The taxonomy and taphonomy of Mio-Pliocene and Late Middle Pleistocene micromammals from the Cape west coast, South Africa

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This thesis describes original research which has not been submitted in any form towards a degree at another university.
I submit it as my own work and acknowledge all assistance received.

Supervised by John E. Parkington and Christiane Denys

ABSTRACT

The study sites investigated in this thesis are situated along the southwest coast of South Africa in an area dominated by the sclerophyllous fynbos of the Strandveld and Sandveld, which supports a well known micromammal (murid, soricid, macroscelid, bathyergid and chrysochlorid) fauna. This study presents the results of a taphonomic, taxonomic and palaeoecological study of micromammal assemblages from two palaeontological sites in the Saldanha Bay/Langebaanweg area on the west coast, in the western Cape Province, South Africa. The micromammalian populations of these two sites are compared both taxonomically, and taphonomically, with other fossil sites on the west coast dating to the Terminal Pleistocene and Holocene.

The older of the two sites is 'E' Quarry at Langebaanweg, a disused phosphate mine, which is the only site in the western Cape Province representing the Mio-Pliocene, a slice of time when modern micromammal genera were emerging. The second site investigated in this thesis is the late Middle Pleistocene site of Hoedjiespunt 1, which fills a significant gap in the continuum of micromammal evolution in the western Cape. This site contained faunal remains accumulated by a brown hyaena *(Hyaena brunnea)*, and micromammal bones and teeth were recovered from the same sediments.

The Hoedjiespunt 1 micromammal assemblages have added to the information available on the past distribution of several species in the Saldanha area, and have confirmed the presence of several endemic species in the west coast area during the late Middle Pleistocene. A comparison between the other west coast fossil sites and Hoedjiespunt 1 indicates that conditions on the west coast in the late Middle Pleistocene were relatively more arid.

The micromammals from Langebaanweg 'E' Quarry indicate that fynbos microhabitats were well established during the Mio-Pliocene on the west coast. Both the fynbos, and most of the micromammal genera present at LBW, have families resident in the west coast area today. The micromammal assemblages from Langebaanweg indicate that the general micromammal population in the area remained relatively unchanged during the period of deposition of the two main fossil-bearing members of the Varswater Formation. There is no compelling evidence to suggest that any marked climatic or environmental change took place during this period.

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I dedicate this thesis to my grandmother, Daphne, and my grandfather, Ewald Baumgarten.

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Introduction

1.1 Micromammals and palaeoecological research

Micromammal bones may become incorporated into palaeontological and archaeological sites, through the deposition of scats from small carnivores or pellets from owls or diurnal birds of prey. The pellets and scats disaggregate over time and become incorporated into the sediment, leaving accumulations of micromammal bones and teeth. Micromammals may also become incorporated into a fossil assemblage when they die as a result of natural disasters such as rock falls, flooding, or suffer aestivation or hibernation deaths. Humans may also be responsible for the accumulation of micromammal assemblages in archaeological sites.

The micromammals from archaeological and palaeontological sites are frequently used in palaeoclimatic and palaeoecological research (Avery 1983, 1990, 1991, 1992a, 1992b, 1992c, 1999, 2002, 2003, Denys 1985, 1996a, 1997, Andrews 1990, Klein 1991, Marean *et al.* 1994, Fernandez-Jalvo 1995, 1996, Vigne and Valladas 1996, Fernandez-Jalvo *et al.* 1998, Manthi 2002). Micromammals are effective environmental indicators because they do not migrate long distances, have small home ranges, and, in many cases, have precise ecological requirements (Falk and Semken 1998). Species, which occupy precise ecological niches, can provide detailed information about the vegetation and/or substrate of the area in which they live.

The evolution of the Rodentia from various African fossil sites has been the focus of much research in recent years as this has provided critical information on the evolution and dispersal of African fauna (Brandy *et al.* 1980, Wesselman 1984, Denys 1987a, 1989, 1990a, 1990b, 1996a, 1999, Lindsay 1988, Chevret *et al.* 1993, Senegas and Avery 1998, Senegas 2001). Information obtained from the study of micromammals has complemented palaeoecological studies on large African mammals (Klein 1983, Kappelman 1984, Marean 1992, Bishop 1999, Vrba 1999), and micromammals found in association with hominids have been used to recreate the habitats in which they lived (Wesselman 1984, Denys 1996a, 1997, 1999, Fernandez-Jalvo *et al.* 1998, Avery 2000b, 2003).

In the past few years, taphonomy has been used increasingly in the study of micromammal assemblages that are being used for palaeoecological analysis (Korth 1979, Andrews 1990,

Fernandez-Jalvo 1995, 1996, Denys *et al.* 1996a, Denys 1997, 2002, Fernandez-Jalvo *et al.* 1998, Matthews 1998, 1999, 2000, Laudet *et al.* 2002, Manthi 2002,). In order to trace changes over time in community structure and population, micromammals representing different time periods, and hence potentially different palaeoclimates and environments may be compared. In the interests of accurate palaeoclimatic and palaeoenvironmental reconstruction, it is necessary to establish to what degree a fossil micromammal assemblage may be considered representative of the original micromammal population that lived in the area. Taphonomy provides the means by which to do this. A taphonomic analysis of a fossil assemblage provides information on the chemical and physical forces that have affected and potentially biased a fossil assemblage since the time of deposition, and also provides information on the site in general.

Andrews (1990) established that different predators produce characteristic breakage and digestion patterns on the bones and teeth of their prey, and it is therefore frequently possible to distinguish between the different families of predator/s involved in the accumulation of fossil assemblages. Identifying the predator responsible for the accumulation of a micromammal assemblage is important as some predators are less selective and have a varied diet, while others are more selective and choose only some of the prey species from the available micromammal population. Identifying the predator allows the analyst to take into account the manner in which particular predators' behaviour may have biased the fossil micromammal assemblage. For example, in a taphonomic study of Elands Bay Cave, an archaeological site on the west coast (see Figure 1.1), Matthews (1998, 1999) showed how different predators influenced the species composition of the micromammal assemblages in the various fossil-bearing horizons.

The study sites investigated in this thesis are situated along the southwest coast of South Africa (Figure 1.1) in an area dominated by the unique, sclerophyllous fynbos of the Strandveld and Sandveld, which supports a well known micromammal fauna (De Graaff 1981, Skinner and Smithers 1990, Stuart and Stuart 2001). Changes in the palaeoenvironment of the west coast during the Late Pleistocene and Holocene have been inferred from several studies on fossil micromammal assemblages (Avery 1992b, 1992c, 1999, Matthews 1998, Avery in press, Manthi 2002). The present study extends the time range investigated much further back to the Mio-Pliocene, when the earliest recorded fynbos, and modern rodent genera, were appearing.

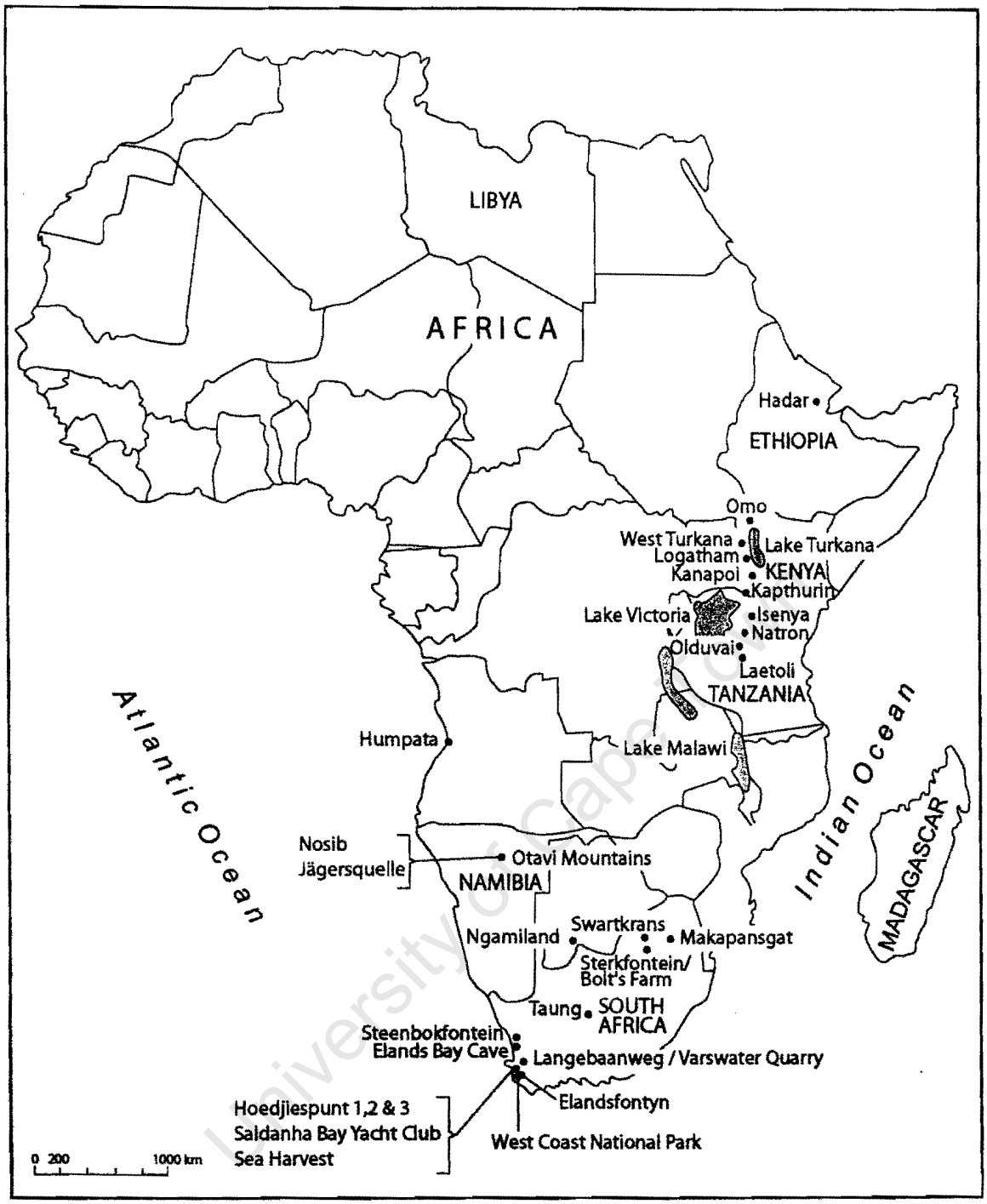


Figure 1.1: The location of archaeological and palaeontological sites referred to in this thesis

1.2 The sites and micromammal assemblages analysed in this thesis

This study presents the results of a taphonomic, taxonomic and palaeoecological study of micromammal assemblages from two palaeontological sites in the Saldanha Bay/Langebaanweg area on the west coast, in the western Cape Province, South Africa. The older of the two sites is 'E' Quarry at Langebaanweg, a disused phosphate mine, which has yielded rich faunal assemblages laid down during the Mio-Pliocene. Mining operations in the

area began in 1943, but Langebaanweg's importance as a fossil site was realised by local and international scientists only in 1958 (Singer 1961, Hendey 1982). LBW offers one of the largest collections of Mio-Pliocene fossils in Africa, and contains an extremely rich and diverse range of over 230 vertebrate and invertebrate taxa, including numerous micromammal bones and teeth (Hendey 1974, 1981a). LBW is the only site in the western Cape Province representing the Mio-Pliocene, a slice of time when modern micromammal genera were emerging, as indicated by both palaeontological and molecular phylogeny studies (Denys 1996a, 1999). LBW is therefore a crucial site for our understanding of the evolution and dispersion of modern rodent taxa from southern Africa. LBW also provides an opportunity to study the fynbos region, which is a centre of endemism for many plant families and genera, primitive invertebrates, and the Amphibia (Bigalke 1972, 1979, Deacon 1983). Several endemic rodent species live in the west coast area today, and this thesis traces the first appearance of some of these, and other genera, in the fossil record at LBW.

The second site investigated in this thesis is the late Middle Pleistocene site of Hoedjiespunt 1 (HDP1). The (HDP1) site contained faunal remains accumulated by a brown hyaena *(Hyaena brunnea)*, and micromammal bones and teeth were recovered from the same sediments (Stynder *et. al.* 2001). Elandsfontyn, the other Middle Pleistocene site in the region (Figure 1.1.), produced no micromammals; and other South African Middle Pleistocene fossil sites which have produced micromammals, such as Wonderwerk Cave and the Cave of Hearths, lie far north of Langebaanweg (Avery 2000a). HDP1 thus fills a significant gap in the continuum of micromammal evolution in the western Cape as there are numerous fossil sites containing micromammals dating to the Holocene, but few Middle or Late Pleistocene sites.

The term 'micromammal' as used in this thesis, includes small mammals up to, and including, the size of mole rats (Family: Bathyerginae). A taxonomic comparison of Langebaanweg and Hoedjiespunt 1 with the micromammal assemblages from three other geographically close west coast fossil sites, dating from the Terminal Pleistocene to the Holocene, are presented in order to trace the development and evolution of the fynbos biota and associated micromammals of this area. The micromammal populations from several modern barn owl pellet collections are included in the comparison.

The East African sites, which are open-air sites, generally show a lower diversity of genera and species than the South African Australopithecine sites. The fact that the East African sites are open-air, lacustrine sites, and the South African australopithecine sites accumulations

in karstic fillings, was thought to be responsible for differences in the diversity of genera and species between the two areas (Denys 1996a, 1999). In general, the number of genera and species are lower in East Africa than in South Africa, even when sites of a comparable age are compared (Denys 1999). It has been suggested that the different depositional histories of the two types of sites may be responsible for the observed differences in diversity between the two areas (Denys 1996a, 1999). Langebaanweg is an open-air site and some of the sediments have been alluvially accumulated. From a taphonomic point of view, therefore, Langebaanweg provides an interesting comparison to the East African sites, and to the other west coast sites mentioned in this thesis, which accumulated under closed conditions.

There is clearly a large gap in the fossil record between Langebaanweg and Hoedjiespunt 1. This gap unfortunately includes the period of time in which taxa such as *Euryotomys* and *Mystromys hausleitneri* disappeared, and modern murid genera replaced those of the Plio-Pleistocene. The micromammals from Langebaanweg, and Hoedjiespunt 1 and the other west coast sites, are compared on a generic, rather than specific level. This comparison is useful, despite the gap, as it contributes to our understanding of how the micromammal population in an area of the west coast has changed over a long period of time. The gaps in the fossil history of the west coast will hopefully be filled in the future, but in the mean time, other sites found in southern Africa, such as Bolt's farm, which is believed to be 5-4 Ma (Senegas and Avery 1998), the 3 Ma Ngamiland fauna from Botswana, and several Namibian sites, many of which are in the Otavi Mountains, are helping to fill in the gaps in the fossil record (Pickford and Mein 1988, Senut *et al.* 1992, Pickford *et al.* 1994,). In East Africa sites such as Hadar (Ethiopia), Ibolé (Tanzania), Omo (Ethiopia) and the Laetoli beds (Tanzania) provide a good record of the micromammals living in East Africa during the Early Pliocene. In North Africa, the Middle Miocene fauna of Sahabi in Libya contributes to our knowledge of the relationship between the faunas of North Africa and Asia, and eastern and southern Africa. The Kenyan site of Kanapoi, dated to around 4 Ma, has yielded only two rodents, *Tatera* and *Hystrix* (Behrensmeyer 1976), however, further excavations will take place at the site very shortly and more taxa are expected to be added to the faunal list (Manthi pers. comm.). The australopithecine sites of South Africa are well documented and have provided a rich rodent fauna, these sites are discussed further in the next chapter.

1.3 Background to the west coast sites

One of the three west coast sites mentioned in this thesis is the Saldanha Bay Yacht Club site (SBYC), which represents a rich micromammal assemblage accumulated in a solution cavity in Langebaan Formation aeolianites. The sediments have been radiocarbon dated to 15 540 ± 70 years B.P (Manthi 2002). There had been some erosion of the deposit at SBYC and micromammal samples were collected from three areas. These included a sample collected from the *in situ* deposit which was called 'hanging remnant', and from two areas below the site where material had eroded out. These sample areas were referred to as the 'upper slope' and the 'down slope' and micromammal samples were collected for the purposes of a taxonomic and taphonomic comparison with the *in situ* material. The micromammals found in these three assemblages are listed in Appendix A. A complete taphonomic analysis, based on Andrews (1990) methods, has indicated that the assemblage was accumulated by an owl, the barn owl being the most likely candidate (Manthi 2002).

The two other sites, Elands Bay Cave (EBC) and Steenbokfontein Cave (STBKC), contain archaeological deposits which range in age from the Terminal Pleistocene to the Late Holocene. EBC is situated in the side of Baboon Point cliff facing north-west towards the sea, approximately 40 m above sea level (Parkington in press). Baboon Point cliff dominates the landscape around the cave, and the tidal zone lies some 150 m away. Behind the cliff stretches sandy, coastal plains and some 2 km from the cave lies a vlei, the Verlorenvlei (Jerardino 1996). The area around EBC is a transitional area in that it lies between the Karroid and Fynbos vegetation types (Sinclair *et al.* 1986). There are two variations of Strandveld found in the area; a dense, dwarf semi-succulent scrub and an open, semi-succulent, fynbos-type form of the Strandveld proper vegetation (Acocks 1975).

EBC was excavated in units defined by differences in stratigraphy. Micromammals were found in units which covered the period from 13 260 BP to 300 BP. A list of the micromammals, showing their percentage occurrence in the various depositional horizons, as well as the dates of the individual units, is available in Appendix B. The barn owl (*Tyto alba afinis*) was found to have been responsible for the deposition of the micromammals in some horizons of the site (units 11, 13, 15b, 15c). The spotted eagle owl (*Bubo africanus),* an unidentified viverrid, and a giant eagle owl (*Bubo lacteus*) were identified as potential predators for the accumulation of the micromammals in various other depositional units (units 3a, 6, 8a, 8b and 9) (Matthews 1998, 1999).

The archaeological cave site of Steenbokfontein is set in a prominent sandstone outcrop which is surrounded by relatively flat terrain, and low sand dunes. The sea is visible from the cave which is oriented west north-west and overlooks nearby reefs and beaches 1.8 km distant (Jerardino 1996). The micromammalian sample studied (listed in Appendix C) was taken from the five uppermost layers. Layer 0 at the very top has not been dated, but layer 1 to 4b have produced dates between 2200 and 6000 BP, and layer 4b yields dates from 3990 BP to 6070 BP 9 (Avery 1999). Although a taphonomic analysis of the STBKC micromammals has not been done, the great density of the micromammal fossils and the extremely low degree of breakage of the micromammals observed at this site strongly indicates that a barn owl was responsible for their accumulation (Jerardino pers. comm).

1.4 Background to the modern, comparative owl pellet collections

Two modern owl pellet collections were gathered for comparative purposes with the fossil material. These comparative assemblages were collected from the rocky koppie (hill) in which Steenbokfontein Cave is found (Avery 1999). The owl pellet sample from Steenbokfontein represents an area in which the environment has been altered by farming as the koppie from which the pellets were collected is surrounded on several sides by farmlands. The other modern barn owl pellet collections mentioned in this thesis were gathered from thirteen roost areas in the national reserve area of the West Coast National Park which lies some 20 km south of Langebaanweg on the west coast, and surrounds the Langebaan lagoon area (Avery 1992b). Several barn owl roost sites in various areas of the nature reserve were sampled over a period of approximately five years, and a comparison was made between the various roost sites in terms of micromammal species composition, seasonal changes in prey, and so on (Avery 1992b). The West Coast National Park pellet collections represent a micromammal population which has comes from a relatively undisturbed area, although farming activities have occurred in areas of the reserve in the past, prior to the declaration of the area as a reserve.

1.5 Present-day vegetation of the west coast

The west coast shows a limited topographical variety (Manning and Goldblatt 1996). The granite hills which dominate the west coast landscape are of early Palaeozoic origin, and the weathered granite soils of intermediate nutrient status support a wide range of plant species (Rutherford and Westfall 1986). The Sandveld and the Strandveld are the two main fynbos vegetation types found on the west coast today, and each grows in a particular kind of soil

(Manning and Goldblatt 1996). The open, scrub vegetation of the Strandveld fynbos includes woody members such as *Rhus, Euclea, Chrysanthemoides* and *Olea,* and generally grows in sandy calcareous soil (Rutherford and Westfall 1986, Manning and Goldblatt 1996). The most characteristic vegetation type on the west coast is the Sandveld, which is dominated by restionaceous genera and small shrubs such as *Phylica stipularis, Staavia radiata, Stoebe plumosa* and *Metalasia densa* (Manning and Goldblatt 1996). In spring annual Asteraceae are abundant. The Sandveld fynbos grows on well drained, coarse sands and gravelly limestones which are poor in nutrients (Manning and Goldblatt 1996). Certain Strandveld species are found only in areas of limestone, which is of Late Tertiary origin (10-2 Ma). The grass species which are found in the Cape fynbos vegetation today, are dominated by C_3 grasses, which favour a cool growing season (Vogel *et. al.* 1978). A third vegetation type, Renosterveld, is not found on the west coast, but slightly inland, in the Swartland area (Manning and Goldblatt 1996). Renosterveld is more nutritious than the Sandveld and Strandveld vegetation and in the past supported relatively large numbers of herbivores (Cowling and Richardson 1995).

Some 210 genera and seven plant families are endemic to the fynbos biome, and some 297 endemic floral species are found in the Saldanha Bay area of the west coast today (White 1983, Low and Pond 2001). Some of the floral species in the Saldanha Bay area occupy stable and unstable dunes, and are mainly restricted to areas of calcareous sands and calcrete (Lubke 1996).

A biome which has been described for the Saldanha area, but which has not been formally recognized, the Thicket Biome, is described by Lubke (1996). The Thicket Biome is relatively mesic and is characterized by dunes which are up to 30 m in height. This biome is comprised of a mosaic of smaller vegetational zones, one of which is the Dune Thicket, which stretches from the Saldanha Bay area and along the western Cape coast to KwaZulu-Natal. Dune Thicket consists of dense thicket and contains vegetation which ranges from closed shrubs such as *Rhus glauca* and *Tetragonia spicata*, to dwarf forests with evergreen, sclerophyllous or succulent trees, vines and shrubs (Lubke 1996).

1.6 Present-day climate and environment of the west coast

The south western and southern tip of the African continent receives winter rainfall from cyclones originating over the South Atlantic (Coetzee 1978), and is located at the interface of temperate westerly and sub-tropical climate systems (Carr *et al.* 2003). The climate on the

west coast is determined by the seasonal shifts and interplay of the prevailing winds over the Benguela region (which are determined by the South Atlantic high pressure system), and by the eastward moving cold fronts (cyclones) across Southern Africa (Tyson 1986). During summer, the South Atlantic high pressure system is well developed, but in the winter months, shifts northwards, allowing cold fronts to move in the same direction (Tyson 1986).

The nutrient-rich Benguela current which flows past the west coast supports a wide range of marine life. The cooling and upwelling of the Benguela current brings moisture-laden sea winds to the west coast which, together with the atmospheric factors, prevent rain from falling in the Namib (Siesser 1978). The affect of the cold, upwelling Benguela current and the persistent, strong South Atlantic high-pressure system (a stable anticyclone which lies above the Atlantic Ocean at 30° S) are two of the main causes for the present aridity along the south-western coast, the Namib and the dryness of the interior of the sub-continent (Siesser 1978; Coetzee 1978, 1980, Coetzee and Rogers 1982).

Coastal fog is a valuable source of moisture for the plants on the west coast during the summer months (Sinclair *et al.* 1986). The Langebaanweg area has an average annual rainfall of approximately 278 mm, and mean annual temperature is about 23°C (Weather Bureau 1986; www.weathersa.co.za/climat/Langebaan_Stats.html). The annual rainfall at Elands Bay Cave is between 275 mm and 150 mm (Parkington in press). Lamberts Bay, the small coastal town which lies approximately 10 km north of Steenbokfontein Cave, receives much less rain than the Elands Bay area, and the site of Steenbokfontein lies on the cusp of these two rainfall zones (Avery 1999).

The Langebaanweg area is presently drained by the Great Berg and Sout Rivers which cut through the Malmesbury formation, the oldest geological strata in the area (Tankard 1974). The Berg River runs into St Helenas Bay, where tidal range is 1.8m (Tankard 1974).

1.7 Layout of thesis

Chapter two provides a background to the modern and fossil rodent faunas of Africa, with an emphasis on South and East Africa. Chapter three provides an overview of the Langebaanweg area in terms of geological succession, present and past climate, fauna and flora, and also previous research done at, and in the vicinity, of 'E' Quarry. Chapter four presents the methodology used to record and describe the taphonomy and taxonomy of the two fossil microfaunal assemblages analysed in this thesis.

Chapters five, six, seven and eight present the results of a taxonomic and taphonomic study of the micromammals from Langebaanweg (LBW). Chapter five presents the results of a taphonomic study of the two main fossil-bearing members at LBW. Chapter six provides a discussion of these results and sketches the depositional history of the LBW micromammals, as suggested by the taphonomy. Chapter seven introduces the various genera and species found at LBW, and places them within the context of the micromammal faunas from other palaeontological sites in Africa. In Chapter eight the faunal assemblages from the two main fossil-bearing members are compared, and various issues relating to the taxonomic mix of micromammal species found in both members are reviewed. The chapter concludes with a discussion of the palaeoecology of LBW, as indicated by the micromammals.

Chapters nine, ten and eleven concentrate on the site of Hoedjiespunt 1 (HDP1). Chapter 9 provides a background to the geology and setting of the Saldanha Bay area, and then focuses on the palaeontological site of HDP1. Previous work done on the site is presented. Chapter ten presents the results of a taphonomic and taxonomic analysis of the HDP1 micromammals. Chapter eleven presents a discussion of these results, and the palaeoenvironmental implications of the micromammal assemblages are discussed.

Chapter twelve provides a taphonomic comparison of the patterns of skeletal element abundance shown by the various west coast fossil sites, namely Hoedjiespunt 1 (HDP1), the Saldanha Bay Yacht club site (SBYC), Elands Bay Cave (EBC), Steenbokfontein Cave (STBKC) and Langebaanweg (LBW). The following chapter, Chapter thirteen, provides an overview of the micromammal populations found in the above-mentioned west coast fossil sites, from the Mio-Pliocene, until the present. Chapter fourteen summarises the main findings of this thesis, and assesses the contributions made towards our understanding of the taphonomy and palaeoecology of HDP1 and LBW, and the micromammal population of the west coast from the Mio-Pliocene to the present.

Chapter Two
Background to the modern and fossil rodent faunas of Africa

This chapter provides some background to the modern and fossil rodent faunas of Africa, as well as the current status of micromammal research regarding the evolution of micromammals in South and East Africa.

2.1 Modern rodent faunas of the biotic zones of Africa.

Establishing the biogeographical affinities of fossil rodent faunas is necessary in order to gain an understanding of speciation and extinction events (Denys 1999). With this in view, Denys (1999) looked at the diversity characteristics of modern micromammal populations in the biogeographical regions of Africa, which are illustrated in Figure 2.1. Table 2.1 presents the generic composition of the modern rodent populations in these regions.

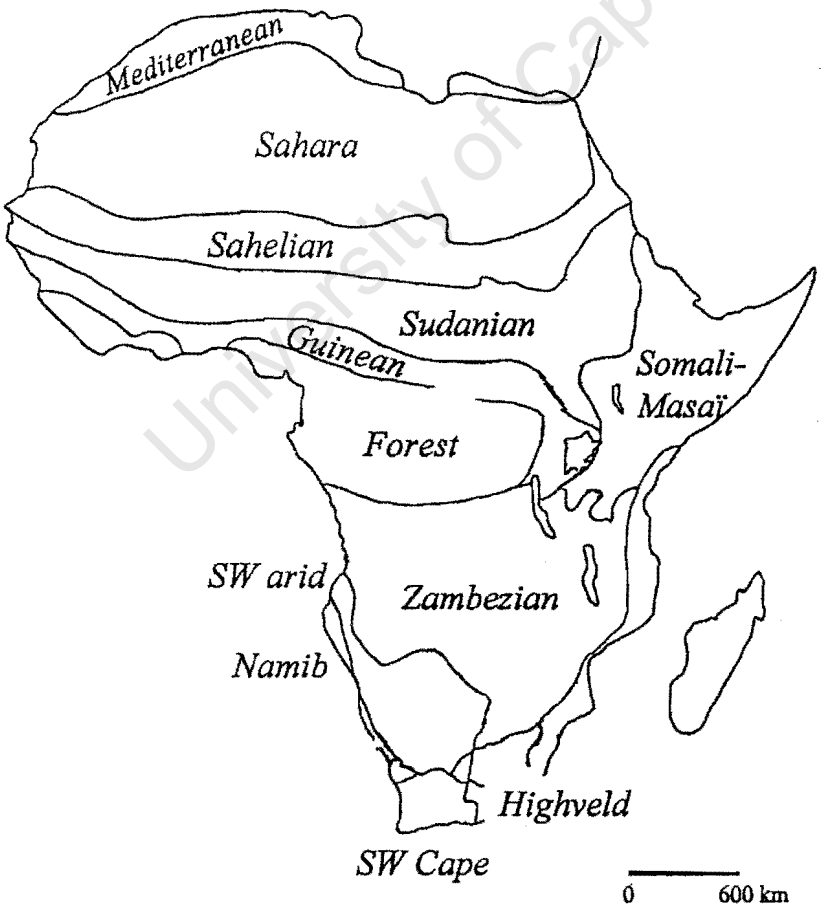


Table 2.1: The biogeographical regions of Africa (After Denys 1999, Figure 16.1, page 227)

Sahara	Sahelian	Sudanian	Guinean	Forest	Montane forest	Regional mosaic of Lake Victoria	Somali-Masai	Zambezian[B]	Highveld[C]	Namib	Kalahari-SW Arid	Cape
<250[A]	250-500	500-1000	1000-1500	1500+	1500+	1000-1500	<500	500-1500	500-1000	<250	<500	250-1000+
Gerbillus	*Desmodilliscus*		*Taterillus*	*Anomalurus*	*Anomalurus*	*Anomalurus*	*Gerbillus*			*Tatera*	*Tatera*	*Tatera*
Meriones	*Gerbillus*	*Gerbillus*	*Tatera*	*Idiurus*		*Tatera*	*Tatera*	*Tatera*	*Tatera*	*Gerbillurus*	*Gerbillurus*	*Gerbillurus*
Pachyuromys	*Tatera*	*Tatera*		*Zenkerella*			*Taterillus*			*Desmodillus*	*Desmodillus*	
Psammomys	*Taterillus*	*Taterillus*	*Heliosciurus*	*Heliosciurus*	*Heliosciurus*	*Heliosciurus*	*Ammodillus*					
				Funisciurus	*Funisciurus*	*Funisciurus*	*Lophiomys*		*Mystromys*	*Petromyscus*	*Petromyscus*	*Mystromys*
		Heliosciurus		*Protoxerus*	*Protoxerus*	*Protoxerus*	*Xerus*	*Xerus*	*Xerus*		*Funisciurus*	
	Xerus	*Xerus*	*Xerus*	*Xerus*	*Paraxerus*	*Paraxerus*	*Paraxerus*	*Paraxerus*			*Xerus*	
						Saccostomus	*Beamys*					
		Cricetomys	*Cricetomys*	*Cricetomys*	*Cricetomys*	*Cricetomys*	*Cricetomys*	*Cricetomys*				
		Steatomys	*Steatomys*	*Deomys*	*Deomys*	*Deomys*	*Saccostomus*	*Saccostomus*		*Saccostomus*	*Saccostomus*	*Saccostomus*
				Prionomys	*Dendromus*	*Steatomys*	*Dendromus*	*Steatomys*	*Steatomys*	*Steatomys*	*Steatomys*	
				Dendroprionomys			*Megadendromus*	*Dendromus*	*Dendromus*		*Dendromus*	*Dendromus*
									Malacothrix		*Malacothrix*	
					Otomys	*Otomys*	*Otomys*	*Otomys*	*Otomys*	*Otomys*	*Otomys*	*Otomys*
Mus	*Mus*	*Mus*	*Mus*	*Mus*		*Mus*	*Mus*	*Mus*	*Mus*	*Parotomys*	*Parotomys*	
	Arvicanthis	*Arvicanthis*	*Arvicanthis*	*Arvicanthis*		*Arvicanthis*	*Muriculus*			*Mus*	*Mus*	*Mus*
Acomys	*Acomys*	*Acomys*	*Acomys*				*Acomys*	*Acomys*				*Acomys*
				Lophuromys	*Lophuromys*		*Arvicanthis*					
		Dasymys	*Dasymys*	*Dasymys*	*Lamottemys*	*Aethomys*	*Aethomys*	*Aethomys*	*Aethomys*	*Aethomys*	*Aethomys*	*Aethomys*
			Aethomys	*Hybomys*	*Hybomys*	*Dasymys*	*Dasymys*	*Dasymys*				*Dasymys*
		Grammomys		*Hylomyscus*	*Hylomyscus*	*Pelomys*	*Grammomys*	*Grammomys*				*Praomys*
		Lemniscomys	*Lemniscomys*	*Malacomys*	*Malacomys*	*Lemniscomys*	*Lemniscomys*	*Pelomys*				*Myomyscus*
	Mastomys	*Mastomys*	*Mastomys*	*Mastomys*		*Mastomys*	*Mastomys*	*Lemniscomys*				
				Oenomys	*Oenomys*	*Oenomys*	*Oenomys*	*Mastomys*	*Mastomys*		*Mastomys*	
			Praomys	*Praomys*	*Praomys*	*Praomys*	*Rhabdomys*	*Rhabdomys*	*Rhabdomys*	*Rhabdomys*	*Rhabdomys*	*Rhabdomys*
		Myomys	*Myomys*	*Stochomys*		*Grammomys*	*Praomys*	*Uranomys*				
				Thamnomys	*Thamnomys*	*Thamnomys*	*Thallomys*	*Thallomys*	*Thallomys*	*Thallomys*	*Thallomys*	
			Uranomys	*Uranomys*		*Lophuromys*	*Zelotomys*	*Zelotomys*			*Zelotomys*	
				Colomys	*Colomys*	*Colomys*	*Colomys*					
Jaculus	*Jaculus*	*Graphiurus*	*Graphiurus*	*Graphiurus*	*Graphiurus*	*Mylomys*	*Stenocephalemys*					
Eliomys							*Desmomys*					
Ctenodactylus			*Thryonomys*	*Thryonomys*		*Uranomys*	*Pelomys*					
						Zelotomys	*Graphiurus*	*Graphiurus*	*Graphiurus*		*Graphiurus*	*Graphiurus*
							Thryonomys	*Thryonomys*	*Thryonomys*			
							Pedetes	*Pedetes*	*Pedetes*	*Pedetes*	*Pedetes*	
Massoutiera	*Felovia*	*Felovia*					*Cryptomys*	*Cryptomys*	*Cryptomys*		*Cryptomys*	*Cryptomys*
						Grahiurus	*Heterocephalus*	*Heliophobius*			*Georychus*	*Georychus*
							Tachyoryctes				*Bathyergus*	
						Tachyoryctes	*Pectinator*			*Petromus*	*Petromus*	
						Thryonomys						
Diversity 10	11	17	18	27	19	30	38	25	16	14	24	16
Gerbillinae 4	4	3	2	0	0	1	4	1	1	3	3	2
Murinae 2	4	8	10	14	9	16	18	12	5	4	6	7

Table 2.1: The generic composition of modern rodent populations in the zoogeographic regions of Africa (After Denys 1999, Table 16.1, page 228.

[A] Average annual rainfall, in millimeters [B] SSW and SSG (South Savanna Woodland and South Savanna Grassland) [C] Temperate subtropical grassland

A study of Table 2.1 shows that the Sahara region is dominated by the Gerbillinae, and there are equal numbers of gerbillid and murine genera in the Sahel. The Sudanian region has similar numbers and genera of Gerbillinae to the Sahel, though Gerbillinae are outnumbered by the Murinae. Some other general trends were observed by Denys (1999). For example, tropical and montane forest showed an increase in diversity from east to west, but decreased with altitude. The highest diversity was found to be in the Somali-Masai region, which contained 38 rodent genera. In this region, rodent genera from the Sahelo-Sudano-Guinean regions are found together with genera from the Zambezian savanna. Southern Kenya and northern Tanzania is the area of contact between Somali-Masai and Zambezian savannas and in this area different species of the same genera are found, for example, *Aethomys chrysophilus* and *A. hindei,* and *Saccostomus mearnsi,* and *S. campestris* (Denys 1999). Some genera are replaced by their ecological equivalents, for example, *Arvicanthis* is replaced by *Pelomys.*

The rodent fauna of the Cape Province was found to show many similarities to that of the Zambezian savannas, but was an exception in terms of the Gerbillinae/Murinae ratio, with two Gerbillinae genera occurring in the area, despite the relatively high rainfall of 500-1500 mm (Denys 1999). Species shared by the Cape, and Kalahari SW Arid regions include *Tatera, Gerbillurus, Saccostomus, Dendromus, Otomys, Mus, Aethomys, Rhabdomys, Graphiurus, Cryptomys* and *Georychus*. Species shared by the Cape, and Namib regions include *Tatera, Gerbillurus, Saccostomus, Otomys, Mus, Aethomys, Rhabdomys, Thallomys, Pedetes* and *Petromus*. The Namib fauna has many affinities with that of the South West Arid Zone, and they share the endemic genera *Petromyscus, Desmodillus, Parotomys,* and *Petromys* (Bigalke 1978, Denys 1999). The rodent fauna found in the Langebaanweg area today shares several genera with the Zambezian and Somali-Masai rodent populations, as well as with the Namib and South West Arid regions. Denys (1999) suggests that differentiation of the southwest Cape Province and of the Southwest Arid region may have occurred as early on as the Early Pliocene.

2.2 Modern and fossil patterns of Endemism

Table 2.2 shows the patterns of endemism shown by several fossil sites dating to the Early and Middle Pliocene.

Fossil Site	Endemic genera	Genera shared with other areas:
Langebaanweg	*Desmodillus*	Southwest Arid and Namib
	Mystromys	Also found in the Highveld
	Bathyergus	Southwest Arid
Namiland	*Malacothrix*	Southern savanna grassland
	Georychus	Southwest Arid
	**Taterillus*	Sahel, Sudanian, Guinean regions
Kosib and Langersquelle	*Gerbillurus*	Namib South west arid Cape
	Malacothrix & Mystromys	Southwest Arid
Langersquelle	*Desmodillus*	Namib South west arid Cape
Makapansgat	*Taterillus* *Mystromys*	
	Myomyscus	Cape
	Malacothrix	Southwest arid
Laetoli	*Heterocephalus*	
Hadar	*Tachyoryctes*	
Omo C	*Oenomys*	

Table 2.2: Fossil patterns of endemism during the Early and Middle Pliocene (After Denys 1999, page 236)

*Identification of this species is uncertain (Denys pers. comm.)

As Table 2.2 illustrates, the South African fossil rodent assemblages contain several modern endemic taxa. The family Chrysochloridae (Golden moles) is endemic to Africa, south of the Sahara, and includes seven genera. Fifteen of the eighteen species are found in the Southern African Subregion (Skinner and Smithers 1990). The Bathyergidae are endemic to Africa, and occur from the Cape, to 10° north of the equator (De Graaff 1981). Bathyergids are well represented in fossil sites of the Early Pliocene, and the extant *B. janetta* and *B. suillus* are endemics of the Cape region (De Graaff 1981). Extant species of rodents endemic to the Southwestern Cape include the Cape gerbil, *Tatera afra*, Verreaux's mouse, *Myomyscus*

verreauxi, and the Cape spiny mouse, *Acomys subspinosus* (Stuart and Stuart 2001). In terms of endemic species, the Cape region shares *Mystromys* with the Highveld grasslands, *Malacothrix*, *Gerbillurus*, and *Bathyergus* with the southwest arid, and *Desmodillus* with the southwest arid and Namib, the only true endemic is *Myomyscus* (Denys 1999). *Rhabdomys*, which is found at Langebaanweg 'E' Quarry, is endemic to the southern savannas.

2.3 The rodent fossil record in East and South Africa during the Miocene

Early Miocene deposits in Kenya, Namibia and Uganda show a rodent fauna with well-diversified Pedetidae, Sciuridae, Bathyergidae, Anomaluridae and Phiomyidae derived from endemic Eocene stock (Denys 1999). Lavocat and Parent (1985) note that the African Miocene Cricedontidae, most notably *Afrocricetodon*, are interesting because morphologically they are at the level of Oligocene European cricetodontids.

The Middle Miocene Muruyur Beds in western Kenya from the Kipsaramon site (15.5 Ma) yielded a diverse rodent fauna with seven rodent families represented, namely pedetids, anomalurids, thryonomyids, diamantomyids, myophiomyids, cricetodontids and ?sciurids (Winkler 1992). The fauna included a mixture of primitive Early Miocene taxa, as well as more derived taxa, for example, a Thryonomyidae genus and species (Winkler 1992). The Muruyur rodents of Kenya from 15.5 Ma show affinities with Early and Middle Miocene sites of East Africa, Namibia, and Saudi Arabia (Winkler 1992, Denys 1999). Contemporaneous sites in Pakistan, the Sivaliks, show a more diversified and advanced cricetid and muroid fauna (Lindsay 1988, Denys 1999). The Kenyan fauna differs from that of North Africa in that it lacks graphiurids and ctenodactylids (Denys 1999).

Around 14 Ma the African faunas show a change in composition, the most significant event being the appearance of the Dendromurinae, Petromyscinae and Myocricetodontinae (Lindsay 1988, Pickford *et al.* 1994, Denys 1999). The fact that some of these taxa are shared by North Africa and the Siwaliks, confirms that exchanges took place in a wide palaeo-Saharo-Indian province (Denys 1999). The Asiatic genera *Potwarmus* and *Antemus*, thought to be direct ancestors of true murinae, are lacking from the East African faunas, however, indicating that these exchanges were not complete, or occurred later (Jacobs 1978). *Myocricetodon* and cf. *Democricetodon*, as well as *Dakkamyoides* species, have been recovered from the Namibian Otavi Breccias, thought to be of Middle Miocene age (Pickford *et al.* 1994). Bishop and Pickford (1975) note the presence of a Dendromurinae gen. nov. and a small and medium sized cricetid from the Ngorora Formation in Kenya which is dated from between 12 and 9

Ma. The Otavi Mountain breccias dating to the Late Miocene yielded Bathyergidae, Sciuridae indet., Cricetidae cf *Brachyuromys* and cf. *Mystromys, Stenodontomys, Myocricetodon, Steatomys, Dendromus, Petromyscus, Protarsomys* and *Dakkamyoides,* among others (Pickford *et al.* 1994).

Around 11.5-11 Ma, the differentiation of the first true Murinae, *Progonomys*, took place in North Africa, Europe and Pakistan, but does not appear in contemporaneous faunas in South or East Africa, where the first true Murinae is an undetermined *Praomys*-like species (Denys 1999). *Progonomys* is found throughout southern Europe and north-west Africa at about the same time (Munthe 1987). A *Praomys* sp. is recorded in Chorora, Ethiopia, at about 10 m.y, and in Namibia around 8-9 Ma (Denys 1999).

The Middle Miocene Sahabi fauna of Libya shows no connection with Langebaanweg and shows total isolation from contemporaneous sub-Saharan faunal elements. The majority of Sahabi micromammals are North African endemics, and may have reached Libya from the Maghreb (Munthe 1987). The taxa *Sayimys,* which is found at Sahabi, is an immigrant from South Asia and represents a late survival of this genus (De Bruijn 1981, Munthe 1987).

In East Africa between 6 and 4 Ma, a wide palaeo-province existed, and the same taxa were found contemporaneously in Afghanistan, Arabia and East Africa. This province was first described by Brandy *et. al.* (1980), but the presence of the Asiatic species, *Saidomys,* in the East African Ibolé fauna indicates that this area is larger than they suggested and may be extended to include Tanzania (Denys 1999). *Saidomys* is also found in the Early Pliocene fauna of Wadi Natrum, and a cf. ? *Saidomys* from undated Plio-Pleistocene deposits has been found in Thailand (Denys 1999).

2.4 East and South African fossil faunas

Appendix D shows the rodent faunal composition of the main Early to Middle Pliocene fossil sites of East and South Africa, including Langebaanweg. The Pleistocene fossil sites of East Africa are rich in Murinae and include 14 genera. These proportions are similar to modern records, except that they show slightly more abundant Murinae (Denys 1996a). South African fossil micromammal assemblages differ in that they show a greater diversity of genera and species, for example, four Otomyinae taxa are represented in fossil sites in South Africa, while only one species is found in East Africa, a situation which prevails today (Denys 1996a). Likewise, five gerbillid species are found in South Africa today, and only two in East

Africa. No sciurids are found in South African fossil sites, although five extant genera live in South Africa today. *Xerus* and *Paraxerus* have been found in East Africa at Olduvai and Omo (Denys 1996a, 1999), and more recently in Chad (Denys pers. comm.).

From the Late Miocene to the Early Pliocene, a common rodent community existed between Africa, Arabia and Pakistan. Although the Hadar fauna contains a large number of taxa of Asian origin, the Laetoli fauna shares only two genera with Hadar and contains no 'Asiatic' genera (Denys *et al.* 1987, Denys 1996a). The two genera common to both Laetoli and Hadar are *Tatera* and *Hystrix*, which are ubiquitous, and it appears that some barrier prevented faunal exchange between the two areas (Denys 1987b). The Middle Pliocene period (4-3 Ma) shows high levels of endemism amongst the rodent faunas in the Eastern Rift area, indicating that the Eastern Rift once contained a series of small basins, isolated from each other by volcanic or tectonic swells (Denys *et al.* 1987). Changes in the composition of local East African fauna may be related to tectonic activity and sedimentological changes, and their affect on the local environment (Denys *et al.* 1987). Differences between the Hadar and Omo B and Omo C rodent communities have been interpreted as resulting from geographical isolation during the Early Pliocene (Denys 1985). Denys (1987b) suggests that around 3.7 Ma, or possibly earlier, there was a relative continuity in the savanna between Laetoli and southern Africa. After this period a geographical barrier prevented the murids from Omo and Hadar from reaching Laetoli, and also prevented the migration into the area of typical southern African forms such as *Saccostomus* and the Bathyergidae (Denys 1987b). The Laetoli Bed faunas have the most genera in common with the Jägersquelle and Makapansgat rodent assemblages (Denys *et al.* 1987, 1999). The eastern murid species differ from the southern ones, however, in showing specialized characteristics which become exaggerated in the Upper Ndolanya beds at Laetoli, and in the Olduvai Bed I (1.75-1.65 Ma). Denys (1987b:165) writes that, "*Given the antiquity of the Laetoli fauna, certain characteristics can be considered as being common, primitive traits that are shared with modern southern African species, in contrast to those of corresponding modern eastern African species*".

Extant species, or subspecies, of rodents such as *Saccostomus*, *Thallomys*, and *Xerus* appear to be represented in southern Africa by species which are generally more primitive than their vicariants from eastern Africa (Denys 1987b). The rodent faunas of South Africa and East Africa show different stages of evolution in contemporaneous faunas, and changes in evolution appear to take place at different periods (Denys 1996a, 1999). Genera cited as evidence of this are *Dendromus*, *Steatomys*, *Aethomys*, *Thallomys* and *Otomys* (Denys 1987b,

Denys 1989, 1994a, 1996a, 1999). The East African faunas show a maximum affinity with the Somali-Masai region between 4 and 3 Ma, and appear to show a differentiation of the region as early as 3.7 Ma (Denys 1999). Seven taxa have not moved from their place of origination, and dispersal southwards is much less common than dispersal northwards (Denys 1999).

During the Early and Middle Pliocene, the rodents from the Ethiopian fossil sites never have more than three genera in common with the South African ones. Even in cases where eastern and southern African sites share common genera, indicate a savanna environment, and are similar in age, the species differ (Denys 1996a). Four to nine genera are held in common between Olduvai Bed I and the Australopithecine cave sites, these include *Tatera, Thallomys, Grammomys, Aethomys, Pelomys, Mastomys, Dendromus, Steatomys* and *Otomys*. *Tatera, Dendromus, Steatomys* and *Mastomys* are the genera held in common between Laetoli and the austropithecine cave sites at 3.7 Ma (Denys 1996a). Table 2.3 provides a summary of Appendix D, which shows the faunal composition of the Early to Middle Pliocene murid faunas of fossil sites in East and South Africa. Table 2.3 shows the rodent genera held in common by LBW and other Early to Middle Pliocene fossil sites.

	LBW	OMB	OMC	LB	UNB	HAD	MKPT	NGA	JAG	NOS
Desmodillus	√								√	
Dendromus	√			√			√		√	√
Aethomys	√						√		√	√
Mystromys	√						√			√
Rhabdomys	√						√			√
Stenodontomys	√						√		√	√
Euryotomys	√									
Zelotomys	√							√	√	√
Thallomys	√	√	√	√	√					
Acomys	√						√		√	
Graphiurus	√								√	√
Bathyergus	√									
Cryptomys	√						√			√

Table 2.3: The Rodent genera held in common by LBW and other Early to Middle Pliocene fossil sites in eastern and southern Africa (After Denys 1999, Table 16.2, page 230 and Senut *et al.* 1992, Table 3, page 730)

Key: LBW = Langebaanweg; OMB & OMC = Omo B and Omo C; LB = Laetoli Beds; UNB = Upper Ndolanya Beds; HAD = Hadar; MKPT = Makapansgat; NGA = Ngamiland; JAG = Jagersquelle; NOS = Nosib1 and Nosib2

As may be seen on the table above, *Aethomys* is found only at LBW, Makapansgat, Nosib and Jägersquelle, while *Acomys* is found at LBW, Makapansgat, Jägersquelle, and also one of the Otavi Mountain sites which are not shown on Table 2.3 (Senut *et al.* 1992). By the Late Pliocene to Early Pleistocene, *Aethomys* is found in many south and east African sites, but *Acomys* is found only at Sterkfontein and Kromdraai (De Graaff 1961, Denys 1999, Avery 2000b).

Stenodontomys, which is also found at LBW, makes a first appearance in breccias from the Otavi mountains in Namibia in what Pickford *et al.* (1984) refer to as 'Late Miocene' deposits. These breccias contain a mixture of Miocene and Early Pliocene micromammal species, and *Myocricetodon, Stenodontomys, Protarsomys* and *Dakkamyoides* are found together with the genera *Steatomys, Dendromus* and *Petromyscus.* Avery (2000a) notes that the Middle and Late Miocene Namibian micromammalian faunas of Harasib and Berg Aukas are quite different to the earlier faunas from the south. *Stenodontomys* survived for a remarkably long period, as indicated by the fact that this species has been found in Late Miocene breccias from the Otavi Mountains, as well as the site of Nosib1 (Ca 3 Ma.) and in deposits at Berg Aukas, Aigamas II, and Uisib I, dating to 1.5 Ma (Senut *et al.* 1992, Pickford *et al.* 1994, Denys 1999).

In Kaokoland, Namibia, breccias dating from the Late Pliocene/Early Pleistocene have yielded a number of genera including *Otomys, Mastomys, Steatomys, Dendromus, Aethomys, Thallomys*, and some other species generally associated with the Namib or SW Arid regions, namely *Petromyscus, Petromus* and *Zelotomys. Thryonomys,* which is most definitely not associated with these regions today, was also found.

The Humpata Plateau in Angola has yielded fossiliferous breccias of Late Pliocene-Early Pleistocene age and one of the sites, Malola, may be approximately the same age as Makapansgat (Pickford *et al.* 1994). *Rhabdomys* was not found in any of the Humpata breccias although the faunal list is long and contains species such as *Aethomys, Zelotomys, Thallomys, Acomys, Dasmys, Dendromus, Steatomys, Petromyscus, Tatera, Otomys, Uranomys, Mus,* and *Grammomys,* among others (Pickford *et al.* 1994).

LBW has no genera in common with Ibolé (Tanzania), and only one genus, *Thallomys,* in common with the Upper Ndolanya beds (Laetoli) and Omo B and Omo C. *Mus* has yet to be postively identified and described at LBW, but is another genus which may be held in

common by LBW, Nosib, Jägersquelle and Omo B. As illustrated by Table 2.3, LBW has seven genera in common with Makapansgat and Jägersquelle, eight in common with Nosib, none in common with Hadar, and one or two in common with the Laetoli beds, Ngamiland and Omo B and Omo C. *Thallomys* was also found at Aigamas II (Senut *et. al.* 1992), in the Kaokoland breccias in Namibia, and a ? *Thallomys* was recorded in the Post-Miocene Otavi breccias (Pickford *et. al.* 1994). The fact that LBW shows the closest similarities with Makapansgat, Nosib and Jägersquelle suggests that a certain affinity existed between the micromammal faunas of what is today the Namib and South West Arid regions, and those of South Africa, as represented by Makapansgat and LBW at approximately 5-3 Ma.

When comparing the Langebaanweg and Namibian faunas as listed by Senut *et al.* (1992), *Malacothrix* and *Steatomys* are noticeable in their absence from LBW as they are found in almost all the Otavi mountain sites. *Mastomys* is absent from both LBW and the Namibian sites, but is found in the Upper Ndolanya beds, the Laetoli beds, Omo B and C, and Makapansgat during the Early-Middle Pliocene.

To conclude, generic and specific diversity is greater in the southern African sites. When comparing the taxa of eastern and southern Africa it becomes clear that few genera are held in common, and no common species have yet been found, even in the case where contemporaneous sites exist (Denys 1996a). After 2.5 m.y, the Tanzanian faunas share between five and eight common genera with the South African cave sites, while Omo F and Omo G from Ethiopia share only two to four genera with East Turkana. The Olduvai rodent faunas are quite distinct from those of Omo and East Turkana in the Pleistocene (Denys 1996a, 1999). Species extinctions occur in East Africa between 3 and 1.7 Ma and between 0.8-0.4 m.y, and in South Africa, between 4 and 3 Ma, and then between 1.5 and 0.3 Ma (Denys 1999).

2.5 First and last appearance of species

Many modern taxa make their first appearance around five million years ago in South Africa and between 8.5-10.5 Ma in Namibia (Denys 1999). There is another peak in the first occurrence of modern taxa in East Africa around 3.7-3.3 Ma, and after 1.7 Ma all modern genera are present (Denys 1999). Table 2.4 shows the first appearance date (FAD) and last appearance date (LAD) occurrences, and dispersal direction, for the rodent genera found in the fossil sites of East and South Africa. As Table 2.4 indicates, Langebaanweg provides vital

information on the first appearance of a number of taxa; including two species of Bathyergidae, a graphiurid sp., and a number of other genera including *Aethomys, Dendromus, Mystromys, Acomys, Euryotomys, Rhabdomys, Zelotomys and Thallomys.* Of all these genera, only *Euryotomys* is extinct.

Taxon	Site	FAD (Ma)	LAD (Ma)	Site of last occurrence	Direction of dispersal
Hystricidae					
Xenohystrix	Laetoli beds	3.7	3.3	Makapansgat ?	SOUTH
Hystrix		?			
Petromuridae					
Petromus	Taung	2.5?	0		SOUTH
Thryonomyida					
Thryonomys	Ibole	6-4?	0		?
Pedetidae					
Pedetes	Laetoli beds	3.7	0		SOUTH
Sciuridae					
Xerus	Laetoli beds	3.7	0		NORTH
Paraxerus	Laetoli beds	3.7	0		NORTH
Bathyergidae					
Bathyergus	Langebaanweg	5	0		None
Cryptomys	Langebaanweg	5	0		NORTH
Georychus	Ngamiland	3.3	0		?
Gypsorychus	Makapansgat	3.3	2.5	Taung	NORTH
Heterocephalus	Kakesio, Lower	4.3	0		NORTH
Cricetomyinae					
Saccostomus	Harasib 3A Namibia	10.5	0		NORTH
Cricetomys	Kapthurin	0.4	0		?
Petromyscinae					
Petromyscus	Harasib 3A Namibia	10.5	0		None
Dendromurina					
Steatomys	BA31 Namibia	8.5	0		NORTH
Dendromus	Langebaanweg	5	0		NORTH
Malacothrix	Makapansgat	3.3	0		None
Gerbillinae					
Desmodillus	Langebaanweg	5	0		None
Tatera	Kanapoi	?4	0		SOUTH
Gerbillurus	Jägersquelle-Nosib	2.5	0		?
Gerbillus	Omo F	2.33	0		SOUTH
Delanymyinae					
Stenodontomys	Namibia: Berg Aukas and Harasib 3a	Late Miocene	1.5	Namibia: Berg Aukas 54, Aigamas II, Uisib I	NORTHWEST
Mystromyinae					
Mystromys	Langebaanweg	5	0		NORTH
Proodontomys	Makapansgat	3.7	1	Kromdraai A & B, Swartkrans I	None

Table 2.4: First appearance date (FAD) and last appearance date (LAD) occurrences and dispersal direction for all rodent genera found in the fossil sites of East and South Africa (After Denys 1999, Table 16.6, page 238)

Table 2.4 continued...

Taxon	Site	FAD (Ma)	LAD (Ma)	Site of last occurrence	Direction of dispersal
Murinae					
Karimata	Chrora, Harasib 3A	10.5	8.5	BA31 Namibia	?
Saidomys	Ibole	6-4	2	Omo G	NORTH
Acomys	Langebaanweg	5	0		NORTH
Eurycolomys	Langebaanweg	5	4-5	Bolt's farm (Senegas and Avery 1998)	NORTH
Aethomys	Langebaanweg	5	0		NORTH
Rhabdomys	Langebaanweg	5	0		NORTH
Zelotomys	Langebaanweg	5	0		NORTH
Thallomys	Langebaanweg	5	0		NORTH
Golunda	Hadar	3.3	2.5	Omo D	SOUTH
Oenomys	Hadar	3.3	0		
Praomys	Hadar	3.3	0		SOUTH
Dasymys	Makapansgat	3.3	0		?NORTH
Grammomys	Makapansgat	3.3	0		?NORTH
Nannomys	Makapansgat	3.3	0		NORTH
Pelomys	Makapansgat	3.3	0		NORTH
Otomys	Makapansgat	3.3	0		NORTH
Myotomys	Makapansgat	3.3	0		None
Prototomys	Makapansgat	3.3	2.5	Taung	None
Millardia	Ngamiland	3	3	Hadar	
Arvicanthis	Omo B	3	0		
Lemniscomys	Omo B	3	0		?
Dipodidae					
Jaculus	Omo F	2.3	0		SOUTH
Graphiurinae					
Graphiurus	Langebaanweg	5	0		NORTH
Tachyoryctinae					
Tachyoryctes	Hadar	3.3	0		SOUTH
Anomaluridae					
Anomalurus	Kipsaramon	15.5	0		None

The endurance of many of the above genera in the Cape region up to the present day is discussed further in Chapter thirteen, where a comparison is made between the micromammal populations of LBW and the west coast fossil sites of HDP1, SBYC, EBC, STBKC, and the faunal assemblages from modern barn owl pellet collections.

Chapter three

Background to the Langebaanweg area

3.1 Introduction

Research carried out on the murids and mole rats from LBW in the 1970's up until the 1990's generally concentrated on the identification and description of new species (Pocock 1976, 1987, Denys, 1990a, 1991, 1994b, 1998). Although Denys (unpublished) made a broad study of the different micromammal taxa at LBW, not all the micromammal material from the LQSM was studied, and none of the micromammals from the recent excavation area have been hitherto analysed. No palaeoecological analysis has been carried out on the site, and previous studies have not looked at the taphonomy of the micromammals. This thesis thus represents the most extensive and detailed study done on the micromammals from the various units at LBW to date.

3.2 The Varswater 'E' Quarry site at Langebaanweg

The phosphate ore mined intermittently at LBW since 1943, came from the Varswater Formation, which was named after the New Varswater Quarry (Tankard 1974). Mining at Varswater 'E' Quarry at Langebaanweg began in 1965, and ceased in 1992.

During the 1960s, and the period up until the late 1980s, fossils from the Varswater Quarry were a focus of research by the South African Museum (now the South African Museum, Iziko Museums of Cape Town), under the leadership of Dr Brett Hendey, who published numerous papers on both the fossil fauna and geology of the LBW area (Hendey 1970a, 1973, 1974, 1976, 1978a, 1978b, 1978c, 1978d, 1980, 1981a, 1981b, 1982). After Dr Hendey's departure from the museum in the late 1980s research at LBW slowed down considerably, and mining of the area ceased in 1992. In 1998, the newly established West Coast Fossil Park was opened to the public under the directorship of Pippa Haarhoff, and in September 1998 the excavation of fossil deposits was resumed at 'E' Quarry.

3.3 The geological succession at Langebaanweg: The Varswater Formation

The Varswater Formation is underlain by the Middle Miocene Elandsfontyn Formation, or by Neoproterozoic to Cambrian bedrock (Roberts in press). Overlying the Varswater formation

is the calcareous aeolionite of the Langebaan Formation, or the quartzose aeolian sands of the Springfontein Formation (Dingle *et al.* 1979, Roberts in press). The Varswater Formation forms part of the Sandveld Group and has been recorded over a large area. Figure 3.1 places the Varswater formation within the Cenozoic geological succession of the Langebaanweg area.

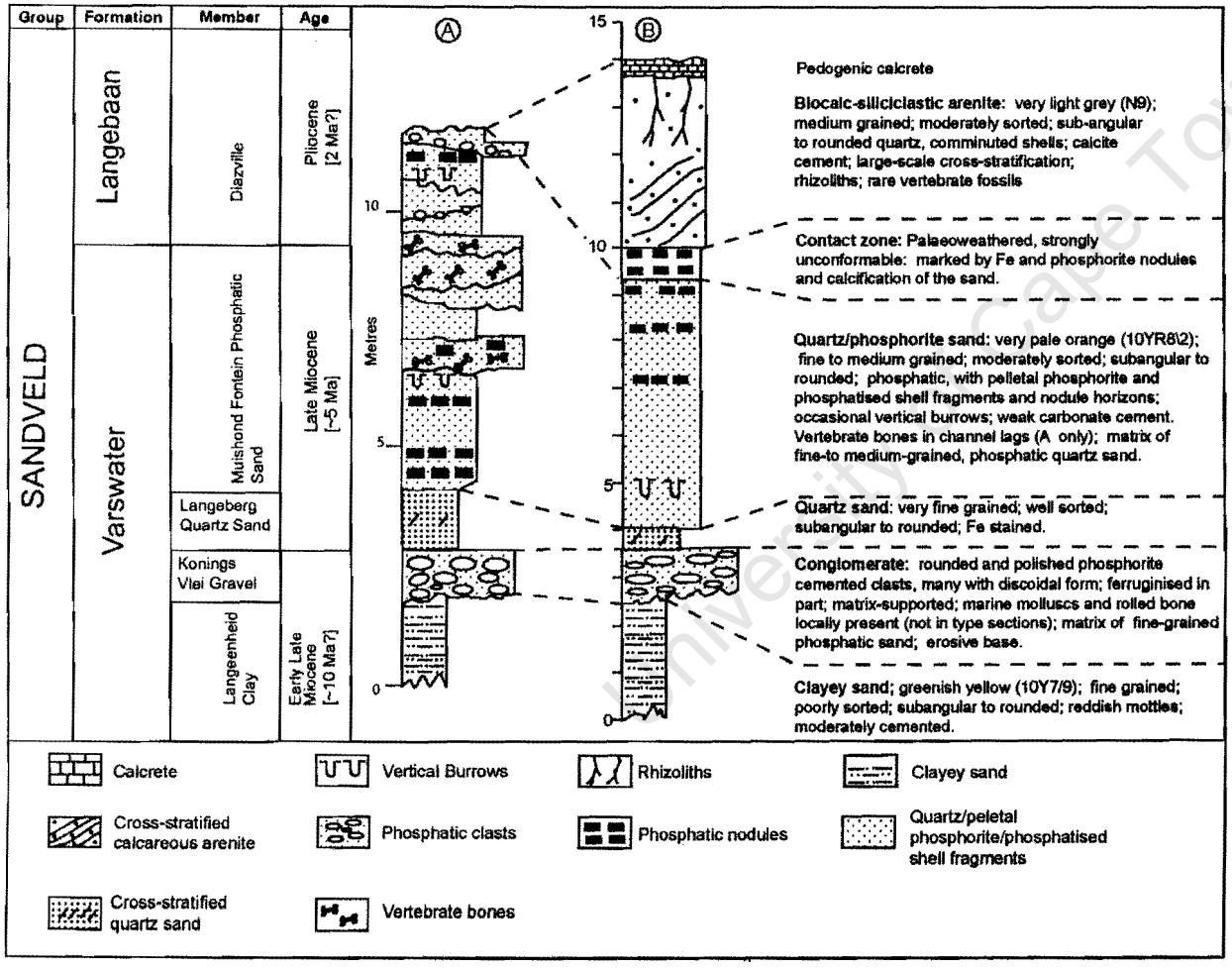


Figure 3.1: The geological succession of the Langebaanweg area

The Varswater Formation succession consists of three members, the oldest of which is the Gravel Member. The Gravel Member is overlain by the Quartzose Sand Member and the Pelletal Phosphate Member. The latter contained the commercially exploitable phosphate ore mined at Langebaanweg. Roberts (in press) has now formally named the lithostratigraphy of the Varswater Formation. The Pelletal Phosphate Member has been renamed the Muishhond Fontein Pelletal Phosphorite Member (MPPM), the Quartzose Sand Member is now the Langeberg Quarz Sand Member (LQSM), and the Gravel Member, the Konings Vlei Gravel Member (KVGM). Pre-KVGM deposits are associated with the Middle Miocene transgression and are found only in boreholes, although small exposures existed at one time in 'C' and 'E' quarries (Hendey 1981a). The LQSM and the MPPM are the main fossil bearing deposits of the formation and are by far the best documented deposits in the Langebaanweg area (Hendey 1976, 1978c, 1981a, 1981b).

The Upper Varswater Formation was probably laid down during a global, early Mio-Pliocene transgression, which has been linked to global sea level changes (Hendey 1981a, Hendey 1981b). The Varswater Formation occurs at ± 90 m at Elandsfontyn (farm 349), and this provides evidence for the sea level reaching ± 90 m at the time of deposition of the LQSM and MPPM (Rogers 1980, Roberts and Brink 2002). These units are found only between elevations of 30 m and 40 m at LBW, however, a feature which may probably be attributed to post-depositional erosion (Roberts and Brink 2002). The maximum elevation of the Varwater Formation is ~45 m amsl and the thickness ~ 40 m (Roberts and Brink 2002). The late Pliocene regression truncated both the MPPM and LQSM in 'E' Quarry to the north and east (Hendey 1981a).

3.3.1 The Konings Vlei Gravel Member (KVGM)

The KVGM has a complex history, and five stages are recognised in the formation of this member (Butzer 1973). These are:

- the deposition of the Middle Miocene phosphatic sediments in a shallow marine/estuarine environment
- the induration of these sediments with phosphorite,
- the reworking of this secondary phosphatic rock into blocks/cobbles by marine processes,
- the partial carbonate cementation and iron-enrichment of this conglomerate,
- then a final reworking of the end products of the above into unconsolidated, white (10YR) medium-to-coarse-grade sands.

The deposition and reworking of the KVGM ceased when the sea level dropped, possibly during the terminal Miocene regression (Hendey 1981a). The molluscs and shark fossil remains found in the KVGM suggest that it accumulated under warm water conditions (Hendey 1981b).

3.3.2 The Langeberg Quarz Sand Member (LQSM) and the Muishhond Fontein Pelletal Phosphorite Member (MPPM)

Hendey (1981a) suggests the following scenario for the deposition of the LQSM and MPPM. During the deposition of the Mio-Pliocene succession of the Varswater Formation, a ± 90 m sea level transgression caused a river, possibly the precursor of the Berg river, entering the sea in the immediate vicinity of 'E' Quarry, to deposit the sediments which were to form the LQSM and MPPM members.

The river which deposited the unconsolidated, ~2 m thick sands of the LQSM, originally followed a channel which lay to the south east and south of 'E' Quarry. The general course of this river is illustrated in Figure 3.2 as 'river channel 1'. After deposition of the LQSM, the river migrated about 500m northwards, cutting diagonally across 'E' quarry, and flowing from north-east to south-west, as illustrated by 'river channel 2' in Figure 3.2. This, and a subsequent northwards shift in the river's course (the third shift is indicated by 'river channel 3') resulted in the deposition of the MPPM member, which represents a channel lag deposit (Hendey 1980). The three shifts of the river's course, and the geology of Langebaanweg and surrounds, are clearly illustrated in Figure 3.2.

The MPPM has been divided into the fossiliferous bed 3a, which consisted of a northerly and southerly part, namely bed 3aS (river channel 2) and bed 3aN (river channel 3), as well as other undifferentiated, largely non-fossil bearing beds (Hendey 1981a). Bed 3aS is thought to have been laid down during the second shift northwards of the river, and bed 3aN by the third northwards shift in the river's course. The third channel still had a north-east to south-west trend, although it swung southwards and cut into the southwesterly parts of bed 3aS, truncating these sediments, as illustrated in Figure 3.2. Substantial sedimentation, together with a rising sea level, may have affected the lower course of the river and could have caused the change in river course from bed 3aS to bed 3aN (Hendey 1981a).

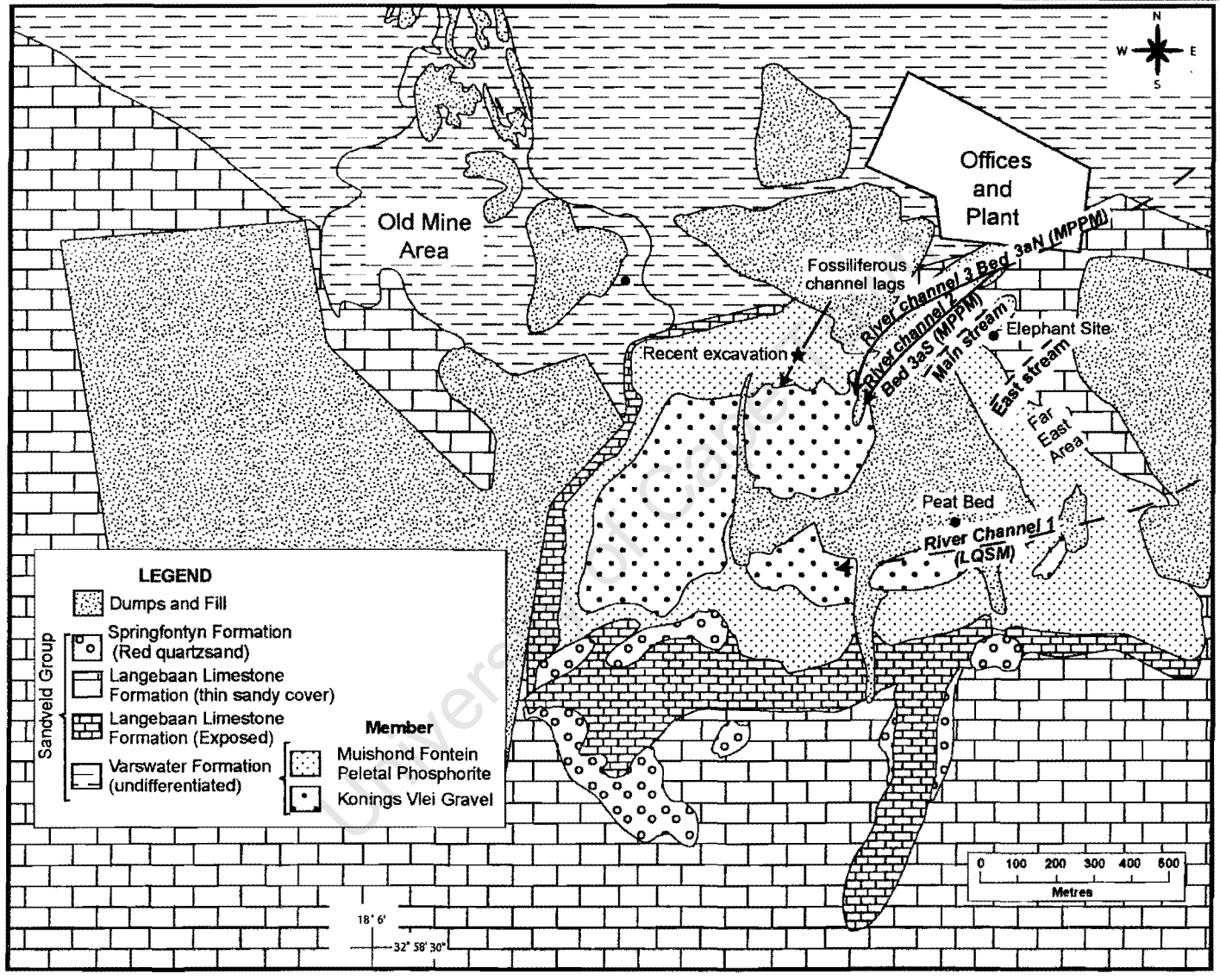


Figure 3.2: The deposition of the LQSM and MPPM, and the geology of Langebaanweg 'E' quarry, and surrounds (After Hendey 1981a, Figure 6, page 28, and Roberts in press)

Note: The areas marked in Figure 3.2, such as 'main stream', 'east stream', 'elephant site', 'far east area' and 'peat bed' show the general areas from which the micromammal assemblages analysed in this thesis came. These areas are mentioned in more detail further on in this chapter. The area marked 'recent excavation' marks the site where excavations have been taking place at LBW since 1998, and from which the MPPM material analysed in this thesis came.

Hendey (1981a) notes that the channel deposits and incorporated fossil assemblages of beds 3aS and 3aN of the MPPM are essentially similar. The difference lies in the fact that bed 3aS appears to have been a relatively straight channel superimposed on unconsolidated stratum, while an outcrop of phosphatic rock deflected the course of the bed 3aN river channel southward. At times of flooding, this phosphatic rock thus provided a consolidated substratum for part of the channel (Hendey 1981a). Both bed 3aS and bed 3aN appear to have been deposited in a fluviatile environment (Hendey 1974, 1981a). Bed 3aN in particular, appears to have been deposited by fast flowing water, although the presence of coprolites suggests that at least some of the fossils were deposited sub-aerially (Hendey 1976).

Bed 3aS generally overlies, and is at a higher elevation, than the LQSM. Bed 3aS deposits may contain some reworked material from the LQSM, but there is no evidence to suggest this is so in the case of bed 3aN (Hendey 1976). Bed 3aN is thought to be younger than bed 3aS (Hendey 1980), however, the relationship between bed 3aN and 3aS is complicated and has not always been clear (Hendey 1981a, Olson 1985). Minor morphological and possible size differences have been observed in some of the species between bed 3aS and bed 3aN (Gentry 1980, De Muizon and Hendey 1980). De Muizon and Hendey (1980) note that differences in morphology are very slight and do not warrant formal nomenclatural recognition as they may simply reflect temporal stages of single species. Some bed 3aN deposits are higher than any bed 3aS deposits, and as mentioned above, have truncated 3aS, but they are not found clearly superimposed in any area. Bed 3aN is situated near the northerly limit of the mineable phosphate (Hendey 1976).

The river must have continued to discharge sediment (MPPM undifferentiated) into the area for a while after bed 3aN was deposited, but as the transgression of the sea progressed, the river mouth must have moved further north or east from the 'E' Quarry area, with a consequent diminuition in the influence of the river on local sedimentation (Hendey 1981a).

The late period of sea-level regression is represented only by some marine and terrestrial deposits found at Anyskop, a 70 m high hill which overlies the MPPM to the South of 'E' Quarry. Anyskop is mentioned in more detail at the end of this chapter.

3.4 The depositional facies of the LQSM

The LQSM represents a number of different depositional environments, which are described briefly in this section. Three main facies are recognized in the LQSM;

- Non-phosphatic quartz sands are thought to represent a riverine floodplain environment, which contains both subaqueously and subaerially accumulated vertebrate fossils (Hendey 1974, Gentry 1980).
- The so-called 'peat bed' is a facies composed of carbonaceous sand and clay, which is thought to represent a salt marsh environment.
- In the southwestern part of the mine, a third facies was identified. The invertebrate fauna and the muddy silt of this deposit indicate that the depositional environment was a tidal mud flat (Hendey 1974, Hendey 1976, Gentry 1980).

A fourth facies, a river channel, was postulated to exist south-east and south of 'E' quarry (Hendey 1981a). Table 3.1 shows the different facies of the LQSM distinguished by Hendey.

