TAXONOMIC AND ECOLOGICAL FUNCTIONAL ANALYSIS OF MODERN AND FOSSIL SOUTHERN AFRICAN RODENT POSTCRANIA

A Dissertation

by

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ABSTRACT

Rodent remains found in many southern African Plio-Pleistocene fossil-bearing deposits are commonly used to reconstruct paleoenvironments using a taxonomic framework. In these studies, craniodental remains are the primary material used to reconstruct rodent paleocommunities while postcranial elements are generally not considered. Utilizing several different methods, this study tests whether analyses of African rodent postcrania can provide useful data for reconstructing past environments. First, this study tests if postcranial remains recovered in modern owl pellets can be considered isotaphonomic with recovered craniodental elements. Second, using both traditional linear measurements and two-dimensional outlines from digital photographs, this study tests if modern rodent postcrania can be used to identify what taxa (i.e. subfamily, genus and species) are present, and thus can be used in a similar manner as craniodental remains to reconstruct rodent community composition. Third, traditional linear measurements are also used to test locomotor habits exhibited by modern rodents within an ecological functional framework. Results from these analyses are then applied to fossil specimens from the hominin-bearing site of Swartkrans, South Africa.

Results from this study show that rodent postcrania are as representative, or better, of the number of individual rodent prey items taken in modern owl roosts compared to estimates based on craniodental remains. Additionally, this study finds significant statistical support for the presence of ecological functional signals, as well as taxonomic signals at the family, subfamily, and genus level using rodent postcranial remains.

Classification rates, however, were generally low unless all postcranial elements included in this analysis were utilized. Rates for analyses of humeri and femora individually were not adequate for application to the fossil record with one exception. Outline based analyses of modern femoral form (i.e. shape + size) at the subfamily level classified correctly 90.1% of the time using linear discriminant function analysis with cross-validation. When these functions are applied to fossil rodent femora from Swartkrans two previously unidentified subfamilies, Cricetomyinae (pouched mice and rats) and Petromyscinae (rock mice), are recovered. The inferred habitat signal from the cricetomyines suggests a wooded component in Members 1 and 2, while that from petromyscines suggests a significant arid component in Members 1-3 during the period in which these deposits accumulated.

DEDICATION

This dissertation is dedicated to my family. Snarf and the late Wookie, cats that decided to grace me with their presence at the beginning of grad school. Angie Campbell, my mother, who lovingly dealt with the prodigal son while he pursued his varied interests - wherever they lead. Upbeat and optimistic, mom always was a voice of encouragement when the inevitable bumps in the road were encountered. Gwen Campbell, my sister, who arguably is the smarter of the siblings for going into the corporate world. Although I am fairly certain she still does not comprehend my fascination with rodents, she at least pretended to be interested, and was always willing to help out when a small grant failed to materialize. And finally, Dan Campbell, my father, who unfortunately passed away during the course of my PhD. Dad prized hard work and education above all things except his family. “Do your shit and do it well” he would say “and then go have your fun”. Hopefully I have done the first in your eye’s dad, as (most) of the journey has fulfilled the latter.

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Contributors

This work was supervised by a dissertation committee consisting of Professor Darryl J. de Ruiter (Chair), Professors Sharon Gursky and Lori Wright of the Department of Anthropology, and Professor Thomas J. DeWitt of the Department of Wildlife and Fisheries Sciences.

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1. INTRODUCTION

1.1 Rodents in Anthropology

Utilizing a variety of different techniques and data, this study tests whether analyses of African rodent postcrania can provide useful data for paleoecological and paleoenvironmental reconstructions of hominin-bearing fossil localities. Many hypotheses of hominin behavioral and morphological evolution have focused on the environments occupied by early members of our lineage in order to provide an adaptive context for major evolutionary events, such as the advent of tool technologies and taxonomic diversification. As a result, a variety of different environmental hypotheses have been put forward such as habitat specific hypotheses (Dart 1925; Jolly 1970; Robinson 1954; Stanley 1992), the turnover-pulse hypothesis (Vrba 1985, 1988, 1995a,b, 1999), and the variability selection hypothesis (Potts 1996, 1998a,b). Implicit to tests of these hypotheses is the need for precise and detailed paleoenvironmental and paleoecological data. To achieve this, different types of proxy data are commonly utilized such as fossil remains of fauna (e.g. Avery 2001; Reed 1997; Reed and Geraads 2012; Vrba 1975, 1995b; White 1995; White et al. 2009) and flora (e.g. Bamford 1999, Bamford et al. 2010; Bonnefille 1984; 1995; Bonnefille et al. 2004; Scott 1995), as well as data from organic and inorganic sources in deep sea cores (e.g. deMenocal 1995, 2004; deMenocal and Bloemendal 1995). Among these different types of proxy data, analyses of faunal remains have played an important role in both the development and testing of environmental hypotheses (e.g. Alemseged 2003; Behrensmeyer et al. 1997; Bobe et al. 2002; Bobe and Behrensmeyer 2004; Faith

and Behrensmeyer 2013; Kimbel 1995; McKee 1995, 2001; Potts 1998a; Reed 1997; Vrba 1995b; White 1995). Within mammals, micromammals (i.e. mammals weighing < 750g) are considered well suited for paleoenvironmental analyses and for testing various evolutionary models (Avery 1982b; Reed 2007). Moreover, actualistic studies have shown that analyses of micromammal community composition can be used to accurately reconstruct habitats within localized settings (Reed 2005, 2007, 2011).

Although analyses of fossilized micromammal remains have played a role in the development of evolutionary hypotheses linking environmental change with events in human evolution (e.g. see Wesselman 1984, 1985 cited in Vrba 1988, 1995b and Andrews 1989; de Graff 1960, Winkler 1995 cited in Potts 1998a), they have not featured prominently in many formal tests utilizing the African fossil record (see Behrensmeyer et al. 1997 and McKee 1995 for the limited use of rodent data). The rodent fossil record has, however, been used in tests of the association between faunal turnovers and climate change in other geographic areas such as North America (Alroy et al. 2000; Prothero and Heaton 1996) and Eurasia (Barry et al. 1995; van Dam et al. 2006). So why are microfaunal data in Africa not generally included in formal tests of evolutionary hypotheses linking environmental change with events in human evolution? Several authors have cited an incomplete fossil record for micromammals as rationale for either their exclusion in analyses or lack of resolution in hypothesis testing (Behrensmeyer et al. 1997; Reed 1997), despite the fact that rodents are found in great abundance at some localities (Avery 1982b, 2001; Denys 1999). At one level, selective sampling efforts that have focused on complete cranio-dental elements or specific groups may have resulted in

micromammalian fossils being overlooked (Bobe and Eck 2001; de Ruiter et al. 2008). Alternately, the depositional environments of fossil bearing localities must also be considered, as many sites that have produced fossils used to test environmental hypotheses represent higher energy fluvial deposits (Alemseged 2003; Bobe and Eck 2001; Hill 1987; Wesselman 1984), conditions generally ill-suited for rodent skeletal preservation (Andrews 1990). Rodent remains have, however, also been found in areas conducive to preservation, yet at low relative abundances. For example, Reed and Geraads (2012) analyzed 28 rodent specimens from Hadar locality A.L. 894 dated to ca. 2.4 Ma and cite the small sample size as limiting the inferences that could be made. Here it is worth noting that these authors comment on the presence of unidentifiable post-cranial elements, of which the number of specimens exceeded that of the cranio-dental remains (D. Reed, pers. comm.).

Regardless of the reason for their sparse representation in some assemblages and depositional environments, if analyses of fossilized microfaunal remains are to play a part in hypothesis testing in human evolutionary theory, all available data must be used. Tests of evolutionary hypotheses are strongest when multiple lines of evidence are utilized, and this project, an analysis of rodent post-cranial remains for taxonomic and ecological functional signals, represents a multifaceted first step in opening up a new source of data in African Plio-Pleistocene paleontology.

1.2 This Study

Utilizing several different methodological approaches, this study tests whether analyses of African rodent postcrania can provide useful data for paleoecological and paleoenvironmental reconstructions of hominin-bearing localities. In general, the purpose of this study is to explore whether analyses rodent postcranial elements can provide useful data for paleoecological and paleoenvironmental reconstructions. This study specifically focuses on Rodentia as it is not only the largest order of living mammals (Wilson and Reeder 2005), but also features prominently in inferred habitat signals in paleoenvironmental reconstructions that utilize micromammal remains (e.g. Avery 2001; Reed 2007; 2011; Wesselman 1985). In doing so the proximate goals of this study are twofold. First, this study seeks to ascertain if modern rodent postcrania can be identified to an environmentally informative taxonomic level. As such, this study represents an extension of approaches that rely on taxonomic lists to study paleocommunity composition and make inferences about past environments. Second, this study also seeks to identify if there are any morphological features in rodent postcranial skeletons associated with functional adaptations that can be used to infer past habitat use. This type of ecological functional analysis can be used to generate environmentally informative functional groupings that do not require taxonomic identification. As the ultimate goal of this dissertation project is to generate comparative data with which to analyze fossil specimens, unstudied rodent postcrania from the well-known southern African hominin-bearing locality of Swartkrans, Members 1-3 are also analyzed. Results obtained using

postcrania are compared with those from previous studies of this site that incorporated only micromammal cranio-dental remains (Avery 1995, 2001).

1.3 Research Objectives, Hypotheses Tested, and Predictions

As previous reconstructions of African Plio-Pleistocene paleoenvironments using micromammals have relied almost exclusively on the analysis of relatively complete cranio-dental remains, numerous questions as to the potential for analyses of postcranial remains to inform on past environments remain unanswered. Therefore, a cascading series of questions must be addressed, as outlined below.

Question 1: Are rodent postcranial remains found in similar proportions to craniodental remains in modern owl accumulations? Owls in general, and barn owls (*Tyto alba*) in particular, are the presumed accumulating agents of many microfaunal fossil deposits, including those at Swartkrans. As many methods for reconstructing past environments rely on taxonomic lists generated from craniodental remains, in order for these methods to be applied to postcrania it necessary to establish equivalency in the representation of craniodental and postcranial remains in modern owl coprocoenoses. For reasons detailed further in Chapter 2, it is predicted that the minimum number of individuals (MNI) calculated from rodent postcranial remains found in modern owl pellet accumulations will be equal to, or slightly higher than those calculated using craniodental remains. Thus, this study tests:

H_1: The MNI calculated using postcranial remains in owl coprocenoses approximates that calculated using craniodental remains from the same assemblages.

H_{1A}: MNIs calculated using both sets of remains do not yield similar results. If so, it may be that the MNIs calculated using postcrania greatly exceeds those calculated using craniodental remains and thus is more indicative of the true proportions of prey taken by the accumulating agent. Alternately, it may be the MNIs calculated using postcrania are much lower that calculated using craniodental remains and that the latter best represent the true proportions of prey taken. While either of these alternatives would be of ecological significance, both would suggest that methods for paleoenvironmental reconstruction based of modern analogs developed using craniodental remains recovered from owl coprocenoses may not be applicable to postcranial data.

Question 2: Is a taxonomic signal recoverable from rodent postcranial remains and, if so, at what level? While the ideal outcome of this study would be to demonstrate that species level identifications are possible using rodent postcrania, this level of taxonomic resolution is not expected due to difficulties in separating out cryptic taxa with ought morphological data (McDonough et al. 2013). Instead, family, subfamily, and genus level signals are predicted to be recoverable. Most taxonomic based methods commonly used to reconstruct past environments require identifications to the level of genus (Reed 2007; Reed and Geraads 2012) or subfamily for calculations of higher taxonomic level ratios (Denys 1999; Fernandez-Jalvo et al. 1998; Jaeger 1976; Matthews et al. 2007; Reed 2007; Reed and Geraads 2012), thus the recovery of taxonomic signals from postcrania at these levels is needed for this portion of the study to be potentially paleoenvironmentally informative. In order to answer this question several different analytical methods are

utilized. As it is possible that the inclusion of multiple skeletal elements from an individual organism may yield a stronger taxonomic signal, this study first tests:

$H_{2.1}$: Taxonomic signals can be detected below the family level utilizing linear measurements and traditional morphometrics on all appendicular long bone elements of a single, individual organism. Linear measurements and traditional morphometrics were selected as these are classic methods by which group separations, and many species diagnoses, have been made.

$H_{2.1A}$: Taxonomic signals cannot be detected below the family level utilizing linear measurements and traditional morphometrics on all appendicular long bone elements of a single, individual organism. Failure to find a taxonomic signal below the family level may indicate that species do not differ in measurements, that the measurements taken are insufficient to recover the taxonomic signal, or that the analytical methods are insufficient to recover the signal. Alternately, a taxonomic signal may be present in some parts/elements of the appendicular postcrania, but is being masked other elements (e.g. shared morphology due to convergence of locomotory patterns).

Unfortunately, as exceptional preservation with articulated skeletal remains is rare (Bottjer et al. 2002), although not unheard of in fossil deposits in close proximity to those studied here (e.g. Berger et al. 2010; Berger et al. 2015; Clark R.J. 1998; Hawks J. et al. 2017), none of the fossils analyzed here were found in articulation. As such, the following hypotheses were also tested:

$H_{2.2}$: Taxonomic signals can be detected below the family level utilizing linear measurements and traditional morphometrics on individual rodent femora and humeri.

Femora and humeri were selected as these are the most robust singular elements and potentially the most likely to be preserved.

$H_{2.2A}$: Taxonomic signals cannot be detected below the family level utilizing linear measurements and traditional morphometrics on individual rodent femora and humeri. Failure to find a taxonomic signal below the family level may indicate that no signal is present, that the measurements taken are insufficient to recover the taxonomic signal, or that the analytical methods are insufficient to recover the signal.

$H_{2.3}$: Taxonomic signals can be detected below the family level utilizing digital 2D outlines and geometric morphometrics on individual femora and humeri. This second approach to individual bone identification was adopted to potentially capture informative shape variation not recovered using linear measurements.

$H_{2.3A}$: Taxonomic signals cannot be detected below the family level utilizing digital 2D outlines and geometric morphometrics on individual femora and humeri. Failure to find a taxonomic signal below the family level may indicate that no signal is present, or that these analytical methods are insufficient to recover the signal.

Question 3: Are there ecological functional signals in southern African rodent postcrania related to substrate use that can aid in reconstructing past habitats? It is possible that similarities in postcranial morphologies may be present, though not driven by shared ancestry. Instead, selection could have led to convergence in postcrania due to functional constraints related to substrate use and locomotory patterns. If so, rodents from divergent lineages that occupying similar ecological niches (e.g. ricochetal taxa in open, arid habitats or arboreal taxa in wooded environments) may share a suite of anatomical characters (e.g.

elongated posterior appendicular elements used for jumping or rounded radial heads for greater rotation of the forearm during climbing) that are independent of phylogeny. As such, the prediction here is that southern African rodents that occupy similar ecological niches share a suite of postcranial characters related to their habitat use and the following hypothesis is tested:

$H_{3.1}$: Rodent groups will differ based on locomotory patterns designated *a priori* using ecological functional indices generated from linear measurements of all appendicular long bone elements.

$H_{3.1A}$: Rodent groups will not differ based on locomotory patterns designated *a priori* using ecological functional indices generated from linear measurements of all appendicular long bone elements. If no significant difference is found it may indicate that no signal is present, or that these methods used here are insufficient to recover the signal. Moreover, as the functional indices adopted have been used in other studies that found significant differences using some of the same taxa (e.g. Samuels and Van Valkenburgh 2008), if this hypothesis is rejected it would suggest that the results of previous studies should be reviewed.

Based on the arguments outlined above for testing Hypothesis 2.2, potential differences between locomotor categories in individual femoral and humeral functional indices are also tested for application to the fossil record. It is predicted that significant differences in locomotor categories found in previous studies will be recovered here. As such, this study also tests:

$H_{3.2}$: Rodent groups will differ based on locomotory patterns designated *a priori* using ecological functional indices generated from linear measurements on individual rodent femora and humeri.

$H_{3.2A}$: Rodent groups will not differ based on locomotory patterns designated *a priori* using ecological functional indices generated from linear measurements on individual rodent femora and humeri. If no significant difference is found it may indicate that no signal is present, or that these methods used here are insufficient to recover the signal. Similarly, rejection of this hypothesis would suggest that the results of previous studies should be reviewed.

Question 4: What is the paleoenvironmental interpretation when the results from the analyses of modern specimens are applied to the rodent fossils from Swartkrans. Utilizing different proxy data, various interpretations of the potential paleoenvironment that existed around Swartkrans in the past have been proposed (Chapter 2). Those based on studies utilizing micromammal craniodental remains have suggested a habitat mosaic consisting of riverine grasslands, and plains with open savannah woodlands (Avery 1995, 2001). It is predicted that a similar paleoenvironmental reconstruction will result from the study of rodent fossil postcrania. As such, this study tests:

H_4: The reconstructed paleoenvironment for Swartkrans using rodent postcrania indicates riverine grasslands, and plains with open savannah woodlands.

H_{4A}: The reconstructed paleoenvironment for Swartkrans using rodent postcrania does not indicate riverine grasslands, and plains with open savannah woodlands. Instead,

the paleoenvironmental signal may suggest the presence of open grasslands or alternately closed woodland type environments.

2. BACKGROUND

2.1 African Rodents

The order Rodentia is the largest living order of mammals with a cosmopolitan distribution and includes around 2,300-2,600 living species, or approximately 40% of extant mammalian species biodiversity (D'Elía, G., Fabre, P.-H., and Lessa, E.P. 2019; Wilson and Reeder 2005). Within Africa, there are currently around 395 recognized species in 98 genera and 15 families, of which 375 (94.9%) species are endemic (Happold 2013). In general, estimates of rodent diversity have increased over time, with the recent increase in new species described roughly corresponding to the advent and application of modern molecular techniques. Analyses of morphological variation, however, remain an integral part to studies of rodent systematics. For example, in a recent review of the state of the field of rodent systematics, D'Elía, Fabre, and Lessa (2019) found that of the 248 new species of rodents described between January 2000 and December 2017, 45 (18.1%) were from Africa. Moreover, in their review of the 41 new species described in the *Journal of Mammalogy* during this timeframe, they note that while 70.7% of the studies used molecular data, and 41.4% used karyotypic data, 100% included some form of morphological data, typically craniodental, in their species delineations. Thus, while our understanding of the diversity and evolutionary relationships among African rodents has greatly increased through the utilization of numerous complementary lines of evidence, rodent systematics is currently an active field of inquiry and numerous taxonomic and phylogenetic issues remain to be resolved.

Although the majority of new African rodent taxa described between 2000-2017 have been found outside southern Africa, with eastern Africa representing the most productive area so far (n = 28 or 68.3%), within the southern African subregion the number of recognized species has also increased with at least three new taxa described in the last 20 years (D'Elía, Fabre, and Lessa 2019). Following Skinner and Chimimba (2005), the southern African subregion is defined here as the mainland area of Africa south of the Kunene and Zambezi rivers, along with the northern border of Namibia, and includes the countries of Namibia, Botswana, Zimbabwe, South Africa, Lesotho, Swaziland, and the southern portion of Mozambique (Figure 2.1). Differences in the number of families, genera, and species reported in three primary treatments of southern African rodents are given in Table 2.1 (De Graaff 1981, Happold 2013, Skinner and Chimimba 2005). Based on the most recent treatment, there are nine families, 37 genera, and 86 species recognized in the southern African subregion, excluding commensal and introduced taxa (Happold 2013). Overall, recognized species level diversity has increased by 22.9% over the time period covered, with some changes having been made at higher taxonomic levels. A list of taxa recognized in the southern African subregion by Hapold (2013) is provided in Table 2.2 with a few exceptions. First, *Aethomys namaquensis* and *A. granti* are here placed in the genus *Micaelamys* following Wilson and Reeder (2005) and Skinner and Chimimba (2005). Similarly, *Otomys sloggetti*, and *O. unisulcatus* are here placed in the genus *Myotomys* following Wilson and Reeder (2005). Finally, taxonomy above the family level used in this study also follows Wilson and Reeder (2005).

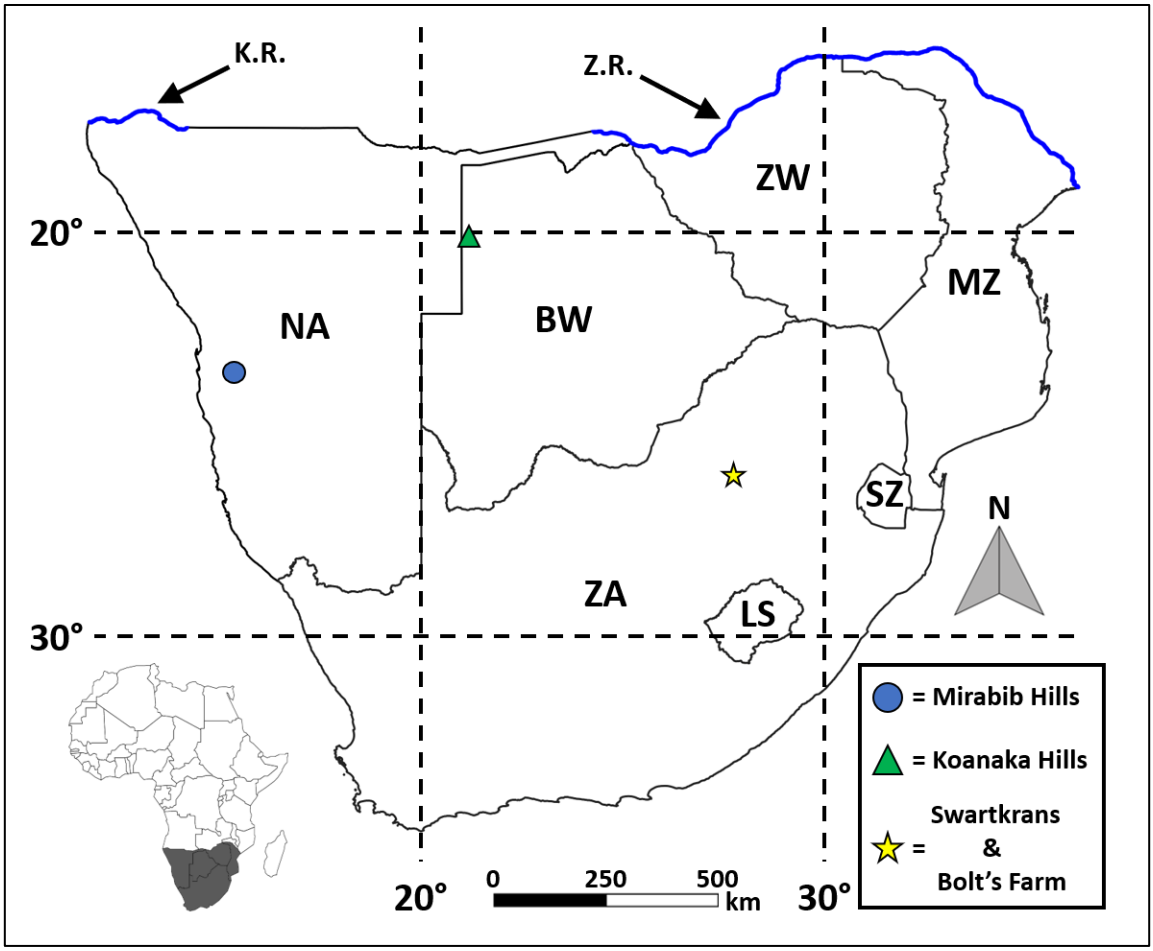


Figure 2.1. Southern African subregion as defined here, and sites used in this study. Abbreviations are as follows: K.R. – Kunene River; Z.R. – Zambezi River; NA – Namibia, BW – Botswana, ZW – Zimbabwe, MZ – Mozambique, ZA – South Africa, LS – Lesotho, SZ – Swaziland.

Table 2.1. Number of families, genera and species recognized in different treatments of southern African rodents. Numbers in parentheses calculated with commensal taxa removed (i.e. *Rattus rattus, R. norvegicus, Mus musculus,* and *Sciurus carolinensis*).

	De Graaff 1981	Skinner & Chimimba 2005	Happold 2013
Families	9	8	9
Genera	38 (37)	37	38 (37)
Species	73 (70)	82	89 (86)

Table 2.2. Southern African rodent taxa in Happold (2013). Subordinal taxonomy following Wilson and Reeder (2005).

Suborder	Family	Subfamily	Genus	Species
Anomaluromorpha	Pedetidae	-	*Pedetes*	*capensis*
Hystricomorpha	Bathyergidae	-	*Bathyergus*	*janetta*
				suillus
			Cryptomys	*bocagei*
				damarensis
				darlingi
				hottentotus
			Georychus	*capensis*
	Hystricidae	-	*Hystrix*	*africaeaustralis*
	Petromuridae	-	*Petromus*	*typicus*
	Thryonomidae	-	*Thryonomys*	*gregorianus*
				swinderianus
Myomorpha	Muridae	Deomyinae	*Acomys*	*spinosissimus*
				subspinosus
			Uranomys	*ruddi*
		Gerbillinae	*Desmodillus*	*auricularis*
			Gerbilliscus	*afra*
				brantsii
				inclusus
				leucogaster
				validus[1]
			Gerbillurus	*paeba*
				setzeri
				tytonis
				vallinus
		Murinae	*Aethomys*	*chrysophilus*
				silindensis
				ineptus
			(*Micaelamys*)[2]	*namaquensis*
			(*Micaelamys*)[2]	*granti*
			Dasymys	*incomtus*
				nudipes
			Grammomys	*cometes*
				dolichurus
			Lemniscomys	*rosalia*
			Mastomys	*coucha*
				natalensis

Table 2.2. Continued.

Suborder	Family	Subfamily	Genus	Species
				shortridgei
			Mus	*indutus*
				minutoides
				musculoides
				neavei
				orangiae
				setzeri
			Myomyscus	*verreauxii*
			Pelomys	*fallax*
			Rhabdomys	*pumilio*
			Thallomys	*nigricauda*
				paedulcus
				shortridgei
			Zelotomys	*woosnami*
		Otomyinae	*Otomys*	*angoniensis*
				irroratus
				laminatus
				saundersiae
			(*Myotomys*)[3]	*sloggetti*
			(*Myotomys*)[3]	*unisulcatus*
			Parotomys	*brantsii*
				littledale
	Nesomyidae	Cricetomyinae	*Cricetomys*	*gambianus*
			Saccostomus	*campestris*
		Dendromurinae	*Dendromus*	*melanotis*
				mesomelas
				mysticalis
				nyikae
			Malacothrix	*typica*
			Steatomys	*krebsii*
				parvus
				pratensis
		Mystromyinae	*Mystromys*	*albicaudatus*
		Petromyscinae	*Petromyscus*	*barbouri*
				collinus
				monticularis
				shortridgei
Sciuriomorpha	Gliridae	-	*Graphiurus*	*kelleni*

Table 2.2. Continued.

Suborder	Family	Subfamily	Genus	Species
				microtis
				murinus
				ocularis
				platyops
				rupicola
	Sciuridae	Xerinae	*Funisciurus*	*congicus*
			Heliosciurus	*mutabilis*
			Paraxerus	*cepapi*
				palliatus
			Xerus	*inauris*
				princeps

[1]While not generally included in southern Africa, the distribution map in Happold (2013:286) shows its presence in northern Zimbabwe thus it has been included here.
[2]Classified as *Aethomys* in Happold (2013).
[3]Classified as *Otomys* in Happold (2013).

2.2 Micromammals in the Fossil Record and Accumulating Agents

Micromammal fossils (e.g. rodents and shrews) are found in many Plio-Pleistocene fossil-bearing localities in Africa (Winkler et al. 2010), and are commonly used to reconstruct paleoenvironments (e.g., Avery 1982a,b, 1984, 1987, 1992b, c, 1995, 2001, 2003; De Graaff 1960a; Fernandez-Jalvo et al. 1998; Louchart et al. 2009; Matthews et al. 2005, 2007; 2009, 2011; Patnaik 2003; Reed 2007; Reed and Denys 2011; Reed and Geraads 2012; Stoetzel et al. 2011; Thackeray 1987; Thackeray and Avery 1990; Wesselman 1984, 1995; Wesselman et al. 2009). Micromammals are considered particularly informative due to their species rich nature, small home range sizes for most taxa, and because some taxa have precise ecological requirements that can provide detailed information on vegetation, substrate type, and climatic conditions within a localized area (De Graaff 1981; Happold 2013, Kingdon 1974; Roberts 1951; Skinner and

Chimimba 2005; Smithers 1971). Moreover, due to how micromammal remains are generally accumulated, particularly in cave deposits, they are often found in great abundance thus allowing for a variety of different analytical techniques to be employed when reconstructing past environments.

Numerous accumulating processes can feasibly introduce micromammal remains into a fossil assemblage. These include geologic processes that can transport remains from some distance as part of a sediment load (i.e. colluvial, fluvial, potentially Aeolian transport), incidental processes where one or a few specimens may inadvertently get introduced as part of a pitfall or burrow collapse, and biotic processes where remains are brought in by an accumulating agent, often as prey (Andrews 1990). Among the latter a wide range of taxa are known to consume micromammals including terrestrial carnivores (Kingdon and Hoffmann, 2013a; Roberts 1951; Skinner and Chimimba 2005; Smithers 1971), avian raptors (Fry et al. 1993; Hokey et al. 2005), snakes and other herpetofauna (Alexander and Marais 2007; Auerbach 1987; Marais 2004), and even hominins (Henshilwood 2008) to name a few.

Of interest here are avian predators in general, and owls in particular, due to known feeding and roosting habits for many species, and because many eject parts of prey items consumed in the form of pellets (Bunn et al. 1982; Mikkola 1983; Steyn 1983; Fry et al. 1993; Taylor 1994; Hokey et al. 2005). These pellets generally consist of undigested vertebrate remains of little nutritional value including bones, teeth, nails, and bills, along with the chitinous remains of invertebrates. These more resilient elements are generally enclosed within softer, yet still indigestible substances such as fur and feathers that

eventually break down over time. Although information on pellet production is lacking for many species, barn owls (*T. alba*) are estimated to eject 1.1-1.4 pellets per day on average (Andrews 1990; Wilson, Wilson, & Fry 1988). Moreover, each pellet can contain numerous prey items, with an average of 2.7 and range of 1-8 vertebrate prey per pellet found in this study. As is evident, continued use of a roosting site by even a single owl over the course of its life can result in the accumulation of remains from several thousand prey items, and over the timeframe in which fossil assemblages probably accumulated, significant deposits can enter the fossil record (Figure 2.2). Due to these factors, and because barn owls generally produce very little damage on the hard tissues of the prey they consume, analyses of prey items found within owl pellets have long been recognized as contributing valuable information on modern faunal community compositions (Davis 1958; Dodson & Wexlar 1979; Avery 1992a; Avenant 2005) with new species having been described (Broom 1907), and range extensions identified for species not previously documented via alternate survey methods, such as trapping (Davis 1959; Skinner et al. 1980; Avery et al. 2003). Furthermore, the contribution of owls to the vertebrate fossil record in Africa was also recognized early on (Broom and Robinson 1952; Cartmill 1967; Cooke 1952; Davis 1959; De Graaff 1960a).

Of the 33 species of owl found in Africa (Fry et al. 1993) barn owls, and possibly spotted eagle owls (*Bubo capensis*), have been inferred to be the accumulating agent at most fossil and archaeological sites where microfaunal prey remains are found in great abundance, and with minimal damage owing to the feeding habits and digestive physiology for these species (Andrews 1990; Bunn et al. 1982; Dodson and Wexlar 1979;

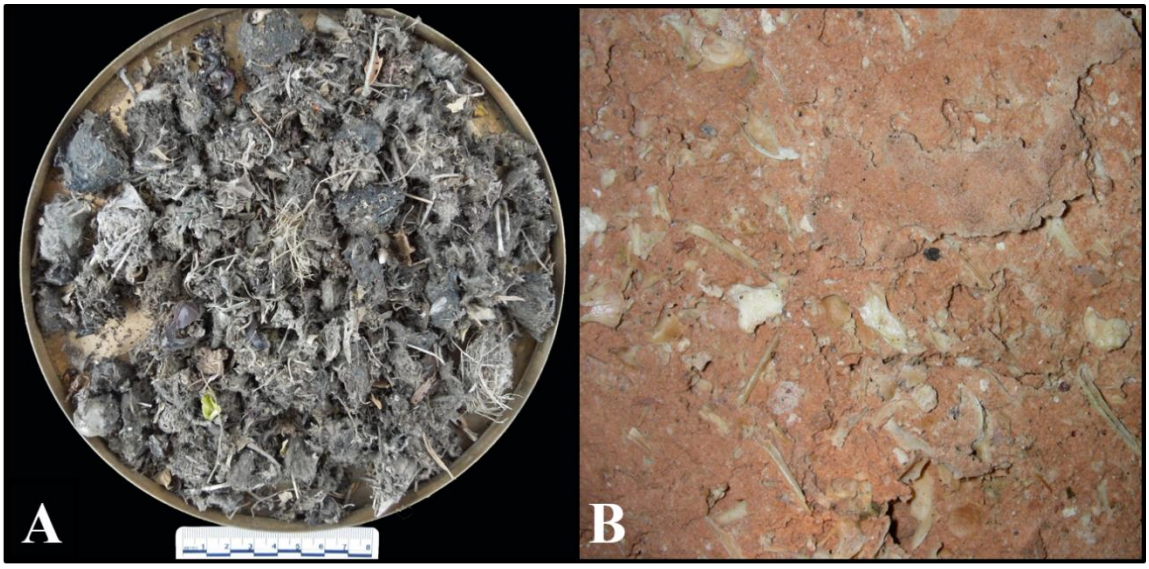


Figure 2.2. Modern owl pellets and microfaunal remains as seen in the fossil record. Panel A: fragmentary pellets collected at Laetoli that had accumulated over a 1 year interval (see Campbell et al. 2018). Panel B: microfaunal fossils incased in breccia from deep within Bone Cave, Koanaka Hills.

Taylor 1994). Roosting preferences for these two species, however, vary with barn owls said to prefer closed environments such as caves, crevasses, hollow trees, building interiors and areas that simulate these conditions (Bunn et al., 1982; Kemp, 2005a; Reed, 2005; Steyn, 1982; Wilson, Wilson & Fry 1988; Wilson, & Fry, 1993), while spotted eagle owls are noted for roosting in open areas such as on the ground in vegetation, along rocky outcrops, or in the crowns of trees (Steyn 1983; Kemp 1993; Kemp 2005b; Reed 2005). These two species have, however, been observed at the same roost in which pellets had accumulated (Campbell et al. 2018). In this instance both a barn owl and a spotted eagle owl were seen in successive years at a candelabra tree in Laetoli, Tanzania, under which a large assemblage of pellets was collected after each siting. Here it was hypothesized that the structure of candelabra trees may offer roosting environments amenable to both

species, with the interiors simulating the dark enclosed spaces preferred by barn owls and the outer branches representing the more open areas preferred by spotted eagle owls. Without compelling evidence for an alternate interpretation, though, barn owls are typically the inferred accumulating agent for most large micromammal cave deposits, and have been implicated at the site examined in this study (Avery 1995; 2001). The degree to which a potential mixing of prey taken by these two species may influence the results of this study, however, are minimal. Analyses of diets of these two species living in the same area indicate that they are largely similar, or identical in terms of prey composition, although roosts occupied by spotted eagle owls can have greater abundance of larger taxa owing to their somewhat larger size (Vernon 1980, Brain 1981; Tilson et al. 1983; Mendelsohn 1989, Dixon and Perrin 1994, Reed 2005, 2007).

