seem to be sensitive to change (Deacon & Lancaster, 1988). Deacon and Lancaster (1988: 110) suggest that "The coastal region in the Cape Ecozone is perhaps the most sensitive to change and the evidence for palaeoclimatic conditions there is of some importance."

The sensitivity of this veld type (coastal fynbos (veld type 47) - Acocks, 1988) to different climatic regimes can be illustrated by looking at South African coastal areas only 1° latitude North, e.g. the Eastern Cape coast, where we find the vegetation to be noticeably different.

## **1.2 Rationale and aims of the study**

Apart from two levels at the Boomplaas A site, representing 1955±65 years BP and 1630 ±50 years BP (Avery, 1982a), one level at Byneskranskop, representing 1880 ±50 years BP (Avery, 1982a), two levels at Wonderwerk, representing 1210 ±50 and 1890 ±50 years BP, and a sequence from Blinkklipkop that covers basically the last millennium (Avery, 1981), the material Avery worked with is all older than 2000 years. There seems to exist a general lack of detailed climatic models based on barn owl pellets <2000 yrs old - more so for the period 2000 - 500 years BP, as compared to the succeeding period (500 BP - 0), when direct climate data started to become available and tree ring data started to increase. Deacon and Lancaster (1988) and Tyson (1986) also note the limited available data on palaeoenvironments for the last 2000 years in southern Africa. Although more African archaeological/ palaeoclimatic research has been done on the most recent 2000-3000 years than on prior periods (Deacon & Thackeray, 1984), most methods used have been incapable of resolving climatic changes on a centennial or the sub-millennial scale addressed in this study. This underlines the importance of this study, focusing as it does on the period with the greatest need for fine-grained climatic models: the last two millennia in southern Africa.



Not only does this study deal with a relatively short time period (roughly the last two millenia), it also deals with a time period during which climatic changes, such as temperature, were generally of a low magnitude (Vogel, 1983; Heaton *et al.*, 1986). As a consequence, the study is a thorough test of the sensitivity of changes in owl pellet composition as proxy indicator of faunal/climatic changes.

The study may be significant in several ways:

- \* It is a contribution to our knowledge about **what barn owl pellets can tell us about climatic trends of the past two millennia.**
- \* It contributes to what is already known about **information on Quarternary climates and theories of climate change.**
- \* Together with other research on past climates **provides a general framework of climatic conditions under which past human settlements developed in the Western Cape coastal region.**
- \* Together with data from other studies, it provides an indication of the natural rhythm of climatic fluctuations, upon which **artificial deviations**, such as the present-day effects of increases in atmospheric greenhouse gasses and stratospheric ozone breakdown, **are imposed.**
- \* The **effects of modern agricultural activities** in adjacent areas can be evaluated in the present pellet samples.
- \* The results from this study contribute to the palaeoclimatic data banks, such as the World Data Center for Paleoclimatology, the Climate Data Catalogue (Germany), the 'Internationale Paläoklima-Datenbank', the Paleoclimate Model Intercomparison Project, the International Geosphere-Biosphere Programme, COHMAP 1988, and many more (Tyson, 1991; Moore *et al.*, 1996; WDC-A for Paleoclimatology, 1999a). These data banks are utilised in programmes aimed at **predicting future climatic trends.**

The study also provides:



- \* **General information on barn owl diets at De Hoop.**
  - \* **New data on distribution of certain species** of micromammals.
  - \* A contribution to an **identification key for micromammals** occurring in the southwestern Cape region (see Appendices 2 and 3; unpublished documents also available to interested parties).
-

## 2. STUDY AREA

### 2.1 Location

The field study was undertaken at De Hoop Nature Reserve, centred on *ca* 34°27'S; 20°26'E (Figure 3), situated in the southern region of the Western Cape Province, South Africa. De Hoop is located approximately 260 km east southeast of Cape Town and 60 km east of the town of Bredasdorp, and covers an area of  $\pm$  40 000 ha (De Hoop Management Plan, 1987). Towards the west the reserve is bordered by the Salt River which terminates in the De Hoop Vlei, to the north by a ridge of limestone/sandstone hills and Potberg Mountain, to the east by the low hills of the Potberg range where the reserve nears the estuarine section of the Breede River, and to the south by the Indian Ocean. It also includes a marine reserve, extending three nautical miles seawards (De Hoop Management Plan, 1987) - see Figure 3.

### 2.2 Geomorphology

The reserve is divided into five biogeographic regions/ major habitat complexes (not to be confused with the vegetation types in Figure 4): (i) coastal plain, (ii) coastline, (iii) limestone hills, (iv) De Hoop vlei and (v) Potberg mountain (Scott, 1986). This study will mainly focus on the coastal plain, although some of the other habitat types may also have direct relevance on the results and will be referred to where necessary.



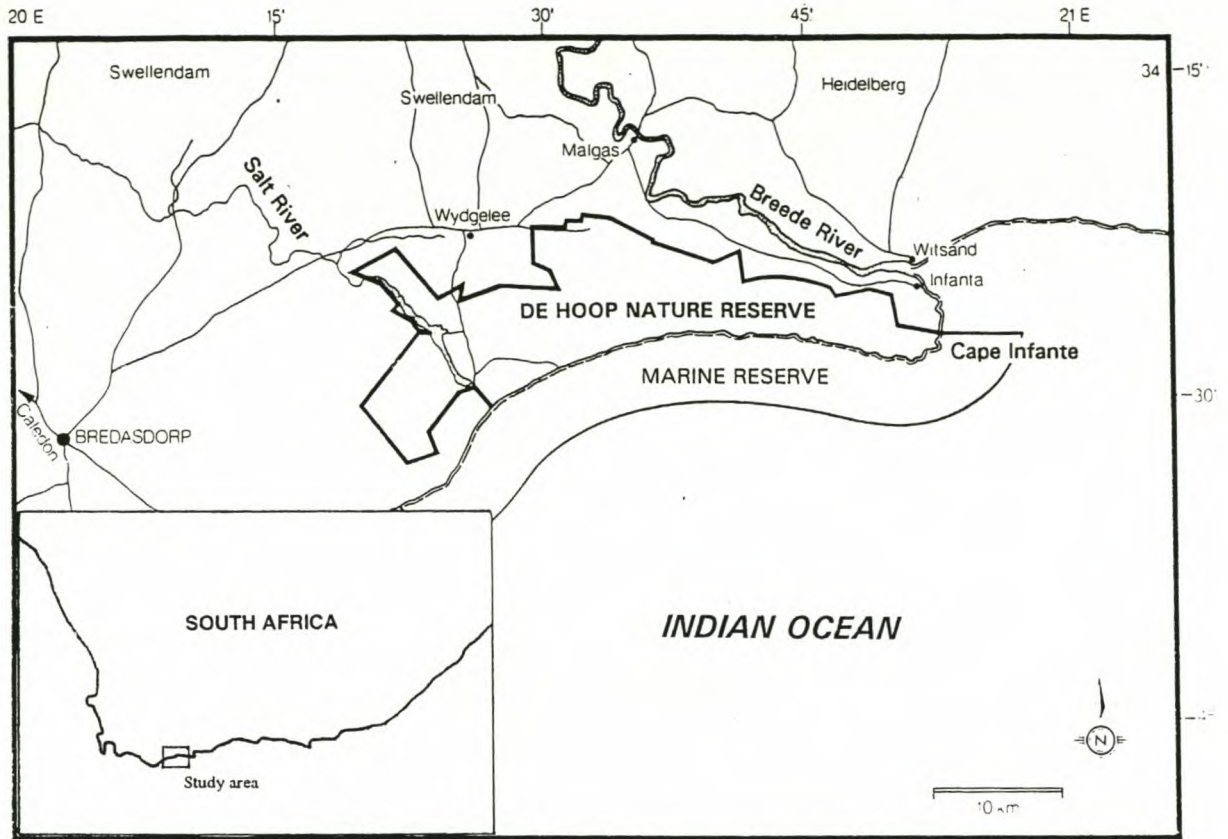


Figure 3: Map of De Hoop Nature Reserve.

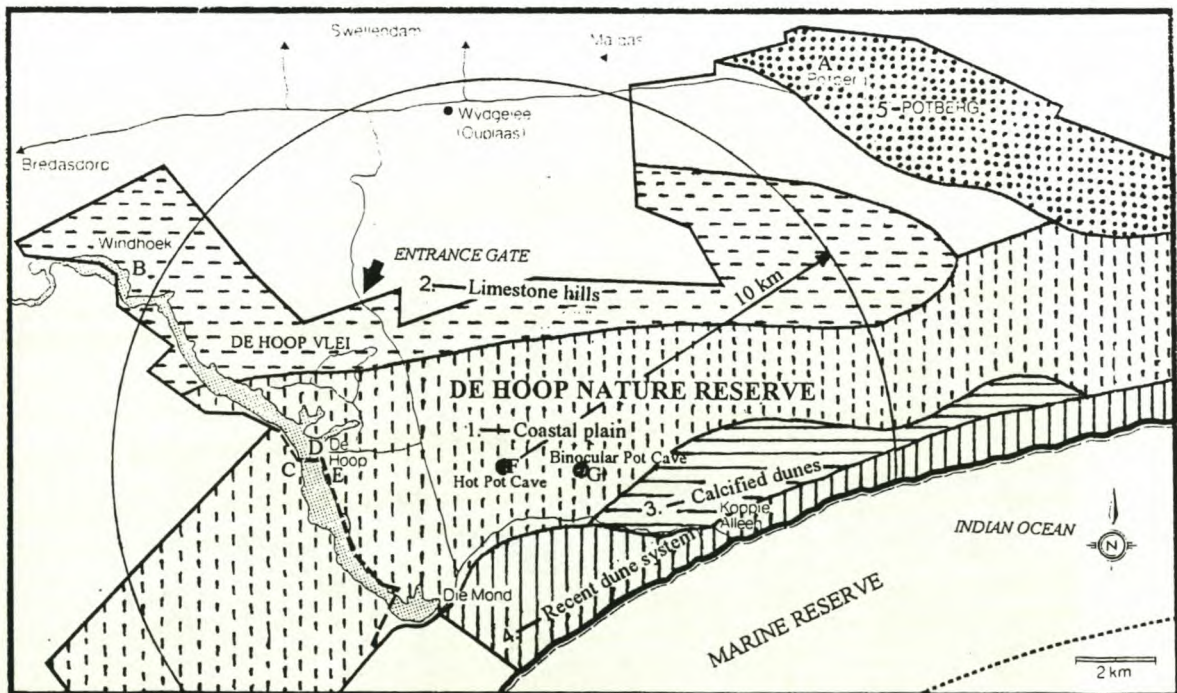


Figure 4: Map indicating the main vegetation types of the study area, Hot Pot Cave and its 10km radius, as well as other sites of importance at .

The owl roosts where pellets were collected: A - Potberg silo; B - Windhoek; C - Milk shed; D - Vlei cliffs; E - Cool room; F - Hot Pot box; G - Binocular Pot



The coastline consists of sandy, as well as rocky (limestone) shores and a number of rivulets enter the ocean in the eastern part of the reserve. The southwestern coastline of the reserve is bordered by an extended open dune field of  $\pm 1000$  ha.

The limestone or "karst" hills, locally known as the hard dunes, were deposited on sandstone in the late Tertiary and rise to a maximum height of *ca* 200 m above sea level (Scott, 1986). These hills also serve as a groundwater reservoir, serving the many springs feeding the De Hoop Vlei (Butcher, 1983).

The brackish De Hoop Vlei is at present landlocked, being separated from the sea by a band of mobile sand dunes *ca* 2,5 km wide (Butcher, 1983). It is believed to have opened to the sea in the past, as relicts of estuarine organisms occur at its southern end (Scott, 1986). The total capacity of the vlei is about 31,6-36,7 million m<sup>3</sup> (Butcher, 1983). The eastern vlei edge (on the De Hoop Centre's side (De Hoop homestead/ Nature Conservation Centre)) of the southern section consists of limestone cliffs, 15 m high at places, and contains numerous caverns. The water level fluctuates considerably (Butcher, 1983). Flooding over the western flat vlei edge occurred in 1906, 1927 (Scott, 1986) and 1957 (Anon., 1983b). The vlei bed was almost completely dry in 1903, 1945, 1975, 1980, 1984 (Scott, 1986) and 1997.

The ecologically isolated mountain habitat of Potberg is partly shadowed from the effects of proximity to the sea by the limestone hills.

Almost the entire reserve comprises a broad coastal plain of low, undulating limestone pavements and ridges interspersed with sandy flats which link the sandstone/limestone ridges in the north with a broad zone of low vegetated dunes to the south (De Hoop Management Plan, 1987). This coastal plain, which forms part of the Bredasdorp Embayment (Lambrechts, 1979 in Day *et al.*, 1979) was incised into the limestone by the sea during Tertiary times (Scott, 1986). Soils are predominantly sandy and of aeolian origin or derived from *in-situ* weathering of sandstones and quartzites and sandy limestones (De Hoop Management Plan, 1987). The coastal plain is underlain by the shales of the Bokkeveld Group and sandstones and quartzites of the Table Mountain Group (age  $\pm 400$  million years) as well as the much younger ( $\pm 5$  million years old) coastal



limestones, recent calcareous sands and in places by acid soils (Schloms *et al.*, 1983 in Deacon *et al.*, 1983). As a result of this diverse geological substrate a complex mosaic of different habitat types with an accompanying diversity of natural plant and animal life is present (Scott, 1986).

A number of caves, i.e. the Hot Pot, Binocular Pot, Edward's Pot, the Onmeetbare Diepgat ("Unmeasurable Deep Hole") and other unnamed caves reported by members of the South African Speleological Society (Butcher pers. comm., 1998), are known to exist under the coastal plain on the boundary between the limestone and underlying shale. Many more are probably yet to be discovered.

### 2.3 Climate

The area is intermediate between Schulze's (1965) climatic regions A and M. It has a temperate mediterranean climate and receives most of its rainfall in winter. Annual mean temperature is *ca* 17.5°C (De Hoop Management Plan, 1987) and precipitation averages *ca* 450 mm per annum, mostly between March and October (Uys, 1983; Lovegrove, 1993). The 25-year rainfall average for 1956 to 1980 was 368 mm/annum (Butcher, 1983). These figures indicate that the area lies on the wetter side of the drier fynbos (lowland and arid fynbos) precipitation range (Rutherford & Westfall, 1986).

The climate is strongly influenced by the proximity of the sea, especially the warm Agulhas current. Temperature extremes are very rare and weak fogs occur.

Winds may reach  $\geq 60$  km/h and blow mostly in summer. Prevailing winds are mostly from the east, west and southwest (Scott, 1986).

### 2.4 Vegetation

The De Hoop Nature Reserve forms part of the Cape Floristic Kingdom (Rutherford & Westfall, 1986) and therefore represents a highly diverse biological system (Kruger &



Taylor, 1980 in: Rutherford & Westfall, 1986). Taylor (1978) points out that this vegetation system, also known as fynbos, characteristically lacks single species dominance. The De Hoop vegetation (like most other fynbos) results from a combination of low nutrient soils, periodic veld fires (either natural or anthropogenic) and a mediterranean climate (Scott, 1986). The effect of climate on vegetation and how the micromammals serve as indicators of the type and structure of the vegetation, will be referred to further below.

Because of the limestone substrate, the area of the present reserve was not suited for agricultural crops and the vegetation remained relatively pristine in historical times (Uys, 1983). Between Bredasdorp and Cape Infanta, and therefore in De Hoop, 81 threatened plant species occur, including six endangered species, while 27 species are endemic to this area. Thirteen of these endemics occur only on the limestone hills and 13 on the Potberg (Anon., 1983a).

Of the three major subdivisions of fynbos, namely coastal, mountain and arid, the largest part of De Hoop's vegetation is represented by coastal fynbos (Kruger, 1977; Taylor, 1978). Three Acocks (1988) veld types are represented on the reserve (Burgers, 1983):

- 1) Coastal Macchia/ Coastal Fynbos (veld type 47) in which the Hot Pot cave is situated and in which most of the micromammal livetrapping was done.
- 2) Macchia/ Mountain Fynbos (veld type 69), represented on the Potberg range and
- 3) Coastal renosterveld (veld type 46)- small pockets at the upper reaches of the vlei and on the southwestern slope of the Potberg Mountain (De Hoop Management Plan, 1987).

In addition De Hoop's diverse vegetation regime includes dense riverine woodland, dominated by the white milkwood *Sideroxylon inerme* and occurring mainly along the vlei edge, as well as 'limestone fynbos' on the limestone/sandstone hills, restioid veld and short grassy plains. The latter may be an artifact of either prolonged human burning practices (Scott, 1986), flooding (Uys, 1983), a different, more clayish substrate, a rich deposition of animal faeces (mostly from De Hoop's grazing animals) in these areas, or a combination of the above.



Coastal fynbos covers most of the area relevant to this study. Parts of the coastal fynbos in the reserve are subjected to infestation by aliens such as *Acacia cyclops* (Butcher, 1983: 14). However, the areas relevant to this study were alien-free. Burgers (1983) distinguishes four areas of coastal fynbos (Figure 4):

- 1) the *coastal plain* - typically a climax of Proteaceae and other larger shrubs, with a lower stratum of ericoids and grassy vegetation
- 2) the *limestone hills* vegetation - 'limestone fynbos', including proteoids, other smaller shrubs and ericoids
- 3) the less rocky and more sandy coastal plain closer to the shore, where the vegetation changes to a very low, dwarflike type of fynbos on the low vegetated dunes, known as the *calcified dunes*. This vegetation is described by Acocks (1975) and Moll *et al.* (1984 in Rutherford & Westfall, 1986) as a variation of southern Strandveld
- 4) *recent dune system*, having little or no vegetation cover. 'Islands' of vegetation may be present in dune slacks.

## 2.5 Fauna

De Hoop is probably best known for its avifauna. The De Hoop Vlei is a wetland which acquired RAMSAR status in 1975 - a wetland of international importance, especially as a waterfowl habitat (Greig, 1983). More than 220 bird species have been recorded in the reserve (Uys, 1983), of which 14 are regarded as threatened (Scott, 1986). Species from other areas also occur in the reserve. Those from drier areas include the Karoo korhaan *Eupodotis vigorsii* and Namaqua sandgrouse *Pterocles namaqua*. Birds from wooded areas, such as those from the Eastern Cape Province and southern Cape, include the southern tchagra *Tchagra tchagra*, forktailed drongo *Dicrurus adsimilis* and the Knysna woodpecker *Campethera notata* (Uys, 1983).

Two freshwater fish species, 14 amphibian species, 36 reptile species and 70 mammal species have been recorded. Of the mammals, 50 species are terrestrial, with 38 being non-



bovid (Scott, 1986). Nine bat species have been recorded in the reserve (Laycock, 1983; Scott, 1986). Some of the non-bovid/equid mammals (local abundance and distributional history will not be discussed here) are listed as follows: the Cape dune mole rat *Bathyergus suillus*, porcupine *Hystrix africaeaustralis*, Cape fox *Vulpes chama*, bat-eared fox *Otocyon megalotis*, black-backed jackal *Canis mesomelas*, caracal *Felis caracal*, African wild cat *Felis lybica* (probably hybridized with feral domestic cats), small-spotted genet *Genetta genetta*, large-spotted genet *Genetta tigrina*, honey badger *Mellivora capensis*, Cape clawless otter *Aonyx capensis*, striped polecat *Ictonyx striatus*, yellow mongoose *Cynictis penicillata*, water mongoose *Atilax paludinosus*, Cape grey mongoose *Galerella perverulenta*, large grey mongoose *Herpestes ichneumon*, hyrax (rock dassie) *Procavia capensis*, the scrub hare *Lepus saxatilis*, red rock hare (probably referring to Smith's red rock rabbit *Pronolagus rupestris*) and the chacma baboon *Papio ursinus* (Gow, 1980; Uys, 1983; Scott, 1986). The Cape hare *Lepus capensis* is not listed, but probably also occurs here.

Several mammal species previously occurred in De Hoop, but are now extinct: the African buffalo *Syncerus caffer*, kudu *Tragelaphus strepsiceros*, hartebeest (Gow, 1980 does not specify the species - probably red hartebeest *Alcelaphus buselaphus*), bushpig *Potamochoerus porcus*, leopard *Panthera pardus*, brown hyena *Hyaena brunnea*, black rhinoceros *Diceros bicornis* and probably hippopotamus *Hippopotamus amphibius*, African elephant *Loxodonta africana* and the aardvark (antbear) *Orycteropus afer* (Gow, 1980; Scott, 1986).

According to information available at the local nature conservation office and a report by Lloyd (1983b), the following micromammal species, occur in the De Hoop Nature Reserve (species in brackets are, according to the De Hoop Nature Reserve lists, expected to occur there, but have not been recorded). These are not all the species expected to occur in De Hoop (according to general distribution maps i.e. Skinner & Smithers, 1990 and Mills & Hes, 1997). The list does not include all the species identified in the pellet material nor all those caught by livetrapping (see Results below):



## Order Insectivora

*Myosorex varius* - forest shrew

*Suncus varilla* - lesser dwarf shrew

*Crocidura cyanea* - reddish-grey musk shrew

*Crocidura flavescens* - greater musk shrew

*Chrysochloris asiatica* - Cape golden mole

(*Amblysomus hottentotus* - Hottentot golden mole)

## Order Macroscelidea

*Macroscelides proboscideus* - round-eared elephant shrew

## Order Rodentia

*Cryptomys hottentotus* - common molerat

*Georychus capensis* - Cape molerat

*Graphiurus ocellatus* - spectacled dormouse

*Otomys karoensis* - Saunders' vlei rat

*Otomys irroratus* - vlei rat

*Otomys slogetti* - Sloggett's rat

(*Acomys subspinosus* - Cape spiny mouse)

*Rhabdomys pumilio* - striped mouse

*Dasymys incomtus* - water rat

*Mus musculus* - house mouse (alien)

*Mus minutoides* - pygmy mouse

*Mastomys natalensis* - Natal multimammate mouse

*Myomyscus (Praomys) verreauxii* - Verreaux's mouse

*Aethomys namaquensis* - Namaqua rock mouse

(*Rattus rattus* - house rat (alien))

(*Rattus norvegicus* - Norwegian/brown rat (alien))

*Tatera afra* - Cape gerbil

*Mystromys albicaudatus* - white-tailed mouse

*Dendromus melanotis* - grey climbing mouse

(*Dendromus mesomelas* - Brants' climbing mouse)

(*Steatomys krebsii* - Kreb's fat mouse)

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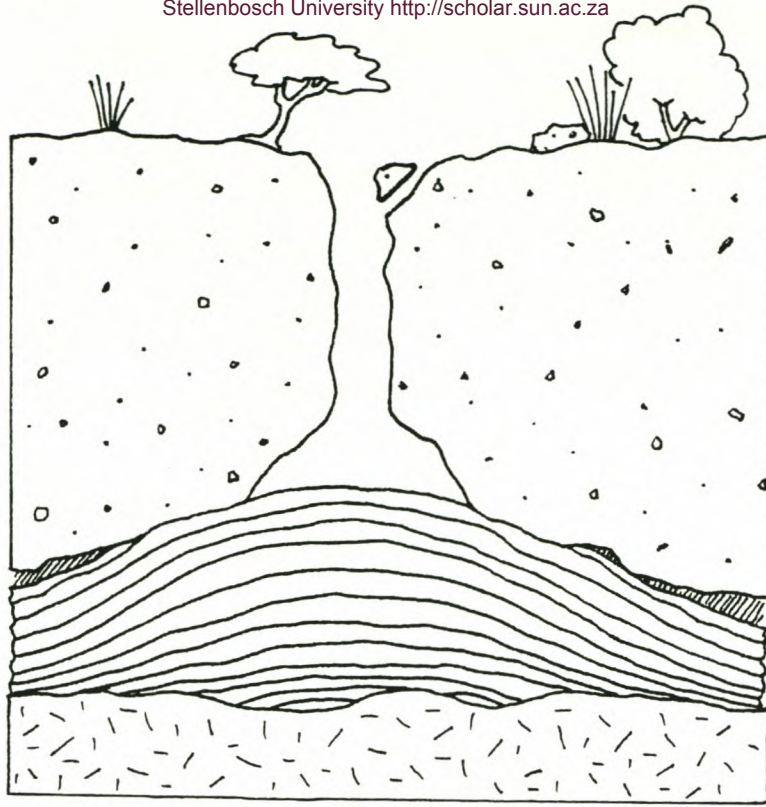
### 3. STUDY SITES

#### 3.1 Hot Pot Cave and surrounding area: ancient owl pellets

The subfossil owl pellet material was excavated from unconsolidated deposits in Hot Pot Cave, 34°27'25"S; 20°26'43.3"E (see Figure 4), in the De Hoop Nature Reserve. Craven & Scott (1989) report the cave to be "situated 0,75 miles (*ca* 1,15 km) southeast of the well (Dronkvlei fountain) and north of the Dronkvlei track".

The site is an approximately horizontal karst-type cave, branching out under the surface of the coastal plain. A system of passageways has developed in the contact horizon between the *ca* 10 m thick upper layer of relatively young Tertiary limestone and the older underlying shales of the Bokkeveld Group, as well as quartzites and sandstones of the Table Mountain Group (Gow, 1980; Scott, 1986). The initial development of the cave occurred below the water table and the cavities are therefore referred to as being phreatic in origin (Hitchcock, 1985). Most of the system consists of sections where the soft limestone roof has dissolved and collapsed to form 'collapsed chambers'. No calcite formations occur (Hitchcock, 1985). Approximately 710 m of the meandering system of low passages have been explored by members of the South African Speleological Association (Hitchcock, 1985).

