Community Structure through Time: ‘Ubeidiya, a Lower Pleistocene Site as a Case Study

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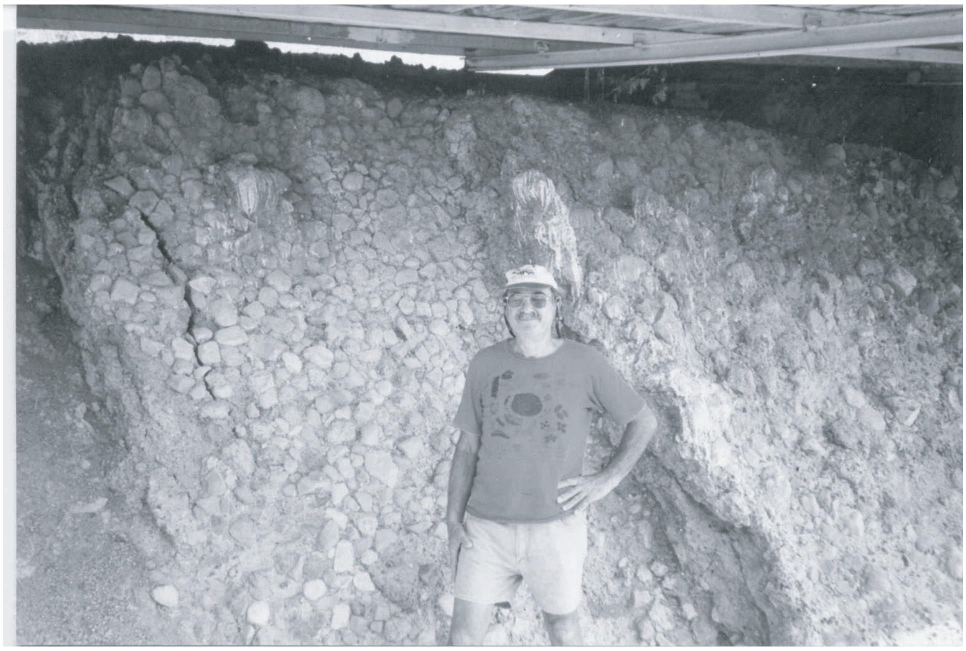
this thesis is dedicated to Eitan Tchernov,
my mentor, without whom this thesis would have never happened



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Abstract

The aim of this thesis is to test paleoecological hypotheses pertaining to early hominin dispersal events. During the Lower Pleistocene, hominins dispersed from Africa into Eurasia via the Levantine corridor. One of the earliest sites which testify to this dispersal event is the site of ‘Ubeidiya. Situated in the central Jordan Valley, the fossil bearing strata are constrained between ca. 1.6 - 1.2 Ma and exhibits a rich lithic and faunal assemblage which span over several distinct stratigraphic units.

Over the history of research, different hypotheses have been put forth in an attempt to explain patterns of hominin evolution and environment change. These may be grouped into habitat specific hypotheses and the Variability Selection (VS) hypothesis.

Habitat specific hypotheses emphasize adaptations that arise as a response to the selection demands of a specific habitat. The savanna hypothesis suggests that early hominins evolved since the Miocene as a response to the increased aridity and open savanna environments. According to this hypothesis, the progressive increase in aridity throughout the Pliocene and Early Pleistocene, was the main selective force for the major morphological (bipedalism, large brains) and behavior (tool making, meat eating) characteristics associated with more developed hominins.

The alternative Variability Selection (VS) hypothesis promotes the idea that hominin adaptation was more influenced by an increase in different types of environments in long temporal time scales. Thus, hominin adaptation is primarily geared towards novelty and the ability to adapt to a variety of environments, as opposed to a single habitat.

This thesis utilizes this conceptual framework developed to the Lower Pleistocene dispersal events. The large mammalian fauna of ‘Ubeidiya was analyzed in order to reconstruct the paleoenvironment at the site and to test for patterns of persistence and change throughout the sequence. Specifically, this study focused on patterns of relative abundance and community structure and its correlation with environmental change. Seven ‘pooled strata’ were analyzed based on adequate sample size and included two ‘pooled strata’ from the Li cycle and five ‘pooled strata’ from the Fi cycle.

In order to address this issues, four detailed research question were formulated in this thesis:

1. What are the agents of accumulation of the large mammalian fauna of ‘Ubeidiya (i.e., hominin primary or secondary access to carcasses, carnivore kill site or scavenging, fluvial transport or natural background fauna)?
2. Can persistence or change be discerned among the large mammalian community structure in ‘Ubeidiya throughout the sequence?
3. Can the observed pattern be attributed to local environmental change (the alternative hypothesis) or to various taphonomic processes (taphonomic null hypotheses)?
4. What is the paleoecological milieu of the ‘Ubeidiya assemblages? are they more similar to that of African biomes, European or Mediterranean ones?

Identification of ecological patterns in the temporal scale depends first and foremost on the removal of the potential taphonomic biases in the fossil assemblages (density mediated processes, weathering, fluvial transport, hominins or carnivores as primary agents of accumulation and post depositional ravaging by hyaenas).

This thesis uses spatial autocorrelation analysis in the temporal scale as an approach to this problem. Biodiversity data (the dependent variables) were correlated with taphonomic variables (the taphonomic independent variables) which formed the null hypotheses as well as with the environmental independent variable which formed the alternative hypothesis.

Methodology included identification of the large mammalian assemblage specimens to species and body elements. Quantification used Number of Identified Specimens (NISP) for all biodiversity calculations (the dependent variables). Taphonomic attributes included weathering, size and shape of specimen and recording of the location of surface marks i.e., cut-marks and carnivore gnaw-marks. A total of 12,098 specimens were analyzed in thesis of which 2582 (29%) were large terrestrial mammals assigned to strata.

Results suggests that the accumulation of the large terrestrial mammalian fauna is similar for most ‘pooled strata’. ‘Ubeidiya assemblages probably represent an amalgamation of several processes. Thus, the faunal assemblages represented kill or near kill sites of large carnivores. These sites where subsequently exposed to low level utilization by hominins. The remains were further scavenged and accumulated by bone crushing carnivores such as the spotted hyaena.

Cut-mark and gnaw mark distribution, the absence of bone marrow processing and body part distribution are more consistent with secondary access of hominins to carcasses at the site which possibly removed selected elements to be processed elsewhere. Body part distribution provide equivocal results, heavily modified by density mediated process and specifically, carnivore ravaging. Nonetheless, I cannot negate the possibility that some early access to carcass was practiced at the site, but it was probably not the modus operandi at the site. It is important to stress that the overall low frequency of cut-marks and the high proportion of specimens with no modification suggests that the hominin involvement in the accumulation of the assemblages is minimal.

The large mammalian fauna of ‘Ubeidiya includes a total of 33 species. Two distinct faunal units can be distinguished. The first faunal unit includes ‘pooled strata’ III 11-13 and III 20 from the Li cycle and is low in species richness. The second faunal unit includes the ‘pooled strata’ in the Fi cycle (II 23-25, III 21-22, II 26-27, II 36 and II 37). Although there is no change in faunal composition throughout the sequence, there is a change in faunal abundance that may be related to the slow trend of desiccation identified both in gross and micro geomorphology. Thus, the older ‘pooled strata’ (II 23-25, III 21-22 and II 26-27) are assigned to sub-faunal unit B1 and the younger ‘pooled strata’ (II 36 and II 37) may be assigned to a sub-faunal unit B2.

The main factor which affects the change in faunal composition (presence-absence and abundance) is local environmental change. This correlation reflects the difference between faunal unit A and B. Local environmental change nor stratigraphy cannot account for the difference between the faunal composition of the two sub-faunal units in the Fi cycle: B1 and B2. There is a weak affect of local environmental change on the relative frequency of taxa throughout the Fi cycle as well as a weak affect of carnivore ravaging. Biodiversity analyses suggests that evenness is highly affected by carnivore ravaging and is a reflection of the selectivity of carnivore, notably hyaenas.

Detailed analysis of individual taxa suggests that this may be related to the change in abundance of forest taxa. Forest taxa (*Capreolous* sp. and *Pseudodama* sp.) abundance is weakly affected of first order environmental changes (between the Li and Fi cycles). ‘Pooled strata’ with high proportions of forest taxa (III 20) reflect periods of greater humidity and thus, greater forest coverage. This is confounded by the taphonomic bias of carnivore ravaging. ‘Pooled strata’ with high proportions of forest taxa, III 20 and II 26-27, were subjected to higher intensities of carnivore ravaging. Within the Fi cycle, the change in relative frequency of forest taxa cannot be attributed statistically either to any of the taphonomic null hypotheses nor to the alternative hypothesis.

The sequence at ‘Ubeidiya can be interpreted as a slow decrease in forest habitat and increase in open habitat. The main decrease can be related to first order environmental change between the Li and Fi cycle (i.e., between ‘pooled strata’ III 20 and II 23-25). Throughout the Fi cycle, there is only a weak affect of the environment and in general a period of stasis. The increase in cervid proportions in ‘pooled stratum’ II 26-27 is related to carnivore ravaging rather to the environment. Recent paleomagnetic studies have suggested that this period may have lasted as long as ca. 325 Ka.