As *T. alba* is the presumed accumulating agent for most of the microfaunal remains at Swartkrans, a summary of 53 studies reporting the prey groups taken by them is provided in Table 2.3. As can be seen, rodents are the most common prey group cited, followed by birds, shrews, and bats. In terms of relative abundance, where reported, 42 of these studies identify rodents as most common prey item taken. Finally, actualistic studies have shown that analyses of micromammal community composition from assemblages produced by these owls can be used to accurately reconstruct habitats within about 1-3 km around a roost and thus analyses of fossilized micromammal remains produced by them are ideal for generating precise, site specific paleoecological data (Reed 2003, 2005, 2007).

Table 2.3. Summary of 53 studies reporting vertebrate prey taken by *Tyto alba* in Africa. Country abbreviations are as follows: NA – Namibia, ZW – Zimbabwe, ZA – South Africa, ML- Malawi, ZM – Zambia, TZ – Tanzania, KE – Kenya, MZ – Mozambique, AG – Angola, NG – Nigeria.

Citation	Date	Country	Rodentia	Sorico-morpha	Afros-oricida	Macro-scelidea	Chiro-ptera	Lago-morpha	Aves	Amphibia	Reptilia
1	1910	ZA	X				X				
2	1923	ZA	X								
3	1944	ZA	X	X	X				X		
4	1946	ZA	X	X			X		X		
5	1956	ZA	X		X		X		X		
6	1958	ZA	X	X							
7	1959	ZA	X	X		X			X		
8	1960	ZA	X	X	X		X		X		
9	1960	ZA	X	X					X		
10	1962	NA			X						
11	1963	ZA	X	X		X	X		X		
12	1963	ML	X	X		X	X		X		X
13	1963	ZA	X								
14	1963	ZA	X						X		
15	1963	ZA	X	X			X		X	X	
16	1963	ZA	X	X					X		
17	1964	ZM							X		
18	1964	NA	X	X							
19	1965	ZA	X	X	X	X	X		X	X	X
20	1966	ZA							X		
21	1966	NA	X	X							X
22	1970	ZW	X								
23	1971	TZ	X	X		X	X		X		X
24	1971	NA	X								
25	1972	KE	X	X					X		
26	1972	ZA, NA	X	X	X	X	X	X	X	X	X
27	1973	ZA	X	X		X			X		
28	1973	ZA	X								

Table 2.3. Continued.

Citation	Date	Country	Rodentia	Soricomorpha	Afrosoricida	Macroscelidea	Chiroptera	Lagomorpha	Aves	Amphibia	Reptilia
29	1973	ZA	X	X	X		X		X		
30	1973	NA	X	X					X		X
31	1974	NA	X		X	X			X		X
32	1974	MZ								X	
33	1974	AG	X	X		X	X		X	X	X
34	1974	ZA, ZW	X								
35	1975	ZA, NA	X	X		X	X		X	X	X
36	1975	NA			X						
37	1977	NA	X			X			X		X
38	1978	ZA	X	X			X		X		
39	1978	NG	X	X					X		
40	1980	ZA	X	X			X		X		
41	1980	ZW	X	X		X	X	X	X	X	
42	1982	ZA	X	?			X		X		
43	1982	ZA	X	X	X		X		X	X	X
44	1983	NA	X	X	X	X			X		X
45	1986	ZA	X	X					X		
46	1987	KE	X	X			X		X	X	X
47	1989	ZA	X	X			X		X	X	X
48	1989	ZA							X		
49	1989	ZA	X	X		X			X		
50	1990	ZA	X	X	X		X		X	X	
51	1991	ZA	X	X	X				X		
52	1992	ZA	X	X	X		X				
53	1997	ZA	X						X		
Count			**48**	**36**	**15**	**15**	**23**	**3**	**40**	**12**	**15**

Citations as follows: 1) Taylor 1910; 2) Fitzsimons 1923; 3) Crass 1944; 4) Kolbe 1946; 5) Skead 1956; 6) Davis 1958; 7) Davis 1959; 8) Bateman 1960; 9) de Graaf 1960b; 10) Meester 1962; 11) Coetzee 1963; 12) Hanney 1963; 13) Malherbe 1963; 14) Reed and Hunter 1963a; 15) Reed and Hunter 1963b; 16) Skead 1963; 17) Mitchell 1964; 18) Winterbottom 1964; 19) Nel and Nolte 1965; 20) Farkas 1966; 21) Winterbottom 1966; 22) Wilson 1970; 23) Laurie 1971; 24) Vernon 1971; 25) Norris 1972; 26) Vernon 1972; 27) Dean 1973a; 28) Dean 1973b; 29) Grindley, Siegfried and Vernon 1973; 30) Stuart 1973; 31) Brain 1974; 32) Broadley 1974; 33) Dean 1974; 34) Pocock 1974; 35) Dean 1975; 36) Stuart 1975; 37) Brain and Brain 1977; 38) Dean 1978; 39) Demeter 1978; 40) van der Merwe 1980; 41) Vernon 1980; 42) Levinson 1982; 43) Perrin 1982; 44) Tilson and LeRoux 1983; 45) Herholdt 1986; 46) Gichuki 1987; 47) Mendelsohn 1989; 48) Neser 1989; 49) Wirminghaus 1989; 50) Avery, Rautenbach, and Randall 1990; 51) Vernon 1991; 52) Avery 1992; 53) Kopij 1997.

Previous reconstructions of African Plio-Pleistocene paleoenvironments that have utilized micromammal fossils have almost exclusively relied on assessments of relatively well-preserved cranial and dental elements in order to generate taxonomic lists and calculate relative abundances. Utilizing these data, community composition analyses are usually then conducted from which paleoecological and paleoenvironmental conditions are then inferred. In these analyses, postcrania are either not considered or are used for taphonomic analyses of the biotic and abiotic factors resulting in their accumulation (e.g. Andrews 1990; Fernandez-Jalvo et al. 1998; Matthews et al. 2006; Stoetzel et al. 2011). In one exception, Fernandez-Jalvo and colleagues (1998) analyzed the rodent assemblages from Olduvai Bed-I and conducted both a taphonomic and community structure analysis using the postcrania. In regards to the latter analysis, inferred locomotor patterns for the fossil taxa were reported to be made based on comparisons with the postcrania of modern taxa with known behaviors. However, in this study it is not clear how the fossil postcrania were attributed to each species as taxonomic identifications were reported to be based on an assessment of the cranio-dental morphology. As such, the degree to which African Plio-Pleistocene rodent postcrania can be used to reconstruct past environments has yet to be addressed.

2.3 Paleoenvironmental Reconstructions: Taxonomic Based Methods

Paleoenvironmental reconstructions that use fossil rodents as proxies for past environmental conditions often rely on the principal of actualism (or transferred ecology/taxonomic uniformitarianism), in which the environmental and habitat

requirements of living taxa are considered to be suitable analogs for the fossil taxa they morphologically resemble (Evans et al. 1981; Patnaik 2003; Reed 2007; Wesselman 1984, 1995; Wesselman et al. 2009). This form of logic follows that if a fossil specimen cannot be morphologically distinguished from an extant taxon, then the known habitat requirements of modern members can be used to reconstruct the past ecosystem. One recognized potential issue for taxon-based paleoenvironmental reconstructions is that over the course of a species existence conditions controlling their biogeography may have changed and that the current factors influencing their distribution may not be same as those that existed in the past. Habitats occupied by modern taxa may differ from those of ancestral populations due to a variety of factors such as competition, habitat loss, or, significantly, anthropogenic interference. Furthermore, diets of closely related yet extinct forms may also differ in ways not predicted by their taxonomic affiliation (e.g. Sponheimer, Reed and Lee-Thorp 2001).

With these qualifications in mind, assessments of modern micromammal habitat use have generally relied on published autecological habitat descriptions (Evans et al. 1981; Matthews et al. 2005), personal observations (Andrews 1990; Fernandez-Jalvo et al. 1998), have borrowed published models and modified them where appropriate (Reed 2007), or have conducted Geographic Information Systems (GIS) assessments of museum specimens in order to generate modern habitat values (Campbell 2010, Campbell et al. 2011, 2012). Once modern habitat use is classified, reconstructions of past environments utilizing taxonomic-based approaches are made through analyses of either individual taxa, or paleocommunity composition. For individual taxa, this is typically referred to as an

indicator species approach and relies on known marked preference or physiological requirement of a specific taxon for a particular habitat (Evans et al. 1981). For example, due to thermoregulatory requirements, hippos (*Hippopotamus amphibius*) require submersion in water during most of the day to prevent overheating (Kingdon and Hoffman 2013b). As such, presence of fossils attributed to them at Swartkrans Member 2, and possibly Member 1, has been used to argue for the close proximity of a permanent body of water during the times these deposits accumulated (Brain 1988; de Ruiter 2003; Watson 1993). Similarly, among rodents the greater cane rat *Thryonomys swinderianus* is a known habitat specialist found in dense grasses or reed beds in the vicinity of swamps, lakes, and rivers (De Graaff 1981; Happold 2013, Kingdon 1974; Roberts 1951; Skinner and Chimimba 2005; Smithers 1971). When identified in the fossil record, specimens attributed to this taxon have been considered indicative of past mesic, wet long-grass and marshland aquatic environments (e.g. Wesselman et al. 2009). Alternately, due to the fossorial nature of modern mole rats (Bathyergidae), their presence in a fossil assemblage is considered an indication of sediments suitable to burrowing and of the past presence of geophytes that they consume (e.g. Matthews et al. 2007). As is apparent, while an indicator species approach can provide detailed information on past environments, application is limited to a select few taxa that are habitat specialists.

In regard to types of community analyses, ratios of higher taxonomic groups generally associated with particular environments have been used to infer paleoenvironments. For instance, Vrba (1975, 1980) pioneered the use of the proportion of Alcelaphini and Antilopini tribes in the family Bovidae as a proxy for open or closed

habitats. Among rodents, members of the subfamily Gerbillinae are generally associated with more xeric, open habitats while those of the subfamily Murinae are generally more abundant in mesic, closed environments (De Graaff 1981; Happold 2013, Kingdon 1974; Roberts 1951; Skinner and Chimimba 2005; Smithers 1971), and calculations of the ratio between these groups have been used as a general index of aridity and/or degree of cover in the environment (Denys 1999; Fernandez-Jalvo et al. 1998; Jaeger 1976; Matthews et al. 2007; Reed 2007; Reed and Geraads 2012). This ratio is calculated by either dividing the number of identified genera of each subfamily found or, when relative abundance data is available, by dividing the minimum number of individuals (MNI). Although numerous additional methods and metrics for community analysis are commonly employed, such as calculations of the Shannon-Weiner index (Avery 1982a, b, 1987, 1992b, c, 1995, 2003; Matthews et al. 2007) and Taxonomic Habitat Indices (Andrews 1990; Fernandez-Jalvo et al. 1998; Matthews et al. 2005; Reed 2007; Stoetzel et al. 2011), all require taxonomic lists be compiled for the fossil assemblage. Additionally, many of these methods also require that taxonomic lists be weighted by the relative abundance of each fossil taxon found. It follows that without complete taxonomic representation in the lists generated and/or accurate relative abundances data, utilization of these methods may result in inaccurate or incomplete inferences about past environments. As such, studies utilizing any form of taxonomic community composition analysis need to consider all sources of data available, including postcranial elements.

2.4 Paleoenvironmental Reconstructions: Ataxonomic Based Methods

In part due the issues inherent with taxonomic uniformitarianism, several methods have been developed that generally do not require taxonomic identification of fossil specimens. These methods are broadly referred to here as "ataxonomic" as they do not rely on uniformitarian assumptions, however, several methods currently incorporate some degree of taxonomic signal in their operation and thus are not truly taxon free. Two recent lines of inquiry that show promise in decoupling rodent taxonomy with paleoenvironmental inference include analyses of dental microwear and stable isotope ecology. These methods also have the additional property of being independent of skeletal element morphology in a broad sense, and thus can be used to check paleoenvironmental signals inferred using other methods.

In general, microwear analyses examine microscopic use wear patterns that accrue on teeth through direct interaction with the environment, typically, though not exclusively, via the acquisition and processing of food. Most microwear studies that have been conducted to date have largely focused on larger mammals (e.g. Scott 2012, Scott et al. 2005, Teaford and Glander 1991; Williams and Patterson 2010), and analyses of microfaunal microwear are still in their infancy (e.g. Burgman et al. 2016; Caporale and Ungar 2016; Hopley, Latham, and Marshall 2006; Ungar et al. In Press; and references therein). In a recent study of rodent incisor microwear for 14 African species from 12 genera, Caporale and Ungar (2016) found significant differences between samples when independently grouped by habitat, substrate, or diet. These authors interpreted their results as indicating that habitat had the strongest effect, although no attempt was made to test for

intraspecific microwear differences in either the three Natal multimammate mouse (*Mastomys natalensis*), or the two Jackson's soft-furred mouse (*Praomys jacksoni*) samples collected from different general habitats (see Caporale and Ungar 2016: Table 1). Alternately, Burgman and colleagues (2016) examined rodent molar microwear in three sympatric species across three habitat types in southern Africa and found differences attributed to both diet and habitat, however, those for the latter varied across species, with one (*Rhabdomys pumilio*) failing to show a significant difference between habitat types. These results were then used as a modern baseline for rodents, and combined with dental microwear analyses of other, better documented groups, in an analysis of the paleocommunity ecology at the East African Pliocene site of Kanapoi (Ungar et al. In Press). Overall, while the results from these preliminary studies of rodent microwear are encouraging, substantial sampling and further testing of is needed to identify if there are any larger patterns in rodent dental microwear patterning that do not require taxonomic identification of the samples used.

In addition to microwear, stable isotope analyses of microfauna also have potential as an additional independent ataxonomic line of evidence in paleoenvironmental reconstructions. As with microwear, the majority of studies to date have focused primarily on larger taxa (Cerling et al. 1997; Franz-Odendaal, Lee-Thorp and Chinsamy, 2002; Lee-Thorp, van der Merwe and Brain, 1994, Lee-Thorp et al., 2010; Luyt, Lee-Thorp, and Avery, 2000; Schoeninger, Reeser, and Hallin, 2003; Sponheimer and Lee-Thorp, 1999; Sponheimer, Reed, and Lee-Thorp 2001; Sponheimer et al. 2005, 2006, 2009; van der Merwe et al. 2003; Zazzo et al. 2000). In these studies, the ratio between carbon's two

stable isotopes, ^{12}C and ^{13}C, is compared to a standard (Pee Dee Belemnite or vPDB) and reported in permil (‰) as $\delta^{13}C$, which broadly reflects the proportion of different plant-based food sources in the diet. The $\delta^{13}C$ of different plants varies depending on their photosynthetic pathway, with most studies assessing the relative contribution of C3 and C4 plants to an organism's diet. These base differences in the $\delta^{13}C$ of plants are subsequently incorporated into various bodily tissues, including those of the skeletal system. Few isotopic analyses of African micromammals have been conducted, and the results have proven somewhat difficult to interpret (Hopley, Latham, and Marshall 2006; Leichliter et al. 2017 and references therein). For example, in a recent study of micromammals from the Sterkfontein Valley, Leichliter and colleagues (2017) examined isotopic ratios for nine rodent genera and two insectivorous families (Soricidae and Macroscelididae) from three modern owl roosts occupying different microhabitats as assessed using 250 m step-point line transects emanating from each roost. These results were then compared with those from a select sample of micromammals from three fossil localities in same general area (Sterkfontein, Swartkrans, Gladysvale). Overall, results from the pooled modern specimens showed no difference in carbon isotopic ratios, though significant differences were recovered when samples were broken down by taxon based on several different exclusion criteria. As such, while currently isotopic analyses of micromammals still need to incorporate some degree of taxonomic signal, it is possible that the results reported may instead reflect a methodological limitation. In particular, the use of 250 m transects around each owl roost to characterize habitats most likely underrepresents the actual range of microhabitats sampled by the accumulating agent (i.e.

1-3 km, see above). An accounting for this may resolve the apparent discrepancies, thereby furthering the application of the method within an ataxonomic framework. Alternately, these signals may simply reflect the rather generalized nature of many terrestrial microfauna, and their ability to utilize food resources in microhabitats not available to larger taxa (Leichliter et al. 2017).

Another ataxonomic approach to reconstructing paleoenvironments relies on the functional morphology of postcranial remains in order to assess locomotor adaptations linked to specific behaviors, substrates, and habitat use. Known as ecological functional morphology, the underlying assumptions are that taxa with similar locomotor patterns and habitat use will show similar morphological features due to selection pressures for similar functionally advantageous structures. These principles have been applied to study a wide range of living and extinct taxa including plesiosaurs (O'Keefe and Carrano 2005), stem mammaliaforms (Meng et al. 2017), marsupials (Argot 2001), cetaceans (Gingerich 2003), bovids (DeGusta and Vrba 2005a, b; Kappelman 1988; Kappelman et al. 1997; Plummer et al. 2008), carnivores (Van Valkenburgh 1987), and rodents (see below) to name a few. These types of studies can be considered ataxonomic as they can be used to generate environmentally informative functional groupings independent of taxonomic identification. Such analyses begin by characterizing the morphological space occupied by modern taxa with distinct ecologies, and then infer the ecologies of fossil specimens from where they group in the defined morphospace. For example, among rodents the presence of a broad, robust distal humerus compared to the overall length is considered a good indication of fossorial digging behavior and has been used in numerous studies of

modern and fossil rodents (Dunn and Rasmussen 2007; Elissamburu and Vizcaino 2004; Fernandez, Vassallo, and Zarate 2000; Hildebrand 1985; Lessa and Stein 1992; Rose and Chinnery 2004). Measured as the ratio of the length of the humerus by the epicondylar breadth, this index gives an indication of the relative area available for the origins of the pronator, supinator, flexor and extensor muscles of the forearm and wrist.

Within Africa these approaches have primarily been applied to large ungulate postcrania (e.g. Barr 2014, 2015; Barr and Scott 2014; DeGusta and Vrba 2005a,b; Kappelman 1988; Kappelman et al. 1997; Plummer et al. 2008; Scott and Barr 2014). Several recent studies, however, have shown that results from these types of analyses may not be truly ataxonomic due to the influence of phylogeny on morphology via canalized bauplans (Barr 2014; Barr and Scott 2014; Scott and Barr 2014). As such, methods such as phylogenetic generalized least squares analysis (PGLS) have been developed for estimating and controlling these influences in studies of ecomorphology, however, they are operationally dependent on the inclusion of an accurate phylogeny and thus are sensitive to tree topology and branch lengths (Scott and Barr 2014). For rodents, most phylogenetic analyses have either focused on relationships within particular lower level taxonomic groups (e.g. Gerbillinae: Abiadh et al. 2010; Colangelo et al. 2007) or have taken representative subsamples to assess higher level relationships (Adkins et al. 2001; Blanga-Kanfi et al. 2009). Even the most comprehensive supertree yet produced, which includes approximately 56% of known rodent taxa, does not include all taxa that are found within southern Africa (Fabre et al. 2012). As such, although these methods show great promise for refining ecomorphological signals, they cannot be utilized in this study.

Previous functional morphology studies of rodents include analyses of fossorial adaptations in gophers (Lessa and Patton, 1989; Lessa and Stein, 1992; Lessa and Thaeler, 1989), semiaquatic locomotion in muskrats (Stein, 1988), and locomotor specializations in caviomorph rodents (Biknevicius 1993; Candela and Picasso 2008; Elissamburu and Vizcaı´no, 2004; Fernandez, Vassallo, and Zarate 2000). To date, few such functional comparisons have been conducted across a wide range of modern rodent groups. When conducted, these studies tend to use a limited number of modern taxa for comparison with fossil specimens (e.g. Dunn and Rasmussen 2007; Rose and Chinnery 2004). In a notable exception, Samuels and Van Valkenburgh (2008) analyzed a global sample of rodent postcrania from 65 extant genera displaying seven different locomotor patterns. Results from their analysis revealed consistent differences in postcranial morphology related to functionally important convergent traits despite distinct evolutionary histories. Moreover, this study further demonstrated the utility of this method in studies of fossil specimens through the identification two distinct ecomorphs of extinct beavers (Castoridae). However, due to the global distribution of the sample selected, only 12 African genera were analyzed. Thus, the presence of functional morphological signals in the postcrania of many African rodent genera remains largely untested.

2.5 Study Sites

This section outlines the various modern and fossil localities used in this study, the specific locations in the southern African subregion of which is given in Figure 2.1.

Information is first provided for the fossil site of Swartkrans, followed by the sites containing modern owl roosts.

2.5.1 Swartkrans

The cave site of Swartkrans is located in the Blaubank Valley, Cradle of Human Kind UNESCO World Heritage Site, Krugersdorp District, Gauteng Province, South Africa (26.017°S 27.724°E). Based on the vegetation classification of Mucina and Rutherford (2006) the site is found in the Grassland Biome, Dry Highveld Grassland Bioregion, and the Gh 15 Carletonville Dolomite Grassland vegetation unit. Altitude for this vegetation unit range between 1,360-1,620 m, though primarily restricted between 1,500-1560 m, with the cave located at approximately 1,480 m. This area is characterized as a species rich grassland set in undulating planes dissected by prominent rocky chert ridges. Vegetation primarily consists of 12 dominant graminoid taxa by biomass, and numerous secondary species. Trees and other woody vegetation are primarily restricted along watercourses and around the entrances of solution cavities and sinkholes. The climate is warm-temperate with high summer temperatures, frequent frosts in the winter, and a mean annual temperature of 16.1°C. Rainfall is concentrated in the summer months (November-March) with the area receiving approximately 600 mm mean annual precipitation.

Located approximately 1 km west from the equally well-known site of Sterkfontein on the north side of the Bloubank River, this area in general is rich in fossil-bearing cave deposits, with seven named sites found within a 3 km distance (Figure 2.3).

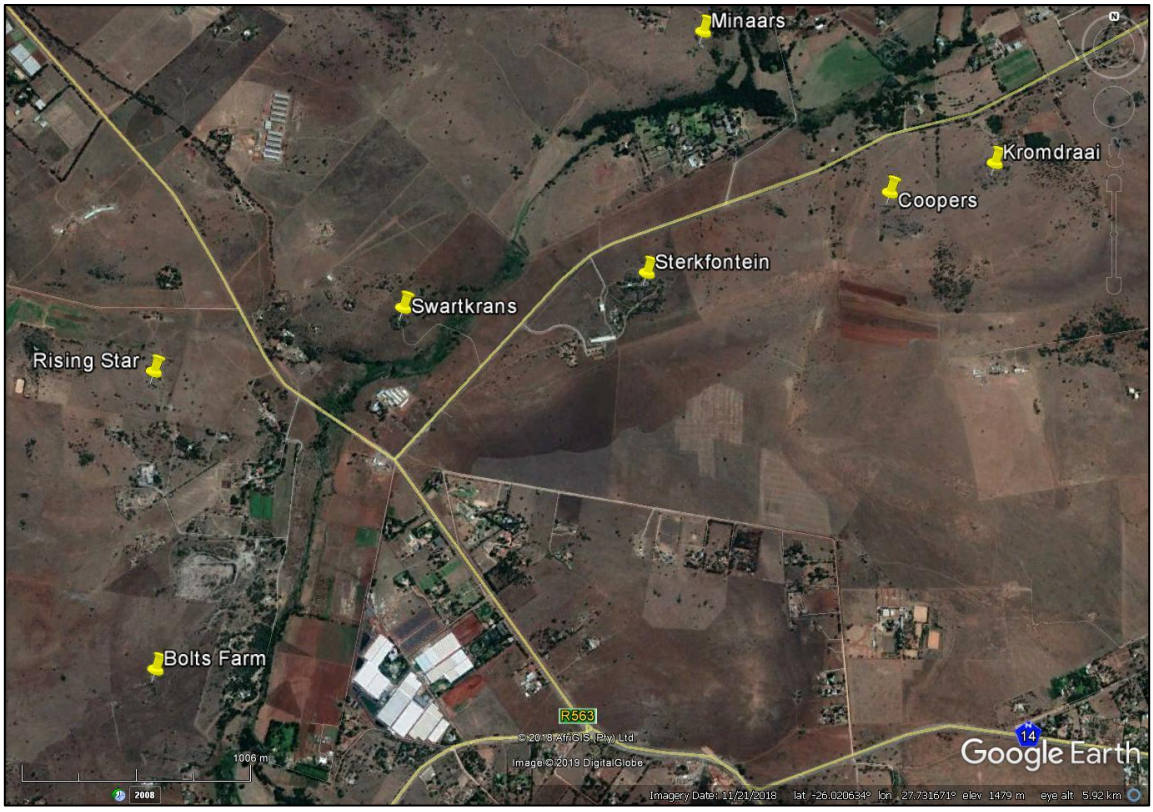


Figure 2.3. Swartkrans, Bolt's Farm, and additional notable fossil-bearing sites.

Although the fossiliferous nature of the site had been known previously, initial exploration of the Swartkrans deposits began in November of 1948 when Robert Broom and John T. Robinson moved a portion of their field team over from the Sterkfontein Type Site under the auspices of the Transvaal Museum and the University of California African Expedition (Broom 1950; Brain 1981; Robinson 1952), the latter of which was run by a rather colorful character named Wendell Phillips (Tucker 2019). Almost immediately after excavations commenced remains of both robust (SK 6 - Broom 1949) and gracile hominin forms (SK 15 - Broom and Robinson 1949) were found, providing early evidence of the co-occurrence of two distinct hominin taxa at one site (Broom and Robinson 1950). These

initial excavations continued until November of 1949 at which time funding was exhausted. Unfortunately, during these early excavations an expansive seam of high-grade travertine had been exposed which, owing to its commercial value, was quickly capitalized on by a local miner who began blasting at the site in December in order to provide lime to a toothpaste manufacturing firm (Brain 1981; Robinson 1952). Due to the primacy given to commercial interests over scientific endeavors by the South African government at the time (Broom and Robinson 1952:10; Robinson 1952:4) this destructive period continued throughout 1950 and into 1951, undoubtedly resulting in the loss of many important fossils. Efforts were made, however, to prospect through the rubble heaps generated by the mining operations and resulted in the recovery of numerous notable fossils including the SK 48 cranium and SK 23 mandible now attributed to *Parathropus robustus* (Broom and Robinson 1952). Upon the cessation of the mining activities in 1951 funds were again obtained allowing work to resume at Swartkrans for a short time. Due to the death of Robert Broom in April of 1951, excavations were taken over by J.T. Robinson and continued into 1953 at which time the site was abandoned for 12 years (Brain 1967; Robinson 1952).

Following the hiatus in field work, excavations at Swartkrans resumed in 1965 under the direction of C.K. Brain and continued unabated until 1986. Brain (1988) conceptualized this period of work as having consisted of three, seven-year phases. During the first two phases the primary objectives included the cleaning up and sorting of the material generated during the chaotic mining episode, followed by the removal of natural overburden in order to expose the full extent of the cave deposits. While this work was

taking place, it became apparent that the cave had suffered from an earlier period of commercial mining prior to the 1950-51 episode (Brain 1967). Other research conducted during this time included attempts to untangle the complex cave stratigraphy (Brain 1976; Butzer 1976), interpret the paleoenvironments and ages for the deposits utilizing fauna (Vrba 1975, 1980), and, significantly, interpret the fossil remains within a taphonomic framework that considered multiple accumulating agents during site formation (Brain 1970). This last part constituted a shift away from the killer ape-man paradigm that had guided many earlier interpretations of hominin fossil sites (e.g. Broom and Robinson 1952; Cooke 1951; Dart 1957) and represented an important advance in the field of paleoanthropology. Much of the work at Swartkrans during these periods was subsequently summarized in Brain's classic contribution *Hunters or the Hunted? An Introduction to African Cave Taphonomy* (1981).

The third round of work at Swartkrans took place between 1979-1986, and it is from these excavations that the fossils used here were recovered (Brain 1993a; 2004). Excavations were conducted in thorough, systematic manner with a permanent metal gird installed over the main excavation area. Larger fossil specimens were individually numbered and cataloged with details including date, provenance, and taxonomic identification (Watson 1993). Alternately, microfaunal remains were aggregated and given a single catalog number per unit/spit. Details on the tags associated with the microfaunal specimens vary with some providing the date, catalog number, unit, spit depth (usually 10 cm), member, and number of specimens contained, while others only provide a catalog number. In total, 351,703 faunal skeletal specimens were recovered during these

excavations, of which ~60% were microfauna (Watson 1993: Table 1). Results from these excavations were largely summarized in the monograph *Swartkrans: A Cave's Chronical of Early Man* (Brain 1993a), which was later reprinted with several additional chapters added (Brain 2004).

Most recently excavations at Swartkrans resumed in 2005 after 19 years with the establishment of the Swartkrans Paleoanthropological Research Project (SPRP) run by Dr. Travis R. Pickering. To date, this period of research has largely focused on further refining the dates and stratigraphy of the site (Gibbon et al. 2014; Sutton et al. 2009), addressing additional taphonomic processes in relation to hominin behavior (Pickering and Brain 2010), analyses of lithic remains (Kuman et al. 2018), and descriptions of new hominin remains recovered (Picketing et al. 2012). Although numerous faunal remains were reportedly recovered, research on these is still ongoing and they have yet to be published.

As with most cave deposits, the stratigraphy at Swartkrans represents a complex history of repeated episodes of dissolution, infill, and collapse. Early work at the site noted the differences between the matrix from which the robust australopithecine and early *Homo* remains were recovered, and postulated that the latter must be younger, however, the question of whether this difference was significant (Broom and Robinson 1949) or not (Broom and Robinson 1950; Robinson 1952) in a geological sense remains open. After much work at the site, Butzer (1976) formally codified 2 different deposits at Swartkrans which he named Member 1 and Member 2. Utilizing these descriptions, and also considering work on the faunal remains, Brain (1976) then reconstructed the caves history as having at least three distinct phases, two in which the primary breccias were laid down,

and a third represented by subsequent dissolution and infill of channels in the named deposits that were possibly variable in age (see also Brain 1981). Subsequent work at the site later revealed a more complex geology and Brain (1988; 1993b) identified 5 members, each separated by an erosional discontinuity. Additionally, Member 1 was further partitioned into two subdivisions; an older lower bank (LB) deposit, and a younger hanging remnant (HR). The most recent series of excavations at Swartkrans have further revealed several new deposits referred to as the Lower Bank East Extension (LBEE), the Talus Cone Deposit (TCD), and the Underground North Excavation (UNE) (Sutton et al. 2009, Pickering et al. 2016). Of these, the LBEE is considered to be a newly recognized portion of the known LB deposit, and thus a part of Member 1. Alternately, the TCD is located above the LBEE deposits and beneath Member 4 in the north east portion of the site and has not yet been formally categorized with the Swartkrans formation member system. Finally, the UNE is also located in the north east portion of the site and is characterized as a highly disturbed deposit which accumulated as a result from earlier mining episodes.

As with the interpretation of the stratigraphy, dating of the Swartkrans deposits has also been proven difficult. Broom and Robinsons initial speculation as to the deposits ages invoked the different matrix in which the SK 13 mandible was recovered and, though not explicitly stated, probably also the more advanced nature of the specimen itself stating "We are thus at present unable to give the age of the deposit except to say that it *must be* (my emphasis) considerably younger than the main deposit. If the main deposit is Upper Pliocene, not improbably the pocket may be Lower Pleistocene." (1949:322). This

statement was quickly walked back, however, with greater uncertainty for the ages for the deposits indicated (Broom and Robinson 1950; Robinson 1952). Over the course of the next 30 years little progress was made on dating the deposits. Best estimates for Members 1 and 2 provided by Brain (1976; 1981) were based primarily on the biostratigraphic work of Elizibeth Vrba using bovids (1975) and suggested a date between 1 and 2 Ma for Member 1, and < 0.5 Ma for member 2. These bovid estimates were subsequently revised to 1.8 -1.6 Ma for Member 1 (both HR and LB), and > 1 Ma for Member 2 (Vrba 1985a), and again later once additional members were recognized to 1.8 Ma - Member 1, 1.1 Ma - Member 2, and 0.7 Ma - Member 3 (Vrba 1995b). Attempts to date the site using equid biostratigraphy were also made by Churcher and Watson (1993) who estimated Member 1 to be approximately 1.7 Ma, Member 2 to be 1.5 Ma, and Member 3 at 1 Ma. While these estimates suggest that the Swartktans Members 1-3 deposits accumulated over the course of approximately 1 Ma, similarities in both the cultural and faunal remains, both micro and macro, have been noted (Avery, 2001; Brain 1993b) and the possibility that the Members 2-3 deposits may be older, and closer in age to Member 1 has been suggested (de Ruiter 2003). Of the other two members, Member 4 was not originally excavated but was interpreted as Middle Stone Age based on observable artifacts, while Member 5 produced a radiocarbon date of 11 Ka BP indicating a Holocene age (Brain 1993b).

Utilizing a variety of new analytical methods, work conducted since 2005 has resulted in more precise dates with associated error estimates for some of the deposits. Drawing on results from a range of studies Herries et al. (2009) produced a seriation of hominin-bearing localities in southern Africa provide best age estimates for Swartkrans of

~2.0 Ma – Member 1, 1.65-1.07 Ma – Member 2, and 1.04-0.62 - Member 3. Subsequent uranium series dating on flowstone deposits within the site produced dates bracketing the Member 1 deposits of 2.31-1.64 Ma when the oldest (flowstone underlying LB) and youngest (flowstone overlying LB) dates are taken with error, or 2.31-1.8 Ma if the flowstone capping the HR is considered (Pickering et al. 2011). Either younger date would also serve as a lower bound for the subsequent Member 2 deposits which were mostly removed during earlier excavations. These dates were further supported by Gibbon et al. (2014) who presented radiometric ages based on cosmogenic nuclide burial of 2.19 ± 0.08 Ma and 1.80 ± 0.09 Ma for Member 1 (LB), and 0.96 ± 0.09 Ma for Member 3. Finally, radiometric uranium series dates representing the lower bound for the Member 4 have also been reported with a mean sample age of 110,300 ± 1,980 years based on a flowstone deposit underlying this deposit (Sutton et al. 2009). Consequently, this date also represents the minimum age for the as yet unassigned TCD which underlies it, although the recovery of robust australopith remains from TCD would argue for a much older age.

In general, paleoenvironmental reconstructions of the Swartkrans deposits have primarily indicated open environments with more recent work suggesting more of a mosaic habitat with areas of increased tree cover. An early paleoenvironmental interpretation based on comparisons with the larger faunal components suggested that southern African hominins in general occupied open plains, similar to baboons, and lived in caves as primary accumulators of many of the recovered fossils (Cooke 1952). Incorporating some of the smaller fauna, including gastropods, Robinson (1952) postulated that the past environment at Swartkrans were no drier, and perhaps even moister

than current conditions. Similar interpretations were provided based on work conducted during the first two phases of excavations under C.K. Brain. While providing the first codification of Members 1 and 2, Butzer (1976) concluded based on sedimentary analyses that the paleoenvironments probably consisted of open grassland or parklands with effective moisture comparable to, or possibly greater than today for the majority of subunits designated. Habitats similar to what are seen today consisting of open grasslands and sparse, low bush cover have also been inferred based on analyses of bovid remains (Vrba 1975, 1980, 1985a, 1988), although different interpretations were given on if these habitats were preceded by more wooded environments represented in earlier deposits found at Sterkfontein (see Shipman and Harris 1988 and Vrba 1988). During this period attempts were also made to reconstruct paleoenvironments utilizing pollen remains, however, these proved problematic due to issues of contamination and degradation (Scott and Bonnefille 1986).