	Facies	Depositional environment	Characteristic sediments
LQSM	I	Deposits, partly subaerially and partly subaqueously deposited, appear to have accumulated on the floodplain of a river. The depositional environment of these sediments appears to be of low energy, such as in a river floodplain. Microenvironments include ponds and minor drainage channels Fossils: Terrestrial vertebrates dominate	Quartz sand
	1(A)	Possible variation of I, ? floodplain closer to channel.	Quartz sand
	II	This bed lies adjacent to LQSM III. LQSMII is a relatively extensive peat bed comprised of black, carbonaceous sands and clays which represent a salt-marsh deposit. Fossils: rich in pollens and vertebrate fossils.	Carbonaceous sand and clay
	III	Vestiges of a tidally inundated mud-flat bed are found in the south-central area of 'E' Quarry. Fossils: extensive invertebrate collection, vertebrate remains rare.	Muddy silt
	IV	? river channel (not exposed, probably exists south-east and south of quarry).	Not known

Table 3.1: The depositional environments and characteristic sediments of the LQSM (After Hendey 1981a, Table 3, page 27, and page 31-33)

Vertebrate fauna were scarce in the tidal mud flat and this facies is very different to others from the LQSM (Hendey 1976). This deposit overlay the peat bed, which differed markedly from it in terms of faunal content (Hendey 1976). According to Hendey, the sands and clays were faunally different from the more typical exposures of LQSM found elsewhere. Hendey (1976:225) wrote, "...a superficial comparison of the peat bed and east stream faunas should

serve to illustrate that different sediments go together with faunal differences". Numerous species found in the east stream area (this area is demarcated in Figure 3.2) are not found in the peat bed (Hendey 1976). For example, the terrestrial francolin was found in abundance in the east stream, but was rarer in the peat bed where water birds were relatively better represented.

3.5 The depositional facies of the MPPM

Table 3.2 shows the depositional environments represented by the MPPM sediments. As the table clearly illustrates, this member contains a number of depositional facies.

	Facies	Depositional environment	Characteristic sediments
MPPM un-differentiated		Marine littoral	Phosphatic sand
MPPM Bed 3aN	I	River bank	Clays and phosphate rock
	II	River channel	Quartz sand and fossil lag on, and in lee, of phosphate rock
	III	Stratigraphically intermediate between II and IV	Quartz sand and fossil lag grading into carbonaceous sand and clay
	IV	Marsh and pond	Carbonaceous sand and clay, sometimes underlying quartz sand and clay horizons
MPPM Bed 3aS	Not sub-divided	River channel and river bank	Quartz sand and fossil lag grading upwards into phosphatic sand

Table 3.2: The depositional environments and characteristic sediments of the MPPM (After Hendey 1981a, Table 3, page 27, and page 31-33)

3.6 Fossil collection and processing at Langebaanweg

The following section describes the manner in which the micromammal remains were retrieved from the LQSM and MPPM. The LQSM material analysed in this thesis was collected during mining operations in 'E' Quarry, under the supervision of Dr Brett Hendey. The MPPM material, however, was recovered during the 1998 excavation season. As mentioned above, the excavation area is marked in Figure 3.2 as 'recent excavation'.

3.6.1 Fossil collection from the LQSM

During mining operations at LBW, the methodology used for the excavation and collection of fossils was variable and depended very much upon circumstances. For example, Hendey (1976) notes that the mining of certain areas in the site had been brought forward, resulting in

an increased urgency in the collecting of specimens in deposits which would be lost if not salvaged properly. Leisurely collecting and excavation was no longer possible in these areas and a hasty rescue operation had to be launched (Hendey 1976). The LQSM fossils all have accession numbers allocated by the South African Museum, and the geological unit from which they came was also recorded, however, the exact provenance of most of the fossils from the LQSM is uncertain. The fossils are more commonly linked to general, rather than specific, areas, some of which are described by Hendey in published work and field notes. This is particularly true of the micromammals which were rarely the focus of collection, but were collected when found in association with the remains of larger animals (Hendey pers. comm.). The micromammals can therefore be linked to general areas in which larger fossils were excavated or processed, but detailed information about the exact position, or context, in which they were found is not available. Hiatuses remain, therefore, in our knowledge of exactly how, and from where, the majority of the micromammals from the Varswater 'E' Quarry were recovered.

The names given to the fossil assemblages frequently refer to a general area in 'E' Quarry from which fossils were collected. For example the micromammals from 'east stream' and 'peat bed' come from general areas (shown in Figure 3.2), rather an actual site. Site names were frequently related to the discovery of *in situ*, and occasionally articulated, body parts of large mammals exposed during mining. Site names were given as a guide for field assistants to watch for associations of material and had no stratigraphic significance (Hendey pers. comm.). For example, the so-called 'elephant site' (see Figure 3.2) was identified because of the largely complete hemi-mandible and other fragments of elephant that were found by workers (Hendey pers. comm.).

The methods of fossil collection used at Varswater 'E' Quarry during the 70's and 80's were:

- Surface collecting – fossils which had become exposed on the surface were picked up by hand.
- Controlled excavation - fossils were excavated using formal excavation methods when, for example, test pits were dug in order to locate fossiliferous deposits and/or to investigate the stratigraphy in an area.
- Uncontrolled excavation (fossils were removed from an area, usually in a 'rescue' dig in an area where mining was about to begin, without precise recording of their position or situation).
- Screening of small sediment samples in the field or lab, using a mesh of 2 mm or less

- ❖ Screening of bulk sediment samples in the field using a double-bank of sieves with mesh of 10 mm and 5 mm (Hendey 1976).

Screening of bulk sediment samples in the field involved the mechanical removal of samples using front-end loaders and tip trucks. The samples, which ranged in size from a few tons to hundreds of tons, were taken by truck to an area where a stand with double-banked sieves was set up, and piped water washed the dumps through the sieves (Hendey 1976). Such processing of the microfauna allowed for the recovery of large samples and rare taxa, but was also very destructive. It is likely to have resulted in further breakage of micromammal bones and loss of teeth, as even gentle handling has been observed to cause further damage to fossil micromammal assemblages (Matthews 1998). The 5 mm and 10 mm sieves used are likely to have led to the under-representation of the smaller micromammal species. The 2 mm sieves are also likely to have led to the loss of isolated micromammal teeth and small bones or bone fragments. The sieve sizes used, as well as the fact that many micromammals finds were surface-collected, may have resulted in a bias against the recovery of small species.

Much of the micromammal fossil material came from the 'east stream' the general area of which has been described (Hendey 1974). 'East stream' was the name given to a modern, narrow channel that developed along the east wall of the mine as a result of mining below the water table (Hendey pers. comm.). This area became the focus of attention as the LQSM was well exposed and highly fossiliferous in this area (Hendey pers. comm.). All the fossils from east stream came from the fine, white sand characteristic of the LQSM, and no stratification was observed (Hendey pers. comm.). East stream formed part of the LQSM I horizon mentioned in Table 3.1.

The water in east stream drained toward the south-western corner of the mine, from whence it was pumped out (Hendey pers. comm.). This artificial east stream concentrated some of the smaller and lighter micromammal and bird fossils (these concentrations are obviously secondary) and some of these fossils were surface-collected as they became exposed (Hendey pers. comm.). The newly exposed floor of the mine was always much disturbed by mining, and it was mainly in areas of active erosion, such as the east stream, that undisturbed deposits could be quickly and confidently identified (Hendey pers. comm.). Micromammals were unsystematically collected from several parts of the east stream area by hand-washing sediment through kitchen sieves (Hendey pers. comm.). The small sieve size used in these collections would have resulted in the smaller species of micromammal being retrieved. The collecting of surface finds by hand would, however, have favoured the retrieval of larger

species which would have been more visible to field assistants (Hendey pers. comm.). When questioned as to ways in which the methods of retrieval used in the east stream area may have biased the fossil micromammal collection, Hendey (pers. comm.) noted the following potential sources of bias;

- ❖ sampling may have been biased in the sense that it was not done on a large scale
- ❖ sampling was haphazard and depended upon the whim of the individual worker, and the proximity of a pool of water to use for the washing of sediment

3.7 The units from the LQSM analysed in this thesis

The LQSM material studied for this thesis was the same as that sent to Craig Black (Carnegie Museum, Pittsburgh) for analysis in the 1970s (Hendey 1976). Dr Black sadly passed away before completion of the study and nothing was published. This section provides information taken from Hendeys' published works and field notes on the main micromammal bearing units of the LQSM investigated in this thesis. The following personal communications noted from Hendey in this, and the following section, were obtained via recent email correspondence.

The unit designated 'main stream' (see Figure 3.2) is a drainage channel which runs from near the north wall to the south west, following the general dip of the deposits. 'Main stream' acts as a boundary between the east and west successions. This drainage line may be of great antiquity, though by 1974 it was only ephemeral as quarry mining below the level of the water table had made it fall due to de-watering of the mine (Hendey 1974).

3.7.1 The east stream area

The LQSM micromammal assemblages collected from the fossiliferous east stream area come from the various depositional facies shown in Table 3.1. Hendey (pers. comm.) noted that his interpretation of the LQSM in the east stream area, was that it represented a floodplain, which in the dry season was the scene of activity by animals both small and large, and in the wet season was partly, or completely, covered by flood waters. Some of the fossils found in the east stream deposits are thought to have been deposited subaqueously, while others appear to have been deposited sub-aerially (Hendey 1976). Channel deposits in the east stream area were deduced from high proportions of fish remains and abraded bones in one area, while in another, the presence of a pond was inferred from a concentration of amphibian bones found together with very few terrestrial vertebrates (Hendey 1976). In some parts of the east stream,

associated bones were found close together lying horizontally within the deposits, indicating that they were lying on a firm surface (Hendey 1976). Redistribution of animal remains appears to have taken place when the area became inundated by flood waters (Hendey 1974). The most complete skeleton found was that of a hyaena, where some 80 of the original ± 200 bones were retrieved. The partly complete skeletons of an elephant, several pigs, a large cat, and several hyaenas were also recovered from this area (Hendey 1981a). Hyaena and small carnivore coprolites were discovered, some of which were very well preserved, and some burnt bones were found *in situ* (Hendey 1976). There were no recorded *in situ* concentrations of micromammals, and though occasionally it appeared that associated bones of smaller species were present, this was never definitively proved (Hendey pers. comm.).

A unit called east stream, square 1 (abbreviation: ES/SQ1) appears to have come from a area that was excavated, however the exact provenance and history of this unit is uncertain, but it may safely be assumed to represent a small area within the east stream. Other units mentioned further on in this thesis also represent discrete areas from which micromammals were collected. These include, east stream (abbreviation: ES), a unit called 'east stream, north end, fish spine' (abbreviation: ES/NE/F.S.) and 'east stream section, section 3, spit 4' (abbreviation: ES/sect 3/sp 4).

3.7.2 East stream/bed2

A particular horizon in the east stream, called bed 2, was identified and the fossil assemblages from the areas labelled, 'east stream/bed2' (abbreviation: ES/bed2), east stream /bed2/Pig#1 (abbreviation: ES/bed2/Pig#1)' and 'east stream /bed2/near Elephant site' (abbreviation: ES/bed2/Eles) were added together as they all came from the same general collection area. The fossils from ES/bed2/Pig#1 were probably recovered from around some *Nyanzachoerus* fossils found in the east stream area. The assemblage compiled from these three sites was called 'combined ES/bed2 sites'. The unit called 'far east area/bed2' was not included in the combined ES/bed2 sites as the provenance of this tiny unit, which contained only three mole rat mandibles, was uncertain. The area referred to as the 'far east area' may be seen in Figure 3.2.

3.7.3 East stream/Dump 2

The LQSM unit which provided the largest assemblage of micromammals was collected from a dump in the east stream area named 'dump 2'. From this point onwards, this fossil assemblage will be referred to as 'east stream, dump 2', abbreviated as 'ES/D2'. The fossils from the unit labelled 'east stream, dump # 1', were added together with ES/D2 for the purposes of analysis as Hendey's field notes state that they are from the same area of Dump 2, and were essentially the same. From this point onwards, when ES/D2 is mentioned, it will include the very small micromammal sample from 'east stream, dump # 1'. The so-called dumps were bulk samples of sediment which were removed from the mine by earth-moving machines and then sieved at leisure near Hendey's field camp. Micromammals are likely to be under-represented in the dump samples owing to the mesh size of the screens used, and the interests of the person(s) doing the screening (Hendey pers. comm.). The recovery of large mammal bones, rather than micromammal bones, frequently tended to be the main focus of sieving activities (Hendey pers. comm.).

3.7.4 The elephant site

The elephant site, mentioned in the previous section (abbreviated as 'Eles' from this point onwards), lay at the northern end of east stream. The site name was given to the general area around which some remains of a single elephant were found, and comprised an area of roughly 3-4 m east to west, and 4-5 m north to south (Hendey pers. comm.).

The majority of relatively large micromammal samples from the LQSM came from the north end of the east stream area. The elephant site mentioned above was recorded in a variety of ways by workers, for example, the area has been described as 'east stream, north end, near elephant site', 'east stream, elephant site, N level', and 'east stream, elephant site'. The labels given differed, but the micromammals were recovered from the same general area (Hendey pers. comm.) and they were therefore added together for the purposes of analysis. From this point onwards, therefore, the term 'combined elephant sites' (abbreviation: combined Eles), will refer to the combined total of the LQSM units, 'east stream/elephant site' (abbreviation: ES/Eles), 'east stream/elephant site/N-level' (abbreviation: ES/Eles/N-level), and 'east stream/north end/elephant site' (abbreviation: ES/NE/Eles).

3.7.5 Pit excavations

Three pits, which were called Tex's pit 1 (TP1), Tex's pit 4 (TP4) and Michael's Pit, represent actual excavations. These pits, which were excavated in the east stream area, were excavations which were usually centred on a surface find (Hendey pers. comm.). The largest of these pits was probably no more than a few metres square and a metre deep. No stratification of sediments was observed and they were also largely unproductive from a fossil point of view (Hendey pers. comm.).

3.7.6 The Peat Bed

The micromammals from the unit labelled 'peat bed', (abbreviation: PB) as it will be referred to from now onwards, come from a peat bed which is described by Hendey (1981a) as a salt-marsh deposit (see Table 3.1). All the micromammal bones and teeth from the Peat Bed facies show dark discolouration.

3.8 The units from the MPPM analysed in this thesis

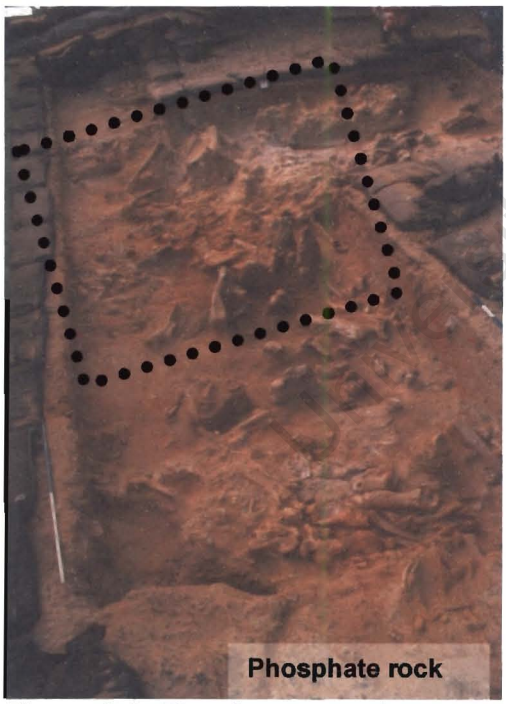


Figure 3.3: The demarcated area on the above picture shows the excavation area of unit F10 and F11, the MPPM units studied in this thesis (Photo: P. Haarhof)

The MPPM deposits analysed in this thesis differ from those of the LQSM in that they were excavated, sieved and sorted under controlled conditions during the new excavations begun in 1998. The particulars relating to this excavation are detailed below. The dig area is shown in Figure 3.3.

3.8.1 Recent excavations at LBW (1998-2003)

The Archaeology Contracts Office of the University of Cape Town were employed by the West Coast Fossil Park to carry out excavations at LBW in 1998 to expose fossil bearing deposits in 'E' Quarry. The *in situ* fossils exposed during this, and subsequent excavations, form part of the West Coast Fossil Park display presently open to the public (Halkett 1999a). The area selected was close to excavations conducted by Hendey in 1976, in "E" quarry, and is believed to be an extension of bed 3aN (the bed laid down during the third northwards shift of the river). Bed

3aN has been the main focus of recent research into the ungulates at LBW (Franz-Odendaal 2002), and is more suitable for a palaeoecological analysis than bed 3aS in that there is no evidence to suggest that bed 3aN contains material derived from the LQSM (Hendey 1976). An extension of the excavated area in the years subsequent to 1998 have resulted in the collection of an extremely large sample of microfauna which still awaits analysis.

3.8.1.1 Method of excavation

1 m^2 blocks were excavated in units which consisted of 10 cm spits, as there was a lack of stratification of the deposit. The sediment was extremely hard and had to be softened with water before a thin layer could be excavated. The excavated material was then wet sieved through a 1.5 mm mesh and the wet bones and fragments were spread out to dry, prior to being bagged (Halkett 1999a). The sediment was then sorted by West Coast Fossil Park staff and all visible micromammal bones and teeth were recovered.

3.8.1.2 The excavation area

It is believed that the current site of excavation, begun in 1998, represents an old river channel which flowed from the north east side of the quarry, sweeping across and around a phosphatic rock outcrop (Halkett 1999a). In the fossil trench the fossils occur adjacent to the phosphate rock outcrop, not above it. It is believed that the river flowing over the phosphate rock created a kind of 'drop zone' for fossil bone in the areas to each side of the rock. The large phosphorite rock outcrop is believed to have protected the river channel deposits from being removed by the action of the drag-line excavators (Halkett 1999a). Excavations revealed a linear feature which runs down the side of the excavation area and appears to be a small channel or gulley (Halkett 1999b). The LQSM is believed to underlie these channel deposits and has been exposed in several of the squares. The two units analysed in this thesis, namely unit F10 and unit F11, were chosen fairly arbitrarily as there were no obvious differences between any of the excavated units. Two adjacent units were chosen for analysis in order to ascertain if there were any marked differences in spatial patterning, or breakage, of micromammals across the site.

In the recent excavation site, microfaunal bones (micromammal, lizard, chameleon, frog and small reptile) and almost complete, large mammal bones, lie in a dense matrix of soil mixed with millions of tiny pieces of fragmented bone. Extremely high concentrations of microfauna were recovered and the Amphibia were the family most commonly represented.

Though preservation of many of the bones is excellent, no obviously articulated large mammal bones have so far been found. The contrast in the condition and preservation of bone within the site, that is, fragments versus complete bones, suggests that the fossils come from a variety of sources and have been exposed to different physical and chemical processes. The fragments of comminuted bone are likely to have come from re-worked deposits. The processes which have produced these fragments can only be guessed at, but may have included sediment compaction, trampling, weathering, transportation and re-deposition by water. The numerous large mammal bones, which are remarkably well preserved, appear to have reached their place of burial before they were exposed to any very destructive chemical or physical forces, and burial appears to have protected and preserved them.

Hendey (pers. comm. to P. Haarhof) suggested that the deposits on the unexcavated side of the phosphate rock represented a floodplain adjacent to a river channel which became inundated with water during the rainy season. The large mammal bones in the excavation area may have been washed into the river from the banks and surrounding areas during the rainy season when the river expanded onto the floodplain. The taphonomy of the micromammal fossils will be discussed further in Chapters five and six.

The variety of animal species found in unit F10 and F11 indicates that there has been mixing of faunal assemblages from animals occupying different parts of the landscape of LBW. Acquatic, subterranean and terrestrial environments are represented as large mammal fossils (mainly large ungulate) are found together with amphibian, reptile, murid, soricid, macroscelid, chrysochlorid and mole rat bones.

Figure 3.4: A short-necked giraffe (*Sivatherium hendeyi*) mandible lies in the river channel deposits of bed 3aN at the site of recent excavations at LBW (Photo: P. Haarhof)

3.9 Background to the taphonomy of the MPPM and LQSM

The MPPM and LQSM represent two separate, depositional events but the time period over which these two horizons were deposited, and the age difference between the two horizons, is uncertain. Hendey (1980) and De Muizon and Hendey (1980) have noted minor morphological and possible size differences between some of the species in bed 3aS and bed 3aN, such as the seal, *Homiphoca capensis*, and the bear, *Agriotherium africanum*. Morphological differences between the badger, *Mellivora benfieldi*, and the otter, *Enhydriodon africanus*, are interpreted as indicating that there was an 'appreciable time interval' between the deposition of beds 3aS and 3aN of the MPPM (Hendey 1978b). Gentry (1980) has noted a possible size increase in tooth size between the *Mesembriportax acrae* from the LQSM and MPPM, and a couple of other bovid species from bed 3aN appear to show an increase in size relative to bed 3aS. The morphological differences between the above-mentioned species from the two MPPM fossil beds are noted as being small, and not sufficient to warrant taxonomic distinction at species level (Hendey 1978b). The length of the 'appreciable time interval' is not specified, but Hendey (1981a) has suggested that the MPPM and LQSM were deposited over a time period of not more than 0.5 Ma. In terms of observed differences between the LQSM and MPPM, broadly the same mammalian taxa were found in the LQSM and MPPM, although the relative abundance of the various species in the two members differ (Klein 1981, 1982). This thesis will investigate if there is a difference between the micromammal populations in the two members, and if so, whether these are related to changes in climate and environment, to taphonomic differences, or to differences in the depositional history of the two members.

Different methods of recovery were used for the micromammals from the MPPM and LQSM assemblages and may, potentially, have caused differences between the two fossil assemblages. Other potential sources of variation are the possibility that the micromammal assemblages represent different areas of the palaeo-landscape, or were accumulated by different predators. In the case of the LQSM fossils, the majority of micromammals come from the east stream area where the non-phosphatic quartz sands are thought to represent a riverine floodplain environment which contained both subaqueously and subaerially accumulated vertebrate fossils (Hendey 1974, Gentry 1980). The recently excavated deposits, units F10 and F11, come from a river channel and potentially contain micromammals which have been washed in from a variety of areas, and have died from a variety of causes. From this point onwards, these two units will be referred to as the MPPM (F) units.

Hendey (1981a) suggests that the LQSM contains the remains of animals that lived in the area, whereas beds 3aN and 3aS of the MPPM are largely comprised of animal remains washed in by the river from elsewhere. He concluded that the presence or absence of species in these two sets of deposits simply reflects the opportunity for their remains to reach their points of deposition, not their presence or absence in the region. Whether accumulations occurred sub-aerially, or sub-acqueously, the predator/s or factors causing the death of the micromammals, together with the agents of accumulation, would affect what skeletal body parts, and what micromammal species, entered the fossil record at LBW.

Maguire and Schrenk (1985) listed the following stages, illustrated in Figure 3.5, in the history of a fossil from being part of a living animal, to becoming a museum specimen.

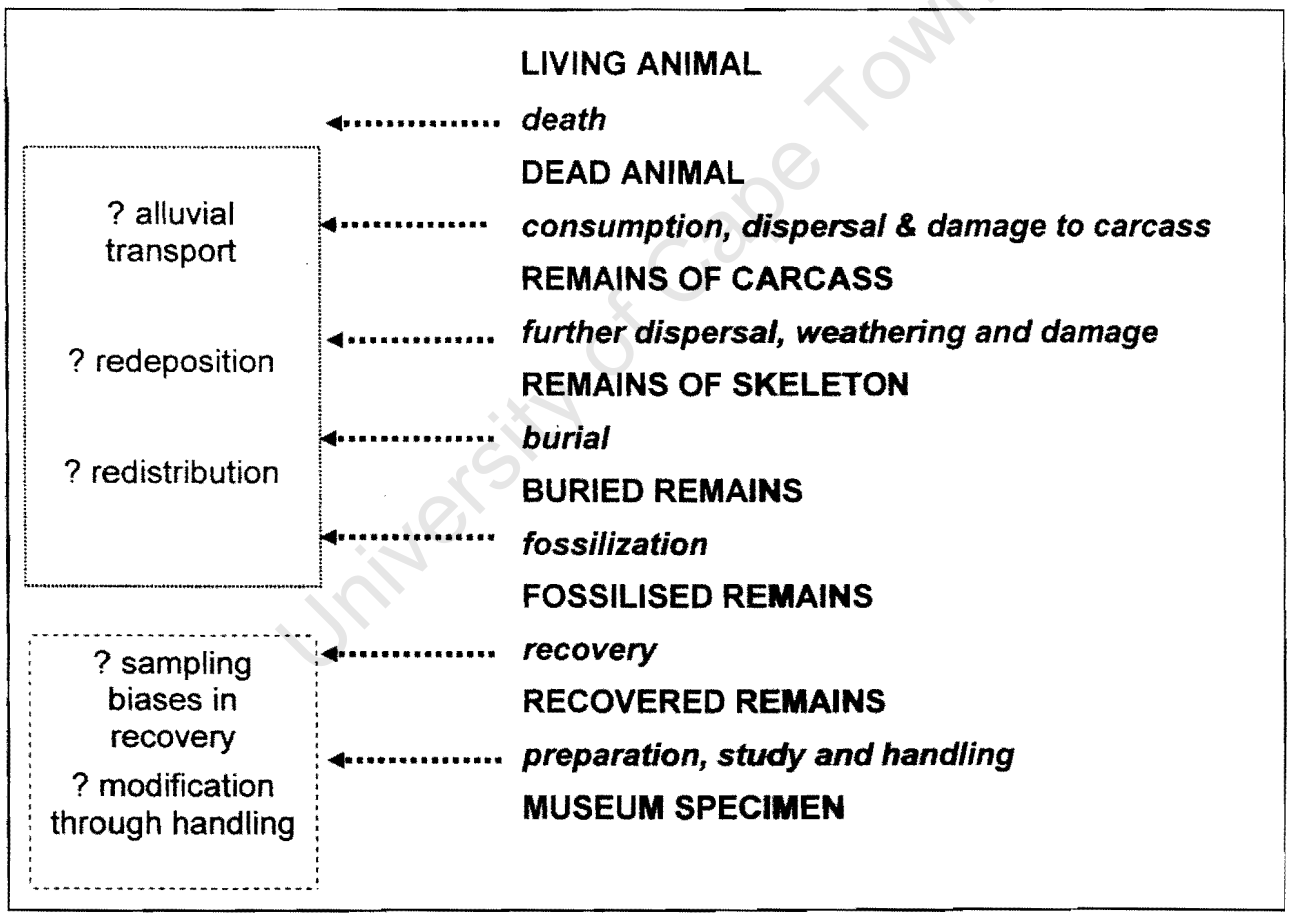


Figure 3.5: The formation and modification of fossil bone assemblages (After Maguire and Schrenk 1985, Figure 3.1, page 71 , and Andrews 1990, Figure 1.2, page 3)

Key: The broken arrows indicate the periods during which information loss may occur as the various processes take place. Further processes, which may have taken place in the case of the Langebaanweg fossils, are shown in the boxes on the far left.

3.9.1 The taphonomy and palaeoecology of the large mammals

Klein (1981, 1982) studied the patterns of ungulate mortality from LBW in order to see if the animals showed attritional or catastrophic mortality profiles. The LQSM was frequently found to contain partly articulated skeletal parts, whereas in the MPPM, many of the bones show abrasion and few articulated bones were found (Hendey 1970a, Klein 1982). These features were interpreted as indicating that the bones from the MPPM had been exposed to alluvial transport (Hendey 1970a, Klein 1982).

The relative abundance of ungulate taxa differed in the two members. No particular species was found to dominate the LQSM assemblages and several species were roughly equally represented (Klein 1981). The attritional profiles of *Mesembriportax acrae,* and *Ceratotherium praecox* from the LQSM suggest that these animals may have died naturally from a variety of factors such as predation, disease, and so on. This is in keeping with the fact that the mode of bone occurrence suggests that after disarticulation, removal, and destruction by scavengers and other biological agents, the bones were buried relatively closely to the area in which they died (Klein 1981, 1982). The mortality profiles of the LQSM large mammals thus support the floodplain scenario proposed by Hendey (1981a).

Alcephaline antelopes such as *Damalcra acalla*, and *Damalcra neanica,* and the giraffids, such as *Sivatherium hendeyi* and *Giraffa* sp., dominate all other species in the MPPM deposits, and all show catastrophic age profiles (Klein 1982). *Mesembriportax acrae* and *Sivatherium demissum,* found together with the bed 3aN giraffids, have attritional mortality profiles. It is suggested that these indicate the secondary incorporation of animals, which died on the floodplain or surrounding areas, into the river channel deposits (Klein 1981).

There were differences between the two beds of the MPPM. Bed 3aS is dominated by grazing alcephalines, and bed 3aN by browsing giraffids. The catastrophic profiles of the giraffids, which dominate bed 3aN, suggest that they may have died through drowning, possibly during flood events (Klein 1982). The abrasion and lack of articulated bones in this member may reflect transport over a relatively long distance (Hendey 1981a, Klein 1981, 1982). Klein (1981) suggests that the abundance of giraffids in bed 3aN may have been caused by an increase in grassland at the expense of bush and forest at the time of deposition of this bed, thus driving the giraffids to the river margins where high bush or trees still existed. The giraffids were then faced with an increased risk of death by drowning, possibly during seasonal flooding (Klein 1982).

Damalcra spp. may have been attracted to the ecotone between riverine forest and fringing grassland, resulting in an increased chance in their becoming incorporated in the Bed 3aN and 3aS fossil assemblages (Klein 1982). Klein (1981) notes that the possibility cannot be ruled out that differences in species representation between beds 3aS and 3aN may be more indicative of how and where the animals died, than of environmental change.

Dental abnormalities in the form of enamel hypoplasia on the teeth of many of the *Sivatheres* and a few of the other ungulate species has been interpreted as reflecting nutritional stress, caused by the reduction in the habitat of these animals, with grassland increasing at the expense of woodland (Hendey 1981a). A recent investigation of mesowear and microwear patterns on the teeth of *Sivatherium hendeyi* do not provide support for this hypothesis, however, as there are some indications that this giraffid was a mixed feeder (Franz-Odendaal 2002). The cause of dental abnormalities in some of the large mammals was investigated by Franz-Odendaal (2002) and the results of this research are presented later on in this chapter.

The presence of a *Nyanzachoerus kanamensis,* at Langebaanweg has been interpreted as representing intermediate and closed habitats (Hendey 1981a, Bishop 1999), however, *Nyanzachoerus* has recently been shown to be cursorial, which may indicate that it occupied open-country environments, rather than closed environments (Benefit 1999). Other species such as two nyala-like bovids (*Tragelaphus* spp.), and two waterbuck (*Kobus subdolus and Kobus sp.*) represent closed country forms (Hendey 1983c). It appears from these taxa that the wooded habitats extended up the river as well as near the river estuary, as they are found in fluviatile and floodplain deposits (Hendey 1983c). The boselaphine (*Mesembriportax acrae*) and reduncines (*Kobus* sp.), which were thought to have favoured more closed habitats, are among the most abundant bovids in the MPPM, while the other common species, a bovine (Simat*herium demissum*), and alcelaphines (*Damalacra* sp.) were probably open area grazers (Hendey 1981a, Klein 1981, 1982, Franz-Odendaal 2002).

The three giraffids (*Giraffa* sp., *Palaeotragus* sp. and *Sivatherium hendeyi*) at LBW are indicative of the presence of trees in the form of woodland, forest or open woodland (Hendey 1983c). A hippopotamus found in the MPPM belongs to a different genus to extant hippos and thus its diet, mixed feeding or pure grazing, has not been determined (Franz-Odendaal 2002). It is likely, however, that it foraged on riverside grasses (Hendey 1984). The rhino found at LBW (*Ceratotherium praecox*) probably inhabited an ecological niche similar to that of an open-country grazer (Franz-Odendaal 2002).

The large and small mammals at LBW were recovered from the same sediments and there is no evidence to suggest that they are not contemporaneous.

3.10 Other fossil sites in the vicinity of 'E' Quarry

The following section contains some brief notes on other fossil assemblages found in the vicinity of 'E' Quarry.

3.10.1 'C' Quarry

'C' Quarry, as the name suggests, was another mining quarry which lay to the North of 'E' Quarry. This Quarry was partly under water and covered by windblown sands and mine dumps in 1972 when it was investigated by Hendey (Hendey 1972). A limited number of identifiable fossils was recovered from this quarry and it played a relatively minor role in the LBW investigations (Hendey 1972).

3.10.2 Anyskop and Baards Quarry

There are only two fossil assemblages dating to the Late Pliocene on the west coast of South Africa, and as they are situated close to 'E' Quarry, they will be briefly mentioned here.

The existing 70 m high hill of Anyskop is a conspicuous feature in the landscape of LBW today, and it has been suggested that Anyskop formed a submerged barrier or barrier island during the Early Pliocene transgression, which prevented erosion of the Varswater sediments. Roberts (in press.) has argued, however, that there is no evidence for the presence of such a sand barrier at any time. Anyskop deposits are clearly younger as they rest uncomformably on the Varswater formation, which suggests that these deposits are probably similar to the calcarenites of the Langebaan formation found elsewhere in the region (Roberts in press). The late period of the Late Pliocene regression is represented by some of the Anyskop deposits which overlie the MPPM to the South of 'E' Quarry (Hendey 1982). Foraminifera suggest that both a marine and a beach, or terrestrial environment, are represented (Hendey 1981a).

Baard's Quarry is situated approximately 2.5 km east of 'E' Quarry (Hendey 1970a), but is now in-filled. Preservation at Baard's Quarry was poor and 90 % of the fossil material consisted of unidentifiable bone fragments (Hendey 1978c). Baard's Quarry has fauna in common with both 'C' and 'E' quarries. Other species such as *Equus*, a mustelid and a

hyaenid are apparently Pleistocene in age (Hendey 1972). No marine fossils were found in the quarry, with the exception of some pinniped fragments (Hendey 1970a).

Hendey (1983c) notes that Baard's Quarry and Anyskop show that by the Late Pliocene/Early Pleistocene, woodland species such as the *Proboscidea* and *Sivatherium* are still represented in the fossil record, but the numbers of more open-country grazers, such as the Equidae, Alcelaphini and Antilopini, appear to be increasing.

3.11 The age of the fossils from LBW

No deposits of Early Tertiary age have been identified in the coastal area of the west coast and in the Overberg and it is thought that during an Oligocene low stand of several hundred metres below sea level, severe erosion removed all the Early Tertiary deposits (Hendey 1983a).

It was initially suggested that the LBW fossils came from Pleistocene and Pliocene sediments (Hendey 1970a, 1970b). A few years later, however, several mistakes as to the interpretation of geology and taxa were recognized, and an age of 4-5 Ma was suggested (Hendey (1972, 1973). Relative dating using faunal comparisons with the East African faunas, which are often securely dated with igneous deposits, has proved problematic as it is difficult to find a broadly contemporaneous fauna (Hendey 1981a). The hipparionids from LBW were interpreted by Boné and Singer (1965) as being similar to those found in the lower layers of south Serengeti which were of Early Pleistocene age. A more recent study concluded that *Hipparion cf. baardi* is probably derived from a Late Miocene/Early Pliocene horse assemblage belonging to the *Eurygnathohippus* lineage (Bernor and Armour-Chelu 1999).

Hyaenas are particularly well represented at LBW, and some five different taxa have been found (Hendey 1981a). The hyaena taxa *Crocuta* only appears in sub-saharan Africa at 4 Ma and the absence of this genus at LBW suggests that the site is older than 4 Ma (Turner 1999). Turner (1999) notes the continued presence of a type 3 (*Hyaenictitherium*) hyaena, which is common in Late Miocene faunas, and a primitive type 4 (*Hyaenictis*) hyaena at LBW, indicating that these primitive forms continued at LBW into the earliest Pliocene, much later than they did in Eurasia.

Bishop (1999) notes that the Old World Pigs, the Suidae, are represented by tetraconodont species such as *Nyanzachoerus devauxi* and *Nyanzachoerus syrticus* throughout the end of the

Miocene, and Early Pliocene assemblages are dominated by *Nyanzachoerus*, and its descendant *Notochoerus*. *Nyanzachoerus kanamensis* is found at Langebaanweg and the presence of this species could be interpreted as indicating an Early Pliocene date for LBW.

The two murids belonging to the genus *Aethomys* at LBW are clearly older than the *Aethomys chrysophilus* and *Aethomys namaquensis* species found at Makapansgat 4. This is the earliest record of *Aethomys* prior to the appearance of this genus at LBW, and Denys (1990) places LBW between 4-5 Ma. Pocock (1976) made a preliminary study of the micromammals and found nothing obviously inconsistent with late Cenozoic fauna, and suggested an age of around 4.5 Ma for LBW. The presence of extinct murid taxa such as *Euryotomys* and *Stenodontomys* at LBW supports a Mio-Pliocene age for the site, though the presence of these two cannot be taken as conclusive evidence. *Stenodontomys* has been found in 'Late Miocene' breccias from the Otavi mountains in Namibia and in Upper Miocene deposits at Berg Aukas and Harasib 3a (Pickford *et. al.* 1994). The genus *Euryotomys* has been found at only one other fossil site, namely Bolt's farm, which is thought to be ~4-5 Ma (Senegas and Avery 1998). The *Euryotomys* from Bolt's farm, *Euryotomys bolti*, shows differences to *E. pelomyoides* which are interpreted as indicating that *E. bolti* is intermediate between *E. pelomyoides* and *Otomys* (Senegas and Avery 1998). The Waypoint 160 deposits from Bolt's Farm, the Makapansgat Limeworks Member 3 (~3 Ma) and Sterkfontein Member 4 (~2.8-2.6 Ma) are the South African sites closest in age to LBW. The micromammalian fauna from these sites will be mentioned further in Chapter seven.

There are obvious problems associated with using fauna to obtain a relative date for a deposit. The most convincing evidence as to the antiquity of the LQSM and MPPM sediments comes from the geology, and the fact that the Varswater Formation shows a maximum elevation of at least ± 90 m above sea level (Rogers 1980, Roberts 2002). This accords with global sea level curves which indicate a Mio-Pliocene highstand of that elevation. Some contention remains as to the exact age of LBW, but there is a general consensus that it is around 4-5 million years old.

3.12 Climatic and environmental conditions at LBW prior to, and during, the deposition of the Varswater formation

The oldest pollen assemblages from the Cape and south western Cape show a close affinity with the flora on other continents (Coetzee 1978). Some of the taxa found are akin to the tertiary microfloras of other southern hemisphere continents such as Australia, New Zealand

and the submerged Ninetyeast Ridge west of Australia (Coetzee and Rogers 1982). Coetzee and Rogers (1982) carried out palynological and lithological studies on a section of Middle Miocene clays of the Elandsfontyn Formation in the Langebaanweg area. This study suggested that a subtropical-tropical gallery forest was followed by a shift towards dominant palm vegetation, which was succeeded by a marsh environment. These changes in vegetation have, in turn, been linked to the lithological evidence for the gradual northward movement of the palaeo-Berg river (Coetzee and Rogers 1982). By the end of the Miocene, both the flora and fauna contained many modern elements (Hendey 1983b). Hendey (1983b) suggests that during the early Pliocene, a climate of relatively low temperatures and rainfall existed, with woodlands and forests probably being confined to river valleys, well-watered mountain slopes, and with wide areas of more open country found on the coastal lowlands. Cowling and Richardson (1995:49) write, "*About five million years ago the coastal lowlands were covered with open shrubland dominated by grasses, restios, geophytes and, for the first time, many members of the daisy family or Asteraceae*'. They go on to note that forest vegetation occurred near the coast, probably on dunes, and inland, in the form of gallery forest along river banks. They note that the abundance of fynbos forms at this time suggests the start of the rise to predominance of the fynbos flora. The presence of large numbers of geophytes was clearly inferred by Cowling and Richardson (1995) from the fact that mole rats had been reported in the literature as being the most common rodent found at LBW. As shown in the following chapters, however, this statement was not strictly correct as some murid species are at least, if not more, common.

Pollen bearing deposits from the south western Cape suggest that Tertiary vegetation had probably disappeared by early Late Miocene times. Coetzee (1978) suggests, however, that the Tertiary vegetation may have become extinct much later, during the Late Miocene/Early Pliocene, when fundamental climatic change led to the extermination of the Palmae and other Tertiary forms. Johnson and Briggs (1981) have suggested that the sclerophyllous communities of the south western Cape have resulted from the progressive development of nutrient deficient soils, rather than the evolution of a mediterranean climate.

The Varswater deposits are not rich in pollen. No quantitative reconstruction of the environment of LBW during the deposition of the Varswater Formation has been made. Earlier pollen studies done on the LBW produced a pollen spectrum in which 92% of the pollens remained unidentified (Tankard and Rogers 1978). The most recent pollen study done

on LBW is reported here as it included, and updated, those done previously (eg. Tankard and Rogers 1978, Coetzee 1980, Coetzee and Rogers 1982). New pollen samples were taken from the quarry floor at LBW, and 6.4 m below the floor (Scott 1995). The pollen spectrum from LBW indicates a variety of environments. Swamps/marshes were certainly present in the LBW area, as indicated by the dominance of pollen (92%) from the acquatic, or semiacquatic Ranunculaceae (Scott 1995). Coastal plains may be inferred from the presence of families such as the Ranunculacea, Cyperaceae, Asteraceae and Umbelliferae, and areas of relative dryness by the Asteraceae, Chenopodiaceae, and Amaranthaceae (Scott 1995). The presence of trees in the area is indicated by the presence of *Podocarpus, Olea* and Proteaceae pollen (Scott 1995). Very few diagnostic elements of open vegetation were found (Scott 1995). The sample taken from the quarry floor indicated swampy conditions with Cyperaceae, and a fynbos component of Proteaceae, Ericaceae, Restionaceae and *Cliffortia.* The 4-6 m sample yielded *Cliffortia,* Restionaceae, palm pollen, and tree pollen (*Podocarpus, Olea* and Proteaceae). Table 3.3 shows the vegetation suggested for various areas of southern Africa, as indicated by pollen studies from fossil sites in South Africa and Nambia.

Period	Southern and southwestern Cape	Namaqualand	Interior plateau	Marine area of Namibia off the west coast
Quaternary	Fynbos (macchia)	Succulent rich dwarf shrub-land or grassland	Woodland savanna or upland grassland or moist mesic woodland	Desert vegetation or dry grassland
Pliocene	Fynbos	-	Similar to Quaternary vegetation	Open desert or dry woodland or shrubland vegetation or dry grassland
Late Miocene/ Pliocene	Transition from sub-tropical woodland to fynbos	Karoid shrubland with fynbos and woodland elements	-	Development of desert elements like Chenopodiaceae
Miocene	Subtropical woodland with swamps	Subhumid subtropical woodland	-	-

Table 3.3: Vegetation in southern Africa during the Neogene according to the Pollen data (After Scott 1995, Table 5.2, page 75)

Key: - = no information available

Recent research done at Langebaanweg includes stable isotope analysis by Franz-Odendaal (2002) of the teeth of several Langebaanweg ungulates. This was done in order to provide an insight into the photosynthetic pathway used by the vegetation in the environment, and the prevailing climatic conditions at LBW.

Cerling *et. al.* (1997) note a period of world-wide faunal turnover in the Late Miocene/Early Pliocene in Pakistan, Europe, North and South America and Africa. This turnover has been related to the world-wide expansion in C_4 grasslands which began between 8 and 6 Ma, and continues to the present day. By 5 Ma C_4 grasslands were widespread, and in Africa faunal assemblages typical of deciduous forest give way to species similar to those found today in savanna woodlands, though browsers dominated (Owen-Smith 1999). Until the research carried out by Franz-Odendaal (2002) it was thought that C_4 grasslands may have extended as far south as LBW during the Early Pliocene. Franz-Odendaal's (2002) research indicated that the expected grazers (eg. alcelaphine, hippopotamus, and rhinoceros), as well as browsing species, showed $\delta^{13}C$ values which indicated that LBW was a C_3 dominated environment. A similar result was obtained in France and Spain and in the eastern Mediterranean where C_3 plants dominate today, and where isotopic research has indicated that C_4 plants were never a significant part of the biomass (Cerling *et al.* 1997). As fynbos has a C_3 signature, it was impossible to differentiate between the type of C_3 vegetation eaten by the ungulates at LBW, that is if they were grazers, or browsing on other C_3 vegetation.

Prior to the research done by Franz-Odendaal (2002), there was no direct evidence to support either a winter-wet, or summer-wet, rainfall regime and indirect evidence was used to ascertain the rainfall pattern. For example, the fact that many of the present taxa of the south-western Cape show rapid growth towards the end of summer when there is little humidity, was taken to suggest that they evolved in a summer rainfall climate (Coetzee 1980, Coetzee and Rogers 1982).

Franz-Odendaal's (2002) research at LBW indicates that a winter rainfall pattern was established on the west coast by the Mio-Pliocene. The presence of cool growing C_3 grasses at LBW during the deposition of the Varswater sediments indicates that the present day climatic regime of winter wet/summer dry was established early in the Pliocene epoch (Franz-Odendaal 2002). The present day flow paths of the Agulhas current, and the Benguela Upwelling System was established during the Mio-Pliocene around 5 Ma (Siesser 1980, Hendey 1983a). The introduction of a cold water current on the west coast accentuated the on-going trend of increased summer drought along the west coast, and strengthening high pressure systems brought drier conditions to the interior (Axelrod and Raven 1978). This would have restricted rain forest and savanna-woodland, lowering their diversity, and encouraging the spread of thorn forest, grassland, and semidesert (Axelrod and Raven 1978). The early development of a Mediterranean climate, which was essentially modern, would

have prevented the spread of tropical C_4 plants as these are favoured by a summer-wet rainfall regime.

3.13 Dental abnormalities in the large mammals from Langebaanweg

No dental abnormalities were observed in the micromammals from LBW. Dental abnormalities, namely hypoplasia, was, however, observed in several of the large mammal species from LBW. These dental abnormalities were not accompanied by any evidence for skeletal disease in the LBW ungulates, suggesting that the local fauna was relatively healthy (Franz-Odendaal 2002). The analysis of serial $\delta^{18}O$ isotopes along the crowns of molars of *Sivatherium hendeyi* indicated that normal seasonal cycles at LBW were interspersed with periods of reduced rainfall and drought. Both adult and sub-adult hippotamus tusks show enamel hypoplasia, but the deciduous teeth of *S. hendeyi* indicate that the hypoplasia in this species occurred after weaning. As pathologies were found only in individuals that had been weaned, Franz-Odendaal (2002) concluded that hypoplasia in the *Sivatheres* was caused by general environmental deterioration, and not diet or weaning behaviour. The hippopotamus (Gen and sp. not det.), *sivathere* (*S. hendeyi)* and reduncines (*Kobus* sp.) were found to show a relatively high incidences of enamel hypoplasia, greater than 20%, as compared to less than 10% in the rhino (*C. praecox*), the giraffe (*Giraffe* cf. *jumae*) and the boselaphine, *M. acrae* (Franz-Odendaal 2002). Fluoride toxicosis has been ruled out as a cause of hypoplasia as the ungulate teeth studied showed no evidence of high levels of fluoride (Franz-Odendaal 2002). Franz-Odendaal (2002) found evidence for decreased seasonal amplitudes, less clearly defined seasons, seasons of varying lengths, and periods of drought and increased aridity, interspersed with periods of normal rainfall. This has been cited as support for the idea, initially proposed by Hendey, that local environments in the area were deteriorating, and seasonality becoming unstable during the period of deposition of bed 3aN (Franz-Odendaal 2002).

The presence of large numbers of burnt bones from the LBW assemblages has also been interpreted as indicating a marked seasonality at LBW as very seasonal rainfall increases the possibility of fires in an area (Hendey 1970a, Hendey 1976, Hendey 1981a, Hendey 1981b, Franz-Odendaal 2002). This idea was, however, originally based on the hypothesis that the high number of burnt bones at LBW reflected a summer rainfall regime, as lightning is much more common in summer-rainfall areas (Hendey 1981a). The fact that many of the large

mammal bones show burning is interpreted by Franz-Odendaal (2002) as indicating a pronounced seasonality, even though a winter rainfall regime is now known to have existed.

3.14 The vertebrate fauna from Langebaanweg

LBW contains a rich array of vertebrate families and species. Table 3.4 provides a faunal list of the mammals from the Varswater Formation, excluding the Rodentia, which are listed further on in this thesis.

A group which shows a puzzling scarcity in the extremely rich vertebrate fauna represented at LBW, is the Primates. Only two isolated cercopithecid molars from one individual have been recovered from the LQSM I deposits (Grine and Hendey 1981). This represents the first appearance of baboons in southern Africa (Benefit 1999). Baboons represent 84 % of the Plio-Pleistocene fossil monkeys from southern Africa, but compose only 10 % of the fossil monkeys from East Africa, and appear to have been endemic to the south (Benefit 1999). Most southern African baboons appear to have been adapted to dry, open savanna habitats, such as those represented by the South African fossil sites of Sterkfontein, Kromdraai and Swartkrans (Benefit 1999).

The absence of crocodiles from the faunal list at LBW is attributed to inappropriate climatic conditions (Hendey 1983c). The birds from LBW are extremely diverse and a rich assemblage of freshwater, terrestrial and marine birds are represented in the fossil record (Rich 1980, Hendey 1981a, Olson 1985, Haarhoff 1988). Tortoises (*Chersina* sp.) were extremely common in LQSM I deposits (Hendey 1981a).

One of the most noteworthy species found at Langebaanweg is the long-legged bear, *Agriotherium africanum*, the first bear to be recorded south of the Sahara. Another noteworthy carnivore found at LBW was the wolverine, *Plesiogulo monspessulanus*, an animal which was widespread in Africa during the Tertiary (Hendey 1982). The most commonly represented carnivore at 'E' Quarry was the seal, *Homiphoca capensis*. This species is only indirectly related to the family of seals (Otariidae) currently found on the southern African coast (Hendey 1982).

	QSM	PPM 3aS	PPM 3aN
ORDER INSECTIVORA			
Family Chrysochloridae (golden moles)			
Chrysochloris species	X	X	X
Family Soricidae (shrews)			
Myosorex sp.	X		
Suncus sp.	X		
Soricidae gen. & sp. not det.	X	X	X
Family Macroscelididae (elephant shrews)			
Elephantulus sp.	X	X	X
ORDER CHIROPTERA			
Family Verspertilionidae (vesper bats)			
Eptesicus sp.	X		
ORDER PRIMATES			
Family Cercopithecidae [Benefit 1999]			
Gen. & sp. indet.	X		
ORDER PHOLIDOTA			
Phataginus sp	X		
ORDER TUBULIDENTATA (aardvarks)			
Gen. & sp. not det.	X		X
ORDER CARNIVORA			
Family Canidae (foxes, jackals etc.)			
Gen. & sp. not det.		X	?
Vulpes sp.		X	X
Family Ursidae (bears)			
Agriotherium africanum		X	X
Family Mustelidae (weasels, martins etc.)			
Plesiogulo monspessulanus	X	?	
Mellivora benfieldi (honey badger)		X	X
Enhydriodon africanus (otter)		X	X
Family Phocidae (seals)			
Homiphoca capensis		X	X
Family Viverridae (mongooses etc.)			
Herpestes spp. A, B	X	X	
Herpestinae spp. C, D, E	X		
Herpestinae not det.		X	X
Viverra leakeyi (civet)	X		X
Viverrinae gen. & not det. (civet)	X	X	X
Genetta sp. (genet)	X		
Family Hyaenidae (hyaenas)			
Adcrocuta australis	X	?	?
Ictitherium preforfex		X	X
Hyaena abronia	X	X	X
Hyaenictitherium namaquense	X	X	X
Euryboas sp. (hunting hyaena)		X	
Hyaenidae sp. E		X	
Hyaenidae not det.		X	X
Family Felidae (cats)			
Machairodus sp. (sabre tooth)	X		
Homotherium sp. (sabre tooth)	X	X	?
Felis sp. (wildcat)	X		

Table 3.4: The mammals from Langebaanweg 'E' Quarry, excluding the Rodentia (After Hendey 1981a, page 50-52)

Table 3.4 continued...

Felis aff. iddiodorensis (lynx)	X	X	X
Felis obscura		X	
Dinofelis diastemata (false sabre-tooth)	X	X	X
Felidae not det.		X	X
Carnivora not det.			
Gen. & sp. not det. (Canidae or Viverridae)	X		
Gen. & sp. not det. (?Procyonidae)	X		
Gen. & sp. not det. (?Lutrinae)	X		
ORDER PROBOSCIDEA (elephants, mastodons etc.)			
Family Gomphotheridae			
Anancus sp.	X	X	
Family Elephantidae	X	?	X
Mammuthus subplanifrons			
ORDER HYRACOIDEA (hyraxes)			
Family Procaviidae			
Procavia *cf.* antiqua	X		?
ORDER PERISSODACTYLA			
Family Equidae (horses)			
Hipparion *cf* . baardi reclassified as Eurygnathohippus cf. baardi [Bernor and Armour Chelu 1999]	X	X	X
Family Rhinocerotidae (rhinos)			
Ceratotherium praecox	X	X	
ORDER ARTIODACTYLA			
Family Tayassuidae (peccaries)			
Pecarichoerus (or *Barberahyus*) *africanus*		X	X
Family Suidae (pigs)			
Nyanzchoerus cf. *pattersone* (or *kanamensis*)	X		
Nyanzachoerus *cf.* jaegeri N. kanamensis [Bishop 1999]		X	
Family Hippopotamidae (hippos)			
Gen. & sp. not det.		X	X
Family Giraffidae (giraffe, okapi etc.)			
Sivatherium hendeyi	X	X	X
Paleotragus *cf.* germaini			X
Giraffa sp.	X	X	X
Family Bovidae (buffaloes, antelopes etc.)			
Tragelaphus sp. A (nyala-like)	X	X	X
Tragelaphus sp. B (nyala-like)			X
Mesembriportax (or *Miotragoceros) acrae* (kudu-like relatives of the nilgai)	X	X	X
Simatherium demissum (buffalo)	X	X	X
Kobus subdolus (kob-like)		X	X
Kobus sp. B (kob-like)			X
Damalcra neanica (hartebeest-like)		X	X
Damalcra acalla (hartebeest-like)	X	X	X
Raphicerus paralius (steenbok)	X	X	X
Gazella sp. (gazelle)	X	X	X
Ovibovini gen. & at least 2 spp. not det.	X	X	X
ORDER LAGOMORPHA			
Family Leporidae (hares, rabbits)			
Pronolagus sp.	X	X	X
ORDER CETACEA (whales, dolphins)			
Gen. & sp. not det.	X	X	X

Note: The references for recent discussions on certain of the above species are given in italics in square brackets after the species name

All three members of the Giraffidae, namely the Palaeotraninae, Sivatheriinae and Giraffinae, are listed among the large mammals at LBW (Harris 1976). The grazers at LBW are as yet relatively unspecialized and large, medium and small species are all represented (Hendey 1983c). These provide some of the best evidence yet obtained on both the character and composition of an early grazing fauna (Hendey 1983c).

LBW is a crucial site for our understanding of the evolution of modern taxa as it provides the earliest recorded appearance of many genera. LBW provides an insight into the transitional fauna which inhabited the southwestern Cape in the Mio-Pliocene, a period when many relict Tertiary taxa are found together with genera which inhabit the southwestern Cape, and southern Africa, today. The fossils found within the LBW sediments enable us to ascertain how the environmental and climatic changes taking places during the Mio-Pliocene affected the evolution of fauna in the area.

Chapter four
Methodology: Recording and describing the fossil assemblages

4.1 Introduction to the fossil assemblages

Andrews (1990), Fernandez-Jalvo and Andrews 1992, Fernandez-Jalvo (1995, 1996,), and Fernandez-Jalvo *et al.* (1998) have described various post-depositional alterations which affect micromammal fossil assemblages. Work by authors such as Denys *et al.* (1995), Denys *et al.* (1996a), Dauphin *et al.* (1999), Sandrock *et al.* (1999), and Fernandez-Jalvo *et al.* (2002) have added to our understanding of the taphonomic and diagenetic alterations that occur in different sedimentological contexts. Many gaps still remain, however, in our understanding of the alterations undergone by micromammal assemblages after deposition. It is difficult to categorise and define taphonomy, but even more difficult to interpret it due to huge gaps in our knowledge of the way biological, and non-biological, bone-damaging processes affect bones (Maguire and Schrenk 1985). There is a lack of detailed research into the way in which bone damaging processes such as transportation by water, trampling, chemical processes, weathering and fossilisation affect micromammal bones and teeth. Experimental work done on micromammal bones to ascertain the affects of transport by water, the affect of acids and digestion on bones and teeth, and so on, have frequently involved small samples or have not been adequately repeated (Denys 2002). Another problem in interpreting the taphonomy of fossils is that experiments cannot replicate the succession of processes which alter a fossil assemblage. The analyst is generally faced with a palimpsest of inextricably bound events, such as may be seen at LBW and, to a lesser extent, HPD1. Any taphonomic examination of fossil material should bear the above limitations in mind. Taphonomy is, however, becoming increasingly integrated into micromammal studies, and as the taphonomy of an increasing number of palaeonotological and archaeological sites is investigated, it should become possible to draw more definite correlations between taphonomic features and their causes.

The following chapter describes the methodology used to record the taphonomy and taxonomy of the micromammal assemblages from Hoedjiespunt (HDP1), and Langebaanweg, 'E' Quarry (LBW). The study of the HDP1 micromammals included all the micromammal species in the assemblage, namely the murids, soricids, chrysochlorids,

macroscelids and bathyergids. In the case of the LBW fauna, the cranial material of the murids and bathyergids from the LQSM and MPPM (F) was analysed. Postcranial bones were excluded from the analysis of the fossil assemblages from the LQSM, as problems relating to the provenance and method of collection of many of the LQSM units had rendered the postcranial bones unsuitable for taphonomic analysis. A taphonomic study was, however, carried out on murid, bathyergid, soricid, macroscelid and chrysochlorid femora and humeri from the MPPM (F), which had been excavated under controlled conditions.

The methodology used to quantify the breakage and digestive etching patterns of the fossil and comparative material is similar to that used by Andrews (1990), Fernandez-Jalvo and Andrews (1992), Fernandez -Jalvo (1995, 1996), and Matthews (1998). All the fossil material studied in this thesis is housed at the South African Museum, Iziko Museums of Cape Town, and all the accession numbers have the prefix "SAM PQL" to denote this collection, although for the sake of brevity only the prefix 'PQL' is used throughout this thesis.

4.2 Recording incisor digestion

The characteristic breakage and digestion patterns produced by the various predators (owls, diurnal birds of prey and small carnivores) on the bones and teeth of their prey have been recorded by Andrews (1990), and may be seen summarised in Appendix E. One of the most useful tools for identifying the predator/s involved in the accumulation of fossil micromammal assemblages is the pattern of digestion on the enamel and dentine of incisors, which is caused during the digestion of prey by predators.

The mixed nature of the LBW micromammal assemblages made it impossible to ascertain the identity of the predator(s) which had contributed to the fossil assemblages. Incisors could, however, be used to ascertain what percentage of teeth had passed through the digestive tract of a predator.

Incisors are generally resistant to post depositional breakage and have relatively large areas of exposed enamel and dentine. It is far easier to assess digestion on incisors, as opposed to molars, as there are fewer structural differences between the incisors of the different rodent taxonomic groups, and the effect of taxonomic differences need not be taken into account (Andrews 1990). In the case of the HDP1 micromammal assemblage, which had been extensively affected by post-depositional corrosion, an attempt was initially made to assess

the digestion on the molars. It proved impossible, however, to distinguish clearly between corrosion and digestion, and the small areas of exposed dentine on many of the murid species made assessing the state of the dentine extremely difficult. No assessment of the digestive etching on the molars from Hoedjiespunt was therefore made as it was felt that trying to separate corrosion from digestion on the molars would have resulted in ambiguous and potentially erroneous results. Though post-depositional corrosion had not affected the LBW assemblages to the same degree of HDP1, it once again proved far more difficult to separate corrosion from digestion in the molars, as compared to the incisors. These difficulties, and the fact that the incisors provided a much clearer, and therefore more accurate picture of digestion, resulted in the attempt to assess molar digestion being abandoned. The incisors, rather than the molars, were therefore used to assess the presence, and degree, of predator-related digestion on the micromammal teeth from both fossil sites. No information on the effect of predator digestion on mole rat incisors was found in the literature and digestion of the mole rat incisors was described in the same way as for the murid incisors.

The following categories (illustrated below in Figure 4.1) were used to record the presence, or absence, of digestion on the enamel and dentine of incisors. The teeth were examined for signs of digestion using a light microscope and variable magnification. The digestion classes listed below are similar to those used by Fernandez-Jalvo (1995, 1996) and Andrews (1990). Class 2b represents a departure from the norm, however, as the literature has suggested that in the early stages of digestion, the enamel alone is affected, with the dentine showing digestion only when the degree of digestion intensifies (Andrews 1990; Fernandez-Jalvo and Andrews 1992). Digestion of the dentine, but not the enamel has, however, been observed on incisors from the micromammals recovered from small carnivore scats (pers. ob.), and has also been observed on the incisors from modern barn owl pellets (Williams pers. comm.). A very low percentage of incisors in the fossil material showed this pattern of digestion.

4.2.1 The digestion classes

Class 0: There is no visible digestion on the incisor. The early stages of digestion may not be detectable with a light microscope and it is possible that some of the incisors falling into this category had sustained very light, but undiscernible, digestion.

Class 1: There is light etching and removal of the upper layers of small areas of both enamel and dentine.

Class 1a: Digestion has affected the dentine, rather than the enamel of the incisor. These incisors show no digestion of enamel, but show light removal and digestion of the dentine.

Class 2: The area of digestion may not be much greater than Class 1, but the digestion has penetrated much deeper through the enamel layers, down to, or very close to, the dentine. The dentine shows a deeper degree of penetration and loss.

Class 3: The area of digestion is more extensive than class 2 digestion, with complete removal of enamel in areas, and digestion and removal of underlying dentine.

Class 4: There is extreme digestion of both enamel and dentine, with some teeth having all the enamel removed and only a dentine core remaining. The edges of the dentine or enamel may be collapsing in on themselves.

4.2.2 'Block' etching

An unusual taphonomic feature seen on a few of the mole rat, and a couple of murid, incisors from the LQSM was a very localised type of etching observed on the tips of the incisors (see Figure 4.1), which was recorded as 'block etching'. The cause of this pattern is uncertain, and it may be the result of corrosion, or digestion.

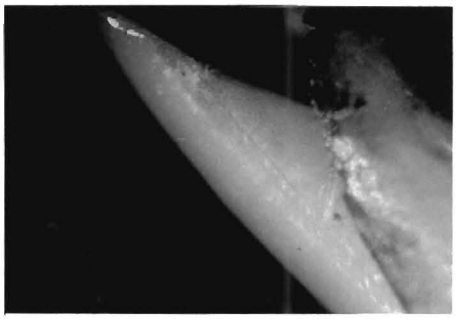
4.3 Recording the breakage patterns of the cranial bones

The breakage patterns of mandibles and maxillae were classified, and the number of *in situ* molars noted in the '*in situ* molars' column. The presence of an *in situ* incisor in a mandible, maxilla or premaxilla was indicated with a 'yes' in the 'incisor *in situ*' column, the column was left blank if no *in situ* incisor was present. The class of digestive etching shown by the incisors was recorded on the database under the column headed 'incisor digestion'. The mandibles and maxillae were recorded as belonging to the left or right hand side of the jaw, or were noted as '?' on the rare occasions the side could not be determined.

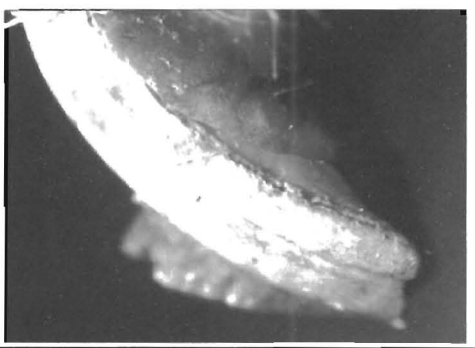
4.3.1 Murid mandibular breakage categories

The murid mandibular breakage categories used to record mandible breakage in this thesis were similar to those used by Andrews (1990) and Fernandez-Jalvo (1995). The presence or absence of molars and the incisors was noted, but this did not affect the classification of mandible breakage.

The following photos of micromammal incisors illustrate some of the digestive etching classes used to assess the digestion on incisors caused by the digestive processes of predators. The following pictures were all taken with a light microscope, using variable magnification (5x - 50x)

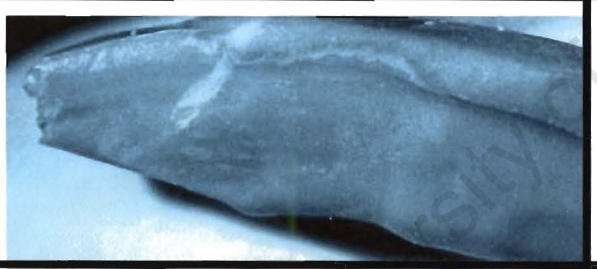


Class 1 digestion



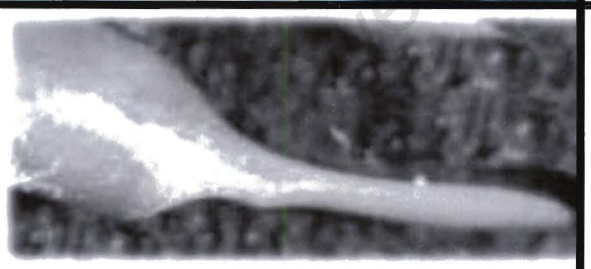
Class 2 digestion

The upper layers of both enamel and dentine have been removed during digestion, which has been accompanied by whitening of the enamel



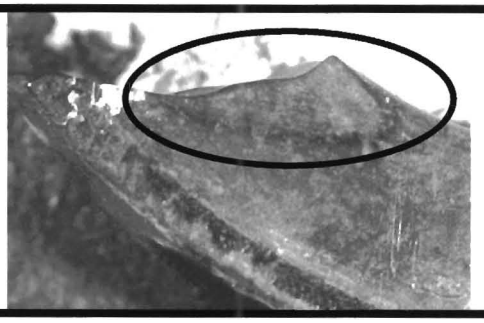
Class 3 digestion

The Murid incisor on the left shows class 3 digestion. Digestion is concentrated on the tip of the incisor, and shows removal of all the enamel in areas, exposing the underlying dentine



Class 4 digestion

The proximal end of the adjacent incisor shows extreme digestion, with only a thin core of dentine remaining



Block etching

The circle in the adjacent photo of a mole rat mandible incisor marks the feature called 'block etching'. The cause of this feature, observed on a small number of incisors was uncertain

Figure 4.1: The incisor digestion classes

Mandibles were recorded under the heading of 'mandible breakage' on the spreadsheet and were recorded as following: Complete mandibles were noted as 'mandible complete' (MC), minimal damage to the ramus was disregarded. If the ramus was broken, it was recorded as 'ascending ramus broken' (ARB), if missing, it was recorded as 'ascending ramus missing' (ARM). All the alveoli, with or without molars, were present in these two categories.

When the inferior border of the mandible was broken, breakage was recorded as 'inferior border broken' (IBB). This category was used to describe the mandibles that had suffered more advanced damage than the two previous categories. Mandibles falling into the 'IBB' category retained anything from one to three alveoli.

The category, 'Ramus/mandible fragment' (R/M frag.) contained fragments of ramus and mandible that did not fall into any of the above categories. Mandibles that had been reduced to just the diastema also fell into this category. Due to selective retrieval by laboratory and field assistants, very few of these fragments were found in the LBW fossil assemblages. Auditory bullae and skull fragments were recorded in the column headed 'skull fragments'. This category, as well as the 'Ramus/mandible fragment' category, was not used in the final data analysis.

The following illustrates how cranial material was recorded on the database. A left mandible with its ascending ramus missing (ARM), three *in situ* molars, and an *in situ* incisor with class 2 digestion would have the following information entered in the row relating to that mandible.

Accession number	Provenance	*In situ* molars	Incisor *in situ*	Incisor digestion	L/R	Mandible breakage
67240	ES/D2	3	yes	2	L	ARM

The 'provenance' column gives the unit name from which the mandible came, in this case east stream/dump 2 (ES/D2).

4.3.2 Murid maxillary breakage categories

Maxillae were recorded under the heading of 'maxilla breakage' on the spreadsheet and were very similar to those used by Andrews (1990). A skull with the left and right premaxilla and maxilla present, including the zygomatic process, was recorded as 'maxilla complete' (MC) and damage to the parietal, occipital and basal regions of the skull was disregarded. The 'complete maxilla' category thus contains two maxillae, all the other maxilla breakage categories, with one exception, contain only one. The other exception is the category that

records instances where the rest of the skull has been removed and only the left and right hand sides of the maxillae, minus the zygomatic process, remain. These maxillae were recorded as 'L&R maxilla'. Maxillae showing this kind of breakage, with five molars *in situ* (three molars in one side of the maxilla and two in the other), would be recorded on the database as follows:

L&R Maxilla	*In situ* molars	Maxilla breakage	L/R
1	5	ZM	L/R

If only the left or right hand half of a maxilla remained, with the zygomatic process intact, it was recorded as 'Maxilla with zygomatic' (M&Z). If the zygomatic bone was missing, it was recorded as 'Maxilla with zygomatic missing' (ZM). These categories contain maxillae which consist of 1-3 alveoli. The number of *in situ* teeth in mandibles and maxillae was noted in the '*in situ* molars' column.

All the premaxillae recovered from both the fossil sites had become separated from the maxilla, and opposing premaxilla. These single premaxillae were recorded under the heading 'premaxilla' and were divided into 'left' or 'right'. The presence of *in situ* incisors were noted and digestion was recorded in the column recording incisor digestion. For example, a right-hand premaxilla with an *in situ* incisor which showed class 2 digestion would be recorded as follows:

Premaxilla	L/R	Incisor *in situ*	Incisor digestion
1	R	yes	2

4.3.3 Shrew and mole rat mandibular and maxillary breakage categories

The morphology of the mole rat mandibles and maxillae differs to that of the murids, but as the kind of breakage observed was very similar, the breakage categories used for the murids proved adequate for the mole rats as well. A mandible with a broken ramus was recorded as 'ascending ramus broken' (ARB), and if missing, as 'ascending ramus missing' (ARM). The number of alveoli in the latter category varied from three to four. The mandibles falling into the 'inferior border broken' (IBB) category may have retained anything from one to four alveoli.

Breakage patterns of the soricid and macroscelid mandibles and maxillae from Hoedjiespunt is recorded slightly differently to that of the murids due to their different morphology. Research by authors such as Manthi (2002) and Denys *et al.* (1996b) suggests that soricid

mandibles may experience preferential preservation relative to murid mandibles from the same fossil assemblage. Complete mandibles were noted as 'mandible complete' (MC), minimal damage to the ramus was disregarded. If the ramus was broken, or missing, it was recorded as 'ascending ramus broken' (ARB) and 'ascending ramus missing' (ARM), respectively. Damage to the proximal end of the mandible was not recorded.

Fragments of soricid and macroscelid maxilla are recorded in the 'ZM' category, as described in the section above. The maxillae from HDP1 were very fragmented and no other categories were necessary for recording maxillary breakage.

4.4 Recording isolated molars and incisors

4.4.1 Isolated Incisors

Single, isolated incisors were identified as a 'maxilla incisor' or 'mandible incisor', and the degree of digestive etching was recorded in the 'incisor digestion' column. The 'proximal end' of the incisor refers to the tip in the following discussion. Almost all incisors showed some breakage, and the majority had sustained some damage to the distal end. It was not always possible to accurately assess the degree of digestion when portions of the incisor were missing, and, in order to take this potential error into account, the degree of completeness, and the presence or absence of the incisor tip, was noted in the 'incisor breakage' column. The latter feature was considered important as digestion frequently occurs on, or towards, the proximal end of an incisor.

If the proximal end and more than half the shaft was present, it was noted as '> tip present'. If the proximal end and less than half the shaft was present, the incisor was described as '< tip present'. If an incisor was missing the proximal end, and more than half the incisor shaft was present, it was described as being '> shaft'. Incisors falling into these three breakage categories were used for the purposes of analysis as they are the most likely to accurately reflect the degree of digestion. If less than half the shaft was present, it was recorded as '< shaft'. If an incisor was too fragmentary to be used for the purposes of analysis it was recorded in the 'incisor fragment' column, and the digestion of the incisor was recorded as a '?'. When assessing digestion on isolated incisors, the incisors falling into the '< shaft' column, as well as incisor fragments, were excluded from the final analysis.

In the case of murid incisors, incisors from mandibles and maxillae were not identified to species but were marked as 'Indeterminate' (Indet.) in the 'identification' column on the database, and mole rat or shrew (very rare) incisors were noted as such.

A murid maxillary incisor, retaining the proximal end and more than half of the shaft, and showing class 3 digestion would be recorded as follows:

Identification	Maxilla incisor	Incisor breakage	Incisor digestion
Indet.	1	>tip present	3

4.4.2 Isolated Molars

Isolated molars were recorded under the column heading 'isolated molars'. 'Field2' is the column on the spreadsheet used to identify the molar, that is whether it was an upper, or lower molar. Molars found in a fragment of bone were recorded as isolated molars. The abbreviations used on the spreadsheet are as follows;

Upper first molar = MU1

Upper second molar = MU2

Upper third molar =MU3

Lower first molar = ML1

Lower second molar = ML2 and

Lower third molar = ML3

From this point onwards, the three molars of the murid mandible will be referred to as the M_1, M_2 and M_3, and the three maxillary molars, as the M^1, M^2 and M^3, respectively. In the case of the mole rats, PM_3 will denote the premolar, and M_1, M_2 and M_3 the three molars (in this case the lower molars).

4.5 Recording the micromammal family, genus or species

Murid M^1 and M_1 teeth (*in situ* and isolated) from the fossil assemblages were identified to species whenever possible, and these were the teeth used to quantify the different species present in the fossil assemblages. The name of the family, genus or species of the micromammal mandibles, maxillae and isolated molars from the fossil assemblages, was noted in the 'identification' column of the database. Occasionally breakage, wear or

digestion of the tooth precluded identification, in which case the mandible, maxilla or isolated molar was noted as being 'indet.' (indeterminate) in the 'identification' column. In some cases extremely worn teeth had lost all identifiable traces of the occlusal dentine and enamel patterns, and these teeth were noted as 'molar worn' in the 'comments' column. Extreme digestion, or advanced wear on teeth was also noted in this column. Worn or digested molars that could be identified to genus, but not to species, were noted in the 'identification' column, as, for example, 'Indet. *Aethomys* sp', or 'Indet. *Rhabdomys* sp.', and these specimens were excluded from analysis. Where there was uncertainty as to the identification of a species, a '?' appears before the name in the identification column. These teeth were not used for the purposes of analysis.

4.5.1 Recording the taxonomy of the LBW micromammals

In the case of the LBW fossil material, the M^2, M^3, M_2 and M_3 molars could frequently not be identified to species or genus, in which case they were simply recorded as 'indeterminate'. In the case of certain species, such as *Aethomys*, *Rhabdomys* and *Acomys*, these teeth were allocated to genus and were recorded as 'Indet. *Aethomys*-like', 'Indet. *Rhabdomys*-like', and so on. The second and third molars of certain species were, however, clearly identifiable, and all the upper and lower molars of the Gerbillid (*Desmodillus* sp.) and the murid, *Euryotomys pelomyoides*, were identified to species.

Murid mandibles and maxillae that were missing all their molars were not identified and were noted as being 'indeterminate' (Indet.). The mole rat *Bathyergus hendeyi* was counted differently, however, as mandibles and maxillae could easily be identified by the patterns of the alveoli, if no molars were present. This obviously increased the number of mole rats relative to the other species present, but not to a significant degree, as only 15 *B. hendeyi* mandibles, and 3 maxillae were identified to species using the alveoli. All of these specimens came from the LQSM unit east stream/dump 2 (ES/D2). The following illustrates how an isolated M^1 from the murid, *Aethomys adamanticola*, would be recorded on the database:

Identification	Field 2	Isolated molar
A. adamanticola	MU1	1

4.5.2 Recording the taxonomy of the HDP1 micromammals

The taxonomy of the HDP1 micromammals was recorded in a similar manner to that of the

LBW fauna, however, the presence of extant species such as *Otomys*, led to a few minor adjustments, which are detailed below. The cranial bones from Hoedjiespunt were so fragmented that the vast majority of material consisted of single teeth. The Otomyinae dominated the species list and *O. unisulcatus, O. saundersae, O. irroratus, O. slogetti* and *Parotomys brantsii*, were present. Identification of isolated teeth from the Otomyinae is difficult as there is individual variation in size of the various species, in some of the features of the molars, and in the number of the laminae within a species. There may also be overlap in size, for example, between *O. saundersae* and *O. irroratus* (Avery pers. comm.). The alveoli patterns were not used to allocate mandibles and maxillae to species when no teeth were present, as there is variation in the number of alveoli of many of the *Otomys* species (Levinson 1985, Avery pers. comm.). The great similarity between the various species made it extremely difficult to identify isolated M_2, M_3, M^2, and M^3 molars, and these teeth were simply recorded as *Otomys/Parotomys* (abbreviated as '*Ot./Parot.*' on database). It was, however, possible to identify the M^1 and M^3, and the M_1 to species.