The large mammalian fauna of ‘Ubeidiya responds to the local environmental change present throughout the sequence either by stasis or by a change in relative frequency only. This is consistent with the recurrent assemblages model and emphasizes the ability of various species to withstand low and medium amplitudes of local environmental change over long time scales.

These results have important implications for paleoecological reconstructions. First, analysis of proportion of taxa is not only a reflection of the habitat but also of the intensity of the carnivore ravaging during this time period. This reduced the fidelity of our paleoecological reconstruction. Thus, 'pooled strata' with a high proportion of small-medium cervids may be erroneously interpreted to represent an environment of dense forest where is fact, the environment is actually more open but the assemblage was subjected to a high intensity of carnivore ravaging. Second, in regions of medium latitudes, where climatic change is often of medium and low magnitude, specific taxon may not respond to a climatic shift. Thus, the appearance of stasis in the fossil record in these regions, does not necessarily reflect environment change.

The fauna at 'Ubeidiya includes a high proportion of taxa of African biogeographic origin. It has been suggested that the presence of these taxa are indicative of savanna type environment. Paleoecological reconstruction of the site suggests that all 'Ubeidiya 'pooled strata' have high affinities with other modern and Plio-Pleistocene Mediterranean sites. Both faunal units present at 'Ubeidiya (faunal unit A and B) reflect various gradients of the Mediterranean biome. Thus, the presence of taxa of African origin such as *Pelerovis oldowayensis*, does not indicate the presence of an African type savanna.

The dispersal of early hominins to 'Ubeidiya during the Lower Pleistocene would have required coping with a novel Mediterranean environment and with the various gradients within it. Successful dispersal events would have required a pre-adaptation to a wide range of habitats as suggested by the variability hypothesis.

The novelty of the thesis is three fold: First, it presents an in-depth paleoecological analysis of a Lower Pleistocene site of 'Ubeidiya with ramifications to early hominin evolution. Second, it analyzes different modes of response of mammalian fauna to low amplitude climatic change, this not only has implications for understanding hominin dispersal events in the Lower Pleistocene but also reveals some inherent biases in paleoecological reconstructions in low and medium latitudes. Third, it presents a methodology to increase the fidelity of paleoecological analysis using spatial autocorrelation in the temporal scale.

Part I

Framework

Chapter 1

Introduction

The purpose of this thesis is to test paleoecological and macro-evolutionary hypotheses of persistence and change through time by the study of the large mammalian paleocommunity found in the the Lower Pleistocene site of ‘Ubeidiya in the Jordan Valley. Three main questions arise from this study: First, what is the paleoecological milieu of the ‘Ubeidiya mammalian community? Second, does the large mammalian fauna respond to the environmental fluctuations present throughout the sequence? Third, what are the implications for early hominin adaptation and specifically, early hominin dispersal events?

The causes and forces which influenced hominin dispersal from Africa into Eurasia in the Late Pliocene and Early Pleistocene are some of the enigmatic phenomena in human evolution. The dating of hominin dispersal events rests upon the precise dating of sites with hominin anthropological or lithic remains, while the analysis of the driving forces for the dispersal requires the combination of data from a multitude of disciplines.

During the Lower Pleistocene, hominins dispersed out of Africa and into Eurasia. The Levant, as Southwest Asia, is one the major dispersal routes used (Tchernov, 1988a). The Levant constitutes a unique province. In the west, it is bordered by a fertile Mediterranean region, which rapidly subsides eastwards to the semi arid steppes of the Syria Arabia desert. In the north it is bounded by the Zagros and Taurus mountains and in the south by the isthmus of the Suez (Tchernov & Belmaker, 2004; Yom-Tov & Tchernov, 1988). Since the onset of the Neogene, the Levant was geographically a corridor between Africa and Eurasia. During different time periods, geological changes (i.e., tectonics, climate and sea level changes) altered the “permeability” of this land bridge. Thus, during certain times, the region allowed for animals to disperse from one region to another as opposed to other periods in which it served as a barrier (Tchernov, 1988a; Tchernov & Belmaker, 2004).

The site of ‘Ubeidiya, in the Jordan Valley (Israel) is one of the earliest sites out-of-Africa to document the dispersal events between the two continents. The site contains rare human remains (Belmaker *et al.*, 2002), rich lithic (Bar-Yosef & Goren-Inbar, 1993) and faunal assemblages (Haas, 1966, 1968; Tchernov, 1986a). Long range biochronological correlation in conjunction with paleomagnetic dating has suggested that the fossil bearing strata may be confined between ca. 1.6 - 1.2 Ma (Tchernov, 1987; Sagi *et al.*, 2005; Sagi, 2005). The paleoecological reconstruction of the Lower Pleistocene sites and specifically that of ‘Ubeidiya can serve a pivotal role in addressing the questions presented above.

Modern ecological studies indicate that taxa respond to environmental change (Barnosky *et al.*, 2003) in one of several ways: adapt to the new habitat, disperse or become extinct (Bennett, 1997). Since niches are usually occupied by other species, the new dispersing species must compete for the new location (Krebs, 2001). To successfully colonize a new region, newly arriving taxa must be better competitors than the present occupiers of the niche. Hence, to understand the forces which affected hominin dispersal events one should study global and local climatic events as a possible impetus for the dispersal and the biological and cultural evolution of the genus *Homo*.

Over the history of research, different hypotheses have been put forth in an attempt to explain patterns of hominin evolution and environment change (Potts, 1998, 2002). Potts (1998) distinguished between two groups of hypotheses; habitat specific hypotheses and the Variablity Selection (VS) hypothesis.

Habitat specific hypotheses emphasize adaptations that arise as a response to the selection demands of a specific habitat. The savanna hypothesis suggests that early hominins evolved since the Miocene as a response to the increased aridity and open savanna environments (Vrba, 1988, 1995; Wynn, 2004). According to this hypothesis, the progressive increase in aridity throughout the Pliocene and Early Pleistocene (Cooke, 1978), was the main selective force for the major morphological (bipedalism, large brains) and behavior (tool making, meat eating) characteristics associated with more developed hominins (Klein, 2000). Conversely, recent evidence promotes the importance of closed vegetation habitats in hominin evolution (Domínguez-Rodrigo, 1997).

The alternative Variablity Selection (VS) hypothesis promotes the idea that hominin adaptation was more influenced by an increase in different types of environments in long temporal time scales. Thus, hominin adaptation is primarily geared towards novelty and the ability to adapt to a variety of environments, e.g., rain-forest environments (Boesch-Aschermann & Boesch, 1994; Mercader, 2002), as opposed to a single habitat (Potts, 1998, 2002). Specifically, this hypothesis suggests that hominins may be pre-adapted to the decoupling of their behavior from any specific ancestral habitat (i.e., African savanna), thus enabling to diversify both its behavioral and ecological options

(Potts, 2002).

This thesis utilizes the conceptual framework developed by Potts (1998) to Lower Pleistocene dispersal events. It has been suggested that the shift in climate may have been the impetus for the dispersal. The biological adaptation which facilitated long range dispersal (Bar-Yosef & Belfer-Cohen, 2001) as well as stone tool technology predate the earliest dispersal event by more than 0.5 Ma and therefore do not appear to be the sole impetus for the dispersal event (Antón *et al.*, 2002). If there was no appreciable change in hominins, biologically or technologically, over this time period, the drive for the dispersal must be sought elsewhere, perhaps in a climatic shift, such as observed during the Olduvai Subchron or in a change in the ability of early hominins to compete for pre-occupied niches (Potts, 1998).

The environmental hypothesis suggests that a climatic shift facilitated the dispersal of large mammals, including hominins (Potts, 1998). The Aullan dispersal event (ca. 1.8 Ma), associated with the new appearance of African faunas in Eurasia, may have included the African genus *Homo* (Martínez-Navarro & Palmqvist, 1995). Alternatively, it has been suggested that the dispersal was an event unique to humans and resulted from technological innovation or an increase in population size (Larick & Ciochon, 1996). The hunting hypothesis suggests that hominins evolved to become active hunters and hence needed larger territories (Walker & Shipman, 1996). Thus, hominins became better competitors for meat, allowing them to occupy new niches.

The ecological-behavioral niche occupied by hominins in Africa is widely debated. Taphonomic analyses of faunal remains has suggested that Plio-Pleistocene hominins had primary access to carcasses and a high proportion of meat in the diet (Brantingham, 1998; Domínguez-Rodrigo, 1997, 2002) but others have contested the data and suggested that hominins may have only had secondary access with a lower intake of meat (Blumenschine, 1988; Blumenschine & Cavallo, 1992; Blumenschine, 1986, 1995). Following the latter paradigm, the scavenging hypothesis suggests that the increased reliance of hominins on meat in the form of carcasses led to the following of large African predators into Eurasia (Arribas & Palmqvist, 1999; Turner, 1999).