Following the completion of systematic excavations conducted during 1979-1986, paleoenvironmental reconstructions for Swartkrans still typically inferred an open savanna type environment, however, greater emphasis was placed on a wooded component usually associated with the paleo-Bloubank River (Avery 2001; Benefit and McCrossin 1990; de Ruiter et al. 2008; Reed 1997; Watson 1993). Although currently an ephemeral watercourse, the presence of aquatic habitat specialists such as hippos, otters, and watermongoose in the Swartkrans deposits (Brain 1988; De Ruiter 2003; Watson 1993) suggests that the Bloubank River was a more prominent landscape feature in the past. Analytical methods used to reconstruct paleoenvironments also broadened with some

analyses using more traditional taxonomic based approaches (Avery 2001, Watson 1993), others relying on community composition comparisons incorporating census data from modern parks and reserves as analogs within both taxonomic and ataxonomic frameworks (de Ruiter et al. 2008; Reed 1997), and others relying on dental functional morphology (Benefit and McCrossin 1990).

2.5.2 Modern Owl Roosts

Modern barn owl pellets used in this analysis were recovered from seven localities found throughout southern Africa: two from South Africa, two from Botswana, and three from Namibia (Figure 2.1).

2.5.2.1 Botswana

The barn owl pellets from Botswana were recovered from the Koanaka Hills (or !Ncumtsa Hills) in the Ngamiland Province, North-West District (20.158°S, 21.195°E). Due to its geographically intermediate nature between the rich hominin-bearing Plio-Pleistocene deposits in South Africa and those of the East African Rift System, exploration of the Koanaka Hills has occurred intermittently since Pleistocene deposits were first recognized (Cooke 1975; Pickford 1990; Pickford and Mein 1988; Pickford, Mein and Senut 1994; Ritter and Mann 1995; Senut 1996; Williams et al. 2012). The pellets used here were collected during fossil and modern faunal surveys conducted in 2008 and 2009, and formed the basis for the master's thesis of R. Tutalo (Bauer et al. 2009; Ferguson et al. 2010; Kennedy et al. 2012; McDonough et al. 2013, Tutalo 2012). Specifically, this

series of pellets were found at Koanaka South, in the entrances of two openings to the Koanaka cave system termed Leopard Cave (Figure 2.4), and Bone Cave (Figure 2.5). The two cave openings are ~200 m from one another, and when last explored no connections between the two were identified within the greater cave system. Due to their close proximity, and because only a single barn owl was visually identified in Leopard Cave during initial survey work in 2007, an argument could be made to combine the assemblages. However, during the initial survey and field work in 2008 barn owl calls audible from a basecamp situated between the two cave openings seemed to emanate from both entrances. Additionally, were these assemblages to enter into the fossil record it is possible they would be treated separately due to the independent entrances and lack of any known connections. As such, following Tutalo (2012) the collections here have been split and considered as separate roosts.

2.5.2.2 Namibia

Modern barn owl pellets from Namibia were collected at Mirabib (or Anachankirab), an isolated granite inselberg located in the Namib-Naukluft National Park, approximately 100 km SE of Walvis Bay, Erongo Region (23.453°S, 15.356°E). Located within the outcrop are numerous weathered crack and fissures, one of which contains the Mirabib Hill Shelter archaeological site. Measuring approximately 10 m x 15 m in area, this site contains both rock art and archaeological deposits recording around 8,000 years of human occupation (Sandelowsky 1974; 1977). Additionally, the shelter site also served as a barn owl roost for nearly as long, as both intact pellets, and microfaunal remains from

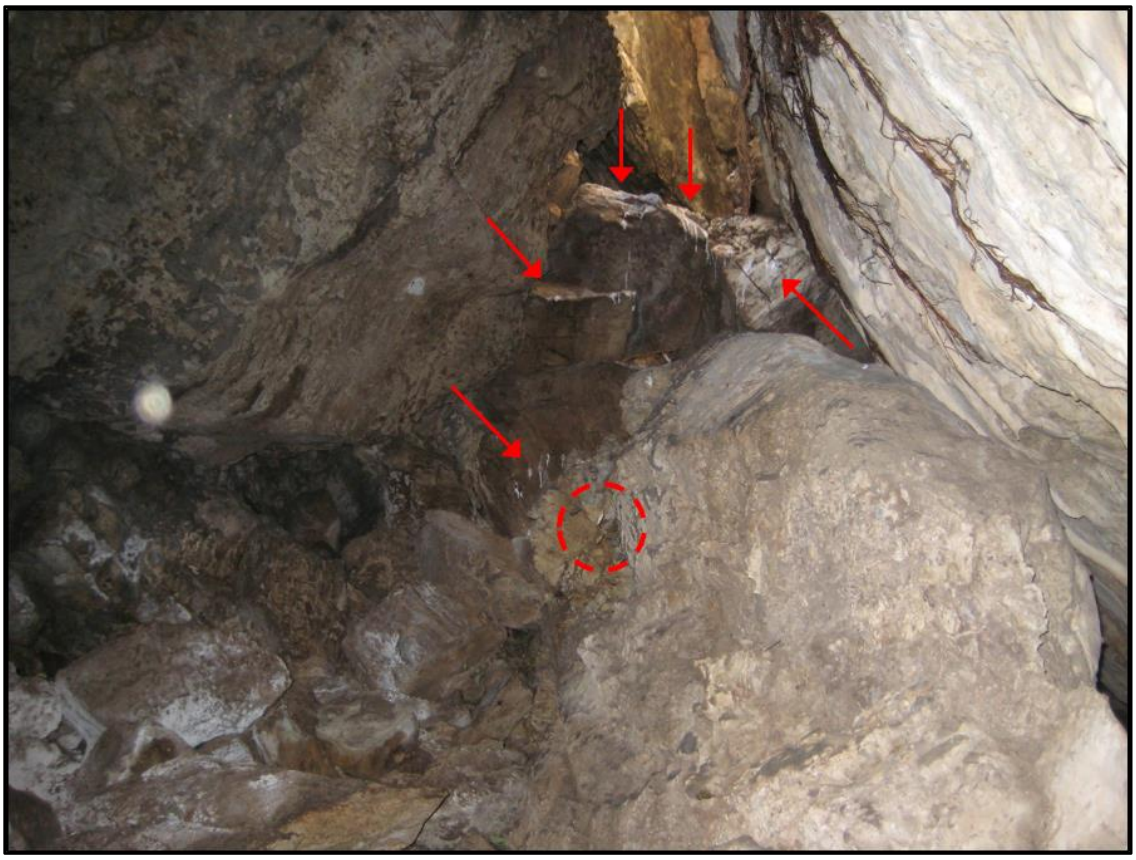


Figure 2.4. Inside the opening of Leopard Cave, Koanaka Hills, Botswana. Notice the accumulated owl excrement (arrows) resulting in the whitewashed appearance of the central, upper ledge and several pellet castings below this in center (circle).

disaggregated pellets were found during excavations in well stratified deposits dating back approximately 6000 BP (Brain and Brain 1977; Sandelowsky 1977). An analysis of these owl accumulated deposits identified an inverse relationship between the two primary prey items recovered, desert gerbils (*Gerbillurus* spp.) and geckos (c.f. *Pachydactylus* sp.), which combined accounted for 87% of all prey items found throughout the strata (Brain and Brain 1977). When these results were compared with those from a previous analysis of modern pellets collected at a second roost close to the archaeological site (i.e. Mirabib

Figure 2.5. Botswanan geologist Mohutsiwa Gabadirwe at the entrance of Bone Cave, Koanaka Hills, Botswana. Notice the accumulated owl excrement (arrows) resulting in the whitewashed appearance of the central, upper and lower entrance. Numerous pellets and disaggregated prey remains were recovered on the floor below.

Owl Crack in Brain 1974), and unpublished data (cited as Stuart and Brain, in prep. in Brain and Brain 1977 – though no such publication could be found, e.g. see Rubidge 2000), this inverse relationship was interpreted to indicate changes in the local environment. Specifically, the higher the relative abundance of gerbils, and thus lower relative abundance of geckos, was associated with increased rainfall resulting in greater grass growth and, correspondingly, a markedly increased the gerbil population. During periods of high gerbil population density barn owls were thought to prey almost exclusively on gerbils as a preferred food source. Alternately, with deteriorating environmental conditions, barn owls switched to geckos as a fall back food due to the

decline in the population of their preferred prey (Brain 1981; Brain and Brain 1977). This pattern was found at an annual level by the almost total exclusion of other prey items observed in pellets recovered in 1974 and 1975 during exceptionally wet years in the Namib Desert compared to those recovered in 1972, and used to interpret similar, longer term paleoenvironmental fluctuations in the area (Brain and Brain 1977).

Barn owl pellets from Mirabib used in this analysis were identified as being recovered during 1974 based on the manifest included with them and are most likely those from which the unpublished data mentioned above were obtained. In total, pellets from three roosts were recovered including the Mirabib Hill Shelter site, the Mirabib Owl Crack, and a third Nest Site reported to be in the Mirabib area. Although it is possible that these pellet accumulations may have been produced by one, or a pair of barn owls, they are treated separately here for the same reason as those from Botswana outlined above.

2.5.2.3 Swartkrans & Bolts Farm

Pellets from the South African roosts both come from two fossil-bearing localities in Cradle of Human Kind UNESCO World Heritage site. Pellets from the first roost were recovered from in the inner cave of Swartkrans by Dr. C. K. Brain between 1974-1975, who discussed their prey composition in a comparison with pellets from Spotted Eagle Owls (*Bubo capensis*) found nearby (Brain 1981). The barn owl pellets were individually labeled and consisted of both craniodental and postcranial remains of prey items. Unfortunately, those pellets attributed to *B. capensis* in the same collection lacked

postcranial elements thus comparisons in prey skeletal part proportions between the two types of owls was not possible. Further details on the site of Swartkrans are given above.

The second series of pellets from South Africa were recovered from Bolt's Farm (26.032°S, 27.713°E), a fossil-bearing locality situated approximately 2 km SW of Swartkrans (Figure 2.3). Fossils from this site were first recovered in 1936 and described as originating in a cave "about a mile south of that in which *Australopithecus* was found…" (i.e. Sterkfontein - Broom 1937:512). Since then numerous excavations and fossil surveys of the area have been conducted revealing an expansive series of fossil deposits which combined document potentially 2 Ma of depositional history spanning the Plio-Pleistocene boundary (see Edwards et al. 2019; Gommery et al. 2012; Thackeray et al. 2008 and references therein for the history of the work at Bolt's Farm). Despite the fossiliferous nature of the varied deposits at Bolt's Farm, no hominin remains have been recovered to date and is probably a major factor in why the locality has historically received less attention than others in area.

Pellets from Bolt's Farm used in this study were collected by both the author and Dr. Frank Sénégas between April-October 2016 during ongoing excavations at the site by the Human Origins and Past Environments Research Unit (HRU), with an additional series of pellets collected in 2010 provided by Dr. Frank Sénégas (Gommery et al. 2012). Pellets were recovered from around the dripline of a shallow cave entrance at the end of wooded channel that slopes downward from the surrounding open grasslands (Figure 2.6). When the pellets were collected the cave was identified as Bridge Cave (e.g. see Gommery et al. 2012; Thackeray et al. 2008), however, a recent study reconciling historical and current

work at Bolt's Farm indicates that names Pit 7, and Elephant Cave have also been used for this location (Edwards et al. 2019).

Figure 2.6. Dr. Frank Sénégas examining owl pellets near the dripline of Bridge Cave/Pit 7/Elephant Cave, Bolt's Farm, South Africa. Notice the extensive accumulated owl excrement (arrows) resulting in the whitewashed appearance along the upper, left ledge.

3. MATERIALS AND METHODS

3.1 Samples

The rodent postcranial remains used in this study were obtained from a variety of different contexts which are detailed as follows.

3.1.1 Modern Owl Pellet Samples & Processing

A total of 279 barn owl pellets from three sites and seven barn owl accumulations were analyzed in this study (Figure 2.3, Table 3.1). Pellets from the Koanaka Hills and Bolts Farm were both processed using the same protocols. Pellets were first individually soaked in water which was stirred occasionally in order to facilitate their breakdown. Once disaggregated, water was then drained, and the remaining osseous and non-osseous material laid out to dry overnight. After drying, osseous material was then separated with all larger rodent skeletal elements (e.g. femora, scapula, craniodental) and most smaller skeletal elements (e.g. ribs, tarsals, caudal vertebra) extracted. The remaining keratinous material, possibly containing some minor skeletal elements, was then bagged separately for future studies. Skeletal remains in the pellets from Swartkrans and Mirabib housed in the Ditsong Museum of Natural History were separated out by previous researchers and thus processing was not required.

Table 3.1. Number of pellets from each owl roost used in this study. Repository abbreviations are as follows: TLC – currently with author; DNMNH – Ditsong National Museum of Natural History; SHNHC – Sam Houston Natural History Collections.

Sites	Country	# Pellets	Repository
Bolts Farm - Bridge Cave	South Africa	38	TLC
Swartkrans	South Africa	38	DNMNH
Mirabib - Crack Owl Roost	Namibia	35	DNMNH
Mirabib - Shelter Site	Namibia	29	DNMNH
Mirabib - Nest Site	Namibia	46	DNMNH
Koanaka Hills - Leopard Cave	Botswana	66	SHNHC
Koanaka Hills - Bone Cave	Botswana	27	SHNHC
Totals	-	**279**	-

3.1.2 Modern African Rodents

In order to generate a modern comparative dataset, skeletons from extant rodent taxa were examined at five institutions: American Museum of Natural History (AMNH), Smithsonian National Museum of Natural History (USNM), Field Museum of Natural History (FM), Natural Science Research Laboratory – Museum of Texas Tech University (NSRL), and the Ditsong National Museum of Natural History (DNMNH). While every attempt was made to visit collections where the most complete taxonomic sampling could be obtained, the historical curation practice of primarily retaining the skins and skulls of micromammals (e.g. Anonymous 1968) inhibited a complete sampling of all southern African rodent taxa. Table 3.2 lists the number of families, subfamilies, genera, species, and specimens examined at each repository. In cases where a taxon does not have a proper subfamily designation the familial name is utilized with the suffix “inae”. Table 3.3 lists the number of specimens examined by taxonomic composition category. In total, 263

Table 3.2. Number of families, genera, species, and specimens by collection.

Repository	Families	Subfamilies	Genera	Species	Specimens
AMNH	6	7	7	8	15
FM	4	5	7	8	19
NSRL	3	4	4	4	7
DNMNH	8	14	31	44	193
USNM	8	13	19	20	29

modern rodent specimens representing 49 species, 33 genera, and 9 families were examined, or approximately 57%, 89%, and 100% of southern African rodent diversity respectively (Table 2.1). Not all specimens, however, were represented by complete skeletons and for eight only femoral and humeral data were collected (Table 3.3). As such, in analyses where the only individual elements were used N=263, while those where the entire skeleton was used for taxonomic identification N=253 as both *Petromus typicus* and *Dasymys incomtus* are represented by only one complete individual. However, during the analyses of functional indices of complete specimens N=255 as neither of these species represent single occurrences for a functional category.

Although at the onset of this project I planned to only sample rodent taxa found within the southern African subregion, and to only sample adult wild caught specimens, I made several exceptions during data collection due to sample size concerns. First, one Cape Dune Mole-Rat (*Bathyergus suillus*) zoo specimen was included to bring the species sample size up to two. Additionally, two juvenile or young adult specimens based, on epiphyseal fusion (TM-44461 *Cryptomys hottentotus*; AMNH-216395 *Thryonomys* sp.), were also included. Next, five individuals of the Silvery Mole-Rat (*Heliophobius*

Table 3.3. Number of specimens sampled by family, subfamily, genus, and species. Values in bold correspond to family level totals. Numbers in brackets indicate specimens for which only humeral and femoral measurements and photographs were available.

Family	Subfamily	Genus	Species	# of Specimens
Pedetidae				**7**
	Pedetinae			7
		Pedetes		7
			capensis	7
Bathergidae				**25**
	Batherignae			25
		Bathyergus		3
			janetta	1
			suillus	2
		Cryptomys		15
			damarensis	4
			hottentotus	11
		Georychus		2
			capensis	2
		Heliophobius		5
			argenteocinereus	5
Hystricidae				**4 (1)**
	Hystricinae			4 (1)
		Hystrix		4 (1)
			africaeaustralis	4 (1)
Petromuridae				**2 (1)**
	Petromurinae			2 (1)
		Petromus		2 (1)
			typicus	2 (1)
Thryonomyidae				**9**
	Thryonomyinae			9
		Thryonomys		9
			swinderianus	8
			sp.	1
Muridae				**148 (6)**
	Deomyinae			10
		Acomys		10
			spinosissimus	9
			subspinosus	1
	Gerbillinae			32
		Desmodillus		6

Table 3.3. Continued.

Family	Subfamily	Genus	Species	# of Specimens	
			auricularis		6
		Gerbilliscus		16	
			brantsii		4
			inclusus		4
			leucogaster		8
		Gerbillurus		10	
			paeba		8
			vallinus		2
	Murinae			93 (5)	
		Aethomys		15	
			chrysophilus		11
			ineptus		4
		Micaelamys		10	
			namaquensis		10
		Dasymys		5 (4)	
			incomtus		5 (4)
		Grammomys		10	
			cometes		4
			dolichurus		6
		Lemniscomys		10	
			rosalia		10
		Mastomys		12	
			coucha		2
			natalensis		8
			sp.		2
		Mus		9	
			indutus		6
			minutoides		3
		Pelomys		2	
			fallax		2
		Rhabdomys		10	
			pumilio		10
		Thallomys		7	
			nigricauda		1
			paedulcus		6
		Zelotomys		3 (1)	
			woosnami		3 (1)
	Otomyinae			13	

Table 3.3. Continued.

Family	Subfamily	Genus	Species	# of Specimens	
		Otomys			10
			angoniensis	4	
			irroratus		6
		Myotomys			3
			unisulcatus		3
Nesomyidae				**39 (1)**	
	Cricetomyinae				14
		Cricetomys			5
			gambianus	5	
		Saccostomus		9	
			campestris		9
	Dendromurinae				19
		Dendromus		9	
			melanotis		7
			mystacalis	2	
		Steatomys			10
			krebsii	2	
			pratensis		8
	Mystromyinae				2
		Mystromys		2	
			albicaudatus		2
	Petromyscinae			4 (1)	
		Petromyscus			4 (1)
			collinus		3 (1)
			sp.		1
Gliridae				**10**	
	Graphiurinae				10
		Graphiurus			10
			murinus	9	
			sp.		1
Sciuridae				**19**	
	Xerinae				19
		Paraxerus		10	
			cepapi		10
		Xerus			9
			inauris	9	

argenteocinereus) were also included here to increase the sample size at higher taxonomic levels due to small sample sizes for two of the three southern African mole-rat genera (Table 3.3). Extralimital to the southern African subregion as defined here, *Heliophobius argenteocinereus* ranges from southern Kenya, west into the eastern portion of the Democratic Republic of the Congo, and south to the Northern bank of the Zambezi river (Happold 2013). An additional fourteen specimens from seven genera and eight species collected outside of southern Africa were also included (Table 3.4). All of these specimens were collected in the Zambezia Province of Mozambique, which is located on the northern bank of the Zambezi River, and all of the species distributions include areas within southern African (Happold 2013). It should be noted that while these specimens reported are known to have been collected outside the subregion, it is possible that several other specimens were as well, however, as no specific locality information was provided on the accession tag, this cannot be determined at this time.

3.1.3 Swartkrans Fossil Rodents

The original goal of this project was to analyze fossil rodent postcrania from the sites of Swartkrans and Sterkfontein in order to compare the results with those obtained previously using craniodental remains (e.g. Avery 1998, 2001). Unfortunately, while visiting the DNMNH in South Africa it was discovered that the microfaunal collection from Sterkfontein could not be located, thus only Swartkrans was available for study. The Swartkrans microfaunal materials examined in this study were recovered from Members 1-3 during excavations carried out by Dr. C.K. Brain from 1979-1986, and are designated

Table 3.4. Taxonomic breakdown and numbers of specimens collected outside the southern African subregion as defined in this study.

Family	Subfamily	Genus	Species	Specimens
Muridae	Deomyinae	*Acomys*	*spinosissimus*	1
	Gerbillinae	*Gerbilliscus*	*leucogaster*	2
		Gerbilliscus	*inclusus*	1
	Murinae	*Micaelamys*	*namaquensis*	1
		Dasymys	*incomtus*	4
		Pelomys	*fallax*	2
Nesomyidae	Cricetomyinae	*Cricetomys*	*gambianus*	2
	Dendromurinae	*Steatomys*	*pratensis*	1

by the SKX prefix. These remains were housed at the DNMNH in eleven 39x42x12 cm boxes containing 1,936 bags in which all microfaunal remains (e.g. avifauna, herpetofauna, afrotheres), minus the micromammal craniodental remains separated out during previous studies, were stored. The number of bags available for sampling in each Member varied and ranged from 138 to 1002 (Table 3.5). Finally, specific provenance of each bag also varied with some representing 10 cm spit levels for 1m x 1m units while others consisted of material from variable units and depths.

Due to the volume of material an exact tally of the number of specimens examined was not made as it would have required an inordinate amount of time for little gain. Some individual bags contained only single specimens while others contained several thousand (Figure 3.1). In her analysis of the larger faunal remains from these excavations however, Watson (1993:Table 1) provides count data for the skeletal specimens recovered indicating that 102,371, 36,213, and 69,850 microfaunal remains were recovered from Members 1-3 respectively, for a total of 208,434. Due to the time needed to sort and clean

Table 3.5. Number of Swartkrans SKX Member microfaunal bags examined.

SKX Member	# of Bags
1	1002
2	138
3	796
Total	**1936**

Figure 3.1. Collage of microfaunal bags from Swartkrans Member 3 with single bag highlighted indicating 229 specimens contained within.

this volume of material, I obtained a permit from the South African Heritage Resource Agency (SAHRA) and the collection was exported to Texas A&M University for processing.

Once at Texas A&M all complete to nearly complete rodent appendicular long bones were extracted, along with all non-rodent remains, and rebagged with the copies of the original tags made to accompany them. Nearly complete here implies that any damage to the specimen would either not affect the linear measurements taken from them, could be reasonably estimated, or that could be digitally reconstructed for an outline analysis (see below). Specimen cleaning consisted of soaking in water for between 20 to 60 minutes with removal of adhering sediments conducted using a soft tipped paintbrush and wooden toothpicks to dislodge material in small fossae and foramina. In total, 126 fossil humeri, and 203 fossil femora were drawn from 215 bags and retained for analysis (Table 3.6).

3.2 Data Acquisition

In this section the types of data extracted from both the modern and fossil rodent samples are detailed.

3.2.1 Modern Owl Pellets

Once the major skeletal elements were separated out for each pellet the skeletal part proportions were calculated with the individual pellet as the unit of analysis. For each pellet the Minimum Number of Elements (MNE) and the Minimum Number of Individuals (MNI) were estimated for the following elements: maxillae, mandibles, humeri, femora, radii, ulnae, and tibiofibulae. In one sense the MNE can be interpreted as a maximum estimate of the number of individuals needed to generate the skeletal sample. Thus, if one were to recover nine right and one left humeri the resulting MNE estimate would be 10.

Table 3.6. Number of specimens by element by Swartkrans SKX Member, and number of bags by member from which specimens were drawn.

SKX Member	Element	# of Bags	# of Specimens
1		145	
	Femora		125
	Humeri		72
2		17	
	Femora		37
	Humeri		22
3		53	
	Femora		41
	Humeri		32
Totals		**215**	**329**

Alternately, the MNI represents a minimum estimate, however, this can be calculated in a variety of ways. One of the most basic MNI calculations involves counting the total number of a specific skeletal element found in a sample and then dividing that value by the number of times that element appears in the skeleton (Binford 1978). Thus, for humeri one would first add up the total number recovered and divide by two. As one can imagine, this method can be problematic in samples where an element from one side predominates. Using the same example as above, in a sample with nine right and one left humeri the resulting MNI would be estimated as five, though this is clearly not possible in a bilaterally symmetrical organism. An alternate approach, developed by Theodore E. White (1953), involves first siding each element and then retaining the greater number counted as the per element estimate. In this case our hypothetical sample would yield an MNI of 9 as the singular left humerus would be considered as a member of a pair with one of the right humeri. Calculations of MNI can be further refined by the addition of more variables, such

as size, sex, and taxonomic affiliation, though the amount of effort needed increases with each new addition (e.g. see cMNI in de Ruiter 2004 and de Ruiter et al. 2008). As such, the method employed here largely follows White (1953) whereby elements were divided by side, although broken elements that could be demonstrably associated (i.e. refits) were also combined and counted as a single specimen.

MNI values were first calculated for each element on a per pellet basis, with the largest value retained per skeletal region. Skeletal regions are defined as either cranial (mandibles and maxillae) or postcranial (humeri, femora, radii, ulnae, and tibiofibulae) and the MNI per pellet per region taken as the highest value obtained for an element in that region. For example, if in a pellet three right and left mandibles, three right maxilla, and four left maxilla were recovered, the resulting MNI for the cranial region of that pellet would be four. The same procedure was then conducted for the postcranial elements and the total MNIs per skeletal region, per pellet were them summed across the entire sample (N=279).

3.2.2 Modern and Fossil African Rodents

Data collection for both the modern and fossil samples consisted of linear caliper measurements and two dimensional geometric morphometric (GM) outlines collected from digital photographs. Linear caliper measures were used to generate ecological functional ratios representing overall limb proportions and mechanical advantages of the primary muscles of locomotion, and are commonly used in rodent functional morphology studies (e.g. Dunn and Rasmussen 2007; Elissamburu and Vizcaino 2004; Lessa and Stein

1992; Rose and Chinnery 2004). Additionally, as linear measurements taken on rodent skulls are commonly used to separate taxa (e.g. Crawford-Cabral 1988; Crawford-Cabral and Pacheco 1991; Granjon 2005; Taylor et al. 2009) these data were also used in a traditional morphometrics (TM) analysis to test for taxonomic differences in the postcrania. Two-dimensional GM outlines were also used to generate shape variables and test for taxonomic differences in femora and humeri. An outline-based analysis was selected in order to capture the variation not accounted for using linear measurements, and have been used in studies of rodent cranio-dental shape variation (Gomez Cano et al. 2013; Cardini and Slice 2004; Hautier et al. 2008; Michaux et al. 2007). Additionally, this method was selected over landmark based GM methods as the latter can be sensitive to the uncertainty of placement of type 2 landmarks (Hautier et al. 2008), or areas of maximum curvature (Bookstein 1991).

Linear measurements drawn from the literature were taken using Paleo-Tech Inc. high-precision dental calipers to the nearest 0.01 mm on one long bone element per specimen (Candela and Picasso 2008; Dunn and Rasmussen 2007; Elissamburu and Vizcaino 2004; Hildebrand 1985; Lessa and Stein 1992; Samuels and Van Valkenburgh 2008). Visual depictions of the measurements are provided in Figures 3.2 and 3.3 and descriptions are detailed in Table 3.7. Right side elements were preferentially selected for modern specimens so as to mitigate any potential influences of bilateral asymmetry, however, contralateral elements were used when right side elements were not available.

Linear measurements were first used to calculate functional indices that represent overall limb proportions and muscular mechanical advantages (Table 3.8). For one murine

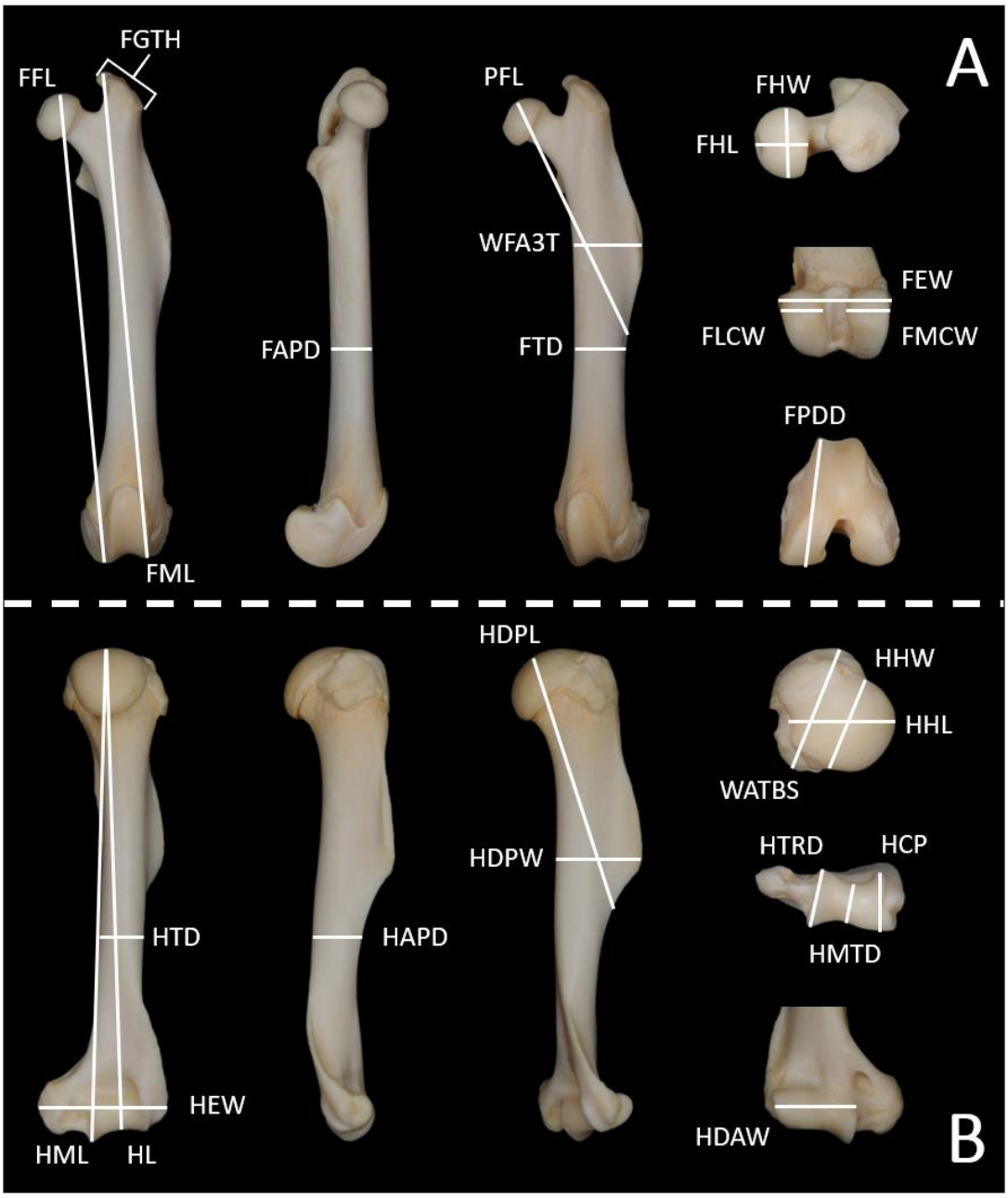


Figure 3.2. Measurements on rodent proximal appendicular long bones. Abbreviations follow Table 3.7. Skeletal elements from *Cricetomys* sp. not used in analysis. Images not to scale. Descriptions begin at the left. Panel A: Extensor surface of left femur, medial view, oblique view with third trochanter leveled, superior view of proximal end, posterior view of the distal end, inferior view of the distal end. Panel B: Extensor surface of right humerus, lateral view, oblique view with deltopectoral crest leveled, superior view of proximal end, inferior view of distal end, anterior view of distal end.

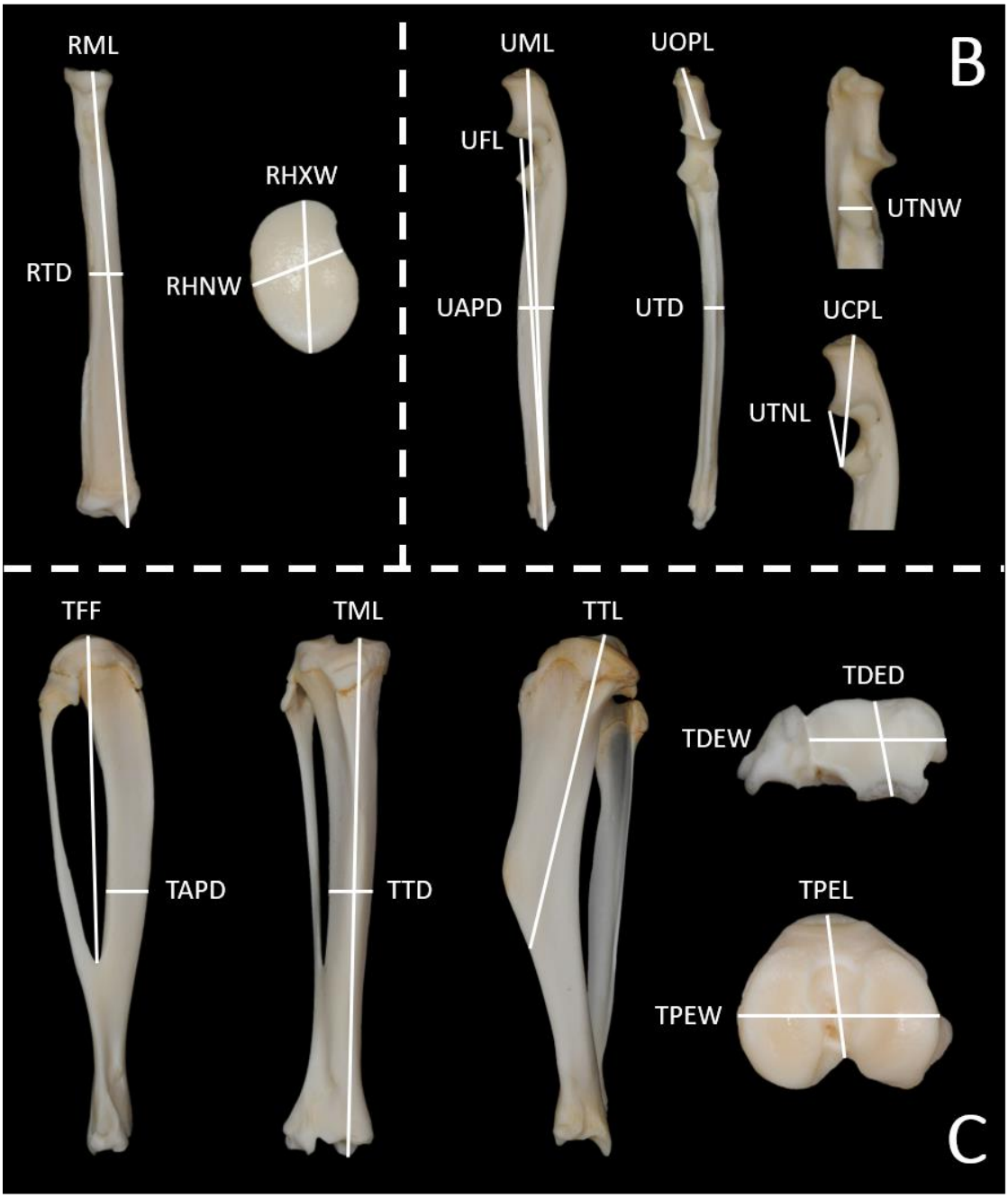


Figure 3.3. Measurements on rodent distal appendicular long bones. Abbreviations follow Table 3.7. Skeletal elements from *Cricetomys* sp. except for third tibiofibula which is from *Thryonomys* sp. Images not to scale and not used in any analyses. Descriptions begin at the left. Panel A: Flexor surface of left radius, superior view of proximal end. Panel B: Lateral view of left ulna, anterior view, oblique view of proximal end, lateral view of proximal end. Panel C: Lateral view of right tibiofibula, extensor surface, medial view, inferior view of distal end, superior view of proximal end.

Table 3.7. Descriptions of osteological measurements taken on each skeletal element.