(a)



(b)

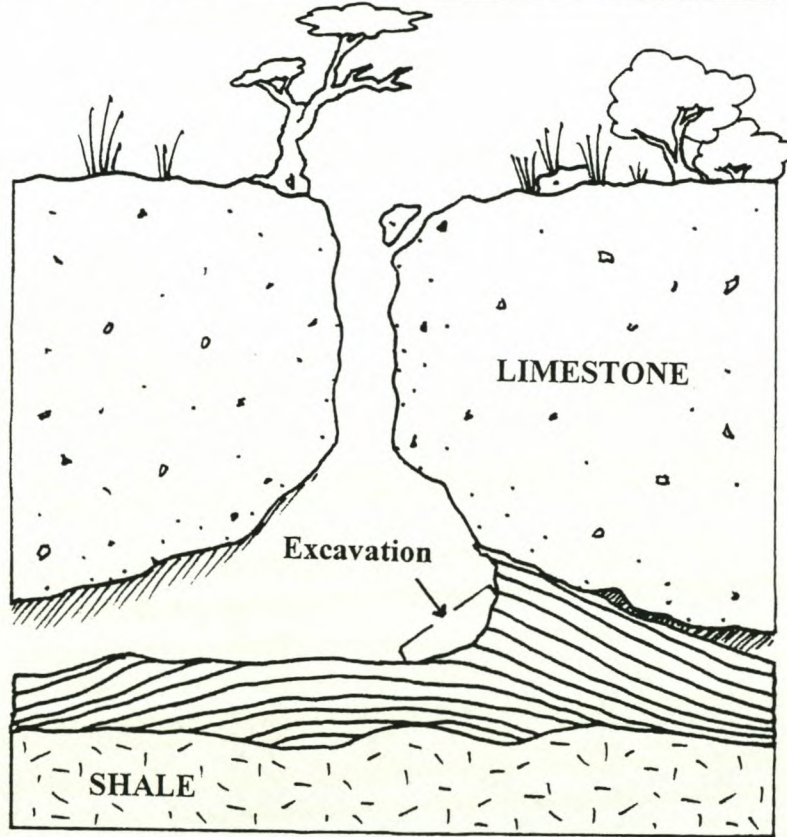


Figure 5: Transect of the first chamber of Hot Pot Cave showing (a) The probable pristine deposit and (b) the deposit after flooding.



Apart from cranial and skeletal material of micromammals and larger animals found on the cave floor surface, a rich microfaunal deposit occurs in the soily matrix underneath the surface. Although the explored section of the cave covers a considerable distance and some micromammal bones were found on the cave floor surface more than 100 m in from the entrance (probably animals that fell in and went further into the cave), all the excavations were undertaken in the first chamber at the bottom of an 8 m vertical entrance shaft. It was assumed that the owl pellet deposit would only occur in the first chamber of Hot Pot Cave, since the owls would probably not have ventured into the pitch darkness of the cave. Gow (1980) suggests that the deposit was once much deeper than its present level, choking the cave's passageway, and that it was subsequently reworked by groundwater. Where the remainder of the deposit now forms the cave floor, Gow determined it to be more than 1 m deep at places. He based his 'groundwater theory' on the remnants of the deposit, such as micromammal bones, found about 0,5 m above the level of the deposit in the rough protuberances of the passage walls, as well as the fact that the micromammal longbones in the deposit were generally orientated horizontally and with their long axes parallel to the walls of the cave passage. Evidence supporting this and showing that it is still an ongoing phenomenon is found in Craven's report (1989), on a visit to Hot Pot Cave. The footprints of the previous survey expedition (1983) had vanished and evidence of flooding to a depth of 1 m was found on the side walls. Craven reports that the then Reserve manager told them that heavy rains ( $\geq 700\text{mm}$ ) fell shortly before their visit (Craven, 1989).

Gow (1980) contends that the deposit choking the side of the first chamber opposite the main passage is relatively undisturbed and that this part of the deposit, continuing into the 'hidden passage' may be quite extensive. It is in this seemingly undisturbed part of the deposit that the excavation was performed (see Figure 5). The substrate intersected in the excavation is a soft peat-like matrix containing the bones. The accumulation extends horizontally (into the 'hidden passage') and vertically (down towards the bedrock), further than exposed in the excavation. The oldest layers in the sequence are yet to be sampled. Figure 5 shows a reconstruction of the manner in which the layers of pellet material were deposited.



The cave is situated in the coastal plain habitat (Figure 4) which consists of coastal fynbos vegetation (De Hoop Management Plan, 1987).

The habitat immediately surrounding the cave entrance generally comprises sandy soil and limestone outcroppings in a *ca* 50/50 ratio, with here and there grass-covered pans. Large restios, Proteaceae, herbaceous plants and alien *Acacia cyclops* trees occur on the sand. In between these the surface is mostly covered with short grass or low ericoid veld. Bare sandy patches also occur. On the limestone areas woody scrubs and small trees, as well as smaller restios, are predominant. Bare patches here consists mostly of limestone. The grass covered pans occur on clayish soil types with a continuous cover of short grass, except where ostrich hollows (shallow bare patches, where the ostriches rest) occur.

### **3.2 Collection sites of recent owl pellets**

The owl roosts which yielded fresh/recent pellet material are, with the exception of the Potberg silo and Windhoek, situated in the coastal plain habitat. Apart from the Potberg silo, all the pellet collection sites were (at least partially) separated from agricultural activities on nearby farms by the limestone hills. Most roosts and all roosts of which the data were used in the calculations are within 10 km of Hot Pot Cave. Radii of barn owl hunting ranges are very seldom more than 6 to 7 km (various authors - see 5.9.2)

#### **3.2.1 Own samples**

Owl pellets were collected at the following sites during the course of this study:

- \* Potberg silo - situated at the foot of the Potberg ('Pot Mountain') and north of the sandstone/limestone ridge. The area in which the owls depositing the pellets hunted was, therefore, in part sheltered from direct maritime influences. The surrounding area comprises mountain fynbos and alien vegetation (*Eucalyptus* trees) with some ravine vegetation, e.g. forest trees and herbaceous undergrowth.



Collecting date - February 1995

- \* Windhoek - the pellets were accumulated in the attic of an old building situated close to the upper reaches of the De Hoop vlei. The surrounding area consists of (1) vlei with its marshy vegetation, but less wooded than the lower areas of the vlei, (2) hill slopes with a more arid vegetation and Proteaceae veld, (3) alien fruit trees and garden plants in the area directly around the Windhoek homestead, and (4) sandstone cliffs with many caves. Currently it is an area with no regular human presence.

Collecting dates - February 1995

- May 1996

- \* Melkkamer - pellets were collected here from an attic in an old building west of the De Hoop vlei. It is surrounded by indigenous woodland with open, grassy patches inbetween and vlei edge reeds and marshes (Uys, 1983).

Collecting dates - February 1995

- May 1996

- \* Vlei cliffs cave - the pellets were collected from a natural location, a cave close to the De Hoop centre. These limestone cliffs constitute the eastern bank of the vlei. Riverine bush, vlei edge vegetation (reeds and marshes) where streams open into the vlei, open grass plains and permanent human structures border the cliffs. The riverine bush is dominated by milkwood *Sideroxylon inerme* and has a similar composition to that of low "southern Cape" forest (Uys, 1983). Further away from the vlei the riverine bush in places becomes more open woodland, with low trees dominating, interspersed with open areas of short grass.

Collecting dates - February 1995

- September 1996

- June 1997



- \* The Cool-room (Koelkamer) - the owl roost is situated under the roof of an old cool-room at the De Hoop Nature Conservation centre. It is approximately 150 m from the vlei cliffs roost and the immediate environment is the same.

Collecting dates - February 1995

- September 1996

- June 1997

- \* Hot Pot Box - a wooden box, 0.6 x 0.4 x 0.4 m, mounted 2.5 m above ground on a wooden pole (see Hosking, 1995). This collecting site differed from the others as barn owls only started roosting here after four years of non-occupation (it has been erected in 1995 and occupied in 1999). The box is situated 50 m from Hot Pot Cave and the surrounding area is therefore the same as described for Hot Pot Cave (see above). No recent owl pellets were present in Hot Pot Cave itself.

Collecting dates - September 1998

- December 1998

- \* Binocular Pot - this is another coastal plain cave, situated at 34°27'25"S; 20°28'04"E (see Figure 4) - approximately 2.1 km East of Hot Pot Cave. The surrounding vegetation is similar to that around Hot Pot Cave, but with less grass and woody scrub. The substrate in the surrounds is more sandy. For the purpose of this study, however, the settings of the two caves are treated as identical.

The Binocular Pot is a cave with basically the same form as Hot Pot Cave, but with the roof of the first chamber seemingly collapsed. It also has a peat-like floor in which micromammal bones were found during a superficial examination. It is possible that, as in the case of the Hot Pot, an extensive micromammal deposit exists in the cave, but that any passageways are completely submerged under the fill of deposit.



This cave was only re-located towards the end of this study. Therefore only one collection was made here.

Collecting dates - September 1998

### 3.2.2 Palmer-Fairall samples

Some pellets used in this study were collected in 1987 by N.Fairall and G.Palmer at the following sites at De Hoop:

#### \* Potberg Silo

Collecting dates of Palmer and Fairall: - 05/01/87

- 16/06/87

#### \* The Cool-room (Koelkamer)

Collecting dates of Palmer and Fairall - 05/01/87

- 30/01/87

- 31/07/87

- 31/08/87

\* De Hoop Silo - situated at the De Hoop centre approximately 100 m from the Koelkamer, with similar surroundings. No collections were made here during this study, because the silo did not contain an owl roost at the time.

Collecting dates of Palmer and Fairall - 02/06/87

- 30/06/87

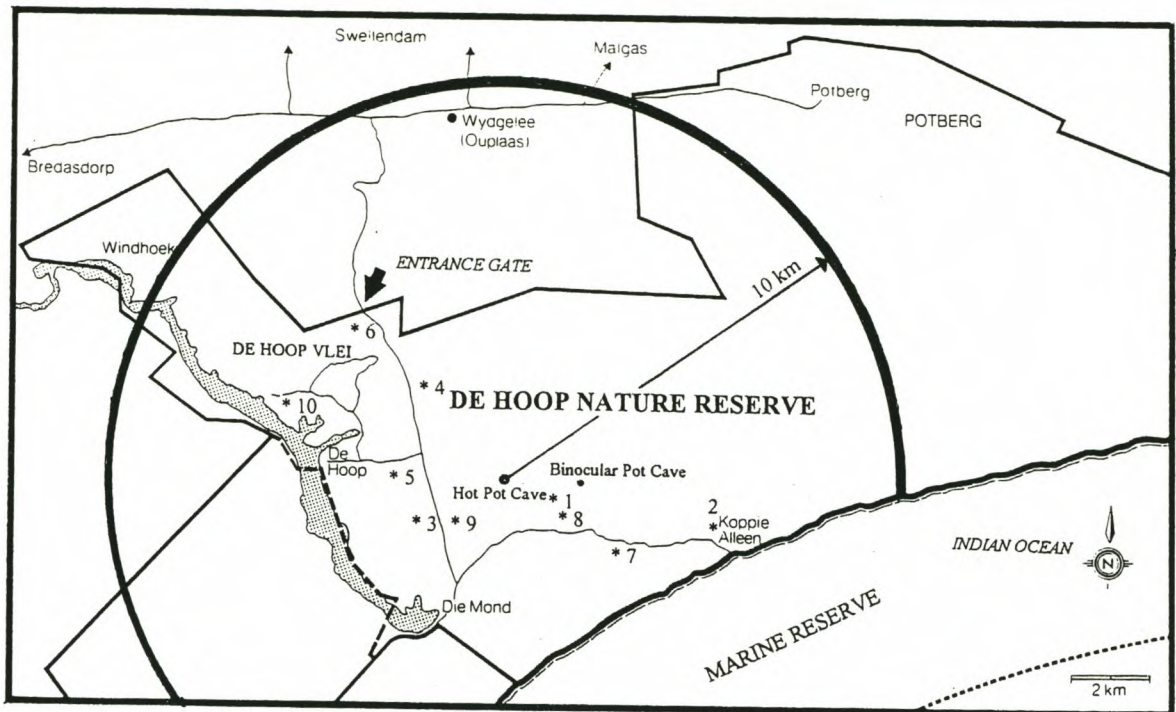
### 3.3 Micromammal livetrapping sites

Livetrapping for micromammals was undertaken in 10 areas of varying vegetation (habitat) within a 10 km radius of Hot Pot Cave (see Figure 6) so as to include most of the possible habitats in which an owl, roosting in Hot Pot Cave, might have hunted (see 'barn owl hunting ranges' below). Livetrapping was not done in the riverine thicket (closed woodland) along the vlei edge, since barn owls prefer to hunt in open areas with a moderate vegetation height (Taylor, 1994) and it is unlikely that they would hunt in the former.

The vegetation in the trapping areas was informally classified as (Figure 6):

1. Low to medium height limestone/sandstone veld - as at the surroundings of Hot Pot Cave.
  2. Coastal fynbos along the coast - near Koppie Alleen on the low, vegetated dunes between the coastal plain and the coastline.
  3. Very short limestone veld.
  4. Medium to high *Protea/Leucodendron* veld at foot of limestone/sandstone hills.
  5. Open woodland with restioids and scrubs.
  6. High, old *Protea/Leucodendron* veld on top of limestone/ sandstone hills.
  7. Medium height scrubland, landwards of sand dunes.
  8. Low, fynbos with grasses on sand
  9. Burnt (6 months previously with first trappings) *Protea/Leucodendron* veld.
  10. Medium height *Leucodendron* veld near vlei.
-





**Figure 6:** Map indicating trapping locations, as well as the 10 km radius around Hot Pot Cave. Habitats represented by trapping locations: 1. Low to medium height limestone/sandstone veld; 2. Coastal fynbos along the coast; 3. Very short limestone veld; 4. Medium to high *Protea/Leucodendron* veld; 5. Open woodland with restioids and scrubs; 6. High, old *Protea/Leucodendron* veld; 7. Medium height scrubland; 8. Low, fynbos with grasses on sand; 9. Burnt (6 months previously with first trap session) *Protea/Leucodendron* veld; 10. Medium height *Leucodendron* veld near vlei.



#### 4. COLLECTING AGENCY AND OWL PELLET ACCUMULATION

Although it would be generally accepted that the barn owl *Tyto alba* (Figure 7) acted as the agency of accumulation for Hot Pot Cave deposits, it is essential to look at the reasons for this assumption.



Figure 7: The barn owl *Tyto alba* (Aves: Tytonidae) - photo: Donald Smith.

The morphology of the cave entrance would imply a bird, and the high proportion of nocturnal/crepuscular prey species suggests an owl. Only three owl species are known to nest in caves - *Tyto alba*, *Bubo capensis* (Cape eagle owl) and *Bubo africanus* (spotted eagle owl) (Maclean, 1985). *Bubo capensis*' prey size range is generally larger (Steyn & Tredgold, 1977) than that found in Hot Pot Cave, and its prey remains tend to be more fragmented (Grindley *et al*, 1973; Steyn, 1984). *Bubo africanus* tends to occur in more rocky areas in the Western Cape (Maclean, 1985). Hot Pot Cave samples' range, as well as the degree of breakage of the bones, is similar to that of the recent barn owl pellets. Furthermore, practically no evidence of bone and tooth digestion on the excavated material, also points towards barn towards barn owls being the responsible predators (Andrews, 1990). This, together with the fact that Gow (1980) found five barn owl bones in Hot Pot



Cave, belonging to at least two individuals, leaves little doubt that *Tyto alba* was the agent of accumulation for the deposit analyzed here. Micromammals that fell into Hot Pot Cave may of course also have contributed to the deposit, but the proportion is unknown and any such contributions were ignored in the calculations for this study.

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## **5. MATERIALS and METHODS**

Material was excavated from Hot Pot Cave, the micromammal bones cleaned, keyed out to species level and the different excavated layers dated. Pellet material was also collected from different roosts in the reserve to compare with the excavated material. The micromammal bones were extracted from the pellets and keyed out to species level. Micromammal livetrapping was done to add to the picture of how local micromammal communities are composed. The results were interpreted from three general perspectives.

### **5.1 The excavation**

Before excavations commenced the first 120 m of Hot Pot Cave was surveyed for the occurrence of micromammal bones. Two excavations were undertaken with the assistance of an archaeologist, Dr Graham Avery, and micromammal specialist, Dr Margaret Avery, both from the South African Museum, Cape Town. A temporary extendable ladder was used to get down the vertical entrance of the cave. A petrol generator and electric tubelight were used throughout work in the cave. A grid of 1 m<sup>2</sup> squares was marked out in the first cave chamber using a theodolite. All excavations were performed within one of the squares using standard excavation equipment i.e. a small trowel and a brush. A small vertical excavation was made to determine the thickness of the layer being excavated before the rest of the layer was excavated in the 1 m wide square. Lifting buckets and rope were used to transport the excavated material to the surface. Four layers were excavated (see Results, below).

### **5.2 Cleaning the excavated material**

Cleaning is the first step in processing excavated material starting by sifting the material through a mesh to remove most of the soily matrix. Initial sifting was done through three meshes of different coarseness up to 1,5 mm, outside the cave. The sifted material was



then transported to the laboratory in plastic bags. Final sifting was done in the laboratory through a 1,5 mm mesh.

The bone particles remaining were subsequently washed with distilled water, as chemicals in tap water might influence subsequent radiocarbon dating, using a smaller hand sieve. The cleaned bone material was then spread out on water-absorbing paper to dry.

### **5.3 Micromammal livetrapping**

Livetrapping for micromammals ( $\leq 100\text{g}$ ) was done as an additional attempt to determine the micromammal community composition under current conditions and in current habitats. Micromammals were trapped using Sherman and Elliot aluminium box traps (230 x 80 x 90mm), set out in grids of 25 or 50 traps, with traps 10 m apart, thus covering areas of either 2500 m<sup>2</sup> or 5000 m<sup>2</sup>. Bait consisted of a mixture of rolled oats, golden syrup, peanut butter, sunflower oil and beef stock. Trapping was done during four visits, representing three seasons: (i) wet season (two visits) - June 1995 and June 1997, (ii) early dry season - September 1996, and (iii) late dry season - February/March 1996. These grids were situated in 10 locations generally representing most habitats in a 10 km radius of Hot Pot Cave (see text above and Figure 6) in which barn owls are likely to hunt.

When caught, animals were weighed in a plastic bag, using a 100 g Pesola spring balance, sexed, their reproductive state (breeding/ non-breeding) determined (breeding males had enlarged testes and breeding females' vaginas were perforated), toe-clipped for individual identification and released at point of capture. Climatic conditions were also recorded.

### **5.4 Collecting recent owl pellets**

Some 1031 Pellets were collected, of which *ca* 600 were analysed (due to its size and limited resources, not all of the 3.468 kg pellet material of the last Hot Pot box sample was processed and analysed), from seven barn owl roosts (see above) in the De Hoop Nature Reserve from February 1995 to December 1998. In addition, 434 pellets collected by



N.Fairall and G.Palmer from three roosts during the period 05/01/1987 to 31/08/1987 augmented my own collection, and allowed a good comparison with the Holocene material from Hot Pot Cave. Pellets were collected randomly from around/beneath the roosts, except in the case of the last sample from the Hot Pot box, where pellets were collected from the roost itself after the chicks had left the roost.

### **5.5 Processing the recent pellets**

The hair in the pellets was dissolved in a solution made up of three teaspoons sodium hydroxide(NaOH) pellets to 1 l water. Ten pellets were put in every 1 l glass beaker and the contents stirred with a glass rod to assist the fur being dissolved. Despite the exothermic character of the sodium hydroxide's reaction with the water, it was still necessary to add external heat by putting the beakers in a hot water bath (not an open flame). If a high temperature water bath is used, the bones contained in the pellets become loose and clean within a few hours.

Bones were then washed in a hand sieve under running tap water, spread out on water absorbing paper, and allowed to dry. The bones tended to become brittle if not washed properly.

### **5.6 Sorting**

Initially all non-bone material (ie. snail shells, plant material etc.) were removed, after which the remaining bone material was separated into cranial and post cranial fractions. The cranial material was then sorted to order level - i.e. Rodentia, Insectivora or Macroscelidea - and non-micromammal cranial material (i.e. lizard jaws etc.), as well as bat skulls, removed.



### **5.7 Identification of cranial remains.**

Keying out of rodent and insectivore cranial material to species level was done by comparing cranial parts with specimens from the J.R. Ellerman museum (University of Stellenbosch) and South African Museum (D.M. Avery collection), as well as available literature, illustrations, and photographs (Meester, 1963; Davis, 1965; Corbet & Hanks, 1968; Meester & Lambrechts, 1971; Meester & Setzer, 1971; Coetzee, 1972; Avery, 1979; Perrin, 1980; De Graaff, 1981; Avery, 1982a; Skinner & Smithers, 1990; Hillson, 1986; Butler, Thorpe & Greenwood, 1989).

Alveolar patterns (see Appendix 2) were used as the primary characteristic in rodent species identification due to their simplicity and because teeth were frequently missing in the rodent material of all the samples, both recent and past. Avery's (1982a) key was particularly useful as it makes use of alveolar patterns.

The insectivore specimens tended to retain most or all of their teeth in all the samples.

### **5.8 $^{14}\text{C}$ dating**

This method was used, because the expected range of dates of excavated material was within 200 to 40 000 years BP, the range of conventional radiocarbon dating where samples contain >50 g carbon, and because bone is suitable for dating by this manner (Gillespie, 1984).

The  $^{14}\text{C}$  dating process measures the level of radioactivity due to  $^{14}\text{C}$  atoms, also known as radiocarbon (Gillespie, 1984), incorporated in organic tissue. This measurement is converted to an age, using the half-life ( $5568 \pm 30$  years) of the  $^{14}\text{C}$  isotope and atmospheric radiocarbon concentrations (Gillespie, 1984; Lowe & Walker, 1984). In the case of bone the protein component is used for dating purposes (Bowman, 1990). The method's accuracy (excluding high precision dating) is generally  $\pm 1\%$  of the age measurement (Gillespie, 1984).

$^{14}\text{C}$  dating was performed at the Quaternary Dating Laboratory of the CSIR at Pretoria using the postcranial bone material from Hot Pot Cave. This material was submitted for dating after as much as possible non-bone material was manually removed.

Ages were calibrated for the southern hemisphere with the Pretoria programme - a system taking into account deviations from the real age of a sample, due to fluctuations in atmospheric radiocarbon.

### **5.9 Interpretation**

The owl pellet material, both recent and sub-fossil, was analyzed to provide data on the following:

- I) physical size measurements of certain cranial criteria of selected species and
- II) community composition
- III) community structure indexes, i.e. species richness and evenness.

These three aspects will be treated in this order for later (see Discussion below) interpretation purposes.

With reference to the term “assemblage”, as used in this study: the material of every excavated layer is an assemblage. The recent pellets also constitute an assemblage. In the Results and Discussion sections the assemblages are referred to as “levels” and labeled by their ages e.g. the recent pellet assemblage = level AD 2000.



### 5.9.1 Physical size measurements

Because micromammals are homoiothermic, long term temperature changes may not always be reflected in distributional shifts. Apart from distributional shifts, micromammals may however react to temperature change by a change in body size (i.e. Bergmann's rule). Some measurements were consequently made on certain species in order to investigate the possible effect of temperature changes among the different assemblages (levels). Bergmann's rule states that animals living in cold climates, and by implication parts of these animals, tend to be larger than their counterparts in warmer climates (Coon, 1962). Because temperature as a climatic feature has bearing on a generally larger area than local vegetational units, it was decided to omit only the Potberg silo data from these calculations. Potberg silo is situated more inland and its immediate environment may to a lesser extent be subjected to the strong marine influence. Furthermore, Potberg's elevation above sea level may affect ambient temperature.

The following measurements were made (Avery's mean coefficients of variation shown between brackets - Avery, 1982a):

1. *Crocidura flavescens*:  $M_1$  to  $M_3$  (A.m.c.v. = 3,44) - from the anterior surface of the first lower molar to the posterior surface of the third lower molar.
2. *Myosorex varius*:  $P_4$  to  $M_3$  (A.m.c.v. = 2,87) - from the anterior surface of the fourth lower premolar to the posterior surface of the third lower molar.
3. *Tatera afra*:  $M_1$  to  $M_2$  (A.m.c.v. = 3,08) - from the anterior surface of the first lower molar to the posterior surface of the second lower molar where teeth were present, but in most cases from the anterior ridge, surrounding the anterior alveolus of the first lower molar to the posterior ridge, surrounding the posterior alveolus of the second lower molar.
4. *Cryptomys hottentotus*:  $M_3$ -sym (A.m.c.v. = 4,65) - From the posterior border of the symphysis surface (where the two mandibles join) to the posterior edge of the third lower



molar where teeth were present, but in most cases to the posterior ridge, surrounding the posterior alveolus of the third lower molar.

5. *Steatomys krebsii*: Upper alveolar length (u.a.l.) or upper tooth row (u.t.r.)- from the anterior surface of the first upper molar to the posterior surface of the third upper molar where teeth were present (u.t.r.), but in most cases from the anterior ridge, surrounding the anterior alveolus of the first upper molar to the posterior ridge, surrounding the posterior alveolus of the third upper molar (u.a.l.).

6. *Steatomys krebsii*: lower alveolar length (l.a.l.) or lower tooth row (l.t.r.) - from the anterior surface of the first lower molar to the posterior surface of the third lower molar where teeth were present (l.t.r.), but in most cases from the anterior ridge, surrounding the anterior alveolus of the first lower molar to the posterior ridge, surrounding the posterior alveolus of the third lower molar (l.a.l.).