Evidence of hominin dispersal into northern latitudes prior to 1.0 Ma is limited. The knowledge of the route and timing of hominin dispersal events depends on the identification of archaeological sites. While most would agree that Eurasia was colonized by 1.0 Ma, older out-of-Africa sites are rare. Dmanisi (Georgia) where several hominin skulls were uncovered and dated to ca. 1.7 - 1.9 Ma (Dzaparidze *et al.*, 1992; Gabunia & Vekua, 1995; Tappen *et al.*, 2002b; Vekua, 1995). Several fragments from Venta Micena (Orce, Granada), dated to ca. 1.65 Ma, have been identified as hominin (Agusti, 1987; Arribas & Palmqvist, 1998; Gilbert & Palmqvist, 1995; Guerreo-Alba & Palmqvist, 1997). A date of ca. 1.8 - 1.6 Ma has been suggested for the sites of Modjokerto and Sangiran (Java) (Huffman, 2001; Larick *et al.*, 2001; Swisher *et al.*, 1994). The authenticity of many of the sites has been contested based on stratigraphy and paleomagnetic dating (Langbroek & Roebroeks, 2000; Sémah *et al.*, 2000) or identification of the human remains (Palmqvist *et al.*, 1996). Thus, the only out of Africa sites with currently uncontested dates of greater than 1.0 Ma are few and include Dmanisi at ca. 1.7 Ma and ‘Ubeidiya at ca. 1.6 - 1.2 Ma.

The paradigm set forth by Potts (1998) presents two questions: First, did hominins disperse into novel environments in the Levant during the Lower Pleistocene and if so, did they employ similar behaviors to those in East Africa and second, given the temporal scale present throughout a site such as ‘Ubeidiya, how did the large mammalian community (to which hominins belong) respond to the climatic change evident throughout the stratigraphic sequence?

Testing the hypotheses requires detailed paleoecological data from well stratified hominin bearing localities. Previous faunal analyses (specifically large mammals) has focused on the relationship between environmental change and hominin speciation. It has been suggested that the radiation of taxa (as well as hominins) is associated with an environmental and climatic shift (Vrba, 1985, 1988, 1995; Zeitoun, 2000). On the converse, Behrensmeyer *et al.* (1997) did not find any evidence for an increase in faunal turnover in this time period in the Turkana Basin.

The contradicting results obtained for faunal turnover analysis shifted the focus to other modes of faunal analyses. Ecological studies have suggested that relative frequency of various species may fluctuate while species presence-absence may remain constant over time (Rahel, 1990). The first phenomenon can be termed *ecological persistence* and the second *evolutionary stability*. Similarly, it has been suggested by Alemseged (2003) and by Bobe & Eck (2001) that relative abundance of taxa may be more sensitive to environmental change than faunal turnover (speciation and extinction).

I suggest analyzing the large mammalian fauna of ‘Ubeidiya to reconstruct the paleoenvironment at the site and to test for patterns of persistence and change of the large mammalian community throughout the sequence. Specifically, I would like to focus on patterns community structure and its correlation with environmental change.

Identification of ecological patterns in the temporal scales depends first and foremost on the removal of potential taphonomic biases in fossil assemblages (density mediated processes, weathering, fluvial transport, hominins or carnivore as primary agents of accumulation and post depositional ravaging by hyaenas). Comparison of two assemblages (or two strata) with different taphonomic biases may result in the identification of apparent change where one did not really exist. Thus it is important to identify change or persistence in the mammalian community that can be related to the environment rather than the appearance of change that is an artifact of taphonomic bias.

The geological evidence indicates an environmental shift throughout the sequence at ‘Ubeidiya (Picard & Baida, 1966a). Picard & Baida (1966a) described four cycles of depositional environments at the site. These have been interpreted by Bar-Yosef & Tchernov (1972) as four large scale climatic periods of alternating lake levels. Sedemintological analysis has suggested first order changes (between cycles) and second order changes (within cycles) attributed to basinal hydrological regime (Feibel, 2004). This has further been confirmed by micropaleontological analysis (Almogi Labin *et al.*, 1995; Siman-Tov *et al.*, 1993, 1994) and micromorphological analysis (Mallol, 2004, 2006) which have attested to climatic fluctuations within the cycles as well. It is important to distinguish between climate and environment. Thus, when there is evidence for local climatic shift, the question is the degree to which these climatic changes are reflected by changes in the large faunal assemblage.

The majority of the studies which have dealt with the taxonomic identification of the paleontological assemblage and its biogeographic and biochronological correlations addressed ‘Ubeidiya as a single biostratigraphic entity for the entire fossil bearing strata (Tchernov, 1987). This contrasts with several faunal studies that have indicated a shift in the faunal composition. Haas (1968) noted that there is shift in the fauna between strata II 23-24 and II 36. Tchernov & Guérin (1986) noted that various diversity indices and environmental characteristics were observed to shift through the sequence of ‘Ubeidiya. Montuire & Girard (1998) identified a change in the cenogram graph derived from the large mammalian community in different ‘Ubeidiya strata.

In order to address this issues, four detailed research question were formulated in this thesis:

1. What are the taphonomic processes which biased the accumulation of the large mammalian fauna of ‘Ubeidiya (i.e., hominin primary or secondary access to carcasses, carnivore kill site or scavenging, fluvial transport or weathering)?
2. Can persistence or change be discerned among the large mammalian community structure in ‘Ubeidiya throughout the sequence?
3. Can the observed pattern be attributed to local environmental change (the alternative hypothesis) or to various taphonomic processes (taphonomic null hypotheses)?
4. What is the paleoecological milieu of the ‘Ubeidiya assemblages? is it more similar to that of African biomes, European or Mediterranean ones?

The results of the analysis of these questions presented in this thesis can help us address issues of early hominin dispersal events, the ecological niche occupied by hominins and the adaptability to environmental change in space and time.

The key element for any paleoecological study is to control for as many potential biases as possible. Previous research (Tchernov, 1986a) focused on taxonomic identification of single families by experts, thereby losing the value of having a single analyst look over the entire assemblage, as a community. The fauna from the first eight years of excavation (1960 - 1968) were studied by Haas (1961, 1963, 1966, 1968). The mammalian fauna from the 1966 - 1974 excavation seasons was analyzed by a team of paleontologists and edited by Tchernov (1986a). Subsequent taxonomic analyses focused on specific taxa only (Martìnez-Navarro *et al.* (n.d.); Martìnez-Navarro (1999, 2000)). Gaudzinski (2002, 2004a,b, 2005) completed an in-depth taphonomic analysis focused on human subsistence patterns on the material from the 1960 - 1974 and 1997 - 1999 seasons.

Despite extensive publication, considerable proportion of the large mammal remains uncovered in ‘Ubeidiya have not been analyzed to date. These included unpublished specimens collected during all the seasons and the finds uncovered during the last seasons of excavations (1989 - 1994 and 1997 - 1999). Moreover, the paleontological type-list studies, by nature, were not concerned with quantification procedures. In addition, the anthropological oriented research (Gaudzinski, 2002, 2004b,a, 2005) was concerned with strata containing lithic material, leaving out strata rich with faunal remains but with almost no stone artifacts. All in all, there has been no attempt to examine the ‘Ubeidiya large mammalian community from a comprehensive, paleoecological, view point as suggested in this thesis.

It is important to note that although certain similarities between the ‘Ubeidiya faunal assemblage and anthropological derived Middle or Upper Pleistocene assemblages in other sites are noted, it is not the intention of this thesis to produce an archaeozoological analysis of the collection. Although some quantification methods common in the archaeozoological literature (MNI and NISP) were applied in the course of this study, other common archaeozoological methodologies (e.g., sexing and aging analyses) were not studied as they did not serve to answer the hypotheses presented here. Rather, this thesis utilizes primarily paleoecological methods of data analyses.

The importance of this analysis of ‘Ubeidiya is not only in the comprehensive presentation of the data but also in the utilization the unique temporal scale of the site to place it within a biogeographical context both in the spatial and temporal scale. Only a multidimensional study including higher organizational levels will help to tease out the various factors influencing mammalian community structure in general and our own hominin evolution in particular.

One of the unique phenomena of the human species is its global dispersion. The current adaptation of humans and their ability of occupy such diverse habitats as the arctic and the tropics, lies in the evolutionary history of the species and the biological and/or cultural mechanisms which drove the initial dispersal event. The results of this thesis are relevant to these core issues of paleoecology and human evolution as well.

Methodologically, in order to further research in science in general and in paleoecology in particular, the interdisciplinary approach is paramount. This study is unique in the interdisciplinary approach it provides. It combines paleoecological research questions with paleontological, anthropological and biogeographical analyses. Such an approach holds promise for illuminating the issues of human dispersal from African into Eurasia. Analysis of the large mammalian faunal assemblage of ‘Ubeidiya provides more than an additional datum point of Plio-Pleistocene archaeological sites, but rather a unique insight into the place of hominins within their ecological milieu during an early period in human evolution.

This thesis contains five parts and are detailed as follows: Part I provides the framework and describes the site of ‘Ubeidiya including the geology, location and dating. Part II includes an in-depth description of the methodology and includes three chapters. First I describe the paleontological methodology used to identify and quantify fossil specimens and which formed the basis of the database. I then describe the taphonomic characteristics obtained from a large sample of the fossils and used to develop the proxies for the independent taphonomic variables as well as the dependent environment variable. And last, I describe the method used for paleoecological reconstructions. Part III describes the results and includes three chapters. First, I describe how the faunal assemblages are effected by each of the taphonomic parameters analyzed. I then describe how different biodiversity parameters are distributed throughout the ‘Ubeidiya sequence and test if the distribution of the biodiversity parameters is related to taphonomic biases (the taphonomic null hypotheses) or environment (the alternative hypothesis). Finally I present the result for the paleoecological analysis of the ‘Ubeidiya assemblages. Part IV presents the discussion and conclusions. The appendices form Part V and include the tables and figures.