Where possible, all of the upper and lower molars of micromammal species other than *Otomys* and *Parotomys* were identified to the species level. Fragments of shrew and elephant shrew teeth, mandibles and maxillae, were identified as 'soricid','macroscelid', or 'shrew', if the fragment was too small to ascertain to which family it belonged.

4.6 Calculating tooth loss

Tooth loss may be used to quantify the breaking up of the cranial bones (Andrews 1990, Matthews 1998). Damage to the inferior border of the mandible, or to the premaxilla, may result in the loss of the incisor, and damage to the alveolar borders of maxillae and mandibles frequently result in molar loss. In the following calculations involving tooth loss from mandibles and maxilla, three molars and one incisor in every murid half-jaw in the sample are assumed to have been present originally.

Tooth loss was calculated for HDP1 (which represented a fossil accumulation in a confined area) but was not calculated for LBW due to the mixed nature of the assemblages from the LQSM and MPPM (F).

4.6.1 Molar loss

Molar loss was calculated by working out the number of molars expected, given the number of mandibles or maxillae in a sample, and subtracting the number of molars present in the jaws (after Andrews 1990). Percentage molar loss was then calculated by dividing molar loss by the number of expected molars, and then multiplying by 100.

4.6.2 Incisor loss

Incisor loss is calculated by working out the number of incisors expected, given the number of mandibles or maxillae in a sample, and subtracting the number of incisors present in the jaws from the number of expected incisors (after Andrews 1990). Percentage incisor loss was then calculated by dividing incisor loss by the number of expected incisors, and multiplying by 100.

Incisor loss was calculated for the mandibles, but not the maxillae, the reason for this being that extremely few premaxillae were found in the fossil material, and no maxilla retaining a premaxilla was recovered.

4.6.3 Comparing isolated molars and incisors with tooth loss from the mandibles and maxillae

The number of empty tooth sockets in murid mandibles and maxillae was calculated for HDP1 in order to see what percentage of missing teeth were accounted for by the loose molars and incisors in the fossil assemblages (after Andrews 1990). A surplus of isolated molars and incisors indicates that maxillae and mandibles have been completely destroyed, with only the single teeth surviving intact in the fossil assemblage. A deficit of isolated teeth indicates that there has been preferential loss of loose teeth from an assemblage. A percentage of around 100% tooth loss indicates that teeth that have come loose from mandibles and maxillae have been retained, undamaged, in the sample. Tooth loss was not calculated for the fossil material from the LQSM and MPPM (F) as both these fossil collections came from mixed sources. In addition, in the case of the LQSM units, there is likely to have been distortion of the original ratio of isolated to *in situ* teeth during recovery.

4.7 The taphonomy of the incisors and molars from the LQSM and MPPM (F)

4.7.1 Recording molar and incisor damage

Damage to *in situ* and isolated molars and incisors from the fossil assemblages was described

in the 'comments' column where it was noted if the enamel and/or dentine of a molar or incisor was chipped, broken, cracked, or absent. The following features were recorded;

- **Molar chipped** - denoted molars where molar enamel and dentine showed chipping from physical damage.
- **Molar broken** - described molars which were missing entire portions of a cusp, or cusps, including the root.
- Physical damage to the enamel and/or dentine of the incisor, such as chipping, was recorded as **incisor dentine damaged** and **incisor enamel damaged**.
- **Incisor dentine absent** - described incisors where the dentine had broken and fallen out, leaving only the enamel. This kind of breakage has been observed on incisors where weathering has caused deep cracking and loss of enamel (pers. ob.). It may also be caused by physical damage (Manthi 2002).

- **Incisor broken** - was used to describe incisors which were *in situ* but which were missing the tip and varying proportions of the shaft, due to breakage.
- **Desquamation** - exfoliation of incisor dentine and/or enamel was noted
- **Cracking** - Many murid and mole rat molars showed a fine cracking of the enamel or dentine, and only large, relatively deep cracks on the enamel and/or dentine of molars and incisors were noted in the 'comments' column as, for example, 'incisor enamel & dentine cracked', 'molar dentine cracked'.

4.7.2 The 'comments' column on the database

The 'comments' column was used to record the features listed above, as well as others, such as burning. In some cases where cranial bones and teeth from the fossil material had been coated for SEM analysis, or where glue had covered the occlusal surfaces of the teeth, it was impossible to ascertain the digestion class with certainty. The etching class was then recorded with a '?' in front of it and was noted as 'coated' in the 'comments' column. These teeth were excluded from the analysis of incisor digestion.

4.8 Recording tooth eruption patterns of the mole rats from the LQSM assemblages

There is debate over the dental formula of the Bathyergidae and various dental formulae have been suggested. It has been suggested that the four molars found in African mole rats consist of two premolars and two molars (Skinner and Smithers 1990). This thesis will, however, use the cheektooth configuration put forward by De Graaff (1981), who proposes that the cheektooth row of adult mole rats consists of a PM_3, M_1, M_2 and M_3.

In order to form a population profile for the mole rat, *Bathyergus hendeyi*, at the time of death, the eruption patterns of this species teeth were recorded. Only the tooth eruption patterns of the mandibles were noted as the mole rat maxillae were generally very fragmented and the sample size was small. Damage to the mole rat mandibles had resulted in the loss of the ascending ramus in the majority of mandibles, and this damage frequently extended into the area where M_3 was situated, causing the loss of this molar, which was as a result the least commonly found *in situ* tooth. The wear patterns on teeth were not included in the analysis of the LQSM mole rats as the M_2 and M_3, in particular the latter, were frequently missing from *B. hendeyi* mandibles. This breakage and tooth loss meant that it was impossible to accurately assess the age of the bulk of mole rats, and the majority of mandibles could provide only a minimum age of the animal at the time of death. Given the fact that post-depositional breakage had, had a big impact on *B. hendeyi* tooth loss, molar eruption patterns provided an adequate way to assess age in the mole rat population. A similar study was not feasible in the case of the two MPPM units, due to the small samples of mole rat mandibles recovered.

The molar eruption patterns are noted in a column on the database entitled 'Eruption'. Fully erupted, *in situ* teeth are recorded with an 'FE' in front. For example, a fully erupted PM_3 would be recorded as 'FE PM_3. When more than one molar was found *in situ*, this was recorded. For example, if the PM_3 and the M_1 and M_2 molars were found *in situ* in a mandible, they would be recorded as 'PM_3, M_1, M_2'. Partially erupted molars, or molars which were just starting to break through the mandible, were recorded in the same way. For example, a partially erupted second molar, would be recorded as 'partial eruption M_2'. Newly erupted molars, that is molars that had just attained full eruption, were distinguishable by their unworn occlusal surfaces and this was also recorded. A mandible in which the second molar had only just erupted would be recorded as 'recently erupted M_2'.

4.9 Recording and classifying the postcranial bones

4.9.1 Breakage patterns of the limb bones

The following sections describe how the postcranial bones from HDP1 and MPPM (F) were recorded. The methodology used follows that of Andrews (1990). The limb bones were not divided into left and right as this was not necessary for calculating an MNI (Minimum Number of Individuals) for the fossil assemblages. The MNI was calculated in the way suggested by Andrews (1990), where the most common skeletal element present in an assemblage was used for the calculation of MNI.

The humerus, tibia and ulna were sorted into the categories, 'complete', 'proximal', 'distal' and 'shaft'. A limb bone fell into the 'complete' category if the proximal and distal parts and the shaft were present. Slight damage to the proximal and distal epiphyses and areas such as the distal, articular end of the humerus, or the head or trochanters of the femur, was ignored. A limb bone was recorded as `proximal' or `distal' if it contained the proximal or distal articular end and a portion, or all, of shaft. If the proximal and distal articular ends were missing, and a portion, or all, of the shaft was present, it was categorised as a `shaft'.

The acronyms in brackets in this, and the following sections, indicate the abbreviations used in the following chapters, and on the database. The femora were categorised in the manner described above, but had an additional breakage category. If only the proximal, articular head, or a small portion of the proximal articular ephiphyses was present, it was recorded under the category of 'femur head' (FH) (illustrated in Figure 4.2). This category was created as this type of breakage is frequent in modern small carnivore assemblages (pers. ob.).

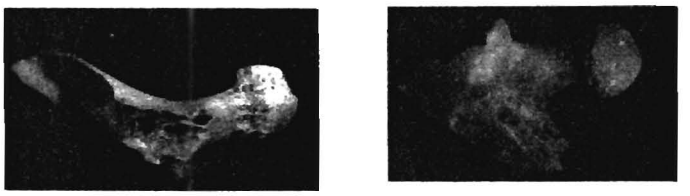


Figure 4.2: The femora above illustrate the breakage category 'femur head' (FH)

This category could, therefore, be used to indicate the contribution of small carnivores to a fossil assemblage. This category was frequently added together to the 'proximal' category (FP) for the purposes of analysis.

Radii were recorded as 'complete' (RC), 'proximal' (RP) or 'distal' (RD) as these categories

were adequate to describe the portions of radii recovered from the fossil assemblages. The reptilian and amphibian microfaunal bones from HDP1 were recorded on the database and the fused tibio-fibula of the frog was recorded under the 'tibia' breakage categories, and the radio-ulna under the 'ulna' breakage categories.

The thin delicate fibula, which is fused to the tibia in the Muridae, was not recovered from the fossil material. Andrews (1990) did not note the presence or absence of these fragile bones in his studies of fossil, and comparative, assemblages. The identification of any bone or tooth, or feature of a bone or tooth which was made tentatively, due to breakage or some other factor, was recorded with a '?' in front of it and was not used for the purposes of analysis.

4.9.2 Recording the epiphyses

The epiphyses of limb bones were not recovered from the LBW fossil assemblages, undoubtedly due to the recovery and sorting processes used at the site. The epiphyses from the proximal humeri, proximal tibia and distal femur were recovered from HDP1, however, and were included in the analysis of the postcranial material. If the number of epiphyses was greater than the number of proximal or distal parts of a limb bone, the epiphyses were taken to represent the distal or proximal portions of a bone. Epiphyses were recorded as follows on the database; ph = proximal humerus, pt = proximal tibia, df = distal femur.

4.9.3 Recording the breakage of the pelvic girdle and the scapula

The pelvic girdle and scapula were recorded under the heading of 'pelvic girdle' and 'scapula' on the database. The acetabulum of the pelvis, and the coracoid of the scapula experienced preferential preservation in the fossil assemblages and were therefore used to represent the pelvic girdle and scapula. The methodology used to record these bones was designed to avoid double-counting and is described below.

The category 'acetabulum present' (AP) included complete pelvic girdles, as well as any pelvic girdle which had retained the acetabulum and any part, or parts, of the ilium, ischium or pubis. A fragment of any part or parts of the ilium, ischium or pubis, which were missing the acetabulum, were recorded under the column 'acetabulum absent' (AA). This last category was not included in the final analysis of the fossil assemblages.

The scapulae falling into the category 'coracoid present' (CP), included both complete scapulae and those which retained the coracoid process but had sustained damage to, and loss of, parts of the blade. Fragments of scapula missing the coracoid process were recorded as 'coracoid absent' (CA). The latter category was not used for the purpose of analysis of the fossil material.

4.9.4 Recording the breakage of the vertebrae

Vertebrae were recorded as 'complete' if they retained the centrum, even if they had sustained damage to the apophyses. Fragments of vertebrae that no longer retained the centrum, or retained only portions of centrum, were recorded under the category 'vertebra damaged'. These vertebrae were excluded from analysis in order to avoid double-counting. The atlas and axis were recorded separately from the other vertebrae, but were added in with the total number of vertebrae for the purposes of analysis.

4.9.5 Recording the numbers of metapodials, phalanges, calcanei, astragali and foot/hand bones

The number of metapodials, phalanges and calcanei and astragali were recorded in the database. Damage to any of these elements was not noted. Generally, however, the majority of these bones from the fossil material were complete. The other bones of the feet were recorded under the heading of 'foot/hand bones' (FB).

4.9.6 Recording the number of ribs

Ribs were counted and recorded regardless of which part of the rib remained. Double counting was unavoidable but was probably kept at a minimum by the fact that generally, the ribs that had survived consisted of the relatively robust capitulum and a portion of shaft.

4.9.7 Recording the chrysochlorid earbones

No chrysochlorid mandibles or maxillae were recovered from either of the fossil sites. The cranium of the golden mole was, however, represented by the earbone, the malleus, which is composed of very dense and durable bone. This bone was recorded under the title 'earbones' on the database and was recovered from both HDP1 and LBW.

4.9.8 Recording species type

The limb bones of the golden moles, the mole rats, and sometimes the shrews, were generally identifiable due to their characteristic shapes. When postcranial bones were recognised as belonging to a particular micromammal species, this was noted in the 'identification' column

of the database. Mole and mole rat bones were labeled as such, and macroscelid and soricid postcranial bones were identified as 'macroscelid' or 'soricid', or, if it was not possible to make this differentiation, as 'shrew'. The majority of postcranial bones, most of which belonged to various murid species, could not be assigned to a particular species and were recorded as indeterminate (indet.). It is possible, however, that some of the less characteristic postcranial bones from shrews, elephant shrews, mole rats and moles may not have been identified accurately to species and have been recorded as 'indet' in the identification column. Bones such as ribs, the calcaneum, astragalus, pelvic girdle, scapula, metapodials, footbones, phalanges and vertebrae are difficult to identify to species, especially when they have sustained damage.

4.9.9 Recording the non-mammalian microfauna from Hoedjiespunt 1

Microfaunal bones from small birds, snakes, lizards and frogs were found in the fossil microfaunal samples from Hoedjiespunt 1, and were recorded along with the micromammals as they provided potential information on predator behaviour and diet. The 'identification' column recorded the microfaunal species involved. If identification was uncertain the species was recorded as a '?', for example, it was uncertain if a bone belonged to a lizard or frog it would be recorded as a '? lizard/frog'. Although the cranial and postcranial bones of non-microfaunal species were recorded, only murid, soricid and macroscelid bones and teeth were included in the taphonomic analysis of the fossil material from Hoedjiespunt. The tibiotarsus from small birds was recorded in the 'tibia' column, but was marked as 'bird' in the 'identification' column. Certain columns were added onto the database to describe the body parts of some of the other species, such as the frogs and small birds. Some of the categories added were;

- The category 'tarso-metatarsals' was created to record these small bird bones.
- The categories, 'clavicle', 'coracoid', 'ilium' and 'urostyle' were added to record these frog bones.

4.10 Recording the taphonomy of the postcranial bones from the MPPM (F)

The femur and the humerus were the bones chosen to assess the postcranial taphonomy of the MPPM (F) units, as these bones are commonly used to quantify breakage, predator digestion, and other taphonomic processes within a site (Andrews 1990, Denys *et al.* 1996a). The taphonomy of these bones was recorded using a light microscope, and variable magnification.

Maguire and Schrenk (1985) point out that the absence of adequate experimental and comparative controls have led to analyses and interpretations of fossil bone damage amounting to little more than informed guesses or opinions. This insight was heeded when recording the obviously complex taphonomic history of the bones from LBW. The micromammal fossils showed a palimpsest of events and it became obvious that accurately separating out all the different taphonomic processes and stages of modification of the fossils would not be easy. With this in mind, the femora and humeri were examined several times and it became clear that certain taphonomic features were frequently observed, though not always together, and in a variety of combinations. These features were recorded and are listed in the following sections. They include flaking and desquamation, damage to the epiphyses, rounding, digestion, punctures and holes, cracking and splitting, digestion and corrosion. These features are described in more detail below.

4.10.1 Flaking and desquamation

The column 'flaking and desquamation' described bones which showed desquamation (exfoliation) and flaking of the surface of the bone. Three different types of desquamation were recognized;

- ***Localized desquamation***, where desquamation occurred in discrete areas
- ***General desquamation***, where desquamation occurred all over the bone surface
- ***Advanced desquamation***, where desquamation occurred all over the bone, and had penetrated deeper through the layers of cortex than the previous category. The desquamation indicated that the bones had been exposed to some sort of corrosive environment, rather than weathering, as the desquamation was not accompanied by the cracking and splitting of bone associated with weathering. It was impossible to ascertain whether the different kinds of desquamation had different, or related, causes. The desquamation appeared to have been caused by different physical or chemical agents to the other types of corrosion observed on the fossils.

4.10.2 Damage to the epiphyses

The epiphyses of the humerus and femur frequently showed chipping and breakage which appeared to have been caused by some physical force, possibly being tumbled in the river. The rough facets of these damaged areas appeared to have been 'smoothed' after they sustained damage, although they were not, in the strict sense of the word, 'rounded'. This smoothing of the damaged areas on the epiphyses of the limb bones was not noted separately

as almost every bone which had sustained damage to the epiphysis showed it, and it appeared to have been caused by physical abrasion, rather than water action. Removal of parts of the epiphysis was clearly associated with breakage, rather than digestion. The epiphyses of the limb bones are more susceptible to digestion, corrosion, and breakage than the shafts, particularly when younger animals are involved.

4.10.3 Rounding

Bones which showed the type of rounding associated with prolonged water action were recorded in the column headed 'rounding'. Digestion may also cause rounding on bones, however, water action may be distinguished from digestion in that it affects all parts of the bone, resulting in a generally smooth and rounded appearance, most noticeable on broken areas. Digestion, on the other hand, is usually concentrated in discrete areas such as the epiphyses, and is accompanied by the removal of the cortex of bone and the exposure of the underlying structure.

4.10.4 Digestion

Femora and humeri showing signs of digestion were noted under the 'digestion' column, which was left blank if no digestion was discerned. If present, digestion was noted with a 'yes' in the column headed 'digestion'. A '?yes' was noted in the case of bones where other taphonomic features, such as damage, corrosion or desquamation made it difficult to ascertain for certain if digestion had taken place.

4.10.5 Punctures and holes

Punctures and holes in the humeri and femora were noted under the column entitled 'punctures/holes'

4.10.6 Cracking and splitting

Very fine cracks in enamel, dentine and bone were not noted as such cracks may have been caused by a number of different factors and would not have been useful for ascertaining events, such as weathering. This category was used to describe those bones which had cracks which were more than superficial and had penetrated the cortex of the bone, and the enamel and/or dentine of teeth. Cracking and splitting of the femora and humeri from the MPPM (F) was noted in a column simply titled 'cracking and splitting'. This feature was noted as extensive cracking and splitting of bone along the bone fibres, or in a mosaic bone pattern, would indicate weathering. The effects of weathering described by Behrensmeyer (1978) for

large mammals are almost identical to that observed on small mammals, although weathering of micromammal bones and teeth occurs at a slower rate (Andrews 1990).

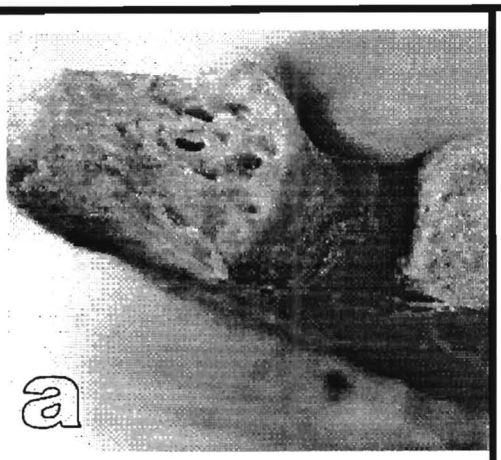
4.10.7 Rootmarks

Provision was originally made to record the presence of rootmarks on the database, however, this turned out to be unnecessary as no rootmarks were recorded on any of the HDP1 or LBW fossils.

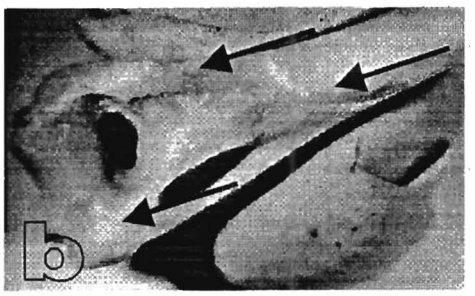
4.10.8 Corrosion

Corrosion on bones and teeth may be caused by a variety of soil types (Andrews 1990). Soil corrosion is distinguishable from weathering as it results in extensive pitting of the teeth and postcrania (Andrews 1990). Acid soils cause the most marked etching on teeth and bone, though etching may also occur in alkaline soils (Andrews 1990). In the case of acid soils, preferential etching occurs first on tooth enamel and, only in more extreme cases, on dentine and bone (Andrews 1990). Very alkaline soil affects bone and the dentine of teeth more than the enamel, and causes a superficial flaking or exfoliation of bone (Fernandez-Jalvo 1995). A similar appearance may result from weathering, however, in this case, the bones would become split and cracked before exfoliation takes place.

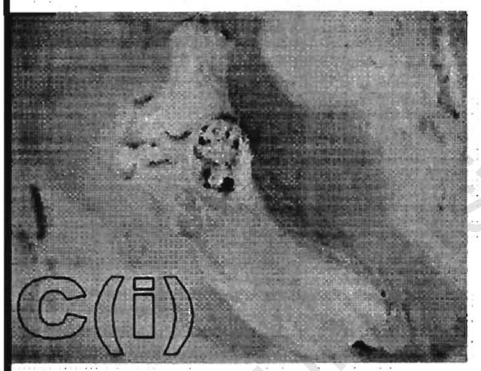
At the site of Gran Dolina, Atapuerca, in Spain, Fernandez-Jalvo and Andrews (1992) discovered that the majority of micromammal fossil bone in the site showed signs of post-depositional corrosion. The bone and tooth dentine appearing chemically dissolved, while the tooth enamel appeared unaffected. This pattern is the opposite to that discernible in cases where the bone has been etched by digestion, or by an acid soil environment, and it was attributed to the preferential etching of bone and dentine by prolonged exposure to an active alkaline environment (Fernandez-Jalvo and Andrews 1992). Figure 4.3 illustrates several taphonomic features of the cranial and postcranial bones from MPPM (F). The following pictures were all taken with a light microscope, using variable magnification (5x - 50x).

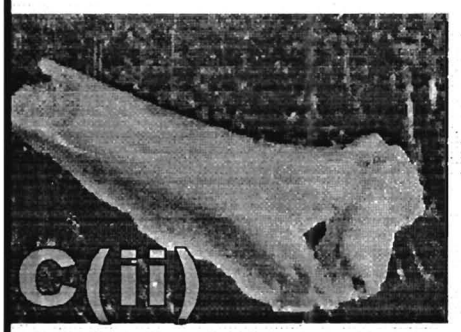


a) This proximal Murid ulna shows signs of abrasion and desquamation



b) The arrows indicate areas of **localized desquamation** on a distal shrew humerus

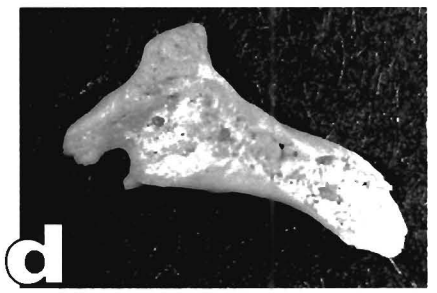




C (i) and C (ii): The adjacent proximal femur and distal humerus illustrate the damage described as **damage to epiphyses** (DTE)

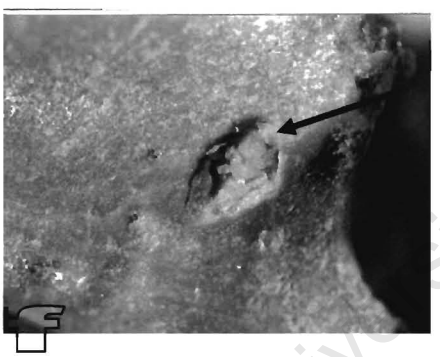
Figure 4.3: Taphonomic features of the fossil assemblages

Figure 4.3: (cont...)

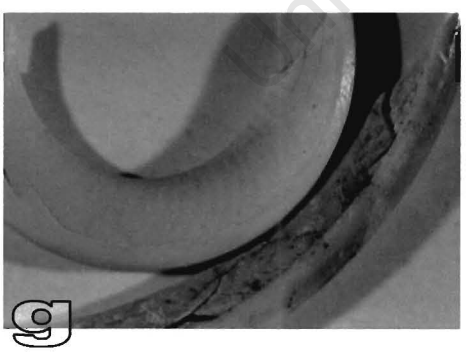


d) Distal shrew humerus showing in-filling with sediment, and rounding from water action on broken areas of bone

e) A small area of digestion is indicated by the arrow on the adjacent picture



f) The arrow indicates a small stone embedded in the cavity. Such damage would be recorded as hole/puncture



g) Photo g shows two incisors (collected from a ledge below a modern owl roost site) which have been exposed to weathering. Both incisors in the photo on the left show traces of weathering. The incisor on the far left is only lightly weathered and shows slight cracking of the dentine. The incisor on the right shows advanced weathering with advanced cracking and splitting of the dentine

The micromammals from both LBW and HDP1 showed evidence of post-depositional corrosion, and this is discussed further in the chapters presenting the taphonomy of the two sites. The term 'corrosion' is used in a broad sense in this thesis to describe any post-

depositional etching on the fossils, which has been caused by some process other than digestion. The broad usage of the word in this thesis reflects our lack of understanding of the processes which cause the various types of corrosion observed on fossil assemblages. The presence of corrosion was recorded on the database under a column titled 'corrosion'. This column was left blank if no corrosion was discerned, and if present, was recorded with a 'yes'.

4.11 Postcranial to cranial proportions

The proportion of postcranial to cranial skeletal elements was calculated for HDP1. The percentage of femora plus humeri, divided by the total number of mandibles and maxillae, was calculated in order to ascertain if there had been selection for, or against, the cranial or postcranial bones (after Andrews 1990):

$$\frac{\text{femur+ humerus}}{\text{mandible + maxilla}} \times \frac{100}{1}$$

The numbers of femora and humeri should approximately equal the numbers of maxillae and mandibles unless either cranial, or postcranial, elements have been selected against.

4.12 Skeletal element proportions

The proportions in which the skeletal elements of prey skeletons appear in scat and pellet assemblages have been used to distinguish between different predator species in both comparative and fossil assemblages (Dodson and Wexlar 1979, Andrews 1990, Fernandez-Jalvo 1995, Fernandez-Jalvo *et al.* 1998, Avery 2002). Skeletal abundance was calculated using the formula:

$R_i = N_i/MNI \times E_i$ (After Andrews 1990)

where,

R_i = the relative abundance of element i

N_i = the number of element i in the sample

MNI = the minimum number of individuals

E_i = the number of element i in the prey skeleton

The MNI is calculated using the highest number of any skeletal element in the assemblage. For example, if the femur is the most abundant skeletal element in an assemblage, 40 femora will yield an MNI of 20.

4.13 Identification of the *Aethomys* and *Rhabdomys* species at LBW

Measurements were made of the length and breadth of the M_1 and M^1 molars of the various *Aethomys* and *Rhabdomys* species from the LQSM and MPPM (F) in order to see if there was variation in the size of species between the two members, and also to see if size could be used to differentiate between species. Molars which were of uncertain identification, or which had suffered damage, wear or digestion that affected tooth measurement, were not used in the analysis.

4.13.1 The molar measurements of *Euryotomys pelomyoides*

Measurements of the length and breadth of *E. pelomyoides* molars made by Christiane Denys and the author were used to assess the degree of variation in size in this species, and to see if there were any differences in tooth size in the specimens from the LQSM and MPPM (F). The MPPM (F) sample of *E. pelomyoides* measured by the author came from the recent excavation area, while the sample measured by Denys came from the micromammals recovered during mining of the MPPM.

4.14 Measuring species diversity with the Shannon Wiener index of general diversity (*H*)

The Shannon Wiener index of general diversity is frequently used for calculating diversity in micromammal assemblages (Avery 1992, Avery 1999, Manthi 2002, Avery in press), and was used for assessing species diversity at LBW. General diversity takes into account both the number of taxa present, and the relative frequency (evenness of representation) of each taxon (Cruz-Uribe 1988). The Shannon Wiener index is calculated using the formula:

$$H = - \Sigma P_i \log P_i,$$

where $P_i = n/N$, that is, the proportion of the total sample represented by each species.

4.15 Assessing the palaeoecology of the HDP1 and LBW micromammal populations

The preferred habitats and habits of extant species of micromammals were used to recreate the environment in which the HDP1 and LBW micromammals lived. Interpretation of the LBW micromammals was hampered by the fact that all the species represented at the site are extinct. Caution was therefore used in applying the habits and characteristics of extant, to extinct, micromammals, and the analysis concentrated on the species which show a strong

correlation of phylogeny with ecology. The reconstruction of the palaeoenvironments of HDP1 and LBW are compared with other lines of evidence, such the large mammal taxa, and pollen data, in the case of LBW.

Chapter five

Results: The taphonomy of the microfaunal collections from Varswater 'E' Quarry, Langebaanweg

5.1 Introduction

This chapter presents the results of a taphonomic study of the micromammals from the LQSM and MPPM. Assorted murid species, and the mole rat, *B. hendeyi*, are the most common rodents found at LBW, though the latter is relatively less well-represented in the MPPM (F). The taphonomy of the mole rat and murid species are presented separately as *B. hendeyi* is larger, and has a different cranial and postcranial morphology. The mole rats may also have been accumulated by different agent/s to the murids. The taphonomic results for the LQSM are presented first, and those for MPPM (F) second.

The term 'corrosion' in this, and subsequent chapters, is used to describe the etching on micromammal bones and teeth which occurred when the micromammals were buried in sediment. The cause of the corrosion is uncertain, but was undoubtedly related to chemical changes which occurred within the sediment. The term 'digestion' refers to the etching on micromammal teeth and bones, caused during digestion of micromammalian prey by the predator.

5.2 Post-depositional corrosion at LBW

Post-depositional corrosion was observed at LBW on the surfaces of bone, and the enamel and dentine of the teeth, however, it did not materially affect identification of digestion on the majority of incisors. When assessing digestion on the incisors it was possible to categorise the digestion when the areas affected by the corrosion were very small, or had occurred in separate areas from the digestion. Incisors that could not be accurately assessed for digestion, due to the presence of corrosion, were excluded from analysis. As corrosion appears to have occurred randomly throughout the site, this would not have affected the results.

5.3 The taphonomy of the LQSM units

5.3.1 Murid and mole rat incisor digestion and breakage

Table 5.1 and Table 5.2 below show the results of the study on digestive etching on the murid and mole rat incisors from the various units of the LQSM. In order to exclude very small assemblages, units which contained samples of fewer than five murid incisors are not shown on Table 5.1, and units which contained samples of fewer than five mole rat incisors are not shown on Table 5.2. Isolated and *in situ* incisors are shown together on the following tables in order to increase sample size.

The majority of incisors shown on the Table 5.1 are *in situ*. Out of the 239 murid incisors appearing on Table 5.1 below, some 105, less than half, are isolated incisors. The relatively low number of isolated incisors in the LQSM units may also be attributable to a bias that appears to have occurred during either collection, sieving and/or sorting, where attention appears to have focussed on retrieving cranial bones, rather than isolated incisors. Maxillary incisors also appear to have experienced bias during collection, only sixteen isolated murid maxilla incisors were found, as opposed to 89 isolated mandible incisors.

No isolated *C. broomi* incisors were found, and the digestion on two i*n situ* incisors, which fell into digestion classes 2 and 0, respectively, is recorded along with those of *B. hendeyi* in Table 5.2.

Unit name	Isolated and *in situ* mandibular and maxillary incisors Digestion classes												
		No visible digestion→		light digestion→		moderate digestion→						extreme digestion	
	(N)	0	%	1	%	1a	%	2	%	3	%	4	%
ES/D2	**148**	49	***33.1***	79	***53.4***	2	***1.4***	13	***8.8***	5	***3.4***	0	***0***
Combined ES/bed2 sites	**6**	1	***16.7***	5	***83.3***	0	***0***	0	***0***	0	***0***	0	***0***
Combined Eles	**39**	7	***17.9***	29	***74.4***	0	***0***	3	***7.7***	0	***0***	0	***0***
ES/SQ1	**35**	7	***20***	26	***74.3***	0	***0***	2	***5.7***	0	***0***	0	***0***
PB	**11**	8	***72.7***	0	***0***	1	***9.1***	1	***9.1***	1	***9.1***	0	***0***

Table 5.1: LQSM Units: Digestion on isolated and *in situ* mandibular and maxillary murid incisors

Unit name	Isolated and *in situ* mandibular and maxillary incisors Digestion classes												
		No visible digestion→		light digestion→		moderate digestion→						extreme digestion	
	N	0	%	1	%	1a	%	2	%	3	%	4	%
ES/D2	**38**	21	***55.3***	8	***21.1***	0	***0***	9	***23.7***	0	***0***	0	***0***
Combined ES/bed2 sites	**43**	20	***46.5***	11	***25.6***	0	***0***	10	***23.3***	2	***4.7***	0	***0***
Combined Eles	**37**	17	***45.9***	9	***24.3***	0	***0***	9	***24.3***	2	***5.4***	0	***0***
PB	**6**	4	***66.7***	1	***16.7***	0	***0***	1	***16.7***	0	***0***	0	***0***
ES	**7**	2	***28.6***	1	***14.3***	0	***0***	3	***42.9***	1	***14.3***	0	***0***
ES/NE/F.S.	**13**	7	***53.8***	4	***30.8***	0	***0***	2	***15***	0	***0***	0	***0***
ES/sect 3 sp 4	**6**	6	***100***	0	***0***	0	***0***	0	***0***	0	***0***	0	***0***
Michaels pit	**7**	2	***28.6***	2	***28.6***	0	***0***	3	**42.9**	0	***0***	0	***0***

Table 5.2: LQSM Units: Digestion on isolated and *in situ* mandibular and maxillary mole rat incisors

Key to unit names: ES/D2 = east stream/dump 2; Combined ES/bed2 sites = combined east stream/bed2 sites; Combined Eles = combined elephant sites, PB = peat bed; ES = east stream; ES/NE/F.S. = east stream, north end, fish spine site; ES/sect 3 sp 4 = east stream, section 3, spit 4

5.3.2 Breakage patterns of the murid and mole rat mandibles and maxillae

The breakage patterns of murid mandibles and maxillae are shown on Table 5.3a, and those of *B. hendeyi* on Table 5.4a. In order to exclude small samples, LQSM units which contained a total of less than 10 mandibles and maxillae are not shown on the following tables. As all the murid and mole rat maxillae from LBW fell into the breakage category ZM, only this maxilla breakage category appears on Tables 5.3b and 5.4b.

	Mandible breakage								
Unit name	Total number of mandibles	Mandible complete (N)	%	Ascending ramus broken (N)	%	Ascending ramus missing (N)	%	Inferior border broken (N)	%
ES/D2	**304**	0	*0*	50	*16.4*	82	*27*	172	*56.6*
Combined Eles	**65**	0	*0*	11	*16.9*	20	*30.8*	34	*52.3*
ES/SQ1	**44**	0	*0*	9	*20.5*	14	*31.8*	21	*47.7*
PB	**5**	0	*0*	0	*0*	3	*60*	2	*40*
ES/TP1	**10**	0	*0*	2	*20*	1	*10*	7	*70*

Table 5.3a: Breakage patterns of the murid mandibles from the LQSM

	Maxilla breakage	
Unit name	Zygomatic missing (N)	%
ES/D2	143	*100*
Combined Eles	36	*100*
ES/SQ1	28	*100*
PB	10	*100*
ES/TP1	7	*100*

Table 5.3b: Breakage patterns of the murid maxillae from the LQSM

Key to unit names: ES/D2 = east stream/Dump 2; Combined Eles = combined elephant sites, ES/SQ1 = east stream/square 1; PB = peat bed; ES/TP1 = east stream, Tex's pit 1

If the two smaller LQSM units in Table 5.3a are disregarded, namely PB and ES/TP1, 48-57 % of murid mandibles fall into the breakage category 'inferior border broken' (IBB), and approximately 27-32 % in the category 'ascending ramus missing' (ARM). The sample size of PB and ES/TP1 is too small to be interpreted with any confidence.

	Mandible breakage								
Unit name	**Total number of mandibles**	**Mandible complete**	**%**	**Ascending ramus broken**	**%**	**Ascending ramus missing**	**%**	**Inferior border broken**	**%**
ES/D2	**175**	0	*0*	10	*5.7*	7	*4.0*	158	*90.3*
Combined Eles	**41**	1	*2.4*	3	*7.3*	3	*7.3*	34	*82.9*
ES	**8**	0	*0*	1	*12.5*	0	*0*	7	*87.5*

Table 5.4a: Breakage patterns of *Bathyergus hendeyi* mandibles from the LQSM

	Maxilla breakage	
Unit name	**Zygomatic missing (N)**	**%**
ES/D2	32	*100*
Combined Eles	9	*100*
ES	6	*100*

Table 5.4b: Breakage patterns of *Bathyergus hendeyi* maxillae from the LQSM

Key to unit names: ES/D2 = east stream/Dump 2 Combined Eles = combined elephant sites
ES = east stream

The vast majority of mole rat mandibles, over 82% in all the units in Table 5.4a, fall into the breakage category IBB, indicating that the morphology of the *B. hendeyi* mandible makes it particularly prone to this kind of damage. The mole rat maxillae from LBW showed considerable post-depositional breakage and only nine *B. hendeyi* maxillae remained attached to the opposing maxilla, all of these were missing the zygomatic bone. Five of these came from east stream/dump2 (ES/D2), two from east stream (ES), one from east stream/elephant site (ES/Eles) and one from an area called 'far east area/bed2'. In terms of Table 5.4b, these maxillae are counted as two maxillae falling into breakage category ZM.

Very few murid and mole rat premaxillae were recovered from the LQSM units. Six single murid premaxillae were recovered from the LQSM units. All of these had become detached from their neighbouring premaxilla, but had retained an *in situ* incisor. Three single *B. hendeyi* premaxillae were found in the LQSM units, and these too had all retained the incisor.

5.3.3 Cranial breakage of *Cryptomys broomi*

The morphology of the *B. hendeyi* mandibles and maxillae was different to that of the smaller mole rat, *C. broomi*, and is therefore shown separately. Thirteen *C. broomi* mandibles, two maxillae, and eleven isolated *C. broomi* molars were found in the LQSM units. Only three

maxillae were retrieved, two of which had remained attached to their partner, though the zygomatic bone was missing. Table 5.5 summarises the breakage patterns of the *C. broomi* mandibles and maxillae found in the LQSM units, although sample size is too small to draw any conclusions.

	Mandible breakage categories				Maxilla breakage categories
	Mandible complete (N)	Inferior border broken (N)	Ascending ramus broken (N)	Ascending ramus missing (N)	Zygomatic missing (N)
LQSM units	0	9	3	1	2

Table 5.5: Breakage patterns of *Cryptomys broomi* mandibles and maxillae from the LQSM

The above mandibles were found in the following LQSM units; east stream/Dump 2 (ES/D2), east stream/north end/elephant site (ES/NE/Eles), peat bed (PB), east stream/bed 2 (ES/bed2), south east face (SE face), east stream/bed 2/near elephant site (ES/bed2/near EleS) and east stream/elephant site (ES/Eles).

5.3.4 The taphonomy of the molars and incisors from the LQSM units

Various taphonomic features observed on micromammal incisors and molars were recorded, and Table 5.6 summarises the taphonomy of the teeth from *all* the LQSM units. Results for the murids and the two mole rat species are presented separately.

The category 'incisor dentine absent', which recorded incisors showing loss of the dentine, is not shown on Table 5.6. In the LQSM units four mole rat, and 2 murid, incisors showed this type of breakage. Both the murid incisors and one *B. hendeyi* incisor, came from the PB area, all the remaining mole rat incisors are from a small, LQSM unit called 'East stream/section 3 spit 4'. As Table 5.6 illustrates, a very low percentage of murid incisors and molars showed damage to the enamel and/or dentine. The murids and mole rats show a very similar taphonomic pattern, and differ only in that a higher percentage of *B. hendeyi* incisors show corrosion, and cracking of enamel and dentine.

	Indet. murid		*B. hendeyi*		*C. broomi*	
Taphonomy of the incisors (isolated and *in situ*)	**(N)**	**%**	**(N)**	**%**	**(N)**	**%**
Incisors showing cracking of enamel and/or dentine	6	*2.05*	18	*8.3*	1	*33.3*
Incisors showing damage to enamel and/or dentine	16	*5.48*	14	*6.5*	1	*33.3*
Incisors showing corrosion (isolated & *in situ*)	33	*11.30*	85	*39.4*	1	*33.3*
Incisors showing desquamation of dentine and/or enamel	3	*1.03*	15	*6.9*	0	*0.0*
Total number of isolated and *in situ* incisors	**292**		**216**		**3**	
Taphonomy of the molars (isolated & *in situ*)	**(N)**	**%**	**(N)**	**%**	**(N)**	**%**
Molars missing cusp/s	46	*3.2*	15	*1.6*	1	*2.7*
Molars showing chipping of enamel	15	*1.1*	23	*2.5*	0	*0.0*
Molars showing cracking of enamel and or dentine	35	*2.5*	157	*17.2*	11	*29.7*
Total number of isolated and *in situ* molars	**1424**		**911**		**37**	

Table 5.6: The taphonomy ofindeterminate murid, *B. hendeyi,* and *C. broomi* incisors and molars from the LQSM

5.4 Molar eruption patterns of *B. hendeyi* from the LQSM units

The results of the molar eruption patterns of the mole rat, *B. hendeyi,* are shown in Table 5.7. As this table indicates, the majority of *B. hendeyi* mandibles contained the PM_3 and M_1 (FE1-2), or the PM_3, M_1, and M_2.

Unit	FE PM_3, M_1	FE PM_3, M_1, M_2	FE PM_3, M_1, M_2, M_3	FE M_1, M_2, M_3	FE M_1, M_2,	FE PM_3	FE M_1	FE M_2,	FE M_3	PE M_1	PE M_2	PE M_3	RE M_2,	RE M_3
ES/D2	42	64	4	1	12	12	4			1	13	4	3	1
Unit ES/Eles and Unit ES/Eles/N Level	10	9	1		2	2	1				2		1	
ES/NE/Eles	4	5			1	1	1						1	
ES	2	4	1					1						
ES/bed2/Pig#1							2				1			
ES/HS	2	1									1			
ES/JPP		1												
ES/NE											1			
ES/NE/F.S.	2													
ES/SQ1			1			1					1	3		
ES/TP4	3	2												
FEA/bed2		2												
PB	1	1				1		1						
SAEW		1												
SE Face														1
SE/ES/WB		1												
Total (N=241)	**66**	**91**	**7**	**1**	**15**	**17**	**8**	**2**	**0**	**1**	**19**	**7**	**5**	**2**

Table 5.7: Molar eruption patterns of *B. hendeyi* mandibles from the LQSM

Key: FE = Fully erupted PE = partial eruption RE = recently erupted

Units names: east stream/Dump 2 = ES/D2
east stream/bed 2/pig #1 = ES/bed 2/pig#1
east stream/north end = ES/NE
east stream/Tex's pit 4 = ES/TP4
stream along east wall = SAEW
east stream/bed 2 = ES/bed2
east stream/north end/elephant site = ES/NE/Eles
east stream/hyaena site = ES/HS
east stream fish spine site = ES/F.S.
far east area/bed 2 = FEA/bed2
south east face = SE face
east stream/bed 2/near elephant site = ES/bed2/near EleS
east stream =ES
east stream/Jimmy's pig pit = ES/JPP
east stream/square 1 = ES/SQ1
peat bed = PB
south end/east stream/west bank = SE/ES/WB
south east face = SE face

5.5 The taphonomy of unit F10 and F11, MPPM (F)

This and the following sections, presents the results from a taphonomic study of the postcranial and cranial bones and teeth from the MPPM (F). Unit F10 and F11 show an essentially similar pattern in terms of post-depositional taphonomy, digestion, and cranial and postcranial breakage. In the following sections the results for these two units are shown both separately, and together, in order to demonstrate this similarity.

5.5.1 Murid incisor digestion

Almost all the incisors from MPPM (F) consisted of isolated incisors. This is the opposite scenario to that observed in the LQSM units, where the majority of the incisors were *in situ*, reflecting a lesser degree of mandible breakage. Only five mandibles in unit F10, and only three mandibles in unit F11, were found to have retained their incisors. This, as well as the fact that no premaxillae were found in Unit F10 and F11, indicates a relatively advanced degree of cranial breakage.

Table 5.8 and 5.9 show the total for each digestion class of all isolated and *in situ* murid and *B. hendeyi* maxillary and mandibular incisors in F10 and F11.

Unit name	Isolated and *in situ* mandibular and maxillary incisors Digestion classes												
	No visible digestion→light digestion→					moderate digestion→					extreme digestion		
Unit F10	**(N)**	**0**	**%**	**1**	**%**	**1a**	**%**	**2**	**%**	**3**	**%**	**4**	**%**
Maxilla incisors	**90**	52	*57. 8*	14	*15.6*	1	*1.1*	16	*17. 8*	6	*6. 7*	1	*1.1*
Mandible incisors	**74**	33	*44.6*	14	*18.9*	0	*0*	23	*31.1*	4	*5.4*	0	*0*
***In situ* incisors**	**5**	0	*0*	5	*100*	0	*0*	0	*0*	0	*0*	0	*0*
Unit F11	**(N)**	**0**	**%**	**1**	**%**	**1a**	**%**	**2**	**%**	**3**	**%**	**4**	**%**
Maxilla incisors	66	43	*65.2*	6	*9.1*	1	*1.5*	14	*21.2*	2	*3.0*	0	*0*
Mandible incisors	48	22	*45.8*	16	*33.3*	0	*0*	7	*14.6*	3	*6.3*	0	*0*
***In situ* incisors**	2	1	*50*	1	*50*	0	*0*	0	*0*	0	*0*	0	*0*
F10 & F11 combined:	**285**	**151**	***53.0***	**56**	***19.6***	**2**	***3.8***	**60**	***21.1***	**15**	***5.3***	**1**	***0.4***

Table 5.8: MPPM (F): Digestion on isolated and *in situ* mandibular and maxillary murid incisors

A detailed breakdown of the digestion of isolated incisors into the incisor breakage categories '>tip present', '< tip present, and '> shaft', for unit F10 and F11 may be seen in Appendix F.

5.5.2 *B. hendeyi* incisor digestion

No cranial remains from the small mole rat, *C. broomi*, were found in either F10 or F11. Due to small sample size, the digestion categories of isolated *B. hendeyi* incisors from F10 and F11 are shown together on Table 5.9. Only isolated incisors are shown as no mandibles and maxillae containing *in situ* incisors were found. A breakdown of the incisor etching patterns into the different breakage categories may be seen in Appendix G.

		Isolated mandibular and maxillary incisors Digestion classes											
		No visible digestion→		light digestion→		moderate digestion→					extreme digestion		
Unit name	(N)	0	%	1	%	1a	%	2	%	3	%	4	%
F11	10	5	*50*	1	*10*	0	*0*	4	*40*	0	*0*	0	*0*
F10	25	12	*48*	10	*40*	0	*0*	2	*8*	1	*4*	0	*0*
F10 & F11 combined:	**35**	**17**	***48.6***	**11**	***31.4***	**0**	***0***	**6**	***17.1***	**1**	***5.9***	**0**	***0***

Table 5.9: MPPM (F): Digestion on isolated mandibular and maxillary *B. hendeyi* incisors

5.5.3 Breakage patterns of murid and mole rat mandibles and maxillae

The breakage patterns of murid mandibles and maxillae are shown on Table 5.10a and 5.10b, and those of *B. hendeyi* on Table 5.11a and 5.11b. Only one breakage category is shown for the maxillae as all the murid maxillae from MPPM (F) were single maxillae with the zygomatic bone missing and thus fell into the breakage category 'ZM'.

	Mandible breakage								
Unit name	Total number of mandibles	Mandible complete (N)	%	Ascending ramus broken (N)	%	Ascending ramus missing (N)	%	Inferior border broken (N)	%
F10	34	0	*0*	0	*0*	11	*32.4*	23	*67.6*
F11	16	0	*0*	0	*0*	5	*31.3*	11	*68.8*

Table 5.10a: Breakage patterns of the murid mandibles and maxillae from the MPPM (F)

Maxilla breakage		
Unit name	Zygomatic missing (N)	%
F10	41	*100*
F11	31	*100*

Table 5.10b: Breakage patterns of the murid mandibles and maxillae from the MPPM (F)

Mandible breakage									
Unit name	Total number of mandibles	Mandible complete (N)	%	Ascending ramus broken (N)	%	Ascending ramus missing (N)	%	Inferior border broken (N)	%
F10	8	0	*0*	0	*0*	0	*0*	8	*100*
F11	2	0	*0*	0	*0*	0	*0*	2	*100*

Table 5.11a: Breakage patterns of the *B. hendeyi* mandibles from MPPM (F)

Maxilla breakage		
Unit name	ZM (N)	%
F10	2	*100*
F11	1	*100*

Table 5.11b: Breakage patterns of the *B. hendeyi* maxillae from MPPM (F)

Some 68% of the murid mandibles, and 100% of the *B. hendeyi* mandibles, fall into the breakage category IBB. The latter result is very similar to that obtained for the LQSM units, where over 82% of the mole rat mandibles showed IBB mandible breakage. A higher percentage of murid mandibles from the MPPM (F) fall into the IBB breakage category as compared to the 48-57 % seen in the LQSM units.

5.6 The taphonomy of the cranial bones from MPPM (F)

The taphonomy of the murid and *B. hendeyi* incisors and molars from the MPPM (F) may be seen on Table 5.12 and Table 5.13, respectively. These tables summarise the breakage on molars and incisors, as well as other taphonomic features such as desquamation, cracking, and physical damage to the enamel and/or dentine of murid incisors and molars.

Only two incisors from F10, and none from F11, showed loss of the dentine, a kind of damage frequently associated with weathering or mechanical damage. The percentage of incisors showing chipping and damage to the enamel and dentine is low, namely 3.9 %, for F10 and F11, combined. The molars show a similar picture, incidence of physical damage is low with only 9.1 % of the molars missing cusps. Cracking, which is likely to be associated with weathering, was not common on the enamel and dentine of incisors and molars, and some 2.4 % of the molars, and 8.4 % of the incisors showed this feature.

	F10	F11	F10 and F11 combined	
Taphonomy of the incisors (isolated and *in situ*)	**(N)**	**(N)**		**%**
Incisors showing cracking of enamel and/or dentine	14	10	24	8.4
Incisors showing damage to enamel and/or dentine	8	3	11	3.9
Incisors showing corrosion	127	64	191	67.0
Incisors showing desquamation of dentine and/or enamel	12	10	22	7.7
Total number of isolated and in situ incisors	**169**	**116**	**285**	
Taphonomy of the molars (isolated and *in situ*)				
Molars missing cusp/s	26	15	41	9.1
Molars showing chipping of enamel	9	4	13	2.9
Molars showing cracking of enamel and/or dentine	6	5	11	2.4
Total number of isolated and *in situ* molars	**301**	**152**	**453**	

Table 5.12: The taphonomy of the murid incisors and molars from Unit F11 and F10 (MPPM)

	F10	F11	F10 and F11 combined	
Taphonomy of the incisors (isolated and *in situ*)	**(N)**	**(N)**		**%**
Incisors showing cracking of enamel and/or dentine	5	0	5	11.6
Incisors showing damage to enamel and/or dentine	0	0	0	0
Incisors showing corrosion	17	6	23	53.5
Incisors showing desquamation of dentine and/or enamel	1	5	6	14.0
Total number of isolated incisors**	**27**	**16**	**43**	
Taphonomy of the molars (isolated and *in situ*)				
Molars missing cusp/s	5	0	5	4.8
Molars showing chipping of enamel	4	0	4	3.8
Molars showing cracking of enamel and or dentine	19	0	19	18.1
Total number of isolated molars (excluding fragments)	57	32	89	
Total number of in situ molars	14	2	16	
Total number of isolated and in situ molars	**71**	**34**	**105**	

Table 5.13: The taphonomy of *B. hendeyi* incisors and molars from unit F11 and F10 (MPPM)

**** No in situ incisors were found in the mole rat mandibles and maxillae from Unit F10 and F11**

The taphonomy of the mole rat molars and incisors is roughly similar to that of the murids, though a relatively higher percentage of murid incisors show corrosion, a feature also observed in the LQSM units. The incidence of mole rat molars showing cracking of enamel and/or dentine is slightly higher than observed in the murids, and more mole rat incisors show desquamation of incisor enamel and dentine. Incisor sample size is small for the mole rats, however, and this may have affected the results. The murid incisors indicate that corrosion is much less common in the LQSM units, where 11.3 % of the incisors show corrosion, as opposed to 53.5 % of the incisors from the MPPM (F).

5.7 Breakage patterns of the limb bones from MPPM (F)

Table 5.14 shows the breakage patterns of the limb bones of the various micromammal species. The NISP (Number of individual specimens) for the different micromammals is given. The various species are shown separately as Manthi (2002) found a difference between the cranial and postcranial breakage patterns of soricids and murids at the Saldanha Bay site of SBYC. Differences in the breakage or digestion patterns of different micromammal species have been noted by researchers in the past (Andrews 1990, Denys *et al.* 1996b, Matthews 1998, Saavedra and Simonetti 1998).

As Table 5.14 indicates, the humerus, femur, tibia and ulna tend to be the most commonly occurring limb bones for many of the micromammal species. The robust mole radii occur in high frequencies relative to the more delicate radii from other micromammal species.

Murid and mole limb bones were found in much higher frequencies than the soricid or mole rat limb bones. Of the two subterranean species, mole limb bones occur in far higher frequencies than that of the mole rats, indicating that moles were more common in the fossil assemblages. No mole mandibles or maxillae were recovered from the MPPM (F) excavations, although 27 golden mole earbones were recovered from F10, and 16 from F11.

F10	TC	TP	TD	TS		UC	UP	UD	US		RC	RP	RD		FP*	FC	FD	FS		HC	HP	HD	HS	
					NISP					*NISP*				*NISP*					*NISP*					*NISP*
Indet. murid	0	2	13	2	***17***	0	34	0	0	***34***	1	7	0	***8***	38	0	5	0	***43***	2	5	43	2	***52***
Soricid	0	1	1	0	***2***	0	0	0	0	***0***	0	0	0	***0***	0	0	0	0	***0***	2	0	6	0	***8***
Mole rat	0	1	6	0	***7***	0	1	0	0	***1***	0	0	0	***0***	11	0	0	0	***11***	0	0	9	0	***9***
Mole	0	0	0	0	***0***	0	29	0	0	***29***	9	5	0	***14***	14	2	0	0	***16***	4	3	17	1	***25***
Macroscelid	0	0	2	0	***2***	0	0	0	0	***0***	0	0	0	***0***	0	0	0	0	***0***	0	0	0	0	***0***
F11	**TC**	**TP**	**TD**	**TS**		**UC**	**UP**	**UD**	**US**		**RC**	**RP**	**RD**		**FP***	**FC**	**FD**	**FS**		**HC**	**HP**	**HD**	**HS**	
					NISP					*NISP*				*NISP*					*NISP*					*NISP*
Indet. murid	0	0	11	0	***11***	0	21	0	0	***21***	0	2	0	***2***	30	0	1	0	***31***	0	1	22	0	***23***
Soricid	0	0	3	0	***3***	0	0	0	0	***0***	0	0	0	***0***	1	0	0	0	***1***	2	0	13	0	***15***
Mole rat	0	0	2	0	***2***	0	0	0	0	***0***	0	0	0	***0***	5	1	0	0	***6***	2	1	1	0	***4***
Mole	2	0	0	3	***5***	2	13	0	0	***15***	8	11	0	***19***	12	0	0	0	***12***	6	3	23	0	***32***
Macroscelid	0	0	0	0	***0***	0	0	0	0	***0***	0	0	0	***0***	0	0	0	0	***0***	0	0	4	0	***4***

Table 5.14: The breakage patterns of the limb bones from MPPM (F)

Key: T = tibia, U = ulna, R= radius, F = femur, H = humerus,
C = complete, P = proximal, D = distal, S = shaft
NISP = number of individual specimens

*This category includes the breakage category f'emur head' (FH)

Soricid cranial material was not analysed, but the low percentage of shrew limb bones suggests that soricids were relatively scarce in the MPPM (F) units, as compared to the mole and murid species. The macroscelids are excluded from Figure 5.1 and 5.2 due to the extremely low number of macroscelid limb bones recovered. Figures 5.1 and 5.2 below illustrate the breakage patterns of the most common limb bones from MPPM (F), namely the tibia, ulna, femur and humerus. The percentages relating to the following two figures may be seen in Appendix H.

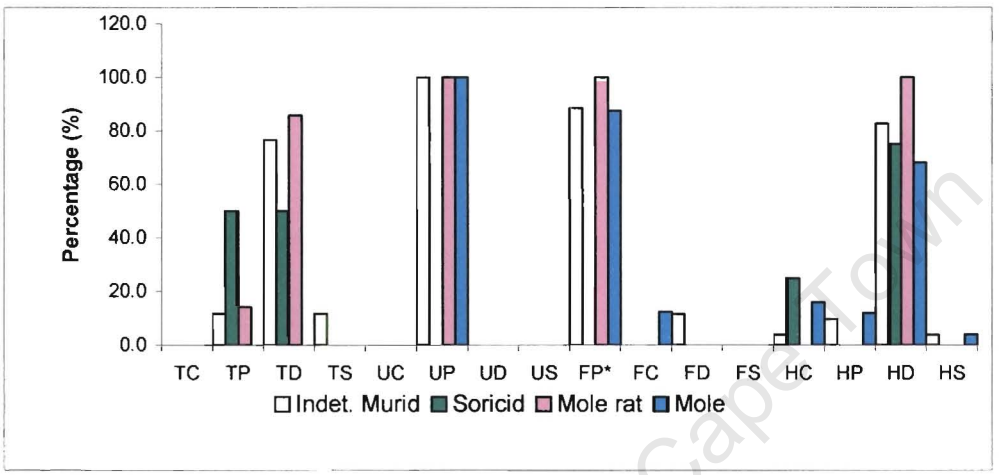


Figure 5.1: The breakage patterns of the tibia, ulna, femur and humerus from unit F10, MPPM (F)

Key: T = tibia, U = ulna, R= radius, F = femur, H = humerus,
C = complete, P = proximal, D = distal, S = shaft

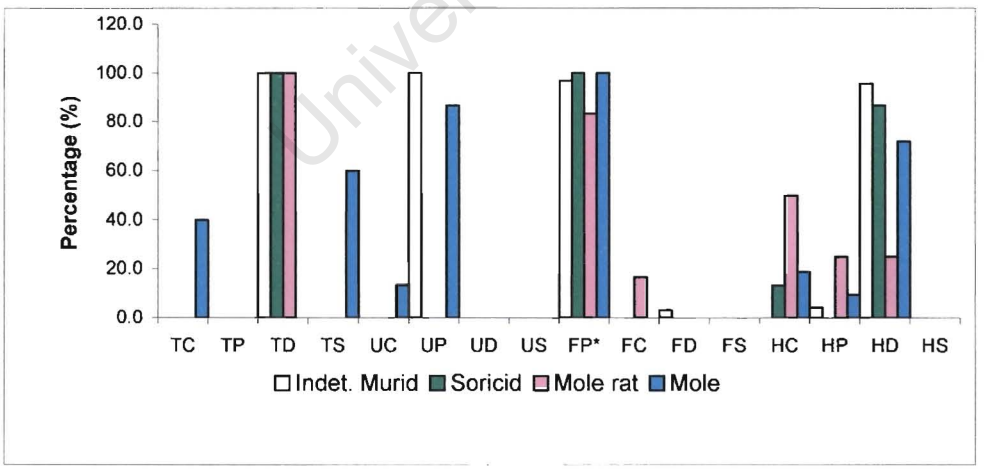


Figure 5.2: The breakage patterns of the tibia, ulna, femur and humerus from unit F11, MPPM (F)

5.8 The taphonomy of the limb bones from MPPM (F)

This section presents the results of the taphonomic study made on the femora and humeri from unit F10 and F11 (MPPM).

5.8.1 Damage to the epiphysis (DTE)

Of the 128 femora and humeri found in Unit F11, 49 (38.3 %) showed damage to the epiphyses. In Unit F10, 69 (41.3 %) out of 167 femora and humeri had sustained this damage.

	Femora and humeri showing damage to the epiphysis	
Species	**F11 (N)**	**F10 (N)**
Murid	19	36
Mole rat	3	10
Mole	23	18
Shrew	4	5
Total number of femora and humeri with DTE	**49**	**69**
Total number of femora and humeri in unit	**128**	**167**

Table 5.15: Damage to the epiphysis (DTE) of micromammal humeri and femora from unit F10 and F11, MPPM (F)

5.8.2 Rootmarks, rounding and burning on the postcranial bones

Rounding, such as is caused by the prolonged action of water, was not common in either F10 or F11, although it was somewhat more prevalent in F10, with 20.3 % of the femora and humeri, as opposed to 7 % (N=9) of the bones in F11, showing rounding.

In F11, one vertebra and one foot/paw bone were found showing evidence of burning. As burnt bones were a feature of the macrofauna, it seems appropriate to mention here that burning was also uncommon in the LQSM units as only one *E. pelomyoides* maxilla, and an incisor, showed evidence of burning.

Rootmarks were not found on any of the fossil material from the LQSM or MPPM (F), which adds to the body of evidence suggesting that they had not spent much of their depositional history close to the surface. In areas of cracking, or breakage, bones showed in-filling with sediment.

5.8.3 Desquamation

Table 5.16 shows the number of micromammal femora and humeri in the different desquamation categories.

Unit	Total number of femora and humeri in unit	Total percentage of femora and humeri with desquamation	Advanced desquamation		General desquamation		Localized desquamation	
	N	(%)	N	(%)	N	(%)	N	(%)
F10	164	32.9	7	4.26	30	18.29	17	10.36
F11	128	26.56	5	3.9	11	8.59	18	14.06

Table 5.16: Desquamation on micromammal femora and humeri in unit F10 and F11, MPPM (F)

The cause or causes of these different types of desquamation is unknown, and as Table 5.16 indicates, showed variability in the manner in which it was manifested in the two units.

5.8.4 Digestion

Unit	Total number of femora and humeri in unit	Digestion evident	%	? digestion evident	%
	N				
F10	164	49	*29.9*	33	*20.1*
F11	128	24	*18.8*	23	*18.0*

Table 5.17: Digestion on micromammal femora and humeri in unit F10 and F11, MPPM (F)

Table 5.17 presents the percentage of femora and humeri showing evidence of digestion. The presence of taphonomic features, such as abrasion, corrosion and desquamation, made it difficult to ascertain for certain if digestion had taken place on certain femora and humeri, these specimens are shown in the '? digestion evident' column.

5.8.5 Other taphonomic features

Only 1.71 % (N=5) of the femora and humeri from F11 and F10 displayed punctures or holes in the bone. An average of 3.7 % (N=10 in F10, and N=1 in F11) of the femora and humeri showed 'cracking and splitting', a type of damage usually associated with weathering. This indicates that the bones did not lie exposed for long periods on the ground surface.

Approximately 55 % of the femora and humeri from unit F10, and 77 % of the femora from unit F11, showed evidence of corrosion. This variability is not surprising, considering that the term 'corrosion' was used in a broad sense to describe more than one type of corrosion.

5.9 The skeletal element proportions of unit F10 and F11

The relative abundance of murid cranial and postcranial bones from Unit F10 and F11 MPPM (F) are shown on the following figures. A breakdown of the figures relating to Figure 5.3 may be seen in Appendix I.

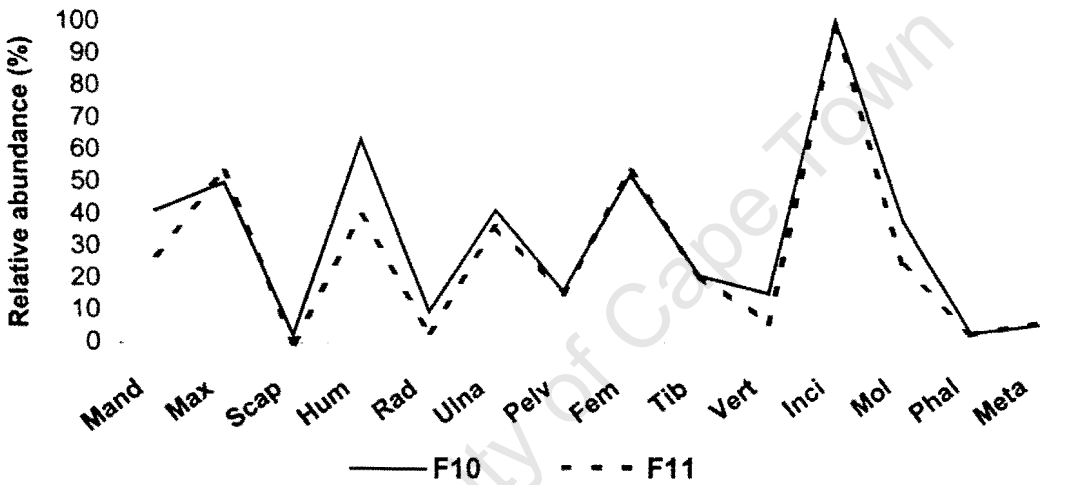


Figure 5.3: The relative abundance of the MPPM (F) assemblages

The general pattern of the skeletal element representation is very similar in F10 and-F11, though there is a relatively higher percentage of mandibles and humeri in F10. The incisor is the skeletal element occurring in the highest relative abundance in both units.

Chapter Six
Discussion: The taphonomy of the LQSM and MPPM (F) micromammals

6.1 Post-depositional corrosion at LBW

The taphonomy at LBW was very complex and it was extremely difficult, if not impossible, to separate out what appeared to be a palimpsest of physical and chemical events. It was impossible to ascertain with any certainty if differences in corrosion were caused by variation in the factor/s causing corrosion, by differences in the degree of corrosion, or, in the manner in which corrosion manifested itself. Post-depositional corrosion was observed in both the LQSM and the MPPM (F) units, although it was relatively more common in the latter.

6.2 The incisor digestion patterns of the LQSM and MPPM (F).

There are obvious problems associated with applying comparative taphonomic information about the patterns extant predators leave on the bones and teeth of their prey, to extinct predators. This is not considered to be an issue at LBW, however, as pin-pointing the identity of the actual predator(s) involved in the accumulation of the micromammals is clearly impossible, given the mixed nature of the fossil assemblages. The MPPM (F) micromammals were recovered from river channel deposits, while the LQSM micromammal assemblages accumulated both subaqueously and subaerially on a floodplain. The digestion on *in situ* and isolated micromammal incisors was used to give an indication of how many of the micromammals and mole rats had died as a result of predation, and to investigate the possibility that a range of different predator species had contributed to the fossil assemblages. The degree of etching provides information which may aid in distinguishing between different categories of predator, as defined by Andrews (1990). The results of the incisor digestion study of the LQSM and MPPM (F) are discussed separately, and are then compared.

6.2.1 Digestion on the murid and mole rat incisors from the LQSM

6.2.1.1 Murid digestion

The pattern of digestion shown by the murid incisors from the various LQSM units is fairly uniform, the unit PB excepted, with approximately 16-33 % of incisors falling into Class 0. Some 53.4 % of the incisors in the largest assemblage, ES/D2, show light etching and fall into digestion class '1' and approximately 74 % of the incisors from two other relatively large

assemblages, namely, the combined elephant sites and ES/SQ1, also fall into class 1. The percentage of incisors falling into class 2, which represents somewhat more advanced digestion, is similar in ES/D2, the combined elephant sites and ES/SQ1 and ranges from 5.7-8.8 %. The fact that the majority of incisors from the LQSM show light etching, indicates that these incisors have passed through the digestive tract of a predator. Incisors are absent or present in percentages of below 4 % in digestion classes 1a, or the more advanced digestion classes, class 3 and 4. PB is an exception, as the majority of incisors in this unit (72.7 %) show no sign of digestion, and 9.1 % of the incisors fall into class 1a and 3, however, sample size (n=11) is unsatisfactorily small.

6.2.1.2 Mole rat digestion

Small sample sizes hampers interpretation of many of the units containing mole rat incisors as ES/D2, the combined ES/bed2 sites, and combined elephant sites are the only units with a sample size of over 30 incisors. Some 46-55 % of the mole rat incisors in the three largest samples, namely ES/D2, the combined ES/bed2 sites, and the combined elephant sites show no signs of digestion, and 21-26% fall into class 1. The mole rat incisors show a similar pattern of digestion to the murids in that the great majority of incisors either show no, or light digestion, but the number of incisors showing no digestion is greater, whereas the majority of murid incisors show class 1 digestion. The mole rat incisors in the ES and Michael's pit assemblages show lower percentages of digestion, but sample size is too small to render this result reliable. Only 5 mole rat incisors in total, fell into class '3', and none are found in class 1a or class 4.

The contribution of predators causing advanced digestion of the incisors is minimal, if present at all, as only 6 murid incisors are found in class 3, and no murid incisor fall into class 4. The mole rats showed a similar pattern with five mole rat incisors falling into class 3, and none into class 4.

6.2.2 Digestion on the murid and mole rat incisors from the MPPM (F)

6.2.2.1 Murid digestion

Over half (53 %) of the isolated murid mandible and maxilla incisors from the two MPPM (F) units fell into etching class '0', and almost all the remainder were roughly divided between class 1 and 2, with 19.6 % of incisors in class 1, and 21 % in class 2. The more advanced digestion classes, class 3 and class 4, were represented by 5.3 % and 0.4 % respectively. Only 3.8 % of the incisors fell into class 1a.

6.2.2.2 Mole rat digestion

The sample size of the *B. hendeyi* incisors from Unit F10 and F11 (MPPM (F)) is rather small, and this hampers interpretation of the results. Slightly more mole rat incisors are found in class 1, but the basic pattern is very similar to the murids, with close to half the incisors showing no etching (48.6 %). The remaining incisors are divided between class 1 and 2, with 31.4 % falling into class 1, and 17.1 % into class 2.

A feature shared by both the mole rats and murids, is the fact that the contribution of predators causing advanced digestion of the incisors is minimal, if present at all, as only 15 murid incisors, and one mole rat incisor showed class 3 digestion, and only 1 murid incisor fell into class 4.

6.3 Interpreting digestion patterns at Langebaanweg

6.3.1 Murid digestion

Owls swallow their prey whole and the breakage and loss of prey bones and teeth is minimal when compared with predators such as diurnal birds of prey, or small carnivores, who dismember their prey, prior to eating. Of all the owl species investigated by Andrews (1990), barn owls caused the least breakage and alteration to bones and teeth, and only 8-13 % of the incisors from barn owl pellets showed digestion. A summary of the various predator categories as defined by Andrews (1990) may be seen in Appendix E. Interpreting the lack of digestion on around 16-33 % of the murid incisors from the LQSM, and 53 % of the incisors from the MPPM (F) units is difficult as these incisors could represent animals that had died from causes other than predation, such as disease, suffocation, aestivation or drowning. Death by drowning has been suggested as an explanation for the high numbers in which *B. hendeyi* is found at LBW (Hendey 1981a), and flooding and death by drowning was suggested as a possible cause of mortality of some of the large ungulates (Klein 1981, 1982). An alternative explanation for the incisors showing class '0' digestion is that they may have been eaten by a 'category 1' predator similar to the barn owl, which causes visible digestion on only a very low percentage of prey incisors. There may, of course, be other factors coming into play here which would be impossible to ascertain from the fossil record, for example, the beheading of prey prior to consumption by a predator. Simmons *et al.* (1991) who made a study of micromammal remains from the pellets of an African Marsh Harrier (*Circus ranivorus*), found that the medium sized prey species, *Rhabdomys,* was less likely to be found in pellet assemblages than larger species, as a small section of the *Rhabdomys* skull, including the jaw,

was often discarded prior to eating. The spotted eagle owl (*Bubo africanus*) routinely tears up prey items and beheads them before feeding young chicks (Steyn 1984). Certain small carnivore species may also discard the heads of prey items (Andrews 1990).

A similarity between the MPPM (F) and LQSM units is the fact that only two incisors from the former, and three from latter fell into digestion class 1a. Just over half of the incisors in the LQSM unit ES/D2, show light etching and fall into digestion class 1, as do approximately 74 % of the incisors from the two other relatively large LQSM assemblages, indicating that the majority of the these incisors have been accumulated by a predator/s. A much lower percentage of incisors fall into class 1 in the MPPM (F) units, namely 19.6 %, and the degree of digestion is slightly more intense in the MPPM (F) units. This more intense degree of digestion is reflected in the fact that around 21 % of the incisors show class 2 digestion, whereas an average of only 7.4 % of incisors from the three largest LQSM units fall into class 2. Also, 15 murid incisors from the MPPM (F) units fell into class three, while only 6 incisors out of the far larger incisor sample from the LQSM, fell into class 3. The presence of incisors showing more intense digestion need not necessarily indicate the contribution of a predator with strong digestion as pellet assemblages from the barn owl may contain a few incisors which show anomalously advanced digestion (pers. ob.). The fact that around a fifth (21 %) of the MPPM (F) units show class 2 digestion does, however, suggest that a predator/predators comparable with Andrews (1990) category 2, or possibly even category 3, predators may have contributed to the fossil micromammal assemblage. The range of digestion classes represented is suggestive of an assemblage to which a number of different category predators have contributed.

Some 50-70 % of the incisors from European and spotted eagle owl pellet assemblages showed digestion, and the degree of digestion described by Andrews (1990) is comparable to the class 3 digestion described in this thesis. In terms of Andrews (1990) results, it is possible to rule out the likelihood of predators similar to these two owls contributing significantly, to the LQSM assemblages, as the degree of observed incisor digestion is generally much lighter. Diurnal birds of prey investigated by Andrews (1990) showed extreme digestion on 60-100% of the incisors. Once again, the degree of digestion is far more advanced than that seen in the vast majority of incisors from the LQSM and MPPM (F), and it appears that once again, on the basis of the degree of etching, diurnal birds of prey have contributed little to the LBW micromammal assemblage.

Given the results of Andrews (1990) study of one felid species, comparative research done by the author on the micromammal assemblages from caracal (*Felis caracal*), jackal (*Canis mesomelas*) and serval scats (*Felis serval*), yielded unexpected results (Matthews 2002). Though 100 % of incisors showed digestion, the digestion classes the majority of the incisors fell into was much lighter than expected, namely classes 1 and 2 (Matthews 2002, Matthews in prep.). The presence of small carnivore coprolites in bed 3aN was noted (Hendey 1976). The contribution of small carnivores to the micromammal assemblages at LBW would therefore appear to have been likely, and cannot be ruled out on the basis of the etching patterns observed in the MPPM (F). Given the mixed nature of the assemblages, and the digestion patterns, it is likely that a number of different predators contributed to the LBW micromammal assemblages.

Teeth which had undergone extreme digestion would be more prone to disappearance from the fossil record. There is, however, no evidence to suggest that the lack of incisors showing heavy and extreme digestion may be due to these teeth being preferentially removed from the fossil record by taphonomic processes. The state of preservation at LBW is generally good, and the incidence of teeth showing advanced digestion uniformly low.

It could be argued that the lower percentage of incisors in the MPPM (F) units showing digestion, relative to those from the LQSM, could be related to the fact that these animals came from a river channel, and thus are more likely to represent animals that died from drowning. There is no way to prove or disprove this suggestion, however, as it is impossible to ascertain if the lack of digestion on incisors from the two members reflects death by predation by a category 1 predator, or natural causes.

6.3.2 Mole rat digestion

The percentage of mole rat digestion in the LQSM and the MPPM (F) units was similar, with close to half of the incisors from both assemblages showing no digestion, and the percentages of incisors in the other classes differing by 10 % or less. In the MPPM (F) units there are slightly more incisors in Class 1, while the LQSM units contain, on average, rather more class 2 incisors. Both assemblages contained a low percentage of class 3 incisors of approximately 5 %. The mole rat assemblages from the LQSM units thus show more similarity in terms of incisor digestion with the MPPM (F) murid and mole rat assemblages, rather than with the murid assemblages in the LQSM units.

B. *hendeyi* is much smaller than the extant *Bathyergus* species and could possibly have been on the menu of some of the predators that took the various murid species. The same reasoning may be applied to *C. broomi*, which was even smaller than *B. hendeyi*.

6.4 Breakage patterns of the mandibles and maxillae from the MPPM (F) and LQSM

6.4.1 Murid cranial breakage

The majority of the micromammals from the LQSM, and those from the MPPM (F), were recovered through the sieving of deposit and thus breakage during retrieval is not likely to be the main cause of any observed differences in cranial breakage between the two members. Also, where recent breakage had taken place, it usually took the form of the breaking off of small pieces of bone, rather than large portions.