Not all species respond equally to Bergmann's rule. The species most inclined to respond according to Bergmann's Rule in temperature change scenarios (whether it be a positive or negative response) were chosen for this exercise. According to Avery (1982a) the two shrew species *Crocidura flavescens* and *Myosorex varius* were inclined to respond to temperature change, although *M. varius* seemingly displayed a negative response to Bergmann's rule (Avery, 1982a). She does, however, mention other lines of evidence which might suggest otherwise (Avery, 1982a). Another species Avery (1982a) deemed potentially useful was the gerbil *Tatera afra*, showing some indications of a positive response to Bergmann's rule. Avery's (1982a) data further indicate definite size changes over time in her samples for measurements on the mole-rat *Cryptomys hottentotus*. Due to similarities between the mole-rat *Spalax ehrenbergi*, which shows some size-change correlation with rainfall (Tchernov, 1968), and *C. hottentotus*, it may be possible that size-changes in *C. hottentotus* may correspond with general fluctuations in precipitation. Although there are some indications of individuals tending to be larger in areas/times of high rainfall, the direction of the trend was not clear throughout Avery's (1982a) data. Klein (1984; 1986) also used a positive correlation between molar size and precipitation to research Holocene climatic conditions in the Western Cape.



As an experiment, measurements were made on *Steatomys krebsii*. This species was chosen because relatively little is known about factors governing their distribution, because of sufficient numbers and because they seem to occur in more open vegetation. This seemingly leaves them with less opportunity to utilise microhabitats in dense vegetation and a need to find an alternative way of coping successfully with temperature changes. No previously estimated coefficients of variance was known to exist for *S. krebsii* cranial measurements and consequently only the first criterium (see below) had bearing on the choice of what to measure for this species. When the measurements on *S. krebsii* were made, the Fairall-Palmer material were not available. That assemblage is not included in the size data for the above-mentioned species.

The choice of what to measure depended on a combination of:

- (1) those characters most frequently preserved and
- (2) those showing a generally low coefficient of variance (Avery, 1982a). This was done to limit the natural variation in the measured parameter, thereby facilitating the selection of more reliable variables.

All measurements were performed along the line of the jaw with a Tricle Brand caliper and recorded in millimetres.

### **5.9.2 Community composition**

Abundance of individual species and, as a result, species community composition tends to be strongly influenced by the local vegetation type, as well as directly or indirectly by climate (see Introduction for references, Figure 2 and Ecological Species Distribution). The recent community composition data was taken to represent the known current climatic regime (see 2.3) and vegetation in Hot Pot Cave area (see 3.1).



Only two roosts - the Hot Pot box and Binocular Pot - were properly situated in the same local vegetation type as Hot Pot Cave, namely coastal plain vegetation (see figure 4).

The other roosts, with the exception of the Potberg silo and Windhoek (situated in different local veld types - see Figure 4) which were omitted from these calculations, are also situated in the general band of coastal plain vegetation. Although these roosts are situated in/close to an artificial environment and immediately surrounded by vlei edge vegetation, it is apparent from information on barn owl hunting ranges (Bodenheimer, 1949; Kowalski, 1971; Hegdal & Blaskiewicz, 1984; Taylor, 1994) that its occupants would most certainly have hunted in the coastal plain habitat and within a 10 km radius of Hot Pot Cave, but not have ventured great distances from their roosts to areas with very different habitats.

Furthermore, the degree of difference between the above-mentioned samples which were taken close to the vlei vs. the samples close to Hot Pot Cave, were calculated, using the Sherman rank correlation coefficient. This was done to see whether the two groups of data could be pooled.

Micromammal species which are specific in their habitat needs (factors governing its distribution i.e. temperature, precipitation and type of vegetation) were especially beneficial in interpreting community composition data. Furthermore, species used in this exercise had to occur in substantial numbers in most samples, since too small sample sizes would yield untrustworthy and possibly meaningless information. Species with substantial numbers were taken as those occurring in at least one assemblage in a proportion of more than 2,5%.

The palaeoclimates represented by the excavated layers were reconstructed relative to the current known climate represented by the recent pellet data (e.g. cooler, slightly drier etc.) and relative to each other. Due to a lack of quantitative background information on habitat requirements for relevant species in the winter rainfall region, palaeoclimatic reconstruction on an absolute scale (e.g. 2,3°C cooler, 75 mm less precipitation per annum etc.) was not attempted (e.g. by means of factor analysis) in this study.



### 5.9.3 Community structure

The Hot Pot box and Binocular Pot, as well as the other 'coastal plain' samples (cool-room, vlei edge, milk shed and De Hoop silo) were used in community structure calculations.

Diversity indices (general diversity, species richness) and an index representing relative abundance of species (species equitability) were calculated as additional tools for comparison with existing climate theories. The basic application here is the concept of decreasing species richness (Krebs, 1978) and equitability (Odum, 1971) further from the warm tropics, towards the colder temperate and polar areas. This is in accord with Kowalski's (1971) statement that in harsh climates mammal communities contain fewer species than in milder climates.

Modern literature is not clear on exactly what can be deduced from a rise or fall in species equitability (= species evenness). Species dominance, the opposite of equitability, has in most cases an inverse relationship with species diversity (Krebs, 1978), implying that a fall in species equitability (i.e. a rise in dominance) may, to a certain extent, reflect more extreme physical conditions and possibly less habitat variety in a given area.

## 5.10 Numerical methods & Statistical analyses

The following bear relevance to both the recent and ancient cranial material.

### 5.10.1 Species Identification

The principle of 'minimum numbers represented' was used to estimate the number of individuals ( $n_x$ ) of species  $x$  in assemblage  $y$ , where the the most abundant element (i.e. left/ right maxilla/ mandible) equals  $n_x$ .

Only cranial elements with more than 50% of the element still intact was keyed out and counted. This was done to eliminate double counting of elements and to limit the "unidentified/ indeterminate"-category.



It was decided to completely rule out “?”(unknown)-categories in a manner illustrated by the examples below.

Example 1: *O. irroratus* and *O. karoensis* mandibles were taken as unassignable *with certainty* to either of the two species, but the maxillae were assignable. If, in a certain assemblage, the maxillae of *Otomys irroratus* and *Otomys karoensis* occur in a ratio of 11:3 and there are 26 mandibles, the following method of division was used:

$$O. irroratus \text{ mandibles} = 26 \times 11/14 = 20 \text{ and}$$

$$O. karoensis \text{ mandibles} = 26 \times 3/14 = 6$$

From here, again the principle of minimum numbers was applied, to estimate the respective species numbers.

Example 2: *Dendromus melanotis* and *D. mesomelas* mandibles were indistinguishable. In all the processed assemblages only two specimens of *D. mesomelas* were encountered, while 186 *D. melanotis* specimens were identified. In this case all *Dendromus* mandibles were assigned to *D. melanotis*.

Example 3: *D. melanotis* and *Steatomys krebsii* mandibles were sometimes indistinguishable, due to breakage. The “?”-quantity mandibular material was divided in the ratio of the distinguishable mandibles. Assume, in a certain assemblage, the mandible ratio between *D. melanotis* and *Steatomys krebsii* is 11:8, 33 mandibles belonging to the former and 24 to the latter, and 15 mandibles are indistinguishable.



$$D. \textit{melanotis} \text{ mandibles} = 11/19 \times 15 + 33 = 42$$

$$S. \textit{krebsii} \text{ mandibles} = 8/19 \times 15 + 24 = 30$$

From here, again the principle of minimum numbers was applied, to estimate the respective species numbers.

### 5.10.2 Physical size measurements

The variation (range), average value, standard deviation and coefficient of variation were estimated for the measured parameters of the selected species in each assemblage. The average of all the coefficients of variation of every parameter, indicated as a percentage (Simpson *et.al.*, 1960), was also calculated.

Differences in a particular measurement between assemblages were compared, using Student's t-test. In many instances the compared data-pair did not pass the normality test (Kolmogorov-Smirnoff test for normality), in which case a Mann-Whitney rank sum test was performed to obtain a *p*-value. Where data sets failed normality, Mann-Whitney-test results were used for interpretation in preference to the t-test results. A *p*-value of <0,05 were taken as indicative of a significant difference between the two data sets. *p*-Values of >0,95 probably indicate a high degree of similarity between groups and were treated as such.

### 5.10.3 Community composition

Firstly a value for every species in each assemblage (i.e. the present pellet assemblage and the four cave layers), called the 'proportion within level' (p.w.l.), was estimated. This is simply the percentage every species constitutes of the micromammal pellet material ('micromammal community') *within every assemblage/level*.

The p.w.l. values indicates the general abundance of a certain species within a certain community (percent occurrence or percentage-contribution to the community).



Secondly a value for every species in each assemblage, called the 'proportion among levels' (p.a.l.) value, was estimated for every p.w.l. value. This is the percentage a given p.w.l. value constitutes of the sum of the p.w.l. values of all the assemblages/levels *within the same species* (relative percent occurrence or relative percentage-contribution).

In formula form:

$$pa_{level\ i} = pw_{level\ i} / (\sum pw_{level\ i}) \times 100$$

Where level i represents Hot Pot Cave and recent assemblages.

$\sum$  the p.w.l. values of a certain *level* = 100 and

$\sum$  the p.a.l. values of a certain *species* = 100.

The p.a.l. values simplified comparisons of the magnitude of change from one level to another between different species.

As an additional exercise the relative percentage-contributions (p.a.l.) of every relevant species was ranked according to how it performed in every level. This was done on a scale of I to V, with rank I being the highest p.a.l value of a given species and rank V the lowest.

Relative percentage-contributions were also grouped and summed, according to the species' habitat requirements (eg. cold and dry, a preference for grass, etc), giving each level (Hot Pot Cave layers or recent assemblage) a "dry"-score, "grass"-score, "cold"-score, etc. Comparisons were done in two ways:

1. including species positively influenced by the presence of man - only ancient levels compared.
2. excluding these species - all levels compared.



#### 5.10.4 Community structure

Basically two variables in the micromammal communities were used in the estimation of the various indices: (1) the number of species ( $S$ ) and (2) the relative contribution (p.a.l.) of the various species ( $p$ ).

Two *species diversity* indices were calculated:

1. The **Shannon-Wiener index of general diversity** (Krebs, 1978), which takes into account both species richness and evenness of representation of different species (Lloyd & Ghelardi, 1964), gives the clearest pattern of differences in community structure between the different assemblages (Avery, 1982a), whilst being relatively independent of sample size (Odum, 1971) - an important prerequisite to make meaningful comparisons between samples of the present study, being of various sizes.. The Shannon-Wiener function is:

$$H = -\sum p_i \log p_i$$

where  $H$  = species diversity

$p_i$  = proportion of community belonging to the  $i$ th species

2. **Simpson's index of diversity** (Simpson, 1949), as an alternative diversity index:

$$D = 1 - \sum (p_i)^2$$

Where  $D$  = species diversity

$p_i$  = proportion of community belonging to the  $i$ th species

One *dominance-related index* was calculated.

3. The **index of species evenness** or equitability (Krebs, 1978):

$$E = H/H_{max} = H/\log S$$

where  $E$  = evenness, on a scale of 0 - 1

$H$  = species diversity (as given by the Shannon-Wiener function)

$H_{max}$  = species diversity under conditions of maximum equitability

$S$  = number of species

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## 6. ECOLOGICAL SPECIES DISTRIBUTION

For a reconstruction of past environmental conditions, a knowledge of the present conditions under which the relevant micromammals species (those occurring at De Hoop) live, is essential. Table 1 supplies summarized information. The biomes in Table 1 are basically those given by Rutherford & Westfall (1986), as adapted by Lovegrove (1993), but the wet savanna includes grassland. The precipitation maps for southern Africa used for comparison with the micromammal species distribution, were those of Lovegrove (1993), and Schulze (1972). Figure 8 shows simplified mean annual precipitation patterns for southern Africa. In general, the trend is for the northeastern and eastern (summer rainfall) and southern (winter rainfall) parts of the subcontinent to be wetter, and the western, northwestern and central parts to be drier. For correlating temperature with micromammal distribution the maps for the mean southern African annual temperature of Schulze (1972; 1980) was used. Figure 9 shows simplified mean annual temperature patterns for southern Africa. Here a general trend for warmer conditions in the north and northeast of the subcontinent is evident, although it is much less pronounced than the rainfall trends. Furthermore, there seem to be no clear temperature trends south of the Tropic of Capricorn. A trend in the temperature range (min.-max.) is, however, detectable, with more fluctuation in temperature throughout the year in the central part of the subcontinent - the northern Karoo and southern Kalahari (Werger, 1978).



**Table 1:** Summary of habitat correlates for micromammal species found in the Hot Pot Cave excavations and De Hoop owl roosts (combined from references used in text). Species occurring in sufficient numbers for interpretation purposes are printed in bold. Shaded areas indicate position and with in relation to certain parameters. Abbreviations: De=desert; SK=succulent Karoo; NK=Nama Karoo; SW=southwest (fynbos); DS=dry savanna (<500 mm/a); WS=wet savanna; Fo=forest; D=dry; W=wet; TEMP.=temperature; C=cold; W=warm; O =open; D =dense; VEGET.=vegetation; d=dry; m=moist; distrib.=distributional; Cult.=cultivation (positive reaction to); *Mva*= *Myosorex varius*; *Sva*= *Suncus varilla*; *Ccy*= *Crocidura cyanea*; *Cfl*= *Crocidura flavescens*; *Cas*= *Chrysochloris asiatica*; *Eed*= *Elephantulus edwardii*; *Cho*= *Cryptomys hottentotus*; *Gca*= *Georchus capensis*; *Oka*= *Otomys karoensis*; *Oir*= *Otomys irroratus*; *Oun*= *Otomys unisulcatus*; *Rpu*= *Rhabdomys pumilio*; *Mmi*= *Mus minutoides*; *Mnc*= *Mastomys natalensis/coucha*; *Ana*= *Aethomys namaquensis*; *Taf*= *Tatera afra*; *Mal*= *Mystromys albicaudatus*; *Dml*= *Dendromus melanotis*; *Dms*= *Dendromus mesomelas*; *Skr*= *Steatomys krebsii*

SPECIES	Southern Afr. BIOMES							HABITAT			TEMP.			VEGET.		Main distrib. factor	Veget. type	Cult.
	De	SK	NK	SW	DS	WS	Fo	D	◇	W	C	◇	W	O	D			
<i>Mva</i>	X			X	X	X								m		Dense vegetation, lower temperature	Forest, scrub & grass	
<i>Sva</i>	X			X	X											Termite mounds	Grass	
<i>Ccy</i>	X	(X)	X	X												Rocks & low rainfall	Scrub	
<i>Cfl</i>	X		X	X	X	(X)								m		Dense, wet vegetation	Scrub & grass	
<i>Cas</i>	X		X											d		Loose soil & open vegetation	Grass & scrub	////
<i>Eed</i>	X	X			X									d		Rocks & low rainfall	Scrub & grass	
<i>Cho</i>	X	X	X		X	X										Moist, loose soil	Geophytes	
<i>Gca</i>				X	X											Sandy soil with geophytes	Geophytes	
<i>Oka</i>	X	X	X													Rocky terrain, lower temperature	Scrub & grass	
<i>Oir</i>	X	X	X	(X)	X	X								m		Dense cover 1-2,5m above ground	Scrub & grass	
<i>Oun</i>	X	X	(X)		(X)									d		Rocks & dry fynbos/scrubs	Scrub	
<i>Rpu</i>	X	X	X	X	X	X	X									Dense cover	Grass (& scrub)	////
<i>Mmi</i>	X	X	X		X	X										Mild temperature & shelter	Scrub & grass	
<i>Mnc</i>			(X)		X	(X)										Relative wet & disturbed areas	Scrub & grass	////
<i>Ana</i>	X	X	X	X	X	X	X							d		Rocks	Scrub (& grass)	
<i>Taf</i>	(X)	X														Sandy soil in SW Cape (& grass)	Grass (& scrub)	////
<i>Mal</i>	(X)	X		X												Relative high rainfall & low temperature	Grass & scrub	
<i>Dml</i>				X	X	X	X									Rank, vegetation	Grass (& scrub)	////
<i>Dms</i>				X	X	X										Rank vegetation & rel. high rainfall	Grass, scrub & trees	
<i>Skr</i>	X	X	(X)	X												Open grassland /bush	Grass	



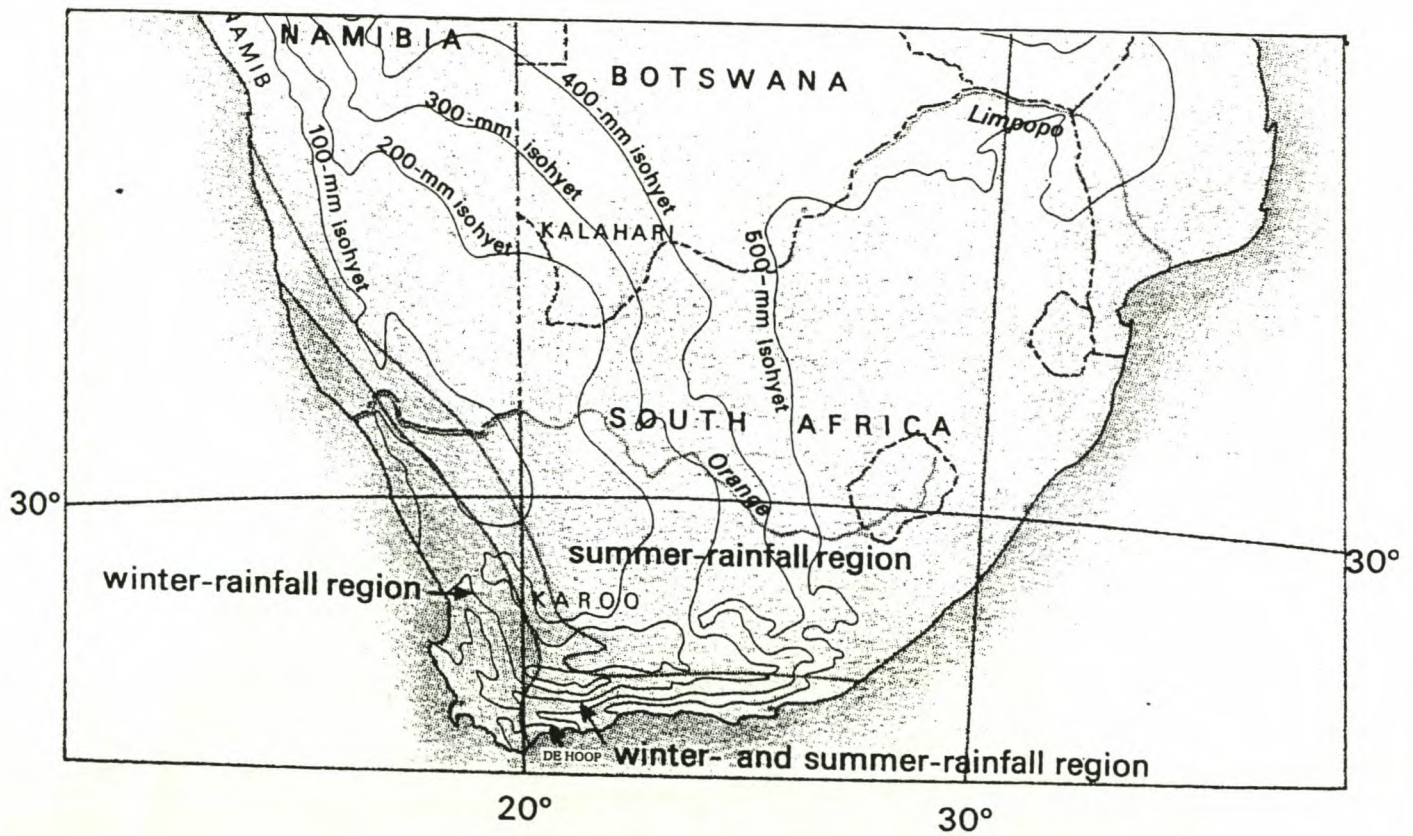


Figure 8: Simplified mean annual precipitation map for southern Africa (after Lovegrove, 1993)

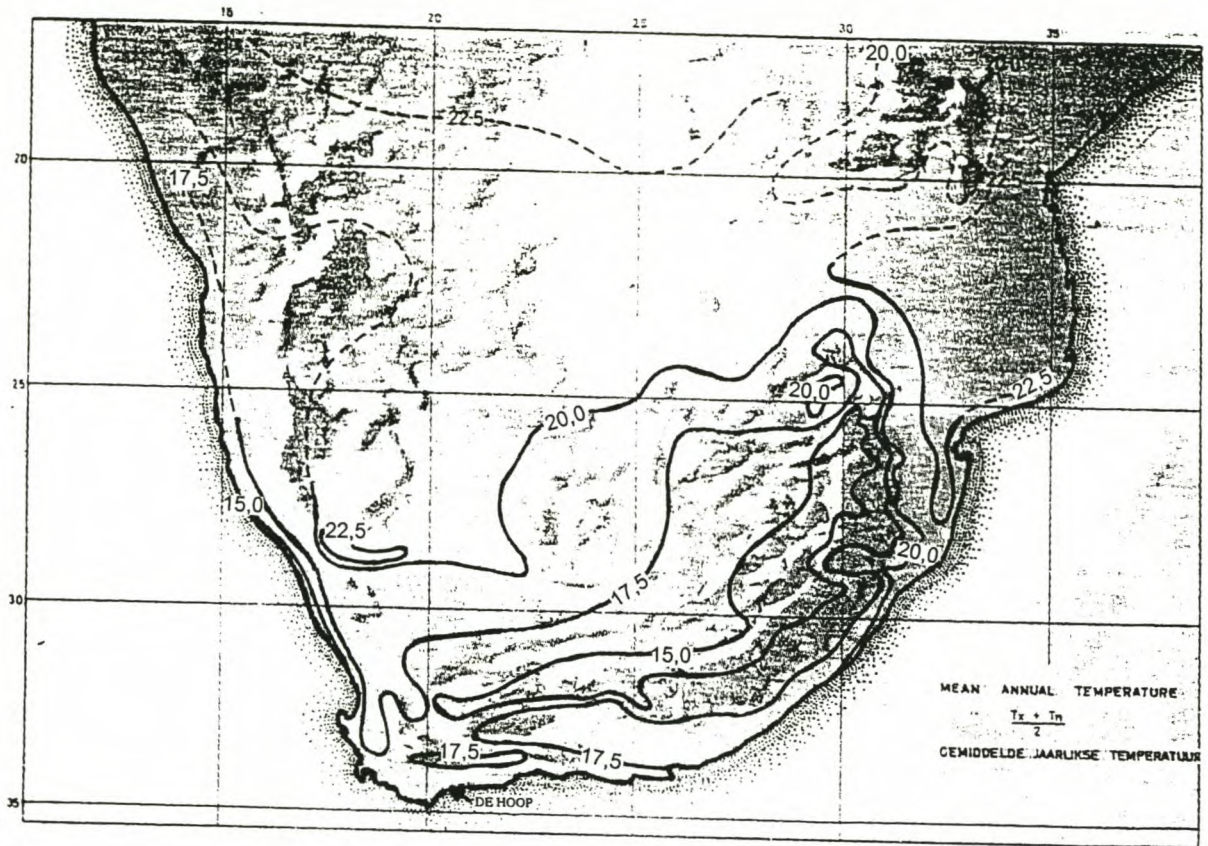


Figure 9: Simplified mean annual temperature map for southern Africa (after Schulze, 1980).



## 6.1 Insectivora

The distributions (various authors in Mills & Hes, 1997) of the five insectivore species tend to show weak geographical correlation with temperature patterns, although the northeastern part of *Crocidura cyanea*'s distribution deviates from this tendency. Generally detectable correlation with precipitation patterns (isohyets) is not evident with this order.

### *Myosorex varius* (Smuts, 1832) - Forest shrew

This species generally occurs in dense, moist vegetation (Skinner & Smithers, 1990), and has the widest distribution of the forest shrews (Dippenaar, 1997). Thackeray (1987) indicates that the species occur in the higher rainfall areas, but also occur in mesic microclimates in drier areas if the vegetation is dense enough and mists occur (Pretorius, 1993, Skinner & Smithers, 1990). There are some indications that it may tolerate sparser vegetation and drier climate than *Crocidura flavescens* (Avery, 1982a). Avery (1982a) notes that they are more sensitive to atmospheric moisture levels than denseness of vegetation. In the Western Cape it inhabits drier areas such as the coastal mountains, with a continuous cover of low succulent bushes that survive on low rainfall, and where mists are frequent (Skinner & Smithers, 1990). It may possibly be associated with colder conditions (Avery, 1982a; Thackeray, 1987). In general Avery (1982a) refers to *M. varius* as an apparent broad-niche species.

### *Suncus varilla* (Thomas, 1895) - Lesser dwarf shrew

These shrews prefer open grassland, and often inhabit large termite mounds (Skinner & Smithers, 1990). They are generally found in a wide range of habitats, mostly in wetter areas, except where they occur in parts of the succulent Karoo (Dippenaar, 1997). A rise in numbers in owl prey may possibly indicate more open vegetation or open patches, since the



smaller micromammals are unlikely to be spotted by owls in denser vegetation (Avery, 1982a).

***Crocidura cyanea cyanea* (Duvernoy, 1838) - Reddish-grey musk shrew**

The species has a wide habitat tolerance - from very dry to very wet and from warm to cold environments (Stuart & Stuart, 1993). *C. c. cyanea*, differs from *C. c. infumata* in its distribution and the structure of M<sub>3</sub> (Meester, 1963), and is the subspecies likely to occur in the present study area. It tends to occur in areas with lower rainfall (< 500 mm/year) (Skinner & Smithers, 1990). Avery (1982a) lists it as indicating scrub vegetation.

***Crocidura flavescens* (Geoffroy, 1827) - Greater musk shrew**

It is generally found in dense, damp vegetation, and nests well above ground (Skinner & Smithers, 1990). According to Meester (1963) *C. flavescens* tends to occur in wetter areas, i.e. those with an annual rainfall of between 500 and 750mm, and valleys in mountainous areas, but is not restricted to any particular type of vegetation (Meester, 1963). More recent information (Swanepoel, 1975; Pretorius, 1993) reports it to also occur in drier areas, given dense enough vegetation and/or frequent mists. Avery (1982a) reports that they tend to avoid very cold conditions and by their presence may, in fact, indicate a general rise in temperature.