Measurement	Description
Humerus	
Maximum length (HML)	Proximal part of humeral head to distal medial tip of the trochlea
Humerus Length (HL)	Proximal part of humeral head to distal mid-point of trochlea
Deltopectoral crest length (HDPL)	Proximal point of articular head to distal end of deltopectoral crest
Deltopectoral crest width (HDPW)	Widest width across humerus at deltopectoral crest
Transverse diameter (HTD)	Medial to the lateral edge distal to deltopectoral crest and proximal to supinator crest
Anteroposterior diameter (HAPD)	Anterior to the posterior edge at ~ level of HTD
Epicondylar width (HEW)	Distance from medial to lateral epicondyle
Head length (HHL)	Distance from "lateral" margin of humeral head between the tubercles to the medial margin
Head width (HHW)	Distance from "anterior" to "posterior" margin of humeral head where it meets the tubercles
Width across Tubercles (WATBS)	Max width across tuberosities form a superior view
Distal articular width (HDAW)	Medial edge of the trochlea to the lateral edge of the capitulum
Trochlea depth (HTRD)	Anteroposterior edge of the medial trochlear ridge
Capitulum depth (HCP)	Anteroposterior edge of the articular surface at the capitulum
Medial trochlear depth (HMTD)	Anteroposterior edge of trochlea in midline
Ulna	
Maximum length (UML)	Proximal edge of the olecranon process to the distal edge of the styloid process
Functional length (UFL)	Proximal edge of the trochlear notch to the distal end of styloid process
Transverse diameter (UTD)	Transverse width of the ulna at the diaphyseal mid-point
Anteroposterior diameter (UAPD)	Anterior edge of the shaft to the posterior edge at midshaft
Olecranon process length (UOPL)	Proximal edge of the olecranon process to the proximal edge of the trochlea notch
Trochlea notch length (UTNL)	Proximal edge of the trochlea notch to the coronoid process
Trochlear notch width (UTNW)	Medial to the lateral edge of the trochlear notch taken in the more distal end
Coronoid process length (UCPL)	Tip of the olecranon process to the coronoid process
Radius	

Table 3.7. Continued.

Measurement	Description
Maximum length (RML)	Proximal edge of the radial head to the distal edge of the styloid process
Transverse diameter (RTD)	Transverse width of the radius at the diaphyseal mid-point
Head maximum width (RHXW)	Measured at widest point
Head minimum width (RHNW)	Measured at narrowest point
Femur	
Maximum length (FML)	Proximal edge of the greater trochanter to the distal edge of the lateral condyle
Functional length (FFL)	Proximal femoral head to the distal end of the medial condyle
Greater trochanter height (FGTH)	Proximal end of the greater trochanter to the distal end on the lateral side
Proximal femoral length (PFL)	Distance from the distal end of the third trochanter to the proximal point of the femoral head. For taxa lacking a third trochanter measurement is taken lateral to the femoral head.
Width across 3rd trochanter (WFA3T)	Width of femur across third trochanter to medial edge of diaphysis. For taxa lacking a third trochanter measurement is essentially the width just below the femoral neck.
Transverse diameter (FTD)	Medial to the lateral edge below third trochanter
Anteroposterior diameter (FAPD)	Anterior to the posterior edge at ~ level of FTD
Head length (FHL)	"Medial" edge of the femoral head to the "lateral edge closest to the greater trochanter
Head width (FHW)	"Anterior" edge of the femoral head to the "medial" edge and ~ right angle to FHL
Epicondylar width (FEW)	Medial edge of the medial epicondyle to the lateral edge of the lateral epicondyle
Patellar distal depth (FPDD)	Anterior point of the patellar ridge to the more posterior edge of the medial condyle from a distal view
Medial condyle width (FMCW)	Medial edge to the lateral edge
Lateral condyle width (FLCW)	Medial edge to the lateral edge
Tibia	
Maximum length (TML)	Proximal end to the distal edge of the posterior process
Tuberosity length (TTL)	Proximal articular surface to the distal end of the tibial crest
Tibiofibular fusion (TFF)	Proximal end of tibia to point of tibiofibular fusion
Transverse diameter (TTD)	Medial edge of the mid-shaft to the lateral edge

Table 3.7. Continued.

Measurement	Description
Anteroposterior diameter (TAPD)	Anterior to the posterior edge at the midshaft level
Proximal end width (TPEW)	Medial edge of the medial condyle to the lateral edge of the lateral condyle
Proximal end length (TPEL)	Anterior edge of the tibial tuberosity to the most posterior edge from a superior view
Distal end width (TDEW)	Medial edge of the medial malleolus to the lateral edge of the distal fibular facet
Distal end depth (TDED)	Anterior to posterior of the distal tibial on the midline from a inferior view

Table 3.8. Morphological indices, references points from which they were derived, their calculations, and inferred functional descriptions. Measurement abbreviations used follow Table 3.6. References are as follows: [1]Dunn & Rasmussen 2007; [2]Elissamburu & Vizcaino 2004; [3]Samuels & Van Valkenburgh 2008.

Index	Description
Shoulder Moment Index[2,3] **(SMI)**	HDPL / HML. Indicates the mechanical advantage of the deltoid and major pectoral muscles acting across the shoulder joint.
Humerus Robustness Index[2,3] **(HRI)**	HTD / HML. Indicates the robustness of the humerus and its ability to resist bending and shearing stresses.
Humeral Epicondyle Index[1-3] **(HEI)**	HEW / HML. Indicates the relative area available for the origins of the flexor, pronator and supinator muscles of the forearm. Considered a good indicator of fossoriality.
Radial Head Index[1] **(RHI)**	RHXW / RHNW. Indicates the relative ability to pronate and supinate the forearm. Arboreal rodents generally have rounder radial heads.
Radial Robustness Index[2] **(RRI)**	RTD / RML. Indicates the robustness of the radius and its ability to resist bending and shearing stresses.
Olecranon Process Index[1-3] **(OPI)**	UOPL / UFL. Indicates relative mechanical advantage of the triceps brachii and dorsoepitrochlearis muscles used in elbow extension. Considered a good indicator of fossoriality.
Ulna Robustness Index[2,3] **(URI)**	UTD / UFL. Indicates the robustness of the ulna and its ability to resist bending and shearing stresses, and relative area available for the origin and insertion of forearm and manus flexors, pronators, and supinators.
Gluteal Index[2,3] **(GI)**	FGTH / FFL. Indicates a measure of the mechanical advantage of the gluteus muscles and the velocity of femur extension.
Femur Robustness Index[2,3] **(FRI)**	FTD / FFL. Indicates the robustness of the femora and its ability to resist bending and shearing stresses.

Table 3.8. Continued.

Index	Description
Femoral Epicondylar Index[3] **(FEI)**	FEW / FFL. Indicates relative area available for the origins of the gastrocnemius and soleus muscles used in extension of the knee and plantar-flexion of the pes.
Tibial Spine Index[2,3] **(TSI)**	TTL / TML. Indicates the mechanical advantage of the hamstrings, biceps femoris, and gracilis muscles acting across the knee and hip joints. Important in flexion of the leg with a more proximal insertion related to greater speed during initial movement.
Tibial Robustness Index[2,3] **(TRI)**	TTD / TML. Indicates the robustness of the tibia, its ability to resist bending and shearing stresses, and the relative width available for the origins of the muscles acting across the ankle.
Intermembral Index[1,3] **(IMI)**	HML + RML / FML + TML. Indicates the length of the forelimb relative to the hind limb. Indicative of ricochetal locomotion in some taxa (e.g. *Pedetes*).
Brachial Index[1,3] **(BI)**	RML / HML. Indicates relative proportions of proximal and distal elements of the forelimb.
Crural Index[1,3] **(CI)**	TML / FML. Indicates relative proportions of proximal and distal elements of the hind limb.

specimen (*Lemniscomys rosalia* – TM 45967) the FML measure was found to be in error (0.84 mm) and was replaced by the average of other specimens in the species. Additionally, one hystricinae (*Hystrix africaeaustralis* – USNM 197190) had a broken third trochanter thus the value was replaced by the average of other specimens in the species. Individual genera were then classified into one of seven locomotor groups based on autecological descriptions of species level habitat use in order to assure genus level locomotor homogeneity in the functional groupings (De Graaff 1981; Happold 2013, Kingdon 1974; Nowak 1991; Roberts 1951; Skinner and Chimimba 2005; Smithers 1971). Following Samuels and Van Valkenburgh (2008) these categorical groups include: terrestrial, semiaquatic, arboreal, semifossorial, fossorial, ricochetal, and gliding categories. Descriptions of each of these categories are found in Table 3.9 and genus level

Table 3.9. Locomotor categories used in this analysis and their definitions after Samuels & Van Valkenburgh 2008.

Locomotor Category	Definition
Terrestrial	Rarely swims or climbs, may dig to make a burrow (but not extensively), may show saltatory behavior (quadrupedal only), never glides (e.g., rats and mice).
Semi-aquatic	Regularly swims for dispersal, escape, or foraging (e.g., beavers and muskrats).
Arboreal	Capable of and regularly seen climbing for escape, shelter, or foraging (includes scansorial species; e.g., tree squirrels and erethizontid porcupines).
Semi-fossorial	Regularly digs to build burrows for shelter, but does not forage underground (e.g., ground squirrels).
Fossorial	Regularly digs to build extensive burrows as shelter or for foraging underground (e.g., gophers and mole rats). Display a predominantly subterranean existence.
Ricochetal	Capable of jumping behavior characterized by simultaneous use of the hind limbs, commonly bipedal (e.g., kangaroo rats and *Pedetes*).
Gliding	Capable of gliding through the use of a patagium, commonly forage in and rarely leave trees (e.g., flying squirrels).

locomotor classifications in Table 3.10. Following this, in order to evaluate the morphological diversity among taxa utilizing TM, linear distances were first log(x+1) transformed for normality and the geometric mean (GMM) calculated as the average of log variables and used as a proxy for size (Jungers et al. 1995). Shape data (as scaled proportions), were created by dividing log(x+1) distances by the size measure.

For the GM based outline analyses, scaled digital photographs of rodent postcrania were taken using a Nikon D300s camera with a 60mm macro lens mounted on a tripod at a right angle to the plane of each specimen. Placement and orientation of each skeletal element was standardized so that images represent the same anatomical two-dimensional area, such as the anterior surface of the femur or extensor surface of the humerus. Once

Table 3.10. Locomotor classifications by genus. Values in bold represent locomotor category totals.

Locomotion Category	Genus	Number
Arboreal	**46**	
	Dendromus spp.	9
	Grammomys spp.	10
	Graphiurus sp.	10
	Paraxerus sp.	10
	Thallomys spp.	7
Fossorial	**25**	
	Bathyergus spp.	3
	Cryptomys spp.	15
	Georychus sp.	2
	Heliophobius sp.	5
Ricochetal	**7**	
	Pedetes sp.	7
Semi-aquatic	**14**	
	Dasymys sp.	5
	Thryonomys sp.	9
Semi-fossorial	**45**	
	Desmodillus sp.	6
	Gerbilliscus spp.	16
	Gerbillurus spp.	10
	Hystrix sp.	4
	Xerus sp.	9
Terrestrial	**126**	
	Acomys spp.	10
	Aethomys spp.	15
	Cricetomys sp.	5
	Lemniscomys sp.	10
	Mastomys spp.	12
	Micaelamys sp.	10
	Mus spp.	9
	Myotomys sp.	3
	Mystromys sp.	2
	Otomys spp.	10
	Pelomys sp.	2
	Petromus sp.	2

Table 3.10. Continued.

Locomotion Category	Genus	Number
	Petromyscus sp.	4
	Rhabdomys sp.	10
	Saccostomus sp.	9
	Steatomys spp.	10
	Zelotomys sp.	3

the images were acquired they were first processed using Adobe Photoshop in order to facilitate further outline thresholding. During this process some degree of interpretation was required to estimate the actual outline of the skeletal element as some of the modern specimens still retained minor pieces of soft tissue, and some of the fossil specimens had chips or imperfections which would have been included when using an automatic outline feature. As such, these problematic areas were either digitally removed, or were filled in where needed (Figure 3.4). In instances where the actual outline of the specimen could not be confidently estimated, the specimen was not used in further analysis. Once all images had been processed outlines were generated as two-dimensional digitized coordinate data using the outline function in tpsDig v. 2.31 (Rohlf 2017). Subsequently, the resulting TPS file was recoded to convert outlines to curves and each specimen curve was resampled to 2000 points. Specimen curves were then subjected to elliptic Fourier analysis (EFA) using EFAWin (Isaev, Denisova 1995). Elliptic Fourier analysis is a generalized procedure designed to fit a closed curve composed of an ordered data points in two-dimensional space with any desired degree of accuracy (Ferson, Rohlf and Koehn 1985; Rolf and Ferson 1992). In doing so, EFA uses an orthogonal decomposition of a curve to produce

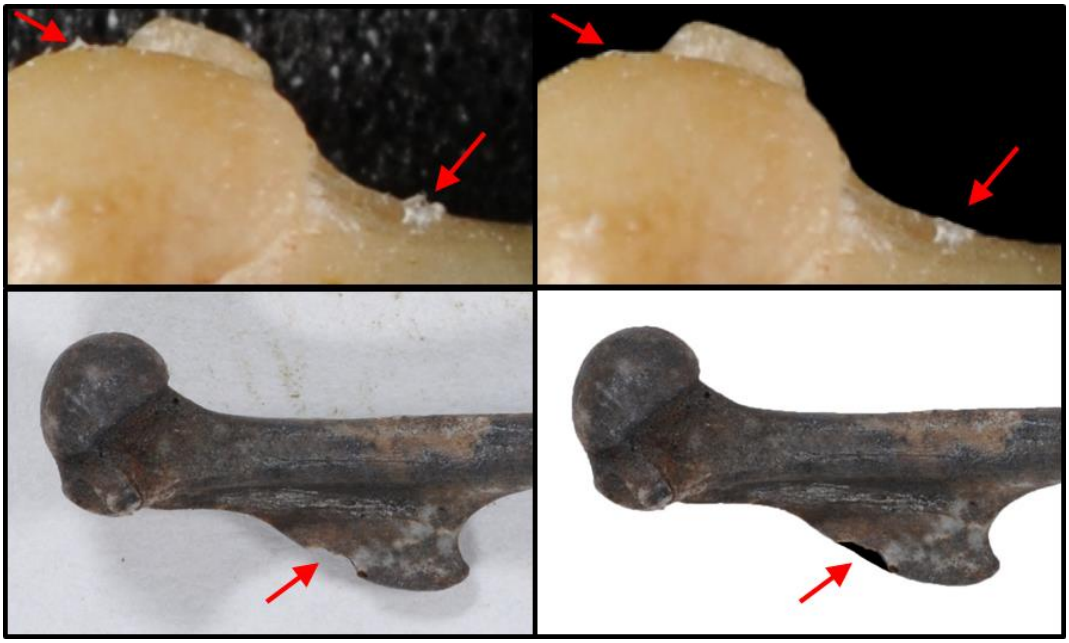


Figure 3.4. Examples of specimens pre (left) and post (right) image processing. Top row demonstrates the digital removal of minor soft tissue while the bottom row shows the filling in of minor chips and breaks.

a series of harmonically related ellipses that define the desired shape. The resulting output consists of a series of four coefficients per harmonic that can be normalized to eliminate certain aspects of the outlines that are not biologically relevant (e.g. location, orientation, outline starting position). Moreover, this method also produces a general estimate of specimen size calculated as the area of the ellipse defined by the first harmonic coefficient, and allows for size standardization by dividing all the resulting harmonic coefficients by the square root of the area estimate. For this study, individual harmonics were sequentially added by eye until outlines generated were judged to fully represent each actual specimen outline (e.g. Ginter et al. 2012). In total, 30 harmonic coefficients resulting in 120 harmonic coefficients (dependent data) were calculated to represent shape information invariant to size, location, rotation, and outline origin.

3.3 Statistical Analyses

Statistical analyses were performed using a combination of SPSS v. 25, PAST v. 3.01, and JMP v. 14 software packages due to differences in features available across platforms. For example, JMP easily allows for unknown specimens to be projected into PC space without influencing the resulting rotation derived from known specimens, and provides the resulting scores. Alternately, SPSS provides both the posterior and typicality probabilities for linear discriminant function analysis (LDFA). Finally, PAST allows for figures to be generated in a user friendly manner, and allows one to easily toggle between the classifications made using a standard LDFA with equal proportions and those made using cross-validation.

3.3.1 Modern Owl Pellets

Differences between MNIs calculated using cranial versus postcranial elements were tested using a chi-square goodness of fit testing the extrinsic hypothesis of equal proportions (Sokal and Rohlf 1995). As the number of elements available to calculate the MNI differ by region (four-cranial, ten-postcranial), a total of three tests were run. The first test included all postcranial long bone elements to estimate MNIs while in the second and third tests postcranial MNIs were calculated utilizing just proximal appendicular elements (femora and humeri), and distal elements (radii, ulnae, and tibiofibulae) respectively.

3.3.2 Modern and Fossil African Rodents: Functional Indices

In order to test for the association between limb morphology and locomotor pattern a multivariate analysis of variance (MANOVA) was first run on the 15 functional indices calculated using the raw linear measurements of all complete modern specimens. Following this, univariate analysis of variance (ANOVA) tests were run on each index to test if individual indices varied between locomotor groups, and Tukey's pairwise post-hoc tests were used to assess differences between categories. For these latter tests a 0.001 alpha value was used as the level of significance to control for the family-wise error rate. Subsequently, a LDFA was used to assess standard, and cross-validated classification rates of posterior probabilities. As the fossil specimens consist of singular femoral and humeral elements the analysis was subsequently rerun on each individual element. Results from these analyses were used as training data and fossil specimens were then classified from the resulting discriminant functions. Following Brophy et al. (2014) correct classification of ≥85% of the training data (with cross-validation) was used for justification of applying the discriminant functions to fossil specimens. When applied to fossil specimens both the classification made, and the typicality probability associated with the classification were examined to identify how specimens classified, and if this classification is potentially accurate. Typicality probabilities represent the probability that a classified individual belongs to each group based on the Mahalanobis distance to each group, and are similar to *p* values returned in many statistical hypothesis tests (Ousley and Jantz 2012). For example, if a fossil classifies as group A with typicality probability of 0.40 this would indicate that 40% of the total sample for that group would be expected to be as far or

farther away from that group's centroid based on the parameters generated from the training dataset. For this study a typicality threshold of ≥ 0.1 was used when deciding if a fossil specimen should be considered correctly classified and represents a compromise between the conservative ≥ 0.15 used by Brophy et al. (2014) to classify unknown bovid teeth using similar methods of data collection, and the ≥ 0.05 cutoff typically employed by forensic anthropologists (Ousley and Jantz 2012).

3.3.3 Modern and Fossil African Rodents: TM Taxonomic Signal

In order to test for a taxonomic signal using TMs, tests of both shape and form (shape + size) were conducted using all elements. Analyses of shape involved using the shape variables created by dividing log distances by the size measure, while the form analyses included the GMM as a dependent variable. For both types of analyses, principal component analyses (PCA) were first run for initial data visualization and distillation to reduce dimensionality (Zelditch et al. 2004). Principal component analyses are rigid data rotations which take a series of potentially correlated original variables and transforms them into new linear combinations, or principal components (PC), as a series of orthogonal axes, each of which explain a proportion of the total variance in decreasing order. As such, these new linear combinations of the original variables not only capture a greater amount of the original variance in reduced dimensions, but the resulting PC scores for each orthogonal axis are also statistically independent. Specimen PC scores for which the axes collectively accounted for greater than 95% of the total variance were retained for most further analyses (see below). Following this step, statistical analyses largely followed the

procedures outlined above for individual elements. First, MANOVAs were run using retained PC scores for the model Family(Subfamily(Genus)) to test for taxonomic signals at different hierarchical levels. Next, LDFAs were then used to assess standard, and cross-validated classification rates of posterior probabilities. Again, as the fossil specimens consist of singular elements, the analyses were subsequently rerun on each individual element. Results from these analyses where correct classification of ≥85% on the training data with cross-validation was used for justification of applying the discriminant functions to fossil specimens, and fossil specimens were considered correctly classified if their typicality probability was ≥0.1.

3.3.4 Modern and Fossil African Rodents: GM Taxonomic Signal

Tests for taxonomic signal using GM based approach follow those using TM, however, the proxy for size in this instance is taken as the square root of the area of the first ellipse, or the area output from EFAWin. Additionally, the PCA for the form analyses were run on the correlation matrix in order to give equal weight to all variables and avoid the size measure from dominating the first PC axis. Following this the procedural steps taken are the same as those using TM.

3.3.5 Reduced Sample TM and GM Shape Analyses

It is the recommendation of some authors that the number of dependent variables (i.e. measurements) not exceed the sample size of the smallest group, and often that the sample size of the smallest group be at least three times greater than minimum sample size

of all groups (e.g. Ousley and Jantz 2012; Tabachnick and Fidell 1996). As such, a reduced sample shape analysis was also performed on both the TM and GM data. In these analyses rodent families with species average masses greater than 1 kg were removed (i.e. Pedetidae, Hystricidae, Thryonomyidae) as these taxa are outside the size prey range of most owls (Andrews 1990). Additionally, the petromurines were also excluded due to small sample size (N=2). Finally, sciurids and glirids (squirrels and dormice) were collapsed into their suborder Sciuromorpha due to sample size (Table 2.1). With the resulting elevated sample sizes (N=241) PC scores were retained that explained 98% (for GM) and 99% (for TM) of the total variance.

4. RESULTS

4.1 Modern Owl Pellets

Postcranial elements were the most commonly recovered parts of the skeleton at four of the seven owl roosts examined (Table 4.1). At two of these sites MNE counts were highest for tibiofibulae, at one femora and tibiofibulae were recovered in equal numbers, and at the fourth site ulnae were the most common element recovered. Alternately, mandibles were more common at two sites, and maxillae at one site. When summed across sites, mandibles were the most common element overall followed by tibiofibulae.

Estimates of the MNIs using rodent cranial versus postcranial remains show that higher values are obtained with postcrania regardless of the method used for calculation (Table 4.2). When all appendicular long bones are used the MNI calculated is significantly greater than when using cranial remains, indicating that postcrania better reflect the number of prey taken on a per pellet basis. However, when only proximal or distal appendicular elements were used no significant difference was found.

4.2 Modern and Fossil African Rodents: Functional Indices

A significant difference between locomotor groups was found using all functional indices on complete modern specimens ($\Lambda < 0.003$; $P < 0.001$). Additionally, all univariate tests of individual indices across locomotor groups were significant, and post hoc tests showed differences in indices between groups at the 0.001 alpha level (Table 4.3).

Table 4.1. Minimum number of elements (MNE) by element across modern owl roosts. Minimum number of individuals (MNI) calculated as the highest estimate obtained across elements, within each pellet, summed across all pellets per site. Site abbreviations are as follows: BFBC – Bolt's Farm Bridge Cave, SK – Swartkrans, MCOR - Mirabib Crack Owl Roost, MSS – Mirabib Shelter Site, MNS – Mirabib Nest site, KHLC – Koanaka Hills Leopard Cave, KHBC – Koanaka Hills Bone Cave. Numbers in bold indicate the most abundant element by site.

Element	Sites							
	BFBC	SK	MCOR	MSS	MNS	KHLC	KHBC	Totals
Maxillae	**117**	153	106	80	132	228	91	907
Mandibles	111	**173**	112	84	**138**	242	118	978
Humeri	106	116	97	51	119	230	108	827
Radii	102	82	106	50	118	218	94	770
Ulnae	108	95	**113**	55	117	219	107	814
Femora	95	143	91	**86**	130	225	113	883
Tibiofibulae	101	149	94	**86**	136	**267**	**120**	953
MNE	740	911	719	492	890	1629	751	6132
MNI	73	118	76	71	94	160	63	655

Table 4.2. Calculations of MNI from cranial (mandibles and maxillae) and postcranial (humeri, femora, radii, ulnae, and tibiofibulae) elements, and results from chi-square test of goodness of fit utilizing 3 methods for postcranial MNI calculation.

Region	MNI Calculations		
	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Cranial	540	540	540
Postcranial	630	576	597
Totals	1170	1116	1137
X^2	6.92	1.16	2.86
P	< 0.01	0.28	0.09

Fossorial taxa differed the most from other locomotor groups across indices, while few differences were recovered between terrestrial and semifossorial taxa. Linear discriminant function analysis of modern specimens resulted in 90.6% of the samples being correctly classified, and an 86.3% correct classification using cross-validation. Alternately, while

Table 4.3. ANOVAs and and Tukey's pairwise post-hoc tests for functional indices across locomotor groups. Functional indices definitions follow Table 3.8. Significate differences between functional groups indicated by initials as follows: A – Arboreal, F – Fossorial, R – Ricochetal, SA – Semiaquatic, SF – Semifossorial, T – Terrestrial.

Index	Arboreal n = 46	Fossorial n = 25	Ricochetal n = 7	Semiaquatic n = 10	Semifossorial n = 44	Terrestrial n = 123
SMI	F, R	A, R, SA, SF, T	A, F, SF	F	F, R	F
HRI	F	A, R, SA, SF, T	F, T	F	F	F, R
HEI	F, R	A, SA, SF, T	A, SA, T	F, R, SF	F, SA	F, R
RHI	R, SA, T	R	A, F, SA, SF, T	A, R	R	A, R
RRI	F, R, SA	A, SF, T	A, SF, T	A, SF, T	F, R, SA	F, R, SA
OPI	F, SA	A, R, SF, T	F, SA	A, R, SF, T	F, SA	F, SA
URI	F, R, SA	A, SF, T	A, SF, T	A, SF, T	F, R, SA	F, R, SA
GI	F, R, SF	A, T	A, SA, T	R	A	F, R
FRI	F, SA	A, R, SF, T	F, SA	A, R, SF	F, SA	F
FEI	F, SA	A, R, SA, SF, T	F	A, F	F	F
TSI	F, R, SA	A, SA, SF, T	A, SA, SF, T	A, F, R, SF, T	F, R, SA, T	F, R, SA, SF
TRI	F, R, SA	A, SF, T	A, SA	A, R, SF, T	F, SA	F, SA
IMI	F, R	A, R, SA, SF, T	A, F, SA, SF, T	F, R	F, R	F, R
BI	F, SA	A, SF, T	SF	A, SF, T	F, R, SA	F, SA
CI	F, SA	A, R, SA, SF	F, SA, T	A, F, R, SF, T	F, SA	R, SA

independent analyses of functional indices for individual elements showed significant differences for both humeri ($n = 3$, $\Lambda = 0.208$, $P < 0.001$) and femora ($n = 3$, $\Lambda = 0.267$, $P < 0.001$), classification rates of known specimens were less than 60% for both elements. As such the resulting discriminant functions were not applied to the fossil sample.

4.3 Modern and Fossil African Rodents: TM Taxonomic Signal

Results of tests for a taxonomic signal in rodent postcrania using TM are presented as follows. First, results using all elements are given, followed by those using just humeri, and femora. In all cases shape analyses preceded form analyses. Abbreviations of measurements follow Table 3.7.

4.3.1. All Elements TM

Principal component analysis of shape utilizing TM and all elements yielded 10 axes that accounted for greater than 95% of the total variance (Figure 4.1). Measurements primarily dealing with element length had high negative loadings on PC1 while most other measures had positive loadings. Negative loadings on PC2 were primarily driven by measurements taken on anterior appendicular elements while those with positive loadings were from posterior elements, particularly the tibiofibula. Significant differences in shape were found for all levels of the model (Table 4.4). Classification rates for all LDFAs run were above 85% with the exception of the Subfamily level with cross-validation (Table 4.5). Misclassifications in LDFAs primarily occurred between the families Muridae and Nesomyidae, or between members within those families at lower taxonomic levels.

Principal component analysis of form utilizing all elements yielded eight axes that accounted for greater than 95% of the total variance (Figure 4.2). Measurements primarily dealing with element length had high negative loadings on PC1 while the GMM had a high positive loading with most other measurements also contributing marginally. Negative loadings on PC2 are primarily driven by measurements taken on anterior

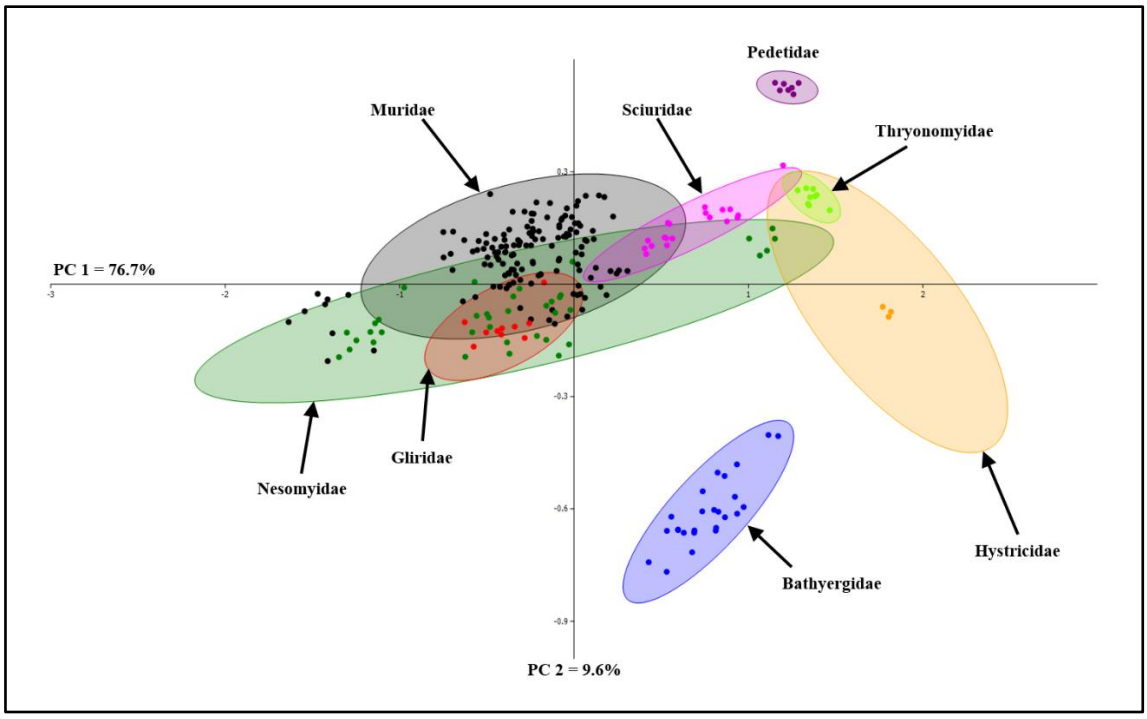


Figure 4.1. First two PCs with 95% confidence ellipses for families from TM analysis of shape using all skeletal elements. Axes not scaled by variance explained. Note the high degree of overlap between the families Muridae and Nesomyidae.

appendicular elements, with those involving the olecranon process of the ulna featuring prominently. Positive loadings on PC2 included the GMM and most of the measurements taken on posterior elements, particularly the tibiofibula. Significant differences in form were found for all levels of the model (Table 4.4). Classification rates for both the Family and Genus level analyses exceeded 85% while those at the Subfamily level were below this threshold (Table 4.5). Again, misclassifications in LDFAs primarily occurred between the Muridae and Nesomyidae, with most occurring between the murines and the petromyscines + mystromyines at the subfamily level.

Table 4.4. MANOVA results for all analyses using TM.

Elements	Analysis	Model	Λ	Approximate F	P
All	Shape	Whole	1.46E-08	37.2	< 0.001
		Family	1.15E-05	107.1	< 0.001
		Family(Subfamily)	7.95E-03	28.2	< 0.001
		Family(Subfamily(Genus))	7.14E-04	13.4	< 0.001
	Form	Whole	3.89E-08	54.2	< 0.001
		Family	5.77E-06	173.6	< 0.001
		Family(Subfamily)	1.30E-02	31.3	< 0.001
		Family(Subfamily(Genus))	8.32E-04	17.9	< 0.001
Humeri	Shape	Whole	1.97E-04	31.2	< 0.001
		Family	2.80E-03	70.1	< 0.001
		Family(Subfamily)	4.83E-02	34.1	< 0.001
		Family(Subfamily(Genus))	2.27E-02	13.6	< 0.001
	Form	Whole	1.62E-03	164.5	< 0.001
		Family	6.26E-03	331.7	< 0.001
		Family(Subfamily)	5.52E-02	123.8	< 0.001
		Family(Subfamily(Genus))	3.42E-02	52.9	< 0.001
Femora	Shape	Whole	1.86E-04	31.6	< 0.001
		Family	2.30E-03	74.5	< 0.001
		Family(Subfamily)	6.04E-02	30.6	< 0.001
		Family(Subfamily(Genus))	2.32E-02	13.5	< 0.001
	Form	Whole	4.84E-04	81.1	< 0.001
		Family	2.71E-03	183.3	< 0.001
		Family(Subfamily)	7.86E-02	52.0	< 0.001
		Family(Subfamily(Genus))	2.08E-02	31.7	< 0.001

Table 4.5. Classification from LDFAs for all analyses using TM. Values in bold exceed 85% threshold.

Elements	Analysis	Grouping	Regular %	Cross-Validation %
All	Shape	Family	**89.7%**	**88.5%**
		Subfamily	**88.5%**	83.8%
		Genus	**94.5%**	**87.8%**
	Form	Family	**87.0%**	**86.2%**
		Subfamily	83.4%	77.1%
		Genus	**94.9%**	**89.3%**
Humeri	Shape	Family	77.9%	75.7%
		Subfamily	71.1%	66.9%
		Genus	74.9%	63.5%
	Form	Family	54.4%	51.7%
		Subfamily	52.5%	51.0%
		Genus	58.2%	48.3%
Femur	Shape	Family	77.2%	74.1%
		Subfamily	64.3%	61.2%
		Genus	76.0%	65.8%
	Form	Family	60.5%	58.6%
		Subfamily	52.5%	50.2%
		Genus	62.0%	56.3%

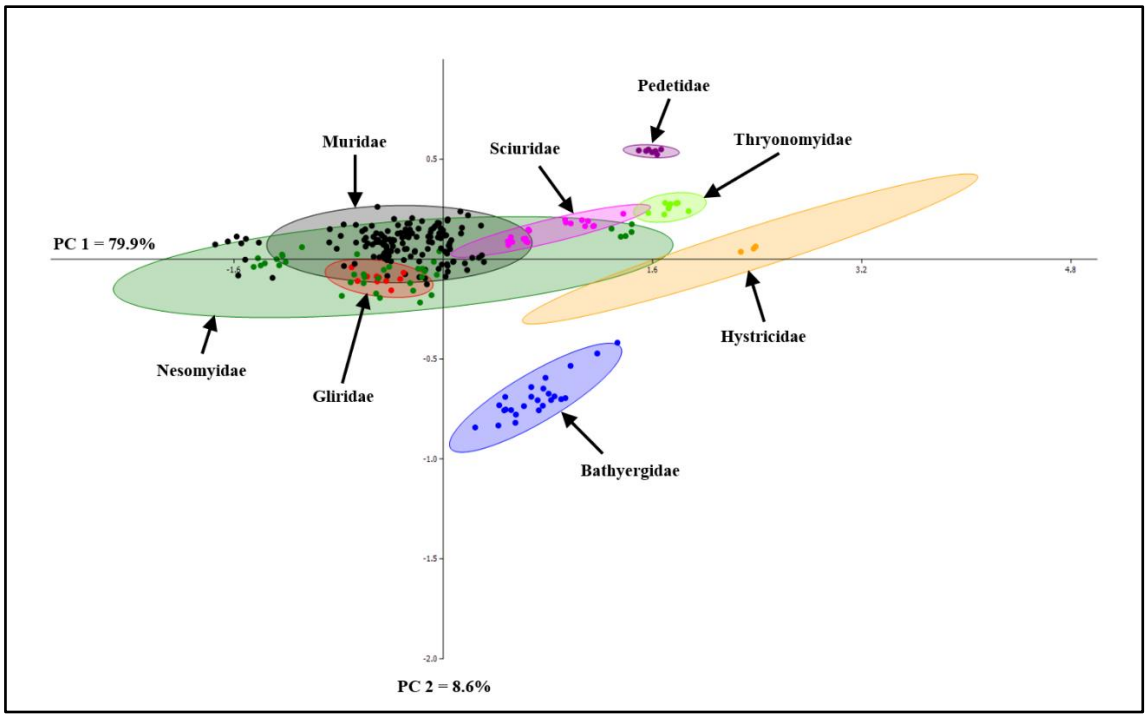


Figure 4.2. First two PCs with 95% confidence ellipses for families from TM analysis of form using all skeletal elements. Axes not scaled by variance explained. Note the high degree of overlap between the families Muridae and Nesomyidae.