Mandible breakage appears to have been somewhat more advanced in the MPPM (F) units as approximately 68% of the mandibles fell into the breakage category containing the most broken mandibles, namely those which had sustained damage to the inferior border (breakage category IBB). In the LQSM units the percentage of mandibles in this category was lower and ranged from 48-57%, in the units of satisfactory sample size. Relatively less breakage in the LQSM units is also indicated by the fact that no mandibles from the breakage category ARB ('ascending ramus broken') were found in the MPPM (F) units, while 16-21% of the mandibles from the LQSM units fell into ARB. No complete mandibles were recovered from either the LQSM or the MPPM (F). The number of mandibles showing ARM ('ascending ramus missing') damage was very similar in both members and approximately 32 % in the MPPM (F) units, and 27-32 % in the LQSM units fell into this category.

The murid maxillae from LBW suffered relatively heavy post-depositional breakage as is indicayed by the fact that all of the murid maxillae from both the MPPM (F) and LQSM fall into the breakage category 'zygomatic missing' (ZM), and have been separated from their opposing half.

A notable difference between the murid cranial bones in the MPPM (F) and LQSM units is that there are more maxillae than mandibles in the former (see Table 7.10, Chapter 7). All the LQSM units, with the exception of the small unit PB, showed a much higher number of mandibles, as opposed to maxillae. The mandible is more resistant to post-depositional breakage and damage than the maxilla, and the large numbers of maxillae relative to mandibles in both the MPPM (F) units is thus unusual. At the Atapuerca-Ibeas cave complex

in Spain, a shortage of mandibles and a large number of maxillae, led Fernandez-Jalvo (1995) to conclude that the assemblage was formed by medium-low energy transportation. Transportation could well have played a role in accumulating the greater number of maxillae, as compared with mandibles, in the MPPM (F) deposits which came from a river channel.

Given the fact that just over 50% of the murid incisors from the MPPM (F) show no etching, it is likely that a relatively large proportion of cranial bones in the MPPM (F) were deposited in a more or less complete state. The skeleton would not have suffered significant breakage prior to deposition if the animal were deposited by a category 1 predator similar to the barn owl, or if the animal died of natural causes other than predation. The lack of complete murid and mole rat mandibles and maxillae in the MPPM (F) units indicates that there has been sufficient post-depositional damage to exacerbate any predator-induced breakage, and to have obscured the initial, predator-related breakage patterns.

In all the LQSM units, PB excepted, the majority of incisors show light to moderate digestion, indicating that predator/s have been responsible for their accumulation. Post-depositional damage appears to have played a lesser role in the LQSM, as compared to the MPPM (F) units, as there is more evidence for predators playing a role in the accumulation of micromammals, yet the cranial bones show higher levels of completeness relative to those from the MPPM (F). In conclusion, cranial breakage indicates that post-depositional breakage has occurred in varying degrees in both the LQSM and MPPM (F) horizons, but has not been too destructive as large numbers of mandibles and maxillae have survived in the fossil record.

Recent research has indicated that prey morphology and size are likely to affect the breakage patterns of micromammal bones. Prey size has been demonstrated by Laudet *et al.* (2002) to affect the breakage and preservation of skeletal body parts, and multi-ejection of skeletal parts, rather than destruction by gastric juices, was found to affect skeletal element representation of bones and teeth. Manthi (2002) recorded different patterns and degrees of breakage in the soricid and murid species from the same assemblages at SBYC. Simmons *et al.* (1991), Denys *et al.* (1996b), Saavedra and Simonetti (1998), and Laudet and Hamdine (2001) have likewise all found evidence for the differential preservation of certain species within predator assemblages. The fact that some facets of predator behaviour may not be ascertained from studying a fossil assemblages needs to be remembered when interpreting patterns of cranial and postcranial breakage, and prey species abundance.

At LBW post depositional breakage appears to some extent to have acted as an equalising agent in terms of the breakage patterns, partially, or totally, erasing the predator-induced breakage patterns which may have existed. Certain of the micromammal species at Langebaanweg appear to show species-specific breakage patterns. This is best illustrated by the *B. hendeyi* mandibles from the LQSM, as the vast majority of *B. hendeyi* mandibles show the breakage pattern 'IBB'. The gerbillid mandibles appear to be relatively more resistant to damage as approximately half fell into the 'IBB' category, and of the remainder, approximately $^{2}/_{3}$ fell into the category 'ARM', and the other third, into 'ARB'. The differential survival and preservation of gerbillid skulls in owl pellet assemblages has been noted by Denys *et al.* (1996b), Laudet and Hamdine (2001) and Manthi (2002). Slightly over 60 % of the *Euryotomys pelomyoides* mandibles fell into the breakage category 'IBB'.

Another area in which research is urgently needed, is the effect that digestion may have on the teeth of different species. In a study of the digestion on the micromammals from a collection of serval (*Felis serval*) scats, the laminate teeth of the vlei rat, *Otomys irroratus*, were observed to show a lesser degree of etching than those of murids such as *Rhabdomys pumilio,* even though they had been ingested by the same animal (Matthews 2002).

6.4.2 Mole rat cranial breakage

All the mole rat maxillae from the LQSM and MPPM (F) were missing the zygomatic process. Some 221 out of a total 255 *B. hendeyi* mandibles found in the LQSM units show an IBB breakage pattern. In the MPPM (F) units 100 % of mandibles fell into the breakage category 'IBB', though sample size for the MPPM (F) units was unsatisfactory (N=10). The fact that the breakage patterns of the mole rat mandibles and maxillae show uniformity, while the pattern of digestion varies between units, and between the LQSM and MPPM (F), suggests that post-depositional breakage has altered the assemblages. The mandibles of the mole rats appear to have broken in areas of morphological weakness, producing a homogenous breakage pattern in the LQSM and MPPM (F) units.

6.5 The taphonomy of the molars and incisors from the MPPM (F) and LQSM

6.5.1 Corrosion

Corrosion has affected 67 % of the murid, and 53.5 % of the mole rat incisors from the MPPM (F) units. The mole rats have been rather less affected than the murids by corrosion. The opposite scenario is shown by the LQSM mole rats as 39.4 % of the mole rat incisors, as

opposed to 11.3 % of the murid incisors show corrosion. Corrosion has affected the LQSM units to a much lesser degree than those from the MPPM (F). Approximately 55 % of the femora and humeri from F10, and 77 % of these limb bones from F11 showed signs of corrosion, indicating that the cause, or causes, of the corrosion had acted differentially on the assemblages from the two units. The cause, or causes, of the corrosion at LBW is unknown and it is not possible to ascertain at which period in the taphonomic history of the fossils it occurred.

6.5.2 Cracking

The taphonomy of the mole rats did not differ noticeably from the other micromammals in the MPPM (F) with the exception that the teeth showed a higher percentage of cracking, with 11.6 % of the mole rat incisors, and 18.1 % of the molars, showing cracking. A similar pattern was observed with the mole rat teeth from the LQSM as the molars and incisors showed a higher percentage of cracking as compared to the murid teeth. The taphonomy of *C. broomi* cannot be assessed due to the small sample size of this species in the LQSM units, however, the high percentage of molars showing cracking (29.7 %) deserves some notice. It would appear that the molars of both mole rat species were relatively more prone to cracking than the murids in both the MPPM (F) and the LQSM. It is difficult to interpret the cause of the higher frequency of cracking in the mole rat teeth and this issue will be discussed further in this chapter.

6.5.3 Desquamation

The level of desquamation of enamel and dentine on the incisors of the MPPM (F) mole rats was also relatively higher (14 %), as opposed to that of the murids (7.7 %), but the small sample size of mole rat incisors (N=43) may have affected the results. Desquamation on LQSM murid and mole rat incisors was rare and 1.03 % of murid, and 6.9 % of *B. hendeyi* incisors showed this feature. There appeared to be no link between desquamation and corrosion in either the MPPM (F) or the LQSM.

It is impossible to say for certain if the type of corrosion or digestion called 'block etching' was caused by predator digestion, or some kind of corrosion. No such pattern has been observed on incisors from bird pellets, or the scats of small carnivores.

6.5.4 Physical damage

Murid and mole rat molars and incisors from the MPPM (F) show low percentages of physical damage, and this was also reflected in the postcranial bones as only 1.71 % (N=5) of the femora and humeri from F11 and F10 showed punctures or holes. Some 3.9 % of the murid incisors in the MPPM (F) units showed damage to the enamel and/or dentine, and 9.1 % of the murid molars had missing cusps. No mole rat incisors showing damage to the enamel and dentine were found, and only 3.8 % of the mole rat molars showed chipping of enamel and/or dentine.

In the LQSM only 4 mole rat, and 2 murid, incisors showed loss of the dentine. In the LQSM units, 5.5% of the murid incisors showed dentine and/or enamel damage, and 3.2 % of the molars showed damage to cusps. This is close to the low percentage of molar and incisor damage in the MPPM (F) units. The mole rats in the LQSM units show a similarly low percentage of damaged molars and incisors. These results indicate that the murid and bathyergid teeth from both the LQSM and MPPM show very little physical damage. Korth (1979) noted that the isolated molars from assemblages which have been transported by water frequently lack roots. This feature was very uncommon in the LQSM and MPPM (F) deposits, though damage to some of the roots on a tooth was common (pers. ob.). It would appear that the molars and incisors from the MPPM (F) showed more resistance to damage from transport than the femora and humeri, as an average of 39.5 % of these bones from unit F10 and F11 showed damage to the epiphyses as a result of transport.

6.6 *B. hendeyi* tooth eruption patterns

As mentioned previously, the vast majority of *B. hendeyi* mandibles show an 'IBB' breakage pattern. In ES/D2, the unit containing the largest assemblage of *B. hendeyi* mandibles, 41 of the 42 mandibles with a fully erupted PM^3 and M^1, and 59 of the 63 mandibles with a fully erupted PM_3, M_1 and M_2, fall into the 'IBB' breakage category. Damage to the distal end of the tooth row and loss of the M_3 made it impossible to assess the age of mole rat mandibles which had sustained such damage. The assemblages are thus biased against the identification of older mole rats. The number of mandibles containing incomplete tooth rows mean that, for the majority of mandibles, it is possible only to ascertain the minimum age of the individual involved. The majority of the mole rat mandibles from the LQSM units contained the PM_3 and the M_1, or the PM_3, M_1 and M_2.

Taylor *et al.* (1985) made a study of the molar eruption patterns of the mole rat *Georychus capensis*, the results of which are tabulated in Table 6.1. *G. capensis* is born with one tooth, the second tooth erupts at 3 weeks of age, and newly weaned juveniles have two teeth (Taylor *et al* 1985).

Class	Breeding status	Mean age	No. of teeth present
1	New born juvenile	-	1
2	Newly weaned juvenile	2.22 months	2
3	Older juvenile	4.04 months	3
4	Adult	12.21 months	4^{th} tooth just erupted or erupting
5	Adult	>20.43 months	4^{th} cheek tooth erupted and showing wear

Table 6.1: The molar eruption patterns of *G. capensis* (After Taylor *et al.* 1985, page 265)

The following demographic reconstruction is based on the tooth eruption patterns of *Georychus capensis*. Although *B. hendeyi* may well have shown a different pattern of tooth eruption, the study on *G. capensis* provides an approximate framework within which to reconstruct a mortality profile for the LBW mole rats. The breakage sustained by the mole rat mandibles makes it impossible to identify whether the mole rats represent attritional or catastrophic populations. They may well represent a mixture of both, as Korth and Evander (1986) have suggested that small mammal bones may accumulate attritionally along the flood plains of streams throughout the year. Periodic flooding may then introduce catastrophic small mammal death assemblages.

Only one mandible (eruption category PE M_2) of a very young individual of approximately 3 weeks of age was found, all other mandibles containing 2 ***in situ*** teeth contained fully erupted molars. Some 108 (44.8 %) of the mandibles had a fully erupted M_2 (see Table 5.7, Chapter 5) indicating that these animals were older than 4.04 months. Another 24 mandibles (9.95 %) show partial or recent eruption of the M_2 and are around 4.04 months of age. This indicates that approximately 54.8 % of the mole rats are at least as old as 4.04 months of age. Many of these mandibles possibly belonged to mole rats that had fully erupted M_3 and were older than 12 months, though breakage precludes their identification.

The last cheek tooth of *G. capensis* erupts when the animal is 9-10 months old (Taylor *et al* 1985) and nine (3.7 %) *B. hendeyi* individuals are around this age. Eight individuals had fully erupted M_3 molars and are older than 12.2 months. The eruption of the M_3 appears to be strongly correlated with the onset of reproductive maturity which occurs at 10 months (Taylor

et al 1985). Thus 7 % of the total mandibles are from individuals older than 9 months, who are reaching, or have reached, sexual maturity. The small number of mole rats falling into this category is undoubtedly due to the selection, caused by breakage, against identification of the older mole rats.

The lack of young mole rats of pre-weaning age suggests that for some reason, this age group was not exposed to predation, or whatever agent/agency caused the death of the older animals. Possibly very young mole rats remained in their burrows and were not taken by predators. Though the breakage of the mole rat mandibles makes it impossible to build up a complete mortality profile, there is sufficient evidence to refute the suggestion made by Hendey (1981a) that the main reason for mole rat mortality was drowning. If flooding had been responsible for the death of the mole rats at Langebaanweg, far more very young individuals should have been found (representing drowned pups) and the majority of incisors should have showed no digestion. Given the evidence from a study of mole rat incisor digestion, predation played a role in the accumulation of around half, and possibly more, of the mole rats in both the MPPM (F) and LQSM. Though drowning may be ruled out as the cause of death of the majority of mole rats, it is probable that water action played a part in the accumulation of some of the mole rats and murids in the LQSM.

6.7 The breakage patterns of the postcranial bones from the MPPM (F)

Both unit F10 and F11 show a selection for the more robust parts of the bones, namely the distal tibia, proximal ulna, and proximal femur and distal humerus. This selection of is a feature shared by murids, shrews, moles and mole rats, indicating a degree of similarity in their morphology. The other limb bones occurred in relatively low frequencies.

The small sample size of soricid and mole rat limb bones recovered from F10 and F11 makes the breakage patterns for these species difficult to interpret, and some of the differences seen between F10 and F11 may be attributed to small sample size. The sample size for F11 is in fact unsatisfactory for almost all limb bones as only the mole humeri are present in numbers greater than 30. The limb bone showing the highest level of completeness was the humeri, and interestingly, this feature was showed by almost all the species. There are very few complete murid and shrew limb bones.

The relative stockiness of the mole limb bones appears to give them an advantage in terms of resistance to breakage, as the mole is the species represented by the most complete bones.

The earbones of the golden moles are all that remained of the cranial bones, indicating that the cranial bones are particularly prone to disappearance from the fossil record, when post-depositional breakage occurs. The robust radii of moles are well represented compared to the more delicate radii of the micromammals and shrews. The breakage patterns of the long bones indicate that post-depositional breakage has occurred, although, as suggested also by the degree of breakage of the cranial bones, this has not been too extensive.

6.8 The taphonomy of the humeri and femora from the MPPM (F)

A taphonomic study of the femora and humeri from unit F10 and F11 (MPPM) indicated that the bones have been though several taphonomic processes. The bones and teeth show various combinations of the following processes:

- Digestion by predators after ingestion
- Corrosion
- Breakage
- In-filling with sediment - Where there were cracks, or bones had experienced breakage, bones have become filled with sediment.
- Rounding from water action
- Abrasion

6.8.1 Damage to the epiphysis (DTE)

The humerus and femur were the bones used to assess the taphonomy of the bones from the MPPM (F). An average of 38 % of the 128 humeri and femora in F11, and 41.3 % of a total 167 humeri and femora in F10, showed damage to the epiphyses. These broken areas, which showed damage to the bone cortex and exposure of underlying cancellous bone, appeared to have experienced a degree of smoothing of these areas after they sustained damage. The shafts of long bones which had also sustained breakage showed no such rounding. This damage to the epiphyses is hard to assess as epiphyses appear to be much more prone to taphonomic alteration, digestion and to damage, than the shafts of the limb bones (pers. ob.). It is possible that some abrasion may have occurred prior to the deposition and transport of the bones in the river. If transport in the river was the cause of the damage, it does not appear to have been sustained enough to affect other, harder, parts of the bone. Approximately 60 % of the femora and humeri in unit F10 and F11 appear to have been deposited soon after

arriving in the river as these bones show no signs of damage to the epiphyses, or abrasion. The relatively low percentage of bones affected by abrasion, together with an assemblage which does not indicate a high degree of post-depositional breakage, suggests that the majority of bones in the assemblage were not subjected to high energy tumbling or transport over long distances.

6.8.2 Rounding

On average, 14.7 % (N=43) of the femora and humeri in MPPM (F) showed rounding. This suggests that the majority of most of the bones were buried relatively soon after ending up in the river, and were not subjected to prolonged water action. The water action in the MPPM river channel was obviously not strong or prolonged enough to result in advanced degrees of fragmentation, or rounding, of the bones.

6.8.3 Desquamation

The percentages of limb bones falling into the different desquamation categories differed, but the overall percentage of limb bones showing desquamation is similar with approximately 27-33 % of the femora and humeri showing this feature. The bones showing general desquamation may at one time have been buried in a corrosive, probably alkaline, environment. The sediment in which the bones were recovered from cannot have been corrosive, however, as preservation is far too good, and it would be difficult to explain why only some bones are affected. The bones that show localized desquamation may have been buried in such a way that they came into contact with a corrosion-inducing agent.

6.8.4 Digestion

The femora and humeri in F10 appear to show a somewhat higher incidence of digestion than those in F11, however, the relatively large number of femora and humeri falling into the '? digestion' category makes it hard to make an assessment of digestion of the two limb bones. At sites where post-depositional taphonomy is complicated, incisors provide a much clearer and more efficient way to assess predator digestion in a fossil assemblage. Digestion occurred on mole, mole rat and murid femora and humeri, and no species-specific patterns of digestion were observed.

6.8.5 Cracking and splitting, rootmarks and punctures

There was little evidence for weathering on the micromammals from the MPPM (F). In the MPPM (F) only 3.7 % of the femora and humeri showed the kind of cracking and splitting

associated with weathering, and only 2.4 % of the murid molars and 8.4 % of the incisors from the MPPM (F) showed cracking. Only two murid incisors from F10, and none from F11, showed loss of the dentine, a kind of damage frequently associated with weathering or mechanical damage.

6.9 Skeletal element proportions in unit F10 and F11 MPPM (F)

With the exception of the higher percentage of mandibles and humeri in F10, the general pattern of skeletal element representation in F10 and F11 is very similar and suggests a uniformity between skeletal element proportions in the two assemblages. Interpreting the pattern of skeletal element abundance is complicated by the fact that the initial predator-related patterning would have been altered by transport and post-depositional breakage. The more fragile parts of the skeleton, namely the scapula, pelvis, vertebra, phalanges and metapodials are all represented, although, as might be expected, they occur in lower frequencies than the more robust bones. Alluvial sorting does not appear to have had much effect on the overall relative abundance of skeletal elements. Experimental studies done on mouse bones indicated that the vertebrae and maxilla were the elements that showed the least resistance to water transport and were the first elements to be dispersed (Dodson 1973). The mandible was the element that showed the most resistance to transport (Dodson 1973). The maxilla in both MPPM (F) units is present in higher proportions than the mandibles, and all body parts are represented, including those which show the least resistance to water transport. The skeletal element abundance in both units suggests that the assemblages were not transported very far from their point of deposition. In fact, the MPPM (F) units show a skeletal element abundance very similar to that from the 'hominid sands' horizon at the west coast fossil site of Hoedjiespunt 1 (this issue is explored further in Chapter thirteen), which represents an accumulation in a closed environment.

A fair degree of cranial breakage is indicated by the fact that the element which occurs in the highest proportions in both units is the isolated incisors. The mandibles and maxillae are present in roughly the same percentages as the relatively robust femur in both F10 and F11, but are more abundant than the ulnae, and tibiae. This is unusual in that mandibles are generally found in high relative frequencies in the majority of scat and pellet assemblages investigated by Andrews (1990). Post-depositional breakage or some other taphonomic feature has probably reduced the number of mandibles, relative to the proportions of the original assemblage. The high number of isolated incisors is consistent with the relatively

low number of mandibles and maxillae in both unit F10 and F11. The low number of isolated molars, relative to incisors suggests, however, that there has been some selection against these teeth. The skeletal element abundance of the MPPM (F) assemblages supports the conclusion reached in previous sections, namely that the micromammals have not been transported over long distances. The skeletal proportions of the MPPM (F) units will be compared with other archaeological and palaeontological sites on the west coast in Chapter thirteen.

6.10 Identifying the agents of micromammal accumulation at Langebaanweg

6.10.1 Mole rat vs murid cranial breakage

The cause of the advanced degree of mole rat mandible breakage, relative to murid cranial breakage, in both the MPPM (F) and LQSM is uncertain. The differences in preservation are difficult to interpret as there are several explanations as to why this may have occurred. It seems unlikely that the size of the mole rat, *B. hendeyi,* somehow made them more prone to post-depositional damage than the murids, as they are not significantly larger than the larger species of murid found at Langebaanweg. It is possible that the morphology of the mole rat cranial bones makes them relatively more susceptible to post-depositional breakage than many of the murid species, but this seems unlikely as they appear to be relatively sturdy. If anything, the mandibles appear to be more, rather than less, robust than murid mandibles. The breakage of mole rat mandibles could be interpreted as indicating that the mole rats have a different taphonomic history to the murids. Other differences between the murid and mole rat assemblages include the fact that the LQSM mole rats showed a higher percentage of corrosion on incisors than the LQSM murids, and the mole rat molars and incisors from both the LQSM and MPPM (F) showed a higher frequency of cracking than was observed in the murid incisors. It is difficult to say if this represents differences in the taphonomic history of the murids and mole rats, or if mole rat dentine and enamel is simply more prone to cracking.

6.10.2 Predation and the Langebaanweg micromammals

Little is know quantitatively about the predation risk for mole rats. Mole rats generally live their lives within their burrow systems, although *Bathyergus* species may come above ground to feed on aerial vegetation and annuals, and will come up to investigate disturbances to the burrow system (De Graaff 1981). Movement above ground by mole rats may be associated with dispersal movements (Bigalke 1978). *Georychus capensis* may travel above ground to establish new burrows in different areas (Bennett and Faulkes 2000). A list of potential predators of extant mole rats includes snakes, owls, and mammalian carnivores such as the

viverrids, foxes, caracal, hyaena, serval and jackal (Kingdon 1974, De Graaff 1981). Mole snakes are sympatric with most of the African mole rats and appear to be able to detect freshly excavated soil (Bennett and Faulkes 2000). Long beaked birds such as the heron and storks have also been observed catching naked mole rats and the common mole rat (Bennett and Faulkes 2000).

The ancestors of many of the above-mentioned predators were present at LBW and are likely to have contributed to the fossil mole rat and micromammal assemblages in the LQSM and MPPM (F). Jackals are missing from the faunal assemblage at LBW, and it is thought that the civet represented the ecological vicariant of the jackal (Hendey 1981a). Small carnivore species at Langebaanweg cited as potential predators of the Langebaanweg micromammals are the Mustelids and Viverrids (Hendey 1978b). The Mustelids include the wolverine, *Plesiogulo monspessulanus,* which is found today only in the Arctic and sub-Arctic Regions, the otter, *Enhydriodon africanus* and the honey badger, *Mellivora benfield* (Hendey 1978b). A genet was identified from the LQSM and MPPM (F), as well as several species of mongoose (Hendey 1981a). The felids were represented by at least two species of sabre-toothed tiger, a false sabre-tooth, a wild-cat type felid and a couple of lynx-like species (Hendey 1981a). Five or more species of hyaena was found in the LQSM and MPPM (F) levels, and birds of prey were represented by at least five species from the Accipitridae and three species from the Strigiformes. As may be seen, there is no shortage of potential predators of the murids and mole rats living in the vicinity of LBW.

6.10.3 Mole rats and the fossil record at Langebaanweg

The high numbers of mole rats relative to murids is an unusual feature of the LBW fauna. High concentrations of mole rats in archaeological and palaeontological sites are usually associated with cave-dwelling carnivores or raptors, or human accumulators (Klein 1991). Bathyergids generally appear in very low proportions relative to murids in other fossil micromammal assemblages in the area (see the faunal lists from HDP1, EBC and STBKC in Appendices A, B and C).

The chrysochlorids are also very well represented at LBW (Hendey 1981a, 1982), indicating that, for some reason, subterranean rodents are present in relatively high proportions in the fossil assemblages. The most likely explanation for the relatively abundant subterranean species recovered from the MPPM (F) and LQSM horizons is likely to be taphonomic. The mole rats may have been more prone to becoming incorporated into the fossil record through

some aspect of their behaviour, for example, a preference for making their burrows in areas of sandy alluvium. Sand dunes along the west coast of the Cape Province are the preferred habitat of the extant *B. janetta* which shows a more diverse distribution than *B. suillus* and is found in more arid areas of the west coast (De Graaff 1981). *B. suillus* is generally limited to the soft sediments of tributaries, rivers, and dunes immediately alongside the coast (De Graaff 1981). Golden moles species prefer light soils such as sandy loam, sandy alluvium, or in the case of *Eremitalpa granti*, loose, dune sand (Andrews and Van Couvering 1975, Skinner and Smithers 1990). The fact that both the Bathyergidae and Chrysochloridae are found in unusually high proportions at LBW, as well as the fact that the extant species inhabit similar habitats, adds support to the argument that some feature of their behaviour led to the inclusion of subterranean species into the fossil assemblages. Death from drowning has been ruled out as the main cause of death of the mole rats at Langebaanweg, however, if *B. hendeyi*'s preferred habitat was areas of sandy alluvium, this species, as well as the chrysochlorids, would have had a good chance of ending up in alluvially accumulated deposits, and in floodplain sediments.

A study of mole rat incisor digestion indicated that predation played a role in the accumulation of around half, and possibly more, of the mole rats in both the MPPM (F) and LQSM. The problem of interpreting the history of incisors which show no visible signs of digestion, and may have been digested by a category 1 predator such as the barn owl, has been mentioned. The relatively fragmented state of the cranial bones of the mole rats as compared to the murids, suggests that they may have come from different areas, or assemblages, to the murids. It is also possible that predation, prior to deposition, caused the relatively advanced breakage found in the mole rat cranial material. The presence of a predator at LBW which specialised in mole rats is yet another possible explanation as to the number of mole rats found at LBW. It is difficult to link the advanced cranial breakage of the mole rats with predation, however, as incisor digestion patterns share many similarities with that of the murids, and there is no clear evidence to indicate that the murids and mole rats were taken by very different categories of predators. Until further evidence is obtained, the effect that predators have had on the LWB mole rat and murid assemblages remains unclear.

6.11 Conclusion

The MPPM (F) units are believed to come from a palaeo-river channel. The taphonomy of the incisors and molars, and the femora and humeri from the MPPM (F) show a decided lack

of evidence of weathering, suggesting that the micromammals were not exposed on the ground surface for any significant period of time during their depositional history. No polishing of bone surfaces, such as may occur when bones lie exposed on a sandy surface, was found, and the lack of rootmarks suggests that the bones did not lie in sediment close to the surface where plants were growing, but were buried deep below the surface.

Wesselman (1984) points out that as experimentation has shown that pellets and scats do not survive transport by water for long distances, it is likely that micromammal assemblages would be incorporated into the channel lag deposits a short distance downstream from where they were accumulated, possibly between 20 and 400 m of arriving in the stream. The same reasoning may be applied to the MPPM (F) assemblages, as prolonged transport in water over long distances is likely to have led to far more fragmentary micromammal assemblages, and a far higher percentage of water worn bones. There is little evidence for weathering in the MPPM (F) micromammals, and the bones seem to have become buried relatively soon after being deposited in the river channel, without being exposed to very high energy water transportation. Hendey (pers. comm. to P. Haarhof) suggested that the deposits to the sides of the phosphatic rock outcrop may have become inundated with water when the river expanded during the rainy season. The MPPM (F) assemblages may thus include the remains of animals that drowned, or whose remains were lying on the river banks, and became incorporated into the channel sediments during flooding. Such a scenario has in fact been proposed for the large ungulates, and their incorporation into the palaeonotolgical assemblages are thought be have occurred either when they died in the vicinity of the river and got washed in during times of flooding, or when they drowned in the actual river (Klein 1982). Death by drowning during flooding may well be an explanation for the lack of incisor digestion on at least some of the murid incisors.

The cause of breakage in the MPPM (F) units, which is greater than that generally observed in the LQSM units, is uncertain. Sediment movement or compaction may well have played a role in post-depositional breakage as the micrommammal bones and teeth were found cemented into the rock-like sediment, which had to be wet in order to soften it sufficiently to remove the bones.

The breakage patterns of the large mammal bones in the MPPM (F) site show some evidence of trampling (pers. comm. to P. Haarhof by K. Behrensmeyer.). Micromammal maxillae are quickly broken down when trampling occurs (Andrews 1990) and there is little evidence to

indicate that trampling played a significant role in the breakage of the micromammal bones in the MPPM (F) units. Firstly, the higher number of maxillae relative to mandibles suggests that post-depositional breakage was not too extensive, and secondly, the bones would have to have been exposed close to, or on, the surface if trampling were to affect them, and there is no evidence, such as weathering or rootmarks, to suggest that this exposure took place. Trampling may leave striations and puncture marks on small mammal remains (Fernandez-jalvo 1995), but this type of damage was rare on the micromammal bones. Denys *et al.* (1997) noted in taphonomic study of small mammals from six African and European fossil sites, that the most striking differences between open-air and cave sites was that the former contained far more bones showing evidence of trampling, weathering and rootmarks. The MPPM (F) and LQSM sediments contain a surprisingly low percentage of bones showing these features.

In conclusion, it appears that the micromammals from the MPPM (F) were transported over short distances in a medium-low or low energy environment. The generally low frequency of bones showing evidence of water-rounding, together with a lack of the degee of breakage associated with prolonged water transport, suggests that they were not exposed to extended periods in the water before being buried well below the ground's surface. The river does not appear to have flowed very strongly and may even have been a relatively ephemeral one. Compaction or movement of sediment may have caused post-depositional breakage of micromammal bones.

The LQSM units investigated in this thesis, with the exception of PB, are thought to represent a floodplain environment. Theoretically, therefore, the micromammal assemblages may have been exposed for some time on the surface, prior to burial, or may have become re-exposed at some period of their depositional history. The taphonomy on the micromammal and mole rat teeth indicates a minimum of weathering, however, and the micromammals appear to have been buried soon after deposition, and if they were ever re-exposed, this was not for a long enough period for weathering to take place. The micromammals also appear to have been buried relatively far below the surface as none of the bones show evidence of rootmarks. Trampling could be expected to have affected some of the micromammals if they had been exposed on the flood plain, however, cranial breakage levels are too low to indicate any significant damage through trampling. The cranial bones from the LQSM units show less cranial breakage than those from the MPPM (F), despite the fact that the recovery methods

used in their recovery were often potentially destructive. The ES/D2 micromammals for example, were recovered from deposits that had been transported by bulldozer and dumped close by Hendey's research station, prior to being water-sieved. Like the MPPM (F) assemblages, the LQSM units appear to have been buried relatively soon after deposition, and do not appear to have been exposed to prolonged or high energy alluvial transport, or any very destructive post-depositional forces.

The taphonomic features of the large mammals from the LQSM studied by Klein (1981, 1982) are noted in Chapter two. The attritional profiles of species such as *Mesembriportax acrae,* and *Ceratotherium praecox* from the LQSM suggest that these animals may have died from a variety of factors, and then, after disarticulation, removal and destruction by scavengers and other biological agents, were buried relatively closely to the area in which they died (Klein 1981, 1982). The large mammals from the LQSM were frequently represented by partly articulated skeletal parts, and abraded bones are rare, whereas in the MPPM, many of the bones show abrasion and few articulated bones were found (Hendey 1970a, Klein 1982). These traits are echoed to some extent in the micromammal cranial bones as they also show less post-depositional damage in the LQSM relative to the MPPM (F) assemblages, and the LQSM assemblages appear to have been buried relatively closely to the area in which the animials died, or in which they were deposited in scats or pellets. Some of the LQSM fossils may have been washed off the floodplain during the rainy season. If some of the LQSM micromammals were alluvially transported, the degree of breakage suggests that, like the MPPM (F) assemblages, transport must have taken place over a short distance, in a low energy environment. The taphonomic processes which affected the LQSM and MPPM (F) units are not thought to include re-working as Wesselman (1984) notes that it is unlikely that alluvially-accumulated micromammal assemblages would survive re-working and re-deposition. This reasoning may be applied to both the LQSM and MPPM (F) micromammal deposits, as neither member shows the degree of breakage and destruction of the assemblages that would, in all probability, be associated with re-working. The LQSM assemblages showed a relatively uniform taphonomic pattern and no particular unit showed evidence of relatively greater post-depositional alteration. The tiny bone fragments in the MPPM (F) deposits found in association with well preserved macrofaunal bones have, as mentioned previously, come from re-worked deposits, and have been reduced to unidentifiable fragments.

The taphonomic pattern shown by the LQSM is very similar to that seen in the MPPM (F), and though some small differences between the assemblages exist, for example, desquamation is somewhat higher in the MPPM (F) than in the LQSM, and more incisors in the LQSM units show signs of digestion, they show a very similar taphonomic pattern. It is hard to interpret this similarity of taphonomy, however, as different taphonomic histories may result in assemblages which have are similar in appearance. It is possible, however, that the taphonomic similarity may indicate that the micromammals from the two members were accumulated by comparable processes. These may have included a mixing of assemblages from the river channel and from the river banks during periods of flooding in low energy environments, quick burial of micromammals after deposition, and the mixing of assemblages from similar predators.

Alluvial transport may result in certain micromammalian species being preferentially destroyed, and this may increase the relative abundance of one species over another (Korth 1979). Such selection of species is not considered to be a problem at LBW as it appears that the micromammals from both the MPPM (F) and LQSM did not travel long distances prior to deposition.

Bones buried in wet environments frequently show manganese staining (Andrews 1990). This feature which was not observed on the LBW micromammals, which may indicate that after burial, their environment was a dry one. Very few burnt bones were found, and the micromammals in this study differ in this feature to that of the larger mammals, many of which showed signs of being burnt (Hendey 1981a, 1982).

In summary, the MPPM (F) and LQSM sediments share many similarities. None of the assemblages from either member show any significant evidence of re-working, or of lying on the ground's surface and being exposed to weathering for any length of time. The lack of rootmarks, and also the lack of evidence for trampling on the assemblages from both members suggest that the bones were buried well beneath the surface.

Post-depositional breakage appears to have affected the LQSM assemblages to a lesser extent than the MPPM (F) units. Given cranial and postcranial breakage patterns, and the pattern of skeletal element abundance, together with low frequencies of bones showing water related rounding, alluvial transport in the river channel of the MPPM (F) appears to have been gentle, and the micromammals appear to have been deposited relatively soon after entering the

channel. As mentioned previously, Hendey has suggested that some of the LQSM assemblages may have been subjected to alluvial transport during periods of flooding. If such transport took place, the degree of breakage and lack of water-related rounding in the LQSM assemblages suggests that the micromammals were not transported over long distances, or subjected to transport in a high energy situation. As in the MPPM (F) units, the lack of taphonomic features associated with weathering suggests that burial occurred soon after deposition, and the bones were not exposed on the ground's surface for any length of time in their depositional history.

A study of mole rat incisor digestion indicates that mole rat digestion in both members show a similar pattern with close to half of the incisors from the LQSM and the MPPM (F) units showing no digestion, and the percentages of incisors in the other classes differing by 10 % or less.

Approximately 18-33% of murid incisors in the LQSM units of satisfactory size, and just over half of the MPPM (F) incisors, show no signs of digestion. It is impossible to ascertain if the lack of digestion on murid incisors from the two members reflects death by natural causes, decapitation of prey, or predation by a category 1 predator as all these would produce assemblages in which the majority of incisors show no signs of digestion. Predation has clearly played a large part in the accumulation of the LQSM assemblages as 53.4 % show class 1 digestion. The difficulty of interpreting incisors which show no digestion makes a comparison between the role of predation in the LQSM and MPPM difficult. It is, however, possible to state that predation clearly played a large part in the accumulation of the LQSM units where roughly 65% of the incisors show signs of digestion. There is less clear evidence for predation in the MPPM (F) units where some 53% of the incisors from the MPPM (F) units show no signs of digestion. The *degree* of digestion, as indicated by murid incisors, is slightly more intense in the MPPM (F) units as compared to those from the LQSM, this is indicated by the fact that a higher percentage of the MPPM (F) incisors, show class 2 digestion. Around a fifth (21%) of the MPPM (F) units show class 2 digestion, as opposed to approximately 8 % in the LQSM units. The range of digestion classes represented, and the differences in the degree of digestion, suggests that a number of different predators may have contributed to the fossil assemblages. The majority of incisors from the LQSM and MPPM assemblages appear to have been taken by category 1and/or category 2 predator(s), or died natural deaths.

Chapter seven
The taxonomy of the Langebaanweg micromammals

This chapter introduces the various genera and species found at LBW, and places them within the context of the micromammal faunas from other palaeontological sites in Africa.

7.1 Previous research on the Rodentia from Langebaanweg, 'E' Quarry

The following section briefly summarises previous research done on the micromammals at LBW, and briefly discusses issues pertinent to these genera.

7.1.1 Family Muridae Subfamily: Murinae Genus: *Aethomys*

Two new species of *Aethomys* were recovered from the LQSM and MPPM during mining operations, and were identified and described by Denys (1990a, 1990b). These two species, *A. admanticola*, and *A. modernis*, represent the oldest *Aethomys* species found to date in Africa. The larger of the two species, *A. adamanticola*, is thought to represent an advanced, early Miocene stage of the species, and shows primitive characteristics which are reminiscent of *A. namaquensis* and *A. hindei*, though it looks different from other modern and fossil *Aethomys* species (Denys 1990a). *A. adamanticola* has many characteristics in common with *Dasymys*, which may indicate a close relationship between the two species. Representatives of the two genera suggest that they separated prior to 5 million years ago (Denys 1990a). *Dasymys* has not so far been recorded at LBW. To date, the earliest occurrence of *Dasmys* is in the Early/Middle Pliocene sites of Makapansgat, Nosib, and at Bolt's farm (*Dasmys bolti*) (De Graaff 1960, Denys 1999). Denys (1990b) has suggested that the extant *Dasymys* is not a direct descendant of any of the fossil forms.

A. modernis looks similar to the South African species of *Aethomys*, particularly *A. chrysophilus*, though the cingular cusps and crests are more strongly developed and are of a smaller size (Denys 1990a). It is unclear if this genus had a southern or eastern African origin, as there is no apparently close relationship between the Plio-Pleistocene *Aethomys* from East Africa (Denys 1990a).

7.1.2 Family Muridae Subfamily: Murinae Genus: *Euryotomys*

Pocock (1976, 1987) described the new murid species, *Euryotomys pelomyoides*, found at

Langebaanweg as being transitional between the Murinae and the Otomyinae. Pocock (1976) points out various cranial features of the Otomyinae which he interprets as linking them with *E. Pelomyoides.* and goes on to suggest that the Otomyinae are derived from the Muridae, and that their probable origin within this family can be linked to the genus *Pelomys.* This standpoint is supported by molecular data from Chevret *et al.* (1993), which points towards a close relationship between the Murinae and the Otomyinae. Cladistic analyses of craniodental data from the tribe Otomyinae have confirmed the monophyly of the Otomyinae, and have also suggested *Pelomys* (rather than *Arvicanthis*) as the sister species of the Otomyinae (Denys in press). Separation between the Arvicanthini and the Otomyinae may have occurred around 8-9 Ma (Senegas 2001), or 7 Ma (Chevret *et al.* 1993). Morphological evidence cited as linking *E. pelomyoides* with the Muridae is that in the M^1, the two posterior rows of cusps are not parallel and lean at an angle as seen in *Otomys* sp., but the angle of inclination of t6 and t9 is greater than that of the first row. This is a feature typical of standard murids and the dental proportions of *E. pelomyoides* are noted as being generally intermediate between the Otomyinae and the murids (Denys *et al.* 1987).

Senegas and Avery (1998) describe *Euryotomys bolti*, a new species of *Eurotomys*, found in the Waypoint 160 deposits from Bolt's Farm, which lies 3 km southwest of Sterkfontein. The Waypoint 160 deposits are, on the basis of the dental pattern of *E. bolti*, thought to be around 4-5 m.y (Senegas and Avery 1998). *E. pelomyoides* and *E. bolti* provide evidence for the murine origins of the Otomyinae, for which a southern African origin, and Early Pliocene radiation of the tribe of Otomyinae is proposed (Pocock 1976, Denys 1989, Senegas and Avery 1998, Senegas 2001). No fossil Otomyinae have been recorded from Plio-Pleistocene East African palaeontological sites, but the family is well-represented in contemporaneous South African sites (Denys 1989). The oldest *Otomys* species found in East Africa, is *O. petteri*, recovered from Olduvai Bed I, which is dated to 2-1.5 Ma (Denys 1989).

There are two schools of thought as to the relationship between *Euryotomys* and the Otomyinae. Senegas (2001) and Senegas and Avery (1998) suggest that *Euryotomys* is an ancestor of the Otomyinae, and that the isolation of *Euryotomys* in the more arid, western part of South Africa may have led to the development of *Parotomys*. Denys (1989) suggests, on the basis of morphological and biogeographical evidence, that *E. pelomyoides* is not an antecedent of the Otomyinae, but rather a murid which was undergoing an enlargement of its molars. Similarities between *E. pelomyoides* and *Saidomys afarensis*, a murid found in

Pliocene sites in Afghanistan and Ethiopia, may indicate that they share a common murid ancestor (Denys *et al.* 1987, Denys in press). Denys *et al.* (1987) suggest that geographic isolation led to the southern African development of *E. pelomyoides.*

If *Euryotomys* is not related to the Otomyinae, there is no representative of the family at Langebaanweg or Bolt's Farm. This would indicate a relatively rapid development of the Otomyinae between the time of deposition of the LBW sediments, and the first appearance of the genus at Makapansgat at 3.3 Ma, and at the Namibian sites of Nosib, Jägersquelle, and some of the other Otavi Mountain sites in Namibia at around ~3 Ma, (Senut *et al.* 1992, Denys 1999). These phylogenetic problems will hopefully be solved when further fossil sites dating to the Middle and Late Pliocene are found in southern Africa. For the purposes of discussion, from this point onwards, the Namibian, microfaunal bearing breccias found in several localities in the Otavi Mountains, will be referred to as the 'Otavi Mountain sites'.

7.1.3 Family Muridae Subfamily: Acomyinae Genus: *Acomys*

The presence of *Acomys mabele* at LBW is evidence that this genus was quite distinct by 5 million years ago (Denys 1992). Morphological and molecular phylogenies support the monophyly of the *spinosissimus* clade (Barome *et al.* 2001). *Acomys*, and also *Uranomys*, are unique among the Murinae for having a t3 cusp on the upper M3, instead of a t1 cusp (Denys *et al.* 1992). Denys *et al.* (1992) note that a phylogenetic analysis of *Acomys*, based on dental characteristics, suggests that *Acomys* and possibly *Uranomys*, could represent one of the early offshoots of the initial radiation of the Murinae. Karyological data agrees with this interpretation (Viégas-Péquignot *et al.* 1983). The analysis also suggests that *Acomys* is not a Cricetinae or a Dendromurinae. It is suggested that it would be irrelevant to present a phylogenetic tree with *Acomys* as a sister-group to other groups as it requires too many reversals in dental evolution (Denys *et al.* 1992). The hypothetical ancestor of *Acomys* remains unknown, both karyotypically, and palaeontologically, but probably occurred in Africa between 14 and 7 Ma (Chevret *et al.*1993, Denys *et. al.* 1994).

7.1.4 Family Muridae Subfamily: Dendromurinae Genus: *Dendromus*

The genus *Dendromus* makes its first appearance at Langebaanweg and is represented by two, new species, namely *D. averyi*, and *D. darti* (Denys 1994a). The smaller species, *Dendromus darti,* shows low-crowned molars with bunodont cusps and Denys (1994a) suggests that its closest relative is *D. melanotis* from the western Cape area. The lophodont *D. averyi* appears to be related to the extant *D. mesomelas* (Denys 1994a). When describing the new

Dendromus species from Langebaanweg, Denys (1994a) noted that the anteroconid of the M_1 exhibited a significant variability both in form, and in the attachment to the first lobe.

The abundance of *Dendromus* and *Mystromys* genera during the Plio-Pleistocene in southern Africa, and their absence in the rich faunal sites of Hadar and Omo, have led to the suggestion that their centre of origin is South Africa (Denys 1990b). *Dendromus* has been found at Jägersquelle, Nosib and a couple of the Otavi Mountain sites, in both Late Miocene and Plio-Pleistocene breccias (Senut *et al.* 1992, Pickford *et. al.* 1994). *Dendromus* has also been found in the Late Pliocene/Early Pleistocene Humpata Plateau breccias of Angola, and from similar aged breccias in north-western Botswana (Pickford *et. al.* 1994). Denys (1990b) notes that the *Dendromus* species found at Makapansgat may represent an intermediary stage of evolution between *D. averyi* and *D. mesomelas*. The *Dendromus sp.* from the Laetoli beds in Tanzania are much more evolved than *D. averyi* (Denys 1990b).

7.1.5 Family Muridae Subfamily: Gerbillinae Genus: *Desmodillus*

The gerbillid found at LBW is among one of the most commonly occurring species at the site and has been identified as belonging to the genus *Desmodillus* (Denys pers. comm.). Other fossil *Desmodillus* sp. have been found at the Early/Middle Pliocene fossil site of Jägersquelle in Namibia (Denys 1999), and in the Otavi Mountains at Aigamas2 (Senut *et al.* 1992).

The extant monospecific species belonging to *Desmodillus* is *D. auricularis* which is found today in the Namib and Kalahari SW Arid Regions, but not the Cape Region, which contains the genera *Tatera* and *Gerbillurus* (De Graaff 1981, Stuart and Stuart 2001). The gerbillid *Tatera afra* is today an endemic of the Cape Region. The genus *Tatera* is ubiquitous and is found at Kanapoi and Hadar, and in the Early to Middle Pliocene in the Upper Ndolanya beds, the Laetoli beds, Omo B, and Makapansgat. The genera *Gerbillurus* and *Tatera* were found at Jägersquelle and Nosib during the Early to Middle Pliocene and at several other of the Otavi Mountain sites in Namibia (Senut *et al.* 1992). *Gerbillurus* is also found at the Sterkfontein type site in the Late Pliocene/Early Pleistocene. The South African gerbillid species *Desmodillus* and *Gerbillurus* are very similar with respect to dental morphology, and both display a primitive horseshoe pattern of anteroconid which may indicate that they are related to the taterilline lineage (Pavlinov 1999).

7.1.6 Family Muridae Subfamily: Delanymyinae Genus: *Stenodontomys*

The Delanymyinae are represented at LBW by *Stenodontomys*. *S. saldanahae* has been

described from Langebaanweg and represents a relict Miocene lineage (Denys 1994b). As mentioned previously, this species appears in Late Miocene breccias from the Otavi mountains at Berg Aukas and Harasib 3a, and in the site of Nosib1, at around 3 Ma. (Senut *et al.* 1992, Pickford *et. al.* 1994). *Stenodontomys darti* was identified by Lavocat, at Makapansgat, Rodent corner *in situ*, Pink breccia collection (Pocock 1987, Denys 1994b). In terms of extant species, *Stenodontomys* shows the closest affinities with *Delanymys* (Denys pers. comm.). Certain characteristics such as the undivided anterocone and short posterior cingulum are some of the features which differentiate *Stenodontomys* from East African Miocene Cricetinae such as *Africricetodon* and *Notocricetodon* (Denys 1994b). Denys (1994b) notes that the existence of a mesoloph(-id) in *Stenodontomys* and *Delanymys*, and not in *Petromyscus*, suggests that the Petromyscinae do not form a natural group and could have their origins in Early Miocene cricetine lineages which are different to those of the Dendromurinae.

The extant *Delanymys brooksi* is a relict species currently found in marshy areas in Eastern Zaire and western Uganda where there is a variety of sedge and grass affiliated species. *Delanymys* is an active climber, and is a very small species, which allows it to exploit very thin stems, without competing with *Dendromus* (Kingdon 1974).

7.1.7 Family Muridae Subfamily: Mystromyinae Genus: *Mystromys*

A new species of *Mystromys*, *Mystromys pocockei*, was described from Langebaanweg (Denys 1991). *M. pocockei* was found in conjunction with a larger species, *M. hausleitneri*, which is also found at Makapansgat and Sterkfontein Valley (Avery 2000a). The presence of *M. hausleitneri* at Langebaanweg indicates that this species survived and flourished over a considerable period of time as it is found at Sterkfontein at 2.8 Ma (de Graaff 1960, Denys 1990b, Avery 2000b) where it dominates the fossil assemblages, together with *Palaeotomys gracilis* (de Graaff 1960). *M. hausleitneri* is also found at the younger Late Pliocene to Early Pleistocene sites of Kromdraai, and the Schurweberg deposits (De Graaff 1961, Denys 1991, Avery 2000a).

Denys (1991) places the new species, *Mystromys pocockei*, with the Cricetinae, but notes that this species shows several features which differentiate it from other representatives of the genus. *M. pocockei* and *Proodontomys cookei* have some characteristics in common, such as the undivided anterocone, which Denys (1991) suggests may be a primitive feature representing an ancestral stage for South African cricetines. Other primitive features shown

by *M. pocockei* include its smaller size, less alternated cusps, a less rectilinear longitudinal crest, and the undivided prelobe of the M_1. *M. pocockei* also has several features which may suggest a parental relationship of *Mystromys* with the Petromyscinae, though further molecular and anatomical research is needed to test this hypothesis (Denys 1991).

M. hausleitneri is noted as being very similar in morphology to the extant *M. albicaudatus*, and size was the only criterion which made it possible to differentiate the fossils from the Makapanagat Cave of Hearths from recent material (de Graaff 1960). Denys (1991) has shown an overlap in the size of the M_1 of *M. hausleitneri* and *M. albicaudatus*, and has noted that they form a chronocline. The validity of a subspecies, *M. hausleitneri barlowi,* found by Broom from Sterkfontein, has been questioned and is generally discounted (De Graaff 1960, Denys 1999). A dwarf species of *Mystromys* has been found at Makapansgat (in the Makapansgat rodent corner *in situ*, and the Makapansgat limework dumps) and is as yet undescribed, though it could prove to be the same as *M. pocockei* (Denys 1991). If so, this would make it contemporaneous with *Proodontomys* which would exclude a phyletic descendance hypothesis involving these two species (Denys 1991). *Mystromys albicaudatus* is the only living representative of the Mystromyinae, a family which was well-represented in South African fossil sites during Plio-Pleistocene times.

7.1.8 Family Bathyergidae Subfamily: Bathyerginae Genus: *Bathyergus*

The Bathyergidae may be divided into two Subfamilies: the Bathyerginae which have grooved upper incisors, and the Georychinae which contains the genera *Georychus* and *Cryptomys* which have smooth incisors (Skinner and Smithers 1990, Bennett and Faulkes 2000). The roots of the upper incisors lie above the molar teeth in the Bathyerginae but lie in the pterygoid region behind the molars in the Georychinae (De Graaff 1981, Skinner and Smithers 1990).

The genus *Bathyergus,* is the only one which exhibits enlarged foreclaws which are used for burrowing, the other genera utilise their incisors (Bigalke 1978). The extant *Bathyergus suillus* (Cape dune mole rat) is the largest of all the bathyergids and is the largest known completely subterranean rodent in the world (Skinner and Smithers 1990). Karotype analysis suggests that mole rats evolved in southern Africa (Nevo *et al.* 1985).

All three genera of mole rats have been found in Early Miocene fossil beds dating to around 25 million years ago in Namibia and East Africa (Bennett and Faulkes 2000). *Bathyergoides*,

the largest of the three fossil genera, is thought to be related to the Bathyergidae, while another of the fossil genera, *Proheliophobius* is similar to the extant *Heterocephalus* and *Heliophobius* (Bennett and Faulkes 2000). *Paracryptomys* was found in the Namibian desert in Early Miocene beds (Bennett and Faulkes 2000). *Heterocephalus* fossils have been found together with extinct bathyergid ancestors, which together with molecular data, suggests that *Heterocephalus* diverged from the family early on (Bennett and Faulkes 2000).

Mole rats are one of the most common rodent species found at LBW, and *Bathyergus hendeyi* and *Cryptomys broomi* are the two new bathyergid species described from LBW (Denys 1998). Langebaanweg provides vital information in that the presence of these two species indicates that the differentiation between *Cryptomys* and *Bathyergus* occurred before 5-4 Ma (Denys 1998). *Bathyergus hendeyi* may be a common ancestor of the extant Cape endemics *B. janetta* and *B. suillus,* though this must remain a theory until intermediate fossils are found. The fact that *Bathyergus* is found clearly differentiated from other bathyergids at LBW, supports an early differentiation of this genus which molecular trees suggest may have occurred around 12 Ma (Nevo *et al.* 1987, Denys 1998). *Bathyergus* cannot be directly related to a Miocene ancestor, however, as the fossil record between 5-12 Ma is incomplete (Denys 1998).

The most striking morphological trait of *C. broomi* are the low-crowned teeth of this species. The molar dimensions of *C. broomi* show a similar variation to that of modern *C. hottentotus* s.l. and *C. robertsi* from Kromdraai B and Sterkfontein sites. *C. broomi* is the earliest known representative of this genus and appears to be closely related to either *C. hottentotus* s. l. or *C. damarensis* (Denys 1998). The fossil *Gypsorychus* does not share common characteristics with *B. hendeyi* or *C. broomi,* clearly suggesting a differentiation before 5 Ma (Denys 1998). *Georychus* and *Bathyergus* appear to have differentiated fairly early on, on the basis of skull and dental morphology (Denys 1998). This is in accord with the molecular evidence (Nevo *et al.* 1987). An investigation of karotype differentiation in three genera and four currently accepted species of mole rat indicated that karotypically 2n = 54, is shared by all species except *C. h. damarensis*, and *B suillus*, and karyotypic evolution is distinct in both diploid numbers and karotype morphology (Nevo *et al.* 1985).

7.1.9 Family: Myoxidae Subfamily: Gliridae Genus: *Graphiurus*

An undescribed *Graphiurus* sp. was found at LBW (Pocock 1976, Hendey 1981a). Today, the genus *Graphiurus* is represented in southern Africa by four species, two of which (*G.*

murinus and *G. parvus*) are associated with woodland savanna and bush, and the other two (*G. platyops* and *G. ocularis*) with rocky areas (Skinner and Smithers 1990, Stuart and Stuart 2001). *G. ocularis* may also be found associated with trees (Stuart and Stuart 2001).

7.1.10 Family: Hystricidae Gen. and sp. not det.

Two porcupine species were recovered, one from the LQSM, and another from bed 3aS and 3aN (MPPM). These have not, as yet, been studied. The family Hystricidae consists of two sub-families, the Atherurinae (brush-tailed porcupines) and the Hystricinae (crested porcupines (De Graaff 1981, Skinner and Smithers 1990). The crested porcupine, *H. cristata,* is found in East Africa and northwards to the coast of the Mediterranean. *Hystrix africaeaustralis* (Cape porcupine) is the species found in the more southerly parts of the continent (Skinner and Smithers 1990). Three subspecies have been described, but are not accepted by Meester *et al.* (1986).

7.2 New additions to the murid faunal list at LBW

This section introduces the various genera which this study has added to the faunal list at LBW.

7.2.1 Family Muridae Subfamily: Murinae Genus: *Zelotomys*

Zelotomys has not previously been recorded at Langebaanweg, but three teeth belonging to these genera were identified in the LQSM and MPPM (F) units. PQL68488 (ES/D2, LQSM) showed features of *Zelotomys,* but slight damage to the M_1, makes this identification somewhat tentative. If it is indeed *Zelotomys*, it is a different species to the other *Zelotomys*-like molar, PQL68980 (F10, MPPM), which was notably larger and showed some morphological differences. PQL68980, an M_1, has been identified as '*Zelotomys*-like sp' as the general cusp physiology appeared similar to *Zelotomys*, though this tooth was shorter than those of extant *Zelotomys* sp. PQL 68906 (F10, MPPM), an M^1, was also identified as belonging to a *Zelotomys* sp.

Zelotomys aff woosnami appears in the Ngamiland fauna at 3 Ma (Pickford and Mein 1988), and a *Zelotomys sp.* is found at Jagergsquelle and Nosib1 (Senut *et. al.* 1992), indicating the early presence of this genus in the Namib/South West Arid Region. By the Late Pliocene/Early Pleistocene *Zelotomys* is relatively common in South African sites, and is also found at Humpata and in East Africa at Olduvai (Denys 1999). In South Africa, during the Middle Pleistocene, *Zelotomys* is found at Makapansgat in the Cave of Hearths, at

Sterkfontein in Horizons of 2-1.7 Ma, and in the Late Pleistocene, at Nelson Bay Cave (Avery 2000a, 2000b). The fossil evidence indicates that *Zelotomys* enjoyed a wide distribution and appears to have been relatively ubiquitous in the Late Pliocene/Early Pleistocene where it is found at Sterkfontein, Kromdraai, Humpata, and Olduvai (Denys 1999).

7.2.2 Family Muridae Subfamily: Murinae Genus: *Thallomys*

A *Thallomys* sp. was identified from an M^1 from the MPPM units (PQL 68912, F10, MPPM (F)). *Thallomys* is not found at Nosib or Jägersquelle, but is found at one of the other, younger, Otavi mountain sites, namely Aigamas 2, which is 2-1 Ma (Senut *et al.* 1992). In South Africa, *T.* cf. *paedulcus* occurs at the Cave of Hearths, and a *Thallomys sp.* was found at Kromdraai B (Denys 1990b). Three different species of *Thallomys* are described at Omo, namely *Thallomys jaegeri, Thallomys quadrilobatus*, and *Thallomys sp. indet.* (Wesselman 1984). *Thallomys laetolilensis* was described by Denys (1987b) from the Laetoli Beds, where it was the most abundant murid. *T. laetolilensis* shows certain primitive characteristics which have lead Denys (1987b) to suggest that the Laetoli form may be ancestral to *T. quadrilobatus*.

One species of extant *Thallomys*, namely *Thallomys paedulcus*, is recognised in Eastern and Southern Africa (Kingdon 1974, Denys 1987b). It is generally thought that these two populations are distinct, although their status, possibly that of sub-species, has not yet been established (Jaeger 1976, Denys 1987b). The southern African *Thallomys paedulcus* shares several primitive traits with the fossil *T. quadrilobatus* and *T. laetolilensis.* The East African *T. paedulcus* appears to be more derived in relation to the primitive Laetoli form (*T. laetolilensis*), and to show fewer primitive traits than fossil forms from Olduvai and the extant *T. paedulcus* in South Africa (Denys 1987b).

7.2.3 Family Muridae Subfamily: Murinae Genus: *Rhabdomys*

It is generally agreed that the Genus *Rhabdomys* currently contains only one species, R. *pumilio* (Avery 1998). This species has an extremely wide distribution and shows variability in size and proportions in the specimens from different areas of southern Africa (Avery 1998). *Rhabdomys* is currently a ubiquitous species and is found in the Somali-Masai, Zambezian, Highveld, Namib, Kalahari-SW Arid and Cape Regions, and is closely related to the *Lemiscomys-Pelomys-Arvicanthis* group on one hand, and the East African *Hybomys*, on the other (Misonne 1969). In terms of the Early-Middle Pliocene fossil sites, this species is found at LBW, Makapansgat, Nosib and Aigamas2 (Senut *et al.* 1992). Two species of *Rhabdomys,*

one large and one small, have also been recorded from the Otavi Mountain breccias listed as being Post-Miocene age by Pickford *et al.* (1994). There appear to be two, or possibly more, species of *Rhabdomys* at LBW, providing evidence of the early differentiation of this genus in South Africa. *Rhabdomys* was found at Kromdraai, Sterkfontein, and in early Pleistocene deposits at Swartkrans (Avery 1998). De Graaff (1960, 1961) adds Bolt's farm (this species was identified as *R.* cf. *pumilio)* and Taung to this list. *Rhabdomys* occurs in Pleistocene deposits at Olduvai, but has not been found in any older East African fossil sites (De Graaff 1960, 1961, Denys 1999). *Rhabdomys* is not found on the faunal list of microfaunal samples recovered from north-western Botswana which are Late Pliocene-Early Pleistocene in age (Pickford *et al.* 1994). There is, however, some evidence that a nocturnal predator accumulated the assemblage. Absence in the faunal assemblage may not, therefore, reflect absence in the region. In conclusion, the present fossil evidence suggests that *Rhabdomys* was represented by more than one species at approximately 5 Ma in Namibia in the Otavi mountain Breccias, and in South Africa at LBW. A single species, *R.* cf. *pumilio,* was recovered from Bolt's farm which, according to Senegas and Avery (1998), is close in age to LBW. The fossil evidence to date thus suggests a southern African derivation for this genus.

7.2.4 Indeterminate species from LBW

This section briefly lists the other murid species found at LBW which have been identified to genus only. Several new *Mus* and *Acomys*-like species were recorded on the spreadsheet under the description of '*Acomys* sp.', '*Mus* sp.', and in one case where the genus was uncertain, '*Mus* or *Acomys* sp.'. One of the *Acomys* species, represented by a single molar, was considerably larger than *A. mabele* and the other *Acomys* specimens, this specimen was recorded as '*Acomys* sp., large'. 7.5

7.3. The Insectivora from Langebaanweg

Shrew, elephant shrew, and golden mole bones and teeth are found in conjunction with the rodents in both the LQSM and MPPM and it is thus appropriate to mention them very briefly at this point. The shrews and golden moles have been included in the taphonomic analysis of the postcranial bones from the MPPM (F).

7.3.1 The Chrysochloridae (Golden moles)

Golden moles differ from true moles in that they have only four digits on their front feet while the latter have five (Skinner and Smithers 1990). There is a general lack of basic information

on the golden moles and golden mole species such as Visagie's golden mole (*Chrysochloris visagiei*) and Van Zyl's golden mole (*Cryptochloris zyli*), were identified by a single specimen each (Skinner and Smithers 1990). The golden moles show a marked evolutionary convergence with the other subterranean species such as the mole rats (Bigalke 1979).

All the golden moles are insectivorous but most will take earthworms (Skinner and Smithers 1990). Most golden moles prefer to live in light, sandy soils, as in the case of *Eremitalpa granti* which lives in light dune sand (Skinner and Smithers 1990). Very dry soils would be unsuitable for chryochlorids as they would lack soil fauna for the insectivores to feed on (Andrews and Van Couvering 1975). Soil types suitable for chrysochlorids could range from intermediate woodland to savanna soils (Andrews and Van Couvering 1975).

Speciation of the Chrysochloridae has taken place mainly in the southern parts of Africa, and this family is found today in non-forested areas of the South West Arid, South West Cape, and the Northern and Southern Savanna zones, in a wide diversity of habitats (Bigalke 1972). For example, *Eremitalpa granti* occupies areas which reach into the Namib desert while *Chrysospalax villosus* occupies areas of moist grassland (Bigalke 1972). Fossil Chrysochloridae found in Pleistocene deposits in southern Africa have undergone minimal morphological change since that time (Skinner and Smithers 1990).

The golden moles at Langebaanweg have not been studied in any detail and are merely recorded as *Chrysochloris* sp. (Hendey 1981a). They have been found in the LQSM and MPPM (beds 3aN and 3aS).

7.3.2 The Soricidae

Shrews are the most common species of insectivore in Africa and are presented in the southern African subregion by four genera and 15 species (Skinner and Smithers 1990). All shrews are capable of burrowing but these tunnels generally consist of short, blind escape tunnels running from the nest (Skinner and Smithers 1990). They are capable of climbing under certain circumstances but are generally terrestrial (Skinner and Smithers 1990). Shrews have a very high metabolic rate and feed throughout a 24 hour period.

All the African species of shrew belong to the subfamily Crocidurinae and are represented by the four genera; *Myosorex*, *Sylvisorex*, *Suncus* and *Crocidura*. Three species of *Myosorex* have been found in the subregion, these are *M. varius*, *M. cafer* and *M. longicaudatus* (Skinner and Smithers 1990). Extant members of the genus *Myosorex* have fossorial

adaptations and are generally confined to moister areas in forests, or near rivers and streams (Skinner and Smithers 1990). *Sylvisorex* is restricted mainly to tropical Africa, but *Suncus* has a far wider distribution and is found in Eurasia and the Oriental Region (Skinner and Smithers 1990). *Crocidura* is the largest genus of African shrews and is represented in the subregion by eight species (Skinner and Smithers 1990).

Genetic differences between *M. varius, M. sclateri* and *M. cafer* are typical of well-differentiated species (Maddalena and Bronner 1992). Maximum parsimony and likelihood analyses of electrophoretic data suggest that *Myosorex* diverged from the Crocidurinae at nearly the same time as the Soricinae (Maddalena and Bronner 1992).

Much research is still needed into the taxonomy and biogeography of shrews. Hendey (1981a) lists an undescribed species of *Mysorex* and *Suncus* in the LQSM, and other, indeterminate species of shrew in both the LQSM and MPPM (Beds 3aN and 3aS).

7.3.3 The Macroscelididae

Members of the Family Macroscelididae are found only in Africa (Skinner and Smithers 1990). As seen in the chrysochlorids, speciation has been most active in the southern part of the continent. These shrews eat insects and fill the role of predators and, despite some differences between the species, they are all rather similar (Bigalke 1972). Their body forms suggest that the Macroscelidae evolved in open areas, a view which is supported by their present distribution (Bigalke 1979). Only two of the present species occur in forests, the others are found in arid and savanna areas.

Early Oligocene beds in Egypt (~ 30-35 million Ma) and deposits in the Namib desert dated to 20-22 Ma were found to contain some of the earliest fossil elephant-shrew remains (Skinner and Smithers 1990). The Macroscelidae are represented at LBW by an undescribed species of *Elephantulus,* which was found in the LQSM and MPPM (Hendey 1981a).

7.4 The *Aethomys* species at Langebaanweg

Identifying *A. modernis* and *A. adamanticola* was not always easy as there was considerable morphological variation within both species, and many of the specimens consisted of isolated teeth. Accession number PQL69250 (F11, MPPM) contained a maxilla with an MU^1 which differed from other *A. adamanticola* specimens and has been called '*Aeth. adamanticola*-like' on the spreadsheet. This MU^1 looked like an *A. adamanticola* but differed in two respects.

Firstly, it had no anterior cingulum as described by Denys (1990a) for *A. adamanticola*, and secondly, it had a well-defined cingular crest on t8, whereas *A. adamanticola* is described as having a trace of a posterior cingulum.

PQL 68918 (F10, PPM) contained a maxilla with an MU^1 which has been recorded as '*Aethomys modernis*-like, pc present'. This molar showed all the features of the M^1 of an *A. modernis*, but had a large, round posterior cingulum, a feature not shown by *A. modernis*.

Several other *Aethomys* and *Rhabdomys*-like species were found and were identified to genus only as these species were for the most part, represented by only one, two or three molars. They were arbitrarily given names, such as *Aethomys* sp. 1, *Aethomys* sp. 2, *Aethomys* intermediate and so on, in order to differentiate between them. A brief description of the following *Aethomys* and *Rhabdomys* species is given in Appendix J, but the exact classification of the new, and as yet indeterminate *Aethomys*, *Rhabdomys* and other species, will have to be delayed until such time as larger samples of the fossil micromammal material from the excavation area becomes available. No attempt was made to match upper with lower molars due to the presence of what appears to be several new species, together with small sample sizes. The following *Aethomys* and *Rhabdomys* species were identified:

- *Aethomys* intermediate and *Aethomys* sp. 3 - identified from an M^1 molar
- *Aethomys* sp. 1 and *Aethomys* sp. 4 - identified from an M_1 molar
- *Rhabdomys* sp. 1, and *Rhabdomys sp.* 2, identified from an M_1 molar
- *Rhabdomys* intermediate identified from M^1 molars

Aethomys sp. 3' is the name arbitrarily given to describe an *Aethomys*-like sp. of which only 3 maxillae were found in Unit F10. These specimens were of particular interest as this species showed similarities to *A. adamanticola,* which showed features not seen in other fossil and modern *Aethomys* species.

The molars called 'small *Aethomys* or small *Rhabdomys*' probably come from more than one species of murid. These molars were markedly smaller than the other, larger species of *Rhabdomys* and *Aethomys*

7.4.1 Measurements of the upper and lower first molars of the *Aethomys* and *Rhabdomys* species at LBW

The length and breadth measurements made of all the *Aethomys* and *Rhabdomys* species

shown in the following figures may be found in Appendix K (M_1) and Appendix L (M^1). Sample size in Figure 7.1, Graph a, is too small to make any conclusive remarks, but there is clearly overlap in size of the various *Aethomys* and *Rhabdomys* species.

The small, and therefore unsatisfactory, sample sizes of the species appearing on the following figures are unsatisfactory, and render the following results provisional. The *A. adamanticola* specimen on the top right in Figure 9.1, Graph b is PQL68758 (Unit F10, MPPM). This was the only measurable *A. adamanticola* M_1 recovered from the MPPM (F) excavation site and this specimen is markedly bigger than the rest, which are all from the LQSM. This relatively large size was not seen in the *A. adamanticola* M^1's from Unit F10.

This suggests either that this molar is an unusually large *A. adamanticola*, or that the tooth came from another *Aethomys* species similar to *Adamanticola*, but larger. The anomalously small *A. adamanticola* M_1 seen on the bottom left of Figure 7.1, Graph b (PQL 68484 ES/Eles, LQSM) was a relatively worn tooth, and this may have affected the measurements, which are clearly smaller than other *A. adamanticola* specimens. Alternately the wear on the tooth may have also affected identification of the species, causing it to be mis-identified, although identification was double-checked.

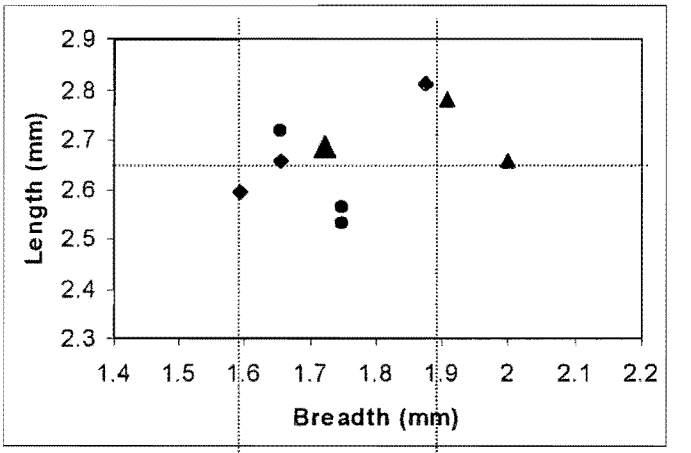
Figure 7.1, Graph c, indicates that *Aethomys modernis* molars are generally smaller than those of *A. adamanticola*, but there is some overlap in the length and breadth of the two species. Breadth, rather than length, appears to be the main feature separating *A. modernis* and *A. adamanticola*. The measurements of *A. modernis* from the LQSM and MPPM (F) were very similar and no size differences were observed.

Figure 7.2 illustrates the measurements made on the M^1 molars from the various *Aethomys* and *Rhabdomys* species. There is not a great deal of variation in the length and breadth of the M_1 of *A. modernis* specimens from the MPPM (F). The smallest *A. modernis* molar in the bottom left of the graph (PQL 68584,TP1, LQSM) is the only positively identified *A. modernis* M_1 recovered from the LQSM units. Interestingly, it is smaller than those from the MPPM (F), but sample size is too small to indicate if this is significant. Unfortunately no positively identified *A. modernis* M^1's were found in the LQSM units. It is possible that the specimens from the LQSM represent another subspecies, or even species.

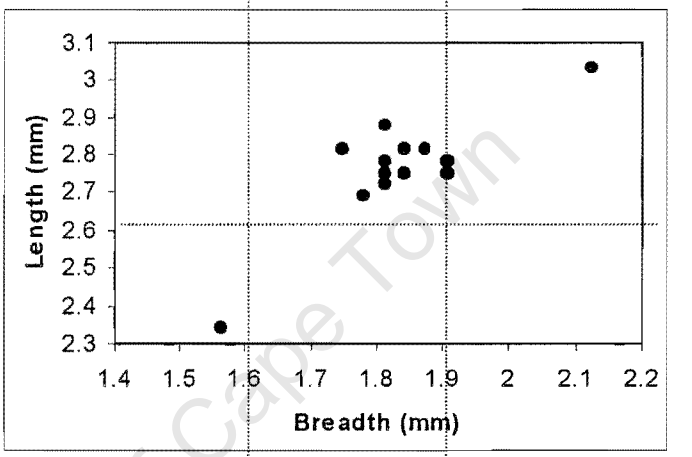
a) M_1 length and breadth measurements of *Aethomys* sp.1, *Aethomys* sp.4, *Rhabdomys* sp. 1 and *Rhabdomys* sp. 2

Key:

● = *Aethomys* sp. 4
◆ = *Aethomys* sp. 1
▲ = *Rhabdomys* sp. 1
▲ = *Rhabdomys* sp. 2



b) M_1 length and breadth measurements of *Aethomys adamanticola*



c) M_1 length and breadth measurements of *Aethomys modernis*

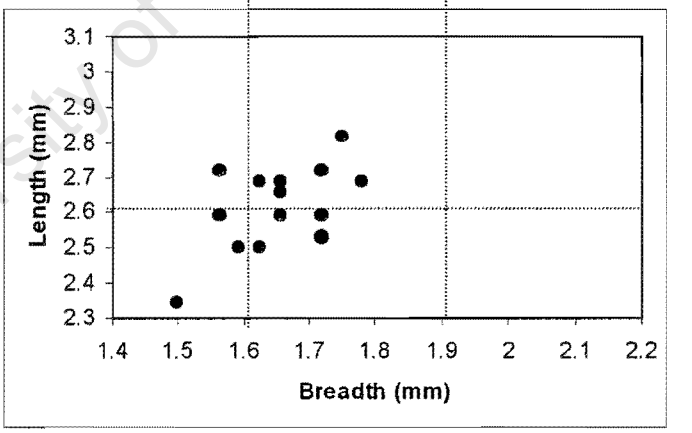
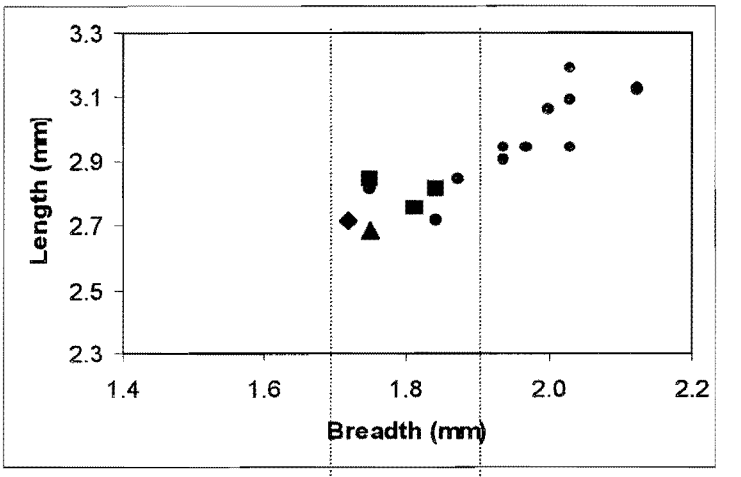


Figure 7.1: A comparison between the length and breadth of the M_1 of the *Aethomys* and *Rhabdomys* species from the MPPM (F) and LQSM units

M^1 length and breadth measurements of *Aethomys adamanticola* and *Aethomys modernis*
Key:

■ = *Aethomys modernis*
● = *Aethomys adamanticola*
◆ = *Aethomys modernis*-like, pc present
▲ = *Aethomys adamanticola*-like



M^1 length and breadth measurements of *Aethomys* and *Rhabdomys*
Key:

▲ = *Aethomys* intermediate
■ = *Aethomys* sp.3
● = *Rhabdomys* Intermediate

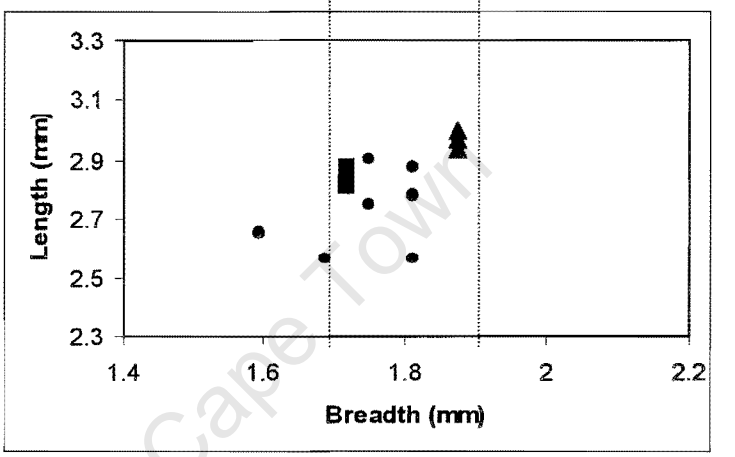


Figure 7.2: A comparison between the length and breadth of the M^1 of the *Aethomys* and *Rhabdomys* species from the MPPM (F) and LQSM units

Upper M^1 molars from *A. Adamanticola* were recovered in relatively high numbers compared with the other *Aethomys* species. There is no marked difference between the size of the *A. adamanticola* specimens from the LQSM and MPPM (F). *A. adamanticola* tends to be larger than *A. modernis*, though, as seen in the M_1's, there is some overlap in size between *A. adamanticola* and *A. modernis*. As may be seen in Fig. 7.2, Graph. 'd', the two molars *Aethomys modernis*-like PQL 68918 (F10, MPPM), and the *Aethomys adamanticola-like* PQL69250 (F11, PPM), are smaller than the other *A. modernis* and *A. adamanticola* molars. This adds support to the identification of these teeth as being different to *A. modernis* and *A. adamanticola.*

Size is clearly not a good indicator to use when separating out *Aethomys* intermediate, *Aethomys* sp. 3 and the other *Aethomys* species found at LBW as Figure 7.2, Graph 'd' and 'e', clearly show overlap in size between the various species. These species also overlap in terms of size with the various indeterminate *Rhabdomys* sp., though on average, the M^1's of the

Rhabdomys intermediate species appear to be smaller than *A. modernis* and the other *Aethomys* sp. The species called '*Aethomys* intermediate' appears to be closer to *A. adamanticola*, rather than *A. modernis*, in size, but this may be an artefact of the tiny sample size. De Graaff (1960) calls *Aethomys* a 'borderline genus", and the similarity of *Aethomys* to others of the Arvicanthis group frequently makes identification of fossil species difficult.