Chapter 2

The Site of ʿUbeidiya

2.1 Geology and stratigraphy of the ʿUbeidiya Formation

The ʿUbeidiya Formation is situated in the Central Jordan Valley, Israel. It is located within the Kinnarot Basin, one of several pull-apart basins within the Dead Seas Transform (DST) (Heinmann & Braun, 2000).

The ʿUbeidiya Formation is composed of a series of layers deposited in the delta and shoreline of a shallow and wide freshwater lake; paleolake ʿUbeidiya. The main exposure of the ʿUbeidiya Formation is located approximately 3 km west of the Jordan outlet of the Sea of Galilee (Lake Kinneret) (coordinates 20255/23290) elevation 160-230 meters below sea level (Figure 1 on page 175).

Several smaller exposures have also been correlated with the formation north of Kibbutz Katzir, east of the Jordan river near Kibbutz Degania B (Um Juna) and one km south of Adasiya, Jordan (Braun, 1992; Picard & Baida, 1966b,a). All data described in this thesis have been retrieved from the main outcrop (Figure 2 on page 176).

The precise geographic extent of the lake is unknown (Mallol, 2004, 2006). It has been estimated that during periods of transgression, it reached as far north at least as the southern region of present-day Lake Kinneret, and eastward, around the mouth of the Yarmouk River (Mallol, 2004, 2006).

A detailed geological analysis of the main exposure was done by Picard & Baida (1966a). First order patterns reflect two alternating cycles of limnic and fluvial strata which comprise four members. The members were named Limnic Inferior (Li), Fluviatile Inferior (Fi), Limnic Upper (Lu) and Fluviatile Upper (Fu). Feibel (2004) has suggested that the first order cycle of the lake transgression and regression most probably reflects climatic control on the basinal hyrographic budget. Within each member, variability on a smaller second order scale represents lateral and temporal changes in the depositional environment:

Li The thickness of this cycle reaches 52 m in the West and 28 m in the East. The majority of the sediments were low energy sediments such as silts, ooliitic limestone and laminated silts. It is also noted for the development of secondary veins of idiomorphic gypsum. It is rich in freshwater mollusks and fish remains.

Fi The thickness of this cycle reaches 22 - 30 m. Sedimentological analysis indicated high energy lakeshore sediments such as conglomerates, fluviatile gravels and mud plains. The majority of vertebrate fauna as well as archaeological material has been found in this cycle. A detailed micromorphological study by Mallol (2004, 2006) of the Fi cycle suggested that desiccation features are abundant and prevail in most zones (across the different microenvironments; beach facies, mudflats, floodplain and swamp facies). These features represent aridity across the site, and increasingly up the stratigraphic sequence. There are only signs of weak pedogenesis, suggesting that the arid conditions were not extreme. Figure 3 on page 177 presents the lithology of the ‘Ubeidiya strata in the Fi cycle (Mallol, 2006).

Lu The thickness of this cycle reaches 52 m and is composed of various layers of silts indicating a transgression of paleolake ‘Ubeidiya.

Fu This cycle is of fluviatile and terrestrial origin. Most of the strata are composed of conglomerate and do not include fauna or artifacts.

Post depositional tectonic events which occurred at the end of the Fu cycle resulted in a complex structure of normal faults and folds. This resulted in two anticlines separated by a small syncline. The dip of the layers vary, at times reaching nearly 80 degrees and including an over-thrust of up to 120 degrees. The formation also includes minor fault displacements and angular discomformaties (Bar-Yosef & Goren-Inbar, 1993; Bar-Yosef & Tchernov, 1972; Picard & Baida, 1966a). Since the Naharayim formation is deposited horizontally, the tectonic events post date ‘Ubeidiya (ca. 1.6 - 1.2 Ma) but pre date the Naharayim Formation (0.8 Ma) (Picard & Baida, 1966b,a).

2.2 Dating of the ‘Ubeidiya Formation

The geochronological position of the ‘Ubeidiya Formation

During the Neogene, the Mediterranean Sea penetrated into the Jordan Valley. A transgression during the end of the Pliocene marks the creation of the rift valley and the deposition of the sediments in a closed basin. These sediments of a fresh to brackish lake and its shorelines, with oxbows and alternating lake levels form the milieu of the Plio-Pleistocene lake deposits in the Jordan Valley: The ‘Erq el Ahmar and ‘Ubeidiya Formations (Horowitz, 1979, 2001).

The Cover Basalt is the oldest formation exposed in the Kinnarot Basin. It was first described by Picard (1936). There is a clear unconformity between the Cover Basalt and the Dead Sea Group which overlies it. It has been dated using K/Ar and ^{40}Ar/^{39}Ar dating methods to ca. 5 - 3.3 Ma (Heinmann & Braun, 2000; Mor, 1993).

The ‘Erq el Ahmar Formation (Blanckenhorn, 1914) is located about 10 km south of ‘Ubeidiya. The formation was deposited in a shallow freshwater lake and is comprised of silt, clay and conglomerates. The ‘Erq el Ahmar Formation overlies the Cover Basalt and underlies the ‘Ubeidiya Formation. The absolute dating of the formation provides the lower limit for the ‘Ubeidiya Formation. It is assigned to the Pliocene based on the presence of Neogene mollusks *Hydrobia acuta* and *Dreissena chantrei*, which suggested a date of ca. 2.0 Ma (Picard, 1943; Tchernov, 1973, 1975). Paleomagnetic studies have shown that the ‘Erq el Ahmar Formation includes both normal and reverse sequences (Braun, 1992; Opdyke *et al.*, 1983; Verosub & Tchernov, 1991). A detailed study has indicated that the normal polarity sequence is correlated with the normal zone within the Olduvai Subchron and dated to 1.96 - 1.78 Ma (Ron & Levi, 2001).

The ‘Ubeidiya Formation was deposited in a delta-shoreline to lake deposits and is comprised of silt, clay and conglomerates. The fossil bearing strata of the formation have been dated to ca. 1.6 - 1.2 Ma. The original date assigned to the ‘Ubeidiya Formation by Picard was the Lower Pleistocene (Picard, 1943). He later revised his assessment and assigned the deposits to the Villafranchian, the lowest part of the Lower Pleistocene (Picard, 1952). This was based on the correlation between the Naharaim Formation which overlies ‘Ubeidiya and the Hatzor and Gesher Benot Ya‘acov Formations which were dated to the Middle Pleistocene (Stekelis *et al.*, 1960).

The Naharaim Formation overlies the ‘Ubeidiya Formation (Heinmann & Braun, 2000) and is dated to the Middle Pleistocene (Braun, 1992). It is comprised mainly of alluvial-colluvial deposits and conglomerates. The Naharayim Formation is composed of four members: Upper and Lower Naharayim Gravels, Yarmuk Basalts and Benot Ya‘aqov Limestone. There is a clear unconformity between the Naharayim Gravels and the ‘Ubeidiya Formation which it overlies. The Yarmuk Basalt overlies the lower conglomerate unit. K/Ar measurements have yield a date of 0.79 ± 0.17 Ma (Braun *et al.*, 1991; Heinmann & Braun, 2000).

The Lisan Formation is exposed from the Sea of Galilee in the north to Hazevah in the South. It is dated to ca. 70 - 15 Ka (Bartov *et al.*, 2002). The formation is composed of laminates of aragonite and gypsum. In the Kinnarot Basin, the exposure has been dated to ca. 24 - 26 Ka, the maximum lake stand (Hazan *et al.*, 2005).

Several additional lava flows which are stratigraphically younger than the ‘Ubeidiya Formation have been radiometrically dated and serve as upper limits for the formation. The Yarda Basalt, located in the Hula Basin overlies Mishmar HaYarden Formation which is considered correlative with the ‘Ubeidiya Formation. A clear unconformity is noted between the Yarda Basalt and Mishmar HaYarden Formation. Radiometric isotope analyses for the Yarda Basalt have yielded dates of 0.64 ± 0.12 Ma (Horowitz *et al.*, 1973).

In summary, regional stratigraphy and absolute dates for the formations below and above the ‘Ubeidiya Formation place upper (Yarmuk Basalt) and lower (‘Erq el Ahmar) limits on the ‘Ubeidiya Formation of 1.78 - 0.79 Ma, securely within the Matuyama Chron (Baksi *et al.*, 1992).

Attempts to date the ‘Ubeidiya Formation radiometrically have not yielded more accurate results. U/Th dates for the sequence between strata II 2 and II 38 of the ‘Ubeidiya Formation provided equivocal results (Bender & Kaufman, 1971) and gave dates between 0.31 - 0.128 Ma. These dates have been regarded as too young compared to the regional stratigraphy and based on comparison of both the faunal and lithic assemblages.