***Chrysochloris asiatica* (Linnaeus, 1758) - Cape golden mole**

*C. asiatica* are mostly restricted to the fynbos, grassland and succulent karroid veld types (but do not occur in the Karoo itself - Bronner, 1997), where they occur in sandy soil under Karoo scrub (Shortridge 1942; Rautenbach, 1971) or in alluvial soil of open grasslands (Shortridge, 1942) - especially that loosened by cultivation activities (Skinner & Smithers, 1990). They coexist well with humans (Bronner, 1997).



## 6.2 Macroscelidea

### *Elephantulus edwardii* (Smith, 1839) - Cape Rock elephant shrew

Not listed for the De Hoop area, but occur in the succulent Karoo and in the Port Elizabeth area of the Eastern Cape Province (Skinner & Smithers, 1990; Stuart & Stuart, 1993; Perrin, 1997) - areas that tend to be drier than De Hoop. They show a tendency to occur in open vegetation and are usually associated with rocky terrain. Avery (1982a) notes that their presence may indicate sparse, possibly semi-arid vegetation. Corbet & Hanks (1968) report them to occur in grassland, although in this study they have been caught in relative high abundance in areas where scrub is predominant, little grass is present and there are limestone outcrops and loose rocks in the vicinity.

## 6.3 Rodentia

### *Cryptomys hottentotus* (Lesson, 1826) - Common mole-rat

These fossorial mammals (Bigalke, 1978), are capable of utilizing a wide range of soil types, except hard and heavy soils, and occur in many different climatic regimes (Skinner & Smithers, 1990). Their distribution is probably limited by the availability of bulbs and tubers (Jarvis, 1997). Avery (1982a) remark that their presence may suggest fairly open grassland, and also the presence of bulbous- and tuberous-species. Soil moisture may also affect distribution, since they are more active when the soil is wet (Skinner & Smithers, 1990) and are, in fact, adapted to conditions in moist soil (Haim & Fairall, 1986). They also have a tendency, like other mole-rats, to move on the surface at night, especially when it rains (Skinner & Smithers, 1990), which, of course, makes it more susceptible to becoming owl prey.



***Georychus capensis* (Palls, 1778) - Cape molerat**

They occur in slightly compact sandy soils, rich in geophytes (Jarvis, 1997). Their distribution tends to be in the less dry montane areas of the Western Cape, various types of fynbos, and coastal sand dunes (Skinner & Smithers, 1990; Jarvis, 1997).

***Otomys karoensis* (= *O. saundersiae*) (Roberts, 1929) - Saunders' vlei rat**

They occur in belts of dry rushes ('sedge meadows' - Stuart & Stuart, 1993) in heath country (probably referring to ericoid vegetation), mostly in mountainous terrain (Shortridge, 1942) and mostly, though not exclusively, in the winter rainfall areas. Restioid/'grassy' vegetation and open scrub cover may also be suggested by the occurrence of this species (Avery, 1982). Kerley (1997) also remarks that it probably feeds mainly on the stems of restios. It is known to prefer rockier situations with more open vegetation than does *Otomys irroratus* (Avery, 1982a). In general, colder conditions seem to be suggested by this species' presence, because Avery detected in her data (1982a) that this species was apparently at an advantage during the Last Glacial maximum, declining in numbers thereafter.

***Otomys irroratus* (Brants, 1827) - Vlei rat**

*O. irroratus* has a wide distribution, but is more abundant in moist, marshy habitats (Stuart & Stuart, 1993), dense waterside vegetation (Avery, 1982a) and areas of generally dense basal and canopy cover (Avery, 1982a). Its habitat preferences are described as >75% scrub cover of 1 to 2,5 m above ground (Bond *et al*, 1980). Especially relevant to the study area, is that Avery (1982a) mentions it to probably indicate the dense microphyllous proteoid vegetation on the limestone ridges. It may also suggest the presence of reedbeds and grasses on which it feeds (Kerley, 1997). Its presence may furthermore suggest mild conditions (Avery, 1982a). Relative to other species, such as *Rhabdomys pumilio* and *Myosorex varius*, *O. irroratus* is described as being a narrow-niche species (Avery, 1982a).



***Otomys unisulcatus* (Cuvier, 1829) - Karoo bush rat .**

This is another species found in this study, but which was not previously recorded from the De Hoop area according to existing distributional information (Skinner & Smithers, 1990; Stuart & Stuart, 1993; Kerley, 1997). It tends to occur in drier, though not sparse, scrub and fynbos areas in association with rocky outcrops as well as in coastal fynbos (Skinner & Smithers, 1990).

***Rhabdomys pumilio* (Sparrmann, 1784) - Striped mouse**

*Rhabdomys pumilio* is described as being essentially a grassland species, although it occurs in a very wide range of climatic conditions and habitats (Skinner & Smithers, 1990) - e.g. found in scrub by Nel & Pretorius (1971). They also thrive in areas where agricultural crops are produced and conifer plantations are grown (De Graaff, 1997). The vegetation type may probably be less important than its preference for dense cover (Avery, 1982a). Avery (1982a) also describes *R. pumilio* as a broad-niche species. Bigalke (1978) refers to the species as scansorial, as well as occurring on the ground surface, because it also climbs into small trees.

***Mus minutoides* (Smith, 1834) - Pygmy mouse**

It has a wide habitat tolerance - from the succulent Karoo and fynbos regions to the Nama-Karoo and savanna regions. The genus is described by Bigalke (1978) as occurring on the ground surface. It tends to shelter under vegetation debris (Skinner & Smithers, 1990). *M. minutoides* may also occur in declining/secondary vegetation (Vesey-Fitzgerald, 1966). Downs & Perrin (1996) state that the species seems to be physiologically warm-adapted. Its distribution indicates that it shuns less-densely vegetated areas (mostly sparse grasslands) - probably due to a lack of plant debris or other shelter on the surface. Even though, Avery (1982a) argues that one might, as in the possible case of *S. varilla*, expect its



numbers to be higher in the owl diet in open vegetation where owls would be more able to spot the smaller micromammal species by sight, Payne (1971, 1958), Knudsen (1981), Knudsen *et al.* (1979), Knudsen and Konishi (1979), Konishi (1973), Konishi and Kenuk (1975) and others found that barn owls can locate and capture prey entirely by the use of sound, especially since the barn owl's night vision is relatively poor for a crepuscular/nocturnal raptor (Taylor, 1994). This implies that dense vegetation with much dry plant debris may actually be beneficial for the owl to locate *M. minutoides* (due to the rustling sound made by the mouse). One might furthermore expect this species' numbers to rise with the onset of mild to warm conditions, because of the small body size (rapid heat loss in cold conditions) of *M. minutoides*. Cold conditions may have the effect of lower numbers in the owl diet, because cold would force it to utilize denser microhabitats and thus be out of reach for the barn owls, and/or it may simply decline in numbers in cold conditions, due to lower reproductive/survival rates. The species' wide habitat tolerance may tend to lessen its interpretive value, however, except perhaps for the interpretation of temperature regimes.

***Mastomys natalensis* (Smith, 1834)/*coucha* (Smith, 1836) - Natal multimammate mouse/multimammate mouse**

These two species are treated together, because, due to a lack of external differences by casual observation, their exact respective areas of distribution has not been determined with certainty. Generally the two species occur in warmer (Thackeray, 1987) and wetter areas (>400 mm/a.) or in river valleys penetrating drier areas. The species' tendency to avoid cold conditions is also demonstrated by Rowe-Rowe & Meester's (1982) results, which indicate that they do not occur above an altitude of 1500 m. Their habitats may include grassland - especially where a cover of low scrub is present (De Graaff, 1997) - forest and rocky areas (Vesey-Fitzgerald, 1966; Avery, 1977). *M. natalensis* tends to live commensally with man (Pienaar, 1964 - before *M. coucha* was described) and is known to be a pioneer species - colonising disturbed or destructed areas, to be replaced by other species in the later stages of succession (Meester *et al.*, 1979).



***Aethomys namaquensis* (Smith, 1834) - Namaqua rock mouse**

*Aethomys namaquensis* utilizes a wide variety of habitats in a wide variety of climatic regimes (Skinner & Smithers, 1990), but prefers rocky terrain (Roberts, 1951; Bond *et al.*, 1980) and scrub-vegetation cover (Hanney, 1965; Bond *et al.*, 1980). Avery (1982a) notes the species to apparently occur in both fynbos and semi-arid scrub, and perhaps more often in the latter. Bond *et al.* (1980) also report the species to dominate the more arid patches of their study area. This agrees with Buffenstein and Jarvis' (1985) findings that the species appears to be physiologically well adapted to the desert environment. Reports of *A. namaquensis* occurring in ericoid and restioid fynbos are made by Nel *et al.* (1980) and David & Jarvis (1983). The species clearly seems to be broad-niched, as is also implied by Avery (1982a). They are terrestrial, but also construct nests 1 - 2m above ground where trees or tall scrubs and grass are present (Skinner & Smithers, 1990) and in riverine vegetation (Pretorius, 1993).

***Tatera afra* (Gray, 1830) - Cape gerbil**

This endemic species of the fynbos biome only occurs in areas of loose, sandy soils (Skinner & Smithers, 1990). It is often associated with open grasslands possessing good drainage (Perrin, 1997) and perhaps scattered trees or bushes (Avery, 1997). It is a primary burrower (Bigalke, 1978), excavating extensive systems (Perrin, 1997). It is also found in cultivated lands (Roberts, 1951). Avery (1982a) notes *T. afra* to have been the dominant species during a wet period, as represented by some the samples she worked with.

***Mystromys albicaudatus* (Smith, 1834) - White-tailed mouse/rat**

Towards the north and east of South Africa it tends to occur in the grassland biome, but it also occurs in parts of the Karoo and the fynbos biome (Skinner & Smithers, 1990). Its presence apparently indicates more open vegetation (Avery, 1982a). Its distribution



roughly corresponds with the higher rainfall areas (Thackeray, 1987). Downs & Perrin (1995) found *M. albicaudatus*' physiology to be typically cold-adapted and some of Avery's data (1982a) seem to confirm this.

### ***Dendromus melanotis* (Smith, 1834) - Grey climbing mouse**

*Dendromus melanotis* is generally associated with tall grass (Stuart & Stuart, 1993) or other tall growth, such as thatching grass, thickened up with other vegetation, such as scrubs and annuals (De Graaff, 1997). The species occurs in a wide habitat range - from sea level to an elevation of 2700 m, and from areas with *ca* 200 mm rainfall/ year in the Kalahari to areas with an annual precipitation of >1200 mm/year (Skinner & Smithers, 1990). The drier edge of its distribution seems to show a rough correlation with the 350 mm/year isohyet, although it deviates from this in the southern Kalahari and northern Namibia, where it occurs in much drier conditions. Its distribution nonetheless seems to have a stronger correlation with precipitation than with temperature patterns. Its occurrence in drier areas, such as the Kalahari, may suggest that this species is better adapted to dry, open vegetation than is *Dendromus mesomelas* (see below).

### ***Dendromus mesomelas* (Brants, 1827) - Brants' climbing mouse**

It generally occurs in bush, woodland (Davis, 1962) and tall grass with scrub (Ansell & Ansell, 1973). Unlike *D. melanotis* it does not occur under such a wide range of precipitation, but tends to prefer the wetter southern and eastern parts of the country. In the Drakensberg, where *D. mesomelas* and *D. melanotis* occur in the same general area, the former seems to be better adapted to tall grass (Skinner & Smithers, 1990).



***Steatomys krebsii* (Peters, 1852) - Krebs' fat mouse**

*Steatomys krebsii* seem to occur in dry, sandy (Skinner & Smithers, 1990) open grassland and bush (Shortridge, 1942) and, according to Avery (1982a), probably also in areas with trees. Distributional data are incomplete due to a lack of collected specimens (De Graaff, 1997). In a comparison between *S. krebsii* and *Tatera afra*, Avery (1982a) suggests *S. krebsii* to prefer more open vegetation, probably drier (based on work on *S. pratensis* by Coetzee, 1969) and warmer conditions.

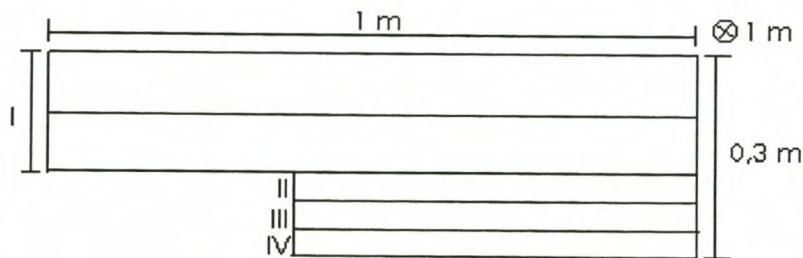
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## 7. RESULTS

### 7.1 Amounts of material collected

Four layers were identified during two excavations, of which the uppermost and youngest was by far the most extensive (Figure 10). The four identified layers form a sequence, with the uppermost (layer 1) being the youngest. Layer 1 is divided into two in the diagram, because with the first excavation it was thought to consist of two separate layers



**Figure 10:** The extent of the excavated Hot Pot cave layers. Layer numbers are indicated on the left.

Table 2 lists the number and locations of collected pellets and excavated material. A total number of *ca* 1465 recent pellets (7578,4 g) was collected during this study and by Palmer and Fairall in the 1980s, of which *ca* 431 (2572,4 g) were analyzed. Average pellet weight was calculated at 5,6 g.

**Table 2:** List of the recent pellet collection sites and Hot Pot cave excavation layers, as well as the amounts of pellet material collected from the roosts/ excavated from Hot Pot Cave in De Hoop Nature Reserve. Abbreviations: P-cran.= postcranial; Cran.= cranial; Vol.(l)= volume (litres).

Location	Date	no. of pellets	Total pellet mass (g)	P-cran.bone mass (g)	Cran.bone mass Rodentia	Cran.bone mass Insectivora
<b><u>RECENT SAMPLES</u></b>						
Potberg silo1	87/1/5	213	676	180.8	43.5	3.6
Potberg silo2	87/6/16	78	363	84.8	30.1	1.7
Potberg silo3	Feb.95	21	83.2	21.7	5	0.5
De Hoop silo1	87/6/2	6	31	9.5	2.3	0
De Hoop silo2	87/6/30	21	97	28.6	9.5	0.1
Windhoek1	Feb.95	36	255.1	60.6	22.3	0.6
Windhoek2	May.96	38	218.6	76	21	1.1
Koelkamer1	87/1/5	41	161.7	46.8	20.5	0.1
Koelkamer2	87/1/30	11	29	8.6	1.4	0.1
Koelkamer3	87/7/31	29	128.5	40.7	12.5	0.2
Koelkamer4	87/8/31	35	165.5	52.4	9.9	0.1
Koelkamer5	Feb.95	38	166.4	58.6	17.5	0.5
Koelkamer6	Sep.96	40	159.4	46.7	14.8	1
Koelkamer7	Jun.97	28	120.7	33	11.6	0.3
Vlei cliffs1	Feb.95	16	100.5	34.4	4.6	0.3
Vlei cliffs3	Sep.96	8	47.3	15.2	3.8	0.4
Vlei cliffs3	Jun.97	30	136.8	58.7	27.4	0.7
Melkkamer1	Feb.95	39	285.9	117	34.1	1.9
Melkkamer2	May.96	42	247.7	80	30.3	1.8
Binocular Pot	26/9/98	80	448	104.1	45.7	3.5
Hot Pot Box1	27/9/98	34	190.4	42.5	7.4	0.3
Hot Pot Box2	Dec.98	150	895.1	39.9	15	0.7
<b>Total</b>		<b>1034</b>	<b>5006.1</b>	<b>1240.6</b>	<b>390.2</b>	<b>19.5</b>
Hot Pot Box2 (not used)	Dec.98	±431	2572.4			
<b><u>HOT POT CAVE SAMPLES</u></b>						
<b>Layer</b>		<b>Vol.(l)</b>				
Layer 1		27.3		378.4	82.5	13.8
Layer 2		8		70.8	10.6	1.1
Layer 3		9		191.7	48.4	5.8
Layer 4		±13		216	30.9	5.9
<b>Cave total</b>		<b>57.3</b>		<b>856.9</b>	<b>172.4</b>	<b>26.6</b>



## 7.2 <sup>14</sup>C dates

The 2 sigma range for the calibrated dates of each of the four excavated layers is given in Table 3. This represents *ca* 95% of the time range covered by each sample (Gillespie, 1984), and therefore indicate basically two standard deviations. The mode is the most probable date. The corrections (in years) take into account variations in isotope fractionation. Ages were converted from years before present (with AD 1950 internationally taken as reference year zero - Gillespie, 1984) to calendar dates (AD).

**Table 3:** Carbon dating results of the excavated bone material from Hot Pot Cave. Anal. no = laboratory analysis number.

Layer	2-sigma range	Mode	Correction	Anal. no
1	AD 1390 - 1446	AD 1417	± 45	Pta-7531
2	AD 934 - 1042	AD 991	± 50	Pta-7525
3	AD 521 - 685	AD 615	± 50	Pta-7522
4	AD 250 - 306	AD 381	± 50	Pta-7532

The different cave levels will henceforth be referred to by their most probable date (although it also includes to the 2 sigma range) and the present level by 'AD 2000'.

## 7.3 Micromammal livetrapping

Table 4 gives the percentages of species caught and site descriptions. A clear trend exists, with *Rhabdomys pumilio* dominating the catches to such a degree that it renders the livetrapping data practically useless (1) as indicative of the coastal plain vegetation and (2) as a comparison with the owl pellet prey content (and thus as an aid to interpret the ancient material). Furthermore, a low number of species (relative to the number occurring in the area) is evident - only seven.

Species trapped, but not previously recorded in the reserve, according to the official micromammal list for De Hoop (see above), are:



Cape rock elephant shrew *Elephantulus edwardii*Brants' climbing mouse *Dendromus mesomelas***Table 4:** Micromammal livetrapping results (%) from different locations in De Hoop Nature Reserve. See Table 1 for species abbreviations.

Habitat	Date	Trap nights	No of traps	Grid size(m <sup>2</sup> )	Percentage of catches						
					Rpu	Mmi	Ana	Dml	Dms	Mva	Eed
Low to medium height limestone veld - ± as at Hot Pot cave	Jun.95	300	50	5000	100	-	-	-	-	-	-
	Feb./Mar.96	100	25	2500	92.9	7.1	-	-	-	-	-
	Sep.96	125	25	2500	100	-	-	-	-	-	-
	Jun.97	125	25	2500	97.7	-	-	-	-	-	2.3
Coastal fynbos at coastal front - near Koppie Alleen	Jun.95	300	50	5000	95.5	4.6	-	-	-	-	-
	Feb./Mar.96	200	50	5000	93.3	6.7	-	-	-	-	-
	Sep.96	250	50	5000	100	-	-	-	-	-	-
	Jun.97	125	25	2500	94.4	-	-	-	-	5.6	-
Very short limestone veld	Jun.95	250	50	5000	-	-	-	-	-	-	-
	Feb./Mar.96	100	25	2500	50	50	-	-	-	-	-
	Jun.97	125	25	2500	80	-	-	-	20	-	-
Medium height to High <i>Protea/Leucodendron</i> veld at foot of limestone hills	Jun.95	250	50	5000	76.9	-	-	-	7.7	-	15.4
	Feb./Mar.96	100	25	2500	100	-	-	-	-	-	-
	Sep.96	100	25	2500	69.2	-	-	-	-	-	30.8
	Jun.97	125	25	2500	92.3	-	-	-	-	-	7.7
Open woodland & shrubs	Jun.95	250	50	5000	100	-	-	-	-	-	-
	Feb./Mar.96	100	25	2500	100	-	-	-	-	-	-
High, old <i>Protea/Leucodendron</i> veld on top of limestone hills	Jun.95	250	50	5000	100	-	-	-	-	-	-
Medium height shrubland landwards of sand dunes.	Feb./Mar.96	100	25	2500	93.1	6.9	-	-	-	-	-
Low grassy fynbos on sand	Sep.96	125	25	2500	100	-	-	-	-	-	-
Burnt (6 months) <i>Protea/Leucodendron</i> veld	Sep.96	5	50	5000	-	-	-	-	-	-	-
Medium height <i>Leucodendron</i> veld near vlei	Sep.96	125	25	2500	30.77	-	7.7	7.7	-	-	53.9

**4 Physical size measurements**

In Table 5 averages of measurements and other statistical indicators are given. The results of the samples in every set of measurements are compared statistically (Student's t-test and/or Mann-Whitney rank sum test) with each other in Table 6. Statistically significant differences ( $p < 0,05$ ) occurred in 7 of the 60 comparisons.



**Table 5:** Averages and other statistical indicators of physical size measurements. R- = negative correlation with rainfall; ? = undetermined reaction to climate change; T+ or T- = positive or negative correlation with temperature change. See Table 1 for species abbreviations.

	<i>Cho</i>	<i>Skr</i>	<i>Skr</i>	<i>Taf</i>	<i>Mva</i>	<i>Cfl</i>
MEASUREMENTS:	M3-sym	u.a.l.	l.a.l.	M1-2	P4 - M3	M1-3
CORRELATION:	R+	?	?	T+	T-	T+
<b>AD 2000</b>						
n	12	5	18	174	99	-
Range	7.1 - 9.5=2.4	4.1 - 4.4=0.3	3.2 - 4=0.8	4.4 - 6.1=1.7	4.5 - 6=1.5	-
Average	8.68	4.28	3.65	5.19	5.48	-
S.D.	0.65	0.13	0.26	0.36	0.25	-
Coeff. of variation	7.51	3.05	7.17	6.98	4.56	-
<b>AD 1417</b>						
n	11	46	52	46	50	17
Range	6.2 - 9.7=3.5	3.7 - 4.7=1	3.2 - 4.2=1	4.9 - 5.9=1	4.9 - 5.9=1	5.2 - 5.9=0.7
Average	8.79	4.28	3.74	5.37	5.54	5.63
S.D.	0.97	0.24	0.22	0.26	0.23	0.19
Coeff. of variation	11.05	5.66	5.86	4.77	4.09	3.31
<b>AD 991</b>						
n	2	12	11	-	7	5
Range	8.5 - 9.8=1.3	3.9 - 4.9=1	3.4 - 4.3=0.9	-	5.4 - 6=0.6	5.4 - 6=0.6
Average	9.15	4.38	3.86	-	5.67	5.74
S.D.	0.92	0.31	0.28	-	0.23	0.24
Coeff. of variation	10.05	7	7.25	-	4.04	4.2
<b>AD 615</b>						
n	7	24	36	42	27	27
Range	8.7 - 10.1=1.4	3.7 - 4.9=1.2	2.9 - 4.2=1.3	4.9 - 6=1.1	5.2 - 5.9=0.7	5.3 - 6.1=0.8
Average	9.27	4.36	3.66	5.43	5.5	5.59
S.D.	0.51	0.26	0.32	0.25	0.2	0.22
Coeff. of variation	5.52	5.92	8.59	4.63	3.72	4
<b>AD 381</b>						
n	7	37	56	37	31	14
Range	7.9 - 9.4=1.5	3.4 - 5=1.6	3.2 - 4.1=0.9	4.9 - 6.5=1.6	4.9 - 5.9=1	5.4 - 6=0.6
Average	8.8	4.29	3.72	5.45	5.51	5.69
S.D.	0.45	0.34	0.21	0.32	0.25	0.18
Coeff. of variation	5.17	7.86	5.75	5.92	4.58	3.15
<b>Average</b>	<b>8.86</b>	<b>4.31</b>	<b>3.72</b>	<b>5.28</b>	<b>5.51</b>	<b>5.62</b>
<b>Coeffs. of variation average</b>	<b>7.86</b>	<b>5.9</b>	<b>6.92</b>	<b>5.58</b>	<b>4.2</b>	<b>3.67</b>



**Table 6:** Statistical comparison of size results. In each comparison block: upper value = *p*-value according to Student's *t*-test; middle value = degrees of freedom; lower value = *p*-value according to Mann-Whitney rank sum test. Values indicating significant difference are printed in bold.

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.094 12			
AD 991	0.45 7	0.804 7		
AD 1417	0.982 16 0.526	0.248 16	0.638 11	
AD 2000	0.683 17	0.057 17	0.385 12	0.756 21 0.23

*Cryptomys hottentotus*: M<sub>3</sub> - symphysis

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.351 59 0.337			
AD 991	0.382 47 0.416	0.832 34		
AD 1417	0.952 81 0.673	0.205 68 0.144	0.231 56 0.182	
AD 2000	0.967 40 0.985	0.497 27	0.485 15	0.981 49 0.862

*Steatomys krebsii*: upper alveolar length

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.406 91 0.34			
AD 991	0.06 65 0.078	0.083 46		
AD 1417	0.638 105 0.908	0.254 86 0.359	0.115 60 0.075	
AD 2000	0.247 72 0.435	0.767 53	<b>0.047</b> 27	0.154 67 0.371

*Steatomys krebsii*: lower alveolar length

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.722 77 0.328			
AD 991	—	—		
AD 1417	0.199 81 0.29	0.278 86	—	
AD 2000	< <b>0.001</b> 209 < <b>0.001</b>	< <b>0.001</b> 214 < <b>0.001</b>	—	< <b>0.001</b> 218 < <b>0.001</b>

*Tatera afro*: M<sub>1-2</sub>

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.922 56 0.338			
AD 991	0.128 36 0.243	0.068 32 <b>0.041</b>		
AD 1417	0.628 79 0.58	0.539 75 0.151	0.145 55 0.279	
AD 2000	0.617 128 0.187	0.705 124 0.969	0.057 104 <b>0.045</b>	0.217 147 <b>0.035</b>

*Myosorex varius*: P<sub>4</sub> - M<sub>3</sub>

	AD 381	AD 615	AD 991	AD 1417
AD 615	0.185 39			
AD 991	0.601 17	0.19 30		
AD 1417	0.401 29	0.574 42	0.286 20	
AD 2000	—	—	—	—

*Crocidura flavescens*: M<sub>1-3</sub>



## 7.5 Community composition

The area surrounding the excavation site (Hot Pot Cave) is at present relatively homogeneous, both geomorphologically and concerning plant communities. This simplifies the palaeoenvironmental reconstruction process substantially.