7.5 Molar length and breadth measurements of *Euryotomys pelomyoides*

The measurements relating to the M_1 of *E pelomyoides*, as illustrated by Figure 7.3, may be seen in Appendix M. The M_1 was the only tooth which showed a size difference between the MPPM (F) and LQSM, and a generally greater length in the molars from the MPPM (F) units was observed. The M^1 and M_2 were also measured but no discernible differences in size were observed.

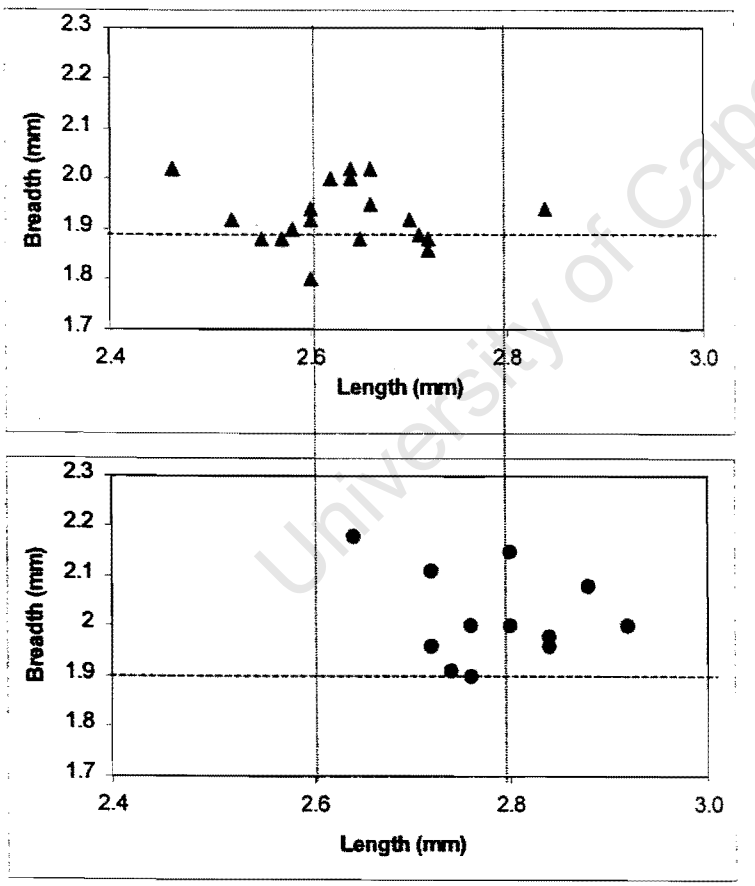


Figure 7.3: Variation in the length and breadth of the molars of *E. pelomyoides* (M_1)

Key: ▲ = LQSM specimens ● = MPPM (F) specimens

The reasons for the increase in molar size in the MPPM (F) units is unclear, but the difference is interesting as it suggests a difference between the LQSM and MPPM (F) in one of the parameters affecting tooth size of *Euryotomys*. The author measured teeth from the recent excavation area (MPPM (F)), and Christiane Denys measured specimens recovered from the MPPM during mining operations. Despite the fact that different samples from the MPPM were measured, both samples contained *E. pelomyoides* teeth of a relatively larger size to those from the LQSM units.

7.6 Summary: The rodent genera and species of Langebaanweg

Table 7.1 presents a list of the various rodents found at Langebaanweg. Species identified during previous research on the micromammals from the MPPM and LQSM are shown separately from the new species identified in this thesis. The term 'indet.' (indeterminate) following the genus name of the new species listed in Table 7.1 is used to indicate that these species were identified to genus only. The new, indeterminate species are noted as being identified from an upper or lower molar, or both. As may be see on Table 7.1, several new species have been identified in this study, but not yet formally described. The majority of these come from the MPPM (F). A detailed breakdown of the species identified in all the LQSM units, and in unit F10 and F11 of the MPPM (F), may be seen in Appendix N (LQSM) and Appendix O (MPPM (F)). The *Aethomys* and *Rhabdomys* species identified as yet only to genera in Table 7.1 may indicate quite profuse speciation of these genera. The enlargement of the sample, and a more detailed identification will clarify the extent of speciation of *Aethomys* and *Rhabdomys* at LBW.

Murid mandibles and maxillae which had retained the first molar were identified to species, as were isolated upper and lower first molars. There is good specific diversity at LBW in that the Dendromurinae are represented by two species, the Mystromyinae by two species, and *Aethomys* and *Rhabdomys* by what may be more than three species. In terms of genera, Langebaanweg shows a generic diversity very close to that of Omo B and C, and the Namibian sites of Jägersquelle and Nosib. The number of undescribed species in many of the East African fossil sites makes a direct comparison of specific diversity with LBW difficult, however, as noted in Chapter two, there is, on average a greater diversity of genera and species in South African sites (Denys 1996a).

Rodentia	LQSM	MPPM	MPPM (F)
Species identified by previous researchers			
Hystricidae			
Gen. and sp. not det. A (Hendey 1981a)	✓	X	X
Gen. and sp. not det. B (Hendey 1981a)	X	✓	X
Bathyergidae			
Cryptomys broomi (Denys 1998)	✓	✓**	X
Bathyergus hendeyi (Denys 1998)	✓	✓	✓
Myoxidae			
Graphiurus sp. (Hendey 1981a)	✓	✓	X
Gerbillidae			
Desmodillus sp. nov.	✓	✓	✓
Dendromurinae			
Dendromus averyi (Denys 1994a)	✓	✓	✓
Dendromus darti (Denys 1994a)	✓	✓	X
Delanymyinae			
Stenodontomys saldhanae (Denys 1994b)	✓	✓	✓
Mystromyinae			
Mystromys pocockei (Denys 1991)	✓	✓	✓
Mystromys hausleitneri (Denys 1991)	✓	✓	✓
? Otomyinae			
Euryotomys pelomyoides (Pocock 1976)	✓	✓	✓
Murinae			
Acomys mabele (Denys 1990c)	✓	✓	✓
Aethomys adamanticola (Denys 1990a)	✓	✓	✓
Aethomys modernis (Denys 1990a)	✓	✓	✓
New species indentified in this study			
Aethomys modernis -like, pc present (Indet.) M^1	X	-	✓
Aeth. adamanticola-like (Indet.) M^1	X	-	✓
Aethomys sp. 1 (Indet.) M_1	✓	-	✓
Aethomys sp. 3 (Indet.) M^1	X	-	✓
Aethomys sp. 4 (Indet.) M_1	X	-	✓
Aethomys intermed. (Indet.) M^1	X	-	✓
Rhabdomys Intermed. (Indet.) M^1	?	-	✓
Rhabdomys sp. 1 (Indet.) M_1	✓	-	X
Rhabdomys sp. 2 (Indet.) M_1	X	-	✓
Mus or *Acomys*-like sp. (Indet.) M^1 and M_1	#	-	#
Small *Aethomys* or small *Rhabdomys* (Indet.) M_1	#	-	#
Acomys sp. (large) (Indet.) M^1	✓	-	X
Thallomys sp. (Indet.) M^1	X	-	✓
Zelotomys-like sp. (Indet.) $M_{1,2}$	?	-	#
Zelotomys sp. (Indet.) M^1	X	-	✓

Table 7.1: The Rodentia at Langebaanweg from the LQSM and MPPM (F) (MPPM faunal list after Hendey 1981a, page 53)

Key: ✓ = species present X = species absent
= more than one indet. species is included in this category
? = identification of genus is uncertain
- = species not recorded in previous studies of MPPM material

The Gerbillinae are represented by an undescribed *Desmodillus* sp. at LBW, and there are approximately six murine genera. If LBW is compared with other Early-Middle Pliocene sites in East and South Africa, LBW shows a ratio of Murine to gerbillid genera which is similar to that of the fossil sites of Hadar and Omo B. The number of Murine genera from the Namibian sites of Jägersquelle and Nosib is slightly lower than LBW, and the number of gerbillid genera slightly higher. Five Murine genera were represented at Hadar, Jägersquelle, and Nosib, together with one, three and two gerbillid genera, respectively (Denys 1999). Five Murinae, and one gerbillid are found at Omo B, and five Murinae (no gerbillid) at Omo C. The Ngamiland caves yielded a large number of gerbillids and Pickford and Mein (1988) list four different species, and three different genera, found together with three Murine genera (Denys 1999).

In terms of the South African Early-Middle Pliocene fossil sites, one gerbillid genus is found at Makapansgat rodent corner *in situ* and at Makapansgat exit quarry red mud, together with eight Murine genera. Makapansgat limework dumps contains no gerbillid genera, but nine Murine genera are represented. As these figures indicate, there are more Murine genera represented at Makapansgat, than LBW, although both sites contain only one gerbillid.

Langebaanweg shows certain similarities in terms of generic and specific diversity with several other fossil sites, both in East and South Africa. The diversity of species and genera observed at LBW is likely to have been affected by a number of factors, including the depositional history of the various horizons, the taphonomy of the site, and many other issues, all of which are explored further in Chapter 8.

Chapter eight

The palaeoecology of the Langebaanweg micromammals

This chapter compares the micromammal assemblages from the LQSM and MPPM (F) and discusses how representative these may be considered to be of the micromammal population living at LBW during the period of deposition of these horizons. Various other taphonomic issues relating to the taxonomic mix of micromammal taxa found in both members are reviewed. The chapter concludes with a palaeolecological reconstruction of the LBW area, as suggested by the fossil micromammal population.

8.1 The effect of sample size on species diversity

Before presenting the results of a taxonomic study of the micromammals from LBW, it is important to say something about the effect that sample size may have on the diversity of a fossil assemblage. This issue is particularly relevant given the fact that many of the units from the LQSM contain very small samples.

It has long been accepted that the diversity and richness of a fossil sample are highly correlated with sample size (Cruz-Uribe 1988). In an extensive study of micromammal fossil-bearing sites throughout Africa, Denys (1999) found that the number of species and genera were dependant upon the MNI. Other micromammal researchers such as Manthi (2002) have also correlated a lower general diversity (*H*) with a relatively smaller sample size. A further discussion of generic and species diversity in the west coast fossil sites and owl-pellet assemblages may be seen in Chapter twelve.

The depositional history of the assemblages from the LQSM and MPPM (F), and in the case of the LQSM units, the manner of recovery, may have affected the taxonomic mix of species, and the species diversity, found in the various assemblages. These so-called 'assemblages' are assemblages only in the sense that they represent micromammals from the LQSM or MPPM (F) fossil horizons. Given their complex depositional and taphonomic histories, these assemblages may potentially have very little in common with the original micromammal accumulations from which they came.

8.1.1 Murid species diversity at LBW

Table 8.1 shows murid species richness for the LQSM and MPPM (F) units. The number of individual specimens (NISP) indicates the total number of M^1 and M_1 molars, both isolated and *in situ* in mandibles and maxillae. Murid species richness is calculated by counting the number of species represented by these molars, which are listed in Appendix P. Molars of uncertain identification are excluded from Table 8.1.

The specific diversity of F11 as shown by the M^1 and M_1 molars is actually 12, however, the identification of an M^3 from a gerbillid in Unit F11, and an M_1 in unit F10, indicated that this species was found in the MPPM (F) and species richness was therefore increased to 13. The number of species found in ES/D2, the combined elephant sites, and the MPPM (F) units F10 and F11, is an under-estimate as a small number of new, undescribed species have been put together under a general heading, such as 'small *Aethomys* or small *Rhabdomys* (Indet.)' (see Table 6.1, Chapter 6).

Unit	Species Richness	NISP
LQSM units		
ES/D2	~13	417
Combined Eles	~11	104
ES/SQ1	7	49
ES/TP1	7	27
PB	4	13
ES/TP4	3	5
Combined ES/bed2	3	3
ES	1	1
LQSM (all units combined)	~16	619
MPPM (F) units		
F10	~19	131
F11	13	66
Unit F10 and F11 combined	~20-22	197

Table 8.1: Murid species richness in the LQSM and MPPM (F)

Figure 8.1 illustrates the figures shown on Table 8.1, and plots murid species richness against the NISP. The number of species in unit F10 and F11 combined, namely ~22, has been calculated with the assumption that the M^1 and M_1 molars from the various *Aethomys* species each represent a different species. Due to the small number of specimens, no attempts have been made to match the upper and lower molars, and it is possible that one or more species

have been double-counted. M^1 molars were more common than the M_1, and if the more numerous M^1 molars are used to calculate the number of species, species richness in unit F10 and unit F11 combined decreases to ~20. Both points are shown in Figure 8.1.

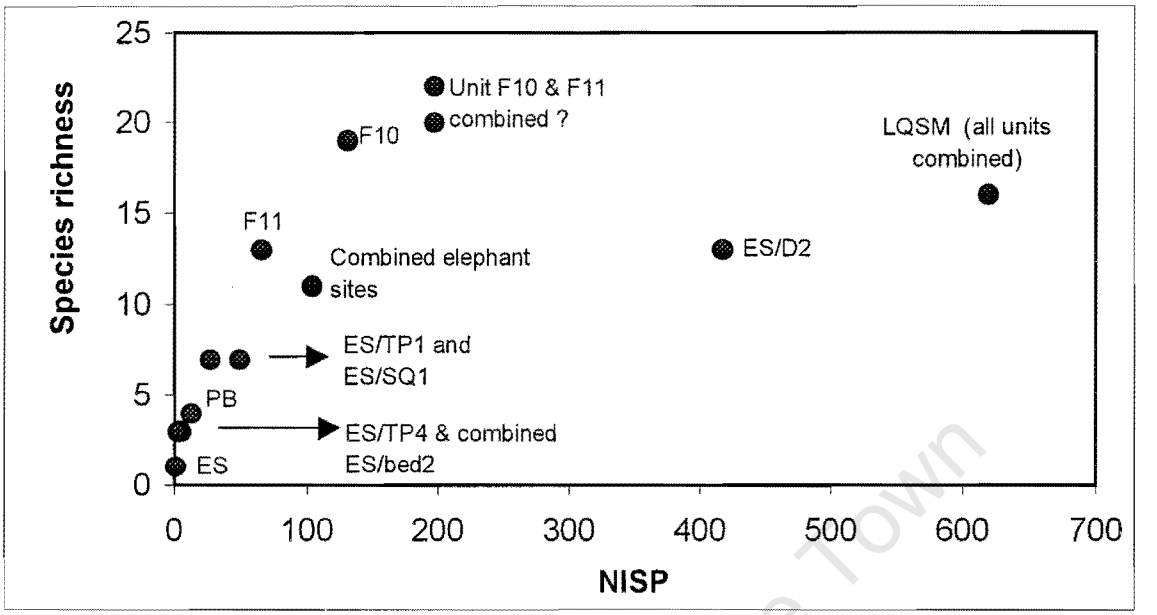


Figure 8.1: The relationship between richness and MNI in the LQSM and MPPM (F) units

ES/D2 represents micromammals recovered from a dump area and contains the largest micromammal assemblage of all the LQSM units. The relatively large sample size of ES/D2, as well as the fact that it was presumed to contain assemblages which came from a number of different areas, led to the expectation that ES/D2 would show a relatively greater richness than the other, smaller LQSM units, recovered from more discrete areas. Surprisingly, this unit does not show a substantially greater richness than the micromammals which came from the combined elephant sites, which represent a relatively small and discrete area at LBW. ES/D2 is distinguished from the other LQSM units in Figure 8.1 by the fact that the relatively large sample size has not resulted in a proportional increase in species richness. This suggests that the available pool of murids in the environment has been sampled. A similar scenario may be seen in ES/SQ1 and ES/TP1, where both units show a richness of seven species, though the former assemblage is almost two times larger than the latter. Combining all the LQSM units together (the point on Figure 8.1 labelled 'LQSM – all units combined') increases sample size, which, predictably, increases species richness. Given the effect that sample size usually has on richness, the MPPM (F) units show a distinctively greater species richness than the large micromammal sample from ES/D2, and indeed from all the LQSM units combined. The markedly higher species richness in the MPPM (F) relative to the

LQSM is clearly illustrated by the fact that Unit F11 (NISP = 66) contains the same variety of species as the considerably larger sample from ES/D2 (NISP = 417).

The relatively high richness of unit F10, as compared to unit F11, is another feature of the MPPM (F) assemblages that should be noted. The higher richness in the former unit cannot be completely explained by sample size and indicates considerable variability in species richness in two adjacent areas of the river channel. Many of the species found in the MPPM (F) assemblages are identified on the basis of one, two or three molars.

Table 8.2 shows the Shannon-Wiener index of diversity for the various units, this index takes into account the number of species and the evenness of their representation.

	L Q S M units							***M P P M (F) units***		
	ES/D2	**Combined elephant sites**	**ES/SQ1**	**PB**	**ES/TP1**	**ES/TP4**	**Combined ES/bed2**	**F10**	**F11**	**F10 and F11**
Shannon-Wiener index of diversity (*H*)	0.61	**0.78**	**0.69**	0.47	0.65	0.46	0.48	**0.78**	**0.71**	0.79

Table 8.2: Murid species diversity in the LQSM and MPPM (F) as indicated by the Shannon Wiener index of general diversity

Using the Shannon Wiener index to calculate diversity presents a somewhat different picture to when a simple count of the number of species is used. When diversity is quantified using this index, the combined elephant sites are seen to show the same diversity as the MPPM (F) unit, F10, and the diversity in F11 is seen to be relatively close to that of ES/SQ1. The units of unsatisfactorily small sample size, namely PB, ES/TP1, ES/TP4 and combined ES/bed2, show a generally low diversity. ES/D2 once again shows a diversity that is considerably lower than that of unit F10 and F11. If the Shannon-Wiener index is used, it becomes evident that the ES/D2 assemblage shows a lower general diversity than the combined elephant sites, and ES/SQ1, which come from more discrete areas. The Shannon-Wiener index thus serves to confirm a feature of the ES/D2 assemblage, namely that ES/D2 shows a surprisingly, relatively low diversity for an assemblage of large sample size which is thought to contain a mixture of assemblages from different areas. There are a number of possible explanations for this, and one of the most likely is that the methods used during recovery have affected species richness in this assemblage. As mentioned in Chapter 3, the dumps were bulk samples of

sediment which were removed from the mine by earth-moving machines and then sieved at leisure near Hendey's field camp. Hendey (pers. comm.) noted that micromammals are likely to be under-represented in the dump samples owing to the mesh size of the screens used, and the interests of the person(s) doing the screening, as the recovery of large mammal bones tended to be the main focus of sieving activities (Hendey pers. comm.). It would appear that the low diversity in ES/D2 may be an artefact of recovery. The fact that the combined elephant site units show the same diversity as unit F10 (MPPM) when the Shannon-Wiener index of diversity is used, suggests that assemblages with a high species diversity (that is, diversity as measured by the Shannon-Wiener Index) were found on the LQSM floodplain. It is perhaps significant that a higher species diversity is observed in the units which came from a relatively small, discrete area of excavation, where there may have been a more concerted effort to recover *all* the micromammals within an area. The lower diversity in terms of actual numbers of species in the LQSM units may be partially the result of recovery methods which were not geared to retrieve rare species represented by one or two molars or jawbones. All micromammal remains were retrieved from the MPPM (F) horizons, however, if sampling had been selective (as may have occurred in the case of many of the LQSM units) and only parts of the assemblage had been recovered, the species represented by one, two or three molars may well have been overlooked, and species richness would have been correspondingly lower.

The MPPM (F) units show a markedly greater diversity than all the LQSM units when a simple count of the number of species is used. When general diversity is calculated using the Shannon-Wiener index of diversity, certain similarities in diversity between some of the LQSM units, and F10 and F11, become evident. This discrepancy in results when using different methods to assess diversity occurs because, as mentioned above, the MPPM (F) units contain a number of species which are generally represented by only one, two or three molars (See Appendix P). The big difference in the actual number of species found in two $1m^2$ areas adjacent to each other in the recent excavation site indicates that variability within an area may greatly affect the results obtained from an excavation. It is sobering to consider the fact that if only the micromammals from unit F11 had been analysed, general species diversity would have been assumed to be similar to that of the LQSM units, and the Shannon-Wiener index would have suggested that diversity in the combined elephant sites was greater than that observed in F11. Other possible reasons for the differences in species richness between the MPPM (F) and LQSM assemblages will be discussed further in this chapter.

8.1.2 Murid species diversity in modern owl pellet assemblages from the west coast

Figure 8.2 below shows the relationship between diversity and MNI of modern owl pellet collections from the West Coast National Park (WCNP) and Steenbokfontein (Stbk) which were investigated by Avery (1992b, 1999).

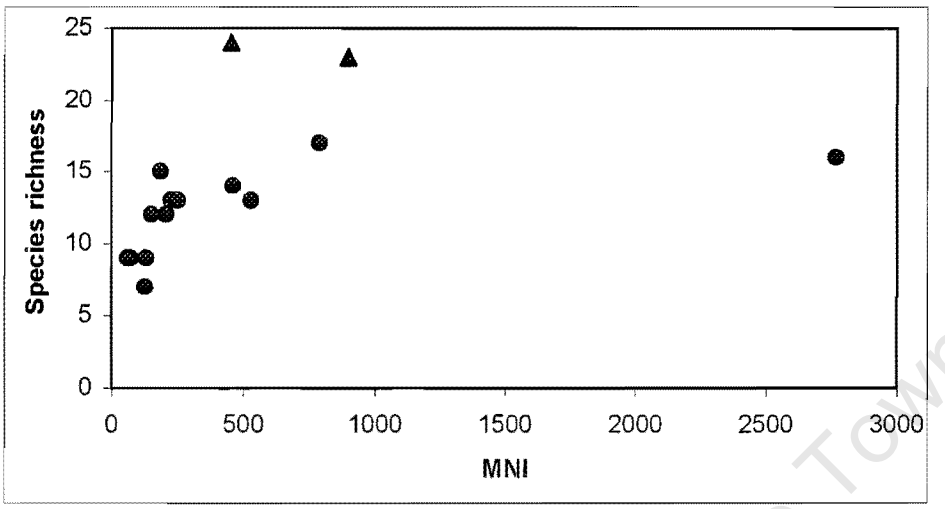


Figure 8.2: The relationship between diversity and MNI in the modern owl pellet collections from the West Coast National Park(WCNP) and Steenbokfontein (Stbk) (After Avery 1992b, Table 3, page 391 and Avery 1999, Table 4, Page 175

Key: ● = *West Coast National Park modern owl pellet collections*

▲ = *Steenbokfontein modern owl pellet collections*

The micromammal assemblages from the modern barn owl pellet collections are obviously very different to the fossil assemblages from LBW which have suffered all kinds of post-depositional alteration and breakage, however, the diversity of patterning observed in Figure 8.2 makes an interesting comparison. Figure 8.2 indicates the difference in diversity which may be observed between assemblages both from the same, and different, areas in the west coast. The Steenbokfontein owl pellet assemblages show a greater diversity than those from the West Coast National Park, indicating that the owls at Steenbokfontein prey on a wider range of species.

The West Coast National Park assemblages illustrate a relatively wide range of diversity which has resulted from pellet assemblages accumulated by the same type of predator (a barn owl), within an area which contains a number of microhabitats. Clearly the range of species diversity shown by one type of predator may vary widely within an area of a few km^2. The diversity shown by an assemblage which has been contributed to by a number of predators, possibly hunting in different areas, could be expected to vary even more. The point to the right of Figure 8.2 indicates an extremely large pellet collection which shows a diversity which

is greater than the majority of others, but which clearly represents a point at which an increase in sample size is unlikely to increase diversity as the majority of micromammal species living within the hunting range have been sampled. Given the range of species diversity shown by the above barn owl pellet assemblages, the spread of species diversity observed in the various units at LBW does not show any particularly striking or anomalous features.

8.2 Proportional representation of the murid and mole rat species at Langebaanweg in the MPPM (F) and LQSM

Figure 8.3 illustrates the percentage of gerbillid mandibles and maxillae present in the various LBW units, relative to those from the other murids, and the bathyergids. The numbers relating to this figure may be seen in Appendix Q.

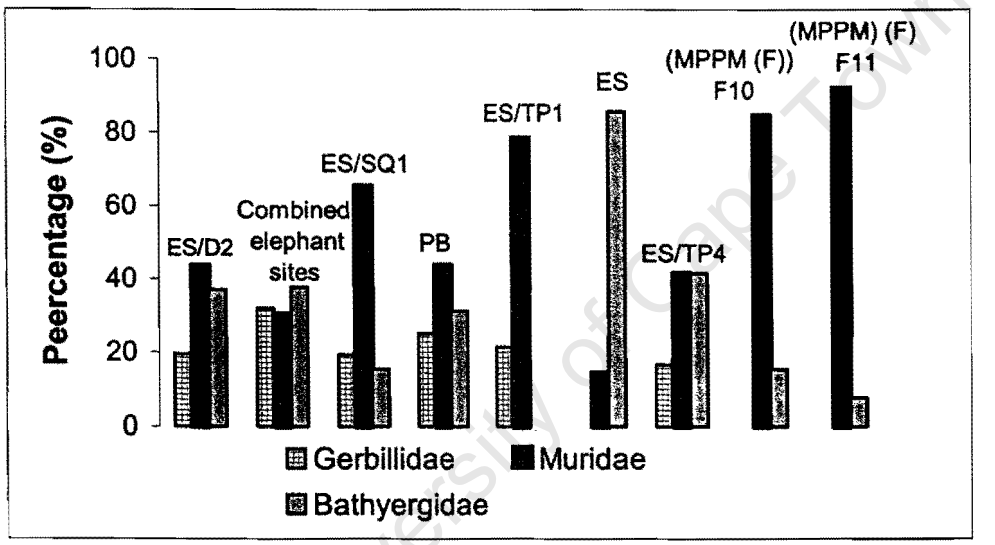


Figure 8.3: The percentage of gerbillids, murids and bathyergids in the LQSM vs the MPPM (f) units

As Figure 8.3 illustrates, the murids dominate all the LBW units, with the exception of ES and the combined elephant sites, which contain a higher percentage of bathyergids. The anomalously high percentage of bathyergids in the unit ES is due to small sample size. This unsatisfactorily sized unit, ES, is the only LQSM unit which does not contain any gerbillid mandibles and maxillae (as mentioned previously, only two isolated gerbillid molars were found in the MPPM (F) units).

The gerbillid species at LBW is found in percentages of 17-32 % in the LQSM units, relative to the various murid and bathyergid species. It is difficult to explain the small number of gerbillids found in the MPPM (F) units relative to the LQSM, as a number of different scenarios may have resulted in this pattern. This issue will be discussed further on in this chapter. The combined elephant sites, which come from a discrete area of the LQSM show a

relatively high percentage of bathyergids, suggesting that bathyergids were common in certain areas of the floodplain. It is interesting to note that bathyergids occur in similar percentages in ES/D2 and the elephant site, even though the former is thought to contain 'mixed' assemblages from several different areas. The gerbillids and bathyergids occur in high percentages relative to the murids, considering that these families are represented by one species in the case of former, and mainly by *B. hendeyi* in the case of the bathygergids.

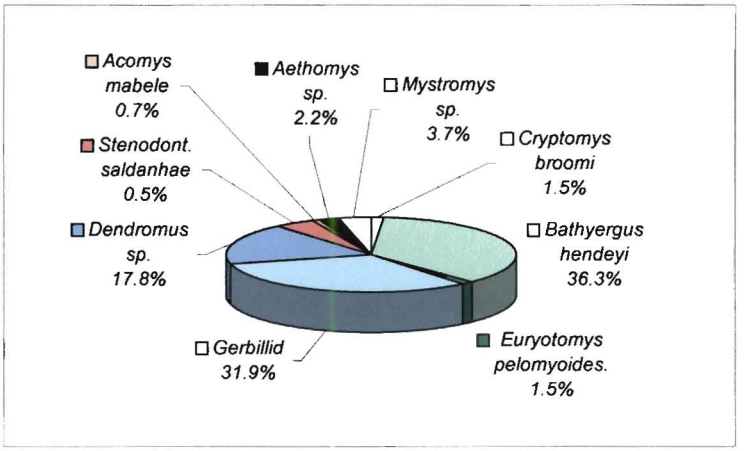
The percentage representation of the various micromammal species found in the LQSM and MPPM (F) are shown in Figure 8.4.and Figure 8.5. The percentages in which the various species occur were calculated using mandibles and maxillae to represent the number of individuals for each species. In order to exclude small samples, LQSM units which contained a total of less than 10 murid mandibles and maxillae are not shown. Isolated teeth, and teeth of doubtful identification, were excluded from the following analysis.

The categories used on the graphs shown in Figures 8.4 and 8.5 include the following species;

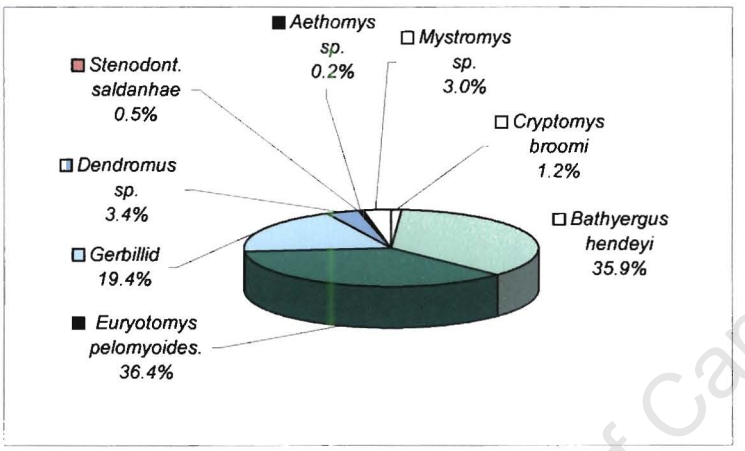
- Murid species identified only to genus, with the exception of *Aethomys* and *Rhabdomys* sp., are shown under the heading **'Other: Indet. sp.'**.
- Indeterminate *Aethomys* and *Rhabomys* species identified only to genus, are shown as **'Indet. Aeth. sp.'** and **'Indet. Rhab. sp.'**, respectively.
- *Aethomys adamanticola*, and *Aethomys modernis* are shown together under the legend ***'Aethomys* sp.'**.
- *Dendromus averyi* and *Dendromus darti* are shown together and appear as ***'Dendromus* sp.'** on the graphs.
- *Mystromys pocockei* and *M. hausleitneri* are shown together as ***'Mystromys sp.'***.
- The **'gerbillid'** legend appearing on the graphs below represents the only gerbillid species appearing at Langebaanweg, a *Desmodillus* sp.

8.2.1 The LQSM units

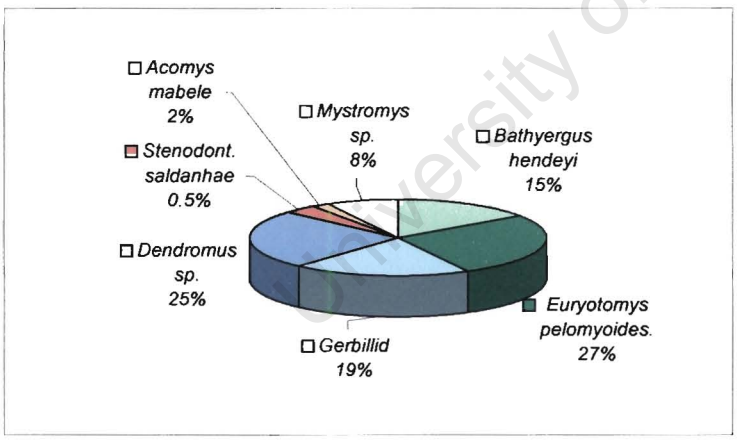
In the LQSM units, indeterminate *Aethomys* and *Rhabdomys* species are represented by single molars and do not therefore appear on the graph. Figure 8.4 illustrates the percentage representation of the micromammals from the LQSM.



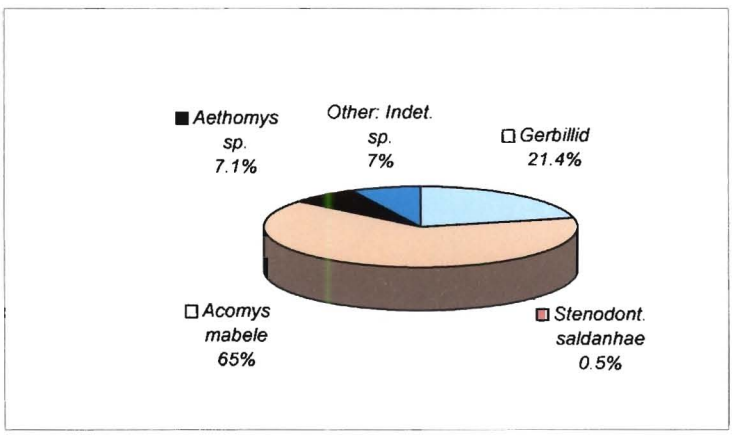
Combined elephant site units (Combined eles)



East stream/dump 2 (ES/D2)



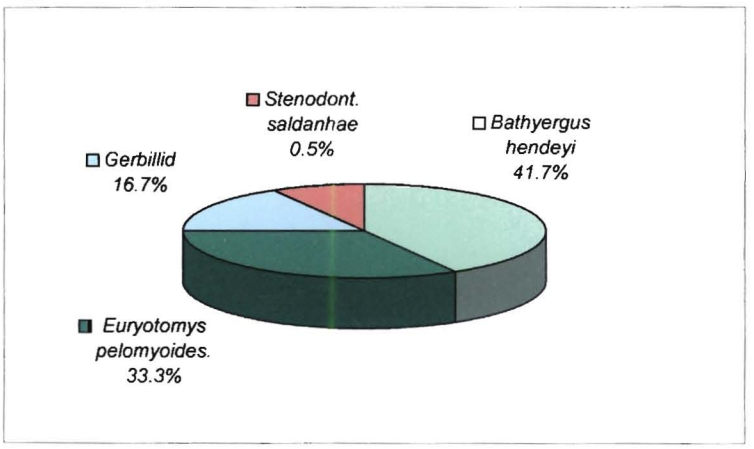
East stream/square 1 (ES/SQ1)



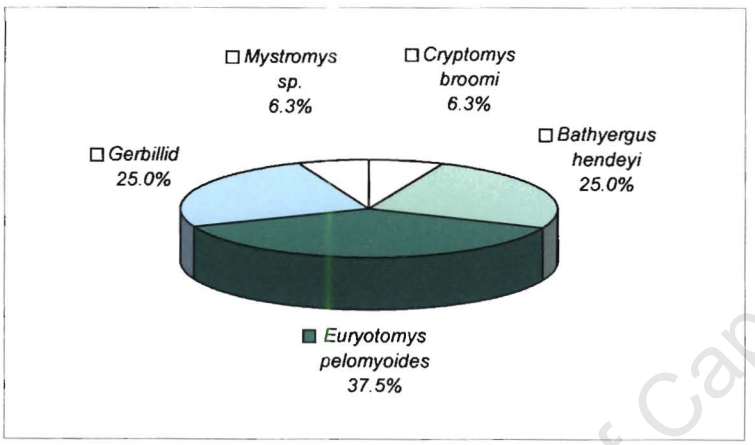
East stream/Tex's pit1 (ES/TP1)

Figure 8.4: The percentage representation of the micromammals from the LQSM units

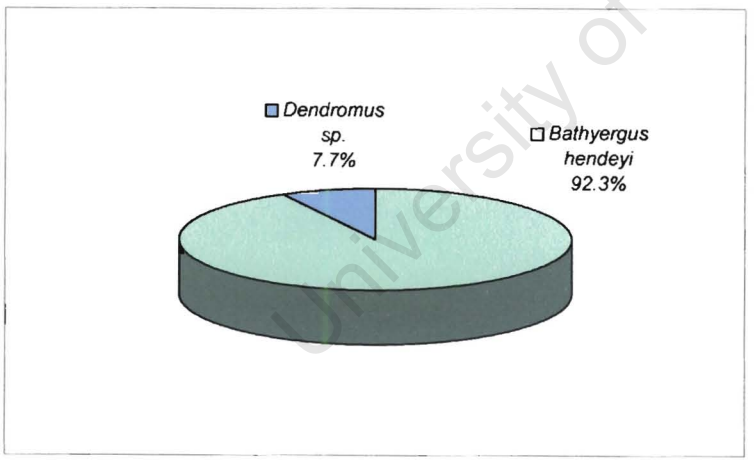
Figure 8.4 (Cont...)



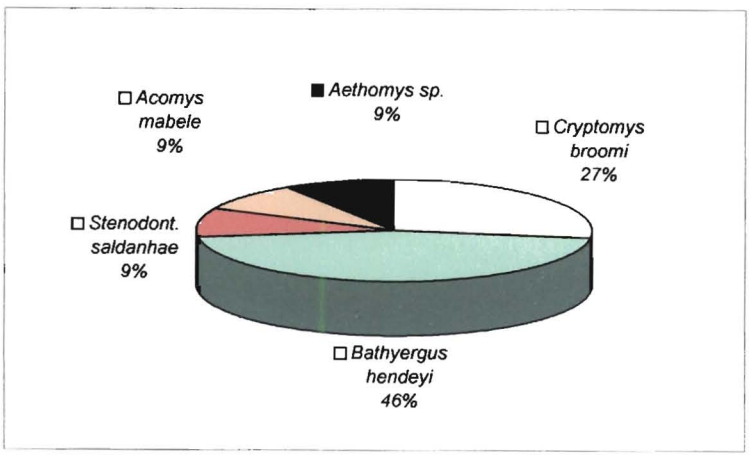
East stream/Tex's Pit 4 (ES/TP4)



East stream/peat bed (ES/PB)



East stream (ES)



Combined east stream/bed2 sites

8.2.2 The MPPM (F) units

Figure 8.5 shows the proportional representation of the micromammal species in the MPPM units F10 and F11, both separately and combined. In this figure, the category 'Indet. Aeth. sp.' includes the various indeterminate *Aethomys* species listed in Table 6.1, Chapter 6. The category 'Indet Rhab.' includes only the species called '*Rhabdomys* intermediate'. The category 'other' includes an *Acomys* sp. and a *Zelotomys*-like sp.

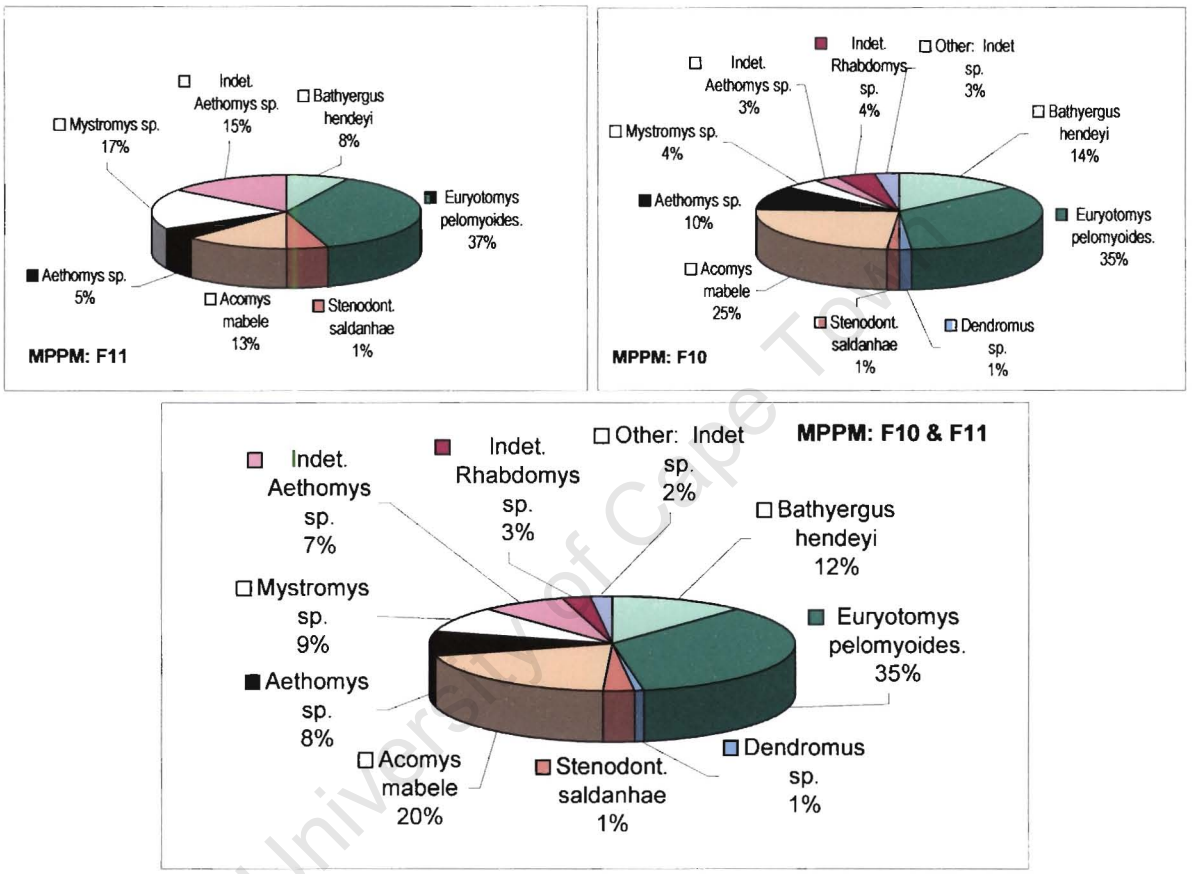


Figure 8.5: The percentage representation of the micromammals from the MPPM (F)

8.2.3 A taxonomic comparison between the MPPM (F) and LQSM units

The LQSM units ES, PB, ES/TP4, ES/TP1 and the combined ES/bed2 sites are all of an unsatisfactorily small sample size, and though percentage representation in these units is mentioned in the following discussion, small sample size renders them unreliable. For the purposes of this discussion, these units will be referred to as the 'small units'. If the small units are excluded from the discussion, *B. hendeyi* shows a percentage representation of 36 % in both the two largest LQSM assemblages, that is ES/D2 and the combined elephant sites, and makes up 15 % of the micromammals in the third largest unit, ES/SQ1. The MPPM (F)

units are closest to the latter unit in that 12 % of the micromammal assemblage in these units is comprised of *B. hendeyi*. The small units show a varied percentage representation of *B. hendeyi* which ranges from 0 % (in the case of TP1), to percentages of 25-90 % in the other units.

Denys (1998) notes that mole rats are the most common rodent found at 'E' Quarry and are well represented in the LQSM and MPPM (F) members, comprising over 80% of the total rodents in the bed 3aN (MPPM) member. As illustrated by Figure 8.5, however, mole rats were not nearly so common in the recently excavated MPPM (F) deposits, and *Acomys mabele* and *Euryotomys pelomyoides* occur in higher frequencies than *B. hendeyi*. Species analysis in this thesis is more encompassing than previous studies as a larger number of fossil material was included in the analysis. This more in-depth study shows that *B. hendeyi* does not dominate the faunal assemblage as much as previous research has suggested, and the murid, *Euryotomys pelomyoides,* and the gerbillid species found at LBW, dominate the various faunal assemblages in both the LQSM and MPPM (F) to an extent which has, as yet, not been recorded or quantified.

Euryotomys pelomyoides is found in all the LQSM units, excluding three of the small units. It is found in percentages of 35 % in unit F10, 37 % in F11, and 36.4 % in the LQSM unit ES/D2. Most of the other LQSM sites show a relatively close percentage representation to the above and occur in percentages of 27 % in ES/SQ1, and 33 % and 38 % in ES/TP4 and ES/PB, respectively, indicating a homogeneity in the percentage occurrence of this species in several units, and in both geological members, at LBW. The combined elephant sites shows a notable exception to this pattern as *E. pelomyoides* forms only 1.5% of the species in this unit. Sample size has in all probability affected the diversity of the small units which lack *E. pelomyoides*, but the combined elephant sites (n=135) contain a more satisfactory sample size and are thus more likely to reflect a real difference in the representation of this species.

The gerbillid appears to occur in similar frequencies of 17-32 % throughout most of the LQSM units. The gerbillid makes up 31.9 % in the combined Elephant site units, 19 % of the species in ES/D2 and ES/SQ1, 21 % in ES/TP1, 25 % in PB, and 16.7 % in ES/TP4. One noticeable difference between the MPPM (F) and LQSM units lies in the lack of gerbillids in Unit F10 and F11. Only two single gerbillid molars were found in the MPPM (F) units and thus no gerbillids appear on the MPPM (F) graph. This low percentage representation of gerbillids does not appear to have occurred in the MPPM micromammal assemblages

retrieved during mining operations, as a preliminary study of the micromammals indicated that this species was relatively common (pers. ob.).

E. pelomyoides, A. mabele and *B. hendeyi* are the three most common species in the MPPM (F) units, in that order. The fact that *A. mabele* occurs in a higher percentage than *B. Hendeyi,* and forms one fifth of the taxa in the MPPM (F), is a feature not seen in any of the LQSM units, excepting ES/TP1, where *A. mabele* greatly dominates the faunal assemblage at 65%. ES/TP1 is, however, one of the small units and thus unreliable. The largest LQSM unit, ES/D2, contained no *A. mabele* mandibles and only thirteen positively identified *A. mabele* isolated molars were retrieved. *A. mabele* is also found in generally low frequencies in the other two larger LQSM units, that is the combined elephant sites and ES/SQ1, at 0.7 and 2 %, respectively.

Mystromys hausleitneri is found in only one of the LQSM units, namely ES/D2, where a total of only one mandible, one maxillae and one M^1 from this species was found. This species was also found in very low frequencies in the MPPM (F) units, where only three jawbones and two M^1's were recovered.

Mystromys pocockei is the more commonly occurring species of *Mystromys* at LBW, and is found in low frequencies of 3-9 % in the combined elephant sites, ES/D2, ES/SQ1, PB and in the MPPM (F) units. This species appears to have been ubiquitous as it appears in all the larger units, and in both geological members.

Stenodontomys saldanhae is another species which appears regularly, in low frequencies of 0.5 % in all three of the larger LQSM units, and in 1 % in the MPPM (F) units. It is only absent in two of the small LQSM units, ES and PB. It is found in the highest frequency, namely 9 %, in the Combined ES/bed 2 unit, however, sample size is tiny and this percentage represents only one mandible. *S. saldanhae* is thus another species which shows homogeneity in its distribution throughout the LBW area. This homogeneity is the more surprising in that this species occurs in such low frequencies that, as a seemingly rare species, it is surprising to see it so consistently represented in both the MPPM (F) and the LQSM.

One *D. averyi* maxilla was the sole representative of the Dendromurinae found in the MPPM (F) units. More *Dendromus* specimens may come to light when a larger sample size from the recently excavated MPPM (F) deposits is analysed, however, it appears as if this genus is relatively scarce when compared with the LQSM deposits. The two *Dendromus* sp. are the

third most common species in the combined elephant units where they form approximately 18 % of the taxa, and appear in frequencies of 25 % in ES/SQ1, and in a rather lower frequency in ES/D2 at 3.4 %. *Dendromus* was absent from all the small units, excepting ES. The smaller *Dendromus*, *D. darti*, appears to be more common than the larger *D. averyi* in the LQSM units.

C. broomi is absent from the MPPM (F) units, the LQSM unit ES/SQ1, and the three smallest LQSM units. In ES/D2 and the combined elephant sites, *C. broomi* makes up 1.2-1.5 % of the murid and mole rat population, respectively. It appears that this species was either absent, or present in only very low frequencies, throughout LBW. The absence of *C. broomi* from the MPPM (F) units is not surprising, considering the fact that, relative to *B. hendeyi, C. broomi* is always present in very low proportions in the LQSM, and mole rats are not present in high frequencies in the MPPM (F) units. *C. broomi* occurs in the highest frequencies in PB at 6.3 % and in the combined ES/bed2 units at 27 %, however, extremely small numbers of mandibles and maxillae are involved, N= 1 in the case of PB, and N=3 in the case of the combined ES/bed2 units.

Two *Rhabdomys* species were identified in the MPPM (F) units (see Table 6.1, Chapter 6). The species, *Rhabdomys* intermediate, was represented mainly by single molars, and is thus slightly under-represented in the MPPM (F) units at 3 % where it appears in Figure 8.3 under the title 'Indet. Rhab. sp.'. The so-called *Rhabdomys* sp. 2 found in unit F10 was represented by a single molar and does not therefore appear on the graph. Only one *Rhabdomys* sp., *Rhabdomys* sp. 1, was found in the LQSM units, ES/D2 and ES/NE/Eles. This species was represented by single molars in both of these units, however, and so does not appear in Figure 8.4.

A. modernis is absent in almost all the LQSM units with the exception of ES/TP1, where one *A. modernis* mandible was found. No other positively identified *A. modernis* mandibles, maxillae or single molars were found in any other LQSM units. *Aethomys modernis* appears in relatively low frequencies in the MPPM (F) as only 4 mandibles and maxillae from unit F10, and 2 from unit F11, of this species were recorded. *Aethomys modernis* is rather under-represented in Figure 8.5, however, as twelve isolated *A. modernis* molars were found in the MPPM (F) units, 10 of which were found in unit F10.

Three *A. adamanticola* jaws, and four isolated upper and lower first molars were found in the MPPM (F). Isolated *A. adamanticola* molars were relatively more abundant in the LQSM unit ES/D2, where ten isolated molars from this species were recorded. Low frequencies of isolated *A. adamanticola* teeth were found in the other LQSM units, indicating that this species may have been relatively more common in the LQSM, as opposed to the MPPM (F). *A. modernis* appears to be relatively more common in the MPPM (F) than in the LQSM. The numbers of specimens involved are, however, small and these patterns should not receive too much emphasis. Three of the small units, namely ES, ES/SQ1 and ES/TP4 are the only LQSM units in Figure 8.4 which did not contain any *A. adamanticola* teeth, isolated or *in situ*.

There are a number of similarities between the MPPM (F) and LQSM in terms of faunal composition, for example;

- *M. pocockei* and *S. saldanahae* are found in low frequencies in the MPPM (F) units, ESD2 and the combined elephant site units.
- *B. hendeyi* features as one of the species occurring in the top three highest percentages in the MPPM (F) assemblages, and the LQSM units ES/D2, ES/SQ1, the combined elephant site units and PB.
- *E. pelomyoides* is the most common rodent in the MPPM (F) units, and the LQSM units ESD2, ES/SQ1 and PB.
- *Mystromys pocockei* appears in the MPPM (F) units, and in the large LQSM units ES/D2, ES/SQ1, and the combined elephant sites, in low frequencies of .3-9 %.
- *C. broomi* is absent, or found in extremely low frequencies in the larger units from the LQSM, and is absent from the MPPM (F). *B. hendeyi* dominates the Bathyergidae in both members.
- There are a minimum of ten murid and one mole rat species held in common by the MPPM (F) and LQSM units.

Differences between the MPPM (F) and LQSM include:

- The lack of gerbillids in Unit F10 and F11. The *Desmodillus* sp. at LBW is found in relatively high percentages in almost all the LQSM units (exceptions were the two small units ES and combined ES/bed2) and was one of the three most commonly occurring

species in these units. A preliminary investigation of the MPPM micromammal assemblages recovered during mining operations indicated that the gerbillid is relatively more abundant in other areas of the MPPM (pers. ob.). The lack of gerbillids in the MPPM units F10 and F11, would thus appear to be a feature of the recently excavated horizons, rather than a widespread faunal difference between the MPPM and LQSM.

- The MPPM (F) units appeared to be relatively depleted in the two *Dendromus* species as only one *D. averyi* maxilla represented this genus in units F10 and F11. A different scenario was observed in some of the LQSM units as *D. darti* was the third most common species found in the combined elephant units, and the second most common species in ES/SQ1 and ES. *Dendromus* was also present in ES/D2, although in low proportions.

- *A. mabele* occurs in generally lower frequencies in the LQSM, as compared with MPPM (F), with the exception of one of the small units (ES/TP1).

- There are a number of new, undescribed *Rhabdomys* and *Aethomys* sp. in the MPPM (F) units which are not found in the LQSM units, and the diversity of species found in the MPPM (F) is much greater.

As the above points indicate, the similarities between the LQSM and MPPM (F) units are generally greater than their differences. The resident micromammal populations at LBW during the time of deposition of the LQSM and MPPM (F) members appear to have been very similar in that they have many species in common, and differences relate to those species appearing in relatively low frequencies. There are no obvious morphological changes in the species from the two members, although *Euryotomys pelomyoides* shows some increase in the size of the M_1 in the MPPM (F), relative to the LQSM, horizons. The most striking differences lie in the lack of gerbillids in the MPPM (F), and in the greater diversity of species observed in the MPPM (F). As noted previously, the lack of gerbillids would appear to be a feature of the recently excavated horizons, rather than a widespread faunal difference between the MPPM and LQSM. Interpreting the difference in diversity between the two members is extremely difficult as these differences may be related to recovery methods used in retrieval of the micromammal assemblages, to differences in the depositional history of the LQSM and MPPM (F) assemblages, or to changes in the environmental and climatic factors governing the micromammal populations. These issues are discussed further in the following section.

8.3 Interpreting the patterns of relative abundance

The micromammals from the fossil assemblages which came originally from pellets or scats would be representative of the micromammal population living within the hunting range of the predator, which may have extended several kilometers beyond the vicinity of 'E' Quarry. Micromammals which came from pellets or scats which were alluvially transported are likely to have been recovered fairly close to the area in which they were deposited because, as argued in Chapter six, scats and pellets are not likely to survive long distance alluvial transport. Korth (1979) noted that owl pellets placed in water became saturated within seconds but continued to float. Slow disintegration followed, with a total break up of the pellets occurring after 200 m of transport.

Hendey (1981a) argued that the MPPM fauna is likely to have washed down river from areas further away and could thus represent different environments to that in the vicinity of 'E' Quarry. The LQSM horizon, on the other hand, was thought to be representative of animals that lived and died in the immediate area of the floodplain (Hendey 1981a). Chapter six has, however, presented a case for the MPPM (F) micromammals in which it is suggested that there is no evidence for long distance transport, or immersion in water for a long period prior to burial of the micromammals, and they are, therefore, likely to have been deposited close to the area in which they died, or were deposited in pellets and scats.

The taphonomic evidence for the LQSM micromammal assemblages indicates minimal, or no, reworking of deposits, and post-depositional transport of micromammal bones over short distances is indicated. The taphonomy thus suggests that both the MPPM (F) and LQSM assemblages are likely to represent the micromammal population in the vicinity and surrounds of 'E' Quarry. The similarity of the micromammal taxa from the LQSM and MPPM (F) fossil assemblages is in accord with, and supports, the taphonomic evidence. There is no evidence to suggest that the micromammals from either the LQSM or MPPM (F) came from re-worked deposits.

The micromammals from LBW represent different areas and, potentially, different micro-habitats. Interpretation of the assemblages from the various units is complicated by the fact that many of these units are likely to contain mixed assemblages which were accumulated by different agents. This is particularly likely in the case of the MPPM (F) assemblages, which are known to be alluvially accumulated, but may also be applied to the LQSM units, as these too may have been affected by alluvial transport. In the case of ES/D2, further mixing of

assemblages would have occurred during removal and dumping of sediment, and during recovery through the sieving of these deposits. The LBW units analysed in this thesis may therefore be expected to provide general, rather than specific, information on the local micromammal population and environment.

An explanation for the general homogeneity in species representation of the larger LQSM units may be that these units all contain mixed, or time averaged assemblages. Homogeneity is, however, also observed in the taphonomy of the micromammals from these units, which suggests that they were accumulated by similar category predator/s. The observed homogeneity may not therefore be entirely attributable to the mixing of deposits. This homogeneity is also not so extensive as to suggest that time averaging has resulted in all loss of characteristics of the original assemblages within an area. There are some differences in terms of species composition between the micromammal populations from the largest assemblages from the LQSM, which suggests that some of the patterning of the original, general patterns of species distribution within the landscape may have been retained. For example, the low frequency in which *E. pelomyoides* occurs in the combined elephant units and ES/TP1 suggests that this species, for some reason, was not accumulated in these areas, although it was clearly common and widespread throughout many areas of LBW. It is the most commonly occurring rodent in the MPPM (F) units, and several LQSM units (ESD2, ES/SQ1 and PB). It is impossible to rule out the possibility that the method of recovery played a role in the low occurrence of the species in these units, although similar recovery methods used elsewhere yielded large samples of *Euryotomys*. The elephant sites were from a relatively discrete area in which the micromammal assemblage contained extremely low frequencies of *E. pelomyoides*, and high frequencies of the gerbillid and *B. hendeyi*. The low frequency of *E. pelomyoides* may indicate the absence in the area of some variable governing the distribution of this species. Alternatively, the assemblages in this area may show some predator-related bias. The many unknown variables regarding the processes and agent/s of accumulation active at LBW make it impossible to substantiate which, if either, case is applicable. If the combined elephant sites do reflect some such bias, it would indicate that certain of the LQSM units have retained a taxonomic pattern which may be related to the area, or manner, in which the fossils were deposited. This would provide further evidence that the LQSM units may generally be considered good indicators of the micromammal population in the surrounds of LBW, 'E' Quarry, and may even provide quite refined information as to the spatial distribution of different species in the landscape.

Another issue which needs to be addressed, is the possibility that the author, or the people who recovered the micromammals, created homogeneity by adding together samples for the purposes of analysis. A look at Appendix N and O, which list the various species found in the LQSM and MPPM (F), indicates that small units, including those too small to appear on Figure 8.2, show a very similar pattern to larger units, with *B. hendeyi, E. pelomyoides* and the gerbillid being the species most commonly found. In other words, the abundance of certain species in the fossil assemblages appears to reflect their prevalence throughout the Langebaanweg area. Species which are found in low frequencies in the larger units are generally scarce in small units as well. For example, a similar consistency in relative abundance is illustrated by species such as *M. pocockei, S. saldanahae,* and *A. adamanticola,* which are consistently found in low frequencies in the MPPM (F) and many of the LQSM units.

The taxonomy and the distribution of micromammal species in the various assemblages may be used to assess how representative the units may be of the original micromammal population from which they came. The MPPM (F) assemblages are mixed in the sense that they are alluvially accumulated, however, it has been argued that the MPPM (F) units should provide a picture of the micromammals found in the general surrounds of LBW at the time of deposition. The MPPM (F) units serve as a kind of control for the LQSM units, in that *all* micromammal bones and teeth were recovered from the deposits, and they were excavated from a discrete area, under controlled conditions. The possible effects of the mixing of different horizons, or bias towards the collection of certain species during recovery, may therefore be discounted. Sampling and recovery methods may have caused the similarities observed between the LQSM units, but this cannot be the explanation for the similarity observed between the MPPM (F) and LQSM assemblages. The fact that the same general micromammal population is observed in the various LQSM units, and in the MPPM (F), adds support to the suggestion that the LQSM units provide a good general reflection of the micromammal population in the surrounds of LBW, 'E' Quarry, despite the rather unsystematic sampling of this member. The many similarities between the MPPM (F) and LQSM assemblages suggests that a similar micromammal population existed during the time of deposition of these members.

8.4 Assessing faunal differences between the MPPM (F) and the LQSM

Differences between the micromammal assemblages of the MPPM (F) and LQSM in terms of specifies diversity could reflect changes in the local micromammal population, and hence in climate and environment, over time at LBW. This is not considered a likely explanation, however, as environmental change would surely involve a more radical transformation and change of the general micromammal population than that observed between the LQSM and MPPM (F) horizons. Faunal differences between the two assemblages are mainly related to those species occurring in low frequencies, and approximately ten Murid species are held in common. The MPPM (F) and the LQSM horizons show the same, or very similar, relative abundance of several micromammal species. The only clear evidence for change in some of the variables influencing the micromammals at LBW during deposition of the MPPM relative to the LQSM, is the fact that *E. pelomyoides* shows an enlargement of the M_1 in the MPPM (F) horizons. There are many different factors which may have lead to such an increase in tooth size, however, and they need not necessarily be related to changes in climate or environment. The lack of compelling evidence for any marked changes in the LBW micromammal population between the time of deposition of the MPPM (F) and LQSM, suggests that the depositional history of the MPPM (F) deposits, and also fossil recovery methods, may have contributed to the high species diversity in the MPPM (F), relative to the LQSM. Further research into a larger sample of rodents from the MPPM is needed, however, before any definite conclusions may be reached as to differences and similarities in the micromammal populations from these two members.

The relatively greater diversity of micromammal species found in the MPPM (F) units may be, at least partially, attributable to the fact that the MPPM (F) sediments were deposited by a river. The river would have acted as an accumulating agent and micromammals from different areas, and different predator assemblages, are likely to have become mixed together. The scarcity of gerbillids in the MPPM (F) units is not shown by the other MPPM horizons and clearly doesn't result from a lack of gerbillids at LBW.

The variety of different predators contributing to a fossil assemblage is likely to influence species diversity. For example, a relatively high species diversity in level FLKN4 at Olduvai bed I was attributed to the fact that two different predators, namely the Verreaux eagle owl (*Bubo lacteus*) and a small carnivore, had contributed to the fossil assemblage (Fernandez-Jalvo *et. al.* 1998). A higher percentage of incisors in the MPPM (F) were noted as showing

rather more intense digestion than was generally observed in the LQSM units, and a far greater percentage of incisors showed digestion in the LQSM units. These differences, together with the greater species diversity observed in the MPPM (F) units, suggests that different combinations of predators may have been involved in the deposition of the micromammals in both horizons. There are however, similarities in the incisor digestion patterns of the MPPM (F) and LQSM in that the incisors showing digestion fall mainly into class 1 or class 2. These similarities have been interpreted as suggesting that generally similar categories of predator/s contributed to the accumulation of the fossil assemblages at LBW. The greater species diversity in the MPPM (F) assemblages is unlikely to be solely attributable to predator-related causes, but this may well have been one of the contributing factors. It has been suggested previously in this chapter that the lower species richness in the LQSM units may also be partially the result of recovery methods which were not geared towards the retrieval of rare species.

In conclusion, it is suggested that the greater species diversity observed in the MPPM (F) may have been caused by a number of variables. These include differences in the manner in which the fossil assemblages from the MPPM (F) and LQSM were accumulated, the contribution of a different variety of predators to the assemblages, and to the recovery methods used for the LQSM micromammal assemblages. There is no compelling evidence to support the idea that marked environmental/climatic change took place during the period of deposition of the LQSM and MPPM (F). The similarities between the faunal assemblages of the two horizons suggest that the time period in which the two members were deposited may even have been relatively short. Hendey (1981a) has suggested that the MPPM and LQSM were deposited over a time period of not more than 0.5 Ma, but a question mark remains over the length of the period of deposition of these members. As mentioned in Chapter 3, minor morphological and possible size differences have been observed in three taxa between bed 3aS and bed 3aN (Hendey 1978b, Hendey 1980, De Muizon and Hendey 1980). These changes have been interpreted as suggesting that an appreciable time interval lapsed between the deposition of the fossil-bearing members (Hendey 1978b, Hendey 1980, De Muizon and Hendey 1980). Interestingly, there is no discussion in the literature of specific morphological differences between animals in the LQSM and MPPM, bed 3aS, though size differences in *Tragelaphus* horn cores have been tentatively identified (Gentry 1980). Hendey (1978b, 1980) has noted the morphological differences in the taxa between bed 3aS and bed 3aN as being small, and not sufficient to warrant taxonomic distinction at species level. It could be argued that, as possible (not definite) morphological differences have been observed in only a small number

of taxa, and as the modifications are small, they need not necessarily have occurred over a long period. The micromammals provide no clear evidence to support the theory that there was a long time break between deposition of the LQSM and MPPM. The question as to whether or not there are significant differences between the taxonomy and morphology of some faunal species from the LQSM and MPPM, and the period involved in the deposition of these horizons, will hopefully be resolved when more of the LBW fauna is studied in detail.

8.5 The palaeoenvironment of Langebaanweg as indicated by the micromammals

Using the habits and characteristics of living micromammal populations to reconstruct that of extinct genera and species carries with it the evident problem that they may not have behaved in a similar way to their antecedents. Fernandez-Jalvo *et al.* (1998) note, however, that the level of inference is particularly good where there is a strong correlation of phylogenetic series with ecology, for example, all gerbils occupy similar ranges of open to arid environments. The following reconstruction of the palaeoenvironment at LBW uses such correlations, and connects them where possible with other lines of evidence.

Components of both the Sandveld and Strandveld vegetation types were found in the LBW pollen samples, which were dominated by the Ranunculaceae, but also contained pollen from the Cyperaceae, Proteaceae, Ericaceae, Restionaceae, and Asteraceae fynbos families (Scott 1995). All these fynbos families have representatives living in the west coast area, and the south western Cape, today.

One requirement that all mole rats have in common is that they are found in areas where there are geophytes, as these form their staple diet, though the genus *Bathyergus* also eats some aerial vegetation (Bennett and Faulkes 2000). There is indeed a symbiotic relationship between geophytes and mole rats as geophytes use mole rats to disperse their underground organs. Some irises produce two kinds of corm clusters, one of which is a large cluster which entices the mole rat, and other, spine tipped corms which reproduce when the larger cluster is consumed (Cowling and Richardson 1995). Lovegrove and Jarvis (1986) have even suggested that some of the Iridaceae co-evolved with mole rats. There are numerous geophytes, including many endemic species, in the west coast area today (Manning and Goldblatt 1996). The extant murid, *Myomyscus verreauxi,* endemic of the southwestern Cape, is thought to be dependent on proteas for its existence, and some ground proteas depend on this murid for pollination (David 1978). Clearly the relationship between many fynbos and

micromammal species is a long-standing one. The presence of two mole rat species at LBW, together with the relatively high frequencies in which *B. hendeyi* appears in the LQSM units of ES/D2, and the combined elephant sites, indicates that there were sufficient geophytes in the area to provide food for a relatively large local mole rat population. The mole rats at LBW thus provide indirect evidence that geophytes were well established at the time of deposition of the LQSM. The pollen evidence suggests that other fynbos species were also well established in the area at this time. Authors such as Cowling and Richardson (1995) and Coetzee (1983), note that by approximately 5 Ma, fynbos appears to have been well established in the west coast, and to have begun its rise to predominance. Climatic conditions at this time were favorable for the growth of fynbos adapted to winter rainfall patterns as modern oceanic circulation patterns were in place, and Franz-Odendaal's (2002) research has provided further evidence for the development of an essentially modern climatic regime at the time of deposition of the Varswater formation. Just to the north of LBW, in Namaqualand, pollen from Mio-Pliocene deposits indicates the presence of Karoid shrubland with fynbos and woodland elements (Scott 1995), and it is probable that a very similar scenario existed to the south in the area of LBW. The extant gerbillid, *Desmodillus auricularis*, which is found in the more arid, western areas of southern Africa, prefers hard ground with some grass cover, or karoid bush (De Graaff 1981, Stuart and Stuart 2001). The presence of a *Desmodillus sp.* at LBW is in accordance with the presence of high proportions of pollen from plant families such as the Asteraceae, Chenopodiaceae, and Amaranthaceae which indicate relative dryness (Scott 1995), as gerbillids are frequently associated with arid conditions (Denys *et al.* 1996b Fernandez-Jalvo *et al.* 1998). The pollen data was noted as containing very few diagnostic elements of an open vegetation (Scott 1985). The presence of the gerbillid in the LQSM units thus supplements the pollen data, and indicates that open, relatively arid areas existed in the surrounds of LBW.

It has been suggested in Chapter 6 that the abundance of *B. hendeyi* in the fossil record in some of the LQSM units, and the presence of this species in the MPPM (F), may have been partially attributable to the preference of this species for making burrows in sandy areas and/or areas of sandy alluvium. The relatively large numbers of *B. Hendeyi*, and possibly a few other micromammal species found in the LQSM and MPPM (F) units, may be taken to indicate the presence of sandy microhabitats at LBW. These sandy areas may have been covered in a vegetation very similar to that of today with grassy and fynbos components. Restionaceae and Asteraceae pollen was recovered from LBW, and many of the species from

these families growing in the area today are associated with sandy flats or coastal forelands (Scott 1985). Further indirect evidence for areas of sandy substrate in the area may be inferred from the presence of large quantities of golden moles, as numerous earbones were recovered from the LQSM (Hendey 1981a). The majority of golden moles utilise sandy soils, although it must be acknowledged that a couple of species are able to cope with light clay or loamy soils, or are found in forested areas (Andrews and Van Couvering 1975).

It has been suggested above that the presence of the gerbillid at LBW indicates relatively arid and open areas. It is also possible that this gerbillid inhabited areas of sandy soil. This suggestion is put forward as most of the extant, southern African gerbillids from the genus *Gerbillurus* and *Tatera*, are associated with sandy soils, and *Desmodillus* is an exception in being associated with hard ground. If the gerbillid and *B. hendeyi* do indeed indicate the presence of areas of sandy soil, the majority of LQSM units would be dominated by species associated with a sandy substrate. The relative abundance of bathyergids and gerbillids in the ES/D2 and combined elephant site assemblages in particular, may have something to do with the preferred habitat of these animals. An alternate explanation is that they were accumulated by a predator(s) which hunted preferentially in more open habitats. There are no obvious differences in the digestion patterns on the incisors from these two assemblages, relative to the others, but it is possible that the same predator(s) hunting in different areas could produce very different assemblages (a point illustrated earlier in this chapter). The LBW gerbillid and *B. hendeyi* may not have had the same habitat requirements, however, as *B. hendeyi* is found in both members, while the gerbillid is barely represented in the MPPM (F) deposits. The virtual non-appearance of the LBW gerbillid in the MPPM (F) is puzzling as this species was recovered from other horizons of the MPPM. It is possible that the gerbillid may have been associated with a particular environmental feature, which led to the representation of this species in the floodplain, but not the river channel, deposits. The gerbillid may not have lived in the immediate vicinity of the river depositing the MPPM (F) sediments.

Whether the gerbillid at LBW was associated with sand, hard ground with some grass cover, or Karoid-like vegetation, the large proportion of gerbillids and *B. hendeyi* specimens found in the LQSM units suggests that the floodplain upon which the majority of the LQSM micromammals were accumulated contained sandy areas and/or areas vegetated with a relatively sparse, scrub-like vegetation. Relative aridity in these areas may also be indicated as most gerbillids are associated with arid environments, and the extant *Bathyergus janetta*

lives in arid areas of the west coast of South Africa today (Fernandez-Jalvo *et al.* 1998, Stuart and Stuart 2001). The present-day fynbos of the west coast is adapted to relatively arid conditions and it is very possible, given the presence of Restionaceae and Asteraceae pollen from LBW, that at least some of the species from these families growing at LBW were associated with relatively arid areas, such as may be seen today in sandy areas and coastal forelands. The mole rats and the gerbillids from the LQSM units thus indicate the presence of microhabits at LBW which have not been connoted by the large mammal species found on the floodplain, which have been interpreted as indicating wooded and grassland habitats, (Klein 1981, 1982, Hendey 1983c).

Extant species of *Acomys* live in a wide variety of conditions which range from extreme desert to moist savanna (Denys 1992). *Acomys subspinosus*, which is today endemic to the western Cape, is found mainly in rocky habitats or woodlands, but may also be found associated with alluvium along rivers and on sandy ground. Any of these habitats may have been favoured by *Acomys mabele*, the *Acomys* species found at LBW.

If the preferred habitat of the extant *Zelotomys* may be applied to the *Zelotomys* at LBW, this species may also be taken to indicate the presence of dry areas at LBW, with sandy soil and sparse vegetation (Stuart and Stuart 2001). As noted in Chapter 2, however, this genus previously enjoyed a far wider distribution than it does today, and there are indications that the adaption of this species to dry conditions is a more recent development (Levinson 1985).

The only extant species of *Mystromys, M. albicaudatus,* is found in a variety of habitats. These include grassland and heath, and, in the western Cape, Succulent Karoo, Cape Macchia and Renosterveld vegetation, indicating that this species is well adjusted to the fynbos vegetation of the west coast and surrounding areas (De Graaff 1981, Stuart and Stuart 2001). The presence of two *Mystromys* species at LBW adds support to the proposed scenario that fynbos may have been a significant part of the environment around LBW. The size difference in the two *Mystromys* species at LBW suggests that they exploited different ecological niches.

The Dendromurinae, or climbing mice, are represented by two species at LBW. The four extant species found in southern Africa are associated with tall grass and rank vegetation, and the presence of two species at LBW possibly indicates the presence of these habitats. The extant *D. melanotis* is frequently associated with riverine conditions, and is also found in dry, savanna environments (Skinner and Smithers 1990). It is therefore possible that the

Dendromus at LBW may represent dry, grassy habitats, or it may have lived in the surrounds of river banks. The presence of *Mystromys* together with *Dendromus*, has been interpreted as indicating a grassland environment by Denys (1994a).

The large percentage of Ranunculaceae pollen found in the Varswater deposits clearly indicates that swamps/marshes were present in the LBW area (Scott 1985). *Delanymys* is an extant species which provides the best analogy for *Stenodontomys* (Denys pers. comm.), and if the habits of the extinct *Stenodontomys saldanahae* may be extrapolated from *Delanymys*, the presence of this species at LBW also testifies to the presence of tall grasses and marshy areas. *Delanymys* uses its small size to avoid competition with *Dendromus* (Kingdon 1974), and the tiny *Stenodontomys* found at LBW may reflect a similar strategy.

The variety of preferred habitats shown by extant species of *Aethomys* makes it difficult to extrapolate as to what environmental parameters are indicated by the presence of the various *Aethomys* species at LBW. This is particularly true in the case of *A. adamanticola* which shows unique dental characteristics. The extant *A. namaquensis* and *A. granti* are mainly restricted to rocky areas, but *A. chrysophilus* is found in a diverse number of habitats which range from grassland to savanna, open woodland, rocky outcrops, or areas of sandy alluvium (De Graaff 1981, Stuart and Stuart 2001).

Species associated with rocky areas are found in all the west coast fossil sites dating from the Late Pleistocene to the present (see Chapter 12) and it is likely that these microhabitats existed in the vicinity of 'E' quarry. The presence of indeterminate macroscelid species at LBW provides evidence for the occurrence of rocky habitats in the area, and such areas may also be represented at LBW by one or more of the *Aethomys* species, by *Acomys mabele*, or the undescribed *Graphiurus* sp. (Hendey 1981a). The presence of the latter species may indicate the presence of rocky areas, woodland savanna or bush, if the habitats of extant species are considered.

A *Thallomys* molar was recovered from the MPPM (F). The presence of this species may be taken to indicate the presence of woodland, as *Thallomys* is associated today with areas of open woodland, particularly in acacia-dominated areas. No *Acacia* pollen has been recovered from LBW to date.