Despite extensive research at ‘Ubeidiya, one of the main caveats has been the lack of absolute dating of the fossil and archaeological beds. Attempts to correlate the sedimentary sequence to the Geomagnetic Polarity Time Scale (GPTS) resulted in a reverse magnetic polarity (Opdyke *et al.*, 1983), which only indicates an age earlier than the Brunhes-Matuyama boundary at 0.78 ma (Baksi *et al.*, 1992). These samples (> 10) were extracted from the Li and Lu cycles (Goren, 1981).

Recent paleomagnetic analysis on the Fi cycle (between strata II 24 and II 50) has indicated a R-N-R-N-R sequence (Sagi, 2005). The first normal episode is in the lower part of stratum II 24 and the second normal episode is located in stratum II 33-34. The total accumulation between the two normal episodes is 30 m. These have been attributed either to the Gilsa (1.575 - 1.567 Ma) to Cobb Mt. (1.215 - 1.190 Ma), a duration of accumulation of ca. 352 Ka or to the Cobb Mt. (1.215 - 1.190 Ma) to Jaramillo Base (1.068 Ma), a duration of accumulation of ca. 122 Ka (Sagi, 2005). The former produces an estimated sedimentation rate of 85 mm Ka^{-1} and a rate of 245 mm Ka^{-1} for the latter.

The estimation of rates of accumulation in alluvial deposits is highly variable (Brown, 1997; Martin, 1999). Estimates for fluvial systems range between 65 and 410,000 mm Ka^{-1} ($n = 15$, $\overline{x} = 86,000$ mm Ka^{-1}) and between 400 - 450,000 mm Ka^{-1} ($n = 28$, $\overline{x} = 112,000$ mm Ka^{-1}) for deltaic systems (Martin, 1999, Table 7.1). River terraces, floodplains, abandoned channels, secondary channels, banks, marginal berms and benches are all products of fluvial erosion, sediment transport and deposition (Steiger *et al.*, 2003). Sedimentation rates can vary with microenvironment (e.g., hydrogeography and sediment availability) (Brown, 1997). Moreover, the estimations of durations of accumulations are increased by the presence of disconformities and diastems (Kowalewski & Bambach, 2003). The calculated rates for ‘Ubeidiya is within the lower range of observed sedimentation rates of fluvial systems and suggest that either the sequence includes diastems or that the estimated duration of accumulation needs to be reconsidered.

The duration of both these sequences is longer than that the rough estimate suggested by Feibel (2004). He suggested that each of the ‘Ubeidiya cycles (Li, Fi, Lu and Fu) represent first order changes that may be related to the Milankovitch cycles and thus the duration of the Fi cycle may be estimated to span ca. 41 Ka (Liu & Herbert, 2004). If this is so, the fossil bearing strata may be confined to a shorter duration i.e., ca. 1.6 - 1.4 Ma. Future studies may reveal additional geomagnetic excursions and paleointensities (e.g., Channell *et al.* (2002)) which would present a possibility for an alternative correlation (and thus perhaps a shorter duration of accumulation) for the ‘Ubeidiya Fi cycle.

The association of the sequence to the paleomagnetic sequence rests on long range biochronological correlations detailed in the following section subsection 2.2 “Biochronological dating and cultural correlations” on page 13.

Biochronological dating and cultural correlations

The original biochronological estimation was based on the malacological fauna of the ‘Ubeidiya Formation which suggested an Upper Pliocene age (Blanckenhorn, 1897).

A detailed description of the fauna by Picard (1934) and a detailed description of the stratigraphic position (Picard, 1932) led him to ascribe the formation to the Upper Pliocene and to place it older than the Cover Basalt and as proceeding the main faulting system. Later, Picard (1952) revised his opinion and suggested the Lower Pleistocene as the date for the formation. Stratigraphically, it was placed post the Cover Basalt and therefore post the main faulting event. The later date was corroborated by N. Schulman (1959).

The onset of full scale excavations in the 1960’s led to a more detailed biochronological analysis of the faunal elements in the ‘Ubeidiya Formation. In the preliminary report after the first season of excavations, Stekelis *et al.* (1960) suggested a Villafranchian age based on faunal comparison to East and North Africa Villafranchian sites. Although the presence of Villafranchian elements was noted by Haas (1961, 1963, 1966, 1968), he also noted the presence of younger and more modern taxa which were not consistent with such an early date.

Long range biochronological correlation were based on rodent and large mammals, both providing similar age estimates. Taxonomic analysis of the rodent assemblage has shown great similarities to East Europe and Central Asia rather than European faunal assemblages. The most indicative for rodent biochronological is the evolutionary lineage of the microtines.

Using microtine genera present in the Early Pleistocene in Hungary, Kretzoi (1956) subdivided the Villafranchian mammal age (ca. 3.5 - 0.6 Ma) into three rodent super-zones: the Villányian (Late Pliocene), Biharian (Lower Pleistocene) and Mosbachaian (Middle Pleistocene).

The presence of *Lagurodon arnakae* together with *Mimomys* sp. in strata II 23-24 in 'Ubeidiya, is similar to the stage denoted by Kretzoi as Biharian (ca. 1.6 - 0.6 Ma) (Haas, 1966, 1968) and the *Microtus* - *Mimomys* rodent stage of Fejfar & Heinrich (1986).

Thus, the biochronological dating of 'Ubeidiya rests on two points, the relative biochronological correlation of the fauna and the absolute dating of the stage. If it is agreed that the fauna of 'Ubeidiya can be best correlated with the Biharian (= MN 19), the question remains of the absolute dating of the biozone, and specifically, its lower boundary.

Repenning & Fejfar (1982) suggested a Late Pliocene age of 2.0 Ma for the 'Ubeidiya Formation based on the identification of the Villányian-Biharian transition at 1.9 Ma below the Olduvai Subchron. Although others supported Repenning & Fejfar (1982) in their assessment that 'Ubeidiya is similar to other Biharian sites, they disagreed with the dating of the Villányian-Biharian boundary and place it younger than the Olduvai Subchron (1.7 Ma), thus providing a lower limit for the date for the 'Ubeidiya Formation (Opdyke *et al.*, 1983; Jaeger, 1983). Current dates for the Biharian correlate it between 1.7 - 0.6 Ma. This range is consistent with the regional stratigraphy.

Long range biochronological correlation based on large mammals provided a more concise chronological estimate. The fauna could be assigned to the Late Villafranchian mammal age (ca. 1.8 - 1.1 Ma). Classic Late Villafranchian elements include, among others, the etruscan bear (*Ursus* cf. *etruscus*), dirk-toothed felid (*Megantereon megantereon)*, mammoth (*Mammuthus merdionalis*) as well as the presence of Etruscan rhino (*Stephanorhinus etruscus etruscus*).

In some of the earlier taxonomic lists, several older and younger taxa were identified (Haas, 1966, 1968). For example; older taxa assigned to the Middle Villafranchian mammal age (ca. 2.6 - 1.8 Ma) included the cervid *Cervus ramosus*, the bovid *gazellospira torticornis*, the hyaena *Crocuta* cf. *perrieri* and the equid *Hipparion*. On the converse, younger Gallerian mammal age (1.0 - 0.6 Ma) fauna included the megacerine cervid *Praemegaceros verticornis*.

Subsequent revision of the fauna by Tchernov (1986a), Belmaker (2002b) and Martìnez-Navarro *et al.* (n.d.) has not confirmed the presence of taxon older than 1.6 or younger than 1.0 Ma (Tchernov, 1987, 1988b).

More specifically, the 'Ubeidiya fauna corresponded to Mammal Neogene Quaternary (MNQ) biozones MNQ 16 through MNQ 20 (Guérin, 1982). Few species provide a more accurate chronological estimate and can serve as biochronological indicator. The most indicative large mammal species is *Stephanorhinus etruscus etruscus*.

The *Stephanorhinus etruscus etruscus* is a typical Villafranchian taxon. Guérin (1982) subdivided this period into four sub-stages based on the faunal associations of Western Europe and specifically the species of rhino. The faunal assemblage in ʻUbeidiya is most similar to the faunal assemblage which is typical of MNQ zone 19 which includes *Stephanorhinus etruscus etruscus* as well as *Sus strozzi* and *Canis etruscus*. This stage has been roughly dated between 1.4 and 1.0 Ma.

Within this time span, the precise position of ʻUbeidiya is difficult to ascertain. No species indicative of MNQ zone 18 (ca. 1.9 - 1.4 Ma) e.g., *Croizetoceros ramosus minor*, *Cervus philisi philisi*, *Eucaldoceros senezensis*) appear in ʻUbeidiya. Similarly, no specimens of *Stephanorhinus etruscus brachycephalus* indicative of MNQ zone 20 (ca. 1.0 - 0.6 Ma) have been found at ʻUbeidiya.

Comparison with the Italian faunal units suggests the greatest similarities of the ʻUbeidiya faunal assemblage are with the Farenta faunal unit (the sites of Selvella and Pieterfitta, Italy) which has been dated to ca. 1.6 - 1.2 Ma (Calio & Palombo, 1997, and references therein). Common species to both regions include *Macaca sylvana*, *Panthera gombaszoegensis*, *Pannonictis pilgrimi*, *Ursus etruscus*, *Mammuthus Merdionalis*, *Pseudodama* sp. and *Leptobos* sp. (Calio & Palombo, 1997).