This degree of homogeneity was tested by calculating the degree of difference between the micromammal species composition of the pellets of two roosts close to Hot Pot Cave (Hot Pot box and Binocular Pot - representing the area in which the ancient Hot Pot Cave owls hunted) vs. that of the roosts close to the vlei, using the Sherman rank correlation coefficient test. The results showed a significant similarity in composition ( $p < 0,025$ ) between the two groups (see Table 7) and, as a result of this, the data was pooled for the community composition exercise.

**Table 7:** A Sherman rank correlation evaluation in micromammal species composition between two groups of samples from the coastal plain of De Hoop Nature Reserve: (1) from roosts near the vlei and (2) near the Hot Pot. Species are listed in order of rank 1's results.

See Table 1 for species abbreviations.

pellets	Eed	Oun	Ccy	Cas	Cho	Mnc	Mmu	Skr	Mmi	Ana	Oka	Mva	Oir	Dml	Sva	Taf	Rpu	Tot.	
<b>Rank 1: SAMPLES near VLEI</b>																			
n	384	0	1	3	3	4	4	5	11	16	20	25	36	62	70	82	99	116	557
Rank	1	2	3.5	3.5	5.5	5.5	7	8	9	10	11	12	13	14	15	16	17		
<b>Rank 2: SAMPLES near HOT POT</b>																			
n	264	8	0	0	1	0	0	0	9	1	0	49	10	50	6	7	3	29	173
Rank	12	3.5	3.5	7.5	3.5	3.5	3.5	13	7.5	3.5	17	14	16	10	11	9	15		
<b>Rank1 - Rank2</b>																			
$=d_i$	-11	-1.5	0	-4	2	2	3.5	-5	1.5	6.5	-6	-2	-3	4	4	7	2		
$d_i^2$	121	2.25	0	16	4	4	12.25	25	2.25	42.3	36	4	9	16	16	49	4		363.
																			<u>1</u>
Sherman rank correlation coefficient ( $r_s$ ) = 0,56																			
The test statistic ( $t_s$ ) = 2,61																			
0,01 < $H_0$ : $p < 0,025$ where $H_0 = 0\%$ correlation between the 2 groups																			

Table 8 gives the composition of all collected pellet samples, for all species. Table 9 shows the community composition from two perspectives: (1) species proportions within each level (p.w.l.-values - see explanation in Material and methods), or percentage contribution, and (2) proportions among the different levels (p.a.l. value), or relative

percentage contribution, of those species occurring in adequate numbers (see below). For the recent (AD 2000) data in Table 9, 648 pellets were used. The p.a.l. values are graphically displayed for all relevant species in Figure 11.

Table 10 ranks the relative percentage contributions of every species in each level in order of I to V. Level 1 (AD 2000) has the highest representation in the extreme rankings (I and V).

In Table 11 relative percentage contributions are grouped and summed, according to the species' habitat requirements. In the columns where no recent value has been calculated the species positively influenced by the presence of man were included in calculations and *vice versa* for the columns with five values.



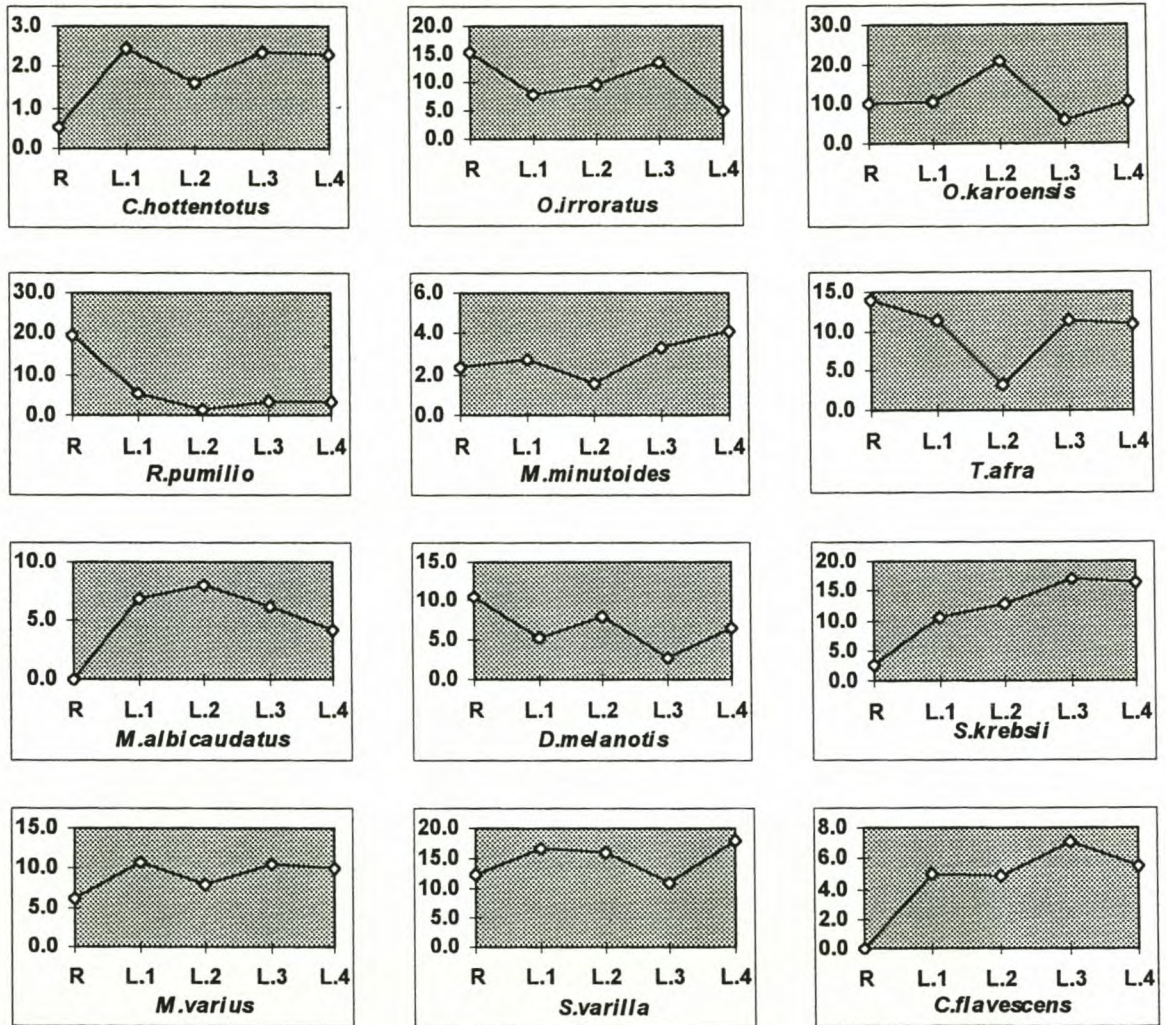
**Table 8:** Numbers of specimens of all species in recent De Hoop owl pellets and Hot Pot Cave samples. Species abbreviations printed in bold represent those that occurred in sufficient numbers to be used in further calculations. See Table 1 for species abbreviations.

	<i>Cho</i>	<i>Gca</i>	<i>Oir</i>	<i>Oka</i>	<i>Oun</i>	<i>Rpu</i>	<i>Mmu</i>	<i>Mmi</i>	<i>Mnc</i>	<i>Ana</i>	<i>Taf</i>	<i>Mal</i>	<i>Dml</i>	<i>Dms</i>	<i>Skr</i>	<i>Mva</i>	<i>Sva</i>	<i>Cfl</i>	<i>Ccy</i>	<i>Cas</i>	<i>Eed</i>	Total specimens		
<b>RECENT SAMPLES</b>																								
Sample	pellets																							
Koelkamer 1	41	2		4		1		1		2	12				1		1					24		
Koelkamer 2	11			1							2								1			4		
Koelkamer 3	29			3		6				3	11				2		5			1		31		
Koelkamer 4	35			2		2				1	12		1			1						19		
Koelkamer 5	38			6		14				2	7		1	1	4	6						41		
Koelkamer 6	40			5	3	18				2	7		1		7	9		1	1			54		
Koelkamer 7	28			5	4	11	1				9		8	3	2	4						47		
De H.silo 1	6										2		1									3		
De H.silo 2	21	1		4		1		3		1	5		6		1		4					26		
Vlei cliffs 1	16					6					6				2		3					17		
Vlei cliffs 2	8			1		6	4	5	2		1		4		1	3	1					28		
Vlei cliffs 3	30			12	5	4		2	1		9		6			2	8					49		
Melkkamer 1	39			13	5	1	19	3	1	4	10		7			10	17			1		91		
Melkkamer 2	42	1		6	8	28		2		5	6		35			7	24		1			123		
Bin. Pot	80			33	17	12							3		3	4	3			1	5	81		
H.Pot Box 1	34			8	6	4		1					2			1	1					23		
H.Pot Box 2	150			9	26	13					3		1		6	5	3				3	69		
<b>Total</b>	<b>648</b>	<b>4</b>	<b>0</b>	<b>112</b>	<b>74</b>	<b>1</b>	<b>145</b>	<b>5</b>	<b>17</b>	<b>4</b>	<b>20</b>	<b>102</b>	<b>0</b>	<b>76</b>	<b>0</b>	<b>20</b>	<b>46</b>	<b>89</b>	<b>0</b>	<b>3</b>	<b>4</b>	<b>8</b>	<b>730</b>	
<b>HOT POT CAVE SAMPLES</b>																								
Level	Vol.(l)																							
AD 1417	27.3	9	4	29	38	1	19			10		2	42	25	19	2	38	39	61	18		6	2	364
AD 991	8	1	1	6	13		1			1	2	5	5		8	5	10	3						62
AD 615	9	5	5	29	13		7		1	1	24	13	6		36	22	23	15			3	1		211
AD 381	13	5	2	11	23		8			9		24	9	14		36	22	39	12			4		218
<b>Total (l)</b>	<b>57.3</b>																							
<b>SAMPLES NOT USED IN CALCULATIONS</b>																								
Location																								
Potb. silo 1	21	1		1	1	1	3			1	4		2		5		4	2	2			3		
Potb. silo 2	213	4		14	5	1	23			38	42	6	5		40		19	19	34			13	1	
Potb. silo 3	78	2		20	11		7			20	1		4		18		40	11	18			1	1	
Windhoek 1	36	1		10		8	4			1		1	1		1			4	4					
Windhoek 2	38			8	4	11	2						2					6	6					
H.Pot Box 2 (unprocessed)	±431																							

**Table 9:** Micromammal species representation of recent De Hoop owl pellets and Hot Pot Cave samples. Abbreviations: pwl = proportion within level; pal = proportion among levels. See Table 1 for species abbreviations.

		<i>Cho</i>	<i>Oir</i>	<i>Oka</i>	<i>Rpu</i>	<i>Mmi</i>	<i>Ana</i>	<i>Taf</i>	<i>Mal</i>	<i>Dml</i>	<i>Skr</i>	<i>Mva</i>	<i>Sva</i>	<i>Cfl</i>
<b>RECENT SAMPLES</b>														
<b>AD 2000</b>	<b>pwl</b>	0.55	15.34	10.14	19.86	2.33	2.74	13.97	0.00	10.41	2.74	6.30	12.19	0.00
	<b>pal</b>	<b>5.92</b>	<b>29.63</b>	<b>17.40</b>	<b>58.97</b>	<b>16.48</b>	<b>51.02</b>	<b>27.33</b>	<b>0.00</b>	<b>31.59</b>	<b>6.43</b>	<b>13.82</b>	<b>16.50</b>	<b>0.00</b>
<b>EXCAVATION SAMPLES</b>														
<b>Level</b>														
<b>AD 1417</b>	<b>pwl</b>	2.47	7.97	10.44	5.22	2.75	0.55	11.54	6.87	5.22	10.44	10.71	16.76	4.95
	<b>pal</b>	<b>26.59</b>	<b>15.39</b>	<b>17.92</b>	<b>8.96</b>	<b>19.45</b>	<b>10.24</b>	<b>22.57</b>	<b>27.24</b>	<b>15.84</b>	<b>24.51</b>	<b>23.49</b>	<b>22.69</b>	<b>22.10</b>
<b>AD 991</b>	<b>pwl</b>	1.61	9.68	20.97	1.61	1.61	1.61	3.23	8.06	8.06	12.90	8.06	16.13	4.84
	<b>pal</b>	<b>17.33</b>	<b>18.69</b>	<b>35.99</b>	<b>2.76</b>	<b>11.39</b>	<b>29.98</b>	<b>6.32</b>	<b>31.96</b>	<b>24.46</b>	<b>30.29</b>	<b>17.68</b>	<b>21.84</b>	<b>21.61</b>
<b>AD 615</b>	<b>pwl</b>	2.37	13.74	6.16	3.32	3.32	0.47	11.37	6.16	2.84	17.06	10.43	10.90	7.11
	<b>pal</b>	<b>25.51</b>	<b>26.54</b>	<b>10.57</b>	<b>5.70</b>	<b>23.48</b>	<b>8.75</b>	<b>22.24</b>	<b>24.43</b>	<b>8.62</b>	<b>40.06</b>	<b>22.88</b>	<b>14.76</b>	<b>31.74</b>
<b>AD 381</b>	<b>pwl</b>	2.29	5.05	10.55	3.67	4.13	0.00	11.01	4.13	6.42	16.51	10.09	17.89	5.50
	<b>pal</b>	<b>24.65</b>	<b>9.75</b>	<b>18.11</b>	<b>6.30</b>	<b>29.21</b>	<b>0.00</b>	<b>21.54</b>	<b>16.38</b>	<b>19.48</b>	<b>38.76</b>	<b>22.13</b>	<b>24.22</b>	<b>24.55</b>





**Figure 11:** Micromammal species representation as a relative percentage-contribution (p.a.l. value) of every assemblage. Levels are indicated on the x-axis and proportional values on the Y-axis. Abbreviations: R = recent (AD 2000); L1 = layer 1 (AD 1417); L2 = layer 2 (AD 991); L3 = layer 3 (AD 615); L4 = layer 4 (AD 381).



**Table 10:** Ranking the relative percentage contribution (p.a.l.-values) of micromammal species in recent De Hoop owl pellets and Hot Pot Cave samples, with rank I being the highest and rank V the lowest. The top value in each block indicates the level (1 the recent data and 5 the oldest) and the bottom value the corresponding p.a.l.-value. The range of every species' p.a.l.-values (maximum - minimum) is also given. See Table 1 for species abbreviations.

RANK	<i>Cho</i>	<i>Oir</i>	<i>Oka</i>	<i>Rpu</i>	<i>Mmi</i>	<i>Ana</i>	<i>Taf</i>	<i>Mal</i>	<i>Dml</i>	<i>Skr</i>	<i>Mva</i>	<i>Sva</i>	<i>Cfl</i>
<b>I</b>	2	1	3	1	5	1	1	3	1	4	2	5	4
	<b>26.59</b>	<b>29.63</b>	<b>35.99</b>	<b>58.97</b>	<b>29.21</b>	<b>51.02</b>	<b>27.33</b>	<b>31.96</b>	<b>31.59</b>	<b>40.06</b>	<b>23.49</b>	<b>24.22</b>	<b>31.74</b>
<b>II</b>	4	4	5	2	4	3	2	2	3	5	4	2	5
	<b>25.51</b>	<b>26.54</b>	<b>18.11</b>	<b>8.96</b>	<b>23.48</b>	<b>29.98</b>	<b>22.57</b>	<b>27.24</b>	<b>24.46</b>	<b>38.76</b>	<b>22.88</b>	<b>22.69</b>	<b>24.55</b>
<b>III</b>	5	3	2	5	2	2	4	4	5	3	5	3	2
	<b>24.65</b>	<b>18.69</b>	<b>17.92</b>	<b>6.30</b>	<b>19.45</b>	<b>10.24</b>	<b>22.24</b>	<b>24.43</b>	<b>19.48</b>	<b>30.29</b>	<b>22.13</b>	<b>21.84</b>	<b>22.10</b>
<b>IV</b>	3	2	1	4	1	4	5	5	2	2	3	1	3
	<b>17.33</b>	<b>15.39</b>	<b>17.40</b>	<b>5.70</b>	<b>16.48</b>	<b>8.75</b>	<b>21.54</b>	<b>16.38</b>	<b>15.84</b>	<b>24.51</b>	<b>17.68</b>	<b>16.50</b>	<b>21.61</b>
<b>V</b>	1	5	4	3	3	5	3	1	4	1	1	4	1
	<b>5.92</b>	<b>9.75</b>	<b>10.57</b>	<b>2.76</b>	<b>11.39</b>	<b>0.00</b>	<b>6.32</b>	<b>0.00</b>	<b>8.62</b>	<b>6.43</b>	<b>13.82</b>	<b>14.76</b>	<b>0.00</b>
<b>Range</b>	<b>20.67</b>	<b>19.88</b>	<b>25.42</b>	<b>56.21</b>	<b>17.82</b>	<b>51.02</b>	<b>21.01</b>	<b>31.96</b>	<b>22.97</b>	<b>33.63</b>	<b>9.67</b>	<b>9.46</b>	<b>31.74</b>



**Table 11:** Relative percentage contributions (p.a.l.-values) grouped for micromammal species in recent De Hoop owl pellets and Hot Pot Cave samples indicating certain environmental parameters. Abbreviations: Art. = 'artificial' - species reacting positively or are adaptable to artificial influences, such as human disturbance, including agriculture; min.A = minus 'artificial' species. See Table 1 for species abbreviations.

Level	Art.	Cold & dry		Cold & wet	Warm & dry	Warm & wet	Grass		Scrub
		min.A					min.A		
AD2000	168.91	17.40	13.82	—	29.63	22.93			
AD1417	57.61	28.16	17.92	50.73	—	37.49	94.57	47.20	10.24
AD991	63.52	65.97	35.99	49.64	—	40.30	85.67	52.13	29.98
AD615	45.31	19.32	10.57	47.31	—	58.28	91.38	54.82	8.75
AD381	47.32	18.11	18.11	38.51	—	34.30	110.30	62.98	0.00
SPECIES	<i>Rpu</i> <i>Ana</i> <i>Taf</i> <i>Dml</i>	<i>Oka</i> <i>Ana</i>	<i>Oka</i>	<i>Mva</i> <i>Mal</i>	—	<i>Cfl</i> <i>Oir</i>	<i>Sva</i> <i>Rpu</i> <i>Taf</i> <i>Dml</i> <i>Skr</i>	<i>Sva</i> <i>Skr</i>	<i>Ana</i>

The species community composition as indicated by the recent pellet material (level AD 2000) in Table 9 can be correlated with the current vegetational composition of the De Hoop coastal plain. This vegetational composition, as indicated by the area surrounding Hot Pot Cave, is roughly:

1. Limestone substrate: *ca* 40%

\* *ca* 30% bare

\* *ca* 20% large shrubs and small trees

\* *ca* 25% small shrubs

\* *ca* 15% herbacious undergrowth

\* *ca* 10% restios

2. Sandy substrate: *ca* 40%

\* *ca* 10% bare

\* ca 25% large shrubs (mostly *Protea* and *Leucodendron* species)

\* ca 25% small shrubs

\* ca 20% grass

\* ca 15% restios

\* ca 5% herbaceous undergrowth

### 3. Pans with clay substrate: ca 20%

\* 100% grass of which some areas are submerged under water during the wet season

Not all species occurred in adequate numbers throughout all the levels. Those not constituting at least 2,5% of an assemblage in at least one assemblage (level) were treated as numerically insufficient and omitted from the general palaeoenvironmental reconstruction process. In Table 8 these species' abbreviations are not printed in bold. The species that did occur in sufficient numbers throughout all the levels (bold in table 8) were:

*Myosorex varius*

*Suncus varilla*

*Crocidura flavescens*

*Cryptomys hottentotus*

*Otomys karoensis*

*Otomys irroratus*

*Rhabdomys pumilio*

*Mus minutoides*

*Aethomys namaquensis*

*Tatera afra*



*Mystromys albicaudatus*

*Dendromus melanotis*

*Steatomys krebsii*

The species occurring in sufficient numbers differed in interpretive value, those being broad-niched and/or adapted for mesic conditions having less interpretive value (e.g. *R. pumilio*), because of their less specific indication of habitat. Those being narrow-niched and/or adapted for more extreme conditions (wet, dry, warm, cold, very dense vegetation, very open vegetation) had better interpretive value. No species used in this study are really adapted for extreme conditions, but some species proved to be good indicators of specific climatic trends, e.g. *M. albicaudatus*, indicating cold and wet conditions. Some species' numbers tend to be influenced by the presence of man, i.e. *R. pumilio*, *T. afra* and *D. melanotis*. The AD 2000 numbers of these species were interpreted in such a way that artificial influences on species numbers were taken into account.

The results show a relatively wide spectrum of species with no outright dominance of any single species, except, to an extent *R. pumilio* and *A. namaquensis*.

Species recorded in the pellet material, but not previously recorded in the reserve, according to the official micromammal list for De Hoop (see above), are (see Table 8):

*Elephantulus edwardii*

*Georychus capensis*

*Otomys unisulcatus*

*Dendromus mesomelas*

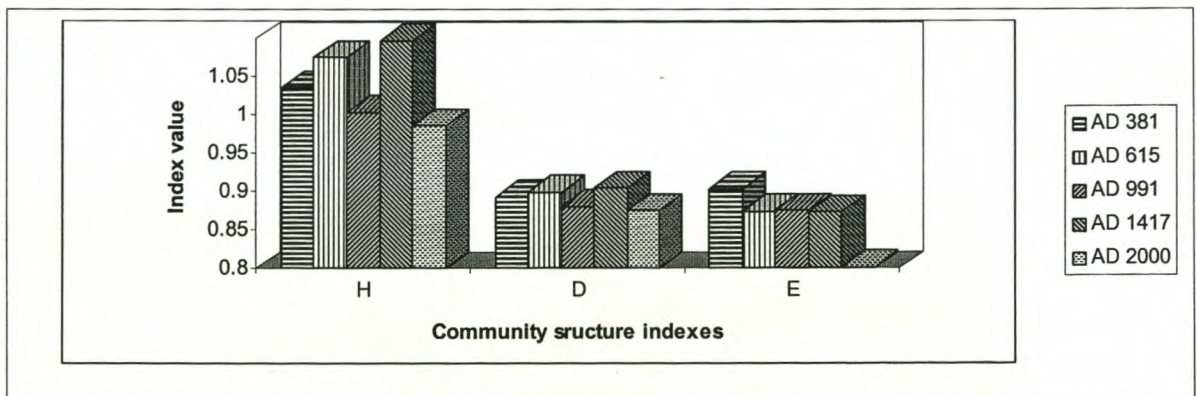
*Steatomys krebsii*

## 7.6 Community structure

Table 12 displays the diversity and evenness index values. In Figure 12 the community structure index values are compared graphically. The results show very similar values throughout, although one detects generally lower values for AD 2000.

**Table 12:** The diversity and evenness values of micromammal species in recent De Hoop owl pellets and Hot Pot Cave samples.

	AD 381	AD 615	AD 991	AD1417	AD 2000
<i>Shannon-Wiener general H diversity index:</i>	1.035	1.075	1.003	1.096	0.985
<i>Simpson's diversity index D</i>	0.893	0.899	0.88	0.904	0.875
<i>Species evenness index: E</i>	0.903	0.874	0.875	0.873	0.801



**Figure 12:** Community structure index values for the different levels: a graphic comparison.



## 8. DISCUSSION

### 8.1 Micromammal livetrapping

The trapping results show a clear dominance in the numbers of *Rhabdomys pumilio* (Table 5). This dominance is of such a degree that it renders the livetrapping results of very little, if any value for comparison with the pellet material, let alone standardising it. The fewer species represented in the trapping results, as opposed to occurring in the pellet material, correspond with trapping results from the S.A.Lombard Nature Reserve (Meester, 1955), showing four less species than Vernon's (1972) results on pellet content studies from the same area. Furthermore, the phenomenon of very few species caught and the dominance of *R. pumilio* numbers corresponds with trapping results obtained at De Hoop (Anon., 1986) by a group of zoology honours students. Their results also showed *R. pumilio* to be the dominant species.

It would seem that the livetrapping data is, as in the case of the pellet data, also subject to certain biases, such as different species being more or less trap-shy and being conditioned quicker. Avery (1982a) remarks that too many variables may be operative to make comparison between trapping results and pellet contents useful for assessing owl pellet biases.

One would expect the diurnal/crepuscular species to show a generally higher representation in the trapping results than in the pellets, since the barn owl would not normally hunt in daylight (although they have been observed to hunt on dull, overcast days - McLachlan & Liversidge, 1970). Furthermore, many micromammal species display, to a greater or lesser extent, trap-shyness or do not take bait (Davis, 1973). The opposite may, of course, also be true that some species/individuals are not deterred by the trap and may actually grow accustomed to the bait, consequently 'coming back for more' the following night. The type of trap used may influence trapping results (Neal & Cock, 1969; Wingate & Meester, 1977). A numerical bias is the effect of 'nonuse'(non-availability), where the event of catching an animal puts that trap out of circulation and lessens the effectivity of the trap



grid, since the area immediately surrounding such a trap are not sampled for the remainder of the trial period.

## **8.2 Background discussion to interpreting the owl prey data**

### **8.2.1 Identification problems**

Most identification problems were similar to those Avery (1982a) encountered in her research (See Appendix 3).

On average the bone material from the recent owl pellets was in good enough condition to identify, but the quality of the excavated bone material seems to have deteriorated with age - those of the oldest/deepest layer being very difficult at times to identify.