The preferred habitats of *Euryotomys pelomyoides* cannot be related to those of extant species with any certainty while the phylogenetic history of this species remains uncertain. Senegas

(2001) suggests that *Euryotomys* was a grazer, however, this suggestion is based on supposition that *Euryotomys* is an ancestor of the Otomyinae.

It appears that more than one *Rhabdomys* species is present at LBW. Extant *Rhabdomys* species occupy a wide range of habitats and it is impossible to make any definite palaeoenvironmental assumptions from the presence of this genus. It is worth noting, however, that in the west coast area today, *Rhabdomys* is common in areas of open scrub, where low bushes are interspersed with sandy areas (pers. ob.).

In summary, the murids and mole rats at LBW suggest a varied environment which contained a number of different habitats. These include marshy areas fringed with tall grass and rank vegetation, open woodland, grasslands, open scrub vegetation, sandy areas (including areas of sandy alluvium), and probably rocky areas or outcrops. Some of the micromammal species at LBW represent genera which are today found on the west coast in association with Strandveld and Sandveld vegetation, and genera, such as *Bathyergus* and *Acomys*, are endemics in the region today. The endurance and continuation of certain genera of micromammals and fynbos on the west coast from the Mio-Pliocene until the present lends support to the suggestion that fynbos microhabitats were well established at the time of deposition of the LBW sediments. As mentioned earlier, it has even been suggested that certain plant and micromammal species evolved together. The fact that approximately nine of the murid, bathyergid and muscardinid genera found in the LQSM and MPPM horizons are found in the west coast area today, or alternately, appear in west coast fossil sites dating from the late Middle Pleistocene to the Holocene, suggests the presence of a developed and established Fynbos vegetation in the west coast area as far back as the Mio-Pliocene.

Chapter nine

The Saldanha Bay area and background to the site of Hoedjiespunt 1

This chapter provides a background to the geology and setting of the Saldanha Bay area, and then focuses on the palaeontological site of HDP1. Previous work done on the site is summarised, and the fauna from the site is introduced.

9.1 The geology of the Saldanha Bay area

Figure 9.1 shows the geological setting of the Saldanha Region. Typical stratigraphic sequences in the area comprise wave cut platforms in granites of the Cambrian Cape Granite Suite, overlain by shallow marine shelly gravel (Velddrif Formation), which in turn is overlain by Langebaan Formation aeolianites (Tankard 1974, Roberts and Brink 2002). This sequence is thought to have been formed during a sea level regression. The wave cut platforms in the vicinity of the 5 sites mentioned below ranges from 6-10 m above mean sea level (amsl) (Roberts pers. comm.).

The Langebaan Formation aeolianite consists mainly of comminuted shell and quartz grains cemented by secondary carbonate, interbedded with calcretes (Roberts and Brink, 2002). Each calcrete-bounded sequence records an episode of dune mobility, followed by the establishment of vegetation and the development of pedogenic calcretes and general dune calcification. These processes may be rapid, occurring within a period as brief as 5-10 ka, a consequence of the high bioclastic carbonate content (Roberts and Berger 1997; Roberts Brink 2002). The Velddrif Formation is not evident at HDP1, HDP2 & HDP3, but can be seen to be overlain by the Langebaan Formation at Sea Harvest and SBYC, and at Bomgat just north of HDP1 (Roberts in press). The younger, unlithified calcareous aeolian deposits form the Witsand Formation.

The age of the aeolianites and marine deposits in the vicinity of the Hoedjiespunt Peninsula, which rest on a wave cut platform at 6-10 m amsl, is contentious. Butzer (as quoted in Grine and Klein 1993) suggested that the sandstone cliff that hosted the Sea Harvest site was formed during one or more of the colder intervals within the Last Interglacial, but there is no evidence to support this. Extinct molluscs in the Velddrif Formation exposures at Sea Harvest and

the nearby Bomgat suggest an earlier Pleistocene age (Pether, as quoted in Dale and Mc Millan, 1999). An infrared stimulated luminescence date of ~1 Ma was obtained on feldspar in primary dune deposits at HDP1 (Roberts in press), but this date is older than the generally accepted limits of this dating technique and may not be reliable. Microfossils indicate a Middle Pleistocene age (Dale and Mc Millan, 1999), but the chronologies linked to the biostratigraphic data is questionable (Roberts and Brink, 2002). It should also be noted that the aeolianites in the Saldanha environs are mainly composite, comprising increments which can vary greatly in age (Roberts and Berger, 1997; Roberts and Brink 2002). As the above discussion clearly indicates, the age of the HDP1 aeolianites remain contentious.

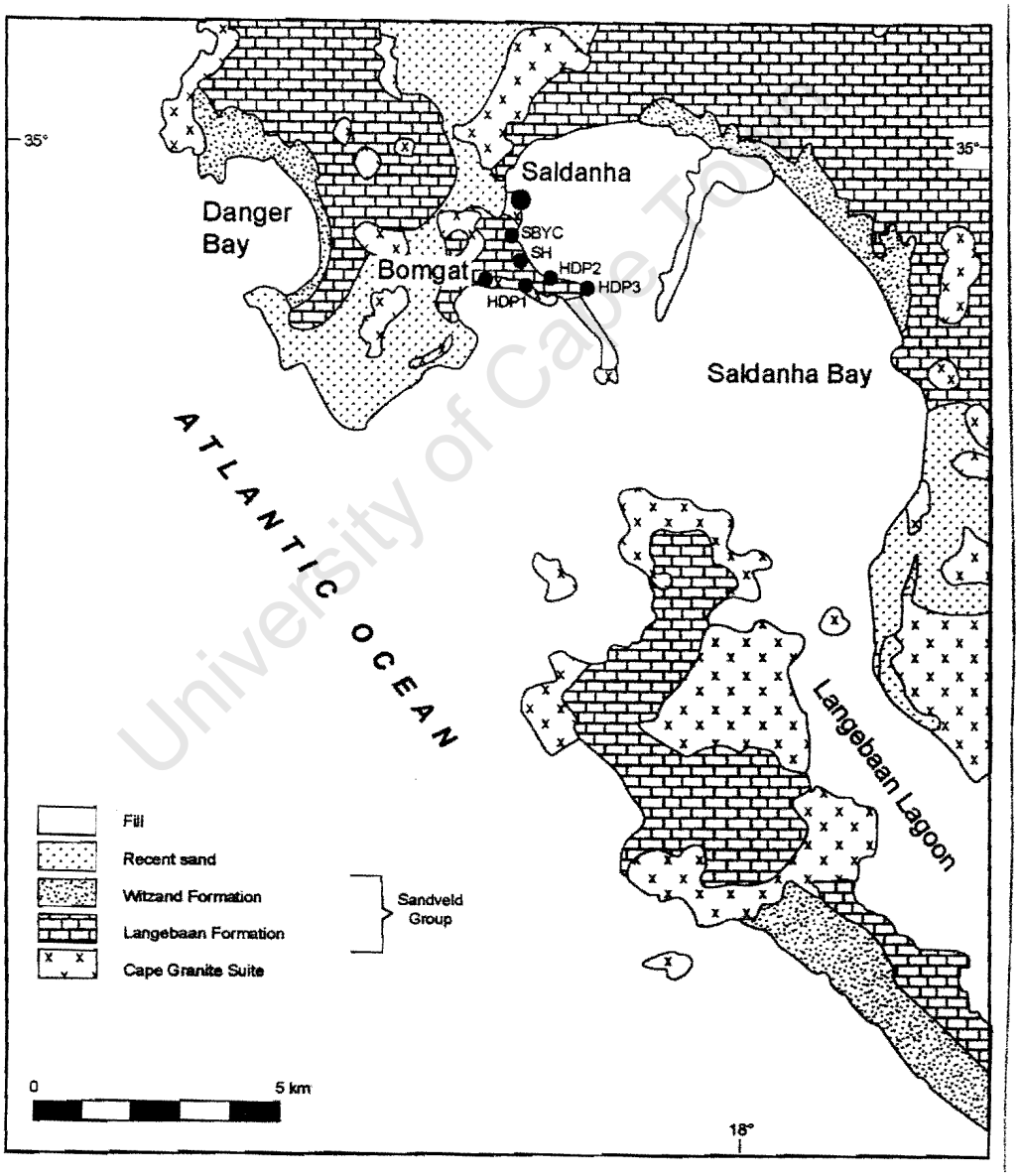


Figure 9.1: The geological setting of the Saldanha Bay area, and location of the Saldanha Bay fossil sites

9.2 Archaeological and palaeontological sites in Saldanha Bay area

Several archaeological and palaeontological sites have been found on, and near, the Hoedjiespunt Peninsula (Grine and Klein 1993, Stynder 1997, Manthi 2002). All of these sites are intrusive into the Langebaan Formation aeolianites. These include the Saldanha Bay Yacht Club site (SBYC), the Sea Harvest site, and the Hoedjiespunt sites, Hoedjiespunt 1 (HDP1), Hoedjiespunt 2 (HDP2) and Hoedjiespunt 3 (HDP3). The site at the Saldanha Bay yacht club, SBYC, has been described in Chapter 1.

9.2.1 The Sea Harvest site

The Sea Harvest site comprises a cemented shell midden situated above the levels of palaeontological deposits. The following site information, unless otherwise stated, is from (Grine and Klein 1993). A hyaena is thought to have been responsible for the palaeontological accumulation of large mammal bones. The latter included a rich mammalian fauna and abundant coprolites, as well as human remains, comprised of a manual distal phalanx and a maxillary premolar. Material was collected from the site as it eroded out of the cliff face and this may have resulted in the mixing of fossils from different depositional horizons (Parkington pers. comm.). In 1977 a particularly rich bone pocket was excavated and Grine and Klein (1993) suggest that this collection provided a representative sample of the fauna. A Last Interglacial age is suggested for the site as the fauna contains no clearly mid-Pleistocene (or older) forms. The most likely minimum age is currently thought to be between 128 000-74 000 years B.P. (Grine and Klein 1993, Stynder 1997). An abundance of grazing ungulates at Sea Harvest has been interpreted as indicating that the ancient vegetation in the area was significantly richer in grasses than during historic times.

9.2.2 The Hoedjiespunt sites 2 and 3

Hoedjiespunt 2 (HDP2), which is situated on the northern side of the peninsula, contains a closely contiguous mixture of human and hyaena occupation horizons (Stynder 1997). A small excavation done at this site revealed thick occupation deposits containing ash, charcoal, bone, stone and ochre (Parkington pers. comm. as quoted by Stynder 1997).

Preliminary investigations at the site of Hoedjiespunt 3 (HDP3) suggest that this site may contain only archaeological material. It has been dated by ESR analysis of marine shell to the Last Interglacial (Yoshida 1996). This date must, however, be considered as provisional until the age of this site is confirmed by further dating (Parkington pers. comm.).

9.3 Hoedjiespunt 1

This section introduces the palaeontological and archaeological site of Hoedjiespunt (HDP1), one of the two sites analysed in this thesis. HDP1 is situated approximately 150km northwest of Cape Town, on the southern edge of the Hoedjiespunt Peninsula at Saldanha Bay (See Figure 9.1). HDP1 is a fossil hyaena lair, intrusive into calcareous aeolianite of the Langebaan Formation.

9.3.1 The stratigraphy of the archaeological deposits

The following description of the stratigraphy of HDP1 and associated assemblages is obtained from Stynder (1997), unless otherwise stated. The aeolianite hill into which HDP1 is set, is capped by approximately 2 m of calcrete, at the base of which is a cemented shell midden, SHEM (shell midden, Fig.). This horizon contained marine shells, stone tools, animal bones, ashy lenses, eggshell fragments and ochre. Beneath SHEM is NOSA (nodular sand), a cemented sand with nodules. DAMA (dark material) lies beneath NOSA and is a dark, loamy horizon, rich in marine vertebrate bone and small animals. The stone tools are mainly in vein quartz, of which 90% are adiagnostic, the remainder are almost certainly Middle Stone Age (MSA).

9.3.1 The stratigraphy of the palaeontological deposits

A fine, stiff, shelly sand horizon called SHES (shelly sand) separates the archaeological from palaeontological assemblages. SHES contained no bones, but a layer of gastropod shells was found in this unit (Parkington pers. comm.). BONS (bone sand) which underlies SHES, is less shelly, and contains bone. Under BONS was a layer of consolidated blocks composed of fine shelly sand, similar to that from SHES, these blocks formed the horizon called ROOF. It is thought that the blocks may represent parts of the roof of the shelter or cave of the original hyaena lair. BONS was differentiated from ROOF during excavation but the division between these two horizons was not clear cut and they graded into one another (Parkington pers. comm.). A few shells are mixed in with the stone roof blocks of ROOF and may have come from the archaeological assemblages above. Below the blocks of ROOF, the horizons consist of fine, and coarser grained sand. Beneath ROOF lies HOMS (hominid sands), the main bone-bearing horizon in the palaeontological assemblage, and the horizon in which hominid remains were found.

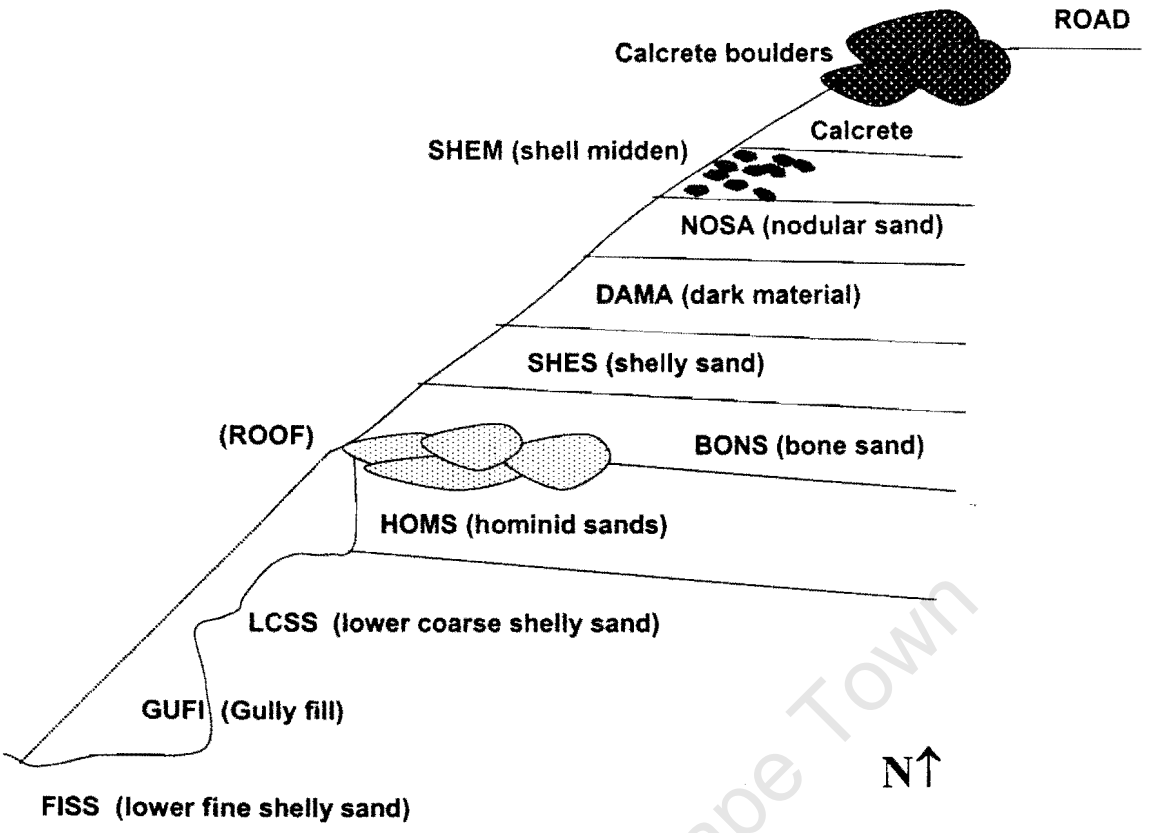


Figure 9.2: The stratigraphic sequence at HDP1 (After Stynder 1997, Figure 3.4, Page 31 - not drawn to scale)

The micromammals analysed from HDP1 came from the horizons ROOF and HOMS. A thin horizon termed HOMS/ROOF was identified in-between the horizons of HOMS and ROOF. This horizon consists of the very lowest portions of ROOF, and the uppermost portions of HOMS. HOMS/ROOF was kept distinct during excavation as a cautionary measure, although it is not a distinct, depositional horizon. HOMS is extremely rich in bone, the majority of which come from large ungulates such as *Connochaetes/Alcelaphus* and carnivores such as the jackal, *Canis mesomelas*. Hominid remains found in HOMS included fragments of a human maxillary molar, a right maxillary third molar, and two mandibular incisors (Stynder *et al.* 2001). In addition, a human tibia was recovered during excavations in 1996 (Stynder *et al.* 2001). Very few marine shells were found in this horizon and those that were, may have filtered down from the archaeological deposits. Ostrich eggshell fragments are common in this horizon.

HOMS can be separated into fossil-bearing and non-fossiliferous deposits. The non-fossiliferous material is more consolidated than the fossiliferous areas and is found in the form of pillar-like structures, which may represent the walls of the original hyaena den. Grain

size analysis confirms that there is indeed a difference between the non-fossiliferous and fossil bearing material as the latter is finer-grained and less well sorted (pers. comm. D. Roberts as quoted by Stynder 1997).

Below HOMS is a smaller, bone-bearing horizon of coarse shelly sand, LCSS (lower coarse shelly sand). A grain size analysis of LCSS indicates that there is a close correspondence between this horizon and the non-fossiliferous HOMS horizon, suggesting a similar derivation of these sediments (pers. comm. Roberts as quoted by Stynder 1997). There is however, not a huge difference in grain size between LCSS and the fossil-bearing horizons in HOMS. Below HOMS is a bone-rich gully, GUFI (gully fill). The state of preservation of the bone in GUFI is different to that of HOMS. HOMS contains many near complete or complete bones from large mammals, whereas GUFI contains fragments of larger bones, and bones from small bovids and carnivores. The gully, GUFI, may represent a separate occupation area from the main hyaena den. A fine, shelly sand (FISS) horizon underlies the palaeontological horizons. A detailed description of the methods of excavation used at HDP1 may be found in Stynder (1997).

9.4 The age of the Hoedjiespunt 1 horizons

9.4.1 The archaeological horizons

The calcrete capping on the Hoedjiespunt hill yielded a date of approximately 300 000 years BP with U series analysis (Vogel, as quoted in Berger and Parkington 1995). Thermoluminescence (TL) and infrared stimulated luminescence (IRSL) dating on sediments from the DAMA horizon gives a date of approximately 117 000 years BP, sometime during the Last Interglacial (marine isotope stage 5e) (Woodborne 2000). Dating of the archaeological horizons to an interglacial period is in agreement with the large number of shell fish and other marine vertebrate fauna found in these horizons (Stynder *et al.* 2001).

9.4.2 The palaeontological horizons

TL and ISRL dates on HOMS suggest an accumulation during the Middle Pleistocene, and a maximum age of 550 000 years BP is given for the site (Woodborne 2000). The fauna from HOMS is typical of the Florisbad Faunal Span which would place a maximum age of 250 000 years BP on the horizon (Stynder *et al.* 2001). It is suggested on the basis of stratigraphic observations, and the dates obtained, that the site was probably deposited some time between 200 000 to 300 000 years ago (Stynder *et al.* 2001). The dental metrical features of the

hominid teeth recovered from HDP1 are noted as being comparable with other African and European hominids from the Late Middle Pleistocene (Stynder et al. 2001). Some uncertainty still remains as to the actual age of HDP1 as the large mammals suggests a broad time period of deposition some time between the Middle Pleistocene and 10 000 years BP. A date for the site, such as marine isotope 6, cannot be ruled out (Parkington pers. comm.).

9.5 The Hoedjiespunt 1 macrofauna

The information in this section, as in the previous section, was obtained from Stynder (1997). Table 9.1 shows the various mammal species found in the excavated sample from HDP1. The HDP1 macrofauna is dominated by grazing ungulates and carnivores. The white rhino is present, but other large herbivores such as the Giraffidae, Proboscidae and Hippopotamidae are absent.

The kudu, *Tragelaphus strepsiceros*, is the only large bodied browser present in the sample. The other small browser found at HDP1 is the extant small grysbok, *Rhaphicerus melanotis*, which shows a present day distribution which is restricted to a narrow belt along the south-western and southern coastal belt, and the adjacent interior (Stuart and Stuart 2001). The kudu found at HDP1 appears to be generally smaller than modern specimens and Stynder (1997) suggests that the species at HDP1 may represent a kudu species, found in the later Pleistocene of the western Cape, which was intermediate in size between the greater and lesser kudu. The palaeontological fauna from HDP1 is basically a modern one, with five, or possibly six, extinct species (Stynder 1997). The extinct species include, *Antidorcas australis, Pelorovis antiquus, Equus quagga, Equus capensis* and *Hippotragus leucophaeus*, and possibly *Tragelaphus* (*strepsiceros*) (Stynder 1997). Of these species, only *Hippotragus leucophaeus* and *Equus quagga* have been recorded locally in historic times, the other species became extinct during the Terminal Pleistocene-Early Holocene (Stynder 1997). The majority of species found in HDP1 were present during the Middle Pleistocene, however, there is an absence of species such as *Rabaticeras arambourgi* which was present in the Middle Pleistocene fauna of Elandsfontein. This suggests that HDP1 may have been deposited after the Middle Pleistocene.

Scientific name	Common name	NISP	MNI
Homo sapiens	Human	14?	2?
Pelea capreolus	vaalribbok	12	2
Antidorcas australis	springbok	64	4
Pelea/Antidorcas	vaalribbok/springbok	57	3
Redunca/arundinum	southern reedbuck	8	3
Damaliscus dorcas	bontebok	16	2
Redunca/Damaliscus	reedbuck/bontebok	56	2
Tragelaphus ?cf. strepsiceros	kudu	34	3
Connochaetes gnou/	black wildebeest		
Alcelaphus buselaphus	Cape hartebeest	479	16
Connochaetes/Alcelaphus/	black wildebeest/hartebeest		
Tragelaphus	kudu	112	2
Raphicerus sp.	steenbok/grysbok	143	10
Hippotragus lecuophaeus	blue antelope	1	1
Taurotragus oryx	eland	29	1
Syncerys caffer	Cape buffalo	10	1
Pelorovis antiquus	giant buffalo	2	1
Taurotragus/Megalotraus/			
Syncerus/Pelorovis		24	2
Hyaena brunnea	brown hyaena	4	1
Crocuta crocuta	spotted hyaena	1	1
Hyaenid general		19	3
Felis lybica	wildcat	14	2
Felis nigripes	small spotted cat	1	1
Felis serval/Felis caracal	serval/caracal	27	2
Panthera pardus	leopard	22	2
Pathera leo	lion	3	1
Lycaon pictus	wild dog	8	1
Vulpes chama	Cape fox	15	2
Canis mesomelas	black-backed jackal	343	11
Mellivora capensis	honey badger	5	1
Aonyx capensis	clawless otter	9	2
Ictonyx striatus	striped polecat	5	2
Herpestes ichneumon	Egyptian mongoose	7	1
Atilax paludinosus	water mongoose	3	1
Genetta tigrina	genet	3	1
Suricata suricatta	suricate	2	1
Viverrids - general		3	1
Equus capensis	giant' Cape zebra	7	1
Equus quagga	plains zebra	1	1
Ceratotherium simum	white rhinoceros	5	1
Suid - general		3	2
Lepus capensis	Cape hare	4	1
Lepus saxatilis	scrub hare	1	1
Bathyergus suillus	dune molerat	32	3
Procavia capensis	rock hyrax	79	8
Hystrix africaeaustralis	porcupine	2	1
Delphinidae gen. and sp. indet.	dolphin	5	1
Arctocephalus pusillus	Cape fur seal	34	2

Table 9.1: The mammals from Hoedjiespunt (excluding the micromammals (After Stynder (1997), Table 4.1, page 45)

Extinct large-bodied forms such as *Pelorovis equus* and *Equus capensis* were extremely large roughage grazers, requiring a grassland high in primary production to survive (Stynder 1997). These species have not been replaced in modern grassland systems. *Syncerus caffer* also eats fibrous food, and this species, together with above-mentioned grazers, prepare the grazing succession for fresh grass grazers that prefer shorter stalks, such as *Alcelaphus buselaphus, Damaliscus dorcas dorcas, Ceratotherium simum, Connochaetes gnou, Redunca arundinum,* and *Hippotragus leucophaeus* (Stynder 1997).

All of the large carnivores found at HDP1 are absent from the area today. The largest of the carnivores that remain are the caracal (*Felis caracal*) and the black-backed jackal (*Canis mesomelas*). Many of the carnivore and ungulate species show a robusticity in their limb bones, a trend which has been noted in other fossil sites such as Florisbad (Brink 1987, as quoted by Stynder). It is thought that this robusticity may reflect a general trend in mammal evolution in southern Africa, rather than being a reflection of cold, climatic episodes and a resultant increase in mean body size.

9.6 The agents of accumulation of the Hoedjiespunt 1 macrofauna

Porcupines do not appear to have been significant agents in the accumulation of the Hoedjiespunt 1 macrofauna as less than 1% of the bones show evidence of gnawing (Stynder 1997). Hyaenas were identified as the main accumulators of the HDP1 fauna for three reasons, the first being that the numerous coprolites found together with the bones were similar in shape and size to those of hyaenas (Stynder 1997). Secondly, the dense accumulation of bone indicates the hyaena as the agent of accumulation as no other carnivores accumulate such large quantities of bone. Hyaenas are known to introduce certain biases into the faunal accumulations that they collect, for example, they produce assemblages which show a high carnivore to ungulate ratio (a feature show by the HDP1 faunal assemblage), and there is selection of certain prey species (Cruz-Uribe 1991). Thirdly, the pockets in which bones are found in the lower horizons of HDP1 may represent sections of the collapsed burrow system of a hyaena den (Stynder 1997). Circumstantial evidence points towards the brown hyaena (*Hyaena brunnea*) as the most likely species to have accumulated the HDP1 assemblage.

9.7 Post-depositional breakage of the Hoedjiespunt 1 macrofauna

Stynder (1997) notes that post-depositional destruction has had a major effect on the

macrofauna from HDP1. Post-depositional destruction appears to have been strongly related to bone density, particularly in the small and small-medium bovid classes. The growth of salt crystals in the bone and root growth have had an extremely detrimental affect on the assemblage. A study of the compact tarsals and carpals from the site indicate that density mediated destruction affected the assemblage, but did not alter it to the degree that it was unsuitable for palaeoenvironmental reconstruction.

9.8 Deposition of the Hoedjiespunt 1 palaeontological assemblages

The position of bones, ostrich eggshell and other fossils were recorded with Geographical Information Systems (GIS) equipment during excavation, and thus detailed information of the position of these faunal remains within the site, and their relation to one another, was recorded.

The section presents the results of an analysis of the distribution of the HDP1 fauna done by Stynder (1997). HDP1 consisted of fossiliferous horizons in which bone was unequally distributed, with clusters of bone in some areas, and low concentrations in other areas (Stynder 1997). Stynder (1997) divided the site into two areas. The division was based on the clusters of bone, and divided the site roughly into two halves, namely HOMS >-2 east and HOMS <-2 east.

Modern hyaenas use different parts of the den for various activities and Stynder (1997) used information on bone distributions within modern hyaena dens to deduce the behaviour of the hyaenas at HDP1. There was an abundance of large, heavy bones from big animals in the area HOMS>-2. The feeding areas of modern hyaena dens are characterised by such concentrations, and Stynder (1997) suggested that the dense accummulation of larger mammal bones in HOMS>-2 represents a feeding area.

Microfauna bones were found to be similarly distributed to ostrich eggshell fragments, small mammal bones and bird eggshell fragments in HOMS (<-2 east). All of these were differently distributed to large, large-medium bovid, small medium bovid/suid, small bovid and carnivore bones Stynder (1997). Coprolites were found to show a distribution similar to that of the small mammal, microfauna, ostrich eggshell and bird eggshell fragments. Latrine areas are frequently situated separately to feeding areas in hyaena dens, and the distribution of coprolites at HDP1 may be a reflection of this. Stynder (1997) suggests that the small

mammal, microfauna and bird and ostrich eggshell fragments may have been deposited in hyaena scats.

It is suggested that the horizon GUFI represents an assemblage from a maternity den where hyaena cubs were reared (Stynder 1997). This conclusion was reached from the fact that small bovid, small medium bovid/suid, marine mammal, bird and carnivore bones were proportionally more common in this horizon, than in the bone cluster (HOMS>-2 east) (Stynder 1997). Hyaena cubs more commonly eat these smaller-sized food items. Large-medium bovid and large animal bones were differently distributed to carnivore, small bovid and marine mammal distributions, all of which were similarly distributed.

The apparently non-random distribution of animal bones, coprolites and bird and ostrich eggshell fragments, together with the evidence that part of the site formed a maternity den, led Stynder (1997) to conclude that the palaeontological accumulation at HDP1 took place in the closed environment of a den, rather than in an open situation. The grain size of the matrix provides evidence that the hyaenas burrowed into the sediments of a partially consolidated dune.

9.9 Palaeoenvironmental implications of the Hoedjiespunt 1 macrofauna

The majority of species in the HDP1 sample are open grassland and open woodland adapted species (Stynder 1997). The species composition of the large mammals at HDP1 indicates a dominance of grazing ungulates, which suggests a grass dominated environment, with relatively little bush or thicket. In addition, the diversity of grazing ungulates suggests an extremely productive grassland which had the capability of carrying a variety of grazing species. The vast majority of these species are adapted to open woodland, and grasslands. The presence of large grazers such as *E. capensis* and *P. antiquus* indicates that the productivity of the ancient grasslands must have been higher in primary production than modern grasslands, and probably functioned in a manner similar to that of the East African woodlands today. The small marine component of the HDP1 assemblage includes dolphins, seals and penguins, indicating that the sea was within reach of the hyaenas occupying HDP1. The presence of fresh water in the area is deduced from the presence of the Egyptian goose (*Alopochen aegptiacus*), the Cape clawless otter (*Aonyx capensis*), and two Vlei rat species (*Otomys irroratus, and O. saundersae).* These two micromammal species are frequently, but

not always, associated with water, however, and cannot be taken as a definite indication of a fresh water source in the area. No freshwater source is found in the area of HDP1 today.

The wild dog, *Lycaon pictus*, is the one species in the HDP1 assemblage which requires relatively open country as it hunts in open habitats where it relies on sight, rather than smell. The Cape Hare (*Lepus capensis)* and scrub hare (*Lepus saxatilis)* found at HDP1 are found today in scrubland, grassland and woodland areas (Skinner and Smithers 1990). The rock hyrax (*Procavia capensis*), which is also found at HDP1, is associated with rocky areas. This species is a grazer and browser and eats a wide variety of plants (Stuart and Stuart 2001).

The two browsing species found at HDP1, the historically absent Kudu (*Tragelaphus strepsiceros*) and the grysbok (*Rhaphicerus melanotis*) indicates a probably limited, woodland and bush component. Large bodied browsers, such as the Giraffids, are absent, suggesting that trees were rare in the area. The spread of grasslands has been linked to glacial episodes during the Pleistocene by Klein (1983). The large number of grazers at HDP1 may indicate that the HDP1 fauna accumulated during a period of sea-level regression (Stynder 1997). Hyaenas living close to the coast usually contain a high percentage of marine animal remains, but only 4.2 % of the animals from HDP1 form the marine component at the site (seals cetaceans and marine birds). This provides evidence for the accumulation of the fossil assemblage during a cooler period of marine regression when the sea may have been 12-15 km away from the coast. The jackal teeth from HDP1 are larger than their modern counterparts. This may also be taken as evidence of cooler conditions, as jackals appear to comply with Bergmann's rule in terms of changes in body size (Klein and Cruz-Uribe 1984).

Klein (1983) notes that the large mammals from the Middle Pleistocene and earlier Late Pleistocene indicate that grasses played a more important role during those periods. Grazers greatly outnumbered browsers, and grasses were far more prominent than in historic times. Mixed feeders later became dominant in historical times in the fynbos (Klein 1983). The large mammals indicate that Quaternary environmental change was more dramatic in the fynbos zone than in any other part of Africa, excepting the Sahara and Maghreb (Klein 1983).

9.10 The Hoedjiespunt 1 microfauna

The sample of microfaunal remains obtained for this study was sorted, by the author, from deposits which had been bagged as unsorted bulk during excavation of HDP1. The unsorted

bulk consisted of sediment which had passed through a 5 mm, and also a 3 mm, sieve. During sorting of these bulk collections, all visible micromammal bones and teeth were retrieved. The 5 mm unsorted bulk contained small, rounded, calcrete pieces. These were extremely hard and it was generally impossible to break them open to see if any microfaunal remains were cemented inside. The square chosen for analysis was L16, as it was relatively centrally situated within the site, and contained a good sample of micromammals from both HOMS and ROOF. The small sample of sieved material from HOMS/ROOF was also analysed.

9.11 The agent of accumulation of the microfaunal sample from Hoedjiespunt 1 according to Stynder (1997)

Stynder (1997) suggests that the micromammals may have come from the coprolites of hyaenas. This suggestion was unsubstantiated, however, in that no study of the digestion patterns on the micromammal bones and teeth was made in order to support this hypothesis. Hyaena's have digestive systems which are geared for digesting large mammal bones and their gastric juices are likely to completely dissolve, or cause considerable digestion to, micromammal bones and teeth.

Stynder (1997) notes that the microfaunal bones showed a distribution similar to that of the small mammal bones, coprolites, ostrich eggshell and bird eggshell fragments. This observation may not be strictly true, however, as during excavation, microfaunal (generally micromammal) bones were plotted when they were observed, but the majority of micromammal remains ended up in the unsorted bulk deposits which were bagged after sieving (pers. ob.). The plotting of microfaunal bones was also dependent upon the whims of the person excavating (pers. ob.). No definite statements can therefore be made about the concentrations of the microfaunal accumulations until all the unsorted bulk has been checked for microfauna. A taphonomic and taxonomic analysis was undertaken in order to verify or refute the various hypotheses relating to the micromammals. The results of this analysis are presented in the following chapter.

9.12 The micromammals from Hoedjiespunt 1

9.12.1 Previous work done on the micromammals

Previous to this study of the micromammals at HDP1, Dr Margaret Avery (South African Museum, Iziko Museums of Cape Town) identified a small sample of selected murid and

soricid jawbones, in order that the micromammal component from HDP1 be included in Stynder's (1997) study. The species identified included *Bathyergus suillus*, *Tatera afra*, *Aethomys namaquensis*, *Myomyscus verreauxi*, *Rhabdomys pumilio*, *Mystromys albicaudatus*, *Otomys irroratus*, *Otomys Saundersae*, *Otomys unisulcatus*, and *Otomys brantsii*. All of these species are found in square L16, but three additional species, all of which were represented by only one mandible, are listed by Stynder (1997). These are *Acomys subspinosus* (the endemic Cape spiny mouse), a soricid, *Myosorex varius*, and the bat, *Rhinolophus clivosus*.

9.12.2 The micromammal assemblages analysed in this thesis

The micromammal species recovered in this study from HDP1, square L16, are listed in Table 9.2. The species noted by Stynder (1997), which did not appear in the sample, are listed as well.

Taxa	HDP1
Soricidae	
C. cyanea	√
M. varius (Stynder 1997)	√
Macroscelididae	
E. rupestris	√
Rhinolophidae	
R. clivosus (Stynder 1997)	√
Muridae	
T. afra	√
M. albicaudatus	√
A. supspinosus (Stynder 1997)	√
M. verreauxi	√
R. pumilio	√
A. namaquensis	√
Z. woosnami	√
O. irroratus	√
O. Saundersae	√
O. unisulcatus	√
O. slogetti	√
P. brantsii	√
Bathyergidae	
B. suillus	√
C. hottentotus	√

Table 9.2: The micromammal taxa from HDP1 (After Stynder 1997, Table 4.4, Page 41)

Appendix R indicates the preferred habitats and habits of the various species listed in Table 9.2, and Appendix S lists the micromammal species currently living in the Saldanha Bay area. According to Stuart and Stuart (2002), *Parotomys brantsii*, which was recovered from HDP1,

is today slightly extra-limital of Saldanha Bay and shows a current distribution from St Helena Bay northwards along the west coast. Skinner and Smithers (1990) suggest a somewhat broader distribution southwards for this species, and suggest that this stretches from slightly south of St Helena Bay, into the Saldanha area. The three species found in the HDP1 fossil assemblage which are not present in the area today are *Zelotomys woosnami*, *Otomys slogetti* and *Elephantulus rupestris* (See Appendix S). The latter is currently found much further to the north, with an extensive distribution beginning slightly to the south of the Orange River, and then stretching northwards along the length of Namibia, but excluding the coastal areas of the Namibian west coast (Stuart and Stuart 2001). The current distribution of *Zelotomys woosnami* is confined to arid and semi-arid areas of the subregion, and *Otomys slogetti* is generally found at high altitudes in rocky areas in the eastern parts of the Cape Province, in Lesotho, and in parts of north-western Natal (Skinner and Smithers 1990, Stuart and Stuart 2001). The appearance of *O. slogetti* at HDP1 supports the statement made by Davis (1962), who, somewhat contrarily to the distribution noted by Skinner and Smithers (1990) and Stuart and Stuart (2001), states that *O. slogetti* ranges fairly extensively in the South West Arid Region. The distribution of micromammalian species is likely to shift within relatively short periods, and the distribution patterns of these species may not be recorded with complete accuracy. This point is emphasised by the fact that *Dendromus mesomelas* was recovered from the Steenbokfontein modern owl pellet collections, although the distribution of this species is noted as not extending further North than St Helena Bay (De Graaff 1981, Stuart and Stuart 2001).

Chapter ten

Results: The taphonomy and taxonomy of the microfaunal assemblages from Hoedjiespunt 1

10.1 Introduction

This chapter presents the results of a taxonomic and taphonomic study of the postcranial and cranial micromammal remains from Hoedjiespunt 1 (HDP1) made by the author. No taphonomic study has previously been done on the micromammals from HDP1, and only a tiny sample of micromammals have been identified. This chapter will explore the differences, if any, between the taxonomy and taphonomy of the two horizons, ROOF and HOMS.

10.2 The taphonomy of the cranial bones and teeth from Hoedjiespunt 1

10.2.1 Digestion

Corrosion and digestion on the micromammals from Hoedjiespunt 1 was examined with a light microscope, using variable magnification. The results from an analysis of HOMS and ROOF, the two main fossil-bearing horizons at HDP1, are presented separately in order to ascertain if they were accumulated by different agent(s), or represent separate depositional events. The use of the terms 'corrosion' and 'digestion' in this chapter are used in the same sense as defined in Chapter five.

10.2.2 Distinguishing digestion and corrosion on the Hoedjiespunt 1 micromammals

It is necessary at this point to discuss the post-depositional corrosion observed on the fossils at HDP1 as this corrosion affected most of the fossil material and complicated identification of digestion. Corrosion was found to have affected, and in some cases completely obscured, the original, predator-induced etching, which resulted during digestion of the micromammals. The corrosion observed on the micromammal bones and teeth at HDP1 affected both the enamel and dentine of teeth equally, and occurred in areas which varied in size and shape. The penetration of the corrosion observed on the HDP1 assemblages varied from superficial to deep penetration. A preliminary investigation of the postcranial bones indicated the same frequency of corrosion as seen on the incisors, and a separate taphonomic assessment was not deemed necessary.

The generally advanced degree of alteration on the surfaces of bones and teeth from corrosion was very different to the relatively light etching that appeared to have occurred as a result of digestion. The corrosion generally etched deeply into the enamel and dentine, while digestion was generally light and affected dentine and enamel relatively superficially.

As mentioned previously, the vast majority of fossils showed evidence of corrosion. This is clearly illustrated by the fact that 286 out of 293 murid and mole rat mandibular and maxillary incisors show evidence of corrosion. The advanced degree of corrosion on many of the incisors made assessing digestion, particularly light digestion, very difficult. In many of the micromammal incisors, corrosion was so extensive, and had etched so deeply into enamel and dentine, that any assessment of digestion was impossible as, if present, it would have been totally removed by the subsequent corrosion. Due to the presence of corrosion on almost all the incisors, classification into digestion classes was, in many cases, made tentatively. Incisors classified tentatively, as well as those that could not be assessed due to advanced corrosion, were excluded from analysis. This is not likely to have affected the results as corrosion affected the incisors in both horizons indiscriminately.

Chapter three describes the methodology used to divide the isolated mandibular and maxillary incisors into breakage categories, for the purpose of assessing digestion on incisors. The incisor breakage categories '> tip present', and '< tip present' (these categories have been explained in Chapter three) are thought to be the most useful for assessing digestion, which frequently occurs at the tip (proximal end) of the incisor. The breakage category '> shaft' was thought to be a less reliable indicator of digestion as the proximal ends are missing from these incisors. This category showed such a similar pattern to that of the other two, however, that it was included on Table 10.1 and Table 10.2, which present the results of a study of mandibular and maxillary incisor digestion in HOMS and ROOF.

If HOMS and ROOF are combined, 169 (82.4 %) of the incisors show no visible signs of etching, 19 (9.3 %) show class 1 digestion, 14 incisors fall into class 2 (6.8 %), and 3 (1.5 %) into category 3. Only two *in situ* mandibular incisors were recovered, these incisors fell into etching classes 2a and class 0, respectively.

The digestive etching patterns observed on the tiny sample of six batheryergid incisors, showed a similar pattern. Two incisors from the breakage category '> shaft', and three of the

four other incisors in the breakage category '> tip present', showed no visible digestion. The remaining incisor fell into digestion class 2.

Unit name	Mandibular incisor breakage categories	Digestion classes: No visible digestion		light digestion				moderate digestion			extreme digestion		
		0	%	1	%	1(a)	%	2	%	3	%	4	%
HOMS	> tip present	15		2		0		1		0		0	
	< tip present)	4		1		0		1		0		0	
	> Shaft	4		2		0		0		0		0	
	Total number of incisors	23	*76.7*	5	*16.7*	0	*0*	2	*6.7*	0	*0*	0	*0*
ROOF	> tip present	33		5		0		3		0		0	
	< tip present)	24		1		0		0		1		0	
	> Shaft	7		0		0		0		1		0	
	Total number of incisors	64	*85.3*	6	*8.0*	0	*0*	3	*4.0*	2	*2.7*	0	*0*
	Total number of incisors: N=105	**87**	*82.9*	**11**	*10.5*	**0**	*0*	**5**	*4.8*	**2**	*1.9*	**0**	*0*

Table 10.1: The breakage and digestion of isolated mandibular incisors

Unit name	Maxillary incisor breakage categories	Digestion classes: No visible digestion		light digestion				moderate digestion			extreme digestion		
		0	%	1	%	1 (a)	%	2	%	3	%	4	%
HOMS	> tip present	16		4		0		3		1		0	
	< tip present)	2		0		0		1		0		0	
	> Shaft	6		0		0		0		0		0	
	Total number of incisors	24	*72.7*	4	*12.1*	0	*0*	4	*12.1*	1	*3*	0	*0*
ROOF	> tip present	44		1		0		4		0		0	
	< tip present)	8		2		0		1		0		0	
	> Shaft	6		1		0		0		0		0	
	Total number of incisors	58	*86.8*	4	*5.9*	0	*0*	5	*7.5*	0	*0*	0	*0*
	Total number of incisors: N=100	**82**	*82*	**8**	*8*	**0**	*0*	**9**	*9*	**1**	*1*	**0**	*0*

Table 10.2: The breakage and digestion of isolated maxillary incisors

10.2.3 Mandibular and maxillary breakage

In the tables below, the maxillary and mandibular breakage patterns of HOMS, ROOF and the small unit of HOMS/ROOF are shown, together with the number of *in situ* teeth. As Table 10.3 illustrates, very low numbers of mandibles and maxillae were recovered from HOMS

and ROOF. The mandibular and maxillary breakage patterns of the different micromammal species are shown separately as this provides information on how breakage may affect tooth loss in different species. For example, only one Otomyinae maxilla containing *in situ* molars was retrieved, indicating that this murid family is relatively more prone to tooth loss from jawbones.

Species	Number of mandibles	Mandibular breakage categories	Number of *in situ* teeth	No. of maxillae	Maxillary breakage categories	Number of *in situ* teeth
Aethomys namaquensis	1	IBB	2	0	-	-
Rhabdomys pumilio	3	IBB	4	1	ZM	1
Crocidura Cyanea	1	ARM	0	0	-	-
Indet. Otomyinae	-			1	ZM	1
Indeterminate murid	9	2x ARM 7x IBB	0	14	ZM	0

Table 10.3: Mandibular and maxillary breakage patterns: ROOF

Key: Mandibular breakage categories: IBB = Inferior border broken
ARM = ascending ramus missing
ARB = ascending ramus broken
Maxillary breakage categories: ZM = zygomatic missing

Species	Number of mandibles	Mandibular breakage categories	Number of *in situ* teeth	Number of maxillae	Maxillary breakage categories	Number of *in situ* teeth
Mystromys albicaudatus	1	IBB	2	0	-	-
Rhabdomys pumilio	0	-	-	3	ZM	5
Crocidura Cyanea	4	2x ARB 2x ARM	6	1	ZM	2
Indeterminate murid	15	1X ARM 14X IBB	0	15	ZM	0

Table 10.4: Mandibular and maxillary breakage patterns: HOMS

Key: Mandibular breakage categories: IBB = Inferior border broken
ARM = ascending ramus missing
ARB = ascending ramus broken
Maxillary breakage categories: ZM = zygomatic missing

Species	Number of mandibles	Mandibular breakage categories	Number of *in situ* teeth	Number of maxillae	Maxillary breakage categories	Number of *in situ* teeth
Rhabdomys pumilio	1	IBB	1	0	-	-
Crocidura Cyanea	1	ARM	2	0	-	-
Indeterminate murid	1	IBB	0	1	ZM	0

Table 10.5: Mandibular and maxillary breakage patterns: HOMS/ROOF

10.2.4 Molar loss

As explained in Chapter 3, tooth loss aids in assessing the degree of cranial breakage in an assemblage. Only six out of 31 murid mandibles, and four out of 35 murid maxillae (three of these were from *R. pumilio*) recovered from HDP1 retained some *in situ* molars. Of six *C. cyanea* mandibles, four retained some of their teeth, and one *C. cyanea* maxillae with a few *in situ* teeth, was recovered.

Table 10.6 and Table 10.7 show the percentage of murid molar tooth loss from mandibles, and maxillae. No soricid, macroscelid or bathyergid cranial material has been included in the following tables as research by Laudet *et al.* (2002) and Manthi (2002) suggests that the morphological differences between these families may result in differential breakage, and preservation patterns. Tooth loss was not calculated for these families as sample size was too small to provide relevant results.

Unit	Number of mandibles	Number of in situ molars	Molar loss (a)	No. molars expected (b)	% molar loss ($^a/_b$ x 100)
ROOF	13	6	33	39	85
HOMS	16	2	46	48	96
HOMS/ROOF	2	1	5	6	83

Table 10.6: Murid mandibular molar loss

Unit	Number of maxillae	Number of in situ molars	Molar loss (a)	No. molars expected (b)	% molar loss ($^a/_b$ x 100)
ROOF	15	1	44	45	98
HOMS	18	5	49	54	91
HOMS/ROOF	1	0	3	3	100

Table 10.7: Murid maxillary molar loss

The advanced degree of cranial breakage at HDP1 has led to an extremely high percentage of mandibular and maxillary molar loss in both HOMS and ROOF. There are no obvious differences between these two units.

10.2.5 Incisor loss

Mandibular incisor loss is shown on Table 10.8. The advanced degree of cranial breakage and fragmentation of the Hoedjiespunt micromammals is indicated by the fact that only one mandible in HOMS, and one in ROOF, retained an incisor, resulting in just over 92 % incisor loss in both units.

Unit	Number of mandibles	Number of in situ incisors	Incisor loss (a)	Number of incisors expected (b)	% incisor loss ($^a/_b$ x 100)
ROOF	13	1	12	13	92.3
HOMS	16	1	15	16	93.8
HOMS/ROOF	2	0	2	2	100

Table 10.8: Mandible incisor loss

Post-depositional breakage resulted in a very low proportion of premaxillae being recovered. This is illustrated by the fact that ROOF contained only three, and HOMS two, premaxillae. Maxilla incisor loss was 100 %, as none of these premaxillae were found to have retained an incisor.

10.2.6 Comparing isolated molars and incisors with tooth loss from the mandibles and maxillae

Cranial breakage is further quantified in Table 10.9, where the high number of isolated molars reflects a corresponding loss of mandibles and maxillae from the fossil assemblage.

Unit	Number of mandibles and maxilla	Number of isolated molars (a)	Mandible and maxilla molar loss (b)	% isolated molars ($^a/_b$ x 100)
ROOF	28	249	95	262
HOMS	34	168	77	218
HOMS/ROOF	3	3	8	38

Table 10.9: Percentage of isolated molars

Cranial breakage appears to be severe in both HOMS and ROOF, with breakage appearing to be somewhat more advanced in ROOF. This unit contains a higher percentage of isolated

molars, 262 %, as compared with 218 % in HOMS. It is hard to assess if the difference in the percentage is significant or not as the numbers involved are not great and a certain amount of in-site variability may be expected.

10.3 The breakage patterns of the postcranial bones

The mole, mole rat and shrew limb bones occurred in very low frequencies. A count of the limb bones from these species yielded eight mole femora, humeri and ulnae, and five mole rat tibiae, femora and ulnae. Some eighteen shrew limb bones were found, and the breakage patterns of these, and the moles and mole rats, may be seen in Table 10.10. Given the small number of mole rat limb bones recovered from HDP1, a surprisingly large number of 53 mole rat phalanges were recovered from HDP1, 21 in HOMS, and the remainder in ROOF.

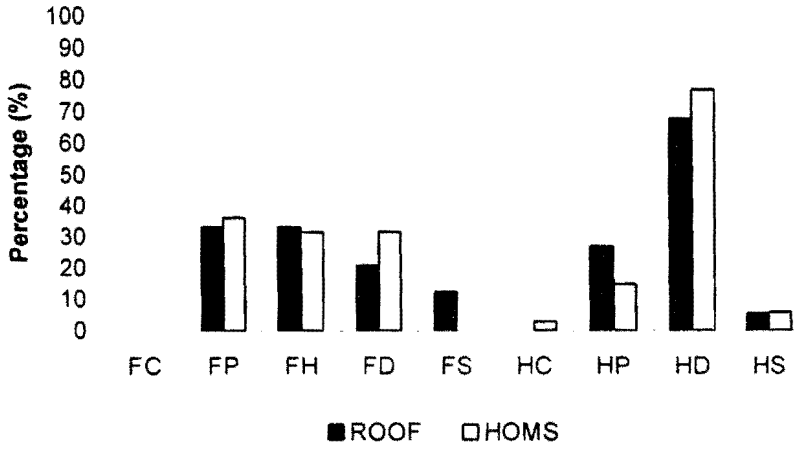
	FC	FP	FD	FS	HC	HP	HD	HS	TC	TP	TD	TS	UC	UP	UD	US	RC	RP	RD
Shrew		4	3		3		3			1		2		2					
Mole		2				1	3						1	1					
Mole rat		1	1								2			1					

Table 10.10: Breakage patterns of the shrew, mole and mole rat limb bones from HDP1

Key: FC= femur complete, FP = femur proximal, FH = femur head, FD = femur distal, FS = femur shaft
HC= humerus complete, HP = humerus proximal, HD = humerus distal, HS = humerus shaft
TC= tibia complete, TP = tibia proximal, TD = tibia distal, TS = tibia shaft
UC= ulna complete, UP = ulna proximal, UD = ulna distal, US = ulna shaft
RC= radius complete, RP = radius proximal, RD = radius distal

Metacarpals were not nearly so common and only six of these bones were recovered from ROOF. Many of the bones belonging to *Bathyergus*, (the largest of the micromammal species found at HDP1) are likely to have been retrieved by excavators, while the smaller micromammal species, together with the smallest foot and paw bones of *Bathyergus*, appear to have been left, unrecovered, in the bulk samples.

Figure 10.1 and Figure 10.2 illustrate the breakage patterns of the murid limb bones. A breakdown of the figures and percentages pertaining to these figures may be seen in Appendix T.



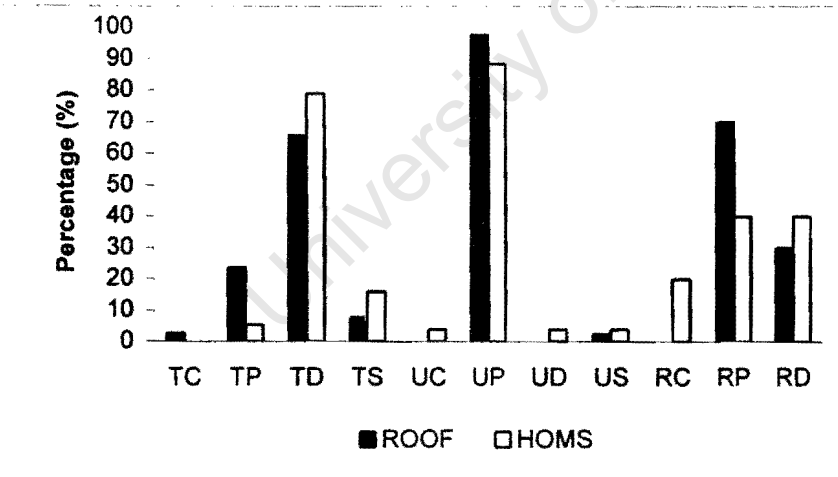
The NISP for the limb bones shown on the adjacent Figure 10.1 are as follows:

HOMS	ROOF
24 femora	28 femora
36 humeri	37 humeri

Figure 10.1: Relative completeness of the femora and humeri from HDP1

Key: FC= femur complete, FP = femur proximal, FH = femur head, FD = femur distal, FS = femur shaft
HC= humerus complete, HP = humerus proximal, HD = humerus distal, HS = humerus shaft

The breakage patterns of the murid postcranial bones in ROOF and HOMS are very similar, and show high percentages of distal and proximal bones, together with very few complete bones, reflecting post-depositional breakage of the fossil assemblages. They differ most as regards radius breakage, however, the sample sizes involved are small and may be affecting the observed patterning.



The NISP for the limb bones shown on the adjacent Figure 10.2 are as follows:

HOMS	ROOF
21 tibiae	38 tibiae
26 ulnae	39 ulnae
5 radii	10 radii

Figure 10.2: Relative completeness of the tibiae, ulnae and radii from HDP1

Key: TC= tibia complete, TP = tibia proximal, TD = tibia distal, TS = tibia shaft
UC= ulna complete, UP = ulna proximal, UD = ulna distal, US = ulna shaft
RC= radius complete, RP = radius proximal, RD = radius distal

10.4 Postcranial and cranial proportions

Postcranial to cranial proportions was calculated, as described in Chapter three, and HOMS yielded a percentage of 177 %, and ROOF 232 %.

HOMS:

$$\frac{24 + 36}{16 + 18} \times \frac{100}{1} = 176.5\%$$

ROOF:

$$\frac{28 + 37}{13 + 15} \times \frac{100}{1} = 232.1\%$$

These results indicate a surplus of femora and humeri, relative to mandibles and maxillae, in both units, although there is a slightly higher proportion of postcranial, relative to cranial, bones in ROOF. The differences are not marked, however, as the numbers involved are relatively small.

10.5 Skeletal element abundance

The skeletal element abundance of the various cranial and postcranial bones from HOMS and ROOF may be seen in Figure 10.3. The numbers and percentages pertaining to this figure may be seen in Appendix U. The skeletal element proportions shown by the barn owl mean calculated by Andrews (after Andrews (1990), Appendix, Table 12), in his extensive analysis of multiple barn owl pellet assemblages, is shown on the same figure.

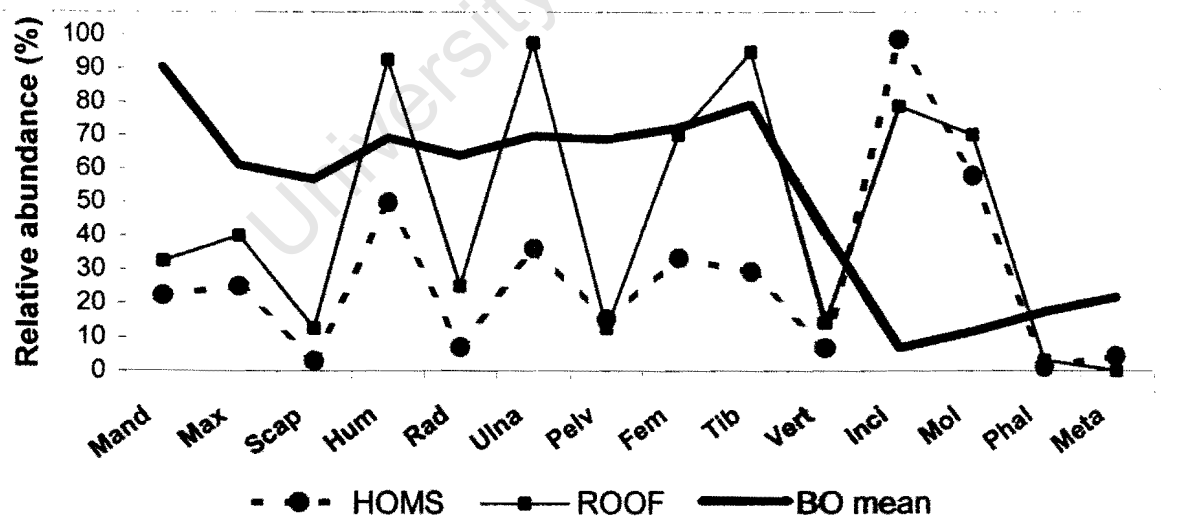


Figure 10.3: The relative abundance of the Hoedjiespunt 1 assemblages compared with the barn owl

The same limb bones have experienced preferential survival in both ROOF and HOMS, however, ROOF shows a far higher relative abundance of humeri, ulnae, femora and tibiae relative to mandibles and maxillae.

10.6 The taxonomy of the micromammal species from Hoedjiespunt 1

Tables 10.11 and 10.12 shows the numbers of isolated and *in situ* molars from the various micromammal species found at HDP1. The soricids, macroscelids and bathyergids, which were found in very low frequencies, are shown separately from the murids in Table 10.11.

Taxa	Isolated and *in situ* molars ROOF	HOMS	ROOF/HOMS
Elephantulus rupestris	0	3	0
Crocidura cyanea	1	10	1
Bathyergus suillus	4	3	0
Cryptomys hottentotus	1	0	0
Mole Rat sp.	0	1	0
Soricid sp.	0	1	0
Macroscelid sp.	1	0	0

Table 10.11: The soricid, macroscelid and bathyergid species from Hoedjiespunt 1: Isolated and *in situ* molars

Table 10.12 shows the upper and lower molars of the various murid species from HDP1. The n/a, 'not applicable', in certain of the rows in Table 10.12 indicates that no numbers are available for these molars as the M_2, M_3 and M^2 molars of the Otomyinae were simply recorded as '*Otomys/Parotomys*'. One *in situ*, and 156 isolated M_2, M_3 and M^2 Otomyinae molars were recorded in this manner.

Murid species	ROOF MU^1	MU^2	MU^3	ML_1	ML_2	ML_3
Aethomys namaquensis	0	0	0	2	2	0
Mystromys albicaudatus	3	0	2	8	7	0
Praomys verreauxi	0	0	0	2	0	0
Rhabdomys pumilio	7	4	5	15	4	1
Tatera afra	0	0	0	1	0	0
Zelotomys woosnami	1	0	0	0	1	0
Otomys irroratus	2	n/a	3	4	0	0
Otomys saundersae	11	n/a	9	2	n/a	n/a
Otomys slogetti	2	n/a	9	2	n/a	n/a
Otomys unisulcatus	9	n/a	5	14	n/a	n/a
Parotomys brantsi	7	n/a	12	4	n/a	n/a

Table 10.12: The murid species from ROOF and HOMS: Isolated and *in situ* molars

Table 10.12 (cont...)

	HOMS					
Murid species	**MU^1**	**MU^2**	**MU^3**	**ML_1**	**ML_2**	**ML_3**
Aethomys namaquensis	0	0	0	1	0	0
Mystromys albicaudatus	0	1	0	3	1	0
Praomys verreauxi	0	0	0	2	0	0
Rhabdomys pumilio	9	4	2	8	5	1
Tatera afra	1	0	0	0	0	0
Zelotomys woosnami	0	0	0	1	0	0
Otomys irroratus	1	n/a	2	7	n/a	n/a
Otomys saundersae	13	n/a	5	4	n/a	n/a
Otomys slogetti	1	n/a	6	2	n/a	n/a
Otomys unisulcatus	0	n/a	2	6	n/a	n/a
Parotomys brantsi	3	n/a	5	2	n/a	n/a

Figure 10.4 shows the percentage representation of the Otomyinae in HOMS and ROOF, relative to one another. The three molars that were used for identification of the Otomyinae, namely the MU^1, MU^3 and ML_1, were used to calculate total numbers for each species.

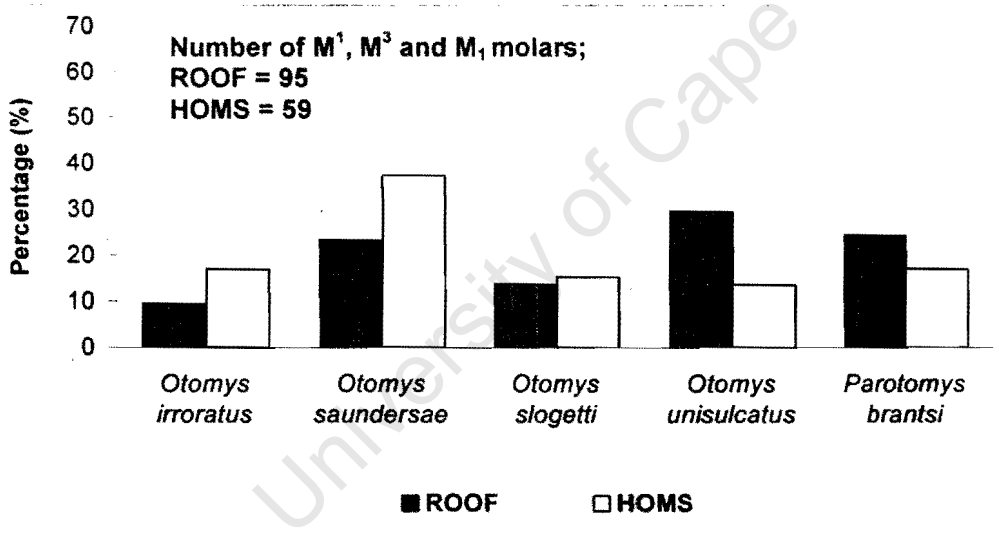


Figure 10.4: Percentage representation of the Otomyinae from HDP1

Using the M^1, M^3 and M_1 molars to represent the Otomyinae results in a pattern similar to that seen when only the M^1 and M_1 molars are used, and it was not deemed necessary to illustrate both situations. Figure 10.4 illustrates the percentages in which the Otomyinae occur in HOMS and ROOF, and indicates that there are some differences between the two horizons. The most marked differences between ROOF and HOMS lie in the relatively high percentage of *O. unisulcatus* in ROOF (30 %, as opposed to 14 % in HOMS), and *O. saundersae* in HOMS, which occurs in percentages of 37 % as compared with 23 % in ROOF. The two species, *O irroratus* and *P. brantsi,* occur in percentages which do not differ by more than 10

%, and *O. slogetti* occurs in very similar percentages in both ROOF and HOMS. The same Otomyinae species are represented in both HOMS and ROOF and they show a pattern which is broadly similar.

Figure 10.5 shows the percentage representation of the other murid species in the site, excluding the Otomyinae. All isolated and *in situ* M^1 and M_1 molars were used to calculate the percentage representation of these murid species, as these were the most abundant molars.

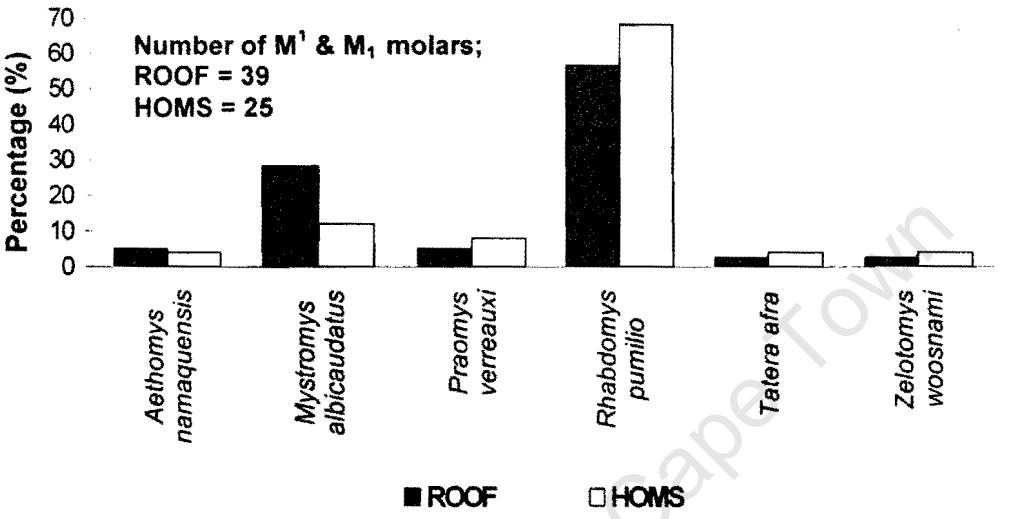


Figure 10.5: Percentage representation of the murids, excluding the Otomyinae, from HDP1

Figure 10.5 illustrates that there are no marked differences in terms of the overall distribution of the murids in HOMS and ROOF, though there are some differences in the percentages in which the individual species occur. For example, though *R. pumilio* dominates in both ROOF and HOMS, it appears in a relatively high percentage in HOMS, and *M. albicaudatus*, the next most frequently appearing species in both units, occurs in relatively high percentages in ROOF.

The soricids, bathyergids and macroscelids do not appear on any of the figures showing species occurrence at HDP1 as they have a different dentition to the murids and occurred in very low frequencies, with an MNI of 1 for all three families.

10.6.1 The non-mammalian microfauna from Hoedjiespunt 1

A study of the limb bones from the non-mammalian microfauna at HDP1 yielded totals of 31 frog, one small bird, and three lizard limb bones. Some 22 small snake vertebrae were recovered from L16, seven of which were found in HOMS, and the remainder in ROOF.

Chapter eleven

The taxonomy, taphonomy and palaeoecology of the micromammals from Hoedjiespunt 1

11.1 Introduction

This chapter discusses the results of the taphonomic and taxonomic study of the postcranial and cranial micromammal remains from HDP1 presented in this thesis. These results are used to assess post-depositional breakage, and to establish the identity of the agent(s) responsible for the accumulation of the HDP1 micromammals. Finally, the palaeoenvironmental implications of the micromammal species from HDP1 are discussed.

11.2 The taphonomy of the cranial bones and teeth from Hoedjiespunt 1

11.2.1 Digestion and corrosion on the micromammals

The two most conspicuous taphonomic features of the HDP1 micromammal assemblages are the advanced degree of breakage of, and the extensive corrosion discernible on, the micromammal bones and teeth. Almost all of the micromammal bones and teeth showed evidence of corrosion, postcranial and cranial bones being equally affected.

Stynder (1997) notes that the macro faunal bones had been affected by corrosion while buried and were frequently very fragile. The most affected bones had a chalky, white appearance and had to be stabilized with paraloid before being excavated (Stynder 1997). The corrosion described sounds very similar to that observed on the HDP1 micromammmals, where affected areas frequently had a white, powder-like appearance.

The fact that corrosion generally occurred in discrete areas on the micromammals from HDP1, rather than all over the surface of the fossil, makes it different to the classic description of corrosion caused by sediment. Digestion is usually distinguishable from corrosion in that the widespread etching caused by soil corrosion differs to the etching of digestion which is usually concentrated in areas, such as the tip of the incisors, or on the epiphyses of limb bones (Andrews 1990). The corrosion at HDP1 indicates that local factors in the environment, rather than gross soil characteristics, may cause 'patchy' corrosion. Figure 11.1 illustrates the post-depositional corrosion observed at HDP1. The same corroded, whitened areas may be seen on bone, and on the enamel and dentine of teeth. The following

photographs of murid and shrew bones, and murid incisors, were taken with a microscope, using variable magnification.

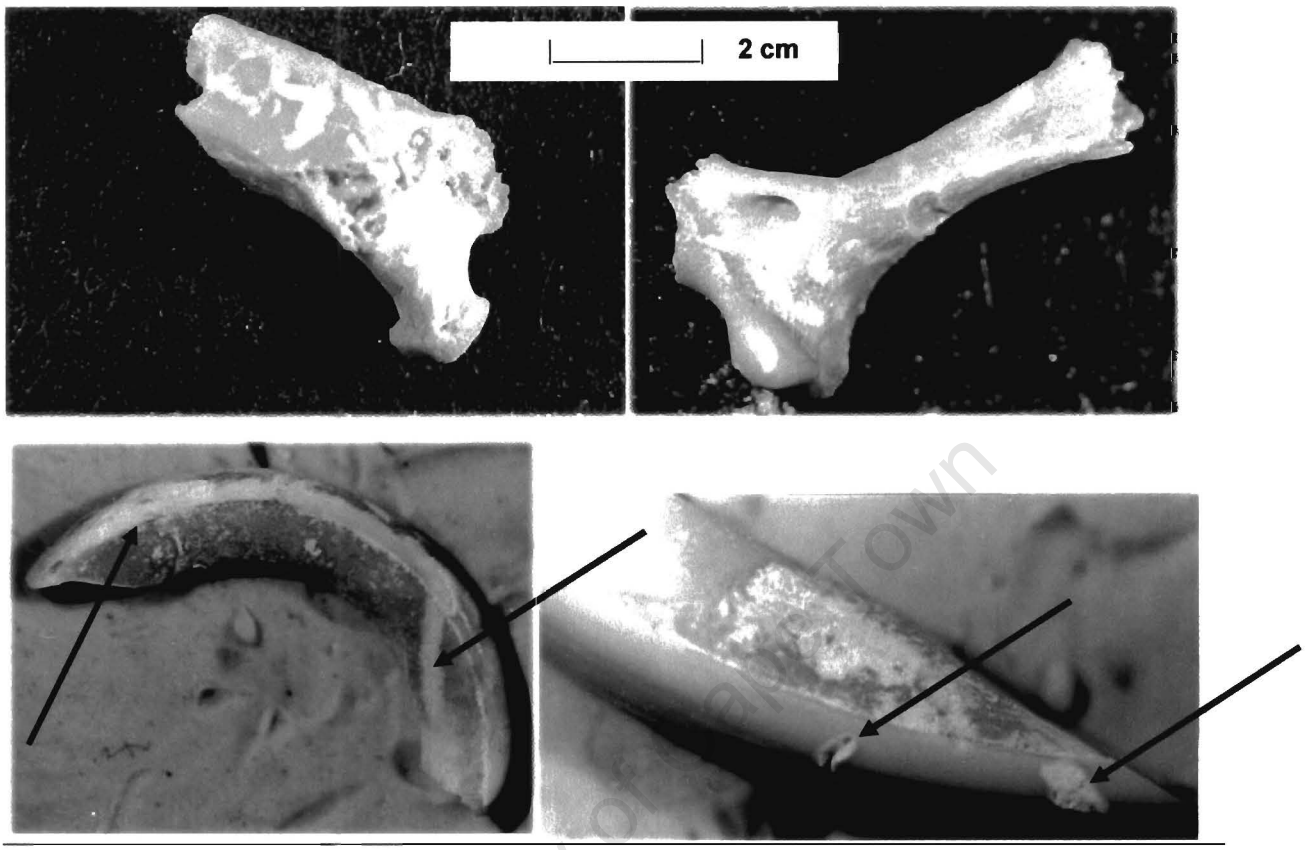


Figure 11.1: The post-depositional corrosion at HDP1

The femur and humerus, top left and right above, illustrate the patchy, variable nature of the corrosion which is visible in the whitened areas of these bones. The murid incisors in the bottom row illustrate how the corrosion manifested on incisors. The right hand photo illustrates how it sometimes etched deeply into a small, discrete area, leaving surrounding areas untouched. The incisor on the left illustrates the problem of differentiating corrosion from digestion. This incisor shows corrosion along the enamel/dentine border, and in the broad strip indicated by the second arrow. Digestion appears to have occurred prior to post-depositional corrosion, but separating out the exact modifications caused by both was extremely difficult, if not impossible.

In differentiating between corrosion and digestion there is likely to be more room for error in the case of incisors which have experienced light digestion, as the light digestion classes of '0' and '1' are difficult to distinguish on incisors where corrosion has taken place. Digestion is more easily distinguished from corrosion in the case of incisors where etching is fairly

advanced. This may have resulted in a bias towards the accurate identification of more advanced degrees of digestion, but despite this, the vast majority of the incisors found in both HOMS and ROOF show no, or light digestion.

Approximately 73-77 % of the mandibular and maxillary incisors in HOMS and ROOF fell into digestion class 0, and showed no visible etching. In HOMS, slightly more incisors, namely 85-87 % showed no signs of etching. A slightly lower percentage of mandibular and maxillary incisors from ROOF fell into digestion class 1, as compared to HOMS. Some 12-16 % of the incisors from HOMS, and 6-8 % of incisors from ROOF, fall into class 1. Although the above percentages indicate some variation between HOMS and ROOF, the differences in the actual numbers of teeth falling into digestion classes 1 and 2 are small. The incisor digestion patterns show a general homogeneity in the horizons of both HOMS and ROOF. There in no compelling evidence to suggest that they have been accumulated by different predators.

If the digestion patterns of the combined horizons of HOMS and ROOF are studied, around 82 % of the incisors showing no visible etching, and some 9 % show light (category 1) digestion. Approximately 8 % of the total incisors in HOMS and ROOF combined, fell into the more advanced etching classes, class 2 and class 3. Andrews (1990) writes that on average, 8-13 % of the incisors from category 1 predator assemblages show signs of digestion. Some 17 % of the mandible incisors, and 18 % of the maxillae incisors from HDP1 showed digestion, which falls close to the range of digestion shown by a category one predator. The barn owl (*Tyto alba afinis*) is the classic example of a category 1 predator which causes minimal digestion and damage to prey bones and teeth. The next category of predator(s), category 2, which includes the giant/verreaux eagle owl (*Bubo lacteus*), may not be ruled out as a potential accumulator in terms of the percentage of incisors showing digestion, as 20-30 % of the incisors from this category predator show digestion. The giant/verreaux eagle owl is not considered a likely accumulator of the HDP1 micromammals, however, as this owl is an opportunistic feeder and is remarkable for its large prey-size range (Andrews 1990a). A category two predator is also not considered likely as digestion is more intense in this category than the previous one, and only 8 % of the incisors from HOMS and ROOF fall into etching classes 2 and 3. The spotted eagle owl (*Bubo africanus*) or Cape eagle owl (*Bubo capensis*) may not entirely be ruled out as contributors to the HDP1 assemblage, however, as the sample size investigated for the former species by Andrews

(1990) was small, and no assemblages from the latter have been examined. The Cape eagle owl is considered a less likely contributor to the HDP1 assemblages than the spotted eagle owl as the Cape eagle owl usually concentrates on one of the larger prey species available, such as the dassie, molerat or hare (Steyn and Tredgold 1977, Andrews 1990). The marsh owl, grass owl and wood owl are all disqualified as potential predators on the basis that they roost and nest in hollows in the grass, or in trees.

The sample of mole rat incisors from the fossil horizons, five out six of which showed no signs of digestion, is too small to reach any definite conclusions. The mole rats may have been taken by a different predator to the micromammals. Lack of digestion may indicate that the heads were not consumed, or that the animals died from natural causes. Spotted eagle owl chicks are, for example, usually fed decapitated prey by their parents (Steyn 1984).

It is interesting to note that the incisor breakage category '> Shaft' showed very similar patterns of digestion to the categories which included the tip, suggesting that the separation of the incisor into different breakage categories when assessing digestion may not be necessary.

11.2.2 The breakage patterns of the cranial bones

The breakage patterns of the mandibles and maxillae, together with the low frequency of etched incisors, clearly indicate that quite extensive post-depositional breakage has taken place as the cranial bones would have been deposited in a relatively complete state if the predator were a category 1 predator. No complete maxillae or mandibles were found in HOMS or ROOF, and all the maxillae found fell into the 'ZM' category which described maxillae which had sustained the most advanced damage. The majority of murid mandibles showed relatively advanced damage and fell into the 'IBB' breakage category. The soricid mandibles were relatively more complete, with the majority showing damage to the ascending ramus, but not the body of the mandible. This relative robusticity of shrew mandibles has been noted by Denys *et al.* (1996b) and Manthi (2002).