4.3.2. Humeri

Principal component analysis of humeri shape utilizing TM yielded five axes that accounted for > 95% of the total variance (Figure 4.3). Measurements primarily dealing with humeral length had high negative loadings on PC1 while those dealing with the anteroposterior depth of the distal end (HMTD, HTrD, HCP) and diaphyseal dimension (HTD, HAPD) all contributed negative loadings. Negative loadings on PC2 were primarily driven by measurements of overall humeral width (HDPW, HTD, HEW, WATBs HDAW) while measures of the anteroposterior depth of the distal end and to a lesser extend humeral length had positive loadings. Significant differences in shape were

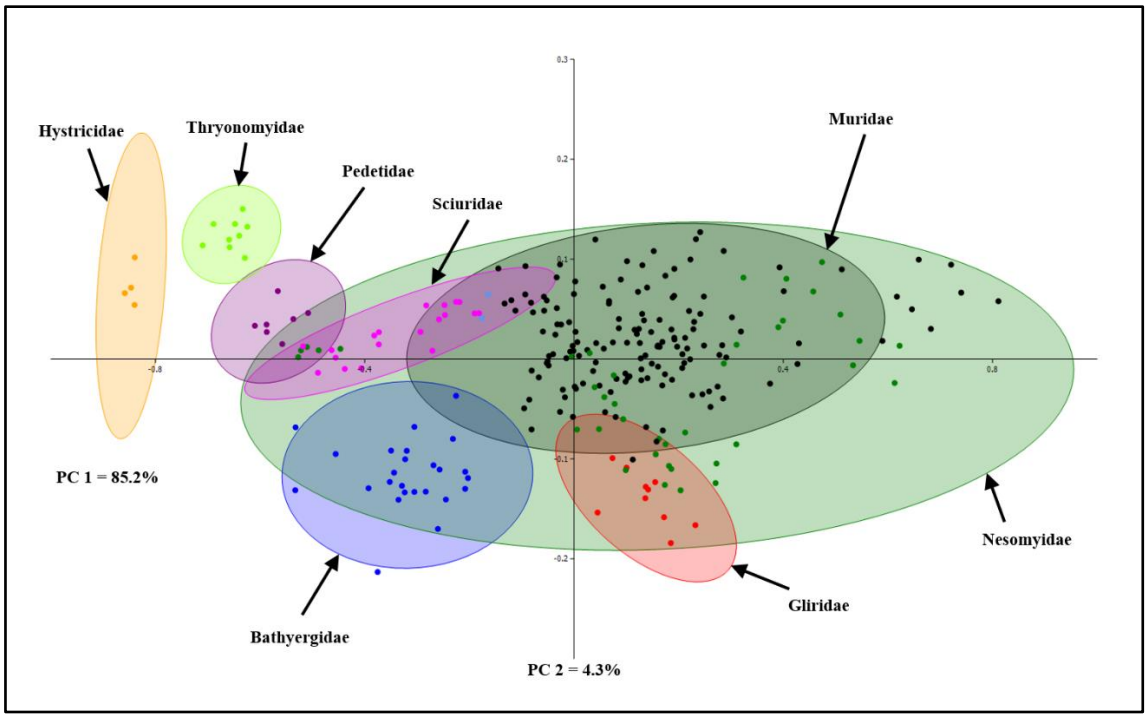


Figure 4.3. First two PCs with 95% confidence ellipses for families from TM analysis of shape using humeri. Axes not scaled by variance explained. Note the high degree of overlap between the families Muridae and Nesomyidae.

found for all levels of the model (Table 4.4). Classification rates from all LDFAs ranged from 63.5% to 77.9% (Table 4.5). At the family level 28% of the murids and 56% of the nesomyids were misclassified, with most misclassifications again occurring primarily between the two families. As no analysis reached the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

Principal component analysis of humeri form utilizing TM yielded two axes that accounted for > 95% of the total variance (Figure 4.4). Measurements primarily dealing with humeral length had high negative loadings on PC1 while the size variable (GMM) dominated the positive loadings of the first axis. Positive loadings on PC2 were driven by

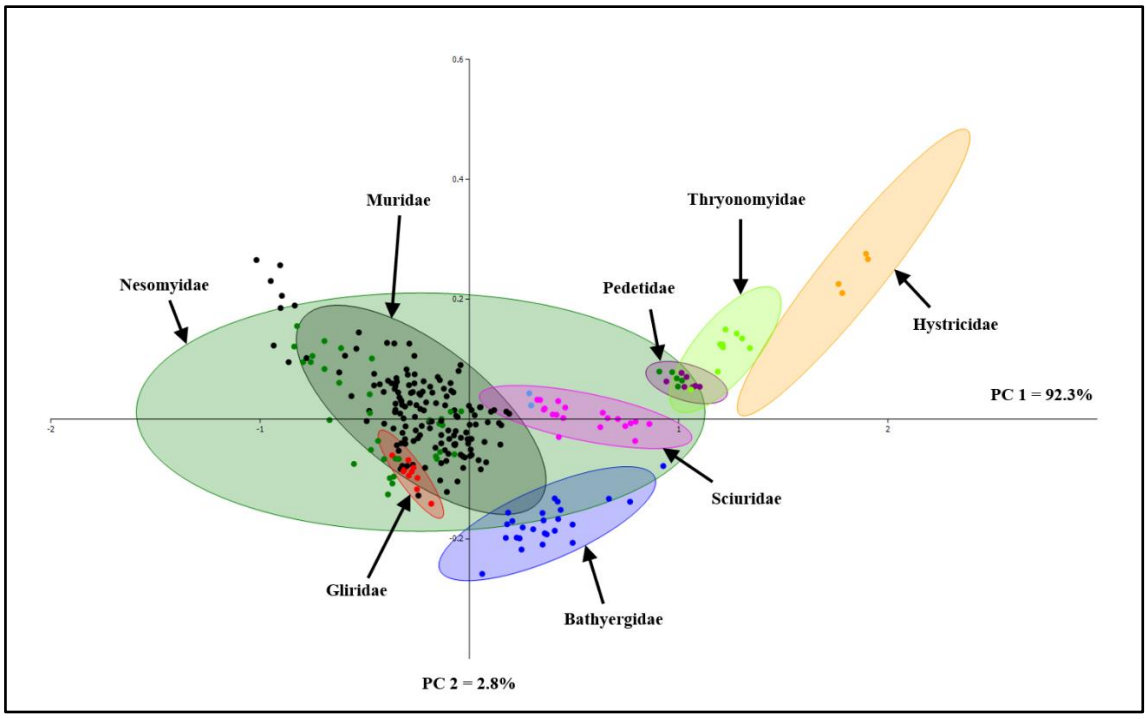


Figure 4.4. First two PCs with 95% confidence ellipses for families from TM analysis of form using humeri. Axes not scaled by variance explained. Note the high degree of overlap between the families Muridae, Nesomyidae, and Gliridae.

size and measures of humeral length, while measures of humeral width contributed negative loadings. Significant differences in shape were found for all levels of the model (Table 4.4). Classification rates from all LDFAs ranged from 48.3% to 58.2% (Table 4.5). Again, most of the misclassifications occurred between murids and nesomyids, however, almost half nesomyids also misclassified as glirids. As no analysis reached the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

4.3.3. Femora

Principal component analysis of femora shape utilizing TM yielded five axes that accounted for > 95% of the total variance (Figure 4.5). Measurements primarily dealing

with femoral length (FML, FFL, PFL) had high loadings on PC1 while the rest of the variables had moderate positive loadings. Positive loadings for PC2 were primarily driven by PFL and to a lesser extent FTD while FML, FGHT and FPDD contributed moderate negative loadings. Significant differences in shape were found for all levels of the model (Table 4.4). Classification rates from all LDFAs ranged from 61.2% to 77.2% (Table 4.5). Again, most of the misclassifications occurred between murids and nesomyids, and to a lesser extent glirids. Additionally, one hystricid (25%) also classified as a pedetid. As no analysis reached the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

Principal component analysis of femora form utilizing TM yielded three axes that accounted for > 95% of the total variance (Figure 4.6). The size variable (GMM) dominated the positive loadings of PC1, while measures of femoral length had the highest negative loadings. Measures of femoral length, GMM, and FPDD had high positive loadings on PC2 while measures of femoral distal breadth, FHL, and FTD had high negative loadings. Significant differences in shape were found for all taxonomic levels of the model (Table 4.4). Classification rates from all LDFAs ranged from 50.2% to 62.0% (Table 4.5). Again, most of the misclassifications occurred between murids and nesomyids, and to a lesser extent glirids. Additionally, one hystricid (25%) also classified as a pedetid. As no analysis reached the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

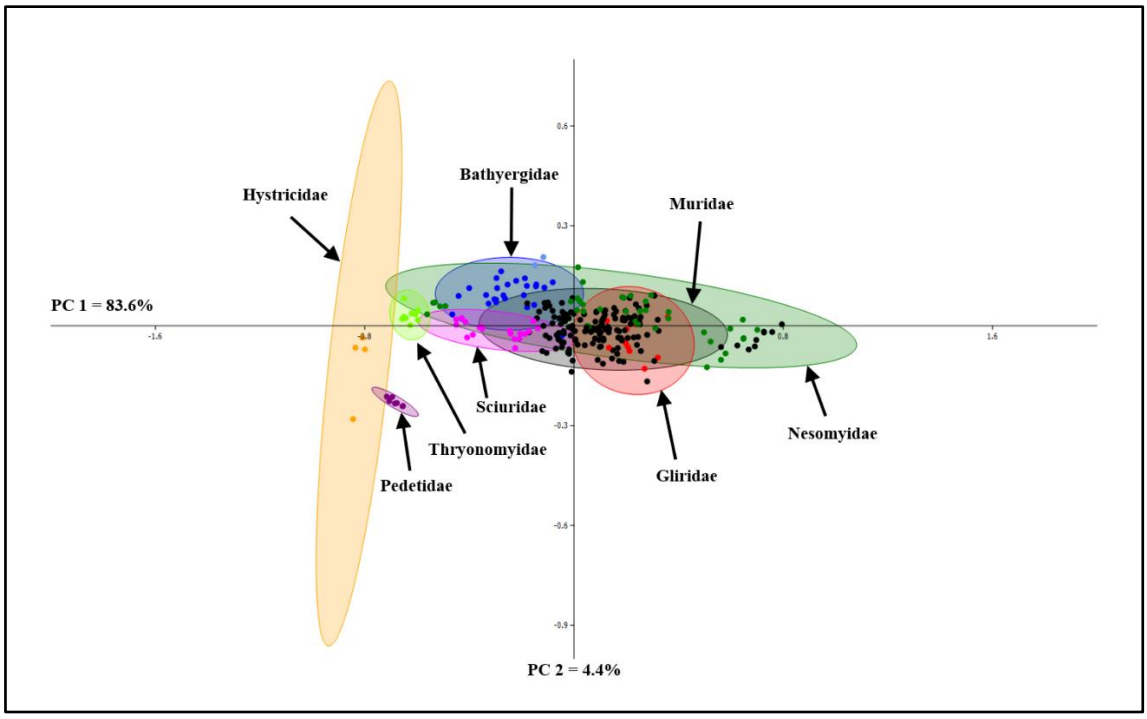


Figure 4.5. First two PCs with 95% confidence ellipses for families from TM analysis of shape using femora. Axes not scaled by variance explained. Note the high degree of overlap between many families, including Hystricidae and Pedetidae.

4.4 Modern and Fossil African Rodents: GM Taxonomic Signal

Results of tests for a taxonomic signal in rodent postcrania using GM follow the same outline as above, with humeri presented first, and shape analyses preceding form. Additionally, as harmonic coefficients are not directly translatable to aspects of element shape (e.g. coefficient three of harmonic 8 cannot be said to measure of femoral length) PC loadings are not provided.

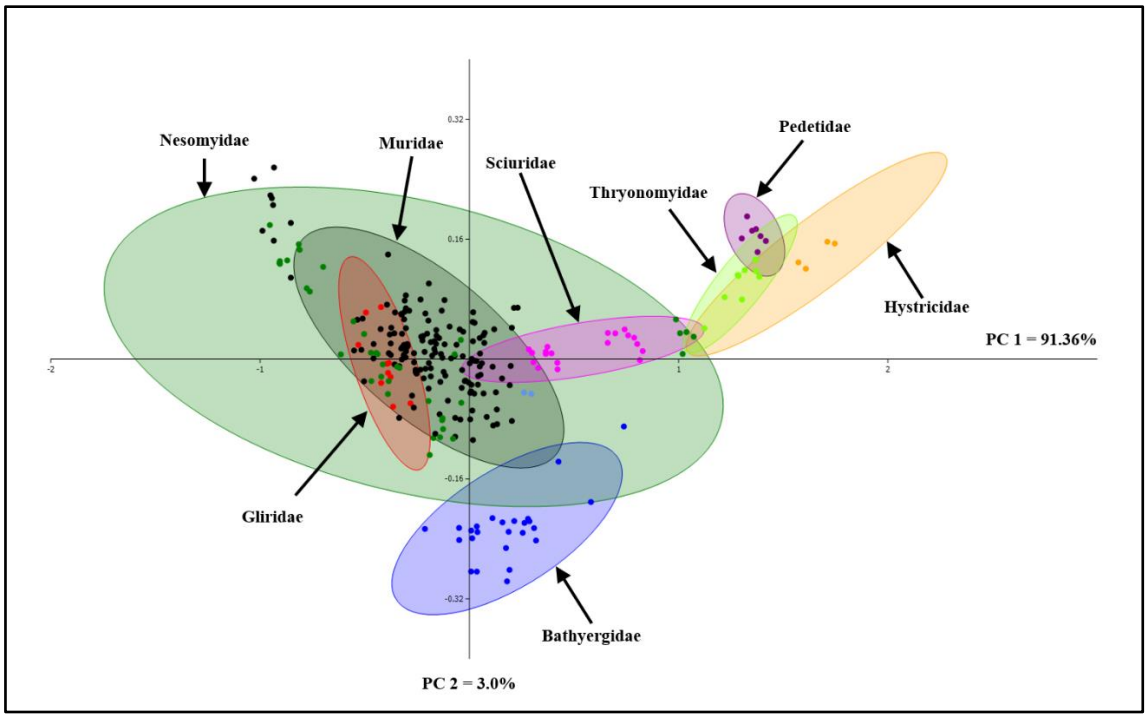


Figure 4.6. First two PCs with 95% confidence ellipses for families from TM analysis of form using femora. Axes not scaled by variance explained. Note the high degree of overlap between many families, including Hystricidae and Pedetidae.

4.4.1 Humeri

Principal component analysis of humeri shape utilizing GM yielded 11 axes that accounted for > 95% of the total variance (Figure 4.7). Significant differences in shape were found for all levels of the model (Table 4.6). Classification rates from all LDFAs ranged from 63.9% to 78.7% (Table 4.7). As in previous analyses, the majority of misclassifications occurred between murids and nesomyids, although 10% of both the nesomyids and glirids also misclassified as sciurids. As no analysis reached the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

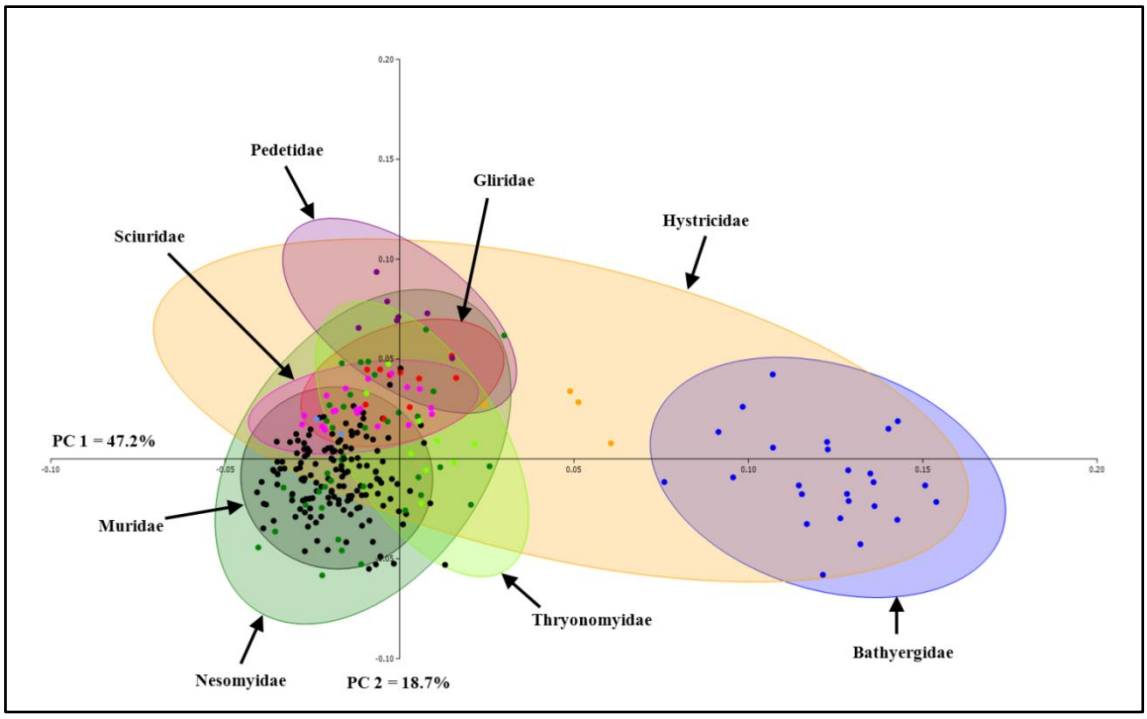


Figure 4.7. First two PCs with 95% confidence ellipses for families from GM analysis of shape using humeri. Axes not scaled by variance explained. Note the significant amount of overlap among families.

Table 4.6. MANOVA results for all analyses using GM.

Elements	Analysis	Model	Λ	Approximate F	P
Humeri	Shape	Whole	3.87E-06	14.7	< 0.001
		Family	8.24E-04	32.9	< 0.001
		Family(Subfamily)	7.42E-02	11.2	< 0.001
		Family(Subfamily(Genus))	1.16E-02	6.0	< 0.001
	Form	Whole	2.19E-12	7.2	< 0.001
		Family	4.79E-06	17.7	< 0.001
		Family(Subfamily)	7.36E-03	6.1	< 0.001
		Family(Subfamily(Genus))	7.27E-06	4.4	< 0.001
Femora	Shape	Whole	1.95E-07	18.5	< 0.001
		Family	5.03E-05	51.5	< 0.001
		Family(Subfamily)	6.33E-02	10.9	< 0.001
		Family(Subfamily(Genus))	1.21E-02	5.3	< 0.001
	Form	Whole	1.35E-11	9.7	< 0.001
		Family	8.42E-07	33.2	< 0.001
		Family(Subfamily)	1.23E-02	7.3	< 0.001
		Family(Subfamily(Genus))	2.66E-04	3.9	< 0.001

Table 4.7. Classification rates from LDFAs for all analyses using GM. Values in bold exceed 85% threshold.

Element	Analysis	Grouping	Regular %	Cross-Validation %
Humeri	Shape	Family	76.8%	72.2%
		Subfamily	72.6%	66.9%
		Genus	78.7%	63.9%
	Form	Family	**90.5%**	84.0%
		Subfamily	**95.8%**	84.4%
		Genus	**95.1%**	76.4%
Femora	Shape	Family	**91.3%**	**90.1%**
		Subfamily	83.3%	79.1%
		Genus	79.1%	67.7%
	Form	Family	**96.2%**	**94.3%**
		Subfamily	**94.3%**	**90.1%**
		Genus	**90.1%**	71.5%

Principal component analysis of humeri form utilizing GM yielded 40 axes that accounted for > 95% of the total variance (Figure 4.8). Significant differences in shape were found for all levels of the model (Table 4.6). Classification rates from all LDFAs ranged from 76.4% to 95.8% and as in previous analyses the majority of misclassifications occurred between murids and nesomyids (Table 4.7). However, as no classifications using cross-validation exceeded the 85% correct classification threshold, discriminant functions were not applied to the Swartkrans fossils.

4.4.2 Femora

Principal component analysis of femora shape utilizing GM yielded 12 axes that accounted for > 95% of the total variance (Figure 4.9). Significant differences in shape were found for all levels of the model (Table 4.6). Classification rates from all LDFAs

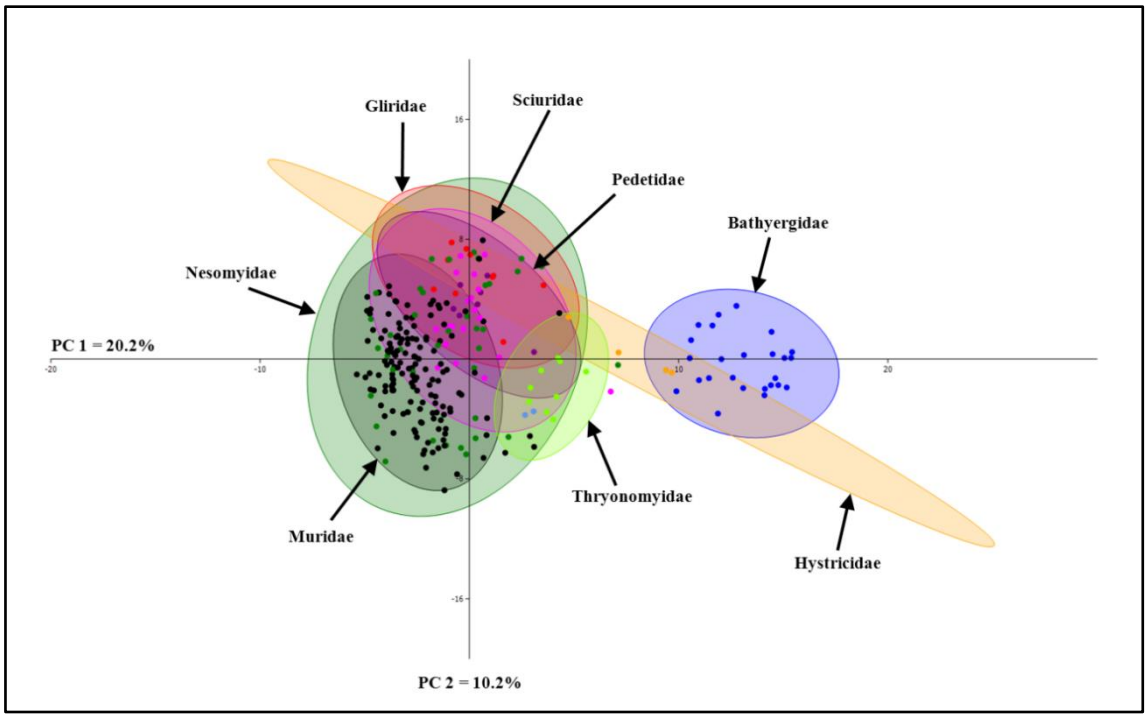


Figure 4.8. First two PCs with 95% confidence ellipses for families from GM analysis of form using humeri. Axes not scaled by variance explained. Note the significant amount of overlap among families.

ranged from 67.7% to 91.3% (Table 4.7). Significantly, classification using cross-validation at the family level exceeded the 85% threshold and thus the resulting discriminant functions were applied to the Swartkrans fossils. Figure 4.10 shows group separation based on the first two canonical axes which collectively account for 67.7% of the variance. Of the 203 fossil femora, 75.4% classified with a typicality probability above the 0.10 threshold (Table 4.8).

Principal component analysis of femora form utilizing GM yielded 30 axes that accounted for > 95% of the total variance (Figure 4.11). Significant differences in shape were found for all levels of the model (Table 4.6). Classification rates from all LDFAs ranged from 71.5% to 96.2% (Table 4.7). Significantly, classification rates using

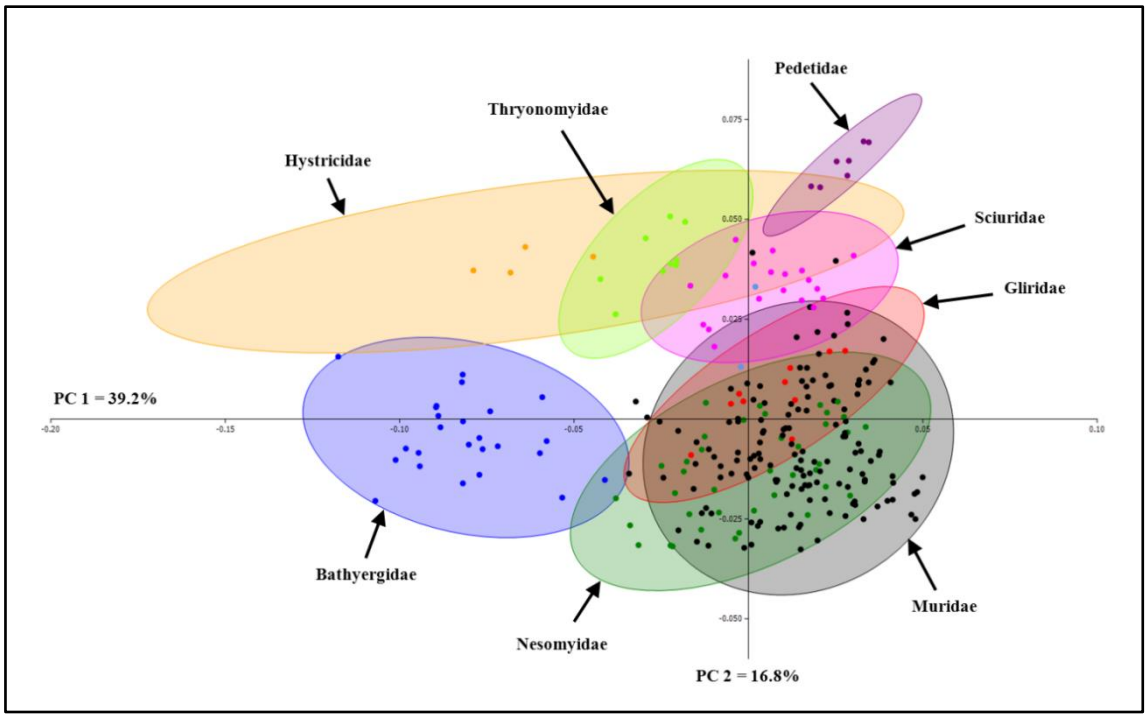


Figure 4.9. First two PCs with 95% confidence ellipses for families from GM analysis of shape using femora. Axes not scaled by variance explained. Note less overlap than in previous analyses.

cross-validation at both the family and subfamily level exceeded the 85% threshold and thus the resulting discriminant functions were applied to the Swartkrans fossils. Figure 4.12 shows family group separation based on the first two canonical axes which collectively account for 73.0% of the variance, while Figure 4.13 shows subfamily group separation with the first two canonical axes accounting for 65.1% of the variance. Of the 203 fossil femora, 56.2% classified with a typicality probability above the 0.10 threshold at the family level, and 58.1% at the subfamily level (Table 4.8).

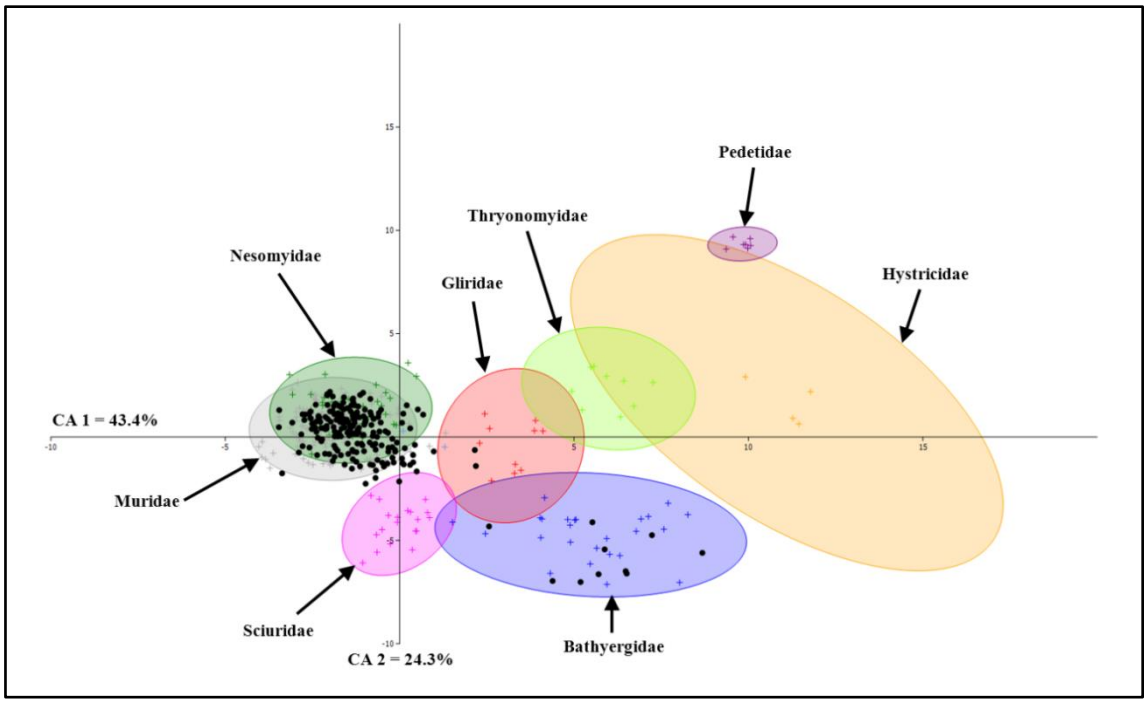


Figure 4.10. First two CAs with 95% confidence ellipses for families from GM analysis of shape using femora. Axes not scaled by variance explained. Plus (+) signs indicate modern specimens while filled circles indicate Swartkrans fossil femora.

Table 4.8. Fossil classifications from LDFAs on GM data that exceeded 0.10 typicality threshold.

Element	Analysis	Level	Group	n =
Femora	Shape	Family	Muridae	104
			Nesomyidae	39
			Bathyergidae	9
			Gliridae	1
	Total			153
	Form	Family	Muridae	58
			Nesomyidae	52
			Bathyergidae	4
	Total			114
	Form	Subfamily	Deomyinae	2
			Murinae	45
			Bathyerginae	5
			Cricetomyinae	3
			Dendromurinae	6
			Otomyinae	24
			Mystromyinae	15
			Petromyscinae	18
	Total			118

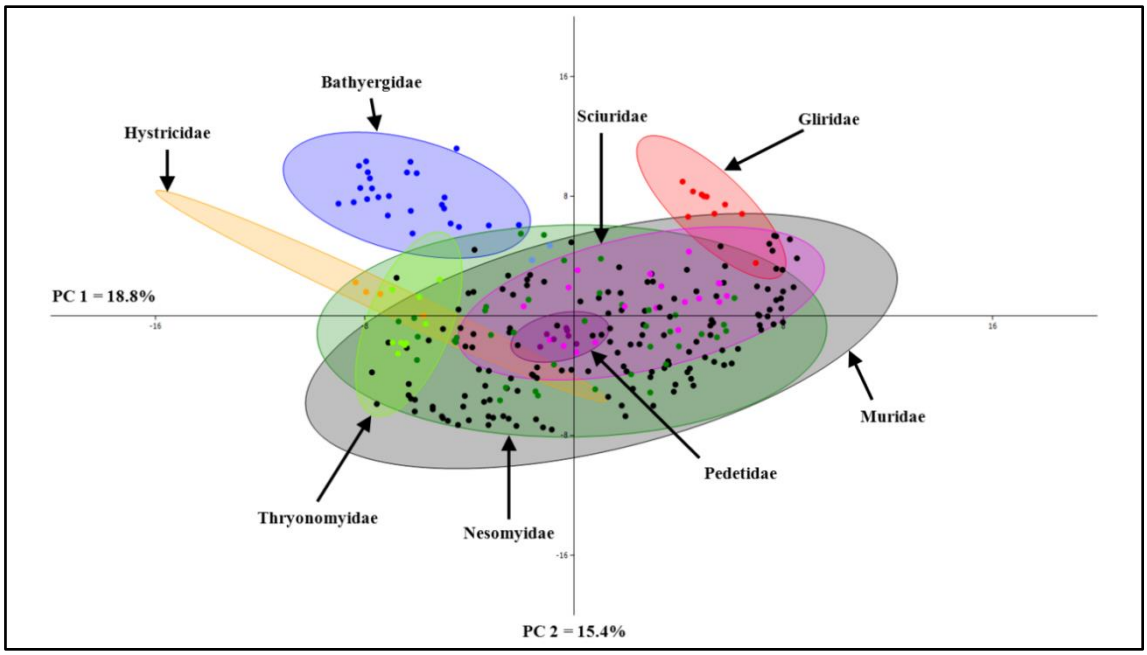


Figure 4.11. First two PCs with 95% confidence ellipses for families from GM analysis of form using femora. Axes not scaled by variance explained.

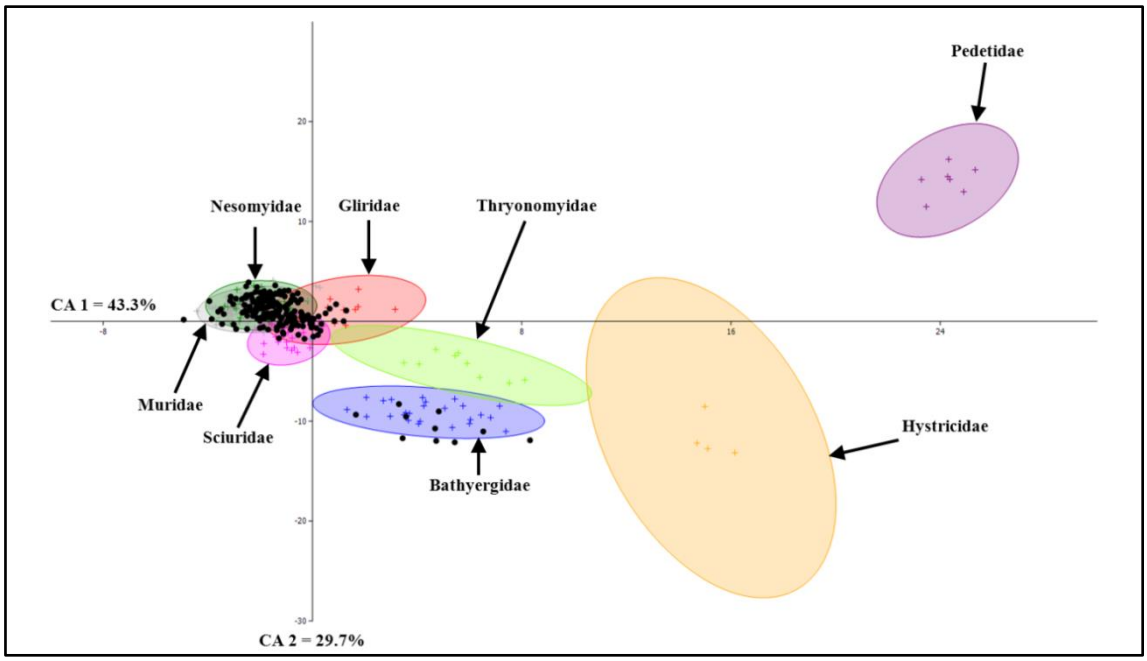


Figure 4.12. First two CAs with 95% confidence ellipses for families from GM analysis of form using femora. Axes not scaled by variance explained. Plus (+) signs indicate modern specimens while filled circles indicate Swartkrans fossil femora.