Although ʻUbeidiya shares some species (e.g., *Canis mosbachensis*) with the following faunal unit of Pirro Nord (ca. 1.2 - 1.0 Ma), it should be considered younger than ʻUbeidiya based on the extinction of forms such as *Pannonictis pilgrimi*, *Lycaon lycaonoides* = (*Xenocyaon falconeri*) and the replacement of *Ursus etrucsus* with advanced arctoid bears (Calio & Palombo, 1997).

This would suggest that the date of ʻUbeidiya should be best confined between ca. 1.6 and 1.2 Ma and consistent with identification of the Fi cycle normal paleomagnetic episodes with the Gilsa (1.575 - 1.567 Ma) to Cobb Mt. (1.215 - 1.190 Ma) as suggested by the recent paleomegnetic studies (Sagi, 2005). Figure 4 on page 178 presents a schematic representation of the ʻUbeidiya formation and other Plio-Pleistocene formations from the Jordan Valley within the GPTS. Further stratigraphic and paleomagnetic studies may determine the precise duration of the ʻUbeidiya fossil bearing strata within this time frame.

This conclusion is further supported by the lithic assemblage. Comparison of the lithic assemblage to East African site such as Olduvai Upper Bed II suggested a Early Pleistocene site. This was based on comparison to North African and South African sites (Stekelis *et al.*, 1969; Bar-Yosef & Goren-Inbar, 1993). Olduvai Upper Bed II is dated to ca. 1.53 - 1.27 Ma (Cerling & Hay, 1986;

Gowlett, 1979).

2.3 Excavation history

The formation was originally described by Blanckenhorn (1897) during initial mapping of the Jordan Valley. He identified the formation as "Melanospsis stage" which was rich in fluviatile and lacustrine sediments. A detailed geological survey and mapping was done by Picard (1932, 1933, 1934, 1943, 1952).

The paleontological and archaeological beds were discovered in June 1959 during agricultural work in the fields of Kibbutz Afikim. The fossil material was sent to the G. Haas from the Hebrew University, who on a short visit to the site found more bones and a pebble tool. Following this, 'Ubeidiya became the focus of both archaeological and paleontological excavations over the next 40 years. A profile section of the site was provided by N. Schulman (1959, 1962), leading to a detailed analysis by Picard & Baida (1966b,a).

There were four periods of excavations:

1960 - 1966 The original work was done under the direction of M. Stekelis (archaeology). Additional team members included G. Haas (paleontology), and L. Picard (geology). In 1962, The Israel Academy of Sciences provided funding for "The Lower Pleistocene of the Central Jordan Valley Project", which supported continued excavation until 1974.

During the first season of 1960 - 1961, excavations began in squares. Squares were opened in three areas: 'Site A' on the top of the hill of the first discovery, 'Site B' in the area of the vineyard and 'Site C' in the open field between the two. A geological trench (12 m) on the edge of 'Site A' was excavated parallel to the main axis of the numbered squares. The numbering of the layers uncovered in the trench followed the order of deposition i.e., from bottom to top.

In 1962, with the beginning of large scale excavations, a series of geological trenches were opened in order to understand the complex stratigraphy of the 'Ubeidiya Formation. Four trenches were excavated, transverse to the N - NE strike of the 'Ubeidiya strata (Picard & Baida, 1966b,a) and numbered with Roman numerals I - IV. Within each trench, the layers were given Arabic numbers, from oldest to youngest. Thus, II 23 is the 23rd stratum of trench II. Faunal material recovered from these seasons are marked by their squares (B5, A5) and layers.

In 1963, O. Bar-Yosef and E. Tchernov introduced the grid system over the tilted surfaced. In this method, layers with no archaeological material were removed along their strike to expose the layer of interest. A grid system of 1×1 m was set up. All material larger than 2 cm was plotted on a

1:10 scale, photographed and drawn. Depth (Z coordinates) was not taken for faunal material and artifacts from these seasons. In addition material from layers was sieved through a 1 mm mesh. Faunal remains from this period were marked by stratum, square and two coordinates.

1967 - 1974 After the untimely death of M. Stekelis on March 12, 1967, O. Bar-Yosef (archaeology) and E. Tchernov (paleontology) were appointed as field directors of the site under the supervision of G. Haas (paleontology), L. Picard (geology) and L.S.B. Leakey (archaeology). A continuation of the grid system set up in 1963 was continued and specimens were plotted by stratum, square and two coordinated. In addition material from layers was sieved through a 1 mm mesh. Faunal remains from this period were marked by stratum, square and two coordinates.

1988 - 1994 Large scale excavations resumed between 1988 - 1994 (Bar-Yosef *et al.*, 1993; Debard *et al.*, 1989, 1990, 1991; Guérin *et al.*, 1996; Guérin *et al.*, 1988, 1992) in a joint Israel-French- American excavation under the directorship of O. Bar-Yosef and J. J. Shea (archaeology) with E. Tchernov and C. Guérin (paleontology). During this period, a three point (x, y, z) system grid was developed which allowed for three point piece plotting for specimens larger than 5 cm.

1997 - 1999 From 1997 1999, a joint Israel-German-American excavation was undertaken (Tchernov *et al.*, 1998). This excavation was directed by O. Bar-Yosef, J. J. Shea and G. Bozinski (archaeology) and E. Tchernov (paleontology). During this period, the three point system (x, y, z) grid continued. During the 1999 season, a sample (one 10 liter bucket) from each square excavated was taken for wet sieving through a 1 mm mesh. Faunal remains from this period were marked by stratum, square and three coordinates.

Figure 5 on page 179 presented the excavation plan for 1960 - 1999 and Figure 6 on page 180 presents the temporal sequence of strata by trenches.

Faunal material retrieved from all seasons of excavation is housed in the paleontological collection of the Hebrew University of Jerusalem. Several specimens are housed in the Israel Museum, Jerusalem and the hominin remains are housed in the Sackler School of Medicine, Tel Aviv University.

2.4 Previous paleoecological research

The mammal fauna Paleontological analyses from the early season of excavations were published by G. Haas in Stekelis *et al.* (1960) and later by Haas (1961, 1963, 1966, 1968). These included the fauna from the 1960-1974 seasons of excavations and were primarily taxonomic lists. E. Tchernov completed a detailed analysis of the rodents (Tchernov, 1981) and edited a comprehensive publication of the mammalian taxa in ‘Ubeidiya by world leading paleontologists (Tchernov, 1986a). These included M. Volokita (Insectivora and Primates) , R. Ballesio (Carnivora), D. Geraads (Suidae and Ruminantia), C. Guérin (Suidae and Rhinocerocidae), M. Faure (Suidae and Hippopotamidae), V. Eisenmann (Equidae), M. Beden (Proboscidae) and E. Tchernov (Rodentia, Lagamorpha, Insectivora and Primates). A revision of the arvicolids was completed by Von Koenigswald *et al.* (1992).

B. Martínez Navarro revised the taxonomy of the bovids and large carnivores of the site (Martìnez-Navarro *et al.*, n.d.; Martìnez-Navarro, 1999, 2000), which included material from all seasons of excavations.

Tchernov & Guérin (1986) suggested the reconstruction of a freshwater lake surrounded by a mosaic Mediterranean park forest. In addition, the occurrence of some arid climate species (*Camelus* sp., *Allactaga* sp.) suggest the existence of more arid environments within the greater catchment area of paleolake ‘Ubeidiya. However, the presence of Africa taxa, adapted to savanna type habitats and specifically *Pelorovis oldowayensis* and *Oryx* cf. *gazella* has been interpreted by others to indicate an arid to semi arid African savanna environment (Dennell, 2004; Martínez Navarro, 2004).

Avian fauna Tchernov (1968, 1980) studied the avian fauna of of ‘Ubeidiya Formation. Results indicates the presence of 48 species from five strata. The species identified represent a variety of environments: the aquatic habitat, swamps and marshes, grasslands, woodland, rocks and cliffs. The reconstruction is of a varied marshland and swampy habitat surrounding the lake. The regions around the lake included a mosaic of woodland and grassland which were bordered by the rifted rocky escarpment.

Reptile, amphibian and fish remains Haas (1961, 1963, 1966, 1968) studied the non mammalian vertebrates at the site. Fish remains are probably the most common vertebrates found in the site and is consistent with the presence of a freshwater lake. Taxa identified included mainly clariids (*Clarias* cf. *lazera*), also cyprinids, cichlids and cyprinodonts (Van Neer *et al.*, 2005). All groups are present today in the Jordan Valley. Amphibian remains include mostly anurans *Bufo* sp. or *Rana* sp. Smaller specimens may be attributed to *Hyla* sp. A single specimen was attributed to *Discoglossus* sp. All anurans support the existence of a wetland region. Reptilian fauna include a crocodile, the aquatic *Varanus niloticus* and the freshwater turtle *trionyx*. All taxa confirm the presence of a freshwater lake.

Malacofauna and crustacean Tchernov (1973) completed an in-depth study of the malacofauna from the ‘Ubeidiya Formation. The relative frequency of the littoral taxa, *Melanopsis* and *Theodoxus* was compared to relative frequency of *Bulimus*, which is a deep lake inhabitant. The relative frequency between the two ecotypes was used as a proxy for hydrological habitats. Results indicated temporal changes between littoral environments and deep lakes.