The Palmer/Fairall material was rather brittle and tended to break easily when handled. One exception to the overall good quality of the modern material was the last sample taken from the Hot Pot Box. It appears to have been subjected to trampling and breakdown from cloacal excretions of the chicks and the parent birds, as well as some digestive effects of the chicks (Andrews, 1990). However, in chick-feeding regurgitation by the parent owls is, however, unlikely (Hosking and Flegg, 1995). The sample consisted mostly of pellets cast by chicks (smaller than those of adults). It contains proportionately less cranial material than the other samples. The postcranial: cranial ratio in all the other pellet samples combined, was 3:1 and in the Hot Pot samples, 4,3:1, while in the second Hot Pot box sample it was 5,5:1. The parent owls may have decapitated prey before taking it to the nestlings (Vernon, 1972; Newman, 1979; Andrews, 1990; Taylor, 1994).

### **8.2.2 Possible biases**

Unfortunately the data that has been generated is the product of a natural environment and not the pure product of those circumstances we would like to have imposed on it as if in a



laboratory. Therefore it contains certain 'impurities' and 'pitfalls', which are essential to consider when interpreting the data.

Biases relevant to comparing excavation sample with pellet sample, rather than excavation sample with biocoenose (life assemblage) were considered. For the purpose of this study it is less important to know the exact composition of the relevant micromammal communities, but rather *changes* in micromammal samples. Were the samples treated equally by nature?

One type of bias concerns the hunting process of the barn owl:

**I. *Prey size limits*** - no influence on this study's results.

Some biases concern the differences in circumstances the material in the Hot Pot has been subjected to as opposed to the modern pellets:

**II. *Micromammals falling into Hot Pot Cave*** - assumed not to have a significant effect on the data, because one would expect species to fall into the cave in an approximate proportion to their abundance and because it is assumed that the amount of individuals that fell into the cave would consist a very small proportion of the excavated material.

**III. *Weathering*** by washing around would not be a factor as the radio-carbon dating showed the material to occur in layers, implying that it had not been washed around extensively. No weathering by wind would have occurred. Apart from this, weathering is not expected to make certain species less identifiable and to bias the compositional data. In other words, no selected preservation is expected to occur. Water corrosion due to stagnant rain water or moisture in the soily matrix is a factor with strong possibility and would explain much of the lower quality of preservation in some of the older samples. It did not, however, have an effect on the species composition data.

**IV. *Trampling*** would only have occurred in the cave area where the excavation was done when a large animal (eg. baboon, ostrich or medium size antelope) fell into the cave. This would not have happened often and should not bias the composition of the samples.



V. *Fires* can be ruled out as a bias, since it is highly unlikely that humans would have occupied the Hot Pot, due to its inaccessibility, and the heat of veld fires could not reach the cave floor.

VI. The *meshes* used should not cause a problem. During the excavation the smallest mesh used was 1,5 mm mesh, which retains all relevant material.

VII. Some rodent populations tend to be subject to *short term fluctuations* such as three or eight year cycles (Honer, 1963; Taylor, 1994). The animals may also have been influenced by climatic cycles of five to seven year cycles (Tyson, 1978), 10 to 12-year cycles and 18-year cycles (Vines, 1980). Even in environmentally stable conditions, fluctuations in community structure occur (Klomp, 1962). These are mere fluctuations in the process of establishing environmental homoeostasis however (Odum, 1971), and should not bias Hot Pot Cave data, since changes in the values of the excavated layers do not represent these short term fluctuations (the compositional data represent an average for the layers' 2 $\sigma$  ranges, and these ranges are too wide). The short term cycles, together with seasonal cycles may well cause skewness in the data of the modern owl pellets as in the case of the Hot Pot box which was sampled only twice, in time slots close to each other, and in the case of Binocular Pot which was sampled only once. Much of this skewness should, however, be mitigated by the fact that the present pellet material used for community composition comparison was collected over a period of five years and in all seasons.

VIII. Some *artificial biases*, introduced by European settlers and for the most part absent during the deposition of the cave material, may influence the data of the present pellet material. Burning practices to improve grazing, as well as cultivation of crops would have benefitted those species able to adapt to these new environments and reduced the numbers of those not able to do so. These phenomena were, as far as possible, incorporated in the interpretation process of the assemblage labeled 'AD 2000'.

Then there are numerical-related artifacts.

IX. *Species' proportional contribution* to the community are relative to each other and *may amplify or subdue each other's* absolute changes in abundance. This scenario may, to a



certain extent, be tempered by the fact that barn owls do not sample prey species in direct proportion to its abundance, but are to a certain extent selective hunters (Glue, 1967; Avery, 1982a; Colvin, 1984 in Taylor, 1994).

These numerical artifacts should not necessarily cause misinterpretations, since this study focuses on relative (not absolute) abundance.

X. Then there is the possibility of *contaminants in the dated samples*, which may affect the accuracy of the ages obtained. Humic acid as a product of surrounding organic material and carbonates in groundwater (both being of a different age than the bone material) may occur, and remain after washing, on the bone material in minute quantities invisible to the human eye (Gillespie, 1984). In most dating laboratories, though, as is the case with the CSIR laboratories, it is general procedure to remove carbonates and humic acids (Gillespie, 1984).

### 8.2.3 Time scale

Before any palaeoenvironmental reconstruction can be attempted, it is important to take into consideration the relevant *time scale*. A sequence covering 100 millennia will show larger amplitude in natural climatic fluctuations than would one covering approximately two millenia, as is the present case. Major climatic trends, or parts thereof, such as between the glacials and interglacials, displayed in cycles of 90 000 to 100 000 years (Delcourt & Delcourt, 1991), are impossible to perceive in as short a time period as 2000 years. This is especially true when the time lag involved for climatic changes to be mirrored in micromammal changes, in many cases via vegetation change (see 8.2.5) is taken into account.

The results to be obtained from a study of a sequence covering such a short time period should be treated with caution and reserve.



### 8.2.4 What can micromammal owl prey tell us?

What are the limits of using terrestrial microfauna as an environmental reconstruction tool? Avery (1982a) proposes that the use of terrestrial indicators, such as the type of data used here, show a tendency to be rather localised in relevance and have to be treated as such.

Compared to other terrestrial fauna, micromammals, as environmental indicators, combine the following aspects: (1) containing a rich amount of information and (2) being relatively (to larger mammals and some other indicators) sensitive reflectors of change, because of their small body size and rapid breeding.

One would expect the time lag in micromammalian changes, as a response to environmental change, to be small. Despite the advantages of micromammalian studies noted above, this is not entirely so. Because of the lag of vegetational change, the lag of migration processes and the small gradients for change caused by the typical lesser environmental changes of the Holocene, one finds five observations cramped into little less than 2000 years (short time lapses in between periods) to be too few and too short in time range for micromammal evidence to document visible environmental change. Avery (1979: 217) suggests that relative to the larger changes shown by Pleistocene sequences "Changes within the Holocene are hardly monitored by the micromammalian evidence and it is suggested that changes must have been relatively minor". Her 1982a data also show a general trend for only monitoring more significant change between layers representing longer time periods. Furthermore, Klein (1983) suggests that climatic conditions during the past 5000-3000 years have been broadly similar to modern conditions.

When analysing the results of the ancient and modern owl pellet material, one should keep in mind that it represents the owl's diet (Raczynski & Ruprecht, 1974) - i.e. *primarily* those prey items preferred by the owl and/or are easiest to obtain and *secondarily* environmental conditions.

Apart from independent population changes (e.g. those resulting from climatic change), changes in the micromammal community may be the result of some interrelated reaction between/among species (referring to prey species), where one species may influence the



distribution of another - mostly due to interspecific competition of some sort. In an area of overlap a narrow-niche species has an advantage over a broad-niche species (Avery, 1982a), as is the case with *Otomys irroratus* (narrow-niche) and *Rhabdomys pumilio* (broad-niche), where both prefer dense vegetation. Although habitat separation occurs, the limited habitat overlap between the two species may have an effect. In such a scenario, under optimal conditions the relative abundance of *R. pumilio* (to *O. irroratus*) may decrease in a given area, even though its 'preferred' habitat increases.

It is therefore important to keep in mind when reconstructing the latter part of the Holocene climate that, as far as community composition and community structure is concerned, *ecological components* (e.g. a species' proportional contribution to a community) are used. Climate is therefore but one of a complex set of variables influencing the ecological component - although probably the largest on a short term scale (see Figure 2).

Although attempts has been made in the past to use micromammal data to indicate absolute (quantitative) changes in climatic parameters, these methods have their limitations and shortcomings (see Palaeoenvironmental Reconstruction below) and in this study micromammal prey was used only to indicate qualitative changes.

One can argue that, despite the virtues of micromammals as environmental indicators, taking the complexities, shortcomings and other relevant biases into account, the interpretation of the micromammal data should, at best, be viewed as a simplification of climatic changes and can therefore be expected to merely show *directional trends*. This is amplified by the shortness (few layers and short period of time) of the sequence, which allows us to see only a very small part of a bigger picture and makes it difficult to determine the exact time period of fluctuations.

### **8.2.5 What causes climate change?**

Even though it is not primarily the aim of this study to research reasons for climate change, but rather an attempt to detect changes, it is still of some importance to give a brief



discussion of the relevant environmental influences. In other words, *what causes climatic change* at De Hoop?

**A. Latitude:** Tectonic movement may cause changes in latitude, but the time scales concerning tectonic movement vastly differ from the time scale relevant to this study.

**B. Topography** (e.g. mountains, altitude and distance from the sea): The latter may be influenced by sea level changes due to ice ages such as the Last Glacial Maximum which ended approximately 12 500 years BP (Avery, 1982a). Although the sea level rose by about 100-130m on the southwestern South African coast (a coastline transgression of 50-100 km) during the last 16 000 years (Dingle & Rogers, 1972; Deacon & Lancaster, 1988), Shackleton & Opdyke (1973) state that the sea reached its modern levels about 6000 BP. After 6000 BP sea level fluctuations were of a much lesser magnitude - less than 3 m - than the preceding period (Martin, 1968; Butzer & Helgren, 1972; Montaggioni, 1976; Birch, 1976; Flemming, 1977; Deacon & Lancaster, 1988; Yates *et al.*, 1986; Suguio *et al.*, 1988; Illenberger & Verhagen, 1990; Jerardino, 1993). These changes were clearly not of the magnitude to have a significant influence on this study's data - the limestone cliffs along De Hoop's shore are approximately 7 to 12 m in height. For the rest, again geological time applies, which therefore also rules out major changes in topography as a viable possibility.

**C. Ocean currents** have dramatic effect on climate. Although the major ocean currents would not have changed over the past two millennia, changes in sea-surface temperatures might have had a pronounced influence on De Hoop's climate. Cohen *et al.* (1992) detected some significant sea-surface temperature fluctuations along the southern African Atlantic shores during the past 1000 years. Greater or lesser cold water input by the Circumpolar Circulation, facilitated by the westerly winds (Jerardino, 1995) into the Benguela Current may have contributed to these fluctuations (Jerardino, 1995). Furthermore, the fact that De Hoop is situated close to the separation between the warm waters of the Agulhas current (flowing in from the east) and the colder Benguela current (to the west), makes the area's climate susceptible to changes in the shoreline areas influenced by the one or the other. Cohen (1993) postulated a wetter and warmer southern Cape



(southern areas of the Western and Eastern Cape Provinces) in the event of a weakening in the Agulhas Current (greater advection of warm water into the Benguela Current).

**D.** Another variable is the general circulation of the atmosphere. A northward shift of the Antarctic Polar Front in the Atlantic Ocean (Hays *et.al.*, 1976) and of the subtropical convergence in the Indian Ocean (Bé & Duplessy, 1976) had a pronounced effect on southern African weather during the Last Glacial Maximum, causing, among other things, the northward shift of the winter rainfall boundary (van Zinderen Bakker, 1976). One can argue that similar, though of a much lesser magnitude, changes in these circulation features during the Holocene might have had similar minor weather changes. Changes in the location of the South Atlantic and Indian Ocean anticyclonic cells (Avery, 1982a) have probably occurred during the past 2000 years, with certain effect on the De Hoop climate.

**E.** The only remaining variables are events that cause global climatic changes on the time scale relevant to this study. These may possibly include changes in the amounts of greenhouse gasses (Chappelaz *et.al.*, 1990; Jouzel *et.al.*, 1993 and others), precession of the equinoxes resulting from the tilting of the earth's axis (Lowe & Walker, 1984), changes in the eccentricity of the earth's orbit and the obliquity of the orbit (Tyson, 1988), volcanism (Porter, 1986) and global scale changes in oceanic and atmospheric circulation.

Apart from the 23 708 yr Milankovitch periodicity in climatic patterns, Campbell *et.al.* (1998) detected strong 1500 yr and weaker century- to millennial-scale periodicities affecting global climates.

### **8.2.6 Anthropomorphic influences on De Hoop**

People occupying the region at the dates under discussion, brought about artificial influences on the environment and as a consequence, on micromammal species numbers.

The oldest layer corresponds in general with the latter part of the Late Stone Age Wilton industry and the first occupations of prehistoric herders (Deacon, 1979), the Khoi-khoi (Rutherford & Westfall, 1986). Sheep might have been introduced into the southern



regions of the Western Cape as early as 2000 BP (Deacon *et al*, 1978), although the oldest sheep remains found by Sealy & Yates (1994) in the region were from Die Kelders, with a calibrated date of  $1325 \pm 60$  years BP. This converts to AD  $625 \pm 60$  years. It is therefore possible that the oldest Hot Pot Cave layer may not have been influenced by any pastoralist activities whatsoever. During the time periods represented by the remaining layers the area would, if occupied by humans at all, probably have been occupied by prehistoric herders, who probably belonged to the the Hessequa tribe (Butcher, 1983), with their field burning practices influencing local vegetation (Skead, 1980), and possibly San people, who were hunter-gatherers (Rutherford & Westfall, 1986). The earliest European human presence dates back to the early 18th century (Butcher, 1983; De Hoop management plan, 1987). The area could therefore be viewed as 'alien-free' (referring to both plants and animals) for all the excavated layers.

Due to the low annual rainfall, shallow soil and rocky substrate, farming activities on the coastal plain have never been very intensive, being mainly restricted to grazing by livestock on the floodplain areas (Butcher, 1983). The study area aquired full conservation status in 1956 (Butcher, 1983) but the bordering areas north of the coastal plain are subject to intensive agricultural activities and the exact influence of these activities on micromammal numbers is not known.

### **8.3 Owl prey data and palaeoenvironmental reconstruction**

Noticeable changes in size measurements, compositional data or community structure data derived from micromammal owl pellet remains have been used in this study to indicate the *direction* of climatic changes (e.g. *a* is warmer than *b*; *c* is drier than *a*, but wetter than *b*), but not the extent of change (e.g. *x* amount of change in micromammal data =  $\Delta y^{\circ}\text{C}$  in ambient temperature). Attempts to use micromammal data as a measure of absolute change has been made by Thackeray (1987, 1995). However, Thackeray's correlation of known micromammal distribution with meteorological records may have some inaccuracies which influenced the choice of interpretation processes in his study:



- \* Existing maps indicating where micromammal species occur in Southern Africa are generalisations and does not indicate where they flourish and where they barely survive. This implies that the calculated precipitation and temperature averages are not necessarily optima for the relevant species.
- \* Furthermore, the above mentioned maps do not indicate areas of local absence (for whatever reason) within their range. This may skew the precipitation and temperature averages calculated for every species, to an extent that they may not even be averages at all.
- \* The single average precipitation and temperature value for every species does not contain any information on the relevant species' niche width - whether it has wide or narrow precipitation and temperature tolerances.
- \* The precipitation and temperature averages for every relevant species' complete distribution will probably differ from the value for its winter rainfall distribution.
- \* The micromammal species for which values are published (Thackeray, 1987), do not contain all the species relevant to the present study.

As described by Avery (1982a), significant changes over a period of a few hundred years, as is the magnitude of this study's time intervals, are viewed as being quite rapid.

In the palaeoenvironmental reconstruction process a general approach was followed by which first the 'most straightforward/ simplest/ easiest to explain' data was interpreted and systematically moving towards the 'less clear/ harder to interpret' data, progressively adding to the palaeoclimatic information of the period under discussion, until a coherent picture emerges.

### **8.3.1 Physical size measurements**

Statistical values mentioned below are from Tables 4 and 5.

The climatic information derived from size measurements is discussed before the community-related data, since it is the simplest to interpret and probably least biased (e.g.



no interspecies competition, human influence, etc.) and will supply a general basis for the community-related interpretations.

Where the  $p$ -value is not indicated to be derived from the Mann-Whitney test (used for data which was not normally distributed), it was derived from Student's  $t$ -test.

The most obvious trend in the size measurements is in the *Tatera afra* data, where all AD 2000 measurements are different from those of the other levels in being significantly smaller ( $p < 0,001$ ). This not only confirms *T.afra*'s positive response to Bergmann's rule (see 5.9.1), but also indicates AD 2000 to be noticeably milder (warmer) than the other levels. In the *Myosorex varius* data the AD 2000 measurements are also noticeably smaller than those of both the AD 1417 (Mann-Whitney:  $p < 0,05$ ) and AD 991 (Mann-Whitney:  $p < 0,05$ ) assemblages. This may indicate that during the accumulation of the latter two layers conditions were generally cooler than during the accumulation of the two earlier cave layers. Taking the *T. afra* results into account, it seems that these data, as opposed to some viewpoints (see Interpretation section), may indicate *M. varius* responds positively to Bergmann's rule. The AD 2000/AD 991 significant difference, together with a significant size difference between AD 991 and AD 615 (Mann-Whitney:  $p < 0,05$ ), seemingly indicate AD 991 to be relatively cool and confirm AD 615 to be milder - probably the mildest of the cave layers. This mildness appears to be confirmed by the high degree of similarity between AD 2000 and AD 615 (Mann-Whitney:  $p > 0,95$ ). Generally low temperatures are also indicated for AD 991 by a significant size difference between AD 2000 and AD 991 ( $p < 0,05$ ) in the *Steatomys krebsii* (lower alveolar length) data, with those of AD 2000 being smaller. Close to significant  $p$ -values (Mann-Whitney and  $t$ -test:  $p < 0.1$ ) between AD 991 and all the other levels in this data set, seem to support this. These findings apparently indicate the lower alveolar length of *S. krebsii* also shows a positive response to Bergmann's rule. Other close to significant  $p$ -values ( $p < 0.1$ ) occur in the data of *Cryptomys hottentotus*, which is generally believed to show a positive size response to precipitation (see 5.9.1). These low  $p$ -values between AD 2000/AD 615 ( $p < 0.1$ ) and AD 615/AD 381 ( $p < 0.1$ ) probably point towards AD 615 being the wettest level and AD 381 and AD 2000 being the driest two levels. This requires confirmation from other sources, though. In the upper alveolar length data of *S. krebsii*, a very high degree of similarity



occurs between AD 2000 and AD 381 ( $p > 0,95$ ). This may indicate both levels to be of similar temperature (mild, according to the above-mentioned findings). In general the environmental parameters to which *S. krebsii*'s u.a.lengths respond and the kind of response (positive/negative) remains uncertain. The *Crocidura flavescens* data do not show any significant trends, but one must add that no AD 2000 data exists for this species.

### 8.3.2 Community composition

See Table 8, 9 and 10, Figure 11 and Ecological Species Distribution.

In this section the term 'numbers' refer to relative percentage contribution (p.a.l. values), unless specifically stated otherwise.

When comparing the different levels' species composition, one notices a trend in the recent data, generally displaying rather marked differences in species numbers (both higher and lower in Table 9) from the species numbers of the ancient data, the latter showing more gentle drops and rises in numbers among each other. Furthermore, Table 10 shows AD 2000 to have the highest representation of all levels in the extreme rankings (I and V). This level (AD 2000) is distinct from the ancient levels in that it shows the greater influence of nearby modern agricultural activities, than the prehistoric herder activities (Lloyd, 1983a). Of the species that increased in abundance (*Otomys irroratus*, *Rhabdomys pumilio*, *Aethomys namaquensis*, *Tatera afra* and *Dendromus melanotis*), *R. pumilio*, *T. afra* and *D. melanotis* are on record (see 7.3) to respond positively, to a lesser or greater extent, to anthropomorphic activities, or occurs in a wide range of habitats, i.e. *A. namaquensis*, and thus probably adaptable to human presence. Even though the De Hoop coastal plain itself is relatively pristine (i.e. no crops being cultivated), the data reflect what seem to be a strong influence of activities in neighbouring areas on the conserved area, probably due to immigration from these areas (possibly through the Windhoek-corridor), the occasional hunting of some coastal plain owls in these areas and anthropomorphic influences in and around the De Hoop Centre. Immediately apparent in the recent data is the drastically lower proportions of four species - *Cryptomys hottentotus*, *Mystromys*



*albicaudatus*, *Steatomys krebsii* and *Crocidura flavescens*. This may be a numerical artifact due to the drastic increases of the 'human-adaptable' species (and, in effect, an overall increase in food in the neighbouring areas, with the possible consequent population explosions "flowing over" to De Hoop), in which case also the numbers of the other (than the four mentioned) 'non-human-adaptable' species will be numerical artifacts, appearing to be lower than they actually are, when compared to the other levels. The apparent marked decrease may, on the other hand, also be indicative of AD 2000 being warmer and drier than any of the ancient levels (confirming the size indications above).

The sum of species representing cold and wet conditions, as indicated by Table 11, is the lowest in AD 2000. Unfortunately no species used in this study are specialists of both warm and dry conditions (see below why *S. krebsii* was not used for indicating a combination of warm and dry conditions). The drier climate is clearly suggested by the lower numbers of *C. hottentotus*, and complete absence of *M. albicaudatus* and *C. flavescens* in AD 2000. These species generally occur in moist habitats. This appears to be confirmed by the low numbers of *Myosorex varius*. While more tolerant of drier climate (given a suitable microhabitat) than the other three species, *M. varius* is indicative of a microclimate of dense, moist vegetation. The relatively higher temperature of AD 2000 may be indicated by the higher numbers of *O. irroratus* (warm-adapted) and lower numbers of *M. albicaudatus* and *M. varius* (cold-adapted). Furthermore, if this 'heat and drought'-situation of AD 2000 is suboptimal (compared to conditions in the ancient levels), generalist species, such as *R. pumilio* and *A. namaquensis* can be expected to have a competitive edge on specialist species. In part, this may explain their higher numbers.

The low numbers of *S. krebsii*, seemingly suited to dry and warm conditions, can only be explained by the influence of the 'human-adaptable'/ generalist species. In the latter respect, it is of some importance to note that Avery (1982a) also detects a reduction in the numbers of *M. albicaudatus*, *S. krebsii* and *C. flavescens* in some of her modern samples relative to the older samples where there was an increase in agricultural activities. Because of this apparent bias, together with some discrepancies the *S. krebsii* data displays (if assumed to indicate warm and dry conditions) towards the general emerging pattern (see rest of discussion below) and the fact that very little is, as yet, known about the habitat



preferences of *S. krebsii*, this species was not used as indicative of a combination of warm and dry conditions. It does, however, seem that *S. krebsii* may, to some extent, indicate grass and possibly warm conditions (see below). If one assumes *M. albicaudatus* to display a correlation with either low temperatures or more open vegetation or both, the presence of this species in conjunction with the size data indicates remarkably similar environmental conditions, indicating AD 2000 to be the milder than any of the ancient levels, AD 1417 and AD 991 to be cooler than AD 615 and AD 381, and AD 991 to be the coolest, with open vegetation. The high numbers of *M. albicaudatus* in AD 991 (indicated by the size data above to be cool and dry) may probably point towards it displaying a stronger correlation with low temperatures than with high precipitation.

Another apparent trend stretching over more than one level is that the higher numbers of *Mus minutoides*, *C. flavescens*, and possibly *S. krebsii*, as well as lower numbers of *M. albicaudatus* in the lower two levels (AD 381 and AD 615) indicate conditions to have been warmer than in the upper two ancient levels (AD 991 and AD 1417). If this is true, the numbers of *A. namaquensis* may imply that this species also displays a strong correlation with low temperatures.

Higher numbers of *S. krebsii* (probably indicating grass) and lower numbers of *A. namaquensis* (probably indicating scrub) in the lower two levels (AD 381 and AD 615), and *vice versa* in the upper three levels (AD 991, AD 1417 and AD 2000) may furthermore indicate predominantly grass in the lower two levels, with an apparent change to more scrub in the upper three levels. This notion lacks support from the other species numbers though.

Second to AD 2000, the level displaying the most fluctuations in species numbers is AD 991 - indicated by the size data to be relatively cooler than the other levels. This notion seems to be confirmed by the low numbers of *M. minutoides*, *C. flavescens* and possibly *S. krebsii* (lower than the preceding two levels), as well as the high numbers of *Otomys karoensis*, *M. albicaudatus* and possibly *A. namaquensis*. There also seem to exist some indications for dry conditions in AD 991 in the low numbers of *T. afra* and, to an extent, *C. hottentotus*, as well as in the high numbers of *O. karoensis*, *A. namaquensis* and possibly



*Dendromus melanotis*. The sum of AD 991's 'cold and dry' species in Table 11 is much higher than any other level. The low numbers of *R. pumilio* and *M. varius* and, to an extent *C. flavescens*, as well as the high numbers of *A. namaquensis* suggest a more open vegetation during the deposition of level AD 991. Apart from the human-influenced numbers of *A. namaquensis* in the recent data, AD 991 shows the highest numbers of this species, suggesting this level to have a more scrub-dominated vegetation than any of the ancient levels.

The species data seem to provide contradictory evidence on whether AD 615 or AD 381 was the warmer period. The lower *O. karoensis* and higher *C. flavescens* numbers seem to suggest AD 615 to be warmer (as implied by the size data), while the *M. minutoides* (higher), *M. albicaudatus* and probably *A. namaquensis* (both lower) numbers apparently suggest AD 381 to be warmer. As far as aridity is concerned, there seems to be a pronounced trend, however. Higher numbers of *C. flavescens* and *M. albicaudatus*, as well as lower numbers of *O. karoensis* and possibly *D. melanotis* indicate wetter conditions for level AD 615 than for level AD 381. In confirmation, lowest numbers of *O. irroratus* in AD 381 indicate this level to be drier and lowest numbers of *Suncus varilla* in AD 615 may indicate a more dense and probably wetter vegetation regime for this level. The data for *A. namaquensis* seem contradictory though, in seemingly indicating AD 615 to be drier. Again this may point towards a stronger correlation of the species with temperature trends. The sum of 'grass' species (both applications, with and without 'artificial' species, in Table 11) seem to indicate AD 381 to possess the grassiest vegetation.