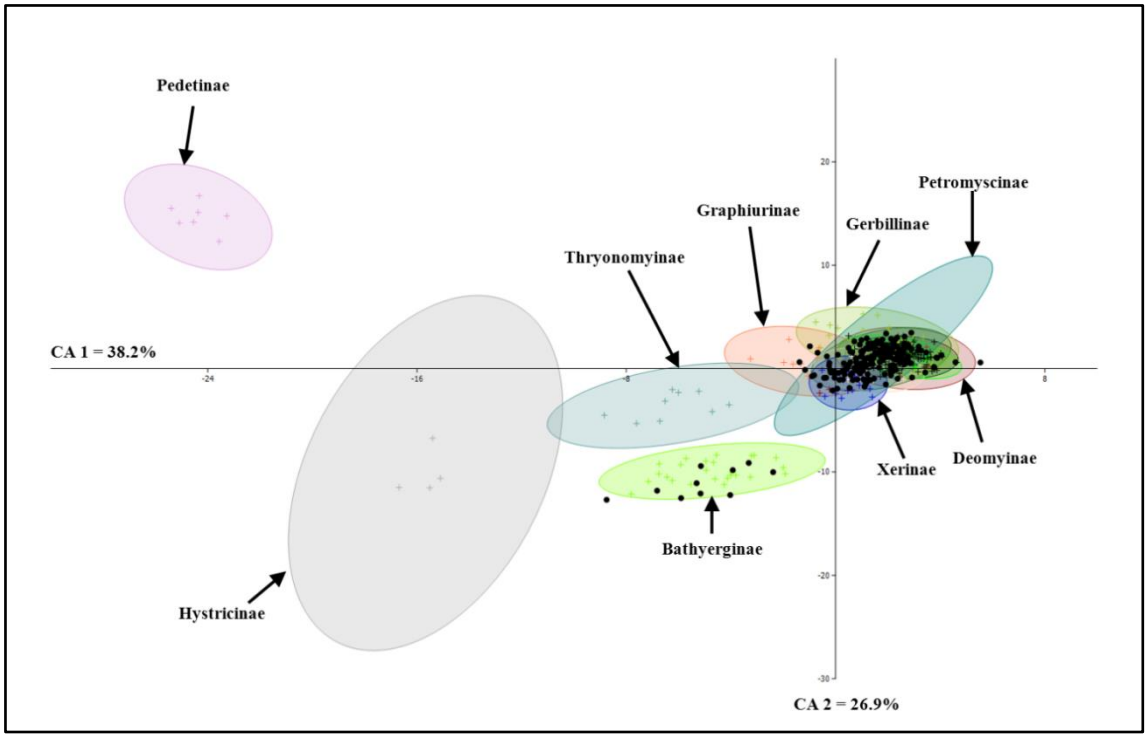


Figure 4.13. First two CAs with 95% confidence ellipses for families from GM analysis of form using femora. Axes not scaled by variance explained. Plus (+) signs indicate modern specimens while filled circles indicate Swartkrans fossil femora. Subfamilies not clearly visible in figure due to significant overlap include Murinae, Cricetomyinae, Dendromurinae, Otomyinae, Mystromyinae, and Petromurinae.

4.5 Reduced Sample TM and GM Shape Analyses

Results of tests for a taxonomic signal in rodent postcrania using TM and GM with a reduced sample size follow a similar outline as above with humeri preceding femora and TM results for each element presented first. Note, PCA were run on form data, however the number of PCs needed to account for > 90% of the total variance using GM data exceeded the sample size of the smallest group (Bathyergidae n =25), thus only shape analyses were conducted.

4.5.1 Humeri

Principal component analysis of the reduced sample humeri shape utilizing TM yielded 11 axes that accounted for > 99% of the total variance (Figure 4.14). Measures of humeral length had high positive loadings of PC1 while the rest of the measures had negative loadings. Positive loadings on PC2 primarily consisted of measures of anteroposterior depth of the distal end (HMTD, HTrD, HCP) while most other measures had negative loadings. Results from a MANOVA indicate a significant family level signal is present in humeral shape ($\Lambda = 0.089$, Approx. $F = 25.8$, $P < 0.0001$). Classification rates from LDFA were 82.6% and 78.0% with cross validation. As with previous analyses most of the misclassifications occurred between murids and nesomyids. As the percent correct classification using cross-validation failed to reach the 85% threshold, discriminant functions were not applied to the Swartkrans fossils.

Principal component analysis of the reduced sample humeri shape utilizing GM yielded 18 axes that accounted for > 98% of the total variance (Figure 4.15). Results from a MANOVA indicate a significant family level signal is present in humeral shape ($\Lambda = 0.009$, Approx. $F = 46.1$, $P < 0.0001$). Classification rates from LDFA were 86.7% and 81.7% with cross validation. As with previous analyses most of the misclassifications occurred between murids and nesomyids. As the percent correct classification using cross-validation failed to reach the 85% threshold, discriminant functions were not applied to the Swartkrans fossils.

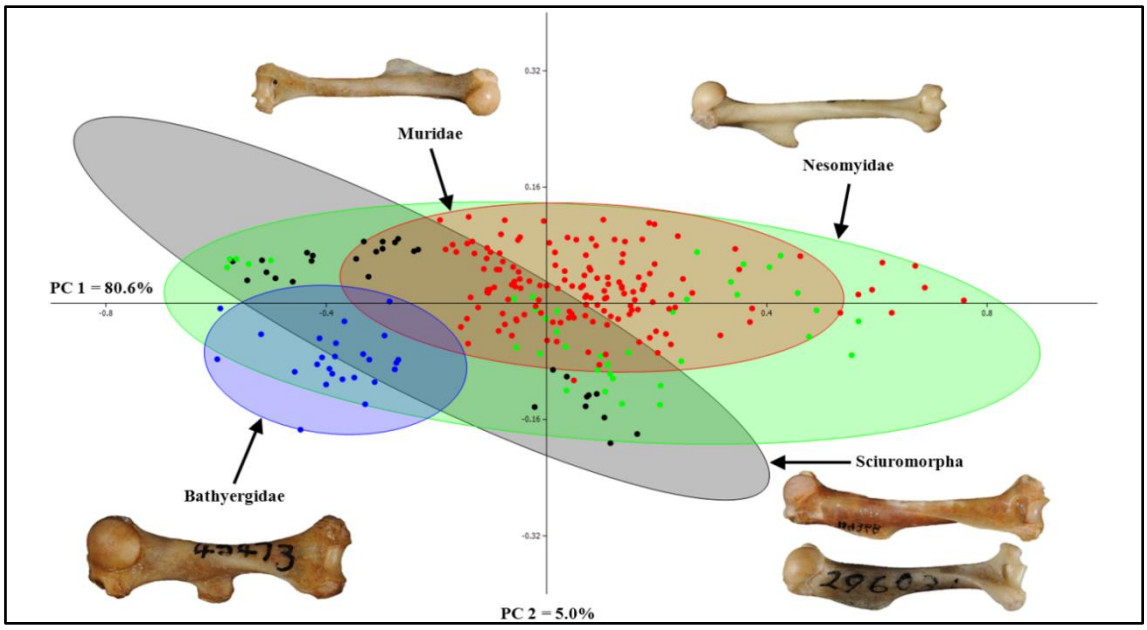


Figure 4.14. First two PCs with 95% confidence ellipses for higher level groupings from TM analysis of humeri shape. Axes not scaled by variance explained. Note the similarity between sciuromorph humeri (top sciurid, bottom glirid).

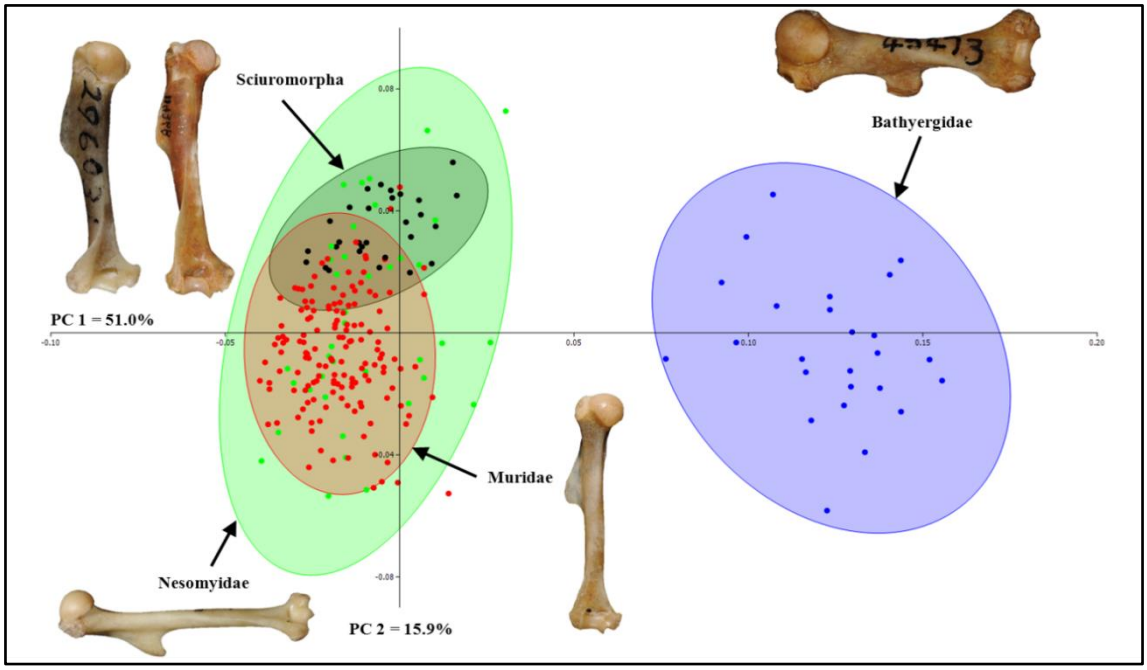


Figure 4.15. First two PCs with 95% confidence ellipses for higher level groupings from GM analysis of humeri shape. Axes not scaled by variance explained. Note the similarity between sciuromorph humeri (right sciurid, left glirid).

4.5.1 Femora

Principal component analysis of the reduced sample femora shape utilizing TM yielded 9 axes that accounted for > 99% of the total variance (Figure 4.16). Measures of femoral length had high positive loadings of PC1 while the rest of the measures had negative loadings. Measures of the femoral head and distal width had high positive loadings on PC2 while FPDD, WFA3T and FGHT had high negative loadings. Results from a MANOVA indicate a significant family level signal is present in femoral shape (Λ = 0.117, Approx. F = 26.9, P < 0.0001). Classification rates from LDFA were 85.5% and 82.6% with cross validation. As with previous analyses most of the misclassifications occurred between murids and nesomyids, however, one bathyergid also misclassified as a sciuromorph. As the percent correct classification using cross-validation failed to reach the 85% threshold, discriminant functions were not applied to the Swartkrans fossils.

Principal component analysis of the reduced sample femora shape utilizing GM yielded 20 axes that accounted for > 98% of the total variance (Figure 4.17). Results from a MANOVA indicate a significant family level signal is present in femoral shape (Λ = 0.005, Approx. F = 51.6, P < 0.0001). Significantly, classification rates from LDFA were 93.4% and 90.0% with cross-validation and all misclassifications occurred between the murids and nesomyids. As the cross-validation correct classification rate exceeded the 85% threshold, resulting discriminant functions were applied to the Swartkrans fossils. Figure 4.18 shows family group separation based on the first two canonical axes which collectively account for 96.8% of the variance. Of the 203 fossil femora, 89.2% classified with a typicality probability above the 0.10 threshold (Table 4.9).

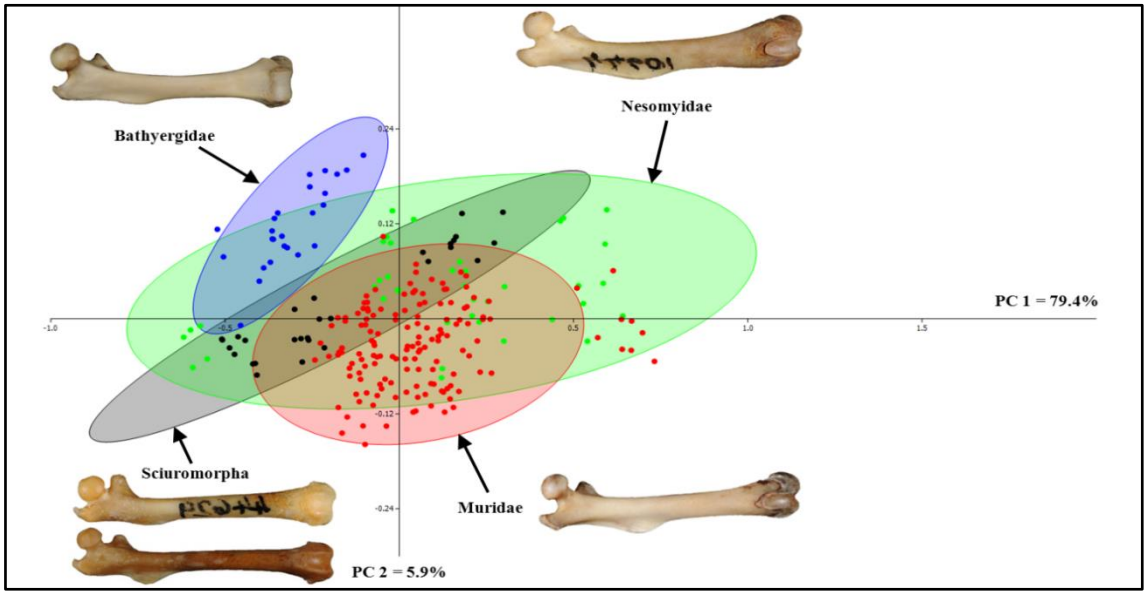


Figure 4.16. First two PCs with 95% confidence ellipses for higher level groupings from TM analysis of femora shape. Axes not scaled by variance explained. Note the similarity between sciuromorph femora (top glirid, bottom sciurid).

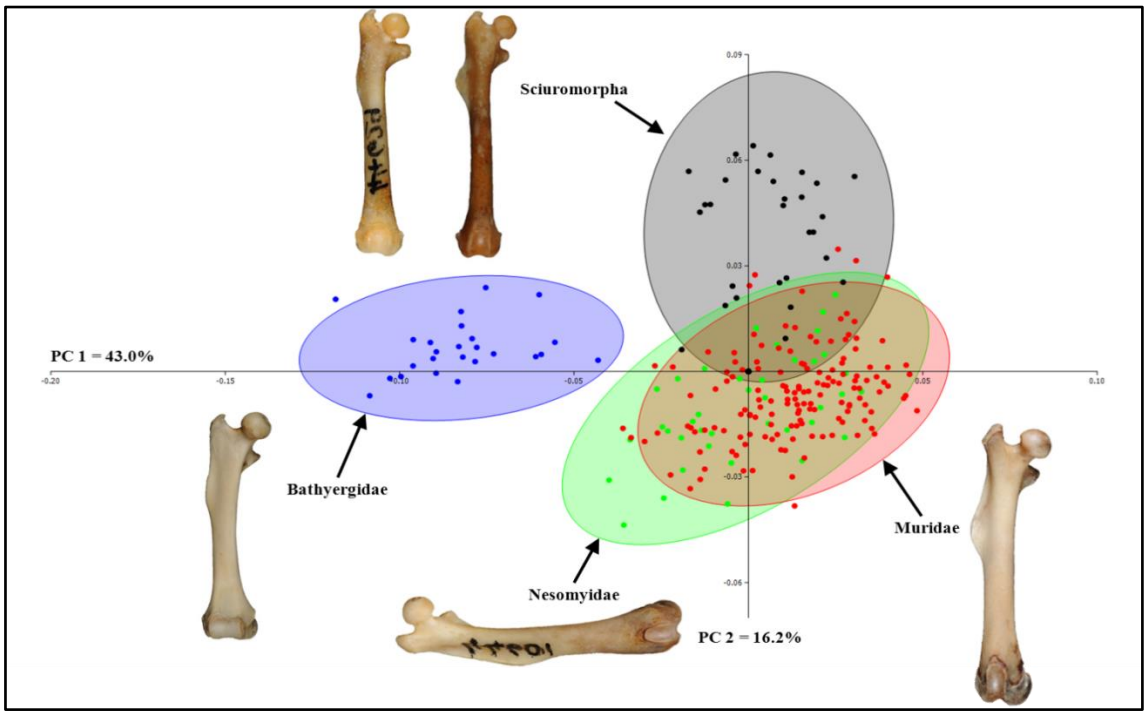


Figure 4.17. First two PCs with 95% confidence ellipses for higher level groupings from TM analysis of femora shape. Axes not scaled by variance explained. Note the similarity between sciuromorph femora (left glirid, right sciurid).

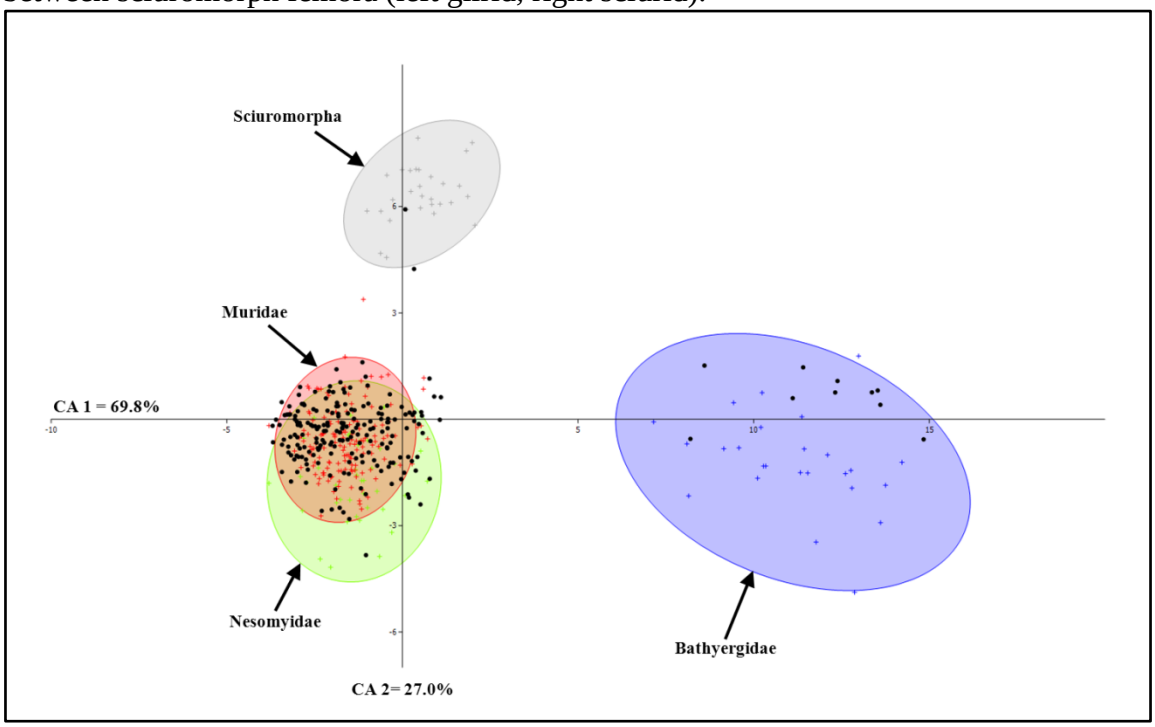


Figure 4.18. First two CAs with 95% confidence ellipses for families from GM analysis of form using femora. Axes not scaled by variance explained. Plus (+) signs indicate modern specimens while filled circles indicate Swartkrans fossil femora.

Table 4.9. Fossil classifications from LDFA on GM reduced sample femora data that exceeded 0.10 typicality threshold.

Element	Analysis	Group	n =
Femora	GM	Muridae	140
		Nesomyidae	37
		Sciuromorpha	2
		Bathyergidae	2
	Total		181

5. DISCUSSION

5.1 Modern Owl Pellets

Estimates of the MNIs using rodent cranial versus postcranial remains show that higher values are obtained with postcrania across all three combinations of elements, however, this difference was only significant when all appendicular long bone elements were included (Table 4.2). These results are not surprising as the inclusion of all long bones yields five sided elements from which an individual can be recorded, as opposed to two when using mandibles and maxillae. When only proximal (humeri and femora) or distal (radii, ulnae, tibiofibulae) postcranial elements are used the differences are not significant. Results from these latter two test thus support Hypothesis 1 and suggest that these skeletal regions can be considered isotaphonomic in regard to estimates of rodent prey taken. By extension, taxonomic based methods for reconstructing paleoenvironments developed using craniodental remains should also be applicable to postcrania, providing a taxonomic signal can be recovered in the latter. Alternately, the results when calculating MNIs using all long bones do not support Hypothesis 1 as the summations are greater than those using craniodental remains. Here it is unclear on how this would influence paleoenvironmental reconstructions. For taxonomic based methods based on presence/absence data, and not weighted by relative abundance, the utilization of all long bone elements may perform better as there would be a greater probability of rare taxa

being recognized in the absence of their craniodental remains. Alternately, assessments of rodent community composition may be affected when relative abundances are incorporated in order to define the pattern of what would be expected for a roost surrounded by a specific habitat. How, and to what degree, however, requires further study.

When the skeletal element counts obtained here (Table 4.1) are compared to what has been reported in the literature, the rank order element abundances found are generally similar (Kendall's $\tau = 0.714$, $p = 0.024$). Table 5.1 provides element count data for 10 barn owl produced assemblages reported across four studies (Andrews 1990; Dodson and Wexlar 1979; Korth 1979; Kusmer 1990). The term assemblages is used, as opposed to roosts, as samples were obtained in different manners. Utilizing a minimum of three individual owls across two institutions, Dodson and Wexlar (1979:276) report skeletal element counts from captive animals provisioned with mice (*Mus* sp.). Alternately, data reported by Kusmer (1990) were from collected from natural roosts in which one barn owl was reported at each site. Those by Korth (1979) also appear to be from a natural setting, however, the nature and number of sites is not indicated. Finally, Andrews (1990) also reports data from natural accumulations, with both roost and nest sites included, although not all are included here. Specifically, although Andrews (1990) lists eight barn owl collections in Appendix Table 1, element counts are only provided for seven of these in Appendix Table 12. Additionally, the assemblage obtained from Gedi, Kenya (Appendix Table 1) states that selection was in favor of skulls and that other elements are poorly represented. As such this last assemblage was not considered.

Table 5.1. Number of skeletal elements and minimum number if individuals (MNI) reported from four studies and ten assemblages. Citations and assemblages are as follows: Andrews (1990: Appendix Table 12) – 1) Salthouse, 2) Stratton, 3) Barton Tuff, 4) Hula, 5) Makapansgat, 6) Boomplaas; Dodson and Wexlar (1979: Table 1) – 7) combined assemblage from several captive owls; Kusmer (1990: Table 2) – 8) barn owl 1, 9) barn owl 2; Korth (1979: Table 1) – 10) barn owl.

Element	Assemblages										
	1	2	3	4	5	6	7	8	9	10	# Elements
Maxillae	65	105	46	**57**	100	**88**	**34**	176	50	36	757
Mandibles	86	**275**	**94**	**59**	**125**	50	32	**177**	61	**38**	997
Humeri	82	172	93	40	103	48	28	155	59	34	814
Radii	60	187	88	33	88	45	29	128	52	26	736
Ulnae	68	214	92	38	89	44	27	149	55	34	810
Femora	**120**	157	**94**	41	99	51	24	153	62	34	835
Tibiofibulae	**120**	209	90	42	106	47	23	157	**66**	36	896
# Elements	601	1319	597	310	710	373	197	1095	405	238	
MNI	60	145	50	30	64	50	17	94	34	20	

When comparing these values, it is also worthwhile to note several additional caveats. First, while two of these studies (Andrews 1990; Kusmer 1990) provided raw count data for all elements, some estimation was required for the others. Dodson and Wexlar (1979: Table 1) do not report maxillae counts but rather skull counts. As there was no indication in their manuscript that any left and right maxillae were separated, skull values were doubled here to produce maxillae estimates. Second, element counts reported for Korth (1979: Table 1) were calculated using the MNI and element percent representation values provided. Finally, aside from the provisioned owls used by Dodson and Wexlar, all other studies examined natural accumulations and thus element proportions are summed across all vertebrate, or at least mammalian taxa as far as can be determined, and thus differ from this analysis which only examined rodent prey remains.

A comparison of Table 4.1 with Table 5.1 shows that mandibles are the most frequent element recovered, followed by tibiofibulae, while radii are the least frequently recovered. All of the other elements are within one rank order place with one exception. Maxillae were the third most common element recovered in this study, while they were the sixth most common reported in the literature.

While the statistical tests employed in this study indicate that MNI counts using postcranial remains are as representative, or better, than counts using cranial elements, it may be worthwhile to try and compare these results to what has been reported in the literature. Unfortunately, these comparisons are made difficult based on methodological differences of how individual prey items were tallied. Recall that individual pellets were the unit of analysis for this study, that MNI values were calculated for each element on a per pellet basis, and that the statistics were run on MNI values per pellet summed across skeletal region (i.e. cranial vs all postcrania, proximal postcrania, or distal postcrania) within sites. Thus, a grand total MNI for each site would be the summation of the highest MNI across elements, per pellet, across pellets.

As stated above, all four of the studies examined here report MNIs, and either raw element counts, or percentages from which element counts could be extrapolated. No study reported sided element data on a per pellet basis. The results here are best compared to those of Kusmer (1990:630) who states "The minimum number of individuals (MNI) in each pellet was calculated by siding and then counting the most frequent element portion for each prey species represented. The MNI for each sample was then obtained by adding the MNI for each individual pellet." While the number of elements present divided

by the expected number of elements per the reported MNI equate, unfortunately the per-pellet data are not reported thus a direct comparison is not possible. For other studies it is far less clear. Dodson and Wexlar (1978: Table 1) report MNI estimates based on mandible counts of 17 for the barn owl pellets they examined, and while most of these values correspond to the percent representation reported, the values for tibia recovered from their great horned owls (*Bubo virginianus*) exceed 100% suggesting that either their study subjects may have retained prey elements from previous meals not accounted for based on mandibular MNI counts, or that some mandibular remains were lost. Andrews (1990) provides element counts and percent representations for each site for which for the majority balance (see Andrews 1990: Appendix Table 12 – Stratton site for the one exception). Here it is assumed that either MNI counts were based on sided elements, and/or the pellet was the unit of analysis as element percentages differ from what would be expected if the analysis was on elements that were not sided at the assemblage level (i.e. % present would either take the form of 100% or ((MNI*2)-1)*100 for the most abundant element). Finally, as for the same argument just made, values reported by Korth (1979) also suggest that either MNI counts were based on sided elements, and/or the pellet was the unit of analysis.

With these caveats in mind, as a heuristic exercise the results from this study are compared to what has been reported in the literature in the following manner. Per element MNI estimates are calculated using the reported, or estimated number elements present divided by the expected number based on the given MNI and rounded up. In other words, the per element MNI estimates are calculated at the assemblage level using a Binford

(1978) based approach detailed in Chapter 3, and do not take siding into account. Recall, however, that 50% element representation could potentially yield a 100% MNI representation if all elements came from the same side. Once per element MNI estimates were generated, the tests were conducted as before using three methods of poscranial MNI calculations. (i.e. cranial vs all postcrania, proximal postcrania, or distal postcrania).

In total five different comparisons are made. Table 5.2 provides results for the recalculations of the data from this study. As can be seen when compared to Table 4.2, MNI estimates are all lower when the site is used as the unit of analysis and skeletal element siding is not considered. Additionally, MNI estimates based on cranial elements are all higher than those using postcrania, although this difference is only significant for the proximal postcrania comparison.

Comparisons two through four are provided in Table 5.3 and consider different numbers of assemblages reported from the literature. In the first of these, all assemblages were included and MNI estimates for cranial elements outnumber those using postcrania in all three calculations. Additionally, these all of these differences are significant, although those using all postcrania are just barely exceed a 0.05 alpha threshold. When examining Table 5.1, however, one assemblage stands out as the number of maxillae is nearly double that of any other element (number 6 or Boomplass of Andrews 1990). In addition to utilizing multiple supplementary hunting roosts where pellets are occasionally accumulated, adult barn owls are known to occasionally decapitate and consume the heads of their prey while bringing back the rest when provisioning an active nest (Bunn et al. 1982; Raczynski and Ruprecht 1974; Steyn 1982; Taylor 1994; Vernon 1972). Although

Table 5.2. Comparison one from text. Calculations of MNI from cranial (mandibles and maxillae) and postcranial (humeri, femora, radii, ulnae, and tibiofibulae) elements utilizing a Binford (1978) based approach, and results from chi-square test of goodness of fit utilizing 3 methods for postcranial MNI calculation.

Region	MNI Calculations		
	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Cranial	493	493	493
Postcranial	491	426	478
Totals	984	919	971
X^2	< 0.01	4.89	0.23
P	0.95	< 0.05	0.63

Table 5.3: Comparisons two through four from text. Calculations of MNI from cranial (mandibles and maxillae) and postcranial (humeri, femora, radii, ulnae, and tibiofibulae) elements utilizing a Binford (1978) based approach, and results from chi-square test of goodness of fit utilizing 3 methods for postcranial MNI calculation.

		MNI Calculations		
	Region	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Comparison 2	Cranial	521	521	521
	Postcranial	459	431	454
	Totals	980	952	975
	X^2	3.99	8.51	4.60
	P	0.048	< 0.01	< 0.05
		MNI Calculations		
	Region	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Comparison 3	Cranial	477	477	477
	Postcranial	433	407	428
	Totals	910	884	905
	X^2	2.13	5.54	2.65
	P	0.14	< 0.05	0.1
		MNI Calculations		
	Region	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Comparison 4	Cranial	434	434	434
	Postcranial	373	366	368
	Totals	807	800	802
	X^2	4.61	5.78	5.43
	P	< 0.05	< 0.05	< 0.05

I am unaware of any study formally testing this hypothesis, if this behavior is prevalent in breeding owls it is possible that hunting roosts may be biased towards cranial remains, while nest sites may be biased towards postcranial remains. If this assemblage represents such a situation (although why the mandibular count is lower than the maxillary count remains an open question), it would seem appropriate to remove this site as was done here in the third comparison. Similarly, in the fourth comparison assemblage one (Salthouse of Andrews 1990) is also removed as this assemblage was a reported nest and the pellets were interpreted to have come from the nestlings. In both comparisons resulting MNI counts by skeletal region again were again highest using cranial elements. When both assemblage one and six were removed the differences were all significant regardless of how the postcrania were aggregated, however, only the comparison with proximal postcranial elements was significant when only assemblage six was removed.

For the final comparison data from all assemblages reported in the literature and all the sites examined in this study were combined (Table 5.4). As with previous comparisons estimates based on cranial remains are higher than those based on postcrania. These differences, however, were only significant for the comparison with proximal postcranial elements, although the comparison with distal postcranial elements approached significant at a 0.05 alpha level.

So what can be made of this exploratory exercise? In all iterations MNI estimates using cranial remains are higher than those using postcranial elements as would be expected due to their numerical superiority. Results from two of the comparisons contrasting cranial to all postcranial, all of the comparisons contrasting cranial to proximal

Table 5.4. Comparison five from text. Calculations of MNI from cranial (mandibles and maxillae) and postcranial (humeri, femora, radii, ulnae, and tibiofibulae) elements utilizing a Binford (1978) based approach, and results from chi-square test of goodness of fit utilizing 3 methods for postcranial MNI calculation.

Region	MNI Calculations		
	Cranial x All Postcranial	Cranial x Proximal Postcranial	Cranial x Distal Postcranial
Cranial	1014	1014	1014
Postcranial	950	857	932
Totals	1964	1871	1946
X^2	2.09	13.17	3.46
P	0.15	< 0.01	0.06

postcranial, and two of the comparisons contrasting cranial to distal postcranial were also found to be significant. When viewed in this manner these results would tend to suggest that cranial remains perform better, in particular to the proximal postcranial elements. For the data reported here (Table 5.2) this result was somewhat surprising as it implies that a significant number of unilateral femora and humeri were lost, which did not occur with the distal elements. Why this would be the case is not known, however, it does illustrate the value of element side data in these types of analyses.

5.2 Taxonomic Signals in Postcrania

Significant differences were found in all tests of taxonomic signal in rodent postcrania using both TM (Table 4.4), and GM (Table 4.6). This includes analyses of shape and form utilizing all postcranial elements, as well as individual those for individual humeri and femora. These results therefore support Hypothesis 2.1 - that taxonomic signals are recoverable below the level of family using TM on all appendicular long bones,

Hypothesis 2.2 - that taxonomic signals are recoverable below the level of family using TM on both humeri and femora, and Hypothesis 2.3 - that taxonomic signals are recoverable below the level of family using 2D GM on both humeri and femora. While statistical support was found for the presence of a taxonomic signal in all cases, the ability of these various approaches to accurately classify specimens varies. Results from the LDFA using TM failed to yield an *a priori* 85% correct classification using cross-validation for all analyses of individual elements, as well at the subfamily level using all appendicular long bone elements (Table 4.5). Although sufficiently high classification rates were found at both the family and genus level using all appendicular elements, as previously noted instances in which articulated specimens are recovered in the fossil record is exceeding rare, and unlikely due to presumed manner in which the Swartkrans deposits were accumulated. As such, while the differences found here using linear measurements are statistically significant, the approach itself is not practical for fossil identification in its current form.

While the majority of classification rates using linear measurements failed to perform at the *a priori* 85% threshold, several LDFA using 2D GM were found to meet this requirement for application to the fossil record (Table 4.7). In particular, femoral shape analysis at the family level, and form analysis at both the family and subfamily level exceeded the predetermined threshold using cross-validation. Additionally, humeral form analyses at both the family and subfamily level also approach this threshold and an argument could be made for their inclusion in the fossil analysis. This suggests that the outline-based approach is able to recover some informative variation that linear measures

are not, such as the degree of curvature for various features on humeral and femoral elements.

5.3 Ecological Functional Signals in Postcrania

A significant difference between locomotor groups was found using all functional indices on complete modern specimens. Additionally, univariate tests also recovered significant differences within indices across locomotor groups (Table 4.3). Multivariate tests on indices associated with the just femora and humeri were also significant. As with many of the tests for taxonomic signal, however, classifications of individual elements performed poorly and well below the *a priori* cutoff of 85%. Thus, from a statistical standpoint these results support Hypothesis 3.1 – that rodent groups differ based on locomotory patterns using ecological functional indices derived from all appendicular long bones, and Hypothesis 3.2 - that rodent groups differ based on locomotory patterns using ecological functional indices derived from only the femora or humeri. In terms applicability, however, without fossil specimens with associated appendicular elements it is not much use as presently formulated.