Manthi (2002) noted that patterns of micromammal cranial breakage in the SBYC palaeontological assemblage appeared to be affected by the dominance of a relatively large and robust species, in this case, high numbers of maxillae from the Gerbillid *Tatera afra*. A similar result was observed at HDP1 where the relatively high percentage of maxillae at the site is attributed to the fact that approximately 60 % of the HDP1 murids belonged to the Otomyinae. These relatively robust maxillae appear to have experienced preferential

preservation relative to many of the other murid species. Other authors such as Laudet and Hamdine (2001), and Denys *et al.* (1996b) have also noted that certain micromammal species experience differential preservation. Caution should therefore be used when using micromammal cranial breakage patterns to identify the predator.

11.2.3 Incisor and molar loss

Incisor and molar loss was calculated in order to ascertain the degree of post-depositional alteration. It became clear in the early stages of analysis that post-depositional breakage was likely to have obscured, or even over-written, any predator-related breakage patterns. Mandibular and maxillary molar loss from HOMS and ROOF is notably higher than the small carnivore assemblages investigated by the author, and all the predators investigated by Andrews (1990), with one exception. This exception is the pine marten, which showed a maxillary molar loss of 92 % (Andrew 1990) and thus came close to the 85 % and 96 % mandibular molar loss, and 98 % and 91 % maxillary molar loss, shown by ROOF and HOMS, respectively. The barn owl assemblages investigated by Andrews, which represent a category 1 predator, showed a 27 % molar loss from the maxilla, and a 34 % molar loss from the mandible. The fact that almost no Otomyinae mandibles or maxillae were found with *in situ* molars suggests that the Otomyinae may lose teeth more easily than certain other murid species. The domination of the Otomyinae of the murid faunal assemblage at HDP1 may have contributed to the high number of isolated molars found in both HOMS and ROOF, although there is a high percentage of molar loss in the other murid species as well.

Mandibular and maxillary incisor loss at HDP1 is very much higher than all the predator assemblages investigated by Andrews, with the exception of the white-tailed mongoose, *Ichneumia albicauda,* which showed a 100% loss. The 93 % incisor loss from HOMS and ROOF is considerably greater than incisor loss from maxillae and mandibles recovered from a category 1 predatory, the barn owl, which showed an incisor loss of 26 % and 3 %, respectively (Andrews 1990). Maxillae are more prone to breakage than mandibles, and it would seem that once a certain level of breakage occurs, most maxillary incisors become isolated. At HDP1 no *in situ* maxillary incisors were recovered.

The results for tooth loss and the percentage of isolated teeth for the unit HOMS/ROOF is very similar to those of HOMS and ROOF, though the small micromammal sample obtained from this unit precludes any real conclusions being reached.

11.2.4 Comparing isolated molars and incisors with tooth loss from the mandibles and maxillae

Andrews (1990) obtained a percentage of 96 % for isolated molars for the barn owl assemblages. This figure suggests that almost all the isolated teeth could be accounted for as coming from the mandibles and maxillae present in the pellet assemblages, and there had been almost no loss of isolated teeth, or loss of jaws, from the pellets. The owl, diurnal bird of prey and small carnivore assemblages investigated by Andrews (1990) generally showed a deficit of isolated molars. The only two of the predators investigated by Andrews showing a surplus of isolated teeth was the little owl, which showed a percentage of 156 % isolated molars, and the kestrel with 139 %. The light degree of etching observed at HDP1 rules out the possibility of this type of predator being responsible for the micromammal accumulations. HOMS and ROOF show a homogenous pattern and a high degree of post-depositional destruction is indicated. The extremely high percentages of isolated molars from both HOMS (218 %) and ROOF (262 %) suggests that the majority of mandibles and maxillae initially present in the sample have been destroyed, and the isolated teeth are all that remain to represent these jaws.

In conclusion, the extensive mandibular and maxillary breakage, extremely high percentages of molar and incisor loss, and the high percentage of isolated molars observed at HDP1, is inconsistent with the incisor digestion patterns of ROOF and HOMS which suggest the involvement of a category 1 predator. An advanced degree of post-depositional breakage at HPD1 is clearly indicated. Post-depositional alteration of the assemblage has erased the original, predator-induced breakage patterns.

11.3 The taphonomy of the postcranial bones

No complete femora were found at HDP1. Under 4 % of the humeri, tibiae, and ulnae were complete. The limb bones show a pattern typical of an advanced degree of breakage, namely low percentages of complete bones, together with a high percentage of the relatively robust, distal humerus and tibia, and proximal ulna, radius, tibia and femur. The categories 'femur head' and 'femur proximal' account for 66.6 % of the femora in ROOF, and 68.1 % in HOMS, indicating an advanced degree of breakage. Over 88 % of the ulnae in both HOMS and ROOF are represented by the proximal ulna. The breakage patterns of the postcranial bones in HOMS and ROOF are very similar, the only marked difference being the relatively high frequencies of complete radii found in HOMS, however, the small sample size, in all

likelihood, affected these results. Incisor digestion indicates that a category 1 predator was involved in the fossil accumulations. Such a predator would not produce the degree of fragmentation observed in the postcranial assemblages from HDP1. As in the cranial bones, postcranial breakage patterns indicate that post-depositional breakage has greatly altered the assemblage.

11.4 Postcranial to cranial proportions

The calculation of postcranial to cranial proportions indicated a surplus of femora and humeri, relative to mandibles and maxillae, in both units. ROOF shows a larger surplus of femora and humeri than HOMS, indicating a greater loss of cranial, relative to postcranial bones, in this unit. This result is in agreement with the fact that ROOF contained a higher percentage of isolated molars, indicating a slightly more advanced degree of cranial breakage in this unit.

11.5 Skeletal element proportions

A common feature of the assemblages in HOMS and ROOF is that a relatively low percentage of mandibles and maxillae are found together with high numbers of isolated incisors and molars. The relative abundance of the limb bones relative to the teeth and cranial bones differs quite considerably, however, in HOMS and ROOF. In HOMS, teeth, in particular the incisors, are found in high frequencies relative to the other skeletal bodyparts, and the relative abundance of all but the teeth shows a relatively 'smooth' pattern in that there are no great differences between the peaks and troughs, and generally, relative abundance is low. A different pattern may be observed in ROOF where the percentage of incisors is high, but this is matched by even higher frequencies in other skeletal elements such as the humerus, ulna, femur and tibia, and overall relative abundance is characterised by very large peaks and troughs. This difference is rather unexpected, given the fact that the breakage patterns of the postcranial and cranial bones in HOMS and ROOF, and the incisor digestion patterns, are generally very similar, although there is evidence that ROOF contains an assemblage which has suffered rather more post-depositional breakage. It is possible that the high percentages in which the humerus, ulna, femur and tibia occur, may have resulted from an increase in the more robust bones, relative to the more fragile ones, in the fossil assemblage, as post-depositional breakage removed the latter from the fossil assemblage. This does not explain the general difference in relative abundance in HOMS and ROOF, however, and issues relating to these differences are discussed further in Chapter 12. Figure 11.2 and Figure 11.3

show the relative abundance of the various small carnivore and owl pellet assemblages investigated by Andrews (1990). The relative abundance of the various diurnal birds of prey, which are not shown in the following figures, show a similar pattern to the small carnivores (Andrews 1990).

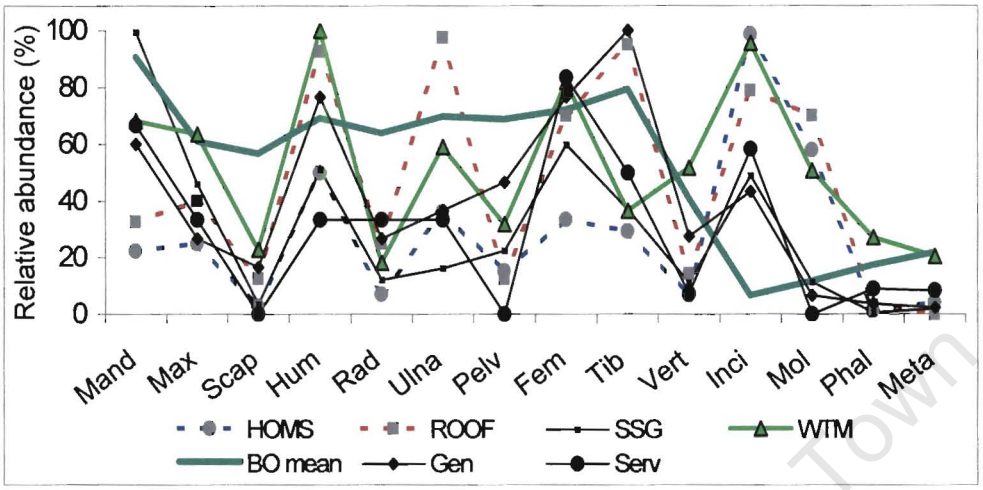


Figure 11.2: The relative abundance of small carnivore assemblages as compared with HOMS and ROOF (After Andrews (1990), Appendix, Table 13, page 213, and Matthews in prep.)

Key: SSG = small spotted genet, WTM = white tailed mongoose BO = barn owl mean
Gen = Genet Serv = serval

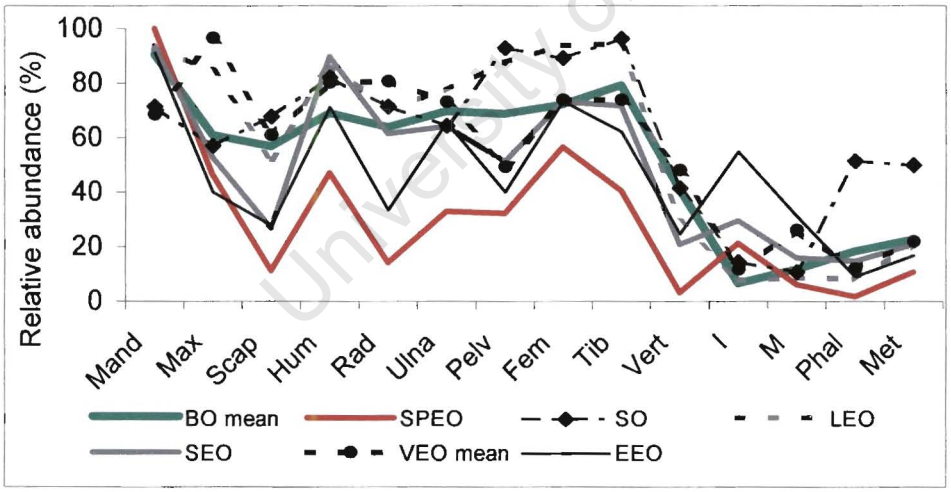


Figure 11.3: The relative abundance of owl pellet assemblages (After Andrews (1990), Appendix, Table 12, page 209-213)

Key: BO mean = barn owl mean SPEO = spotted eagle owl, SO = snowy owl LEO = long eared owl
SEO = short eared owl VEO = Verreaux (giant) eagle owl EEO = European eagle owl

The owls, small carnivores and diurnal birds of prey show a common pattern in that mandibles and maxillae are found in high proportions relative to the other postcranial bones, indicating the relative robusticity, and survival, of the cranial bones in predator scats and

pellets. There are generally slightly more mandibles than maxillae in these assemblages. ROOF and HOMS differ from almost all the predator assemblages investigated by Andrews (1990) in the relatively low abundance in which mandibles and maxillae occur. This is found together with a correspondingly high proportion of isolated molars and incisors. It would appear that HOMS and ROOF have been subjected to post depositional damage which has overwritten the original, predator-related pattern of skeletal element abundance, and the preferential survival of mandibles and maxillae shown by predator assemblages has been erased.

11.6 Summary of the taphonomy

ROOF was found to contain a higher percentage of isolated molars than HOMS, and also showed a greater loss of cranial, relative to postcranial, bones. This may be interpreted as indicating that there has been relatively more post-depositional breakage in ROOF which has negatively impacted preservation of the cranial bones. The situation is not clear cut, however, as HOMS shows a slightly higher percentage of mandibular and maxillary tooth loss. A study of skeletal element proportions indicated a difference between HOMS and ROOF, with the latter showing a pattern of greater abundance in the more robust limb bones and teeth, relative to the mandibles and maxillae. The reason for these differences are not clear.

An advanced degree of breakage at HDP1 is indicated by the cranial and postcranial breakage patterns, substantial tooth loss, high percentages of isolated teeth relative to mandibles and maxillae, and the pattern of skeletal element abundance. All of the indices measuring breakage show a degree of breakage which is far greater than the patterns observed in almost all the predator assemblages investigated by Andrews (1990). The HDP1 pattern of skeletal element abundance of the cranial bones, relative to isolated teeth, differs from all but one of the predator assemblages investigated by Andrews (1990). Once again, post-depositional breakage has clearly affected the original patterning of the assemblage.

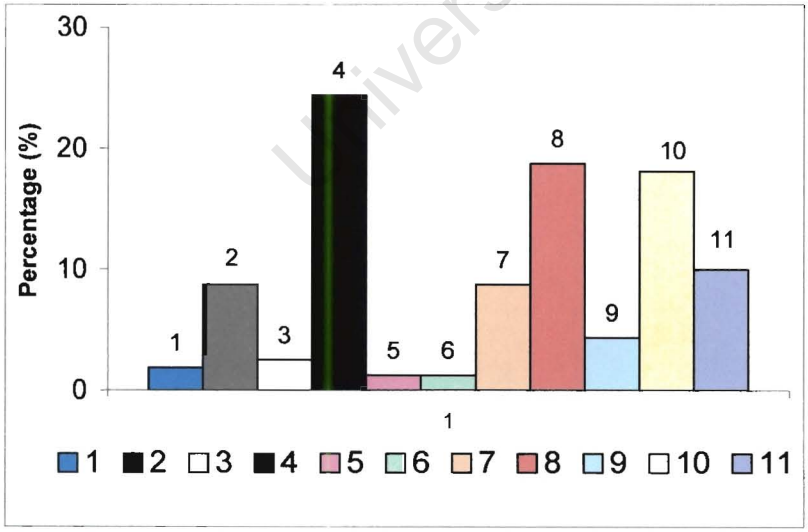
The incisors in both HOMS and ROOF show relatively similar patterns of digestion, with approximately 73-77 % of the incisors in HOMS, and 85-87 % of the incisors in ROOF falling into digestion class 0. The percentage of incisors falling into the other digestion classes in HOMS and ROOF vary by less than 10 %. The advanced degree of cranial and postcranial breakage observed at HDP1 is incompatible with the incisor digestion patterns of ROOF and HOMS which suggest the involvement of a category 1 predator. Post-depositional

breakage at HDP1 complicates the interpretation of differences and similarities between the two units. It could be argued that post-depositional breakage has led to the homogeneity of the cranial and postcranial breakage patterns shown by HOMS and ROOF. These similarities are, however, repeated in the patterns of incisor digestion and it appears that the majority of the HDP1 micromammals were accumulated by the same predator.

11.7 The taxonomy of the Hoedjiespunt 1 micromammal species

As demonstrated in the previous chapter in Figure 10.4 and Figure 10.5, the murids from ROOF and HOMS show a general pattern of species distribution which shows no marked differences in terms of the overall distribution, though there are some differences in the percentages in which the individual species occur. A comparison between the percentage representation of all the murid species in HOMS and ROOF combined, is shown in Figure 11.4. Isolated and *in situ* M^1 and M_1 molars were used to represent the various species.

In terms of individual species, *R. pumilio,* dominates the faunal assemblage. *O. saundersae* is the next most common species, closely followed by *O. slogetti*. *M. albicaudatus* and *O. irroratus* show the same percentage occurrence and are the fourth most common species. As a family, the Otomyinae are very well represented and account for 59 % of the murid species in ROOF, and 61 % in HOMS.



Species list as numbered on graph	ROOF & HOMS combined	
	(N)	(%)
1 *A. namaquensis*	3	1.9
2 *M. albicaudatus*	14	8.8
3 *P. verreauxi*	4	2.5
4 *R. pumilio*	39	24.4
5 *T. Afra*	2	1.3
6 *Z. woosnami*	2	1.3
7 *O. irroratus*	14	8.8
8 *O. saundersae*	30	18.8
9 *O. slogetti*	7	4.4
10 *O. unisulcatus*	29	18.1
11 *P. brantsi*	16	10.0

Figure 11.4: The percentage representation of the muridae at HDP1

In conclusion, the great similarity observed between the taphonomy, and the micromammal taxa found in ROOF and HOMS, suggests that both horizons represent the same assemblage.

Establishing the identity of the predator(s) responsible for accumulating the HDP1 assemblage is vital if the micromammals are to be used to make inferences about the palaeoenvironment.

11.8 The agent of accumulation of the Hoedjiespunt 1 microfaunal assemblage

The hyaena may be safely ruled out as a potential accumulator of almost all the HDP1 micromammals as the bulk of incisors show light, or no, etching. The number of incisors showing etching suggests that a category one predator, the barn owl, was responsible for the accumulation of the majority of the HDP1 micromammals. The spotted eagle owl may probably be ruled out in that the degree of etching is not as intense as would be expected from this species which is generally recognized as a category 3 predator in terms of digestion (Andrews 1990). It is, however, impossible to completely rule out the possibility of some contribution to the HDP1 fossil assemblage by a spotted eagle owl, or indeed, small carnivores. Research by the author into the scats of several small carnivore species indicates that some small carnivores, such as the caracal, serval and genet, produce assemblages in which the majority of digested incisors fall into digestion classes 1 and 2 (Matthews 2002, Matthews in prep.). The great degree of post-depositional breakage at HDP1 prevents the identification of any variation in breakage, such as may be associated with predators other than the barn owl, or may aid in differentiating an owl roost, from an owl nesting, area.

The body mass of the micromammals from HDP1 ranges from 9-130 g, excluding the relatively large mole rat, *Bathyerus suillus* (see Appendix R). It is possible that the *Bathyergus* specimens at HDP1 may have been deposited by an agent other than that responsible for the deposition of the other micromammal species, although juveniles of this species, as well as other, smaller mole rat taxa are found in owl pellets (Avery 1992b, Avery 1999). Lack of digestion on five out of the six mole rat incisors recovered may indicate that the heads were not consumed, or that the animals died from natural causes. The golden mole bones and teeth may represent animals that died in the sediment, or were taken by the predator(s) active at HDP1. The size range of the micromammals taken at HDP1 fit into the prey spectrum taken by the barn owl, which is cited as ranging from 9-164 g (Morris 1979, Perrin 1982, Taylor 1994), and also the spotted eagle owl, which is noted as taking a great diversity of taxa up to the size of 100-140 g (Steyn 1982). Seven to nine murine and gerbillid species were recovered from a study of several *Bubo bubo ascalaphus* pellet assemblages from Algeria, and a variety of other, larger rodent species were taken (Denys et al. 1996b).

The spotted eagle owl is an opportunistic feeder and produces assemblages which do not necessarily reflect the characteristic taxa found in a particular biogeographical region or vegetation zone (Denys *et al.* 1996b).

The spotted eagle owl (*Bubo africanus*) is a nocturnal species while the barn owl is not strictly nocturnal but is also active in the early evening and in the morning (Andrews 1990, Taylor 1994). Seven of the eighteen species found at HDP1 are diurnal, or predominantly diurnal, which provides further support for the identification of the predator as a barn owl. *Otomys irroratus* and *Otomys angoniensis* have been found in spotted eagle owl pellets from Clarens (Denys pers. comm.), however, these species are predominantly, not strictly, diurnal in their habits. The presence of three other *Otomys* species at HDP1 which are diurnal in behaviour provides further evidence that the barn owl, rather than the nocturnal eagle owl may have responsible for the accumulation of the assemblage.

Species	Activity pattern
Otomys irroratus	Predominantly diurnal
Otomys saundersae	Diurnal
Otomys slogetti	Diurnal
Otomys unisulcatus	Diurnal
Parotomys brantsi	Largely diurnal
Rhabdomys pumilio	Mainly diurnal but also active at night
Elephantulus rupestris	Predominantly diurnal, but also show nocturnal activity
Myosorex varius	Active sporadically throughout the night and day
Crocidura Cyanea	Active sporadically throughout the night and day
Zelotomys woosnami	Primarily nocturnal
Acomys subspinosus	Nocturnal, but also active in early morning or late afternoon
Aethomys namaquensis	Nocturnal
Mystromys albicaudatus	Nocturnal
Mastomys verreauxi	Nocturnal
Tatera afra	Nocturnal
Rhinolophus clivosus	Nocturnal
Bathyergus suillus	Fossorial
Cryptomys hottentotus	Fossorial

Table 11.1: The activity patterns of the micromammal prey species from HDP1

The diversity, and mix, of micromammal species at HDP1 is similar to that observed in the other west coast fossil sites (see Chapter thirteen), and the modern owl pellet collections from the West Coast National Park and Steenbokfontein (Avery 1992b, Avery 1999, Manthi 2002, Avery in press). The non-micromammalian microfauna found at HDP1, which were found in relatively low frequencies, were represented by frog, lizard, small bird, and snake remains. All of these species, with the exception of the snake, are relatively common in barn owl

pellets, although they may also have become associated with the faunal assemblage through some other means.

It is impossible to determine at which stage the micromammals became associated with the site, but they would appear to be roughly contemporaneous with the macro fauna as they are found within the same sediments of HOMS and ROOF. It is possible that the hyaena den was occupied by owls during periods when it was vacated by the hyaenas, or they may have co-existed if roosting and nesting ledges were available in areas above the den. The pellets could have collected in both HOMS and ROOF, or microfaunal bones and teeth could have filtered from ROOF down to HOMS when pellets disaggregated. It is common to find bones and teeth, which have been released from pellets, scattered around the area surrounding, and below, a roosting site (pers. ob.).

The general pattern of species distribution of the murids in HOMS and ROOF is the same and the micromammals in both horizons appear to have come from the same, original assemblage. The similarity observed in the micromammal taxonomy of HOMS and ROOF is echoed in the taphonomy, and it would appear that the HDP1 micromammals may represent a single accumulation of pellets at a roost site. The period over which the assemblage accumulated is uncertain, however, as the assemblage appears to represent a single occurrence, it may provide an insight into the climatic conditions on the west coast during a relatively short period of time.

11.9 Palaeoenvironmental implications of the Hoedjiespunt 1 micromammals

Stynder (1997) deduced the presence of freshwater in the vicinity of HDP1 from species such as the Egyptian goose and Cape clawless otter. The presence of these species may not necessarily indicate a water source nearby, however, as Stuart and Stuart (2001) note that the otter may wander several kilometers from water, and the Egyptian goose would be able to fly to water sources some distance away. As mentioned previously in section 9.9 (Chapter 9), the micromammal species cited by Stynder (1997) as being indicative of a water source in the area, provide inconclusive evidence.

The presence of *O. irroratus, M. verreauxi* and *M. varius* at HDP1 may indicate the presence of relatively moister and more densely vegetated microhabitats, but their presence does not provide unequivocal proof of this as these species also occupy other habitats. *Mastomys*

verreauxi inhabits river banks close to the sea and areas of damp, meadow grass in the Knysna region, however, this species also has a wide habitat tolerance. One of the two shrew species found at HDP1, *Myosorex varius*, is frequently associated with moist, more densely vegetated microhabitats, but is also found in drier conditions and its presence on the arid west coast today appears to depend on the dense succulent vegetation (Bigalke 1979).

Bathyergus suillus and *Tatera afra* appear to be associated with sandy soil, rather than with any type of vegetation (Bigalke 1979). An arid component of the environment is indicated by the presence of *Zelotomys woosnami*, *Otomys unisulcatus*, *Parotomys brantsii* and *Elephantulus rupestris*, as all these species are associated with relatively arid habitats today. *Z. woosnami* is presently found in areas such as the Kalahari, and *P. brantsii* is found in the arid, western areas of South Africa and Namibia. *Z. woosnami* is usually associated with sparse vegetation and sandy soil, while *Otomys unisulcatus* is found in shrub and Karoo-like vegetation, usually interspersed with stones and rocks. *Parotomys brantsii* lives in sandy arid environments and makes burrows in hard, sandy soil. A sandy environment, together with a relatively open, shrub like vegetation is thus suggested by many of the micromammals. An open, shrub vegetation is also probably indicated by the presence of *A. namaquensis*, which is generally associated with open areas such as open shrub with scattered trees, though this species may also be found in rocky habitats.

There appears to have been a significant rocky component in the environment around HDP1 as several of the micromammal are associated with rocky habitats. The macroscelid, *Elephantulus rupestris*, occupies rocky, open environments with semi-arid scrub and the presence of this species suggests the occurrence of such habitats in the surrounds of HDP1. There is not much information available on *Otomys slogetti* which is generally associated with rocky habitats. This rat appears to be relatively hardy and is known as the 'ice rat' by the Basotho people because of its habit of leaving its rocky retreat to sit and sun itself when snow is lying on the ground (De Graaff 1981). *Aethomys namaquensis* and *Crocidura cyanea* are also frequently, though not exclusively, associated with rocky habitats. *Crociudura cyanea* is a versatile and ubiquitous species. Its presence may also indicate a rocky environment with sandy and scrub microhabitats as it is currently found in scrub on Kalahari sands, and in karroid scrub in the Cape Macchia Zone, where it is frequently associated with rocks (Skinner and Smithers 1990).

The presence of ubiquitous species, such as *Rhabdomys pumilio* and *Cryptomys hottentotus*, does not provide a great deal of information as these two species are not very habitat specific and enjoy a wide distribution. Both of these species would, however, be able to survive in a relatively arid environment. *Rhabdomys* is a near endemic of the Southern Savanna Grassland zones, but it is also found throughout the South West Cape and South West Arid zones (De Graaff 1981). The presence of *Rhabdomys* at HDP1 may be taken to represent grasslands, but this is not necessarily so. The one requirement of *Rhabdomys pumilio* is the presence of ground cover, and after a fire *Rhabdomys pumilio* will only occupy an area once reasonable cover has grown (Rowe-Rowe and Lowry 1982.). In the west coast area today *Rhabdomys* is common in areas of open scrub, where low bushes are interspersed with sandy areas (pers. ob.). *Rhabdomys* is frequently taken by barn owls living in the west coast area today, and is found in all the west coast fossil sites mentioned in this thesis (Avery 1992b, Avery 1999, Manthi 2002, Avery in press).

It is significant that none of the HDP1 micromammals, with perhaps the exception of *O. irroratus, M. verreauxi* and *M. varius*, indicate moist conditions. Species adapted to arid and semi-arid conditions dominate the assemblage. Given the large number of arid-adapted species, and the presence of the extra-limital *Z. woosnami*, *Parotomys brantsii* and *Elephantulus rupestris*, it would appear that the environment was arid relative to today. Several species commonly found in the other west coast fossil sites of SBYC, EBC and STBK are missing from HDP1. These species include *C. flavescens, S. varilla, E. edwardii, D. melanotis, S. krebsii* and *G. paeba*. The possible reasons for the lack of these species from the HDP1 faunal list will be discussed further in Chapter thirteen, when a comparison is made between the micromammal faunal lists of the west coast fossil sites.

The large mammals from HDP1 indicate an extremely productive, grass dominated environment (Stynder 1997). In terms of the micromammals, *Rhabdomys* and some of the *Otomyinae* may be associated with grasslands as these two genera dominate in the grasslands of the Northern Province. *Dendromus melanotis*, which is frequently associated with grass, is, however, missing from the HDP1, although it is found in all the other west coast fossil sites, and in the modern owl pellet assemblages investigated in this thesis (See Chapter 13, Table 13.1). There is some discrepancy in the environment indicated by the micromammals and large mammals at HDP1 in that murid species associated with sandy and/or arid habitats, rather than grasslands, dominate the assemblage.

There are two possible reasons as to why the micromammals show a rather different picture to the large mammals. Firstly, the micromammals may represent microhabitats in the environment which are not reflected in studies of the macro fauna which occupy less specific habitats and have far wider home ranges. Another likely reason for the observed discrepancies between the two assemblages is that the hyaenas hunted in different areas to the owl(s) responsible for accumulating the micromammal assemblage. The micromammal assemblage from HDP1 may represent the environment in the vicinity of the hyaena den, whereas the macrofauna may represent environments from further afield. The territory size of *Hyaena brunnea* varies with the availability of food sources. Territory size ranges of modern brown hyaenas are listed as extending from 13.4 to 23.6 km^2 (Skinner and Smithers 1990, Stuart and Stuart 2001). In more arid areas, such as the southern Kalahari and Namibia, the territory size may range from between 235 km^2 to 481 km^2 (Skinner and Smithers 1990, Stuart and Stuart 2001).

The usual hunting range of the barn owl may vary from a radius of 400-500 m to 3 km (Andrews 1990, Avery 1992b). Both barn and spotted eagle owls are known to prefer hunting in open environments (Andrews 1990, Fernandez-Jalvo *et al.* 1996). The emphasis on open vegetation, and open, sandy areas shown by the micromammals may indicate that the owl responsible for accumulating the HDP1 microfauna concentrated its hunting in areas of open scrub, sand, and rock. These microhabitats are likely to reflect the immediate environment around the site. The hunting grounds of extant barn owls living in the West Coast National Park were rarely found to extend further than 1 km from the roost (Avery 1992b). Avery's (1992b) study of multiple barn owl roost sites at the West Coast National Park indicated that the various pellet assemblages provided very specific information as to the available micromammal populations in the vicinity of the roost sites. Given the differences in hunting ranges between the owl and the hyaena, the micromammals are likely to reflect the environment close to, if not immediately around the site, whereas the hyaena-accumulated macrofauna would be likely to represent more distant areas of the environment.

The spread of grasslands has been linked to glacial episodes during the Pleistocene (Klein 1983), and Stynder (1997) has suggested that the large number of grazers at HDP1 may indicate that the HDP1 fauna accumulated during a period of cooling and sea-level regression. The micromammals lend some support to this suggestion as they indicate an environment which was more arid than that of today, and aridity is frequently associated with cooler

periods. The fact that the HDP1 micromammals are dominated by arid-adapted species, and are lacking several species common to the west coast, such as *C. asiatica, C. flavescens, S. varilla, E. edwardii, D. melanotis, S. krebsii* and *G. paeba,* supports the suggestion made in the previous section, namely that this assemblage may have accumulated over a period of a few months, and may thus provide a short, rather than long-term, insight into climatic conditions on the west coast. More west coast sites of a similar age to HDP1 need to be analysed in order to ascertain the extent of climatic and environmental change in the area during the late Middle Pleistocene, as well as the duration of the period of aridity reflected in the HDP1 micromammal assemblage.

Chapter twelve
Overview of the skeletal element proportions of the of the west coast fossil sites

In this chapter a taphonomic comparison is made between the west coast fossil sites in terms of skeletal element abundance. The suitability of using skeletal element abundance to assess the taphonomic history of a fossil assemblage is discussed.

12.1 Skeletal element proportions: A comparison

Andrews (1990) notes that the relative abundance of skeletal parts is not sufficiently adequate to distinguish between a diurnal raptor, some of the owls and mammalian carnivores. These issues become even more complicated when post depositional alteration occurs on top of predator-related patterning. Skeletal element abundance is, however, frequently used in the assessment of the taphonomy of fossil assemblages (Andrews 1990, Fernandez-Yalvo 1995, Avery 2002, Manthi 2002). This section provides a taphonomic comparison between the west coast fossil sites in terms of skeletal element abundance. The numbers relating to the following figures may be seen in Appendix I (MPPM (F)), Appendix U (HDP1), Appendix V (SBYC), and Appendix W (EBC). Figure 12.1 compares the skeletal element abundance of the various west coast fossil sites.

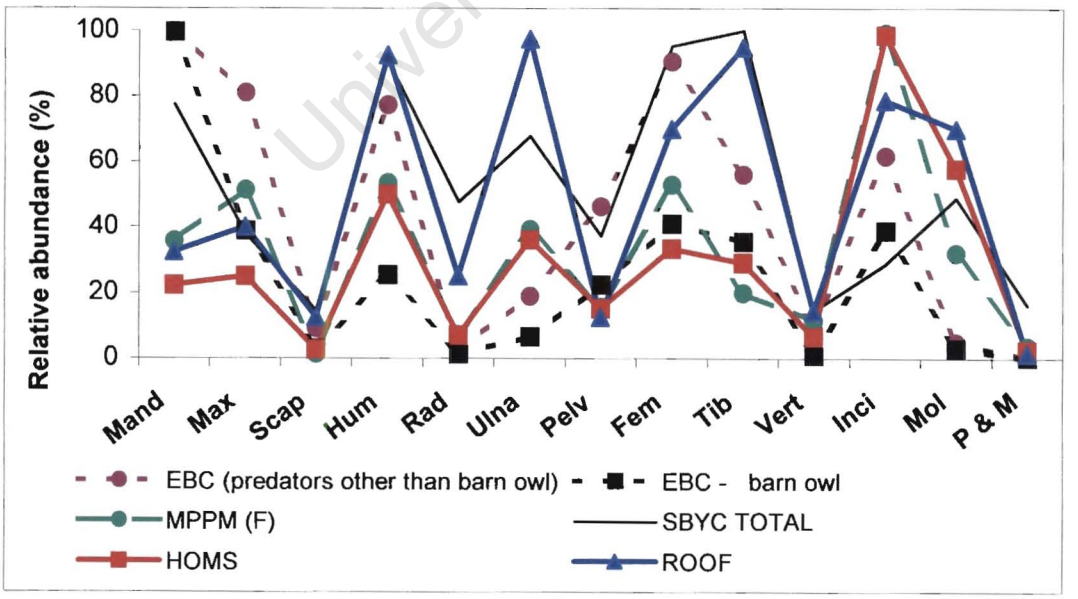


Figure 12.1: Skeletal element abundance of the west coast fossil sites

Key: Mand = mandible, Max = maxilla, Scap = scapula, Hum = humerus, Rad = radius, Pelv = pelvic girdle =, Fem = femur, Tib = tibia, Vert = vertebra, Inci = incisor, Mol = molar, P & M = phalanges and metapodials

Figure 12.1 illustrates that HOMS, ROOF and the MPPM (F) units show a low proportion of mandibles and maxillae relative to the other fossil sites, and a correspondingly higher percentage of isolated incisors, and to a lesser extent, molars. SBYC and the two EBC assemblages show a higher proportion of mandibles and maxillae, together with a lower percentage of isolated molars, indicating that there has been relatively less post depositional breakage in these sites.

A taphonomic examination of the EBC micromammals by Matthews (1998) indicated that a barn owl had been responsible for the accumulation of the micromammals in various depositional horizons of the site. In other horizons, a mixture of predator species had contributed to the accumulation of the micromammal assemblages. The two sets of assemblages are shown separately in Figure 12.2, and are compared to the barn owl mean calculated by Andrews (1990) in an investigation of several barn owl pellet collections from a number of areas.

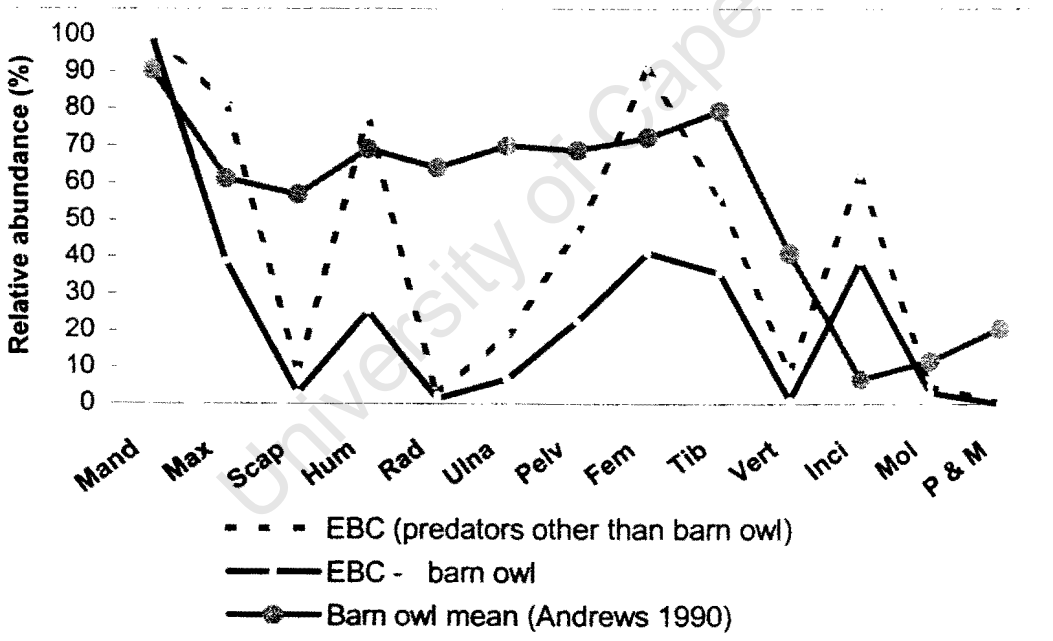


Figure 12.2: Skeletal element abundance of the EBC assemblages

Key: Mand = mandible, Max = maxilla, Scap = scapula, Hum = humerus, Rad = radius, Pelv = pelvic girdle =, Fem = femur, Tib = tibia, Vert = vertebra, Inci = incisor, M = molar, P & M = phalanges and metapodials

The barn owl mean represents the relative abundance of micromammals which come from pellets and are unaffected by post-depositional alteration and breakage. The barn owl assemblages from EBC provides an opportunity to see how post-depositional damage has altered the original barn owl pattern. As Figure 12.2 illustrates, post-depositional breakage

and loss have altered the pattern of skeletal element abundance beyond recognition. The EBC barn owl relative abundance has retained some traces of the original patterning in that it shows a somewhat smoother relative abundance than the EBC units of mixed origin, and does not show the marked peaks of the mixed-predator units. There has been a large decrease in the relative abundance of cranial, relative to postcranial, bones in the owl assemblage (Matthews 1998). The cause of this pattern is probably taphonomic. The mixed predator assemblage shows an increase in abundance in the relatively durable femur, humerus, tibia and incisors. A corresponding increase in proximal femora and distal humeri was noted in units where completeness was low, and a decrease when completeness was high (Matthews 1998).

Mandibles are the most abundant skeletal bodypart in all three assemblages in Figure 12.2. An increase in the number of isolated incisors in the two EBC fossil assemblages, together with a low relative abundance of fragile body parts, and high relative abundance of the more robust bones, indicates fairly extensive post-depositional damage. Trampling and sediment compaction are thought to have been responsible for the post-depositional breakage (Matthews 1998). Figure 12.3 compares the HDP1 horizons, HOMS and ROOF, to the skeletal element abundance shown by SBYC.

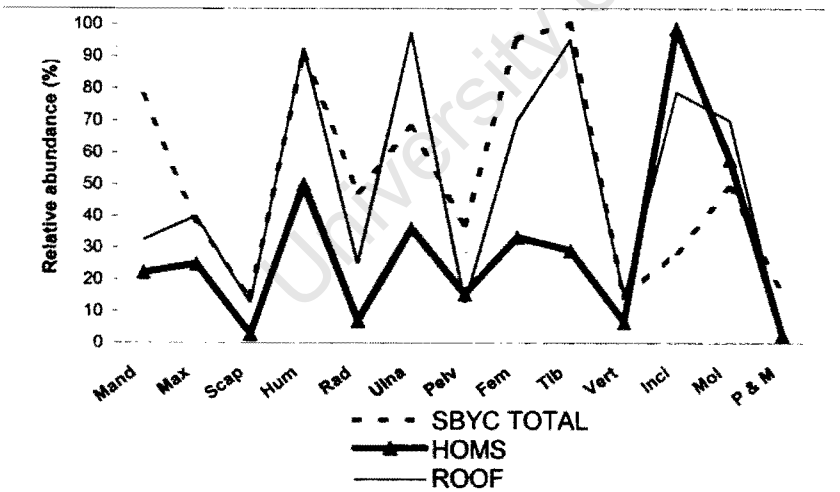


Figure 12.3: Skeletal element abundance of the SBYC, HOMS and ROOF assemblages

As illustrated in Figure 12.3, HOMS has a far lower relative abundance of postcranial body parts than ROOF, even though both horizons are thought to represent the same assemblage. The similarities and discrepancies in the skeletal element abundance of HOMS and ROOF were discussed in Chapter 10 and Chapter 11 and it was concluded that HOMS and ROOF have been subjected to post depositional damage which has overwritten the original, predator-

related pattern of skeletal element abundance. Research has suggested that barn owls produce a very characteristic pattern of skeletal element abundance (Andrews 1990), although authors such as Saavedra and Simonetti (1998) and Laudet *et al.* (2002) suggest that this is not as clear cut as previously assumed. Laudet *et al.* (2002) have found a difference between the skeletal element representation of modern barn owl roosts from different areas, as the pellets from one locality showed a more marked loss of hindlimbs from all prey size classes (Laudet *et al.* 2002). Saavedra and Simonetti (1998) have recorded quite marked differences in skeletal element preservation in the barn owl assemblages from different areas. Factors such as these may have caused some of the discrepancies in skeletal element abundance observed between the horizons of HOMS and ROOF in HDP1, although this is impossible to prove, and does not sufficiently explain the differences. The complexities of interpreting the skeletal element abundance of fossil assemblages are demonstrated by the fact that the three assemblages from SBYC showed an almost identical pattern of skeletal element representation (Manthi 2002). This was unexpected as one of the SBYC assemblages came from *in situ* fossil horizons, while the other two came from deposits which had eroded out from the fossil assemblage and lay in the upper and lower areas of a slope below the site. The latter two assemblages were exposed on the ground's surface and would presumably be exposed to more damage and alteration than the *in situ* deposits. This expectation was supported by the fact that preservation was better in the *in situ* material, and differences between the three assemblages were observed in terms of the breakage patterns of some of the bones, and in micromammal species representation (Manthi 2002). In the case of SBYC, assemblages which have been exposed to different stresses since deposition show the same pattern of skeletal element abundance, while HOMS and ROOF, which have presumably been exposed to similar post-depositional stresses, show very different patterns of skeletal element abundance. The differences between the skeletal element abundance patterns of the barn owl and mixed predator assemblages at EBC could be attributed to the fact that they were accumulated by different predators. This argument cannot be applied to the assemblages of HOMS and ROOF, however, as both appear to have been accumulated by a barn owl. The discrepancies in skeletal element abundance in HOMS and ROOF may be interpreted as providing evidence that post depositional events may act upon an assemblage in such a way as to cause marked differences in skeletal element abundance in different horizons of the site. Alternatively, some unknown variables may have affected skeletal element abundance at HDP1. One such obvious variable would be that in some parts of the site more than one predator has

contributed to the assemblage, although incisor digestion patterns do not lend support to this suggestion.

The skeletal element abundance of SBYC is roughly similar to that of ROOF, although the greater proportion of mandibles, a lower percentage of isolated incisors, and the greater relative abundance of the relatively fragile radius and pelvic bone indicate less post-depositional breakage. As seen in EBC, the skeletal element abundance of SBYC has altered to the extent that the original barn owl pattern is now longer recognizable. The general pattern of skeletal element abundance shown by HOMS, ROOF and SBYC is roughly similar, with a high relative abundance of the more robust bones. They differ mainly in the relative proportions of mandibles to isolated teeth, as discussed in the beginning of this chapter. In Chapter 11 a relatively high percentage of mandibles was found to be characteristic of almost all the predator assemblages investigated by Andrews (1990). It appears that this pattern survives in fossil sites until a certain degree of post-depositional breakage occurs. The fossil horizons of HDP1 and the MPPM (F) appear to have crossed this point, while EBC and SBYC have not. Both EBC and SBYC show an increase in isolated incisors, however, indicating that though the mandibles have remained within the assemblage, damage to the mandibles has resulted in the release of the incisor.

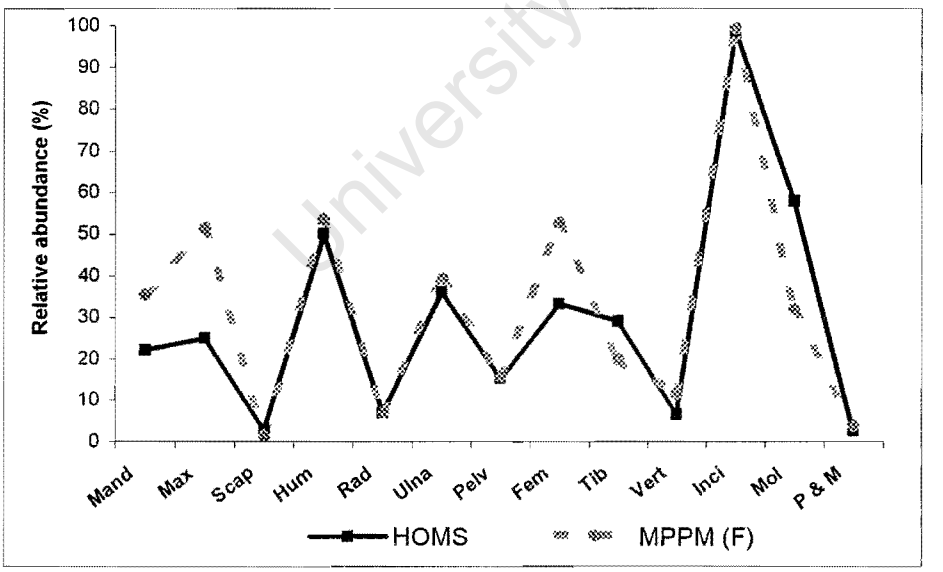


Figure 12.4: Skeletal element abundance of the HOMS (HDP1) and MPPM (F) (LBW)

Figure 12.4 compares the skeletal element abundance of HOMS and the MPPM (F) units. The two sites show a remarkably similar pattern of relative abundance, although mandibles, maxillae and femora are rather more abundant in MPPM (F). The fact that the MPPM (F)

units, which were accumulated in an open site, show a taphonomic pattern very similar to that of HOMS, which represents an accumulation in a closed environment, suggests that micromammal assemblages accumulated under very different conditions may produce very similar patterns of skeletal abundance. This has obvious implications for using skeletal element abundance to trace the taphonomic history of an assemblage.

It was concluded in Chapter six that the skeletal element abundance of the MPPM (F) assemblages supports the conclusion reached from studying the taphonomy of the micromammal assemblages, namely that the micromammals have not been transported over long distances. Alluvial transport has been noted as causing damage to the cranial bones (Korth 1979). The MPPM (F) assemblage, which has been subjected to transport, albeit gentle transport over a short distance, shows better preservation of both mandibles and maxillae than HOMS, which has not. Alluvial transport has been recorded as causing sorting in bones, however, the similarity between the skeletal relative abundance of HOMS and the MPPM (F) units indicates that skeletal element abundance may not be a good method to assess if alluvial transport has taken place. In the case of MPPM (F), short-distance transport has produced an assemblage which shows no obvious signs of transport in terms of the skeletal element abundance. Identifying the effects of alluvial transport on micromammals from a river channel is obviously complicated by the fact that micromammal bones and teeth are likely to enter the channel all along the course of the river and, as a result, no clear pattern of body part distribution may emerge.

Different units in the same site frequently show peaks of abundance of the same skeletal elements, even if there are differences in the general pattern of skeletal abundance. For example, the mandible, humerus, femur and incisors occur in relatively high proportions in both the assemblages at EBC, while the ulna, which is generally more abundant than the more fragile skeletal elements in predator assemblages (see Chapter 11, Figures 11.2 and 11.3), occurs in anomalously low proportions in both assemblages. The site shows a characteristic lack, or loss, of ulnae in assemblages deposited by different predators.

The general pattern of the two HDP1 units was similar in that relatively low percentages of mandibles and maxillae were found together with high numbers of isolated incisors and molars, and the more robust bones such as the distal humerus, proximal femur and so on, occurred in relatively high frequencies, relative to the more fragile skeletal elements. The three assemblages from the SBYC site investigated by Manthi (2002) showed an almost

identical pattern of skeletal element representation even though they had come from different areas, and differences between the assemblages in terms of the breakage patterns of some of the bones, and in micromammal species representation were observed.

The MPPM (F) units, F10 and F11, showed a very similar pattern of relative abundance, even though they came from a river channel and could be expected to contain very mixed assemblages (Chapter 5, Figure 5.3).

The fact that each of the west coast fossil sites show certain similarities between the assemblages in different horizons, even those accumulated by different predators, suggests that certain, site-specific patterns have resulted from post-depositional taphonomic processes. These patterns appear to have altered the original, predator-related patterning beyond recognition. A site-specific pattern of skeletal element abundance may be seen in the open-air site of LBW, and in all the cave/closed west coast fossil sites.

The relative abundance of isolated teeth to mandibles and maxillae appears to be the one feature that shows fairly consistent results, as all the fossil sites showed a proportional increase in isolated teeth, relative to a decrease in the percentage of mandibles and maxillae. No clear pattern of how post-depositional breakage affects skeletal element abundance has emerged from this study of the west coast fossil sites, and the general impression obtained is that taphonomic processes may act erratically and unevenly on the skeletal elements within a site. This study indicates that, unless post-depositional breakage and alteration of a fossil assemblge is minimal, skeletal element abundance can contribute little to identifying the predator of a fossil assemblage as post-depositional breakage is likely to erase or alter the original patterning. Skeletal element abundance provides useful information relating to the degree of general breakage in an assemblage, but should be used with great caution when trying to identify the taphonomic forces which have affected a fossil assemblage.

Chapter thirteen
Overview of the micromammals on the west coast, past and present

This chapter provides an overview of the micromammal populations found in archaeological and palaeontological sites on the west coast from the Saldanha Bay/Langebaanweg area, northwards to Steenbokfontein, from the Mio-Pliocene, until the present. Comparisons are made on a specific level in the case of the Pleistocene and Holocene sites, and on a generic level in the case of LBW.

13.1 Overview of the west coast fossil sites dating from the late Middle Pleistocene to the Holocene

Table 12.1 shows the micromammal faunal lists for the palaeontological and archaeological sites of Hoedjiespunt 1 (HDP1), the Saldanha Bay Yacht Club site (SBYC), Elands Bay Cave (EBC) and Steenbokfontein Cave (STBKC). The modern barn owl pellet collections from Steenbokfontein and the West Coast National Park introduced in Chapter one are also included.

The MNI for the various units at STBKC and EBC was calculated from the number of mandibles and maxillae (Avery 1999, Avery in press). The total MNI for these two assemblages was calculated by adding the MNI for each depositional unit. In the case of HDP1 and SBYC, more detailed information was available as postcranial bones had been included in the study, and MNI's were calculated by using the highest number of any single element in the assemblage (see Appendix U (HDP1), and Appendix V (SBYC)).

	Hoedjies-punt 1 (HDP1)	Saldanha Bay Yacht Club (SBYC*)	Elands Bay Cave (EBC**)	Steenbok-fontein Cave (STBKC***)	Steenbok-fontein owl roost samples***	West Coast National Park owl roost samples****
Age of site	200 00 – 300 000 BP	~15 540 BP	13 600 - 300 BP	6000-2200 BP	Modern	Modern
Climate	? Glacial	Late glacial	Terminal glacial and Interglacial	Inter-glacial	Inter-glacial	Inter-glacial
Chyrsochloridae						
C. zyli			✓			
C. asiatica		✓	✓	✓	✓	✓
E. granti			✓			✓
E. capensis						✓
Chiroptera						
T. aegyptiaca						✓
R. clivosus	✓	✓				
Soricidae						
C. cyanea	✓	**cf. C. cyanea**	✓	✓	✓	✓
C. flavescens		✓	✓	✓	✓	
M. varius	✓	✓	✓	✓	✓	✓
S. varilla		✓	✓	✓	✓	✓
Macroscelididae						
E. granti				✓	✓	
E. edwardii		✓	✓	✓	✓	
E. rupestris	✓		✓			
Muridae						
D. melanotis		✓	✓	✓	✓	✓
D. mesomelas		✓		✓	✓	✓
S. krebsii		✓	✓	✓	✓	✓
G. paeba		✓	✓	✓	✓	✓
T. afra	✓	✓	✓	✓	✓	✓
D. auricularis					✓	
M. albicaudatus	✓	✓	✓	✓		
A. supspinosus	✓		✓		✓	
M. verreauxi	✓		✓			
R. pumilio	✓	✓	✓	✓	✓	✓
M. typica				✓	✓	
A. namaquensis	✓		✓	✓	✓	
Z. woosnami	✓					
G. ocularis						
Mus minutoides			✓	✓	✓	✓
G. ocularis			✓	✓		
O. irroratus	✓	✓	✓	✓	✓	✓
O. Saundersae	✓	✓	✓	✓		
O. unisulcatus	✓	✓	✓	✓	✓	✓
O. slogetti	✓					
P. brantsii	✓			✓		
R. rattus					✓	
M. musculus						✓
Bathyergidae						
B. suillus	✓	✓		✓	✓	
C. hottentotus	✓	✓	✓	✓	✓	
G. capensis			✓			✓
MNI	**52**	**804**	**315**	**3457**	**1351**	**5971**
Diversity	**18**	**19**	**25**	**24**	**22**	**18**

Table 13.1: The micromammalian fauna of the west coast fossil sites from the Late Middle Pleistocene to the Holocene

*After Manthi (2002), Table 7.2.2 and Table 7.2.3, page 80-81, **After Avery in press
***After Avery (1999), Page 155, Table 4 ****After Avery (1992b), Table 3, Page 391)

In order to distinguish the modern owl pellet assemblages from the fossil assemblages, the modern owl pellet assemblages from Steenbokfontein and the West Coast National Park will be referred as STBK-modern and WCNP-modern from this point forwards. A relatively wide range of 9-17 species was obtained per roost site from the thirteen owl roost sites at different areas in the WCNP-modern, giving an average of 12.2 species. Sample size was satisfactory for all the collections with the smallest sample containing an MNI of 62, and the largest 2770. The pellet collections showing a lower species diversity were not necessarily those of smaller sample size.

The two barn owl pellet collections from Steenbokfontein (STBK-modern) yielded a diversity of 23 and 22 species, respectively. It is interesting that species diversity in the Steenbokfontein area, which is currently being farmed, is higher than that in the WCNP-modern assemblages. This may have something to do with the fact that barn owls have a narrower and more specialised diet in more productive habitats, and a wider spectrum diet in areas that are more arid and have lower micromammal densities (Taylor 1994). Increases in the diversity of fossil assemblages are usually taken to represent an increase in the amelioration of environmental conditions, and an increase in available niches, as diversity has been shown to be directly related to habitat diversity and the availability of food resources (Brown 1973). Taylor's (1994) research suggests, however, that the opposite may be true, and that a barn owl hunting in a relatively less productive area may produce assemblages which show greater diversity. Care should thus be taken when interpreting the diversity of fossil micromammal assemblages. The STBK-modern barn owl assemblages showed a similar diversity to the fossil assemblages from STBKC, which showed a range of 11-21 species, with an average diversity of 17 species, in the six depositional horizons.

The three pulses (pulses were composed of several depositional units) containing the largest micromammal samples at EBC, namely, pulse B, D and E, yielded an average diversity of 18.1 species per pulse (Avery in press).

SBYC yielded a diversity of 19 species from the entire assemblage (Manthi 2002). HDP1 contained the lowest diversity of species of the fossil assemblages, namely 18. The MNI from HDP1 is lower than that of the other fossil sites, and this may also have contributed to the slightly lower species diversity in the site. The diversity is not markedly different from the average obtained in the other fossil sites, however, if separate depositional horizons are considered.

The micromammal species listed in Table 12.1 show the following features:

- *C. cyanea, M. varius, T. afra, R. pumilio, O. irroratus* and *O. unisulcatus* are found in all the west coast fossil sites, as well as the modern barn owl pellet assemblages from Steenbokfontein (STBK-modern) and the West Coast National Park (WCNP-modern-modern).

- *C. flavescens, M. varius, S. varilla, E. edwardii, D. melanotis, S. krebsii* and *G. paeba* are found in the fossil sites of SBYC, EBC, STBKC and the STBK-modern assemblages. Of these species, the WCNP-modern assemblages lack *C. flavescens* and *E. edwardii*. All of the above species, with the exception of *M. varius*, are missing from HDP1.

- *D. mesomelas* is found at SBYC, STBKC and in both the modern barn owl pellet assemblages, but not at HDP1 or EBC.

- The endemic *A. subspinosus* is found at HDP1, EBC, and in the STBK-modern owl pellet assemblages.

- *O. slogetti* and *Z. woosnami* were only found at HDP1.

- *E. rupestris* is found only at HDP1 and EBC

- *P. brantsii* is found only at HDP1 and STBKC.

- *A namaquensis* is found in all of the assemblages, with the exception of SBYC and the WCNP-modern barn owl assemblages.

- *M. albicaudatus* and *O. saundersae* are found in all the fossil sites, but not in either the WCNP-modern or STBK-modern barn owl collections.

- The gerbillid, *Desmodillus auricularis,* was found only in the STBK-modern owl pellets.

- In terms of bat species, *R. clivosus,* came from SBYC, and HDP1 and *T. aegyptiaca* from the WCNP-modern owl pellets. Bat bones are particularly prone to post depositional breakage (Manthi pers. com.) and their scarcity in the fossil sites may be largely due to taphonomic causes.

- The golden mole, *E. capensis,* was found only in the WCNP-modern assemblages. *C. asiatica* was found in all the west coast fossil sites, and in the WCNP-modern barn owl pellets.

- The mole rat *G. capensis* is only found at EBC and in the WCNP-modern pellets.

- *B. suillus* is found in all the fossil sites, and in some owl pellets from the WCNP-modern.

- *C. hottentotus* is found at all the fossil sites, and in the STBK-modern pellets, but does not appear in the WCNP-modern pellets.

- *M. verreauxi,* which is currently found in the south western parts of the Cape Region up to the Knysna district in the south, is found only at HDP1 and at EBC.

- Commensal species, namely *Rattus rattus* and *Mus musculus,* were only found in the STBK-modern and WCNP-modern pellet assemblages.

Many of the conclusions reached in the following discussion are tentative as there may be a number of unknown variables influencing the distribution of species and the general character of the micromammal populations represented by the various fossil assemblages. Having acknowledged this, certain inferences may still be made on the basis of the available fossil evidence.

The general pattern observed in the west coast fossil sites and in the modern barn owl pellet assemblages, with the exception of HDP1, is that the Soricidae, Otomyinae and Gerbillidae (either *T. afra* or *G. paeba*) generally dominate the assemblages (Avery 1992b, Avery 1999, Manthi 2002, Avery in press). In the fossil sites, two species of gerbillid (*T. afra* and *G. paeba*), four soricid species, and three species from the Otomyinae are always represented, although one particular gerbillid or otomyine species usually dominates in terms of overall numbers. HDP1 was an exception in that five species of *Otomys* are represented, but only one gerbillid, and two soricid species are found.

The fossil assemblages at STBKC were dominated by both *G. paeba* and *O. unisulcatus.* The soricids occurred in low frequencies, but were well represented in that out of the six depositional horizons at STBKC, two contained two soricid species, and in the other four horizons, three to four soricid species were found in each horizon (Avery 1999).

The gerbillid, *T. afra,* and the soricids, *M. varius* and *S. varilla,* dominated the micromammal assemblage at SBYC. The Otomyinae, in particular *O. saundersae,* were also well represented at SBYC, relative to the other murid species (Manthi 2002).

At EBC, *A. namaquensis* and *O. unisulcatus* dominated the Holocene packages which appear to have been accumulated by a mixture of predators other than the barn owl, while the Terminal Pleistocene packages which were deposited by a barn owl were overwhelmingly dominated by *O. unisulcatus* (Matthews 1998, Avery in press). Each depositional unit at EBC contained at least one soricid species, and overall, four species of soricid was represented at EBC.

The Soricidae are well represented in all the west coast sites, with the exception of HDP1 which contains only two species; *C. cyanea*, a species notable for its ability to survive in very dry areas, and *M. varius*, which is generally associated in moister environments, but on the other hand, is widely distributed up the relatively arid west coast, stopping just short of the Orange River. The fact that only two soricid species is found at HDP1 distinguishes it from the other fossil sites, as four soricid species are found in all the fossil sites, and in the STBK-modern owl pellet assemblage. Three soricid species are found in the WCNP-modern assemblages.

Another noticeable gap in the species list when comparing HDP1 and the other west coast sites is the lack of *Dendromus* species. *D. mesomelas* is generally associated with rank vegetation, especially tall grass with scrub (Skinner and Smithers 1990). *D. melanotis* may be found in association with tall stands of grass, but may also be associated with riverine conditions, and dry scrub in the Kalahari (Skinner and Smithers 1990). Both these species are currently found on the west coast, although the present distribution of *mesomelas* does not extend further north than St Helena Bay according to De Graaff (1981), Skinner and Smithers (1990) and Stuart and Stuart (2001). The presence of both *Dendromus* species in the modern owl pellet collections from STBK-modern indicates that *mesomelas* enjoys a wider distribution than is generally accepted. A dominance of grazing ungulates at HDP1 was interpreted as indicating a grass-dominated environment (Stynder 1997), which should have provided a suitable habitat for *Dendromus*. The presence of *M. albicaudatus* at HDP1 may also indicate that grasses occurred locally, though this is not conclusive, as this species is also associated with the macchia vegetation of the west coast (De Graaff 1981). The general pattern indicated by the micromammals at HDP1 is one of aridity. The absence of both

Dendromurinae, and in particular *D. melanotis,* from the HDP1 assemblage is puzzling as the latter species enjoys a current distribution in the dry, Kalahari area. It is possible that the distribution of the Dendromurinae in the late Middle Pleistocene did not extend into the Saldanha area. Alternately, a suitable habitat for the Dendromurines may have been lacking from the area in which the owl hunted.

The absence of *Steatomys krebsii* at HDP1, which is common in the other west coast fossil sites is surprising, given the fact that this species is hardy (it is able to reduce body temperature and food intake during periods of stress) and frequently associated with relatively dry environments (De Graaff 1981, Avery 1992b). This murid appears to be restricted to open, sandy, grass-covered substrates (De Graaff 1981, Stuart and Stuart 2001) and these microhabitats appear to have been present at HDP1 as indicated by species such as *Bathyergus suillus*, *Zelotomys woosnami* and *Tatera afra* (Bigalke 1979). Barring predator and other sample-related biases, it is possible that the absence of *Steatomys krebsii* may indicate a different distribution pattern of this species in the past, which excluded the area in the surrounds of HDP1.

The Otomyinae are well represented in all the west coast sites, with *Parotomys* occurring at STBKC and HDP1. The presence of this species at STBKC and HDP1 clearly indicates that *Parotomys* has extended its distribution further southwards at various periods in the past as it is presently found slightly to the north of the Saldanha area (Stuart and Stuart 2001).

The occurrence of *O. slogetti* and *Z. woosnami* at HDP1 is not repeated in any of the other fossil sites, suggesting that the distribution of these species changed at some period between the late Middle Pleistocene and the Terminal Pleistocene. As mentioned in Chapter 9, Davis (1962) (contrary to some other, more recently published authors) noted that *O. slogetti* ranges fairly extensively in the South West Arid Region, which makes the appearance of this species at HDP1 less unexpected. *O. slogetti* was found at Sterkfontein in horizons dating to approximately 1.5 Ma and in other horizons bearing ESA and MSA stone tools, indicating that this species enjoyed a much wider distribution in the past. The presence of *Z. woosnami* at HDP1 would appear to be linked to an increase in aridity in the west coast at the time of deposition of the HDP1 micromammals, as this species is found today in more arid areas to the North (See Appendix R). *E. rupestris,* which appears only at HDP1 and EBC, is also found today in arid, rocky areas of Namibia, and the very northern part of the South

African west coast, indicating that this species has also shown a northward shift in distribution along the west coast since the late Middle Pleistocene.

The endemic gerbillid, *Tatera afra,* is present at HDP1 and all the other west coast sites, but *Gerbillurus paeba,* which is prevalent in all the west coast sites, as well as the barn owl assemblages, is conspicuously absent from HDP1. *G. paeba* prefers desert and subdesert conditions and is widely spread in the South West Arid biotic zone, but encroaches marginally into the Southern Savanna and South West Cape biotic zones (De Graaff 1981). *G. paeba* should have been able to cope easily with the arid conditions which appear to have existed at HDP1. This species, along with *T. afra*, is also a common prey item taken by owls and it is likely that it would be represented in the HDP1 assemblage if it had been present in the area. It is thus tentatively suggested that the absence of this species may indicate that its distribution did not extend to the Saldanha Bay area during the late Middle Pleistocene.

Desmodillus auricularis is found only in the STBK-modern owl pellet sample. The distribution of this species today is noted as being widespread in the South West Arid zone, with peripheral extensions into the Southern Savanna and the South West Cape Biotic Zones (De Graaff 1981, Stuart and Stuart 2001). Gerbillids are a favoured prey item of both barn and eagle owls, and if present in the area would be likely to be accumulated by such predators. The total lack of *D. auricularis* from all the Pleistocene/Holocene fossil sites suggests that the earlier distribution of this species may not have extended as far south as it does today.

M. verreauxi makes an appearance in low frequencies, at HDP1 and EBC, but does not occur at SBYC, STBKC or in the modern owl pellet assemblages. Surprisingly, the catholic *R. pumilio* doesn't appear at SBYC either. This ubiquitous species usually appears in low frequencies in barn owl pellets (Avery 1992b, Avery 1999).

P. brantsii is found only at HDP1 and STBKC, and not in the modern owl pellets. As mentioned in Chapter 9, there is some discrepancy as to the present-day distribution of this species which may, or may not, extend into the Saldanha area. Evidence from the West Coast National Park owl pellet collections suggests that it does not extend as far south as the reserve.

M. albicaudatus and *O. saundersae* are present in all the west coast fossil sites, but not in the modern barn owl assemblages. The lack of *M. albicaudatus*, the sole extant representative of

the Mystromyinae, may very well be linked to the fact that this species is recorded as becomingly increasingly rare (South African Red Data Book 1986). The prominance of *O. saundersae* in Last Glacial samples in South Africa led Avery (1991) to suggest that an increase in the numbers of this species in a fossil assemblage may reflect colder weather. This correlation should be applied with caution, however, as the presence of *O. saundersae* throughout the fossil records of the west coast indicates that this species has been consistently present throughout many cycles of climatic change.

Mole rats generally appear in very low frequencies in barn owl accumulated assemblages and this is reflected by the fact that *Bathyergus suillus* and *Cryptomys hottentotus* are found in low frequencies in almost all the fossil sites, and in the STBK-modern owl pellets. This does not appear to be a hard and fast rule, however, as *Cryptomys hottentotus,* together with *Otomys irroratus,* and *Desmodillus auricularis,* formed the main three prey species at Abbot's Cave in the Middelburg District, southwestern Cape (Avery 1991). No taphonomic studies were carried out to confirm that the predator responsible for the micromammal assemblages was a barn owl, however, and the possibility exists that an eagle owl may have been responsible for this fossil accumulation.

Manthi (2002) concluded that the conditions under which SBYC accumulated were essentially modern, although temperatures may have been slightly lower. This conclusion may well be applied to all the other, younger west coast fossil sites as, although differences in faunal composition between the different fossil horizons reflect shifts in the dominance of various vegetational parameters, the general environment and resident micromammal population appears basically similar to that of today (Avery 1992b, Avery 1999, Stuart and Stuart 2001, Manthi 2002, Avery in press). Climatic change in the Holocene, as deduced from micromammalian evidence, tends to be reflected in changes in the proportions of various species, rather than in the species represented (Avery 1990). Palaeoenvironmental and palaeoclimatic reconstructions should therefore be made in conjunction with a thorough taphonomic analysis in order to ascertain how predator selection of prey may have affected fossil micromammal assemblages. The problem with interpreting the above absence of certain species is that it is impossible to ascertain if this reflects actual absence from the area, or some predator–related bias, such as sampling of the micromammals in only one part of the landscape, or selection of favoured prey species. Taphonomically-induced biases should be, to some extent, identifiable.

Species such as *C. asiatica, C. flavescens, S. varilla, E. edwardii, D. melanotis, S. krebsii* and *G. paeba* are found in all the west coast fossil sites, and in the modern STBK-modern pellet samples, but are missing from HDP1. HDP1 is thus lacking many of what the other fossil sites and modern pellet assemblages suggest are typical west coast species. HDP1 also differs in that it contains species, such as *Z. woosnami* and *O. slogetti*, which are not represented in any known fossil or modern micromammal assemblages from the west coast area. The HDP1 fauna contains some 'typical' west coast features, however, in that all four endemic micromammal species of the south western Cape are present (that is the mole rat *B. suillus*, and the murids, *Tatera afra*, *Myomyscus verreauxi* and *Acomys subspinosus*), suggesting that these species were well established in the area during the late Middle Pleistocene. The analysis done on the pattern of incisor digestion at HDP1 suggests that the predator responsible for the accumulation of the HDP1 micromammals is a barn owl, which is known to provide a good sample of the available micromammal population within the hunting range. This species may, however, produce an assemblage which is biased in the sense that its hunting range may encompass only certain microhabitats within the landscape. It is possible that the absence of some species at HDP1, such as *Dendromus*, may have resulted from the owl sampling the micromammal population living in the immediate vicinity of the roost site, and not further afield. The fact that HDP1 is missing many characteristic west coast species, together with the presence of species such as *Z. woosnami* and *O. sloggetti*, suggests that conditions on the west coast in the late Middle Pleistocene differed quite markedly to climatic and environmental conditions that prevailed during the periods represented by the fossil sites of STBKC, SBYC and EBC. Conditions appear to have been relatively more arid at the time of deposition of the HDP1 micromammals.

13.2 Overview of the generic composition of the micromammal populations from the west coast fossil sites

Table 13.2 provides a summary of the rodent genera appearing to date in archaeological and palaeontological sites on the west coast. As may be seen, there is a large gap in the fossil record from the Early Pliocene until the late Middle Pleistocene, however, several genera which were found in this area during the Mio-Pliocene, are found in the other west coast fossil sites. *Mystromys, Rhabdomys* and *Cryptomys* are found in all the west coast fossil sites. *Dendromus* is found in all the sites but HDP1, and *Aethomys* appears in all the fossil assemblages but those from SBYC. *Acomys* is represented at LBW by *A. mabele* and at HDP1 and EBC by the endemic *A. subspinosus. Graphiurus* appears at LBW, and then again

in the Terminal-Pleistocene/Holocene where it is found at EBC and STBKC. *Bathyergus* is found in all the fossil sites. *Zelotomys* was found only at LBW and HDP1. To summarise, nine micromammal genera found at LBW are present in some, or all, of the west coast fossil sites dating from the late Middle Pleistocene until the Holocene. These are; *Aethomys, Rhabdomys, Mystromys, Dendromus, Acomys, Zelotomys, Cryptomys, Bathyergus* and *Graphiurus*. Not all of these genera are represented in both the LQSM and MPPM (F) units. Their absence in the MPPM (F) units is not necessarily reflected in the other MPPM horizons. For example *Cryptomys* and the *Graphiurus* sp. have been recovered from MPPM horizons, but not MPPM (F).

	Langebaan-weg	**Hoedjiespunt 1**	**Saldanha Bay Yacht club site**	**Elands Bay Cave**	**Steenbok-fontein Cave**
Age of site	Mio-Pliocene	late Middle Pleistocene	Late Pleistocene	Late Pleistocene to Holocene	Holocene
Genus					
Dendromus	✓		✓	✓	✓
Steatomys			✓	✓	✓
Gerbillurus			✓	✓	✓
Tatera		✓	✓	✓	✓
Desmodillus	✓				
Mystromys	✓	✓	✓	✓	✓
Acomys	✓			✓	
Praomys		✓		✓	
Rhabdomys	✓	✓	✓	✓	✓
Mus	?			✓	✓
Aethomys	✓	✓		✓	✓
Zelotomys	✓	✓			
Thallomys	✓				
Graphiurus	✓			✓	✓
Pelomyoides	✓				
Otomys		✓	✓	✓	✓
Parotomys		✓			✓
Euryotomys	✓				
Stenodontomys	✓				
Bathyergidae					
Bathyergus	✓	✓	✓		✓
Cryptomys	✓	✓	✓	✓	✓
Georychus				✓	
No. of genera	**14**	**10**	**9**	**14**	**13**

Table 13.2: The murid and bathyergid genera represented in the west coast fossil sites dated from the Mio-Pliocene to the Holocene

The only two genera which have so far been recovered from the MPPM (that is, the recently excavated horizons of MPPM (F)), but not the LQSM, are *Thallomys* and *Zelotomys*, although a ? *Zelotomys* has been tentatively identified in the LQSM. As mentioned in Chapter 7, *Zelotomys* previously enjoyed a wide distribution in South Africa throughout the Late Pliocene/Early Pleistocene, although it is currently confined to arid and semi-arid areas of the subregion. Levinson (1985) notes that *Zelotomys* is likely to have undergone a habitat change since 250 000 years ago as this species shows very few marked desertic adaptations, such as enlarged bullae, long hind legs, or a bushy tip to the tail. HDP1 provides evidence for the association of this species with an arid habitat during the late Middle Pleistocene.

Denys (1996a) suggests that the persistence of extinct rodent taxa until relatively recently in South Africa may be due to a long phase of isolation. Only two of the genera found at LBW are now extinct, these are *Stenodontomys* and *Euryotomys*. *Euryotomys* appears again in the fossil record at Bolt's farm, which is thought to be around 4-5 million years old, and then disappears from the fossil record (Senegas and Avery 1998). *Stenodontomys* makes a last appearance at Makapansgat (Denys 1994b), and at and Nosib1 in Namibia (Ca 3 Ma.).

Micromammal genera shared by the Cape, and Kalahari SW Arid Regions today include *Tatera, Gerbillurus, Saccostomus, Dendromus, Otomys, Mus, Aethomys, Rhabdomys, Graphiurus, Cryptomys* and *Georychus* (Denys 1999). Genera shared by the Cape, and Namib Region includes *Tatera, Gerbillurus, Saccostomus, Otomys, Mus, Aethomys,* and *Rhabdomys* (Denys 1999). All of above-mentioned genera were recovered from Namibia in Otavi Mountain breccias of Post Miocene age (Pickford *et al.* 1994), and *Dendromus, Aethomys, Rhabdomys, Graphiurus, ?Mus* and *Cryptomys* are found at LBW. The fact that LBW shares many genera with Nosib and Jägersquelle (see Chapter 2, Table 2.3), as well as with other Namibian sites similar in age to LBW, indicates that a certain similarity existed between the micromammal faunas of what is today the Namib and Kalahari SW arid Regions, and the Cape Region, approximately 4-5 Ma. The number of genera currently held in common by the Cape, Namib and Kalahari SW Arid Regions indicates that this long-standing similarity has endured up until the present day. Denys (1999) suggests that regional differentiation of the southwest Cape Province and the South West Arid biomes in terms of rodent taxa took place in South Africa between 6 and 4 Ma. The evidence from this thesis supports this suggestion as nine of the micromammal genera found at LBW are present in some, or all, of the west coast fossil sites dating from the late Middle Pleistocene until the

Holocene. This indicates the endurance of many of the genera present at LBW, and in the Kalahari South West Arid and Namib Regions, from the Mio-Pliocene, up until the present.

Chapter fourteen
Conclusion

This chapter summarises the main findings of this thesis, and assesses the contributions made towards understanding the taphonomy and palaeoecology of HDP1 and LBW. Recommendations are made as to areas in which further research is urgently required.

14.1 The taphonomic contribution of the micromammal assemblages investigated in this thesis

14.1.1 Skeletal element proportions

The study of the west coast fossil sites presented in Chapter thirteen suggests that, unless there is exceptional preservation, skeletal element abundance can contribute little to identifying the predator of a fossil assemblage, and should be used with caution when trying to ascertain the taphonomic history of a site. The fact that each of the west coast fossil sites show certain similarities between the assemblages in different horizons, even those accumulated by different predators, indicates that a site-specific patterning has over-written the original, predator-induced patterns of skeletal element abundance. Skeletal element abundance does, however, provide useful information relating to the degree of general breakage in a site, and in this regard the relative abundance of isolated teeth to mandibles and maxillae is particularly useful.

More experimental work is urgently needed into the various taphonomic agents and processes which may effect, and alter, a fossil assemblage. The situation is complex and, as pointed out by Fernandez-Jalvo *et al.* (2002), the same processes acting on fossil, and freshly deposited assemblages, will not necessarily produce the same result. Fossil sites such as HDP1, EBC and STBKC indicate that in a 'closed' environment, skeletal elements disappear from the assemblage after deposition. This is undoubtedly related to post-depositional breakage, however, as yet, we do not have a full understanding of the exact processes which lead to the breakage, and then disappearance, of bones and teeth within a fossil assemblage. Further research into the effects caused by damaging processes such as transportation by water, trampling, and sediment compaction is urgently needed.