A study by Heller & Sivan (2002) analyzed the *Melanopsis* spp. They determined that three species and two hybrids existed throughout the sequence which differed in their ecological niche requirements. Thus, the presence of *M. buccinoidea* suggests an ecological landscape representing a spring or perhaps a deep lake with a nearby stream and is the dominant taxon in the Li cycle; *M. costata* indicates an ecological landscape of a shallow, non-turbulent, well-aerated lake with a slow current and is the dominant taxon in the Fi cycle; and the *Phanesiana obediensis* is suggestive of an ecological landscape of a turbulent, well-aerated lake and is the dominate taxon in the Lu cycle. All crustacean may be attributed to the freshwater crab *Potamion* cf. *potamios* (Haas, 1966), which is extant in the freshwaters system of the Jordan valley.

Micropaleontology Micropaleontological samples were extracted from the Li and Lu cycles. The foraminifera *Ammonia berccarii tepida* and *Ammonia berccarii cf. parkinsonia* were found at the base of the Li cycle. Diatoms were found throughout the cycle. Two distinct phases of salinity, a fresh phase ($< 5‰$) and a mesohaline phase ($5 - 30‰$) can be distinguished based on diatom and foraminifera assemblages (Almogi Labin *et al.*, 1995; Siman-Tov *et al.*, 1993, 1994).

Based on the micropaleontological remains, it is interpreted that the Fi cycle sediments were deposited in a freshwater lake with a mesohaline stage during its early and late phases. In its intermediate stage (III 12), reworked Paleocene foraminifera suggests strong fluviatille activity (Almogi Labin *et al.*, 1995; Siman-Tov *et al.*, 1993, 1994).

The botany Few botanical remains have been retrieved from the site, all from the Li cycle. Macrofloral remains of fossilized leaves have been found in stratum III 19. These have been identified as *Pistacia lentiscus*, *Rhus tripratita* and *Myriophyllum* (Lorch, 1966).

Pollen spectra were extracted from stratum III 12 and analyzed by A. Horowitz (in Bar-Yosef & Tchernov, 1972). The analysis indicated 82% arboreal species of which the overwhelming majority are *Quercus* sp. followed by *Juniperus* sp. and *Olea* sp. Non arboreal families include Gramineae, Cruciferae and Compositae. Cyperaceae comprise 8.4% of the pollen and attest to the water habitat present at the site. Both analyses support the presence of a Mediterranean park-forest with rocky and steppe terrain.

Water quality Analyses of Ca, Ba/Ca and ^{87}Sr/^{86}Sr isotopes from ‘Ubeidiya *Melanopsis* gastropods has indicated that the water in paleolake ‘Ubeidiya consisted mostly of basaltic water ($> 80\%$) with a small contribution of Rift brines. The influence of carbonates on the chemistry of the water must have been negligible as indicated by its low salinity (Rosenthal *et al.*, 1990). The basaltic water was probably received via the Yarmuk river during erosion of the basaltic plains of the Golan Heights following the post-Cover Basalt tectonic phase (Rosenthal *et al.*, 1990).

2.5 The presence of early hominins at ʿUbeidiya

Evidence for the presence of early hominins in the site is indicated by anthropological osteological remains (albeit scant) and and evidence for human activity at the site:

1. **Anthropogenic remains**

Several cranial fragments (UB 1703, 1704, 1705 and 1706), an incisor (UB 1700) and a molar (UB 1701), retrieved as surface finds, have been assigned to *Homo* indet. (Tobias, 1966b,a) and later revised as *Homo* cf. *erectus* (Tchernov & Volokita, 1986).

Belmaker *et al.* (2002) described a right lateral hominin incisor (UB 335) from stratum I-26a of ʻUbeidiya. UB 335 exhibits similar taphonomic affinities to the macromammal fauna of I-26a, including heavy fossilization, almost metallic in color and heavy in weight, suggesting a similar depositional environment. All previously identified of hominin specimens (UB 1700, 1701, 1703, 1704, 1705 and 1706) have been shown to be younger than the surrounding deposits (Molleson & Oakley, 1966). While it has since been agreed that the cranial fragments represent intrusive elements, the molar (UB 1701) and incisor (UB 1700) were assigned to the Lower Pleistocene deposits based on provenience data (Tchernov & Volokita, 1986). However, due to the small size, the teeth were not tested for radiometric assay but for level of fluorination, which allows only a semi-quantative analysis (Molleson & Oakley, 1966). Moreover, fluorine tests have been shown to be problematic (Johnsson, 1997). Thus, while the antiquity of the previous finds has been contested, the new hominin incisor (UB 335) described is the only one that can be securely assigned to the Lower Pleistocene deposits.

The UB 335 incisor did not differ significantly from Lower Pleistocene hominins of other sites but did differ significantly from other known Middle and Upper Pleistocene hominin fossil populations. Two-tailed student t-test and single classification Model II ANOVA of the buccolingual diameter could not distinguish among the Lower Pleistocene species: *Homo habilis*, *H. ergaster* and *H.* cf. *erectus*. Thus, UB 335 can be identified as a Lower Pleistocene hominin although it cannot be securely assigned to any particular species within that time frame. The current date of the ʻUbeidiya deposits and the location of the site within the Levantine corridor suggests a tentative identification as *H. ergaster* (Belmaker *et al.*, 2002).

2. **Evidence for hominin behavior**

This can be derived from several lines of evidence; the large lithic assemblage, cut-marks and possible modified living floors:

Lithic assemblage A large lithic assemblage was found at the site, dispersed throughout the strata but mostly concentrated in the Fi cycle. The lithic assemblage was analyzed by Stekelis (Stekelis, 1965, 1966; Stekelis *et al.*, 1969, 1960). A detailed analysis of the lithics from 1960 - 1974 was undertaken as a Ph.D. dissertation by Goren (1981) and later published in a monograph (Bar-Yosef & Goren-Inbar, 1993). The lithics from the 1988 - 1994 seasons were published by Shea & Bar-Yosef (1999) and Shea (1999).

The three main sources for raw material used for tool manufacture in ‘Ubeidiya were flint, limestone and basalt. The lithic assemblage as a whole reflects a high degree of homogeneity and includes high frequencies of core tools, notches, denticulates and scrapers (Bar-Yosef & Tchernov, 1972).

Stekelis *et al.* (1969) identified two distinct cultures at the site. The first, Developed Oldowan, is characterized by chopping tools, spheroids and sub-spheroids and well as scrapers and used flakes. The second culture, the Lower Acheulian, includes a high percent of hand axes and a lower percent of light-duty tools (scrapers and used flakes). This change in assemblage throughout the sequence observed by Stekelis has not been supported in later studies (Bar-Yosef & Goren-Inbar, 1993).

Cut-marks and evidence for bone marrow processing An analysis of cut-marks was done on the faunal assemblage from 1969 - 1974 and 1997 - 1999 (Gaudzinski, 2002, 2004b,a, 2005). Results suggests that cut-marks are present in low proportions and evidence for bone marrow extraction (i.e., percussion marks on bone fragments) is absent.

It has been suggested that the overall percent of percussion marks and location of cut-marks on skeletal elements is consistent with early access of hominins to carcasses (Gaudzinski, 2002, 2004b,a, 2005).

Living floors The exposure of thin “pavements”, a pebble or two thick, have been dubbed “living floors”. While the appearance of the “living floors” is similar to that of a natural rocky beach, the size and compact organization of the cobbles suggested they may have been partially modified by humans (Bar-Yosef & Tchernov, 1972). Goren (1981) points out the restricted thickness of the deposits, the association between the lithic artifacts and bone specimens and the high artifact density is consistent with the characteristics of “living floors” as defined by Villa (1977). Nonetheless, granulometric studies aimed at comparison between naturally deposited shorelines and the ‘Ubeidiya strata were inconclusive (Bowman & Giladi, 1979). Further studies on the distribution of lithics could not confirm or refute any of the hypotheses (Bar-Yosef & Goren-Inbar, 1993).

Part II

Methodology

Chapter 3

Paleontological Methodology

Over years of excavation, different methods of collection (see chapter 2.3 on page 15) have led to various levels of stratigraphic information recorded for each specimen. In order to provide a uniform method, all specimens were labeled with new numbers. This ensured that specimens could be retrieved for cross-checking in the future.

Labeling procedure included the application of acrylic PB 72 on a small area of each bone, followed by numbering with Indian ink and then application with another thin layer of PB 72. Each specimen was placed in a separate plastic bag with a paper label denoting the stratigraphic information, taxon, body part and previous catalogue numbers. Bones were repaired as necessary to facilitate identification and compared to published reports. Data was recorded using FILEMAKER Pro 7.0 database program.

3.1 Stratigraphy

3.1.1 Assignment of specimens to stratigraphic units

Each specimen was assigned all the data which could be ascribed to it and included sub-stratum, square and when applicable, the three dimensions on the grid system. This was retrieved from existing information on the specimens, associated notes or information on boxes and bags, field diaries, catalogues and publications. In case of discrepancies in stratigraphic information between the tags attached to the specimens and that which appears in publications, I preferred the data on the specimens themselves. Mammalian faunal remains were retrieved from 114 strata or substrata.