Although unfortunate, the failure of the functional indices calculated here from individual elements to correctly classify known specimens at a sufficiently high rate is not totally unexpected. Rodent studies that have used functional indices to infer locomotor habits of extinct fossil forms have utilized multiple elements, either from well preserved individual specimens of from composite specimens where the taxon-element association is assumed (e.g. Dunn and Rasmussen, 2007; Samuels and Van Valkenburgh 2008). As

all organisms are integrated systems, the use of a limited number of measurements on just one element, or the indices derived from them, is unlikely to fully capture the adaptations allowing for a specific behavioral repertoire. In order to assess if the single element functional analysis attempted here would be similar to results from other studies, a comparison of the locomotor classification average index values and standard deviations for humeri and femora reported by Samuels and Van Valkenburgh (2008) and recovered here is provided in Table 5.5. As can be seen, for each functional group most index averages recovered here are within one standard deviation of those reported by Samuels and Van Valkenburgh, and all are within two standard deviations. The larger index differences can likely be attributed to the different taxonomic compositions of the samples used as Samuels and Van Valkenburgh selected from a global sample of rodents for their functional groups, while this study was limited geographically to southern Africa. While only suggestive without formal testing, it is likely that individual element locomotor classifications would fail to correctly classify at the cutoff rate used here for application to the fossil record regardless of what dataset is used.

One final aspect that should be considered for the ecological functional analysis in general, and the individual element analysis in particular, is the taxon functional classifications themselves. While some taxa are highly specialized and thus fall easily within a specific category (e.g. Bathyergids are fossorial), many present with a generalized *bauplan* and exhibit a range of behaviors which could fall into two or more locomotor categories. When classifying taxa to locomotor groups here either the classifications of Samuels and Van Valkenburgh (2008) were used, or attempts were made to emulate these

Table 5.5. Comparison of means and standard deviations (SD) for functional indices calculated using humeri and femora reported in Samuels and Van Valkenburgh (2008: Table 5) and found in this study. Index abbreviations follow Table 3.8 with the FEI index corresponding the FEB index of Samuels and Van Valkenburgh. Numbers under each locomotor classification correspond to the number of species, and individuals used in each study. Values in bold and italics for this study are means that are within 2 SD of those reported in Samuels and Van Valkenburgh. All other means recovered here are within 1 SD.

	Samuels and Van Valkenburgh 2008											
	Terestrial		Semiaquatic		Arboreal		Semifossorial		Fossorial		Ricochetal	
	n = 14, 53		n = 8, 38		n = 9, 46		n = 9, 44		n = 16, 67		n = 7, 27	
Index	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
SMI	0.416	0.062	0.474	0.042	0.447	0.039	0.463	0.054	0.539	0.059	0.435	0.05
HRI	0.086	0.011	0.105	0.019	0.094	0.013	0.095	0.008	0.112	0.012	0.094	0.006
HEB	0.247	0.026	0.307	0.068	0.271	0.021	0.289	0.046	0.368	0.057	0.31	0.019
GI	0.092	0.022	0.119	0.015	0.112	0.024	0.116	0.024	0.125	0.027	0.115	0.017
FRI	0.084	0.01	0.105	0.018	0.087	0.012	0.086	0.012	0.104	0.013	0.079	0.008
FEI	0.179	0.032	0.268	0.051	0.218	0.033	0.208	0.032	0.247	0.023	0.181	0.023
	This Study											
	Terestrial		Semiaquatic		Arboreal		Semifossorial		Fossorial		Ricochetal	
	n = 23, 126		n = 2, 14		n = 8, 46		n = 8, 45		n = 6, 25		n = 1, 7	
Index	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
SMI	***0.488***	0.023	0.477	0.023	0.457	0.029	0.469	0.043	0.583	0.027	***0.516***	0.017
HRI	***0.074***	0.008	***0.081***	0.006	***0.079***	0.01	***0.081***	0.007	0.111	0.012	0.088	0.009
HEB	0.233	0.028	***0.227***	0.017	***0.241***	0.031	0.257	0.021	***0.298***	0.023	***0.286***	0.011
GI	0.108	0.011	0.118	0.007	0.103	0.01	0.121	0.015	0.125	0.016	***0.134***	0.008
FRI	***0.098***	0.012	0.109	0.011	0.089	0.007	0.092	0.011	***0.127***	0.03	***0.089***	0.005
FEI	0.184	0.016	***0.2***	0.016	***0.175***	0.013	0.187	0.027	0.256	0.018	0.0195	0.015

based on autecological descriptions of their habitat use (De Graaff 1981; Happold 2013, Kingdon 1974; Nowak 1991; Roberts 1951; Skinner and Chimimba 2005; Smithers 1971), however, some taxa could conceivably have been placed in an alternate locomotor group. As such, the following is a short discussion on some potential alternate locomotor behaviors to those used here (Table 3.9).

Arboreal: Arboreal taxa are defined here as capable of, and regularly seen climbing for escape, shelter, or foraging. In part due to their small size and generalized morphology, many rodents have at least some ability to climb when foraging or avoiding predators as has probably been noted by any casual observer of commensal rats and mice (i.e. *Rattus rattus, Rattus norvegicus, Mus musculus*) in urban environments. As such, the locomotor patterns of some taxa are referred to as terrestrial and scansorial, with the latter term indicating at least some climbing habits, while climbing proficiency is noted in others. Two taxa used in this analysis, the southern African pouched mouse (*Saccoostomus campestris*) and the four-striped grass mouse (*Rhabdomys pumilio*), are described as scansorial by Happold (2013), however, no remarks on their climbing abilities were found in other species descriptions (e.g. Skinner and Chimimba 2005) thus they were classified as terrestrial. The climbing ability of Woosnam's broad-headed mouse (*Zelotomys woosnami*) is noted by both Skinner and Chimimba (2005) and Happold (2013), while that of the pygmy rock rat (*Petromyscus collinus*) only by the latter. These taxa, however, are described as terrestrial and were also classified as such here. An alternate arboreal classification for these taxa, or the use of a semi-arboreal category may be justified.

Semi-aquatic: In addition to the taxa classified here as semi-aquatic, Happold (2013) notes that several species of creek rats are known to be semi-aquatic, though not morphologically adapted to water, including the East African creek rat (*Pelomys fallax*) analyzed here. Thus, while this taxon was classified as terrestrial, a semi-aquatic classification could also be justified.

Ricochetal: Ricochetal taxa are defined by jumping behaviors characterized by simultaneous use of the hind limbs and are commonly bipedal. Of the taxa examined here, only the springhare (*Pedetes capensis*) is considered bipedal, although several taxa in general, and most gerbils in particular are listed as terrestrial yet are adept jumpers. For example, both the hairy-footed gerbils (*Gerbillurus* spp.) and standard gerbils (*Gerbilliscus* spp.) examined here move via quadrupedal saltation facilitated by elongated hind feet and limbs (Happold 2013), however, none of these taxa are strictly bipedal as in the small dipodids *Allactaga* and *Jaculus* used by Samules and Van Valkenburgh (2008). Alternately, Cape short-tailed gerbils (*Desmodillus auricularis*) are terrestrial, non-saltatorial, with short and thick fore- and hindlimbs (Happold 2013). While the terrestrial definition does include some quadrupedal saltatory behavior, due to the hindlimb adaptations for jumping in most gerbils an argument could be made to add a quadrupedal jumping category.

Terrestrial: Recall terrestrial taxa are said to rarely swim or climb, may dig to make a burrow (but not extensively), may show saltatory behavior (quadrupedal only), and never glide. While this definition provides flexibility to account for varied behaviors exhibited by different taxa, it also makes classifications difficult for some groups. As noted above, although gerbils are described as terrestrial, and most are adept quadrupedal jumpers, they also are known to build complex burrows (Happold 2013). Owing to this last part they were classified as semi-fossorial here but may warrant a terrestrial classification. Alternately, veld rats (*Aethomys* spp.) are known to occasionally climb trees, while the least spiny mouse (*Acomys spinosissimus*) are known to burrow feeding

tunnels leading to roots and bulbs which they consume (Happold 2013). While these taxa were classified as terrestrial here, potential alternate classifications could be considered.

5.4 Paleoenvironmental Implications

So what can rodent postcrania tell us about Pleistocene environments at Swartkrans? Unfortunately, small sample sizes and high taxonomic resolution allow for few inferences to be made at this time. Despite over 200,000 microfaunal remains reported for Members 1-3 (Watson 1993), and the identification of over 10,000 individual rodents using craniodental remains (Avery 2001), few (N=329) complete femora and humeri were found. The scarcity of complete proximal appendicular elements was not expected as barn owls are known to do relatively little damage to the skeletal remains of their prey. For example, Andrews (1990:Table 3.3) analyzed the breakage patterns of major skeletal elements for a variety of avian predators and found that for barn owls 99% of humeri and 97% of femora recovered were "complete". In his analysis, however, breakage to the epiphyses, damage to the greater trochanter of the femur, and damage to the distal articulation of the humerus was not considered thus, it is not known how many specimens one could expect to be found intact in modern barn owl pellets. As these features are all needed for the various measurements taken here, and in order to generate accurate outlines of the specimens, if a majority of rodent remains found in modern barn owl lose their epiphyses the type of analyses conducted here may be of limited use.

Although statistical support was found for differentiation of rodent postcrania at the family through genus level, and significant differences were found between locomotor

categories, classifications of known specimens using cross-validation typically performed poorly and only the analysis of fossil femoral form using GM was possible below the family level. A comparison between the subfamilies recovered here using postcrania, and those found utilizing craniodental remains by Avery (2001) is given in Table 5.6. As can be seen this study failed to identify any dormice graphiurines, or gerbillines, although both groups were previously found at low abundances. Additionally, the proportions of higher taxa identified differ, with murids representing the most abundant family found here while nesomyids were found to be the most abundant using craniodental remains. These differences are potentially due to the small sample size found here and thus care should be taken before inferring to much from these results.

While this study failed to recover members from two rodent subfamilies, it did identify specimens of the pouched mice and rats (Cricetomyinae) and rock mice (Petromyscinae) which have not previously been reported at Swartkrans. The subfamily Cricetomyinae currently is represented by two species in southern Africa, the Gambian giant pouched rat (*Cricetomys gambianus*), and the southern African pouched mouse (*Saccostomus campestris*). Owing to the larger size of *C. gambianus*, the specimens recovered here most likely represent a form of pouched mouse. Modern *S. campestris* are characterized as terrestrial/scansorial, and occur in many types of woodlands, grasslands, and close to marshes (Happold 2013). Relying on the principal of transferred ecology, their presence is thus consistent with a mosaic habitat type, while possibly indicating a greater degree of woody cover in Members 1 and 2 (Reed 2007).

Table 5.6. Proportional representation of rodent taxa from Swartkrans Members 1-3 recovered by Avery (2001) and in this study.

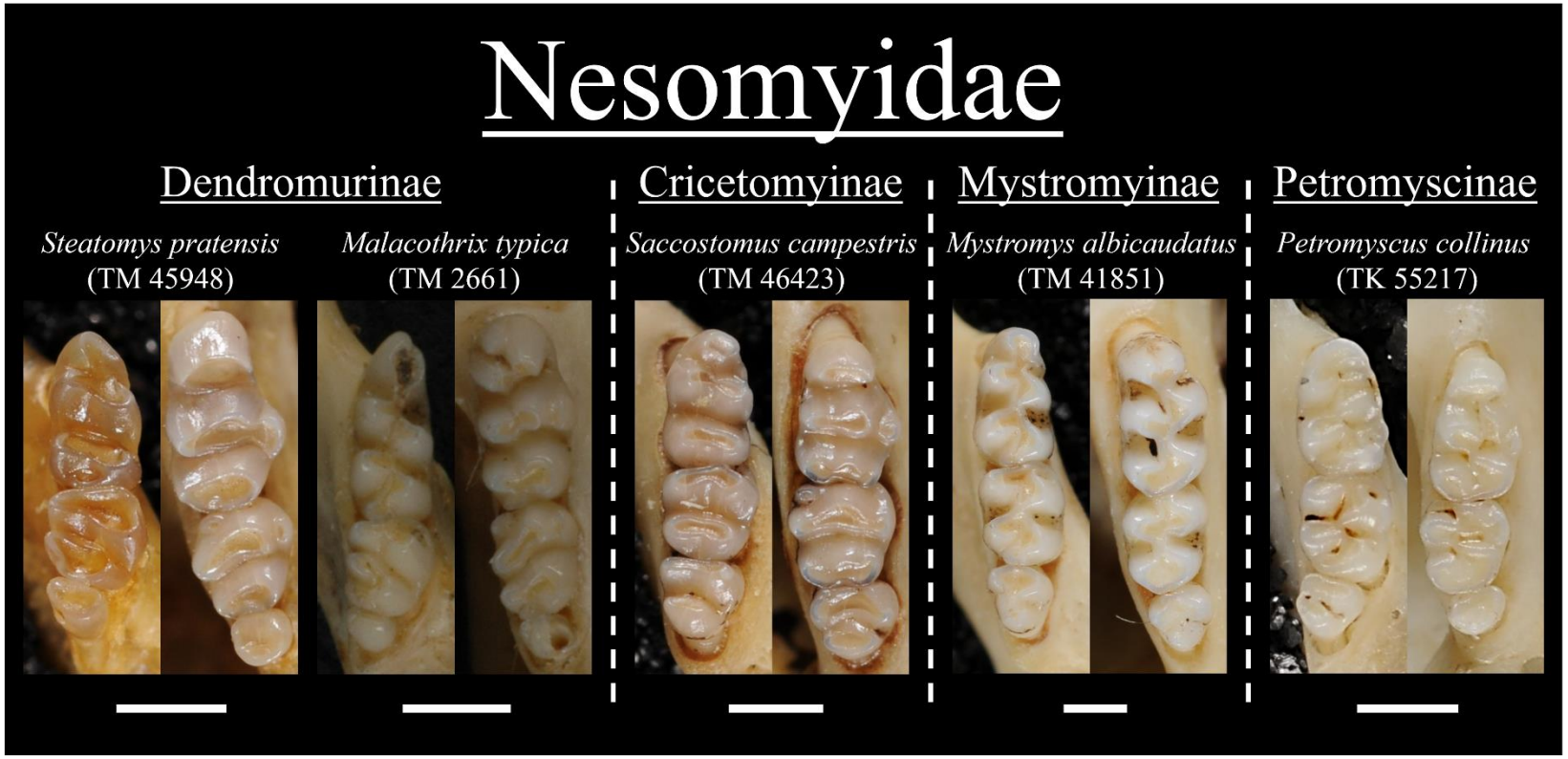
Taxa		**Avery 2001**			**This Study**		
Family	Subfamily	SKX 1	SKX 2	SKX 3	SKX 1	SKX 2	SKX 3
Bathergidae		**11.4**	**15.6**	**11.7**	-	**16.0**	**4.3**
	Batherignae	11.4	15.6	11.7	-	16.0	4.3
Gliridae		1.1	1.5	1.1	-	-	-
	Graphiurinae	1.1	1.5	1.1	-	-	-
Muridae		**22.6**	**25.3**	**23.0**	**54.3**	**68.0**	**69.6**
	Gerbillinae	1.5	0.8	1.3	-	-	-
	Deomyinae	0.1	0.1	< 0.1	-	8.0	-
	Otomyinae	12.7	13.5	13.7	18.6	32.0	13.0
	Murinae	8.4	11.0	8.0	35.7	28.0	56.5
Nesomyidae		**64.9**	**57.5**	**64.1**	**45.7**	**16.0**	**26.1**
	Cricetomyinae	-	-	-	2.9	4.0	-
	Dendromurinae	1.3	2.1	0.7	5.7	4.0	4.3
	Mystromyinae	63.6	55.5	63.5	17.1	-	13.0
	Petromyscinae	-	-	-	20.0	8.0	8.7
	Totals	5411	2136	2669	70	25	23

While the presence of cricetomyines may indicate more wooded habitats in the earlier members of Swartkrans, an alternate habitat signal is inferred from the presence of petromyscines. This subfamily currently consists of one genus (*Petromyscus*) and four species, (*P. montiularis, P. barbourin, P. collinus, P. shortridgei*) found in the xeric areas of western South Africa, Namibia, and into southern Angola. These areas consist of arid to semi-arid habitats and members of this genus are restricted to rocky hills and outcrops within which they find shelter (Happold 2013). Their presence in all three members at Swartkrans suggests a significant arid component during the times these deposits accumulated.

Why no members of these two subfamilies were identified from craniodental remains at Swartkrans remains unclear. As both groups are in the family Nesomyidae they share a suite of unique dental characters and it is unlikely that specimens would be misidentified for members of other families. Within the family, however, there is enough similarity that misidentifications are possible, particularly when dealing with fragmentary specimens lacking the entire molar complement (Figure 5.1). Due to the results of this study, it may be worthwhile to reexamine the craniodental remains attributed to *Steatomys pratensis* from Swartkrans and take into consideration the possibility that they represent remains *S. campestris*. These taxa both have similarly sized maxillary first molars (M1), and lack a T1 cusp on the lingual side of M1, however, they differ in terms of the development of the third maxillary molars, presence of an incipient T7 on M1 in *Saccostomus*, posterior extension of the anterior palatal foramen, and development of a masseteric knob in *Steatomys* (Pierce et al. in prep). A second comparison that may be warranted is between *Mystromys albicaudatus*, the most numerically dominant taxa using craniodental remains, and *Petromyscus* spp. as a sister taxa relationship has been suggested between the monogeneric Mystromyinae, and Petromyscinae (Happold 2013), and their molar morphology bear some resemblance. Both genera are characterized by an offset molar cusp arrangement that results in what has been described as a zig-zag enamel pattern (Skinner and Chimimba 2005). Modern specimens differ, however, in that *Mystromys* are notably larger, have a greater posterior extension of the anterior palatal foramen, and lack an additional lingual cusp (T4?) along the primary lingual series as seen in *Petromyscus* (Happold 2013). The degree to which these features are apparent in

Pleistocene members, or evident in fragmentary or heavily worn specimens is not known and may warrant further investigation.

Figure 5.1. Select sample representing the four subfamilies of nesomyids in southern Africa. For each species the right mandibular tooth row is presented first, then the right maxillary. Scale bar underneath each taxon represent 1 mm. Collections abbreviations as follows: TM – Ditsong National Museum of Natural History, TK - Natural Science Research Laboratory – Museum of Texas Tech University.



6. CONCLUSION

After a careful analysis of the representation of individual prey items based on rodent postcranial appendicular elements compared to craniodental remains in modern owl coprocoenoses, and of both the ecological functional and taxonomic signals present in southern African rodent postcrania, several conclusions can be made.

First, counts of rodent prey taken using postcrania are as representative, or better than counts of craniodental remains providing that counts are made using sided elements on a per pellet basis. Although most studies of modern owl accumulations appear to tabulate their data in this manner, reports of only percent representation and/or raw element counts are insufficient for comparisons of the number of individuals recovered. In the future it is recommended that sided element counts be provided. Additionally, these types of studies should also explicitly state the protocols used for counting and tabulating their data.

Second, there is strong statistical support for the differentiation of southern African rodents by locomotor pattern when all appendicular elements are used, and for differences in individual functional indices across locomotor groups. When all indices are used for classification, accuracy is sufficiently high so that they can be applied to an unknown sample. Alternately, when only the indices derived from humeri or femora are used in a single element analysis classification rates are low and do not warrant application to an unknown sample.

Third, there is strong statistical support for a taxonomic signal in southern African rodents at the family, subfamily, and genus levels using linear measurements and TM. This signal is present when all elements are analyzed together, when only humeri or femora are considered individually, and when the analyses are run on either specimen shapes of forms. When used for classification, however, only analyses using all appendicular postcranial elements had accuracy sufficiently high to warrant application to an unknown sample.

Fourth, there is strong statistical support for a taxonomic signal in southern African rodents at the family, subfamily, and genus levels using an outline-based analysis and GM. This signal is present for both the humeri and femora, and when the analyses are run on either specimen shapes of forms. When used for classification, however, only femoral shape analysis at the family level, and femoral form analyses at the family and subfamily levels presented sufficiently high classification rates to be applied to an unknown sample.

Fifth, when the results from the GM analysis of femoral form are used to classify fossil rodent femora from Swartkrans specimens from two previously unidentified subfamilies are recovered. These two subfamilies, the Cricetomyinae and Petromyscinae, potentially indicate a more wooded habitat, and an arid or semi-arid habitat respectively. As both of these taxa are in the family Nesoymidae, and share some dental features with other members of this group, a reexamination of the craniodental remains attributed to allied taxa is recommended.

In summary, this study finds that African rodent postcranial remains are as representative as craniodental remains in modern owl produced assemblages, and that both

taxonomic and ecological functional signals are present in these remains. Analyses of these signals, however, generally require the use of all appendicular long bone elements in order to achieve a high enough classification accuracy to justify their application to the fossil record. At present, only the analysis of femoral form can provide taxonomic resolution below the family level. When applied to fossil rodent femora at Swartkrans two previously unidentified subfamilies are recovered which suggest both a wooded component in Members 1 and 2, and a significant arid component in Members 1-3 during the period in which these deposits accumulated.

REFERENCES

Abiadh, A., Chetoui, M., Lamine-Cheniti, T., Capanna, E., Colangelo, P., 2010. Molecular phylogenetics of the genus *Gerbillus* (Rodentia, Gerbillinae): Implications for systematics, taxonomy and chromosomal evolution. Molecular Phylogenetics and Evolution 56, 513-518.

Adkins, R.M., Gelke, E.L., Rowe, D., Honeycutt, R.L., 2001. Molecular phylogeny and divergence time estimates for major rodent groups: Evidence from multiple genes. Molecular Biology and Evolution 18, 777-791.

Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. Journal of Human Evolution 44, 451-478.

Alexander, G, Marais, J., 2007. A Guide to the Reptiles of Southern Africa. Struik Publishers, Cape Town.

Alroy, J., Koch, P.L., Zachos, J.C., 2000. Global climate change and North American mammalian evolution. Paleobiology 26, 259-288.

Andrews, P., 1989. Paleoecology of Laetoli. Journal of Human Evolution 18, 173–181.

Andrews, P., 1990. Owls, Caves and Fossils. The University of Chicago Press, Chicago.

Argot, C., 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. Journal of Morphology 247, 51–79.

Auerbach, R.D., 1987. The Amphibians and Reptiles of Botswana. Mokwepa Consultants, Gaborone.

Avery, D.M., 1982a. The micromammalian fauna from Border Cave, Kwazulu, South Africa. Journal of Archaeological Science 9, 187-204.

Avery, D.M., 1982b. Micromammals as palaeoenvironmental indicators and an interpretation of the Late Quaternary in the Southern Cape Province, South Africa. Annals of the South African Museum 85, 183-374.

Avery, D.M., 1984. Micromammalian population dynamics and environmental change: The last 18 000 years in the southern Cape. In: Vogel, J.C. (Ed.), Late Cainozoic Palaeoclimates of the Southern Hemisphere. A. A. Balkema, Rotterdam, pp. 361-369.

Abiadh, A., Chetoui, M., Lamine-Cheniti, T., Capanna, E., Colangelo, P., 2010. Molecular phylogenetics of the genus *Gerbillus* (Rodentia, Gerbillinae): Implications for systematics, taxonomy and chromosomal evolution. Molecular Phylogenetics and Evolution 56, 513-518.

Adkins, R.M., Gelke, E.L., Rowe, D., Honeycutt, R.L., 2001. Molecular phylogeny and divergence time estimates for major rodent groups: Evidence from multiple genes. Molecular Biology and Evolution 18, 777-791.

Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. Journal of Human Evolution 44, 451-478.

Alexander, G, Marais, J., 2007. A Guide to the Reptiles of Southern Africa. Struik Publishers, Cape Town.

Alroy, J., Koch, P.L., Zachos, J.C., 2000. Global climate change and North American mammalian evolution. Paleobiology 26, 259-288.

Andrews, P., 1989. Paleoecology of Laetoli. Journal of Human Evolution 18, 173–181.

Andrews, P., 1990. Owls, Caves and Fossils. The University of Chicago Press, Chicago.

Argot, C., 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. Journal of Morphology 247, 51–79.

Auerbach, R.D., 1987. The Amphibians and Reptiles of Botswana. Mokwepa Consultants, Gaborone.

Avery, D.M., 1982a. The micromammalian fauna from Border Cave, Kwazulu, South Africa. Journal of Archaeological Science 9, 187-204.

Avery, D.M., 1982b. Micromammals as palaeoenvironmental indicators and an interpretation of the Late Quaternary in the Southern Cape Province, South Africa. Annals of the South African Museum 85, 183-374.

Avery, D.M., 1984. Micromammalian population dynamics and environmental change: The last 18 000 years in the southern Cape. In: Vogel, J.C. (Ed.), Late Cainozoic Palaeoclimates of the Southern Hemisphere. A. A. Balkema, Rotterdam, pp. 361-369.

Avery, D.M., 1987. Late Pleistocene coastal environment of the Southern Cape Province of South Africa: Micromammals from Klasies River Mouth. Journal of Archaeological Science 14, 405-421.

Avery, D.M., 1992a. Ecological data on micromammals collected by barn owls *Tyto alba* in the West Coast National Park, South Africa. Israel Journal of Zoology 38, 385-397.

Avery, D.M., 1992b. Man and/or climate? Environmental degradation and micromammalian community structure in South Africa during the last millennium. South African Journal of Science 88, 483-489.

Avery, D.M., 1992c. The environment of early modern humans at Border Cave, South Africa: Micromammalian evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 91, 71-87.

Avery, D.M., 1995. Southern savannas and Pleistocene hominid adaptations: The micromammalian perspective. In: Vrba, E.S., Denton, G.H., Partridge, T.C. Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 459-478.

Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. Journal of Human Evolution 41, 113-132.

Avery, D.M., 2003. Early and Middle Pleistocene environments and hominid biogeography; micromammalian evidence from Kabwe, Twin Rivers and Mumbwa Caves in central Zambia. Palaeogeography, Palaeoclimatology, Palaeoecology 189, 55-69.

Avery, D.M., Avery G., Colahan, B.D., 2003. Micromammals and barn owls in the Free State, South Africa: Prey distribution and predator behaviour. Researches- Nasionale Museum Bloemfontein 19, 1-18.

Avery, D.M., Rautenbach, I.L, Randall, R.M., 1990. An annotated check list of the land mammal fauna of the West Coast National Park. Koedoe 33, 1-18.

Avenant, N.L., 2005. Barn owl pellets: A useful tool for monitoring small mammal communities? Belgian Journal of Zoology 135, 39-43.

Bamford, M., 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. South African Journal of Science 95, 231-237.

Bamford, M.K., Neumann, F.H., Pereira, L.M., Scott, L., Dirks, P.H.G.M., Berger, L.R., 2010. Botanical remains from a coprolite from the Pleistocene hominin site of Malapa, Sterkfontein Valley, South Africa. Palaeontologia africana 45, 23-28.

Barr, W.A., 2014. Functional morphology of the bovid astragalus in relation to habitat: Controlling phylogenetic signal in ecomorphology. Journal of Morphology 275, 1201-1216.

Barr, W.A., 2015. Paleoenvironments of the Shungura Formation (Plio-Pleistocene: Ethiopia) based on ecomorphology of the bovid astragalus. Journal of Human Evolution 88, 97-107.

Barr, W.A., Scott, R.S., 2014. Phylogenetic comparative methods complement discriminant function analysis in ecomorphology. American Journal of Physical Anthropology 153, 663-674.

Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Jacobs, L.L., Lindsay, E.H., Raxa, S.M., Solounais, N., 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of Northern Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology 115, 209-226.

Bateman, J.A., 1960. Owl habits from pellets. Zoological Society of South Africa News Bulletin 1, 20-21.

Bauer, A.M., Kennedy, A.M., Lewis, P.J., Thies, M.L., Gabadirwe, M., 2009. The herpetofauna of Koanaka South and adjacent regions, Ngamiland, Botswana. Herpetological Bulletin 107, 16-26.

Behrensmeyer, A.K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. Science 278, 1589-1594.

Benefit, B.R., McCrossin, M.L., 1990. Diet, species diversity and distribution of African fossil baboons. Kroeber Anthropological Society Papers 71/72, 77-93.

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: A new species of *Homo*-like australopith from South Africa. Science 328, 195-204.

Berger, L.R., Hawks, J., de Ruiter, D.J., Churchill, S.E., Schmid, P., Delezene, L.K., Kivell, T.L., Garvin, H.M., Williams, S.A., DeSilva, J.M., Skinner, M.M., Musiba, C.M., Cameron, N., Holliday, T.W., Harcourt-Smith, W., Ackermann, R.R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z.D., Congdon, K.A., Deane, A.S., Dembo, M., Drapeau, M., Elliott, M.C., Feuerreigel, E.M., Garcia-Martinez, D., Green, D.J., Gurtov, A., Irish, J.D., Kruger, A., Laird, M.F., Marchi, D., Meyer, M.R., Nalla, S., Negash, E.W., Orr, C.M., Racovcic, D., Schroeder, L., Scott, J.E., Throckmorton, Z., Tocheri, M.W., VanSickle, C., Walker, C.S., Wei, P., Zipfel, B., 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4, e09560.

Biknevicius, A.R., 1993. Biomechanical scaling of limb bones and differential limb use in caviomorph rodents. Journal of Mammalogy 74, 95–107.

Blanga-Kanfi, S., Miranda, H., Penn, O., Pupko, T., DeBry, R.W., Huchon, D., 2009. Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. BMC Evolutionary Biology 9, 1-12.

Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 399-420.

Bobe, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. Journal of Human Evolution 42, 475-497.

Bobe, R., Eck, G.G., 2001. Responses of African bovids to Piocene climatic change. Paleobiology 27, 1-47.

Bonnefille, R., 1984. Cenozoic vegetation and environments of early hominids in east Africa. In: Whyte, R.O. (Ed.), The Evolution of East Asian Environments, Volume II, Paleobotany, Paleozoology, and Paleoanthropology. University of Hong Kong, Center of Asian Studies, pp. 579-612.

Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record in East Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C. Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 299-310.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proceedings of the National Academy of Sciences 101, 12125-12129.

Bottjer, D.J., Etter, W., Hagadorn, J.W., Tang, C.M., 2002. Fossil-Lagerstatten: Jewels of the fossil record. In: Bottjer, D.J., Etter, W., Hagadorn, J.W., Tang, C.M. (Eds.), Exceptional fossil preservation. Columbia University Press, New York, pp. 1-10.

Brain, C.K., 1970. New finds at the Swartkrans australopithecine site. Nature 225, 1112-1119.

Brain, C.K., 1974. The use of microfaunal remains as habitat indicators in the Namib. Goodwin Series 2, 55-60.

Brain, C.K., 1976. A re-interpretation of the Swartkrans site and its remains. South African Journal of Science 72, 141-146.

Brain, C.K., 1981. Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.

Brain, C.K., 1988. New Information from the Swartkrans Cave of Relevance to "Robust" Australopithecines. In: Grine, F.E. (Ed), Evolutionary History of the "Robust" Australopithecines. Aldine de Gruyter, New York, pp. 311-316.

Brain, C.K., 1993a. Swartkrans: A Cave's Chronical of Early Man. Transvaal Museum Monograph 8, Pretoria.

Brain, C.K., 1993b. Structure and stratigraphy of the Swartkrans cave in the light of the new excavations. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph 8, Pretoria, pp. 23-33.

Brain, C.K., 2004. Swartkrans: A Cave's Chronical of Early Man, Second Eddition. Transvaal Museum Monograph 8, Pretoria.

Brain, C.K., Brain, V., 1977. Microfaunal remains from Mirabib: Some evidence of palaeo-ecological changes in the Namib. Madoqua 10, 285-293.

Broadley, D.G., 1974. Predation by birds by reptiles and amphibians in South-Eastern Africa. The Honeyguide 78, 11-19.

Broom, R., 1907. On some new species of *Chrysochloris*. Journal of Natural History 19, 262-268.

Broom, R., 1937. Notices of a few more new fossil mammals from the caves of the Transvaal. Annals and Magazine of Natural History 20, 509-514.

Broom, R., 1949. Another new type of fossil ape-man. Nature 163, 57.

Broom, R., 1950. Finding the Missing Link: An account of Recent Discoveries Throwing New Light on the Origin of Man. Watts & Co, London.

Broom, R., Robinson, J.T., 1949. A new type of fossil man. Nature 164, 322-323.

Broom, R., Robinson, J.T., 1950. Man contemporaneous with the Swartkrans ape-man. American Journal of Physical Anthropology 8, 151-155.

Broom, R., Robinson, J.T., 1952. Swartkrans ape-man *Paranthropus crassidents.* Transvaal Museum Memoir 6, Pretoria.

Bunn, D.S., Warburton, A.B., Wilson, R.D.S., 1982. The Barn Owl. Buteo Books, Vermillion.

Burgman, J.H.E., Leichliter, J., Avenant, N.L., Ungar, P.S., 2016. Dental microwear of sympatric rodent species sampled across habitats in southern Africa: Implications for environmental influence. Integrative Zoology 11, 111-127.

Butzer, K.W., 1976. Lithostratigraphy of the Swartkrans formation. South African Journal of Science 72, 136-141.

Campbell, T.L., 2010. Genus level assessment of the environmental tolerences of southern African rodents with implications for Plio-Pleistocene paleoenvironmental reconstructions. Master's Thesis: Department of Biological Sciences, Sam Houston State University.

Campbell, T.L., Lewis, P.J., Williams, J.K., 2011. Analysis of the modern distribution of South African *Gerbilliscus* (Rodentia: Gerbillinae) with implications for Plio-Pleistocene palaeoenvironmental reconstruction. South African Journal of Science 107, 1-8.

Campbell, T.L., Lewis, P.J., Thies, M.L., Williams, J.K., 2012. A Geographic Information Systems (GIS)-based analysis of modern South African rodent distributions, habitat use, and environmental tolerances. Ecology and Evolution 2, 2881-2894.

Campbell, T.L., Pierce, Z.W., Dollman, K.N., Bamford, M.K., Musiba, C.M., Magori, C., 2018. Syntopy and co-utilization of a "roosting area" by the barn owl (*Tyto alba*) and spotted eagle owl (*Bubo africanus*) in Tanzania. African Journal of Ecology 58, 664-668.

Candela, A.M., Picasso, M.B.J., 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): Indicators of locomotor behavior in Miocene porcupines. Journal of Morphology 269, 552-593.

Caporale, S.S., Ungar, P.S., 2016. Rodent incisor microwear as a proxy for ecological reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 446, 225-233.

Carrión, J.S., Scott, L., 1999. The challenge of pollen analysis in paleoenvironmental studies of hominid beds: The record from Sterkfontein caves. Journal of Human Evolution 36, 401-408.

Cartmill, M., 1967. The early Pleistocene mammalian microfaunas of sub-Saharan Africa and their ecological significance. Quaternaria 9, 169-198.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153-158.

Churcher, C.S., Watson, V., 1993. Additionaly fossil Equidae from Swartkrans. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph 8, pp. 137-150.

Clarke R.J., 1998. First ever discovery of a well preserved skull and associated skeleton of *Australopithecus.* South African Journal of Science 94, 460–463.

Coetzee, C.G., 1963. The prey of owls in the Kruger National Park as indicated by owl pellets collected during 1960-61. Koedoe 6, 115-125.

Colangelo, P., Granjon, L., Taylor, P.J., Corti, M., 2007. Evolutionary systematics in African gerbilline rodents of the genus *Gerbilliscus*: Inference from mitochondrial genes. Molecular Phylogenetics and Evolution 42, 797-806.

Cooke, H.B.S., 1952. Mammals, ape-men and Stone Age men in southern Africa. The South African Archaeological Bulletin 7, 59-69.

Cooke, H.J., 1975. The paleoclimatic significance of caves and adjacent landforms in western Ngamiland, Botswana. The Georaphical Journal 141, 430-444.