14.1.2 The taphonomy of predator assemblages

This thesis finds further evidence that indices such as cranial breakage and tooth loss are affected by the species of micromammal involved. This finding is in agreement with results obtained by authors such as Simmons *et al.* (1991), Denys *et al.* (1996b), Saavedra and Simonetti (1998), Laudet and Hamdine (2001), Laudet *et al.* (2002), and Manthi (2002). This indicates that research into the effect of the various predators on micromammal assemblages needs to take into account the size and species of micromammal involved.

Research by the author suggests that some felids and canids may produce assemblages which show less breakage and loss of bone than previous studies of species from these families have indicated (Matthews 2002, Matthews in prep.). Micromammal assemblages recovered from South African caracal, genet and jackal scats suggest that these predators produce bones and teeth which show a much lighter degree of digestion, and less breakage and destruction of cranial and postcranial bones, than expected (Matthews 2002, Matthews in prep.). More research is needed into the characteristic breakage and digestion patterns produced by African small carnivores, diurnal birds of prey, and owls as many species produce assemblages which have not yet been investigated. Saavedra and Simonetti (1998) and Laudet *et al.* (2002) have found that barn owl pellet assemblages from different areas show taphonomic differences. Further research into the patterns produced by African predators need to take place in conjunction with a study of the variation in the taphonomic patterns produced by the same species of predator, in different areas.

14.1.3 The taphonomy of the Langebaanweg micromammals

The taphonomic analyses done on the LBW sediments have provided important information on the events that led to, and the conditions under which, deposition of the LQSM and MPPM (F) sediments took place. These may be listed as follows;

- If some of the LQSM micromammals were alluvially transported, as suggested by Hendey (1981a), the degree of cranial breakage suggests that transport must have taken place over a short distance, in a low energy environment.
- Certain taphonomic features of the larger fauna from the LQSM noted by Hendey (1981a) and Klein (1981, 1982) are echoed by the taphonomy of the micromammals. For example, micromammal cranial bones from the LQSM indicate that there has been less post-depositional damage in the LQSM horizons, relative to those from the MPPM (F).

Also, as observed in the large mammal assemblages, the LQSM micromammals appear to have been buried relatively closely to the area in which they died, or in which they were deposited in scats or pellets.

- The vast majority of micromammals from the MPPM (F) were transported over short distances before being buried well below the ground's surface. The general degree of breakage of cranial and postcranial bones and lack of rounding on the bones, together with a skeletal element abundance which indicates minimal alluvial transport, suggests that the river was slow-flowing. This is contrary to the scenario proposed by Hendey (1976), who suggested that Bed 3aN appeared to have been deposited by fast-flowing water. The taphonomy of the micromammals suggests that the MPPM (F) sediments may represent a small, subsidiary channel. Compaction or movement of sediment may have caused some of the observed post-depositional breakage of micromammal bones.

- The assemblages from both the LQSM and MPPM (F) show little sign of being exposed on the surface for a long period as very few of the teeth, and bones in the case of the MPPM (F) units, show the taphonomic features associated with weathering.

- Neither the LQSM, nor MPPM (F), assemblages show the degree of breakage or destruction that would, in all probability, be associated with re-working. Damage to incisors and molars has occurred in very low frequencies in both the LQSM and MPPM (F).

- Approximately 18-33% of murid incisors in the LQSM units of satisfactory size, and just over half of the MPPM (F) incisors, show no signs of digestion. It is impossible to ascertain if the lack of digestion on murid incisors from the two members reflects death by natural causes, or predation, as category 1 predators produce assemblages in which the majority of incisors show no signs of digestion. The degree of digestion, as indicated by murid incisors, is slightly more intense in the MPPM (F) as indicated by the fact that a higher percentage of the MPPM (F) incisors, show class 2 digestion. The majority of incisors from the LQSM and MPPM (F) assemblages suggest, however, that they were taken by category 1 and/or category 2 predators, or died natural deaths.

- There is no obvious indication that trampling has affected breakage of the micromammals observed in either the LQSM, or the MPPM (F).

- ❖ The presence of large numbers of burnt bones from the LBW assemblages has been interpreted as indicating a marked seasonality at LBW (Hendey 1970a, Hendey 1976, Gentry 1980, Hendey 1981a, Hendey 1981b, Franz-Odendaal 2002). The micromammals in this study differ in this feature to that of the larger mammals, as only four burnt fossil bones were recovered.

The cause of the pathologies observed on the large mammals at LBW has not been completely explained. Issues such as why some taxa show high incidence of hypoplasia, while others show none is unclear, and no correlations between dietary strategies, such as grazing or browsing, and tooth defects were found (Franz-Odendaal 2002). Problems with the interpretation of the large mammal assemblages are noted as, firstly, there may have been some time-averaging of different populations and, secondly, the observed teeth defects in some of the animals may not have resulted from the same stress episode, or the same causes, if different species are being compared (Franz-Odendaal 2002). The issues raised by this study of the micromammals, that is, what each depositional 'assemblage' may be expected to represent, given the complicated taphonomic history of the assemblages, are also applicable to the large mammals and undoubtedly added to the complications of analysis. Such complications may have hampered the drawing of associations between pathologies and diet, or pathologies and other variables acting upon the fauna. Future research at LBW should adapt the methodologies used in faunal analysis to take into account the possible limitations and/or problems imposed on analysis by the taphonomic history of the LBW assemblages.

14.1.4 The Langebaanweg mole rats

The mole rats do not dominate the LBW micromammal assemblage to the extent suggested by previous research. The gerbillid found at LBW, and the extinct murid *Euryotomys pelomyoides,* are as common as, or more common than, the bathyergids in many of the units at LBW.

Death from drowning has been ruled out as the main cause of death of the mole rats from the LQSM as the mortality profile indicates that unweaned and very young individuals are not represented in the fossil assemblages. Close to half of the mole rat incisors from the LQSM and the MPPM (F) units show no evidence of digestion. It is uncertain if this indicates that predation has not taken place, or if these animals were taken by a category 1 predator. Predator behaviour, such as the beheading of prey prior to consumption, may not be ruled out.

It is suggested that the high proportion of mole rats in some of the LQSM units may reflect the fact that *B. hendeyi* frequented the soft, sandy sediments of tributaries, rivers, and dunes, much like the extant *Bathyergus* species. Such behaviour would have increased the likelihood of this species being incorporated into the floodplain deposits of the LQSM, and the river channel deposits of the MPPM (F).

14.2 Present and past distributions of micromammals

This thesis has noted certain disparities in the distribution of modern-day micromammal species as recorded by different authors. Studies of modern owl pellet assemblages from the west coast have indicated that the current distribution of micromammal species as described in the literature may not be strictly correct. This may be related to changes in species distribution over relatively short periods of time, as well as difficulties relating to recording and updating the records of the micromammal population living an area. The current distribution of many micromammal species clearly needs to be updated. There is a need for studies, such as those done on modern owl pellet assemblages by Avery (1992b, 1999), as these contribute information on the current distribution of micromammal species, and add to understanding how seasonal change may affect the species represented in pellet assemblages. The study of different owl roosts within the same area provides important information on how the immediate environment around a roost site, and predator-prey selection, may affect micromammal species representation in pellet assemblages. An understanding of issues such as these is vital if fossil assemblages are to be used for palaeoecological reconstruction.

14.2.1 HDP1

HDP1 indicates that the distribution patterns of *O. slogetti* and *Z. woosnami* have changed quite markedly since the late Middle Pleistocene. *E. rupestris*, present on the west coast during the late Middle Pleistocene, appears to have shown a northwards shift in distribution on the west coast since its appearance throughout the Holocene deposits from EBC, until approximately 750 BP. Further research into the present-day west coast micromammal communities, and the discovery of other Pleistocene and Holocene micromammal-bearing fossil sites in the area, will confirm which of the changes in distribution postulated for several species in the previous chapter are correct.

14.2.2 LBW

This study has contributed three new murid genera to the microfaunal list at LBW, namely *Thallomys*, *Zelotomys* and *Rhabdomys*, and it is possible that further research on the micromammal assemblages from the new excavation area will add even more. These three genera may now be added to the several other taxa making an earliest recorded appearance at LBW. Several new *Aethomys* and *Rhabdomys* species have been identified from the MPPM (F) and the LQSM, indicating the speciation of these taxa during the Mio-Pliocene in southern Africa.

14.3 Langebaanweg: The relationship of the MPPM and LQSM members

The present study contributes towards understanding the complex and confusing relationship between the MPPM and LQSM horizons, and provides evidence which suggests that there may not have been, as has been suggested previously, an appreciable time interval between the deposition of the two members. The unexpected similarity observed between the general micromammal populations of the two members indicates that there may have been a relatively short period of time between their deposition. This suggestion is in agreement with the geology in that there are no obvious uncomformities at the interface between the MPPM and LQSM. The LQSM persisted over a large area in a horizon which was found to be consistently ~2 m thick, strongly suggesting that there has been no significant post-depositional erosion, and the MPPM and LQSM are inter-fingered in some places (Roberts in press.).

Klein's (1981, 1982) study of the ungulates indicated that broadly the same mammalian taxa were found in the LQSM and MPPM. The micromammals show a similar picture, and do not indicate any morphological differences between species common to both the LQSM and MPPM (F). Differences between the micromammal taxa in terms of the species present, and species diversity, found in the MPPM (F) and LQSM may be related to a number of different factors, and this hampers interpretation. Previous research has noted morphological differences between large mammal taxa from the two members, and between bed 3aS and bed 3aN, as being very slight. Differences appear to have been small and somewhat tentatively identified (Gentry 1980, Hendey 1980). Further research into the fauna from the MPPM and LQSM should aid in clarifying what, if any, marked morphological differences exist between the taxa from these horizons. Such information should also aid in clarifying the time period involved between the deposition of the LQSM and MPPM members.

The increase in molar size observed in *Euryotomys pelomyoides* in the MPPM (F) is interesting as a similar increase in size in a few of the large mammal taxa from bed 3aN, relative to bed 3aS, has been noted (Hendey 1978b, Gentry 1980, De Muizon and Hendey 1980). Future research at LBW should aim to increase the sample size of micromammals studied in order to see if similar increases in body size may be observed in other species.

14.4 The contribution of the micromammals from HDP1 and LBW towards interpreting diversity in fossil assemblages

The diversity of species found in the LQSM units, namely ~16 species, is lower than that of the MPPM (F) units at ~20-22 species. The number of species found in the LQSM units is slightly lower than the range of diversity shown by modern barn owl pellet collections (see Chapter 13), and indeed all the other west coast fossil sites. Diversity in the LQSM units is somewhat low considering the large sample size of this unit, which is thought to contain a mixture of assemblages. The various issues which may have contributed to the higher species diversity of the MPPM (F) assemblages relative to those from the LQSM, were discussed in some detail in Chapter 8. These issues included the manner in which recovery methods may have affected species diversity, differences in the depositional history of the LQSM and MPPM (F) units, the contribution of predators to species diversity in the fossil assemblage, and changes in environmental and climatic parameters. These many variables complicate assessing the diversity at LBW. The MPPM (F) fossil assemblages show a similar diversity of species to the other west coast fossil sites, with HDP1 and SBYC showing a somewhat lower, and EBC and STBKC, a slightly higher, diversity. The diversity of species found in the MPPM (F) horizons is not, therefore, in any way exceptional when compared with other west coast fossil sites. Climatic or environmental change cannot be entirely ruled out, however, there would appear to be a number of different factors which may also have led to this scenario. Until a larger sample of micromammals from the MPPM (F) horizons are analysed, and further research into the micromammal assemblages from bed 3as (MPPM) are completed, the cause of differences in diversity between the two members must remain, to a certain extent, unresolved.

In Chapter One the issue was raised that the greater diversity of genera and species in the South African Australopithecine sites relative to the East African sites, which are open-air, lacustrine sites, may be attributable to the different depositional histories of the two types of sites (Denys 1996a, 1999). LBW, which contained sediments which were accumulated on a

floodplain, as well as other, alluvially accumulated sediments, provided an opportunity to test this hypothesis.

The river channel deposits of MPPM (F) show a diversity of species which is similar to that of fossil sites in the same region which accumulated in caves, in the case of STBKC and EBC, and in hollows/cavities within calcarenite in the case of HDP1 and SBYC. This suggests that alluvially accumulated, open-air sites need not necessarily produce assemblages which show a low diversity of species.

In Chapter six, it was mentioned that LBW shows a murine species diversity which is similar to two of the Makapansgat fossil horizons, namely the Makapansgat rodent corner and Makapansgat Limework dumps, which show a species diversity of 23 and 22, respectively. LBW thus provides evidence that suggests that the greater diversity of murine genera and species observed in the South African australopithecine sites relative to the East African sites, may not be attributable to the different depositional histories of the two types of sites, but may reflect the greater differentiation of genera and species in South, as opposed to East, Africa.

14.5 Environmental change at Langebaanweg

The LBW micromammals have contributed towards assessing what environmental change occurred between the time of deposition of the MPPM and the LQSM. A comparison of the micromammalian data with that of the most recent work on the large mammal taxa from LBW done by Franz-Odendaal (2002) raises some interesting issues which future research needs to address.

Franz-Odendaal (2002) suggests that nutritional stress from diet has not been the cause of the observed tooth defects, on the basis that the young *Sivatheres* indicate a stress-free, *in utero* period, and defects on tooth enamel are not related to the weaning period. Episodic periods of stress were deduced from a study of the $\delta^{18}O$ sequences across the *Sivathere* tooth crowns, and Franz-Odendaal (2002) suggested that the occurrence of defects in certain taxa may be related to water-dependance, and periods of drought and increased aridity (Franz-Odendaal 2002). No support for this theory may be found in the micromammalian taxa in that the micromammal populations of the LQSM and MPPM (F) show many similarities, and there is no indication of marked environmental change. The question arises as to whether the micromammal species could be expected to reflect the stress which appears to have affected the large mammals, when many of them appear to have occupied different areas of the

landscape to the large taxa. It could be argued that the large and small mammals at LBW occupy different ecological niches and have different sized home ranges, and so may be affected differently by changes in environmental parameters. A palaeoecological study of the micromammals at Olduvai bed I and Lower bed II indicated the same large-scale habitat changes shown by the bovids, suggesting that the large and small mammals from a site can provide very similar palaeoenvironmental information (Kappelman 1984). This study did not, however, take into account the effect that the predators responsible for accumulating the micromammals may have had in terms of prey selection (Fernandez-Jalvo *et al.* 1998).

The ratio of Murinae to Gerbillinae has been used as an indicator of aridity by several authors as the number of gerbillids are known to increase, and the number of Murinae decrease, with an increase in aridity (Denys *et al.* 1996b, Fernandez-Jalvo *et al.* 1989, Denys 1999). This is clearly indicated by the high number of gerbillid, relative to murid, species found in the Sahara, Sahelian and Sudanian Regions today (see Chapter 2). The presence of only one gerbillid species at LBW indicates that open, and relatively arid, areas existed, but does not indicate general aridity in the area. LBW is clearly less arid than the Namibian fossil sites as three gerbillid genera were represented at Jägersquelle, and two at Nosib (Denys 1999). The Gerbillidae show no increase in abundance in the MPPM (F), relative to the LQSM, deposits. In fact, there is a paucity of gerbillids in the MPPM (F) river channel deposits, suggesting that the gerbillid did not enjoy a widespread distribution throughout LBW. The micromammals do not thus provide support for Franz-Odendaal's (2002) suggestion that periods of drought and increased aridity occurred during deposition of the bed 3aN horizons.

In conclusion, the micromammal assemblages from LBW suggest that the general micromammal population in the area remained relatively unchanged during the period of deposition of the MPPM (F) and LQSM, and there is no compelling evidence to suggest that any marked climatic or environmental change took place during this period.. This provides support for the suggestion made by Franz-Odendaal (2002), namely, that the pathologies observed in the large mammals at LBW were not related to dietary factors. Dietary stress would, presumably, be linked to environmental change. The greater diversity in the MPPM (F) assemblages, relative to those from the LQSM, is an issue which cannot be ignored in that it could be interpreted as indicating some kind of environmental or climatic change. There are, however, a number of variables which may have led to the greater species diversity observed in the MPPM (F). These have been discussed in detail in Chapter 8. In addition, the diversity in the MPPM (F) units is similar to that of the other west coast fossil sites, while that

of the LQSM units is somewhat lower. This provides support for the suggestion that the relatively lower diversity in the LQSM units may be an artefact of recovery, taphonomy, or perhaps a combination of factors. A final verdict on the matter must be delayed until more conclusive evidence is obtained.

Research into other taxa which are sensitive to the availability of water is needed at LBW in order to ascertain if other species indicate the increasing aridity postulated to have occurred during the deposition of the MPPM (Franz-Odendaal 2002). This will hopefully serve to contribute to our understanding of the prevailing climatic conditions at LBW during the deposition of the fossiliferous horizons, and will assist in ascertaining whether different environmental or climatic variables were acting upon the fauna from the LQSM and MPPM.

14.6 The contribution of the micromammal assemblages from HDP1 and LBW towards palaeontology and palaeoecology

The HDP1 micromammal assemblages have added to the information available on the past distribution of several species in the Saldanha area, and have confirmed the presence of several endemic species in the west coast area during the late Middle Pleistocene. A comparison between the west coast fossil sites and HDP1 indicates that conditions on the west coast in the late Middle Pleistocene differed quite markedly to climatic and environmental conditions that prevailed during the Terminal Pleistocene and Holocene, and appear to have been relatively more arid. A comparison between the micromammal populations of SBYC, EBC, STBKC and modern owl pellet assemblages indicates that the general environment and resident micromammal population from the Late Pleistocene, to the present day, has remained very much the same (Avery 1992b, 1999, Manthi 2002, Avery in press). The HDP1 micromammal assemblage appears to represent an accumulation of barn owl pellets which were deposited during a single episode of occupation of the site. HDP1 may thus provide a brief glimpse of the environs of HDP1 during the period the owl roosted at the site.

The discrepancy observed between the palaeoenvironments indicated by the large mammals and the micromammals at LBW is similar to that observed at HDP1, namely that the various micromammal species indicate the existence of microhabitats not detected by a study of the large ungulates. The ungulates from LBW and HDP1 have been analysed in terms of being grazers, browsers, or mixed feeders, and this classification excluded the identification of microhabitats such as sandy, rocky, arid or open areas. The micromammals from both the

sites investigated in this thesis have provided a fine-tuning to the palaeoecological picture provided by larger animals.

On the basis of the micromammals, it was suggested in Chapter 8 that certain fynbos components may have been well established in the environment at LBW some 4-5 Ma, and that relatively dry microhabitats with an open, scrub vegetation, similar to that seen in the west coast Sandveld today, existed. This study of the micromammals from LBW, and the other west coast fossil sites, indicates that certain genera have persisted in the area over a long period of time. It would appear that at LBW, during the Mio-Pliocene, a micromammal fauna existed which exploited ecological niches in the fynbos. Both the fynbos and micromammal genera present at LBW have families resident in the west coast area today, and further north in the Namib and South West Arid Regions. This suggests the endurance and continuation of certain aspects in the environment of the west coast from the Mio-Pliocene, until the present, and lends support to the suggestion that fynbos microhabitats were well established at the time of deposition of the LBW sediments.

The micromammal populations from west coast fossil sites dating to the Terminal Pleistocene and Holocene are essentially similar to the present-day micromammals resident in the west coast area. HDP1 has, however, provided an insight into the shifts in distribution of several species which appear at the site, but are no longer found in the area. More west coast sites of a similar age to HDP1 need to be analysed in order to ascertain the extent of climatic and environmental change in the area during the late Middle Pleistocene, as well as the duration of the period of aridity reflected in the HDP1 micromammal assemblage.

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Appendices

Appendix A: The percentage representation of micromammalian species from the Saldanha Bay Yacht Club site (SBYC), Saldanha

Taxon	Down slope		Upper slope		Hanging remnant	
	N	%	N	%	N	%
Insectivora						
C. asiatica	2	1.1	12	2.4		
cf. C. cyanea	7	3.7	3	0.6	3	3.4
C. flavescens	4	2.1	5	1	1	1.1
M. varius	49	26	164	32.7	12	13.5
cf. M. varius	3	1.6	16	3.2	1	1.1
S. varilla	20	10.6	63	12.5	19	21.3
cf. S. varilla			1	0.2		
Chiroptera						
R. clivosus	1	0.53	1	0.2		
Muridae						
D. melanotis	2	1.1	9	1.8	2	2.25
D. mesomelas			2	0.4		
Dendromus spp.			2	0.4	2	2.25
S. krebsii	8	4.2	22	4.4	3	3.4
G. paeba	7	3.7	9	1.8	3	3.4
T. afra	50	26.5	121	24.1	25	28.1
M. albicaudatus	2	1.1	4	0.8	2	2.25
R. pumilio	4	2.1	4	0.8		
cf. R. pumilio	1	0.53				
O. irroratus	1	0.53	7	1.4	1	1.1
O. saundersiae	10	5.3	24	4.8	12	13.5
O. unisulcatus	5	2.65	6	1.2		
Otomys spp.	9	4.8	17	3.4	3	3.4
Bathyergidae						
B. suillus			1	0.2		
C. hottentotus	4	2.1	8	1.6		
Macroscelididae						
E. edwardii			1	0.2		
Shannon Weiner Indices*	**2.16**		**2.04**		**1.95**	
MNI*	***189***		***502***		***89***	

After Manthi (2002), Table 7.2.2 and Table 7.2.3, page 80-81

* based on number of maxillae and mandibles

Appendix B: Percentage representation of micromammalian species in the various units at Elands Bay Cave (EBC), Elands Bay

Unit	1-2b	3a-4c	5a-5c	6-7	8	9	10a-10d	11-12	13	14	15-19
Age	330 - 550 BP	900 – 750 BP	1550 – 2200 BP	3400 – 4150 BP	3750 – 3800 BP	3900 – 4350	8000 – 8750 BP	8900 – 9500 BP	9200 –9659 BP	9950 – 10050 BP	10450 –13260 BP
Muridae											
O. unisulcatus	20	33.3	27.3	57.4	42.1	32.6	80.5	83.3	79.1	87.5	52.9
A. namaquensis	37.5	31.1	39.4	20.6	23.7	29.2	2.4	2.6	2.7	5	5.7
O. saundersiae		3.3	3		1.3	1.4			0.9		1.1
O. irroratus				1.5	1.3	0.4					5.7
S. krebsii	12.5	2.2	3		2.6	2.1					2.3
T. afra						0.7	2.4	1.3	1.8	2.3	2.3
G. paeba	2.5		3		2.6	2.1		1.3			
M. minutoides		1.1			1.3	0.7					
M. verreauxi	2.5	2.2		1.5		0.7	2.4				
A. subspinosus					1.3						
R. pumilio		4.4	9.1	1.5	1.3	8.3	2.4	3.8	5.5	5	10.3
D. melanotis						0.7					
Dendromus sp.	2.5										
M. albicaudatus	2.5	1.1				0.7		2.6	1.8		1.1
G. ocularis		1.1									
Macroscelididae											
Elephantulus sp.											1.1
E. rupestris		5.6	3	2.9	1.3	6.3	4.9	1.3			
E. edwardii	7.5	3.3	3	4.4	6.6	2.1		1.3	2.7		
Soricidae											
M. varius		1.1		4.4	2.6	2.8		1.3			3.4
S. varilla	2.5										2.3
C. flavescens				1.5		1.4			0.9		3.4
C. cyanea	5	6.7	9.1	1.5	5.3	3.5	2.4		1.8		
Bathyergidae*											
C. hottentotus	2.5	2.2	0	2.9	5.3	2.1	2.4	1.3	0.9	2.5	2.3
G. capensis									1.8		
Chrysochloridae					1.3						1.1
C. zyli		1.1				0.7					
E. granti						0.7					
C. asiatica	2.5										
MNI	***40***	***90***	***33***	***68***	***76***	***144***	***41***	***78***	***110***	***40***	***87***

After Avery (in press), Table 4

**Bathyergus suillus* was present at EBC, but was not included in the analysis of the micromammals done by Avery (in press)

Appendix C: The micromammalian species from Steenbokfontein Cave (STBKC), Steenbokfontein farm, and a modern barn owl pellet collection from the area

	Unit 0	Unit 1	Unit 2	Unit 3	Unit 4a	Unit 4b	Modern owl pellet assemblage
Age	-	~2200 – 2300 BP			~3300 BP	~3990 – 6070 BP	
Soricidae							
M. varius		7.5	8.4	9.2	4.3	8.7	1.9
C. flavescens	4.2	1.1	0.6	0.5		0.7	0.2
C. cyanea			0.3	0.2			1.6
S. varilla	8.3	7.9	9	4.6	4.3	4.2	4.3
Chrysochloridae							
C. asiatica		0.6					0.3
E. granti	4.2	4.4	3	2.3	4.3	0.7	1.3
Bathyergidae							
B. suillus		0.4	0.7	0.2			1.1
C. hottentotus		0.3	0.2	0.3		0.3	0.7
Macroscelididae							
E. edwardii	4.2	4.6	2.7	5.3	2.2	4.5	0.1
Muridae							
P. brantsii			0.6				
O. saundersiae	8.3	8.1	7.4	10.2	8.7	6.3	
O. irroratus		1	2.1	0.7	4.3	2.1	4.1
O. unisulcatus	25.0	22.5	25.8	21.7	30.4	20.9	5.6
D. auricularis							1.4
G. paeba	25.0	15.3	14.3	17.1	10.9	24.4	12
T. afra	4.2	5.2	4.7	6.2	8.7	6.3	49.6
M. albicaudatus	4.2	6.2	6.2	7.5	8.7	7.0	
D. melanotis		0.6	0.9	0.9	2.2	0.3	1.2
D. mesomelas		0.1	0.1	0.1			0.7
M. typica						0.3	0.7
S. krebsii	8.3	7.6	6.5	6.6	6.5	7.7	4.3
A. subspinosus							0.1
R. pumilio	4.2	5.9	5.1	4.9	4.3	4.9	0.9
M. minutoides			0.5	0.3			7.1
A. namaquensis		0.4	0.7	1.1		0.7	0.6
R. rattus							0.1
G. ocularis		0.3					
MNI	***24***	***724***	***886***	***1490***	***46***	***287***	***898***

After Avery (1999), Table 4, page 175

Appendix D: Faunal composition of the Early to Middle Pliocene murid faunas of fossil sites in East and South Africa

Genus	IBL	UNB	LB	OMB	OMC	LQSM*	MPPM*	EXQR	MRCIS	MLWD	NGA	HAD	JAG	NOS
Age of site→	4-5 Ma	3.7 Ma	3.7-3.59 Ma	~3.3 Ma	~2.48 MA	4-5 Ma	4-5 Ma	~3.3-3.7			3 Ma	3.6 Ma	~ 3 Ma	Plio-Pleistocene
Xerus		1	1	1	1									
Paraxerus			1	1	1									
Gerbillinae, indet.			1											
Gerbillurus													1	1
Tatera		1	1	1					1			1	1	
Desmodillus						1	1						1	
Taterillus								1	1		1			
Saccostomus	1	1	1										1	
Dendromus			1			1	1	1	1	1	1		1	1
Steatomys			1					1	1	1			1	1
Malacothrix								1	1	1	1		1	1
Golunda				1	1							1		
Millardia												1		
Lemniscomys				1	1									
Thallomys		1	1	1	1		1						1	
Mastomys		1	1	1	1				1	1				
Oenomys					1									
Arvicanthis				1										
Aethomys						1	1	1	1	1				
Acomys						1	1	1	1	1			1	
Dasymys								1	1	1				1
Grammomys									1	1				
Mus				1		1	?	1	1	1	1	1	1	1
Myomyscus									1	1	1			
Pelomys										1	1			
Praomys												1		
Rhabdomys						1	1	1	1	1				1
Proceromys	1													
Saidomys	1											1		

Appendix D (cont...)

	IBL	UNB	LB	OMB	OMC	LQSM	PPM	EXQR	MRCIS	MLWD	NGA	HAD	JAG	NOS
Zelotomys						?	1				1		1	1
Mystromys						1	1	1	1	1				1
Stenodontomys						1	1	1	1				1	1
Proodontomys								1	1	1				
Otomys								1	1	1	1			1
Myotomys								1	1	1				
Prototomys										1	1			
Cryptomys						1	1	1	1	1				1
Gypsorychus										1				
Bathyergus						1	1							
Euryotomys						1	1							
Georychus											1			
Graphiurus						1	1						1	1
Heterocephalus		1	1											
Thryonomys	1	1		1	1									
Pedetes			1											
Tachyoryctes												1		
Diversity	**4**	**17**	**11**	**10**	**8**	**~13**	**~14**	**15**	**19**	**19**	**10**	**7**	**11**	**13**

After Denys (1999), Table 16.2, page 230

Key: **IBL** = Ibolé, (Tanzania) **UNB** = Upper Ndolanya Beds (Tanzania)
LB = Laetoli beds (Tanzania)
OMC = Omo C (Ethiopia) **OMB** = Omo B (Ethiopia)
MPPM = Muishond Pelletal Phosphate Member (Western Cape, S. A.) **LQSM** = Langeberg Quartzose Sand Member (Western Cape, S. A.)
EXQRM = Makapansgat exit quarry red mud (Northern province, S. A.) **MRCIS** = Makapansgat rodent corner in situ, (Northern province, S. A.)
MLWD = Makapansgat limework dumps (Northern province, S. A.),
NGA = Ngamiland (Botswana), **HAD** = Hadar (Ethiopia), **JAG** = Jägersquelle (Namibia) **NOS** = Nosib (Namibia)

Appendix E: Andrews' (1990) predator categories

	Category 1	Category 2	Category 3	Category 4	Category 5
Breakage of skulls	Bo, So, Leo, Geo , Ggo	Seo, Speo, Eeo, T	Lit, Kes, H	-	Mam. Carn.
Breakage of mandibles	Bo, Leo, Geo, Ggo	So, Seo, Eeo, T	Speo, Kes, H	LIT, Mam. Carn.	--
Mandibular tooth loss	Bo, So, Leo, Seo, Ggo, Eeo	Geo, Speo, T	Lit, Kes, Coy, Art, Pine	H, Mong, Gen, Bat, Red	-
Maxillary tooth loss	Bo, So, Leo, Geo ,	Ggo, T	Seo, Eeo, Speo, Bat, Coy	Lit, Kes, H, Gen, Mong, Red, Art, Pine	-
Proportions isolated teeth	Bo, So, Leo, Seo, Geo, Eeo, Speo	Ggo, Coy, Mong	T, LIT, Bat	Kes, Gen, Red, Pine	H, Art
Postcranial/ cranial proportions	Bo, Leo, Seo, Eeo, Ggo, Pine, Bat	T, Geo , Speo, Kes, Gen	H, Art,	So, Lit, Mong, Coy, Red	-
Loss of distal elements of postcrania	Bo, So, Leo, Geo, T	Seo, Eeo, Ggo, Coy, Art	LIT, Kes	Speo, H, Red	Pine, Mong, Gen, Bat
Incisor digestion	Bo, So, Seo	Leo, Geo, Bat, Ggo	Eeo, Speo, LIT, Mong, Gen, T, Pine	K	Hen, Coy, Red, Art
Breakage of teeth	Bo, So, Leo, Ggo,	Seo, Geo , Speo, LIT	Eeo, T	Kes, H	Mam. Carn.
Breakage of postcrania	Bo, Ggo, Leo, Seo, Geo	So, Eeo	Speo, T,	LIT, Kes, H, Mong, Gen, Bat	Pine, Art, Coy, Red

After Andrews (1990), Table 3.16, page 90

Key: Bo = barn owl
Gen = genet
So = snowy owl
H = hen harrier
Kes = kestrel
Mam. Carn. = mammalian carnivores
Lit = little owl
K = kestrel
T = tawny owl
Mong = mongoose
Bat = bat-eared fox
Art = arctic fox
Ggo = great grey owl
Red = red fox
Pine = pine marten
Eeo = European eagle owl
Speo = spotted eagle owl
Leo = long-eared owl
Coy = coyote
Seo = short-eared owl
Geo = giant eagle owl

Appendix F: The digestive etching of the murid incisors from the MPPM (F), Langebaanweg

Unit F10 (PPM): Digestive etching on isolated murid maxillary incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated maxilla incisors					
			Etching classes					
			0	1	1a	2	3	4
F10	15	< tip present	17	2	1	6	2	1
F10	12	> tip present	32	12	0	9	4	0
F10	6	> shaft	3	0	0	1	0	0
Total (n=123)	*33*		*52*	*14*	*1*	*16*	*6*	*1*

Unit F10 (PPM): Digestive etching on isolated murid mandibular incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated mandible incisors					
			Etching classes					
			0	1	1a	2	3	4
F10	13	< tip present	15	4	0	11	3	0
F10	9	> tip present	17	8	0	8	1	0
F10	2	> shaft	1	2	0	4	0	0
Total (n=98)	*24*		*33*	*14*	*0*	*23*	*4*	*0*

Unit F11 (PPM): Digestive etching on the isolated murid maxillary incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated maxilla incisors					
			Etching classes					
			0	1	1a	2	3	4
F11	3	< tip present	10	1	0	2	0	0
F11	12	> tip present	28	4	1	12	1	0
F11	2	> shaft	5	1	0	0	1	0
Total (n=83)	17		43	6	1	14	2	0

Appendix F (cont...)

Unit F11 (PPM): Digestive etching on the isolated murid mandibular incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated mandible incisors					
			Etching classes					
			0	1	1a	2	3	4
F11	4	**< tip present**	9	1	0	3	1	0
F11	7	**> tip present**	11	15	0	3	2	0
F11	1	**> shaft**	2	0	0	1	0	0
Total (n= 60)	*12*		*22*	*16*	*0*	*7*	*3*	*0*

Appendix G: The digestive etching of *B. hendeyi* incisors from the MPPM (F), Langebaanweg

Unit F10 (PPM): Digestive etching on isolated *B. hendeyi* mandibular and maxillary incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated mandible and maxilla incisors					
			Etching classes					
			0	1	1a	2	3	4
F10	0	< tip present	4	3	0	1	0	0
F10	1	> tip present	8	7	0	1	1	0
F10	0	> shaft	1	0	0	0	0	0
Total (n= 27)	*1*		*13*	*10*	*0*	*2*	*1*	*0*

Unit F11 (PPM): Digestive etching on isolated *B. hendeyi* mandibular and maxillary incisors

Unit name	No. of incisors that could not be assessed	Incisor breakage categories	Isolated mandible and maxilla incisors					
			Etching classes					
			0	1	1a	2	3	4
F11	0	< tip present	3	1	0	1	0	0
F11	1	> tip present	2	0	0	3	0	0
F11	1	> shaft	2	1	0	0	1	0
Total (n= 16)	*2*		*7*	*2*	*0*	*4*	*1*	*0*

Appendix H: Breakage patterns of the limb bones from the MPPM (F), Langebaanweg

F10	TC	TP	TD	TS	UC	UP	UD	US	FP*	FC	FD	FS	HC	HP	HD	HS
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
Indet. Murid	0.0	11.8	76.5	11.8	0.0	100.0	0.0	0.0	88.4	0.0	11.6	0.0	3.8	9.6	82.7	3.8
Soricid	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	75.0	0.0
Mole rat	0.0	14.3	85.7	0.0	0.0	100.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Mole	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	87.5	12.5	0.0	0.0	16.0	12.0	68.0	4.0
F11	**TC**	**TP**	**TD**	**TS**	**UC**	**UP**	**UD**	**US**	**FP***	**FC**	**FD**	**FS**	**HC**	**HP**	**HD**	**HS**
Indet. Murid	0.0	0.0	100.0	0.0	0.0	100.0	0.0	0.0	96.8	0.0	3.2	0.0	0.0	4.3	95.7	0.0
Soricid	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	13.3	0.0	86.7	0.0
Mole rat	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	83.3	16.7	0.0	0.0	50.0	25.0	25.0	0.0
Mole	40.0	0.0	0.0	60.0	13.3	86.7	0.0	0.0	100.0	0.0	0.0	0.0	18.8	9.4	71.9	0.0

Key: **TC = tibia complete,** **TP = tibia proximal,** **TD = tibia distal,** **TS = tibia shaft**
UC = ulna complete, UP = ulna proximal, UD = ulna distal, US = ulna shaft
FP = femur proximal* FC= femur complete, FD = femur distal, FS = femur shaft
HC= humerus complete, HP = humerus proximal, HD = humerus distal, HS = humerus shaft

* The category 'femur proximal' includes the breakage category 'femur head'

Appendix I: The relative abundance of bodyparts in Unit F10 and F11 (MPPM (F)), Langebaanweg

	F10		F11		Unit F10 and F11 combined)	
	(N)	%	(N)	%	(N)	%
Mandible	34	**41.5**	16	**27.6**	50	**35.7**
Maxilla	41	**50.0**	31	**53.4**	72	**51.4**
Scapula	2	**2.4**	0	**0.0**	2	**1.4**
Humerus	52	**63.4**	23	**39.7**	75	**53.6**
Radius	8	**9.8**	2	**3.4**	10	**7.1**
Ulna	34	**41.5**	21	**36.2**	55	**39.3**
Pelvic girdle	13	**15.9**	9	**15.5**	22	**15.7**
Femur	43	**52.4**	31	**53.4**	74	**52.9**
Tibia	17	**20.7**	11	**19.0**	28	**20.0**
Vertebra	200	**15.2**	57	**6.1**	257	**11.5**
Incisor	164	**100.0**	114	**98.3**	278	**99.3**
Molar	186	**37.8**	83	**23.9**	269	**32.0**
Phalange	57	**2.5**	37	**2.3**	94	**2.4**
Metapodial	41	**5.0**	32	**5.5**	73	**5.2**
MNI	***41***		***29***		***70***	

Appendix J: The undescribed *Aethomys* and *Rhabdomys* species from Langebaanweg

The terminology used for the description of the molars follows that used by Misonne (1969) and Wesselman (1984).

The M^1 of *Aethomys* intermediate

Accession no: PQL69323 (F11, MPPM (F)), PQL69249 (F11, MPPM (F) - 2 molars)

- t1 lies behind the t2 and t3 and t1is more clearly separated from the t2 than in Aeth. sp 3.
- the central row of cups is more dominant than *Aeth.* sp. 3 or *A. adamanticola*, and t2, t5 and t8 and are arranged longitudinally, one behind the other.
- the cusps are more hypsodont than in the other LBW *Aethomys* sp.
- t4 and t6 lie posterior to the t5
- t3 and t6 are large cusps and are similar in size to t1 and t4
- t9 is a well-defined cusp and is situated to the side of t8, it is set more to the posterior of t9, than seen in *Aethomys sp. 3*
- there is no link between t6 and t9
- the size of the anterior cingulum ranges in size from a vestigial cusplet, to a small cingulum. PQL 69323 had no cingulum.
- t7 is absent, there is a link between the t8 and t9

The M_1 of *Aethomys* sp. 1

Accession no: PQL68768 (F10, MPPM (F)), 69268 (F11, MPPM (F)),and PQL 68567 (LQSM)

- this *Aethomys* is similar in size to *A. modernis*
- the cusps are less alternated than *A. modernis*
- PQL68768 has no anterocentral cusp, PQL68768 have a small, vestigial cusp
- The anterolingual cusp is larger than the anterolabial cusp
- the 2nd and 3rd cusp rows have a wider angle between them than A. modernis

PQL68779 is too worn to make a positive id., but may belong to the same *Aethomys* species

The M^1 of *Aethomys* sp. 3

Accession no: PQL69245, PQL69246, PQL69247 (MPPM (F): F11)

- the occlusal surfaces of the t1, t2 and t3 are aligned, as seen in *A. adamanticola*

- t4 and t6 lie posterior to the t5
- t3 and t6 are small relative to t1 and t4
- t9 lies transversely to the t8 and lies more posteriorly when compared to Aethomys intermediate
- PQL 69245 is more worn than the other two molars, and shows a connection between t8 and t9, and t4, t5 and t6.
- There is a small posterior cingulum on PQL69246 and PQL69247, but not PQL69245
- the cusps are orientated towards the back of the tooth

The M^2 of *Aethomys* sp. 3

- t1 and t3 are positioned opposite one another, t3 is small relative to t1
- t2 and t7 are absent
- t4 and t6 lie behind the t5 and are positioned opposite one another
- t5 and t8 are large and dominate the central row of cusps to a greater degree than in the M^1
- t9 is positioned next to the t8 in the same position as seen in the M^1, but is slightly smaller than t9 on the MU^1
- there is a link between t6 and t9

The M_1 of *Aethomys* sp. 4

Accession no: PQL68767(F10, MPPM (F), PQL68772 (F10, MPPM (F), PQL69264 (F11, MPPM (F)

- the cusps are alternate and relatively hypsodont
- the anterolabial and anterolingual cusps are approximately equal in size
- the anterolabial cusplet lies transversely on the hypoconid
- the posterior cingulum is relatively large and lies between the hyonconid and entoconid
- a small vestigial anterocentral cusplet is present
- the anterolabial and anterolingual cusps are narrower than the metaconid, protoconid, hypoconid and entoconid.
- All cusps are clearly separated, there is no liasion between the prelobe and the second row of cusps

The M_1 of *Rhabdomys* sp. 1

Accession no: PQL68513 (LQSM), PQL68492 (LQSM)

This *Rhabdomys* species is bigger than the other *Rhabdomys* species at LBW, namely *Rhabdomys* sp. 2 (Accession no. PQL68766).

- the anterolabial and anterolingual cusps are approximately the same size
- the cusps are only slightly alternated
- PQL68513 has no anterocentral cusp, PQL68492 has a vestigial anterocentral cusp
- the anterolabial cusplet is situated more posteriorly than on Rhabdomys sp. 2
- a small cingular crest runs along the labial anterocentral cusp
- there is a lingual link between the anterolabial and anterolingual cusps, and between the hypoconid and entoconid

The M_1 of *Rhabdomys* sp. 2

Accession no.: PQL68766 (F10, MPPM (F))

- the cusps are less robust than the other *Rhabdomys* sp. 1
- the anterocentral cusp is rounded
- the angle between the hypoconid and entoconid is greater than in *Rhabdomys sp.*1
- the posterior cingulum is relatively large compared with the other *Rhabdomys* species at LBW.
- both this, and the other *Rhabdomys sp.* 1 are much larger than the extant *R. pumilio*
- the cusps are slightly more alternated than *R. pumilio*, but the shape and angles of the cusps are otherwise very similar to *R. pumilio*

The M^1 of *Rhabdomys*, indeterminate

Accession no: PQL68986, PQL68923, PQL68924, 68811, 68812, 68827, 68835, 68911, 68917, 68928 (F10, MPPM (F))

- t1 lies posteriorly to t2 and t3
- t4 and t6 lie posteriorly to t5
- t9 is round and lies transversely on the t8, somewhat towards the posterior of t8
- t8 has a cingular crest
- t6 leans at an angle towards t9, and the two cusps almost touch. With wear a link develops between the two cusps

Accession numbers: PQL69248 (F11, PPM), - This tooth is rather too worn to be positively identified as a *Rhabdomys*, intermediate. This molar shows a connection between t1, t2 and t3. There is a trace of an anterior cingulum in this specimen.

Accession number PQL68569 (Unit SAEW/bed 2/S of EleS, LQSM): As far as may be ascertained, given the advanced degree of wear on this tooth, this tooth is identified as a ? *Rhabdomys* intermed.

The M^2 of *Rhabdomys*, indeterminate

- t2 is absent, t3 is smaller than t1
- t4 and t6 lie behind t5, opposite one another
- t1 and t4 are large relative to t3 and t6
- t9 is smaller than in the MU^1
- t5 and t8 are large, t8 is the same size as in the MU^1

Appendix K: M_1 length and breadth of the *Aethomys* and *Rhabdomys* species from the LQSM and MPPM (F), Langebaanweg

Member	Unit	Accession number	Species	Breadth (mm)	Length (mm)
MPPM (F)	F11	69268	Aeth. modernis	1.65625	2.59375
MPPM (F)	F11	69266	Aeth. modernis	1.625	2.5
MPPM (F)	F11	69270	Aeth. modernis	1.59375	2.5
MPPM (F)	F10	68762	Aeth. modernis	1.71875	2.71875
MPPM (F)	F10	68763	Aeth. modernis	1.625	2.6875
MPPM (F)	F10	68769	Aeth. modernis	1.5625	2.59375
MPPM (F)	F10	68770	Aeth. modernis	1.65625	2.6875
MPPM (F)	F10	68771	Aeth. modernis	1.59375	2.5
MPPM (F)	F10	68773	Aeth. modernis	1.75	2.8125
MPPM (F)	F10	68774	Aeth. modernis	1.65625	2.59375
MPPM (F)	F10	68775	Aeth. modernis	1.65625	2.65625
MPPM (F)	F10	68777	Aeth. modernis	1.71875	2.53125
MPPM (F)	F10	68793	Aeth. modernis	1.5625	2.71875
MPPM (F)	F10	68778	Aeth. modernis	1.71875	2.59375
MPPM (F)	F10	68761	Aeth. modernis ?	1.6875	2.5625
MPPM (F)	F11	69261	Aeth. modernis	1.78125	2.6875
MPPM (F)	TP1	68584	Aeth. modernis	1.5	2.34375
MPPM (F)	F10	68767	Aethomys sp. 4	1.75	2.5625
MPPM (F)	F11	69264	Aethomys sp. 4	1.65625	2.71875
MPPM (F)	F10	68772	Aethomys sp. 4	1.75	2.53125
MPPM (F)	F11	69268	Aethomys sp. 1	1.65625	2.65625
MPPM (F)	F10	68768	Aethomys sp. 1	1.59375	2.59375
MPPM (F)	TP1	68567	Aethomys sp. 1	1.874	2.8125
LQSM	ES/D2	68492	Rhabdomys sp. 1	2	2.65625
LQSM	NE/ES/Eles	68513	Rhabdomys sp. 1	1.90625	2.78125
MPPM (F)	F10	68766	Rhabdomys sp. 2	1.723	2.6875
MPPM (F)	F10	68758	Aeth. adamanticola	2.125	3.03125
LQSM	ES/Eles	68484	Aeth. adamanticola	1.5625	2.34375
LQSM	ES/D2	68492	Aeth. adamanticola	1.875	2.8125
LQSM	ES/D2	68492	Aeth. adamanticola	1.78125	2.6875
LQSM	ES/D2	68492	Aeth. adamanticola	1.8125	2.75
LQSM	ES/D2	68492	Aeth. adamanticola	1.75	2.8125
LQSM	ES/Eles	68511	Aeth. adamanticola	1.8125	2.875
LQSM	NE/ES/Eles	68512	Aeth. adamanticola	1.90625	2.75
LQSM	NE/ES/Eles	68513	Aeth. Adamanticola	1.84375	2.75
LQSM	ES/D2	68492	Aeth. adamanticola	1.8125	2.78125
LQSM	ES/D2	68567	Aeth. adamanticola	1.84375	2.8125
LQSM	ES/D2	68567	Aeth. adamanticola	1.90625	2.78125

Appendix K: (cont...)

Member	Unit	Accession number	Species	Breadth (mm)	Length (mm)
LQSM	ES/D2	68567	Aeth. adamanticola	1.8125	2.71875
LQSM	ES/ bed2	68570	Aeth. adamanticola	1.875	2.8125
MPPM (F)	F11	69268	Aeth. modernis	1.65625	2.59375
MPPM (F)	F11	69266	Aeth. modernis	1.625	2.5
MPPM (F)	F11	69270	Aeth. modernis	1.59375	2.5
MPPM (F)	F10	68762	Aeth. modernis	1.71875	2.71875
MPPM (F)	F10	68763	Aeth. modernis	1.625	2.6875
MPPM (F)	F10	68769	Aeth. modernis	1.5625	2.59375
MPPM (F)	F10	68770	Aeth. modernis	1.65625	2.6875
MPPM (F)	F10	68771	Aeth. modernis	1.59375	2.5
MPPM (F)	F10	68773	Aeth. modernis	1.75	2.8125
MPPM (F)	F10	68774	Aeth. modernis	1.65625	2.59375
MPPM (F)	F10	68775	Aeth. modernis	1.65625	2.65625
MPPM (F)	F10	68777	Aeth. modernis	1.71875	2.53125
MPPM (F)	F10	68793	Aeth. modernis	1.5625	2.71875
MPPM (F)	F10	68778	Aeth. modernis	1.71875	2.59375
MPPM (F)	F11	69261	Aeth. modernis	1.78125	2.6875
LQSM	TP1	68584	Aeth. modernis	1.5	2.34375

Abbreviations on table:
Acc. No. = Accession number
Aeth. modernis = Aethomys modernis, Aeth. adamanticola = Aethomys adamanticola
Aeth. intermed. = Aethomys intermediate, Aeth. sp. 3 = Aethomys sp. 3
Rhab. intermed. = Rhabdomys intermediate

Appendix L: M^1 length and breadth of the *Aethomys* and *Rhabdomys* species from the LQSM and MPPM (F), Langebaanweg

Member	Unit	Accession number	Species	Breadth (mm)	Length (mm)
LQSM	Michaels Pit	68568	Aeth. adamanticola	2.03	3.19
LQSM	NE/ES/EleS	68515	Aeth. adamanticola	1.97	2.94
LQSM	PB	68485	Aeth. adamanticola	1.88	2.84
LQSM	TP1	68567	Aeth. adamanticola	1.94	2.91
LQSM	Bed 2/stream along east wall/S of Eles/sieved	68569	Aeth. adamanticola	2.03	3.19
LQSM	ES/D2	68490	Aeth. adamanticola	1.97	2.94
LQSM	ES/D2	68504	Aeth. adamanticola	2.03	2.94
LQSM	ES/D2	68504	Aeth. adamanticola	1.75	2.81
LQSM	ES/D2	68504	Aeth. adamanticola	2.00	3.06
MPPM (F)	F10	68828	Aeth. adamanticola	2.125	3.125
MPPM (F)	F10	68914	Aeth. adamanticola	1.84375	2.71875
MPPM (F)	F10	68922	Aeth. adamanticola	1.9375	2.9375
MPPM (F)	F11	69253	Aeth. adamanticola	2.03125	3.09375
MPPM (F)	F11	69250	Aeth. adamanticola-like	1.75	2.6875
MPPM (F)	F10	68920	Aeth. modernis	1.84375	2.8125
MPPM (F)	F10	68921	Aeth. modernis	1.75	2.84375
MPPM (F)	F10	68927	Aeth. modernis	1.8125	2.75
MPPM (F)	F10	68918	Aeth. modernis (pc present)	1.71875	2.71875
MPPM (F)	F10	68835	Rhabdomys intermed.	1.75	2.75
MPPM (F)	F10	68917	Rhabdomys intermed.	1.8125	2.5625
MPPM (F)	F10	68928	Rhabdomys intermed.	1.8125	2.78125
MPPM (F)	F10	68811	Rhabdomys intermed.	1.6875	2.5625
MPPM (F)	F10	68812	Rhabdomys intermed.	1.59375	2.65625
MPPM (F)	F10	68923	Rhabdomys intermed.	1.8125	2.875
MPPM (F)	F10	68924	Rhabdomys intermed.	1.875	2.96875
MPPM (F)	F11	69255	Rhabdomys intermed.	1.6875	2.5625
MPPM (F)	F10	68986	Rhabdomys intermed.	1.75	2.90625
MPPM (F)	F11	69245	Aeth. sp. 3	1.71875	2.875
MPPM (F)	F11	69246	Aeth. sp. 3	1.71875	2.8125
MPPM (F)	F11	69247	Aeth. sp. 3	1.71875	2.84
MPPM (F)	F11	69249	Aeth. intermed.	1.875	2.96875
MPPM (F)	F11	69249	Aeth. intermed.	1.875	3
MPPM (F)	F11	69323	Aeth. intermed.	1.875	2.9375

Appendix M: M_1 length and breadth of *Euryotomys pelomyoides*

Accession number	Member	Length (mm)	Breadth (mm)
25891	LQSM	2.66	1.95
25891	LQSM	2.6	1.92
25891	LQSM	2.72	1.86
25891	LQSM	2.84	1.94
25891	LQSM	2.6	1.92
25891	LQSM	2.71	1.89
25891	LQSM	2.64	2.02
25891	LQSM	2.6	1.92
25891	LQSM	2.72	1.88
25891	LQSM	2.46	2.02
25891	LQSM	2.6	1.8
25891	LQSM	2.7	1.92
25891	LQSM	2.66	2.02
25891	LQSM	2.65	1.88
25891	LQSM	2.57	1.88
25891	LQSM	2.58	1.9
25891	LQSM	2.55	1.88
25891	LQSM	2.64	2
25891	LQSM	2.62	2
25891	LQSM	2.52	1.92
25891	LQSM	2.6	1.94
25891	LQSM	2.66	1.95
25891	LQSM	2.6	1.92
25891	LQSM	2.72	1.86
25891	LQSM	2.84	1.94
25891	LQSM	2.6	1.92
25891	LQSM	2.71	1.89
25891	LQSM	2.64	2.02
25891	LQSM	2.6	1.92
25891	LQSM	2.72	1.88
25891	LQSM	2.46	2.02
25891	LQSM	2.6	1.8
25891	LQSM	2.7	1.92
25891	LQSM	2.66	2.02
25891	LQSM	2.65	1.88
25891	LQSM	2.57	1.88
25891	LQSM	2.58	1.9
25891	LQSM	2.55	1.88
25891	LQSM	2.64	2
25891	LQSM	2.62	2
25891	LQSM	2.52	1.92
25891	LQSM	2.6	1.94

Accession number	Member	Length (mm)	Breadth (mm)
50606	MPPM	2.74	1.91
50606	MPPM	2.76	1.9
50606	MPPM	2.84	1.96
50606	MPPM	2.64	1.68
50606	MPPM	2.72	1.96
50606	MPPM	2.92	2
50606	MPPM	2.88	2.08
63462	MPPM	2.64	2.18
14821	MPPM	2.84	1.98
14821	MPPM	2.72	2.11
14821	MPPM	2.8	2.15
14821	MPPM	2.8	2
14821	MPPM	2.76	2
25891	MPPM	2.74	1.91
25891	MPPM	2.76	1.9
25891	MPPM	2.84	1.96
50606	MPPM	2.64	1.68
50606	MPPM	2.72	1.96
50606	MPPM	2.92	2
50606	MPPM	2.88	2.08
50606	MPPM	2.64	2.18
50606	MPPM	2.84	1.98
50606	MPPM	2.72	2.11
63462	MPPM	2.8	2.15
14821	MPPM	2.8	2
14821	MPPM	2.76	2

Appendix N: Murid and mole rat mandibles, maxillae and isolated molars in the LQSM units, Langebaanweg

All the mandibles, maxillae and single molars of the various species found in the LQSM and MPPM (F) units are shown below. Species identified tentatively due to damage or digestion are marked with a '?' after the species name.

	East stream (ES)			East stream/bed 2 (ES/bed2)			East stream/bed 2/near elephant site (ES/bed2/near Eles)			East stream/bed 2/pig #1 (ES/bed2/Pig #1)			East stream/Dump2 (ES/D2) *includes ES/D1		
Species	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi				1			1	1					6	1	9
Bathyergus hendeyi	8	4								3	2	8	175	27	156
Euryotomys pelomyoides.													149	56	73
Gerbillid													52	57	22
Dendromus averyi													2		1
Dendromus darti	1												13	4	6
Stenodontomys saldanhae				1									3	0	1
Stenodontomys saldanhae ?				1											
Acomys mabele				1											13
Acomys mabele?													1		
Aethomys adamanticola				1									1		10
Aethomys adamanticola?															1
Aethomys modernis															
Aethomys modernis?															1
Aethomys intermediate															
Aethomys intermediate?															
Rhabdomys intermediate															
Mystromys pocockei													9	6	
Mystromys hausleitneri													1	1	1
Mus or Acomys-like sp.															1
Acomys sp. (large)															
Small *Aethomys or* small *Rhabdomys*															5
Zelotomys															
Zelotomys-like sp.															1
Rhabdomys sp. 1															1

Appendix N (cont...)

	East stream/elephant site *and* east stream/elephant site/N-level (ES/Eles & ES/ELES/N LEVEL)			East stream/hyaena site (ES/HS)			East stream.Jimmy's pig pit (ES/JPP)			East stream/KP2 (ES/KP2)			East stream/north end (ES/NE)		
Species	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi	1	0	0												
Bathyergus hendeyi	28	5	9	4		1	1	1					1		
Euryotomys pelomyoides.	0	1	6	2			5	1	2		1		4		
Gerbillid	10	8	4	2	1			1					1		
Dendromus averyi	2														
Dendromus darti	7	1													
Stenodontomys saldanhae	1														
Stenodontomys saldanhae ?															
Acomys mabele			2												
Acomys mabele?															
Aethomys adamanticola	1		1												
Aethomys adamanticola?															
Aethomys modernis															
Aethomys modernis?															
Aethomys intermediate															
Aethomys intermediate?															
Rhabdomys intermediate															
Mystromys pocockei			2												
Mystromys hausleitneri															
Mus or *Acomys*-like sp.															
Acomys sp. (large)			1												
Small *Aethomys or* small *Rhabdomys*															
Zelotomys															
Zelotomys?															

Appendix N (cont...)

Species	East stream/north end/elephant site (ES/NE/Eles)			East stream/north end/fish spine site (ES/NE/F.S.)			East stream/section 3, spit 4 (ES/sect 3 sp 4)			East stream/square 1 (ES/SQ1)			East stream/test pit 1 (ES/TP1)		
	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi	1											1			1
Bathyergus hendeyi	13	3	1	2				3	5	6	2	4			1
Euryotomys pelomyoides.	1		1	2	3					7	7	1			
Gerbillid	8	17	3		1					4	6	2	2	1	10
Dendromus averyi	4											2			
Dendromus darti	6	4		1						7	6	1			
Stenodontomys saldanhae	5									2					
Stenodontomys saldanhae ?															
Acomys mabele	1		4								1		4	5	
Acomys mabele?										1					
Aethomys adamanticola	1	1	1												4
Aethomys adamanticola?															
Aethomys modernis													1		
Aethomys modernis?															
Aethomys intermediate															
Aethomys intermediate?															
Aethomys sp. 1															1
Rhabdomys intermediate															
Rhabdomys sp. 1			1												
Mystromys pocockei	4	1	1							3	1	3			1
Mystromys hausleitneri															
Mus or Acomys-like sp.			1											1	
Acomys sp. (large)															
Small *Aethomys* or small *Rhabdomys*															
Zelotomys															
Zelotomys?															

Appendix N (cont...)

	East stream/test pit 4 (ES/TP4)			Far east area/bed 2 (FEA/bed2)			Michaels Pit			Peat bed (PB)			South area east wall *and* south east wall/bed2/south of elephant site (SAEW & SAEW/bed 2/S of EleS_		
Species	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi										1					
Bathyergus hendeyi	5			2	1					4		7	1		
Euryotomys pelomyoides.	2	2							2	4	2	3	1	1	2
Gerbillid	2									1	3	1		1	
Dendromus averyi									1						
Dendromus darti															
Stenodontomys saldanhae	1														
Stenodontomys saldanhae ?															
Acomys mabele														1	
Acomys mabele?															
Aethomys adamanticola								1				1		1	
Aethomys adamanticola?															
Aethomys modernis															
Aethomys modernis?															
Aethomys intermediate															
Aethomys intermediate?									1						
Rhabdomys intermediate															
Rhabdomys intermediate ?														1	
Mystromys pocockei											1				
Mystromys hausleitneri															
Mus or Acomys-like sp.															
Acomys sp. (large)															
Small *Aethomys* or small *Rhabdomys*															
Zelotomys															
Zelotomys?															

Appendix N (cont...)

	South east face (SE Face)			South end/east stream/west bank (SE/ES/WB)			South east corner deepening/bed 2/location #1 (SECD/bed 2/Loc #1)		
Species	Md	Mx	Isolated molars	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi	2								
Bathyergus hendeyi	1			1					
Euryotomys pelomyoides.									
Gerbillid	1	1	3						
Dendromus averyi						1			
Dendromus darti									
Stenodontomys saldanhae									
Stenodontomys saldanhae ?									
Acomys mabele									
Acomys mabele?									
Aethomys adamanticola									
Aethomys adamanticola?									
Aethomys modernis									
Aethomys modernis?									
Aethomys intermediate									
Aethomys intermediate?									
Rhabdomys intermediate									
Mystromys pocockei				1			1		
Mystromys hausleitneri									
Mus or Acomys-like sp.									
Acomys sp. (large)									
Small *Aethomys* or small *Rhabdomys*									
Zelotomys									
Zelotomys?									

Appendix O: Murid and mole rat mandibles, maxillae and isolated molars in the MPPM (F) units, Langebaanweg

	F10			F11		
Species	Md	Mx	Isolated molars	Md	Mx	Isolated molars
Cryptomys broomi						
Bathyergus hendeyi	8	2	57	2	1	32
Euryotomys pelomyoides.	9	15	105	3	12	50
Gerbillid			1			1
Dendromus averyi		1				
Dendromus darti						
Stenodontomys saldanhae	1			1	1	
Acomys mabele	9	8	2	1	4	
Aethomys adamanticola		3	3			1
Aethomys adamanticola?			2			
Aethomys adamanticola-like					1	
Aethomys modernis	1	3	10	2		2
Aethomys modernis?	1		1	1	1	1
Aethomys modernis -like, cp present		1				
Aethomys intermediate					1	2
Aethomys sp. 4	1		1	1		
Aethomys sp. 3					3	
Aethomys sp. 1			1			1
Rhabdomys Intermediate		3	7			1
Rhabdomys Intermediate?					1	
Rhabdomys sp. 2			1			
Mystromys pocockei	1	1		2	3	
Mystromys hausleitneri		1		2		2
Mus or Acomys-like sp.						
Small *Aethomys* or small *Rhabdomys*			1			
Acomys sp.		1				
Acomys sp. ?		1				
Thallomys sp.			1			
Zelotomys sp,			1			
Zelotomys-like sp.		1	1			

Appendix P: Diversity in the LQSM and MPPM (F) units, Langebaanweg*

Species	ES/D2	Combined Eles	ES/SQ1	PB	ES/TP1	ES	ES/TP4	Combined ES/bed2	F10	F11
Euryotomys pelomyoides.	216	8	14	7			2		66	38
Gerbillid	120	46	12	4	10		2		1	
Dendromus averyi	2	4	1						1	
Dendromus darti	22	18	14			1				
Stenodontomys saldanhae	4	6	2				1	1	1	2
Acomys mabele	13	7	1		9			1	18	4
Aethomys adamanticola	15	5		1	4			1	6	1
Aethomys modernis					1				14	4
Aethomys intermediate										3
Aethomys sp. 1					1				1	1
Aethomys sp. 3										3
Aethomys sp. 4									2	1
Aethomy modernis-like, cp present									1	
Rhabdomys intermediate									10	1
Rhabdomys sp. 1	1	1								
Rhabdomys sp. 2									1	
Mystromys pocockei	14	7	5	1	1				2	5
Mystromys hausleitneri	3								1	3
Mus or Acomys-like sp.	1	1			1				1	
Acomys sp. (large)		1								
Small *Aethomys* or small *Rhabdomys*	5								1	
Zelotomys									1	
Zelotomys-like	1								2	
Thallomys									1	
Species diversity	13	11	7	4	7	1	3	3	19	12

* Calculated using isolated and *in situ* M^1 and M_1 molars)

Appendix Q: The percentage of Gerbillidae, Muridae and Bathyergidae in the LQSM and MPPM (F) units, Langebaanweg

LQSM units	ES/D2		Combined Eles		ES/SQ1		PB		ES/TP1		ES		ES/TP4	
	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%
Gerbillidae	109	19	43	32	10	19	4	25	3	21	0	0	2	17
Muridae	245	44	41	30	34	65	7	44	11	79	2	14	5	42
Bathyergidae	209	37	51	38	8	15	5	31	0	0	12	86	5	42

MPPM (F) units	F10		F11	
	No. of mandibles and maxillae	%	No. of mandibles and maxillae	%
Gerbillidae	0	0	0	0
Muridae	55	85	36	92
Bathyergidae	10	15	3	8

Appendix R: The distribution and habits of the micromammals from Hoedjiespunt 1, Saldanha

Unless otherwise stated, the table is based on information from Stuart and Stuart (2001) and De Graaff (1981).

Species	Habitat	Additional information	Current Distribution in the western Cape	Activity pattern	Mass
Aethomys namaquensis Namaqua rock mouse	Largely restricted to rocky habitats but also found in open shrub with scattered trees and in riverside woodland. Tends to inhabit more level country.	Lives in small colonies, and breeds in summer months. Nests are built of stalks and grass stuffed into rock crevices. When rocks are not available may also build nests around tree bases.	Distributed widely throughout South Africa.	Nocturnal, partly arboreal but mainly terrestrial	50g
Mystromys albicaudatus White-tailed mouse	Grassland, heath, succulent Karoo, Cape Macchia, and Karoo vegetation. They live in cracks or holes in the ground and have been seen using Suricate burrows.	They fall prey to owls and are taken by the barn, marsh, spotted eagle owl, and the grass owl. They were found to occur in consistently low proportions in barn owl pellets.	Swaziland, Lesotho and south and east areas of South Africa.	*M. albicaudatus* is nocturnal and especially active during wet weather.	75-110g
Mastomys verreauxi Verreaux's mouse	In the Knysna region this mouse inhabits riverbanks close to the sea, and areas of damp, meadow grass.	Multimammate mice have a wide habitat tolerance.	Found only in the south western Cape from the Olifants River in the northwest to Knysna in the south.	Nocturnal and terr estrial	40g
Rhabdomys pumilio Striped field mouse	Very versatile and lives in habitats which range from desert fringe to high rainfall areas. Has been described as primarily a savanna form.	Only constant requirement is the presence of grass.	Spread throughout most of South Africa and Namibia, but only in parts of Zambia, Botswana and Mozambique.	Mainly diurnal but also active at night	30-50g
Acomys subspinosus Cape Spiny mouse	Found in rocky habitats, but also in woodland and forest.	This species may live singly, or in groups.	The Cape spiny mouse occurs only in the western Cape.	Nocturnal, but also active in early morning or late afternoon	22 g
Tatera afra Cape Gerbil	Found in loose sand, sandy alluvium soils, and open grassland.	*T. afra* is endemic to the western cape biotic zone.	Found in sandy areas of the western Cape Town, northwards to Nieuwoudtville and eastwards along the coast to Herold's Bay.	Nocturnal	100g

Appendix R (cont...)

Species	Habitat	Additional information	Current Distribution in the western Cape	Activity pattern	Mass
Zelotomys woosnami Woosnam's Desert Rat	Found in arid areas with sparse vegetation and sandy soil. Trapping indicates individuals are solitary and widely spaced.	Digs own burrow, or uses the abandoned burrows of other animals. The localities where this species has been found in Botswana all have a mean annual rainfall of 200-500 mm per annum.	North central and north western areas of the subregion.	Primarily nocturnal and terrestrial	55g
Otomys irroratus Vlei rat	Associated with moist, marshy habitats but may also be found in drier habitats, such as grassy hillsides.	Depending on the surrounding habitat, may become partly aqueous.	Found over most of the country, but not the areas to the south of the Orange river.	Predominantly diurnal	120g
Otomys saundersiae Saunder's Vlei rat	Prefers mountainous habitats, but is not confined to these, inhabits belts of dry rushes in heath country and on mountain slopes.	Sloggett's vlei rat is the only other Otomys sp. associated with rocky, mountainous areas.	Found from Cape Town to north of St Helena;s Bay Distribution in areas of the south coast uncertain, but it is found in parts of the south coast and in a corridor stretching into Lesotho .	Diurnal	100g
Otomys slogetti Sloggett's Rat	Associated with rocky habitats, usually at high altitudes.	Lives in rock crevices and around boulders.	Found in east-central parts of South Africa, in Lesotho and at high altitudes such as the Drakensberg	Diurnal	130 g
Otomys unisulcatus Bush Karoo Rat	Of all the Otomys sp., only O. unisulcatus is found in arid areas.	This species shuns damp situations, and is found in shrub and Karoo-like vegetation, usually interspersed with stones and rocks.	This species is mainly found in the South West Arid and South West Cape biotic zones.	Diurnal	125 g
Parotomys brantsi Brant's Whistling rat	Lives in arid, sandy environments. Found in Botswana within the limits of the 300 mm isohyet.	May live in colonies or solitary in burrows Burrows in hard, sandy soils.	Found only in the arid, western areas of South Africa and Namibia, with a limited distribution in south-western Botswana. only found in Southern Africa.	Largely diurnal and completely terrestrial	120 g
Elephantulus rupestris Smith's rock elephant-shrew**	This is one of the three species of elephant-shrew living in a rocky habitat. It is restricted to areas where there are rocky outcrops, or piles of boulders.	*Elephantulus* is a large genus and has seven species distributed throughout the Savanna and Arid zones and this distribution appears to be associated with elevated altitudes (Bigalke 1978).	Distribution is confined to the Subregion and is found in a narrow strip running from Kaokoland in northwest Namibia, through the central parts of the Cape Province, to the coastal surrounds of East London.	Predominantly diurnal, but also show nocturnal activity	65 g

Appendix R (cont...)

Species	Habitat	Additional information	Current Distribution	Activity pattern	Mass
Crocidura Cyanea Reddish-grey Musk Shrew**	This species shows a wide habitat tolerance and are found in a variety of habitats. They are found in scrub on Kalahari sands, in reed beds around waterholes, and in karroid scrub in the Cape Macchia Zone where they are frequently associated with rocks (Skinner and Smithers 1990).	*C. c. cyanea* is found in the South West Arid Zone in areas which receive less than 500mm, but *C. C. infumata* is found in wetter areas in the Southern Savanna Zone and in the Eastern Parts of the subregion (Skinner and Smithers 1990).	Found over almost all of South Africa and Botswana, and in the western areas of Namibia.	Active sporadically throughout the night and day	9 g
Bathyergus suillus Cape Dune Mole rat*	This species is found in a wide range of soils ranging from fine clays to coarse arenosols, and alluvial sands.	Prefer loose, coastal sand dunes. They are not found on rocky mountain slopes and are found below 300m above sea level. Mole rats do not drink but get all the moisture they need from their food (Bennett and Faulkes 2000).	Restricted to the Southwestern Cape, at low altitudes along the coast. Ranges from south of the Olifants river to Knysna.	Fossorial	Exhibits sexual dimorphism Males: 933 g Females: 635 g
Cryptomys hottentotus Common mole rat*	Found in areas with very different rainfall patterns, ranging from the dry and arid northwest, to areas of high humidity. They are found in diverse types of substrates. Heavy clay soils or very brecciated soils are avoided.	Live in small colonies in underground burrows and burrow actively after rain. They are easily trapped as they come to investigate any damage to their burrows.	This species is one of the most widely distributed and is found all over South Africa, most of Namibia, Botswana and the southern areas of Mozambique and Angola.	Fossorial	Exhibits sexual dimorphism Males: 77 g Females: 57 g
Rhinolophus clivosus Geoffroy's Horseshoe Bat	Predominantly associated with savanna woodlands, but may be found on forest fringes, and even in deserts.	All *Rhinolophus* species are principally cave roosters. They leave their roosts approximately half an hour after sunset to forage , and return before the first light.	They are widespread in Zimbabwe, in Mozambique south of the Zambezi River in the central areas of the country and in the west to about 24°S. In the Northern Province they occur in the north and east, southwards to about 24°S.	Nocturnal	Mean mass: Males: 13-20 g Females: 12-25 g

Appendix S: Soricid and mole rat species found in the Saldanha Bay area today

Family	Species
Macroscelidae	*Macroscelides probosideus* *Elephantulus edwardii*
Soricidae	*Myosorex varius* *Myosorex tenuis* *Crocidura cyanea* *Suncus varilla*
Bathyergidae	*Bathyergus suillus* *Cryptomys hottentotus* *Georychus capensis*
Muridae	*Mystromys albicaudatus* *Steatomys krebsii* *Dendromus melanotis* *Dendromus mesomelas* *Malacothrix typica* *Desmodillus auricularis* *Gerbillurus paeba* *Tatera afra* *Acomy subspinosus* *Aethomys namaquensis* *Rhabdomys pumilio* *Mus minutoides* *Mus musculus* *Myomyscus verreauxi* *Rattus rattus* *Otomys laminatus* *Otomys irroratus* *Otomys unisulcatus* *Otomys saundersiae*

Information supplied from Stuart and Stuart (2001)

Appendix T: Breakage patterns of the indeterminate murid limb bones from Hoedjiespunt 1, Saldanha

ROOF	No.	%	HOMS	No.	%
FC	0	0	**FC**	0	0
FP	8	28.6	**FP**	8	33.3
FH	8	28.6	**FH**	7	29.2
FD	9	32.1	**FD**	9	37.5
FS	3	10.7	**FS**	0	0
Total number of femora	*28*		Total number of femora	*24*	
HC	0	0	**HC**	1	2.8
HP	10	27.0	**HP**	7	19.4
HD	25	67.6	**HD**	26	72.2
HS	2	5.4	**HS**	2	5.6
Total number of humeri	*37*		Total number of humeri	*36*	
TC	1	2.6	**TC**	0	0
TP	9	23.7	**TP**	3	14.3
TD	25	65.8	**TD**	15	71.4
TS	3	7.9	**TS**	3	14.3
Total number of tibiae	*38*		Total number of tibiae	*21*	
UC	0	0	**UC**	1	3.8
UP	38	97.4	**UP**	23	88.5
UD	0	0	**UD**	1	3.8
US	1	2.6	**US**	1	3.8
Total number of ulnae	*39*		Total number of ulnae	*26*	
RC	0	0	**RC**	1	20
RP	7	70	**RP**	2	40
RD	3	30	**RD**	2	40
Total number of radii	*10*		Total number of radii	*5*	

Key: FC= femur complete, FP = femur proximal, FH = femur head, FD = femur distal, FS = femur shaft
HC= humerus complete, HP = humerus proximal, HD = humerus distal, HS = humerus shaft
TC= tibia complete, TP = tibia proximal, TD = tibia distal, TS = tibia shaft
UC= ulna complete, UP = ulna proximal, UD = ulna distal, US = ulna shaft
RC= radius complete, RP = radius proximal, RD = radius distal

Appendix U: Murid skeletal element abundance at Hoedjiespunt 1 (HDP1), Saldanha

	HOMS		ROOF		HOMS & ROOF combined	
	N	%	N	%	N	%
Mandible	16	22.2	13	32.5	29	27.9
Maxilla	18	25.0	16	40.0	34	32.7
Scapula	2	2.8	5	12.5	7	6.7
Humerus	36	50.0	37	92.5	73	70.2
Radius	5	6.9	10	25.0	15	14.4
Ulna	26	36.1	39	97.5	65	62.5
Pelvic girdle	11	15.3	5	12.5	16	15.4
Femur	24	33.3	28	70.0	52	50.0
Tibia	21	29.2	38	95.0	59	56.7
Vertebra	76	6.6	91	14.2	167	10.0
Incisor	142	98.6	63	78.8	205	98.6
Molar	250	57.9	168	70.0	418	67.0
Phalange	22	1.1	34	3.0	56	1.9
Metapodial	30	4.2	0	0.0	30	2.9
MNI	***36***		***20***		***52***	

Appendix V: Skeletal element abundance at Steenbokfontein Cave (STBKC), Steenbokfontein farm

	SBYC	
	N	%
Mandible	1275	77.6
Maxilla	662	37.9
Scapula	310	14.4
Humerus	1243	90.8
Radius	665	47.7
Ulna	1202	67.8
Pelvic girdle	565	37.4
Femur	1217	95.4
Tibia	1607	100.0
Vertebra	5279	14.4
Incisor	1622	28.7
Molar	4829	48.9
Phalange	5110	6.5
Metapodial	3966	25.7
MNI	***804***	

After Manthi (2002), Table 7.1.1, page 78

Appendix W: Skeletal element abundance at Elands Bay Cave (EBC), Elands Bay

	EBC - mix of predators (other than barn owl) Units; 3a, 6, 8a, 8b and 9 (N)	%	EBC - barn owl assemblages Units; 11, 13, 15b, 15c (N)	%
Mandible	318	100.0	311	99.7
Maxilla	258	81.1	121	38.8
Scapula	29	9.1	9	2.9
Humerus	246	77.4	79	25.3
Radius	8	2.5	4	1.3
Ulna	60	18.9	21	6.7
Pelvic girdle	147	46.2	70	22.4
Femur	288	90.6	128	41.0
Tibia	178	56.0	111	35.6
Vertebra	460	9.0	51	1.0
Incisors	393	61.8	242	38.8
Molars	95	5.0	58	3.1
Phalanges and metapodials	18	0.2	5	0.1
MNI	***159***		***156***	

After Matthews 1998, Table 5.1, page 57, and Table 5.2, page 58