In the level AD 1417 the trends are not pronounced. The species numbers tend to indicate this time interval to be generally cooler than the lowest two levels, but not as cool as AD 991 (see discussion above). There are, however, slight indications that AD 1417 was wetter - *S. krebsii* and possibly *D. melanotis* (both lower numbers), and *M. albicaudatus* and *O. irroratus* (both higher numbers) - and had denser vegetation - *O. irroratus* (higher numbers) and *R. pumilio* (slightly higher numbers) than AD 381. *A. namaquensis* seemingly contradicts this, implying AD 1417 to be drier (stronger temperature-correlation?).



Furthermore indications exist that AD 1417 was slightly drier - *O. irroratus* (lower numbers), *O. karoensis* (higher numbers) and probably *D. melanotis* (higher numbers) - and possessed a more open vegetation regime - *S. varilla* (higher numbers) and *O. irroratus* (lower numbers) - than AD 615. The *R. pumilio* data are not in agreement with this - slightly higher numbers seem to imply the vegetation to be denser during AD 1417. *R. pumilio* is less specific in its habitat requirements than the other mentioned species, though, and should, at best, supply supportive, but not rejective arguments to the trends in the more specific species' numbers.

The *Tatera afra* numbers were the most difficult to interpret. No major differences occurred among levels except that AD 991 showed much lower numbers. Being an endemic to the winter rainfall region, and occurring, among other places, on the winter rainfall mountains, the probable low temperatures of AD 991 should not restrict *T. afra*'s abundance. Taking into account that it was often found to be dominant in wet conditions, as indicated by Avery (1982a), it was probably restricted by AD 991's dry climate. It may also have been restricted by AD 991's scrubby vegetation, implying very little grass. Although it has high numbers in the recent level, which is also dry (see above), its numbers may have been artificially boosted by the proximity of cultivated lands.

The cranial mass results (Table 2) show a rodent: insectivore ratio of *ca* 20: 1 in the case of the modern material, compared to *ca* 7: 1 in the case of the ancient material. Apart from teeth frequently being missing from the ancient rodent crania, this phenomenon could not be explained.

### 8.3.3 Community structure

The index values and graphic detail of the data under discussion can be seen in Table 12 and Figure 12. Differences between index values are very small throughout and therefore do not convey much information. In both diversity indexes and the evenness index AD 2000's values are the lowest, probably portraying the artificial influence of nearby



agricultural activities on species numbers. The two instances where index values differ most (with  $>0,1$ ) are:

\*The first is a difference in the Shannon-Wiener diversity index values between AD 2000 and AD 1417. This may (apart from the agricultural artifact) be the result of the difference between the dry and warm climate of AD 2000 and the relatively moderate climate of AD 1417.

\*The second instance is a difference in the species evenness index values of AD 2000 and AD 381. The reason for this difference remains uncertain and may well be artificial.

#### **8.3.4 Summary**

The climatic reconstruction (graphically depicted in a comparison with other existing climate models in Figure 13) is derived from a combination of physical size, community composition and community structure data and can be summarised in the following manner:

**GENERAL** (general trends stretching over more than one level)

**AD 381 & AD 615: milder, with possibly more grass**

**AD 991 & AD 1417: cooler, with possibly more scrub**

**AD 2000: milder than any of the preceding levels, also with predominantly scrub**

**LEVEL SPECIFIC** (trends unique to each level)

**AD 381: Relative dry and mild**

**AD 615: Wettest level and possibly milder than AD 381**



**AD 991: Coolest of all the levels and driest of the ancient levels**

**AD 1417: Relatively cool and probably drier than AD 615, but wetter than AD 381**

**AD 2000: Mildest and driest of all levels, with artificial influence of nearby agricultural activities**

#### **8.4 Existing climate change models and comparisons**

Research aimed at palaeoenvironmental reconstruction was already conducted in Africa as early as the 1890's, mapping glacial features and past high lake levels in the East African Rift valley (Deacon & Lancaster, 1988). Palaeoenvironmental research utilizes a wide range of methods of marine, aquatic and terrestrial of origin - both geomorphic/sedimentary and biological. Those used for the Quaternary period include deep-sea cores/ ocean sediments (e.g. foraminifera content) and ice cores (measuring  $^{18}\text{O}$ -isotope level), vertebrate faunal remains, insect remains, palaeosols, pollen, tree rings, tree fire scars, corals, borehole data, plant macrofossils and other forms of floral remains, to name but a few. Apart from micromammals, other small vertebrate evidence such as that of snakes, frogs (Stuckenberg, 1969) and lizards (Mouton, 1986) have also been used in palaeoenvironmental studies. Some give very complete information for long uninterrupted periods (e.g. deep-sea cores), and are good for general global climate theories (e.g. marine evidence). Others may be less complete and range from very general to very particular (regional). When making comparisons with this or other studies' data, every set of reconstructed information should be applied within the range of its restrictions.

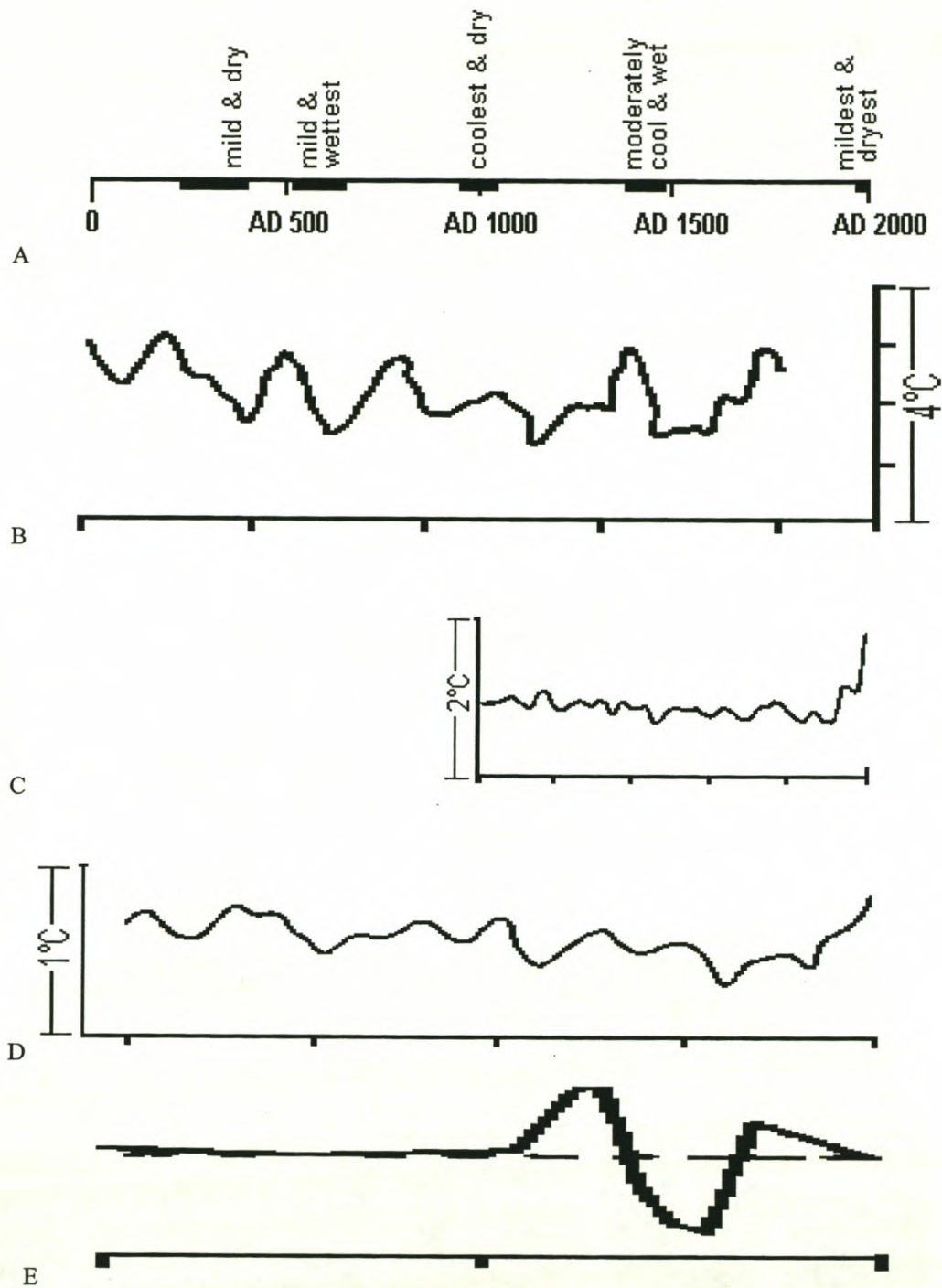
Not all the palaeoenvironmental methods will be discussed here. The findings of those that generated late Holocene (with emphasis on the last two millennia) information, for comparison with the results of this study are mainly of interest. Short additional notes on the rest of the Holocene and the preceding few millennia are also given. A comparison with some results of other authors from the same region is made in Figure 13. The lengths of the bars in Figure 13A correspond with the two- $\sigma$  ranges in the dates of every level.



When comparing existing information with this study's data, it is important to keep in mind that the Western Cape is seemingly out of phase with the interior of southern Africa, as far as relative humidity is concerned (van Zinderen Bakker & Butzer, 1973; Butzer *et.al.*, 1978; Jerardino, 1993) e.g. when the interior experiences a wet period, the Western Cape will probably experience a dry period (not referring to seasons). This is a general trend, though, and conflicting evidence does exist. There are some indications that wetter conditions tend to coincide with higher temperatures in the southern Cape (Butzer & Helgren, 1972; van Zinderen Bakker & Butzer, 1973; Butzer *et.al.*, 1978). Because of this tendency of rainfall patterns to be very local, the models used for comparison of humidity/precipitation concerned only those from the southern and southwestern Cape. As far as temperature is concerned, the application seems to be generally wider, although not all causes of temperature changes have a global influence (see the section above on What causes climate change). Models from other areas on the globe were therefore used cautiously in comparisons, and secondary to local temperature change models.

Despite the probable time lag of environmental change to be displayed in the micromammal data (see above), a 'time lag factor' was not incorporated in the comparisons with other data, since the other data itself is in most cases subject to a time lag and since no database exist, as yet, on how the lags differ from one method to the next.





**Figure 13:** Graphical comparison of the palaeoclimatic results with some existing climate models. All time axes correspond with that of A. A: The findings of this study; B: Cango Cave, southwestern Cape - after Talma, & Vogel, 1992; C: Northern hemisphere temperature variation (various indicators) - after Mann *et al.*, 1999; D: global mean temperature variations, Greenland ice core - after Saltzman, 1983; E: south- Atlantic sea-surface temperature fluctuations - after Cohen *et al.*, 1992 and Jerardino, 1995.



#### 8.4.1 Existing models for the preceding period

In general, models are in accord. Since the Last Glacial Maximum - *ca* 18000 years BP (Butzer & Helgren, 1972; Tankard & Schweitzer, 1974 and numerous others) to 16000 BP (Tyson, 1991), when temperatures were up to 7°C colder than at present in the southern Cape interior (Talma & Vogel, 1992) - climatic conditions improved. This is especially since 12 000 BP and by *ca* 8000 BP the modern or Holocene norms were reached. Even though southern Africa was not glaciated, it is evident from the extent of temperature increases since the Glacial Maximum that there was a rapid swing towards warmer conditions immediately following the glacial events of the Quaternary (Moore *et al.*, 1996). Furthermore, other local evidence such as isotopic analysis of molluscs from Nelson Bay Cave, in the southern Cape region, east of De Hoop, has shown the Holocene to be generally warmer than the preceding period (Shackleton, 1973). Pollen analyses from Europe and the Near East by Van der Hammen *et al.* (1971) show four noticeable climatic events in the few millennia before the climatic 'stability' of the Holocene, the most recent being a cold and dry period, called the Younger Dryas (*ca* 12 500 to 11 500 years BP, according to Johnsen *et al.*, 1992 or 10 800 to 10 000 BP, according to Moore *et al.*, 1996), roughly representing the start of Shackleton's <sup>18</sup>O stage 1 (see below). After 8000 BP climatic fluctuations still occurred, but they were of a much smaller magnitude than those defining glacial maxima, inter-glacial stages and interstadials.

The complete time range covered by this study (*ca* 2000 BP to present) falls within Emiliani's (1955; 1966) <sup>18</sup>O stage 1, derived from deep sea core-data, and dated by Shackleton (1975) as 13 000 BP to present. Fluctuations monitored are therefore trends within a part of the interglacial stage we find ourselves in at present.

Holocene climate changes, according to various authors, using various methods, are:

*ca* 10 000 BP - rapid temperature rise, according to micromammal data in the southern parts of Southern Africa (Avery, 1982a)

*ca* 10 000 to 7800 BP - increase of *ca* 1,5°C/millennium, based on factor analysis of micromammal data in the Northern Province, South Africa (Thackeray, 1995).



*ca 10 000 to 4200 BP* - relatively warm and dry, with more open vegetation, according to pollen data from the southern Cape (Butzer & Helgren, 1972; Butzer, 1973; Butzer *et.al.*, 1978)

*ca 9000 BP* - colder and drier (Avery, 1982a)

*ca 8000 to 7000 BP* - probably relatively wet, according to tree pollen levels from the southern Cape (Martin, 1968, 1969)

*ca 8000 to ca 6500 BP* - warmer (milder) than average (Avery, 1982a)

*Early Holocene (before 6000-5000 BP)* - warm, moist on the southern Cape coast, according to mammal size data (Klein, 1986)

*ca 6400* - warmer conditions indicated by fossil oyster beds from the Cape west coast (Flemming, 1977)

*ca 6800 to 2000 BP* - tree pollen levels from the southern Cape probably indicating relatively dry conditions (Martin, 1968)

*ca 6000 BP* - short cold (harsh) period (Avery, 1982a)

*ca 6500 to 3500 BP* - drier (and according to the above mentioned tendency for the southern Cape region, probably cooler) than the preceding period (Avery, 1982a)

*After 6000 to 5000 BP* - more scrub and less grass than the preceding periods, according to macromammal data from the Little Karoo in the southern Cape region (Deacon, 1979).

*Late Holocene (after 5000 BP)* - cooler and drier on the southern Cape coast, according to mammal size data (Klein, 1986)

*ca 4200 BP* - colder and wetter, according to charcoal data from the Western Cape west coast (February, 1990)

*ca 4500 BP* - Generally colder, according to speleothem evidence from the southern Cape interior (Talma & Vogel, 1992)



*ca 3600 to 3300 BP* - general temperature rise (Avery, 1982a)

*After ca 4000 BP* - relatively warm and moister than the preceding period, according to pollen data from the southern Cape (Butzer & Helgren, 1972; Butzer, 1973)

*ca 3080 BP* - Wet, according to palaeosol data from the western coast of the Western Cape Province (Miller *et al.*, 1993)

*ca 4010 to 1300 BP* - wetter, with more forest and bush, according to pollen data from the southern Cape (Butzer & Helgren, 1972; Butzer *et al.*, 1978)

*ca 3200 to 2600 BP* - generally colder, according to speleothem evidence from the southern Cape interior (Tyson, 1991; Talma & Vogel, 1992)

*3500 to 2300 BP* - cold sea-surface temperatures on the southern African Atlantic shores, according to oxygen isotope analyses of shells (Cohen *et al.*, 1992; Jerardino, 1995)

*3100 to 2500* - several cold events according to speleothem evidence from the southern Cape interior (Talma & Vogel, 1992)

*ca 3000 to 2000 BP* - colder and wetter, according to charcoal data (February, 1990) and micromammal data (Avery, 1992) from the Western Cape west coast

*ca 2400 BP* - warmer, according to speleothem evidence from the southern Cape interior (Talma & Vogel, 1992)

*ca 2000 BP* - rapid temperature rise (Avery, 1982a)

*After 2000 BP* - wetter, according to tree pollen data from the southern Cape (Martin, 1968)

#### **8.4.2 2000 BP to Present: a comparison**

Existing models for the past two millenia provide the following picture:



*ca 2000* - Wetter and cooler, according to large mammal data from the southern Cape (Klein, 1980).

*Up to ca 1050 BP* - wetter, with more forest and bush, according to pollen data from the southern Cape (Butzer *et.al.*, 1978)

*ca 1300 BP* - a cold event, according to speleothem evidence from the southern Cape interior (Talma & Vogel, 1992).

*Up to ca 1350 BP (from ca 4000 BP)* - wetter, with more forest and bush, according to palaeosol data from the southern Cape (Butzer & Helgren, 1972). **These wet conditions are also monitored by the data of the AD 615 level.**

*The earlier period of the past 2000 years to the present day* - Avery (1982a) found a gradual replacement of grass/restioid vegetation by scrub. **The two earlier levels of this study indicate a similar probable predominance of grass.**

*ca 1950 (AD 50) to 1850 BP (AD 150)* - warm (Avery, 1982a)

*ca 1850 BP (AD 150)* - warmer conditions indicated by fossil oyster beds from the Cape west coast (Flemming, 1977). **Similar temperatures probably continued to the AD 381 level.**

*ca 1650 BP (AD 250)* - cooler (fluctuating), according to micromammal evidence (Avery, 1982a)

*Towards ca 1050 BP (AD 950)* - becoming drier, according to charcoal studies in the Little Karoo, southern Cape region (Scholtz, 1986). **This agrees with the dry conditions of the AD 991 level.**

*ca 1050 to 650 BP (AD 950 to AD 1350)* - a seemingly colder period, according to Lara & Villalba's findings (1993) in tree ring studies of southern Chile. **These findings may correspond with the general cooler conditions indicated in the AD 991 and AD 1417 levels**



*ca 1050 BP (AD 950)* - dry, according to micromammal evidence from the western part of the fynbos region (Avery, 1983), large mammal data (Klein, 1980) and pollen data (Martin, 1968) from the southern Cape. **Another strong concurrence with the dry conditions of AD 991.**

*ca 1050 BP (AD 950) to the present day* - coarse sands, indicating drier conditions and/or human agricultural activities, according to palaeosol data from the southern Cape (Butzer & Helgren, 1972; Butzer *et.al.*, 1978) = **Dry conditions of AD 991.**

*ca 800 BP (ca AD 1200)* - Relative warm sea-surface temperatures on the southern Atlantic southern African coasts, according to oxygen isotope analyses of shells (Cohen *et al.*, 1992; Jerardino, 1995)

*650 - 450 BP (AD 1350 - 1550)* - lowest sea-surface temperatures for the past two millennia on the southern Atlantic southern African coasts, according to oxygen isotope analyses of shells (Cohen *et al.*, 1992; Jerardino, 1995). **Probably concurrent with the relatively cool conditions of level AD 1417.**

*ca 550 BP (AD 1450)* - wetter, with more forest and bush, according to palaeosol data from the southern Cape region (Butzer, 1984) – **correspond with the relatively moist conditions of level AD 1417.**

In Figure 13 the findings of this study are compared with some graphic presentations of other existing climate models.

The weak indications of more grass in the oldest level of this study is supported by the findings of Talma & Vogel (1992) that C4 grass invasion reached an optimum in the southern Cape hinterland at about 2000 BP.

The cool weather of the AD 1417 and AD 991 levels of this study correspond with an extended period of below-average temperatures in the southern Cape hinterland from about AD 1000 to the middle of the sixteenth century (Talma, 1989) - see Figure 13 - and that of the AD 1417 level with probable early effects of the southern African Little Ice Age,



occurring from AD 1500 to AD 1675 (Avery, 1997). The mildly cool, moderate fluctuations displayed by this level (AD 1417), probably indicates it to lie in a transitory time slot between the time of warm sea-surface temperatures on the southern Atlantic southern African coasts proposed by Cohen *et al.*(1992) and Jerardino (1995) for *ca* AD 1200 (see above) and the above-mentioned cold period from AD 1500 to AD 1675.

The relatively cool weather of the youngest cave layer also corresponds with narrower than average (indicating slow growth probably due to cold conditions) yellow wood tree rings from Natal, South Africa for roughly the same time period (Tyson, 1991). Acocks (1975) proposes a recreation of the southern Cape vegetation of AD 1400 which consists of extensive forests – probably corresponding with the relatively cool and moist conditions of level AD 1417.

Cohen *et al.* (1992) and Jerardino (1995) found sea-surface temperatures along the southern African Atlantic coast to be generally lower during the past 4000 years than at present. This is in accord with this study's findings that the present pellet assemblage (AD 2000) represents a warmer era than any of the others. The same similarity in principle agrees with Varekamp & Thomas' (1999) findings that the modern rate of sea level rise exceeds that of the past 2000 years - probably indicating a global rise in temperature. Furthermore, Mann *et al.* (1999) postulate that the latter part of the twentieth century was warmer than any period during the preceding millennium in the Northern Hemisphere. Campbell *et al.* (1998) detected a natural warming trend in western Canada that is expected to continue until *ca* AD 2400, and 616 individual temperature change rate reconstructions, using borehole data from all five continents, give a global perspective of a continued rise in surface temperature change rate - all over the globe it is getting warmer faster (WDC-A for palaeoclimatology, 1999b). This is rather similar to this study's findings for the recent time slot, being warmer than any of the preceding. These similarities between Northern and Southern Hemisphere data clearly indicate climate changes on a global scale and of apparently the same origin.

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## 9. CONCLUSION

From the results of this study the general picture emerged that levels dated AD 381 and AD 615 were milder (warmer), with possibly more grass; AD 991 and AD 1417 were cooler, with possibly more scrub and AD 2000 was milder than any of the preceding levels, also with predominantly scrub.

Looking specifically at each level, it was found that AD 381 was relatively dry and mild; AD 615 was the wettest level and possibly milder than AD 381; AD 991 was the coolest of all the levels and the driest of the ancient levels; AD 1417 was relatively cool and probably drier than AD 615, but wetter than AD 381 and in comparison with the cave assemblages the present (AD 2000) climate is the mildest and driest of all levels, with artificial influence of adjacent agricultural activities.

These findings generally correspond with other palaeoclimate models for the region and proved micromammal remains yet again to be an effective tool for reconstructing palaeoclimates, even on such a fine scale.

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## LIST OF APPENDICES

**Appendix 1: Species list of all micromammals encountered in the study**

**Appendix 2: Micromammal alveolar patterns**

**Appendix 3: Problem areas in cranial identification**



**APPENDIX 1: SPECIES LIST OF ALL MICROMAMMALS ENCOUNTERED IN THE STUDY (PELLET MATERIAL & LIVETRAPPING)**

Listed for species below: Latin name, common name and abbreviation used elsewhere.

Taxonomic listing order according to Skinner & Smithers (1990)(with new names where it has changed).

Species not previously recorded in the De Hoop area are indicated with an asterisk.

**ORDER INSECTIVORA**

Family SORICIDAE

Subfamily CROCIDURINAE

*Myosorex varius* - forest shrew - Mva

*Suncus varilla* - lesser dwarf shrew - Sva

*Crocidura cyanea* (cf. *cyanea*) - reddish-grey musk shrew - Ccy

*Crocidura flavescens* - greater musk shrew - Cfl

Family CHRYSOCHLORIDAE

*Chrysochloris asiatica* - Cape golden mole - Cas

**ORDER MACROSCELIDEA**

Family MACROSCELIDIDAE

Subfamily MACROSCELIDINAE

*Elephantulus edwardii* \* - Cape rock elephant-shrew - Eed



**ORDER RODENTIA**

## Family BATHYERGIDAE

## Subfamily GEORYCHINAE

*Cryptomys hottentotus* - common molerat - Cho*Georychus capensis* \* - Cape molerat - Gca

## Family MURIDAE

## Subfamily OTOMYINAE

*Otomys karoensis* - Saunders' vlei rat - Oka*Otomys irroratus* - vlei rat - Oir*Otomys unisulcatus* \* - bush Karoo rat - Oun

## Subfamily MURINAE

*Rhabdomys pumilio* - striped mouse - Rpu*Mus musculus* (alien) - house mouse - Mmu*Mus minutoides* - pygmy mouse - Mmi*Mastomys natalensis/coucha* - Natal multimammate mouse/

multimammate mouse - Mnc

*Aethomys namaquensis* - Namaqua rock mouse - Ana

## Subfamily GERBILLINAE

*Tatera afra* - Cape gerbil - Taf

## Subfamily CRICETINAE

*Mystromys albicaudatus* - white-tailed mouse - Mal



Subfamily DENDROMURINAE

*Dendromus melanotis* - grey climbing mouse - Dml

*Dendromus mesomelas* \* - Brants' climbing mouse - Dms

*Steatomys krebsii* \* - Krebs' fat mouse - Skr

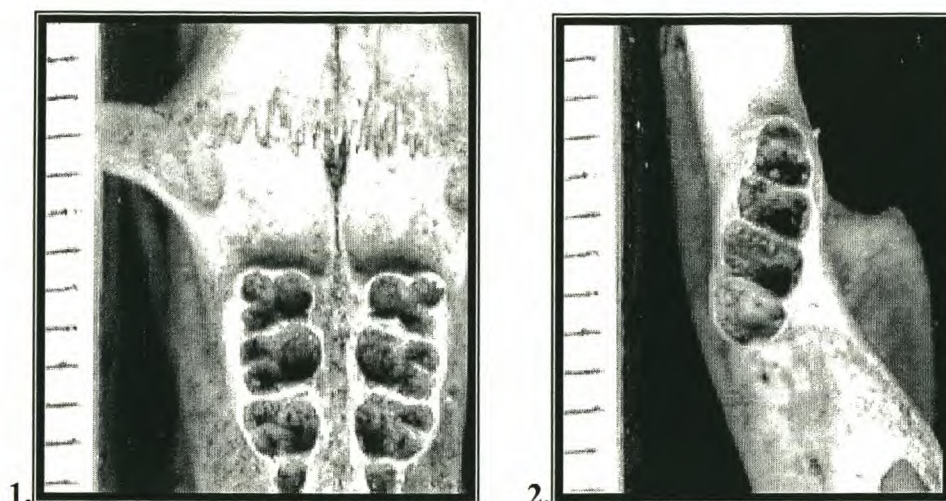
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## Appendix 2: Rodent alveolar patterns

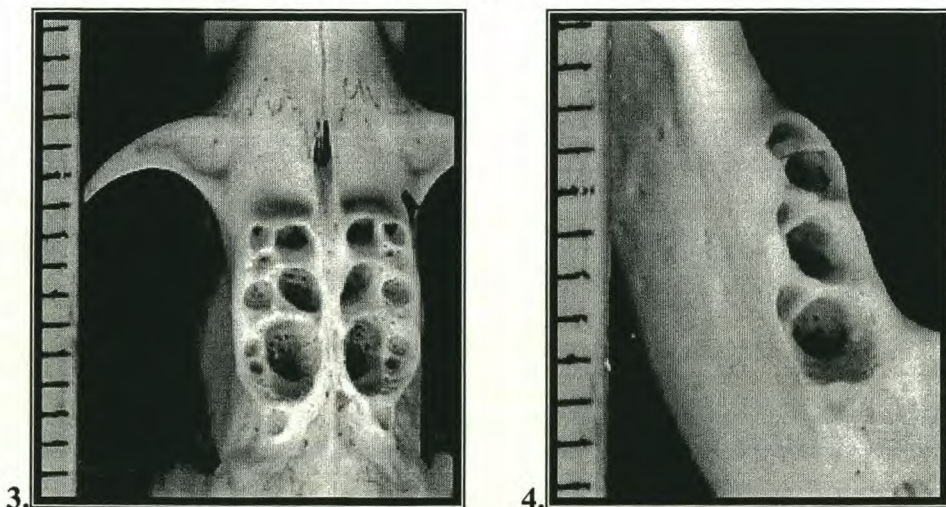
The photographs of alveolar patterns should be a convenient visual aid to existing keys, such as those of Avery (1979) and Coetzee (1971). The guide compiled for identification use in this study is by all means available to other researchers.