Crass, R.S., 1944. The birds of Sulenkama, Qumbu District, Cape Province. Ostrich 15, 10-20.

Dart, R.A., 1925. *Australopithecus africanus*: The man-ape of South Africa. Nature 115, 195-199.

Dart, R.A., 1957. The osteodontokeratic culture of *Australopithecus prometheus*. Transvaal Museum Memoir 6, Pretoria.

Davis, D.H.S., 1958. Notes on some small mammals in the Kalahari Gemsbok National Park, with special reference to those preyed upon by barn owls. Koedo*e* 1, 184-188.

Davis, D.H.S., 1959. The barn owl's contribution to ecology and palaeoecology. Ostrich 30, 144-153.

Dean, W.R.J., 1973a. Analysis of a collection of barn owl *Tyto alba* pellets from Warmbaths, Transvaal. Zoologica Africana 8, 75-81.

Dean, W.R.J., 1973b. Age distribution of *Praomys natalensis* prey in *Tyto alba* pellets. Zoologica Africana 8, 140.

Dean, W.R.J., 1974. Analysis of *Tyto alba* pellets from Angola. Zoologica Africana 9, 89-90.

Dean, W.R.J. (1975). *Tyto alba* prey in South West Africa and the northern Cape. *Zoologica Africana* 10:217-219.

Dean, W.R.J., 1978. The ecology of owls at Barberspan, Transvaal. Symposium on African Predatory Birds, Northern Transvaal Ornithological Society, Pretoria, pp. 25-45.

De Graaff, G., 1960a. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal System. Palaeontologia Africana 7, 59-118.

De Graaff, G., 1960b. N Ontleding van Uilklonte van die Nonnetjiesuil *Tyto alba*. Ostrich 31, 1-5.

De Graaff, G., 1981. The Rodents of Southern Africa. Butterworths, Durban.

D'Elía, G., Fabre, P.-H., Lessa, E.P., 2019. Rodent systematics in an age of discovery: recent advances and prospects. Journal of Mammalogy 100, 852-871.

de Ruiter, D.J., 2003. Revised faunal lists for Members 1-3 of Swartkrans, South Africa. Annals of the Transvaal Museum 40, 29-41.

de Ruiter, D.J., 2004. Relative abundance, skeletal part representation and accumulating agents of macromammals at Swartkrans. In: Brain, C.K. (Ed.), A Cave's Chronical of Early Man, Second Eddition. Transvaal Museum Monograph 8, Pretoria, pp. 265-278.

de Ruiter, D.J., Sponheimer, M., Lee-Thorp, J.A., 2008. Indications of habitat association of *Australopithecus robustus* in the Bloubank Valley, South Africa. Journal of Human Evolution 55, 1015-1030.

DeGusta D., Vrba E.S., 2005a. Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton. Journal of Archaeological Science 32, 1115-1123.

DeGusta, D., Vrba, E.S., 2005b. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. Journal of Archaeological Science 32, 1099-1113.

deMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53-59.

deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. Earth and Planetary Science Letters 220, 3-24.

deMenocal, P.B., Bloemendal, J. (1995). Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: A combined data-model approach. *Paleoclimate and evolution with emphasis on human origins*. Vrba, E.S., Denton, G.H., Partridge, T.C. Burckle, L.H. eds. New Haven, Yale University Press:262-288.

Demeter, A., 1978. Food of a barn owl, *Tyto alba* in Nigeria. Nigerian Ornithologists' Society Bulletin 14, 9-13.

Denys, C., 1999. Of mice and men: Evolution in East and South Africa during Plio-Pleistocene times. In: Bromage, T.G., Schrenk, F. (Eds.), African Biogeography, Climate Change, and Human Evolution. Oxford University Press, New York, pp. 226–252.

Dixon, J.E.W., Perrin, M.R., 1994. Prey selection by owls in the Etosha National Park. Journal of Ornithology 135, 172.

Dodson, P., Wexlar, D., 1979. Taphonomic Investigations of Owl Pellets. Paleobiology 5, 275-284.

Dunn, R.H., Rasmussen, D.T., 2007. Skeletal morphology and locomotor behavior of *Pseudotomus eugenei* (Rodentia, Paramyinae) from the Uinta Formation, Utah. Journal of Vertebrate Paleontology 27, 987-1006.

Edwards, T.R., Armstrong, B.J., Birkett-Rees, J., Blackwood, A.F., Herries, A.I.R., Penzo-Kajewski, P., Pickering, R., Adams, J.W., 2019. Combining legacy data with new drone and DGPS mapping to identify the provenance of Plio-Pleistocene fossils from Bolt's Farm, Cradle of Humankind (South Africa). PeerJ 7, e6202.

Elissamburu, A., Vizcaino, S.F. (2004). Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). Journal of Zoology 262:145-159.

Evans, E.M.N., Van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in western Kenya. Journal of Human Evolution 10, 99-116.

Fabre, P.-H., Hautier, L., Dimitar, D., Douzery, E.J.P., 2012. A glimpse on the pattern of rodent diversification: A phylogenetic approach. BMC Evolutionary Biology 12, 1-19.

Faith, J.T., Behrensmeyer, A.K., 2013. Climate change and faunal turnover: testing the mechanics of the turnover-pulse hypothesis with South African fossil data. Paleobiology 39, 609-627.

Farkas, T., 1966. The birds of Barberspan: III. Some structural changes in the avifauna of the Barberspan Nature Reserve. Ostrich 37, 463-491.

Ferguson, A., McDonough, M.M., Thies, M.L., Lewis, P.J., Gabadirwe, M., 2010. Mammals of the Koanaka Hills region in Ngamiland: A provisional checklist. Botswana Notes and Records 42, 163-171.

Fernandez, M.E., Vassallo, A.I., Zarate, M., 2000. Functional morphology and paleobiology of the Pliocene rodent *Actenomys* (Caviomorpha: Odontodidae): The evolution to a subterranean mode of life. Biological Journal of the Linnean Society 71, 71–90.

Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). Journal of Human Evolution 34, 137-172.

Fitzsimons, F.W., 1923. The Natural History of South Africa: Birds, Volumes 1 & 2. Longmans, Green and Co, New York.

Franz-Odendaal, T.A., Lee-Thorp, J.A., Chinsamy, A., 2002. New evidence for the lack of C4 grassland expansions during the early Pliocene at Langebaanweg, South Africa. Paleobiology 28, 378-388.

Fry C.H., Keith S., Urban E.K. (Eds), 1993. The Birds of Africa, Volume 1. Academic Press, New York.

Gibbon, R.J., Pickering, T.R., Sutton, M.B., Heaton, J.L., Kuman, K., Clarke, R.J., Brain, C.K., Granger, D.E., 2014. Cosmogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa. Quaternary Geochronology 24, 10-15.

Gichuki, C., 1987. The diet of the barn owl, *Tyto alba* (Scopoli), in Nairobi, Kenya. Journal of the East Africa Natural History Society and National Museum 75, 1-7.

Gingerich, P.D., 2003. Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. Paleobiology 29, 429–454.

Gommery, D., Badenhorst, S., Potze, S., Sénégas, F., Kgasi, L., Thackeray, J.F., 2012. Preliminary results concerning the discovery of new fossiliferous sites at Bolt's Farm

(Cradle of Humankind, South Africa). Annals of the Ditsong National Museum of Natural History 2, 33-45.

Grindley, J., Siegfried, W.R., Vernon, C.J., 1973. Diet of the barn owl in the Cape Province. Ostrich 44, 266-267.

Hanney, P., 1963. Observations upon the food of the barn owl (*Tyto alba*) in Southern Nyasaland, with a method of ascertaining population dynamics of rodent prey. Annals and Magazine of Natural History, London 6, 305-313.

Happold, D.C.D. (Ed.), 2013. Mammals of Africa: Volume. III. Rodents, Hares and Rabbits. Bloomsbury Publishing, London.

Hawks, J., Elliott, M., Schmid, P., Churchill, S.E., de Ruiter, D.J., Roberts, E.M., Hilbert-Wolf, H., Garvin, H.M., Williams, S.A., Delezene, L.K., Feuerriegel, E.M., Randolph-Quinney, P., Kivell, T.L., Laird, M.F., Tawane, G., DeSilva, J.M., Bailey, S.E., Brophy, J.K., Meyer, M.R., Skinner, M.M., Tocheri, M.W., VanSickle, C., Walker, C.S., Campbell, T.L., Kuhn, B., Kruger, A., Tucker, S., Gurtov, A., Hlophe, N., Hunter, R., Morris, H., Peixotto, B., Ramalepa, M., van Rooyen, D. Tskioane, M., Boshoff, P., Dirks, P.H., Berger, L.R., 2017. New fossil remains of *Homo naledi* from the Lesedi Chamber, South Africa. eLife 6, e24232.

Henshilwood, C.S., 2008. Holocene prehistory of the Southern Cape, South Africa. Cambridge Monographs in African Archaeology 75, 1-171.

Herholdt, J.J., 1986. Diet of the barn owl at a riverine roost in the central Orange Free State. Ostrich 57, 185-192.

Herries, A.I.R., Hopley, P.J., Adams, J.W., Curnoe, D. Maslin, M.A., 2010. Letter to the editor: Geochronology and palaeoenvironments of southern African hominin-bearing Localities—A reply to Wrangham et al., 2009. ‘‘Shallow-water habitats as sources of fallback foods for hominins’’. American Journal of Physical Anthropology 143, 640-646.

Hildebrand, M., 1985. Digging of quadrupeds. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.), Functional Vertebrate Morphology. Harvard University Press, Cambridge, pp. 89-109.

Hill, A., 1987. Causes of perceived faunal change in the later Neogene of East Africa. Journal of Human Evolution 16, 583-596.

Hockey, P.A.R., Dean, W.R.J., Ryan, P.G. (Eds), 2005. Roberts birds of southern Africa, Seventh Edition. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Hopley, P.J., Latham, A.G., Marshall, J.D., 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: A stable isotope and dental microwear approach. Palaeogeography, Palaeoclimatology, Palaeoecology 233, 235-251.

Horowitz, A., 1975. Preliminary palaeoenvironmental implications of pollen analysis of Middle Breccia from Sterkfontein. Nature 258, 417-418.

Hughes, A.R., Tobias, P.V., 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. Nature 265, 310-312.

Isaev, M.A., Denisova, L.N., 1995. The computer programs for shape analysis of plant leaves. Proceedings of the “Mathematics. Computer. Education" International conference, Pushchino.

Jaeger, J-J., 1976. Les rongeurs (Mammalia, Rodentia) du Pleistocene Inferieur d'Olduvai Bed I (Tanzanie), IERE. In: Savage, J.G., Coryndon, S.C. (Eds.), Fossil Vertebrates of Africa. Academic Press, London, pp. 57-124.

Jolly, C.J., 1970. The seed eaters: A new model of hominid differentiation based on a baboon analogy. Man 5, 5–26.

Kappelman, J., 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. Journal of Morphology 198, 119–130.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997. Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. Journal of Human Evolution 32, 229-256.

Kemp, A.C., 1993. Strigidae, typical owls. In: Fry, C.H., Keith, S., Urban, E.K. (Eds), The Birds of Africa, Volume 3. Academic Press, New York, pp. 110-155.

Kemp, A.V., 2005a. Barn owl. In: Hockey, P.A.R., Dean, W.R.J., Ryan, P.G. (Eds.), Roberts Birds of Southern Africa, Seventh Edition. Trustees of the John Voelcker Bird Book Fund, Cape Town, pp. 251-252.

Kennedy, A.M., Marais, J., Bauer, A.M., Lewis, P.J., Thies, M.L., 2012. Effect of fire on the herpetofauna of the Koanaka Hills, Ngamiland, Botswana. Check List 8, 666-674.

Kimbel, W., 1995. Hominid speciation and Pliocene climatic change. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds, Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 425-437.

Kingdon, J., 1974. East African Mammals: An Atlas of Evolution in Africa, Volume II, Part B (Hares and Rodents). Academic Press, London.

Kingdon, J., Hoffman, M. (Eds.), 2013a. Mammals of Africa Volume V: Carnivores, Pangolins, Equids, and Rhinoceroses. Bloomsbury Publishing, London.

Kingdon, J., Hoffman, M. (Eds.), 2013b. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe and Bovids. Bloomsbury Publishing, London.

Kolbe, F.F., 1946. The case for the barn owl. African Wildlife 1, 69-73.

Kopij, G., 1997. Food of the barn owl *Tyto alba* in a farmland near Bloemfontein, South Africa. Journal of African Raptor Biology 12, 20-23.

Korth, W.W., 1979. Taphonomy of microvertebrate fossil assemblages. Annals of Carnegie Museum 48, 235-285.

Kuman, K., Sutton, M.B., Pickering, T.R., Heaton, J.L., 2018. The Oldowan industry from Swartkrans cave, South Africa, and its relevance for the African Oldowan. Journal of Human Evolution 123, 52-69.

Kusmer, K.D., 1990. Taphonomy of owl pellet deposition. Journal of Paleontology 64, 629-637.

Laurie, W.A., 1971. The food of the barn owl in the Serengeti National Park, Tanzania. Journal of the East Africa Natural History Society and National Museum 28, 1-4.

Lee-Thorp, J.A., Sponheimer, M., Passey, B.H., de Ruiter, D.J., Cerling, T.E., 2010. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. Philosophical Transactions of the Royal Society: Series B 365, 3389-3396.

Lee-Thorp, J.A., van der Merwe, N.J , Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. Journal of Human Evolution 27, 361-372.

Leichliter, J., Sandberg, P., Passey, B., Codron, D., Avenant, N.L., Pain, O.C.C., Codron, J., de Ruiter, D., Sponheimer, M., 2017. Stable carbon isotope ecology of small mammals from the Sterkfontein Valley: Implications for habitat reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 485, 57-67.

Lessa, E.P., Patton, J.L., 1989. Structural constraints, recurrent shapes, and allometry in pocket gophers (genus *Thomomys*). Biological Journal of the Linnean Society 36, 349–363.

Lessa, E.P., Stein, B.R., 1992. Morphological constraints in the digging apparatus of pocket gophers (Mammalia: Geomyidae). Biological Journal of the Linnean Society 47, 439–453.

Lessa, E.P., Thaeler Jr., C.S., 1989. A reassessment of morphological specializations for digging in pocket gophers. Journal of Mammalogy 70, 689–700.

Levinson, M., 1982. Taphonomy of microvertebrates from owl pellets to cave breccia. Annals of the Transvaal Museum 33, 115-121.

Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M., White, T.D., 2009. Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. Science 326, 66e61-66e64.

Luyt, J., Lee-Thorp, J.A., Avery, G., 2000. New light on Middle Pleistocene west coast environments from Elandsfontein, Western Cape Province, South Africa. South African Journal of Science 96, 399-403.

Malherbe, A.P., 1963. Notes on birds of prey and some others at Boshoek, north of Rustenburg during a rodent plague. Ostrich 34, 95-96.

Marais, J., 2004. A complete guide to the snakes of southern Africa. Struik Publishers, Cape Town.

Matthews, T., Denys, C., Parkington, J.E., 2005. The palaeoecology of the micromammals from the late middle Pleistocene site of Hoedjiespunt 1 (Cape Province, South Africa). Journal of Human Evolution 49, 432-451.

Matthews, T., Parkington, J.E., Denys, C., 2006. The taphonomy of the micromammals from the Late Middle Pleistocene site of Hoedjiespunt 1 (Cape Province, South Africa). Journal of Taphonomy 4, 1-16.

Matthews, T., Denys, C., Parkington, J.E., 2007. Community evolution of Neogene micromammals from Langebaanweg `E' Quarry and other west coast fossil sites, south-western Cape, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 245, 332-352.

Matthews, T., Marean, C., Nilssen, P., 2009. Micromammals from the Middle Stone Age (92-167 ka) at Cave PP13B, Pinnacle Point, south coast, South Africa. Palaeontologia Africana 44, 112-120.

Matthews, T., Rector, A., Jacobs, J., Herries, A.I.R., Marean, C., 2011. Environmental implications of micromammals accumulated close to the MIS 6 to MIS 5 transition at

Pinnacle Point Cave 9 (Mossel Bay, Western Cape Province, South Africa). Palaeogeography, Palaeoclimatology, Palaeoecology 302, 213-229.

McDonough, M.M., Sotero-Caio, C.G., Ferguson, A.W., Lewis, P.J., Tswiio, M., Thies, M.L., 2013. Mitochondrial DNA and karyotypic data confirm the presence of *Mus indutus* and *Mus minutoides* (Mammalia, Rodentia, Muridae, Nannomys) in Botswana. Zookeys 359, 35-51.

McKee, J.K., 1991. Palaeo-ecology of the Sterkfontein hominids: a review and synthesis. Palaeontologia Africana 28, 41-51.

McKee, J.K., 1995. Turnover patterns and species longevity of large mammals from the Late Pliocene and Pleistocene of southern Africa: A comparison of simulated and empirical data. Journal of Theoretical Biology 172, 141-147.

McKee, J.K., 2001. Faunal turnover rates and mammalian biodiversity of the Late Pliocene and Pleistocene of Eastern Africa. Paleobiology 27, 500-511.

Meester, J., 1962. Some mammals from the Namib Desert. Annals of the Transvaal Museum 24, 241-248.

Mendelsohn, J.M., 1989. Habitat preferences, population size, food and breeding of six owl species in the Springbok Flats, South Africa. Ostrich 60, 183-190.

Meng, Q.-J., Grossnickle, D.M., Liu, D., Zhang, Y.-G., Neander, A.I., Ji, A.I., Ji, Q., Luo, Z.-X., 2017. New gliding mammaliaforms from the Jurassic. Nature 548, 291-296.

Mikkola, H., 1983. Owls of Europe. Buteo Books, Vermillion.

Mitchell, B.L., 1964. Owl prey. Puku 2, 129.

Nel, J.A.J., Nolte, H., 1965. Notes on the prey of owls in the Kalahari Gemsbok National Park, with special reference to the small mammals. Koedoe 8, 75-81.

Neser, W., 1989. Note on the prey of the barn owl (*Tyto alba affinis*). Laniarius 38, 9.

Norris, C.E., 1972. Barn owl pellets. East Africa Natural History Society Bulletin, 129.

O'Keefe, F.R., Carrano, M.T., 2005. Correlated trends in the evolution of the plesiosaur locomotor system. Paleobiology 31, 656–675.

Ousley, S.D., Jantz, R.L., 2012. Fordisc 3 and Statistical Methods for Estimating Sex and Ancestry. In: Dirkmaat, D.C. (Ed.), A Companion to Forensic Anthropology. Blackwell Publishing, London, pp. 311-329.

Patnaik, R., 2003. Reconstruction of Upper Siwalik palaeoecology and palaeoclimatology using microfossil palaeocommunities. Palaeogeography, Palaeoclimatology, Palaeoecology 197, 133-150.

Perrin, M.R., 1982. Prey specificity of the barn owl, *Tyto alba*, in the Great Fish River valley of the Eastern Cape Province. South African Journal of Wildlife Research 12, 14-25.

Pickering, T.R., Brain, C.K., 2010. What taphonomically oriented research at Swartkrans Cave reveals about early hominid behavior. Journal of Taphonomy 8, 215-232.

Pickering, T.R., Heaton, J.L., Clarke, R.J., Sutton, M.B., Brain, C.K., Kuman, K., 2012. New hominid fossils from Member 1 of the Swartkrans formation, South Africa. Journal of Human Evolution 62, 618-628.

Pickering, R., Kramers, J.D., 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. Journal of Human Evolution 59, 70-86.

Pickford, M., 1990. Some fossiliferous Plio-Pleistocene cave systems of Ngamiland, Botswana. Botswana Notes and Records 22, 1-15.

Pickford, M., Mein, P., 1988. The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana. Comptes rendus de l'Academie des sciences. Serie 2 307, 1681-1686.

Pickford, M., Mein, P., Senut, B., 1994. Fossiliferous Neogene karst fillings in Angola, Botswana, and Namibia. South African Journal of Science 90, 227-230.

Plummer, T.W., Bishop, L.C., Hertel, F., 2008. Habitat preference of extant African bovids based on astragalus morphology: Operationalizing ecomorphology for palaeoenvironmental reconstruction. Journal of Archaeological Science 35, 3016-3027.

Pocock, T.N., 1974. New mammal record for genus *Mus* for southern Africa. South African Journal of Science 70, 315.

Potts, R., 1996. Evolution and climate variability. Science 273, 922-923.

Potts, R., 1998a. Environmental hypotheses of Hominin evolution. Yearbook of Physical Anthropology 41, 93-136.

Potts, R., 1998b. Variability selection in hominid evolution. Evolutionary Anthropology 7, 81-96.

Prothero, D.R., Heaton, T.H., 1996. Faunal stability during the Early Oligocene climatic crash. Palaeogeography, Palaeoclimatology, Palaeoecology 127, 257-283.

Raczynski, J., Ruprecht, A.L., 1974. The effect of digestion on the osteological composition of owl pellets. Acta Ornithologica 14, 1-12.

Reed, D.N., 2003. Micromammal paleoecology: Past and present relationships between African small mammals and their habitats. Anthropology, Stony Brook University. Doctor of Philosophy: 242.

Reed, D.N., 2005. Taphonomic implications of roosting behavior and trophic habits in two species of African owl. Journal of Archaeological Science 32, 1669-1676.

Reed, D.N., 2007. Serengeti micromammals and their implications for Olduvai paleoenvironments. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.), Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence. Springer, Dordrecht, pp. 217-255.

Reed, D.N., 2011. Serengeti micromammal communities and the paleoecology of Laetoli, Tanzania. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 1: Geology, Geochronology, Paleoecology and Paleoenvironment. Springer, Dordrecht, pp. 253-264.

Reed, D.N., Denys, C., 2011. The taphonomy and paleoenvironmental implications of the Laetoli micromammals. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 1: Geology, Geochronology, Paleoecology and Paleoenvironment. Springer, Dordrecht, pp. 265-278.

Reed, D.N., Geraads, D., 2012. Evidence for a Late Pleistocene faunal transition based on a new rodent assemblage from Oldowan locality Hadar A.L. 894, Afar Region, Ethiopia. Journal of Human Evolution 62, 328-337.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution 32, 289-322.

Reed, R., Hunter, C., 1963a. Bird diet. Witwatersrand Bird Club New 43, 4-8.

Reed, R., Hunter, C., 1963b. Records of bird diets and feeding habits received since publication of the last news sheet. Witwatersrand Bird Club News 44, 2-4.

Ritter, R., Mann, P., 1995. Discovery and exploration of two new caves in the Northwest District. Botswana Notes and Records 27, 1–12.

Roberts, A., 1951. The Mammals of South Africa. Trustees of Mammals of South Africa Book Fund, Johannesburg.

Robinson, J.T., 1952. The Australopithecine-bearing deposits of the Sterkfontein Area. Annals of the Transvaal Museum 22, 1-19.

Robinson, J.T., 1954. The genera and species of the Australopithecinae. American Journal of Physical Anthropology 12, 181–200.

Rohlf, F.J., 2017. tpsDig2, version 2.31. Ecology & Evolution and Anthropology, Stony Brook University.

Rose, K.D., Chinnery, B.J., 2004. The postcranial skeleton of early Eocene rodents. Bulletin of the Carnegie Museum 36, 211-244.

Rubidge, B.S., 2000. Charles Kimberlin (Bob) Brain - A tribute. Palaeontologia Africana 36, 1-9.

Samuels, J.X., Van Valkenburgh, B., 2008. Skeletal indicators of locomotor adaptations in living and extinct rodents. Journal of Morphology 269, 1387-1411.

Sandelowsky, B.H., 1974. Archaeological investigations at Mirabib Hill Rock Shelter. Goodwin Series 2, 65-72.

Sandelowsky, B.H., 1977. Mirabib – An archaeological study in the Namib. Madoqua 10, 221-253.

Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: Evidence from mammalian herbivore enamel stable isotopes. Journal of Anthropological Archaeology 22, 200-207.

Scott, L., 1982. Pollen analyses of Late Cainozoic deposits in the Transvaal, South Africa, and their bearing on palaeoclimates. Palaeoecology of Africa and the Surrounding Islands 15, 101-107.

Scott, L., 1995. Pollen evidence for vegetational and climatic change in southern Africa during the Neogene and Quaternary. In: Vrba, E.S., Denton, G.H., Partridge, T.C. Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 65-76.

Scott, L., Bonnefille, R., 1986. Search for pollen from the hominid deposits of Kromdraai, Sterkfontein and Swartkrans: Some problems and preliminary results. South African Journal of Science 82, 380-382.

Scott, R.S., Barr, W.A., 2014. Ecomorphology and phylogenetic risk: Implications for habitat reconstruction using fossil bovids. Journal of Human Evolution 73, 47-57.

Senut, B., 1996. Plio-Pleistocene Cercopithecoidea from the Koanaka Hills (Ngamiland, Botswana). Comptes rendus de l'Academie des sciences. Serie 2 322, 423–428.

Shipman, P., Harris, J.M., 1988. Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In: Grine, F.E. (Ed.), Evolutionary History of the "Robust" Australopithecines. Aldine de Gruyter, New York, pp. 343-381.

Skead, C.J., 1956. Prey of the barn owl *Tyto alba*. Ostrich 27, 148.

Skead, C.J., 1963. Contents of pellets of barn owl *Tyto alba* at a rural roost. Ostrich 34, 171-172.

Skinner, J.D., Chimimba, T., 2005. The Mammals of the Southern African Subregion, Third Edition. Cambridge University Press, Cape Town.

Skinner, J.D., Lindeque, M., Van Aarde, R.J., Dieckmann R.C., 1980. The prey of owls from Koichab pan in the southern Namib Desert. Madaqua 12, 181-182.

Smithers, R.H.N., 1971. The mammals of Botswana. Memoirs of the National Museum of Rhodesia 4, 1-340.

Sponheimer, M., Codron, D., Passey, B.H., de Ruiter, D.J., Cerling, T.E., Lee-Thorp, J.A., 2009. Using Carbon Isotopes to Track Dietary Change in Modern, Historical, and Ancient Primates. American Journal of Physical Anthropology 140, 661-670.

Sponheimer, M., Lee-Thorp, J.A., 1999. Isotopic evidence for the diet of an early Hominid, *Australopithecus africanus*. Science 283, 368-370.

Sponheimer, M., Lee-Thorp, J.A, de Ruiter, D., Condron, D., Condron, J., Baugh, A.T., Thackeray, F., 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. Journal of Human Evolution 48, 301-312.

Sponheimer, M., Passey, B.H., de Ruiter, D.J., Gutatelli-Steinberg, D., Cerling, T.E., Lee-Thorp, JA., 2006. Isotopic evidence for dietary variability in the early Hominin *Paranthropus robustus*. Science 341, 980-982.

Sponheimer, M., Reed, K., Lee-Thorp, J.A., 2001. Isotopic palaeoecology of Makapansgat Limeworks Perissodactyla. South African Journal of Science 97, 327-329.

Stanley, S.M., 1992. An ecological theory for the origin of *Homo.* Paleobiology 18, 237–257.

Stein, B., 1988. Morphology and allometry in several genera of semiaquatic rodents (*Ondatra, Nectomys,* and *Oryzomys*). Journal of Mammalogy 69, 500–511.

Steyn, P., 1983. Birds of Prey of Southern Africa. Tanager Books, Dover.

Stoetzel, E., Marion, L., Nespoulet, R., El Hajraoui, M.A., Denys, C., 2011. Taphonomy and palaeoecology of the late Pleistocene to Middle Holocene small mammal succession of El Harhoura 2 cave (Rabat-Témara, Morocco). Journal of Human Evolution 60, 1-33.

Stuart, C.T., 1973. A short note on the diet of *Tyto alba* at Sandwich Harbour, Namib Desert Park, South West Africa. Madoqua 4, 103.

Stuart, C.T., 1975. Preliminary notes on the mammals of the Namib Desert Park. Madoqua 4, 5-36.

Susman, R.L., de Ruiter, D., Brain, C.K., 2001. Recently identified postcranial remains of *Paranthropus* and Early *Homo* from Swartkrans Cave, South Africa. Journal of Human Evolution 41, 607-629.

Sutton, M.B., Pickering, T.R., Pickering, R., Brain, C.K., Clarke, R.J., Heaton, J.L., Kuman, K., 2009. Newly discovered fossil- and artifact-bearing deposits, uranium-series ages, and Plio-Pleistocene hominids at Swartkrans Cave, South Africa. Journal of Human Evolution 57, 688-696.

Taylor, I., 1994. Barn Owls: Predator-Prey Relationships and Conservation. Cambridge University Press, Cambridge.

Taylor, L.E., 1910. Notes from Cape Colony. The Journal of the South African Ornithologists' Union 5, 81-87.

Thackeray, J.F., 1987. Late Quaternary environmental changes inferred from small mammalian fauna, southern Africa. Climatic Change 10, 285-305.

Thackeray, J.F., Avery, D.M., 1990. A comparison between temperature indices for Late Pleistocene sequences at Klasies River and Border Cave, South Africa. Palaeoecology of Africa and the Surrounding Islands 21, 311-315.

Thackeray, J.F., Gommery, D., Senegas, F., Potze, S., Kgasi, L., McCrae, C., Prat, C., 2008. A survey of past and present work on Plio-Pleistocene deposits on Bolt's Farm, Cradle of Humankind, South Africa. Annals of the Transvaal Museum 45, 83-89.

Tilson, R.L., LeRoux, P., 1983. Resource partitioning in coexisting Namib Desert owls, *Bubo africanus* and *Tyto alba*. Madoqua 13, 221-227.

Tucker, A., 2019. The complex legacy of America's Lawrence of Arabia. Smithsonian Magazine - March: Available at https://www.smithsonianmag.com/history/revisiting-complex-legacy-americas-lawrence-arabia-180971446/

Tutalo, R.S., 2012. The identification of prey remains from barn owl (*Tyto alba*) pellets and their use in identifying taphonomic biases in fossil deposits of Northwestern Botswana. Biological Sciences, Sam Houston State University, Masters of Science: 104.

Ungar, P.S., Abella, E.F., Burgman, J.H.E., Lazagabaster, I.A., Scott, J.R., Delezene, L.K., Manthi, F.K., Plavcan, J.M., Ward, C.V., In Press. Dental microwear and Pliocene paleocommunity ecology of bovids, primates, rodents, and suids at Kanapoi. Journal of Human Evolution http://dx.doi.org/10.1016/j.jhevol.2017.03.005

van Dam., A.J., Abdul, H.A., Sierra, M.A.A., Hilgen, F.J., van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., van der Meulen, A.J., Pelaez-Campomanes, P., 2006. Long-period astronomical forcing of mammal turnover. Nature 443, 687-691.

van der Merwe, M., 1980. Importance of *Miniopterus schreibersi natalensis* in the diet of barn owls. South African Journal of Wildlife Research 10, 15-17.

van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A., Luyt, J., 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. Journal of Human Evolution 44, 581-597.

Van Valkenburgh B., 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. Journal of Vertebrate Paleontology 7, 162–182.

Vernon, C., 1991. Border Notes: Prey of the barn owl near East London and Stutterheim. The Bee-eater and ECWBS News 42, 31.

Vernon, C.J., 1971. Owl foods and other notes from a trip to South West Africa. Ostrich 42, 153-154.

Vernon, C.J., 1980. Prey of six species of owl at the Zimbabwe Ruins–1970-1975. The Honeyguide 101, 26-28.

Vrba, E.S., 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. Nature 254, 301-304.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns. Fossils in the Making. University of Chicago Press: Chicago, pp. 247-271.

Vrba, E.S., 1985a. Early hominids in southern Africa: Updated observations on chronological and ecological background. In: Tobias, P.V. (Ed), Hominid Evolution: Past, Present, and Future. Alan Liss, New York, pp. 195-200.

Vrba, E.S.,1985b. Environment and evolution: Alternative causes of the temporal distribution of evolutionary events. South African Journal of Science 81, 229–236.

Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), Evolutionary History of the ‘‘Robust’’ Australopithecines. Aldine de Gruyter, New York, pp. 405–426.

Vrba, E.S., 1995a. On the connection between paleoclimate and evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution With Emphasis on Human Origins. Yale University Press, New Haven, pp. 24–45.

Vrba, E.S., 1995b. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 385–424.

Vrba, E.S., 1999. Habitat theory in relation to the evolution in African Neogene biota and hominids. In: Bromage, T.G., Schrenk, F. (Eds.), African Biogeography, Climate Change, and Human Evolution. Oxford University Press, New York, pp.19-34.

Watson, V., 1993. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph 8, 35-73.

Wesselman, H.B., 1984. The Omo micromammals: Systematics and paleoecology of early man sites from Ethiopia. Contributions to Vertebrate Evolution 7, 1-219.

Wesselman, H.B., 1985. Fossil micromammals as indicators of climate change about 2.4 Myr ago in the Omo Valley, Ethiopia. South African Journal of Science 81, 260-261.

Wesselman, H.B.,1995 Of mice and almost-men: Regional paleoecology and human evolution in the Turkana Basin. In: Vrba, E.S., Denton, G.H., Partridge, T.C. Burckle,

L.H. (Eds.) Paleoclimate and Evolution With Emphasis on Human Origins. Yale University Press, New Haven, pp. 256-268.

Wesselman, H.B., Black, M.T., Asnake, M., 2009. Small mammals. In: Haile-Selassie, Y., WoldeGabriel, G. (Eds.), *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp. 105-133.

Williams, B.A., Ross, C.F., Frost, S.R., Waddle, D.M., Gabadirwe, M., Brook, G.A., 2012. Fossil *Pap*io cranium from !Ncumtsa (Koanaka) Hills, Western Ngamiland, Botswana. American Journal of Physical Anthropology 149, 1-17.

Wilson, D., Reeder, D.M. (Eds.), 2005. Mammal Species of the World 3rd ed. Smithsonian Institution Press, Washington, DC.

Wilson, V.J., 1970. Notes on the breeding and feeding habits of a pair of barn owls, *Tyto alba* (Scopoli), in Rhodesia. Arnoldia Rhodesia 4, 1-8.

Wilson, R.T., Wilson, M.P., Fry, C.H., 1988. Tytonidae, barn owls and bay owls. In: Fry CH, Keith S, Urban EK (Eds.), The Birds of Africa, Voluime 3. Academic Press, New York, pp. 110-155.

Winkler, A.J., 1995. Small mammals from the early Pliocene at Kanapoi, West Turkana, northern Kenya. Journal of Vertebrate Paleontology 15(S3), 60A.

Winkler, A.J., Denys, C., Avery, D.M., 2010. Rodentia, In: Werdelin, L. Sanders, W.J. (Eds.), Cenozoic mammals of Africa. Berkeley, University of California Press, pp. 263-304.

Winterbottom, J.M., 1964. Report on the birds of Game Reserve No 2. Cimbebasia, 9, 1-75.

Winterbottom, J.M., 1966. Results of the Percy FitzPatrick Institute of African Ornithology-Windhoek State Museum ornithological expeditions. 4. Notes on the food of *Tyto alba* in the Etosha Pan. Ostrich 37, 139-140.

Wirminghaus, J.O.,1989. The diet of barn owls at a roost near Grahmstown. South African Journal of Zoology 24, 232-234.

White, T.D., 1995. African omnivores: Global climatic change and Plio-Pleistocene hominids and suids. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution With Emphasis on Human Origins. New Haven, Yale University Press, pp. 369-384.

White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S. et al., 2009. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. Science 326 87-93.

Zazzo, A., Bocherens, H., Brunet, M., Beauvilaian, A., Billiou, D., Mackaye, H.T., Vignaud, P., Mariotii, A., 2000. Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate. Paleobiology 26, 294-309.