The scale with every picture indicates millimetre units.



Appendix 2.1: *Cryptomys hottentotus* maxillae (subadult)

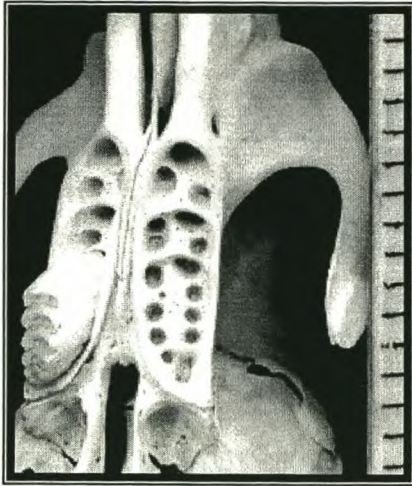
Appendix 2.2: *C. hottentotus* right mandible (subadult)



Appendix 2.3: *Georychus capensis* maxillae (juvenile)

Appendix 2.4: *G. capensis* right mandible (juvenile)

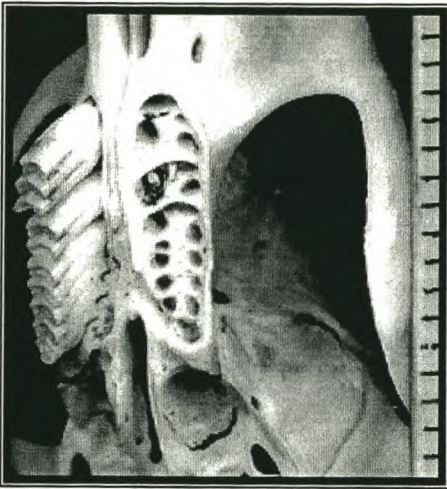




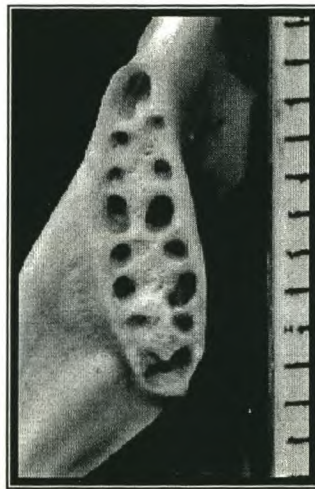
5.

Appendix 2.5: *Otomys karoensis* maxillae

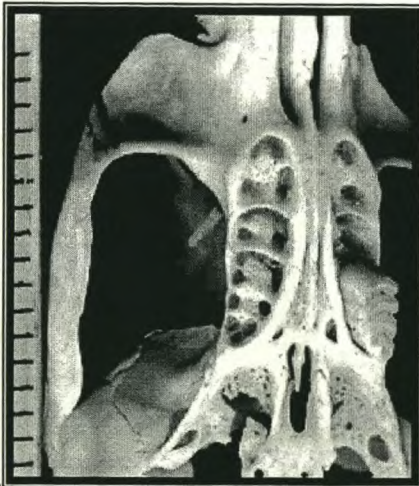
6.

Appendix 2.6: *O. karoensis* right mandible

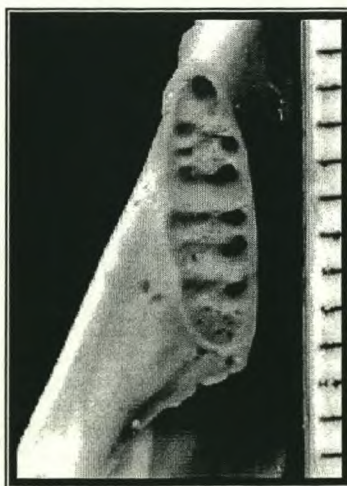
7.

Appendix 2.7: *Otomys irroratus* maxillae

8.

Appendix 2.8: *O. irroratus* left mandible

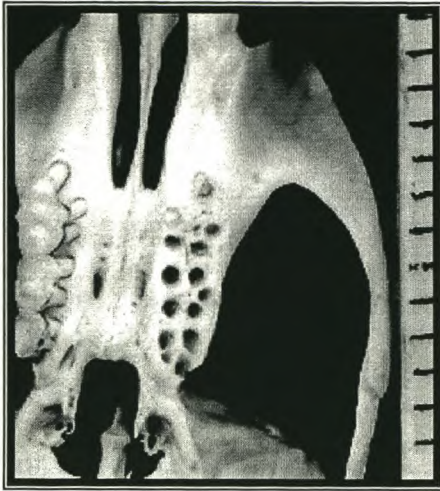
9.

Appendix 2.9: *Otomys unisulcatus* maxillae

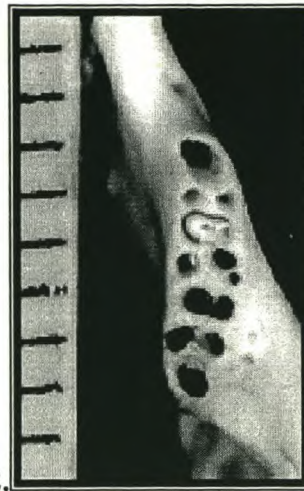
10.

Appendix 2.10: *O. unisulcatus* left mandible

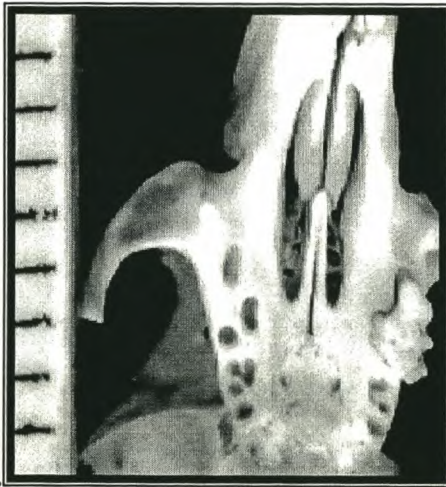




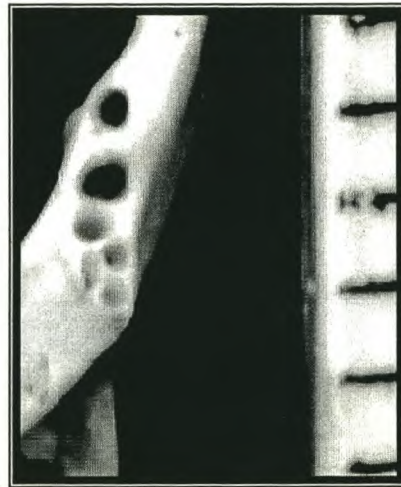
11.

Appendix 2.11: *Rhabdomys pumilio* maxillae

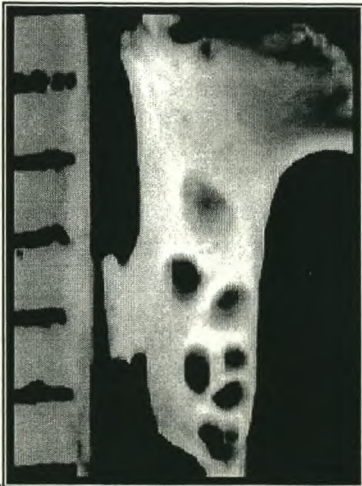
12.

Appendix 2.12: *R. pumilio* right mandible

13.

Appendix 2.13: *Mus minutoides* maxillae

14.

Appendix 2.14: *M. minutoides* left mandible

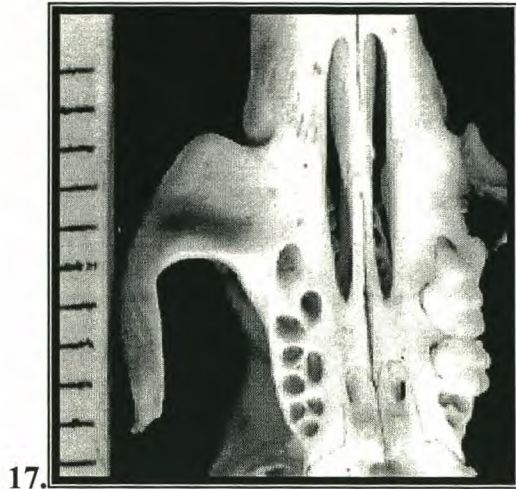
15.

Appendix 2.15: *Mus musculus* left maxilla

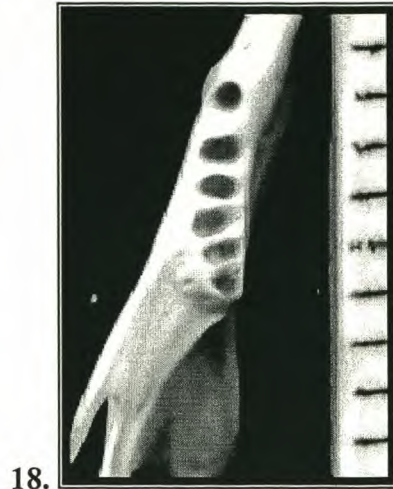
16.

Appendix 2.16: *M. musculus* right mandible

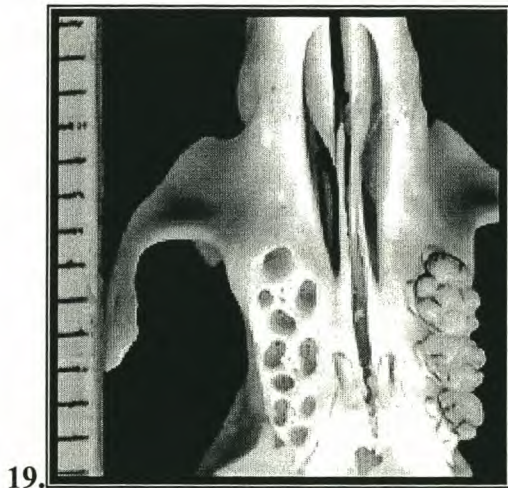




Appendix 2.17: *Mastomys natalensis/coucha* maxillae



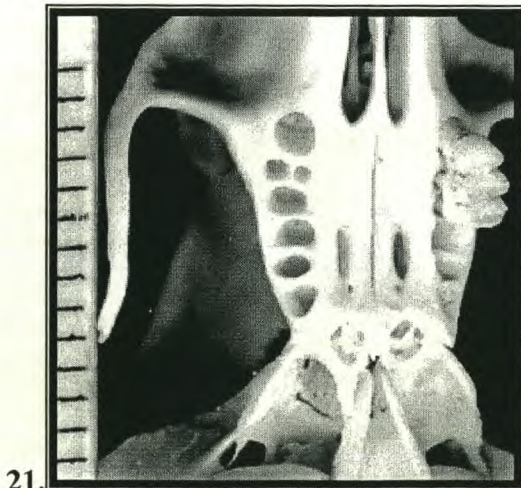
Appendix 2.18: *M. natalensis/coucha* left mandible



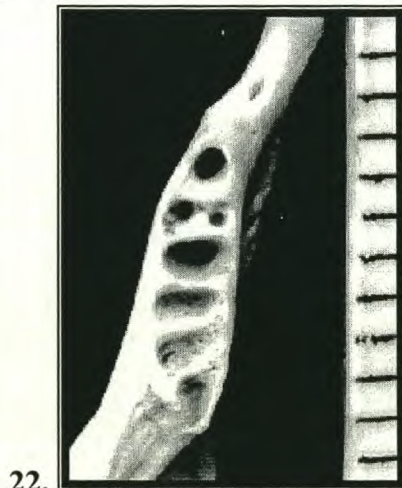
Appendix 2.19: *Aethomys namaquensis* maxillae



Appendix 2.20: *A. namaquensis* right mandible

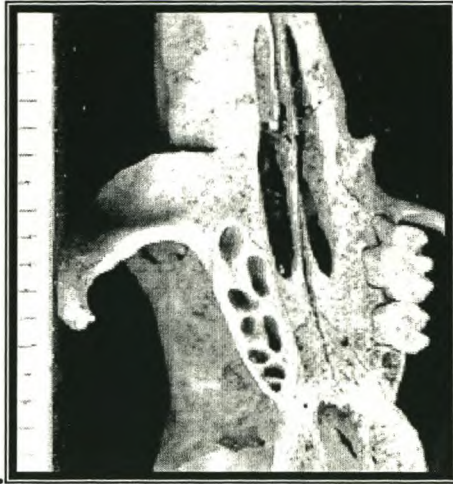


Appendix 2.21: *Tatera afra* maxillae



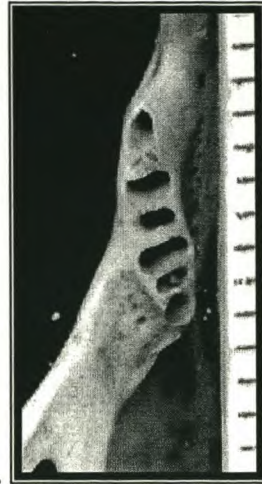
Appendix 2.22: *T. afra* left mandible





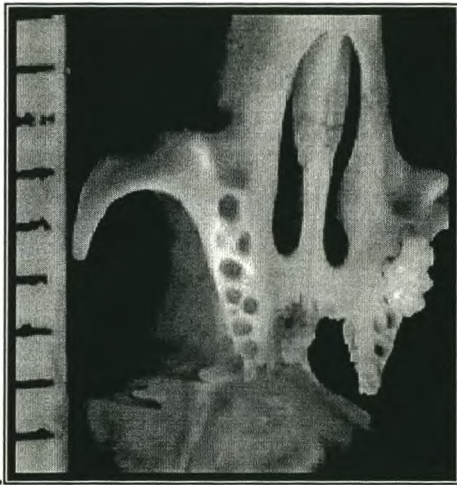
23.

Appendix 2.23: *Mystromys albicaudatus* maxillae



24.

Appendix 2.24: *M. albicaudatus* left mandible



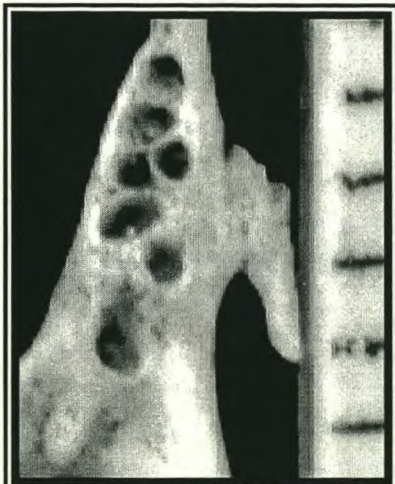
25.

Appendix 2.25: *Dendromus melanotis* maxillae



26.

Appendix 2.26: *D. melanotis* right mandible



27.

Appendix 2.27: *Steatomys krebsii* left maxilla



28.

Appendix 2.28: *S. krebsii* left mandible



### Appendix 3: Problem areas of cranial identification

#### *Myosorex varius* and *Crocidura cyanea*

Distinguishing between these two species was not extremely difficult, but the following points may prove valuable to students initially attempting identification. This is especially the case since they are very similar in skull size, although *C. cyanea* tends to be marginally smaller. The most useful distinguishing feature of the *M. varius* skull is the presence of two small holes dorsally at the posterior end of the nasal bones and just frontal to the braincase. When the skulls of the two species are viewed from the front *C. cyanea*'s roughly resembles that of a "n", while *M. varius*' is more triangular. The palate of *M. varius* is a little wider than that of *C. cyanea*. Viewed laterally, the zygomatic plate is wider in *M. varius* with an indent, lacking in *C. cyanea*. Also lacking in the latter species is a P<sup>3</sup>, which is present in a reduced form in *M. varius*, anteromedial to P<sup>4</sup>. *M. varius* has an extra cusp posteromedial on P<sup>4</sup>, which is not present with *C. flavescens*. The *M. varius* mandible has a small knob laterally on the coronoid process. With *C. cyanea* the knob is situated dorsally. When viewed from posteriorly the condylar process resemble an obtuse angle with *C. cyanea* and a right angle with *M. varius*.

#### *Chrysochloris asiatica* and *Amblysomus hottentotus*

In general the *A. hottentotus* skull is more slender. The temporal bullae are very conspicuous with *C. asiatica* and are visible from dorsally. This is not the case with *A. hottentotus*. *C. asiatica* has one more tooth in both the maxilla (10:10) and mandible (9:9) halves (*A. hottentotus*: <sup>9,9</sup>/<sub>8,8</sub>).

#### *Macroscelides proboscideus* and *Elephantulus edwardii*

If complete skulls with intact teeth of these two elephant shrew species are compared, identification is not difficult. However, skulls from owl pellets are frequently broken and the teeth lost. It is therefore necessary to look at a spectrum of diagnostic features.



The zygomatic arch (from lateral) and the braincase seem wider with *M. proboscideus*. Also in the latter species the temporal bullae are enormous and are visible from a dorsal viewpoint - not so with *E. edwardii*. The palatal foramina seem a little larger in *E. edwardii*. The rostrum tends to be longer in *E. edwardii* and there is a bigger separation between I<sup>3</sup> and C. Furthermore, in *E. edwardii* both C and P<sup>1</sup> are double rooted, with the roots one behind the other. In *M. proboscideus* they are single rooted. P<sup>2</sup> and P<sup>3</sup> are both clearly two lobed from a lateral view and P<sup>2</sup> has lingual cusps in the case of *M. proboscideus*. None of these features are present with *E. edwardii*. The *M. proboscideus* mandible is a little more curved ventrally and the coronoid process is narrower. P<sub>1</sub> is single rooted with *E. edwardii*, but not so with *M. proboscideus*.

#### ***Bathyergus suillus* and *Cryptomys hottentotus***

Both these skulls are sturdy and are seldom very broken. Distinction should not prove difficult for the trained eye. Alveolar patterns are described clearly by Avery (1979) and other cranial features by De Graaff (1981). It is worth while to note two distinctive features not mentioned in these sources.

Seen from the anterior, the infraorbital foramen is clearly bigger in *C. hottentotus*. The ventrolingual edge of the angular process forms a thicker ridge in *B. suillus*.

#### ***Otomys irroratus* and *Otomys karoensis***

Of the three species of *Otomys* encountered in this study, *O. unisulcatus* could be distinguished with relative ease and will not be discussed. *O. karoensis* and *O. irroratus*, however, proved difficult to distinguish from each other. Trends exist, but there were many areas of overlap and exceptions to the trends can occur. Differences listed by Avery (1982a) are not be discussed, except to stress that the *O. irroratus* skull is generally larger than that of *O. karoensis*.

It was found that the molar tooth row length and nasal width used by Coetzee (1971) can at best be viewed as trends, since many exceptions occur. In the light of this study, these measurements may be influenced by Bergmann's Rule and as a result will differ through time



and over its current range. The features described below refer to *O. karoensis* with the implication that *O. irroratus* displays the opposite characteristics.

*O. karoensis* has a shorter snout and as a result a shorter diastema. Viewed from anteriorly the groove between the premaxillae tends to be deeper. The ridges formed by the anterior parts of the premaxillae tend to be shorter and to divert less anteriorly. The frontal ridge of the zygomatic process tends to be lower and rounder. Viewed both anteriorly and laterally the zygomatic plate tends to be narrower and smaller. The attribute listed by De Graaff (1981) that the anterior palatal foramina tends to be long and narrow, extending almost to the incisors, proved to be a very convenient diagnostic feature. It was furthermore noted that these foramina tended to almost reach the first root of  $M^1$  posteriorly. The *O. irroratus* palatal foramina does not tend to reach as close to the incisors and the molars. The postal areas of the frontal bones tend to be more convex. Viewed ventrally the posterior process of the basisphenoid tends to be shorter. In lateral view the fissura sphenodalis seems less visible. In both the maxillae and mandibles the incisors and molars tend to be smaller and narrower. Looking at the mandible, the lingual root of the second lamellum of  $M_1$  tends to be absent or reduced. The medial part of  $M_1$ 's lamellae tends to curve more to the front than that of *O. irroratus*. Despite these features, the mandibles could not be distinguished with certainty and a formula was used to divide them between the two species - see Materials and methods.

#### ***Mastomys natalensis* and *Mastomys coucha***

With the methods applied in this study it was not possible to distinguish between the cranial material of these species. Until more information is available, the ecological data are treated as applying to both species (Mills & Hess, 1997: 146). For these reasons the two species of *Mastomys* were treated as one.

#### ***Mastomys natalensis/coucha* and *Myomyscus verreauxii***

It was possible to distinguish between the upper jaws of these 'two' species by the position of the posterior palatal foramina and the extent to which the anterior palatal foramina reach posteriorly (Rosevear, 1969). However, it was not possible to distinguish between the



mandibles of the 'two' species'. As no *M. verreauxii* upper jaw material was encountered in this study, it was taken that there were no mandibles of this species.

### ***Aethomys namaquensis* and *Rhabdomys pumilio***

The maxillae of these two species are distinguishable. The mandibular differences are, despite *A. namaquensis* being slightly larger, not always apparent when teeth are absent.

The most diagnostic feature in the *A. namaquensis* mandible is the two anterior alveoli of M<sub>2</sub> which do not appear as distinct alveoli as is the case with *R. pumilio*. There are specimens where these alveoli do appear distinct in *A. namaquensis*, but such examples are rare. On the *R. pumilio* mandible a minute lateral alveolus usually exists between the first and second alveolar rows of M<sub>2</sub>. This is absent in *A. namaquensis*. Furthermore the *A. namaquensis* alveolar tooth row is generally somewhat wider, but appears narrower towards the anterior end. At the symphysis *A. namaquensis* displays a sharper medioventral ridge than *R. pumilio*. The lateral mandibular ridge tends to be more prominent in *A. namaquensis* and the anterior end tends to be closer to the mental foramen. Another useful feature was found to be the position of the mental foramen. In *A. namaquensis* it tends to be situated more dorsally and in *R. pumilio* more laterally.

### ***Dendromus melanotis* and *D. mesomelas***

Although it was impossible to distinguish between the mandibles of the two species when teeth were absent, certain distinctive characteristics do exist in the skull and maxillae. As only one (possible) *D. mesomelas* maxilla was found in all the material, the *Dendromus* mandibles were all taken to belong to *D. melanotis*. The following results were obtained from the D.M.Avery collection.

As the maxillae tend to break loose from the skull, the most important distinctive features are those of the zygomatic plate and masseter knob. The *D. melanotis* zygomatic plate is narrower and the masseter knob more pronounced. The part of the zygomatic process joining the maxilla appears thinner in *D. melanotis*. It was found that from an exact lateral/frontal view the masseter knob silhouette is visible only in *D. melanotis*. The skull of *D. melanotis* is



in general smaller than that of *D. mesomelas*. The *D. melanotis* snout is relatively shorter. The zygomatic arch tends to turn lower (more ventral) in *D. melanotis*. From a frontal view the infraorbital foramina of *D. melanotis* appears marginally smaller and rounder.

#### ***Dendromus* and *Steatomys krebsii* mandible**

The *Steatomys* angular process tends to be longer. The alveoli of *S. krebsii* are more oblong and a wider gap exists between the first and second mandibular alveoli. The posterior end of the lower alveolar tooth row tends to turn more medially with *S. krebsii*. Small differences also occur between the coronoid and condylar processes.

#### ***Steatomys krebsii* and *Mus minutoides* maxillae**

Apart from the fact that *M. minutoides* is generally smaller the most distinctive feature in the maxilla is the area where the zygomatic plate joins the main body of the maxilla. In this area the *S. krebsii* zygomatic plate is narrower, whereas no constriction occurs here with *M. minutoides*. Furthermore, a masseter knob is present in *S. krebsii* (as in all Dendromurinae), while being absent in *M. minutoides*.

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