Unfortunately, most of these 114 strata and substrata had small sample sizes which were inadequate for meaningful paleoecological analyses. In order to facilitate such analyses, several procedures were undertaken to enable analyses of larger sample sizes. This included grouping of substrata and strata into more inclusive stratigraphic units, thereby including as many fossil specimens as possible. Grouping was based was geological correlation and grouping of substrata as detailed below. In this thesis, stratigraphic units originally defined by the excavators are termed ‘strata’ and the inclusive stratigraphic units used in this analysis were termed ‘pooled strata’.

Geological correlations

Picard & Baida (1966a) and Bar-Yosef & Tchernov (1972) suggested geological correlations between strata. Some of these were done by following the strike of each layer. A good example is stratum I 15. In trench I it was excavated along its strike until trench II, where it met stratum II 26 indicating that they are the same strata. Thus, correlated strata from different trenches were analyzed as a single unit (e.g., III 23-25 and K 29-30).

Also, specimens from early seasons of surveys and excavations (1959 - 1962) and which were assigned units other than the trench-layer system (e.g., the samples described by Schulman (1959) and square system (Stekelis *et al.*, 1960)) were converted into this system.

Following Schulman (Schulman, 1959, 1962; Stekelis *et al.*, 1960) the correlations are as follows (the old system is given on the left and the trench-layer system on the right) :
Sample 1 = II 19; Sample 2 = II 20; Sample 3 = II 21; Sample 4 = II 22; Sample 5 = II 23; Sample 6 = II 24; Sample 7 = II 25; Sample 8 = II 26; Sample 9 = II 27; Sample 10 = II 28; Sample 11 = II 29; Sample 12 = II 30; Vineyard = K 29-30; K1 to K4 = K28; K5 = K 29; K6 = K 30; Square A6 from date 24.4.1960 was assigned to II 23-25.

In addition, specimens assigned to L.F. and no data from 1966 squares EF 78 - 80 were assigned to stratum I 15-16 based on field diaries.

Figure 7 on page 181 presents the strata grouped together and their stratigraphic relationship. The assignment of strata to pooled strata is described in detail in Appendix E on page 277.

Grouping of substrata

In order to facilitate analysis using larger sample sizes, substrata were analyzed together as a single unit. This was supported by the presence of conjoined specimens in two separate substrata suggesting that they are a single stratigraphic unit e.g., UB 731 from stratum I 26 and UB 610 from I 26c. Moreover, grouping of these substrata was also supported by the analysis of microfacies and their interpretation based on soil micromorphology (Mallol, 2004, 2006). Thus, strata II 23 and II 24 have both been identified as bioturbated gleyed sandy clay and all substrata of III 22 (with the exclusion of III 22a) have been identified as bioturbated pseudogleyed silty clay (Mallol, 2004, 2006).

Also, stratigraphic units which were considered as possible belonging to either one of two consecutive strata (e.g., II 23-24 or I 15-16) were analyzed together with specimens which were definitely assigned to either strata (e.g., II 23 and II 24, I 15 and I 16). This was also supported by the presence of conjoined specimens between consecutive strata e.g., UB 199 from stratum II 24 and UB 10699 from stratum II 23.

Of the total of 32 'pooled strata', 12 'pooled strata' had a sample size larger than 10. This was determined as the cut off point for subsequent analysis (See subsection 3.1.2 on page 25).

Figure 7 on page 181 presents the strata grouped together and their stratigraphic relationship. The assignment of strata to 'pooled strata' is described in detail in Appendix E on page 277.

3.1.2 Choice of strata for analysis

Despite increased sample sizes by the use of 'pooled strata', sample sizes of some units remained low. A logarithmic relationship exists between sampling effort (volume of excavation) and sample size and in turn between sample size and richness. Thus, in low sample sizes, a small increase will greatly increase our richness but after a given sample size (the asymptote), further sampling will not result in significant increase in richness and we may infer that the assemblage has been adequately sampled (Gotelli & Graves, 1996). Thus, species comparisons among assemblages with low sample size that are not adequately sampled, will not yield scientifically valid results.

In order to use assemblages with adequate sample size, 'pooled strata' were chosen using point by point individual based rarefaction curves. Rarefaction is used to compare species richness between two samples in paleontological and archaeological assemblages of unequal size by estimating the species richness expected based on random sub-samples of individuals (Gotelli & Graves, 1996).

By performing the procedure for several abundances (from 1 to the maximum sample size available), we can plot a point by point rarefaction curve for the expected number of species (ordinate) for every sample size (abscissa). If the graph has reached an asymptote, the sample was considered as adequately sampled (Bonuso *et al.*, 2002b,a; Zohar & Belmaker, 2005).

Rarefaction was calculated using freeware Analytic Rarefaction 1.3 by S.M. Holland. The rarefaction equation is based on a modification of the original equation by Sanders (1968) as developed by Hulbert (1971) and is based on hypergeometric distribution sampling without replacement from a parent distribution (the observed assemblage). The equation used for rarefaction is described in Equation 1 on page 271. The variance calculated follows the equation developed by

Heck *et al.* (1975) and is presented in Equation 2 on page 271. The upper and lower 95% confidence limits are calculated as estimated number of species $\pm 1.96 \times \sqrt{\sigma^2(\hat{S}_n)}$; the 99% confidence limits are calculated as estimated number of species $\pm 2.58 \times \sqrt{\sigma^2(\hat{S}_n)}$.

Following the methodology suggesting by Gotelli & Graves (1996), assemblages were compared by plotting their rarefaction curves and 95% confidence limits. Rarefaction curves were based on the maximum quantification method (Number of Identified Specimens (NISP) quantification).

To determine which of the rarefaction curves reached an asymptote, I calculated the increment of the rarefaction curve (Equation 3 on page 271) for the last ten consecutive pairs of n (number of identified specimens NISP) and $\hat{S}_n$ (expected number of species). A 'pooled stratum' was considered to reach an asymptote if the average of the last ten pairs was 0.05 or less.

A total of 24 'pooled strata' had specimens which were identifiable to the species level. The number of specimens per 'pooled stratum' ranged from 1 to 814. In order to select which ones were adequately sampled, the 12 'pooled strata' with a sample size larger than 10 were subjected to point by point rarefaction.

Results are presented in Figure 8 on page 182. Of the 12 'pooled strata' tested, seven met the criteria set above and are listed in stratigraphic order from oldest to youngest: III 11-13, III 20, III 23-25, III 21-22, II 26-27, II 36 and II 37.

3.2 Taxonomy

3.2.1 Identification of specimens

This thesis included all the identifiable specimens of large mammal bones from all seasons of excavations. For the taphonomic analysis, the sample was augmented by a sample of unidentified specimens as explained in Section 4.2 "Independent variables of the null hypotheses: The taphonomy of the 'Ubeidiya large mammal assemblages" on page 37. Specimens identified to other taxa (small mammals, birds, reptiles, turtle, fish and invertebrates) were not included in this study. It is important to stress that the large bulk of these taxa have not been studied to date.

A large bulk of large mammal fragments (ca. 10,000 specimens) also remains unidentified, with the overwhelming majority less than 2 cm in length. Previous researchers (Prof. Haas and Prof. Tchernov) had separated the identifiable specimens from those that were deemed undeterminable. All the material studies in this thesis comes from the identifiable section supplemented with a sample of the undeterminable one.

Taxonomic identification is the foundation for biodiversity analysis. There are levels of taxonomic identification, each with different applicability to different studies (Belmaker, 2005a).

I identified all specimens (both craniodental and post cranial) by comparison with fossil taxa that were previously published from the site (Ballesio, 1986; Beden, 1986; Eisenmann, 1986; Faure, 1986; Geraads, 1986; Geraads *et al.*, 1986; Guérin, 1986; Haas, 1961, 1963, 1966, 1968; Martìnez-Navarro, 1999, 2000; Martìnez-Navarro *et al.*, n.d.; Tchernov, 1986b; Tchernov & Volokita, 1986). If unpublished material could not be identified by comparison with identified specimens in the published material from the ‘Ubeidiya collection, identification was done by comparison with comparative mammal and paleontological collections worldwide or publications in the literature. A list of museum collections visited in this study is presented in Appendix D on page 276.

The question of dispersal of hominins from Africa, emphasizes the importance of the identification of the biogeographic origin of the mammals identified at ‘Ubeidiya and their quantification. The biogeographic origin of taxa was determined based on data obtained from the literature. The mammals of African origin in ‘Ubeidiya that can be related to the Lower Pleistocene dispersal events was quantified as a proportion of total species and as a proportion of total individuals.

Not all fragments are identifiable to species or genus, resulting in a large collection of bones which could only be identified to higher taxonomic levels (family or order). Specimens identified to higher taxon levels were assigned body size groups which roughly corresponded to the estimated weight of the identified taxa:

A: $\leqslant$ 0.5 kg Included all micromammals; Rodentia (with the exclusion of *Hystrix indica*, Chiroptera and Insectivora (with the exclusion of *Erinaceus europaeus*).

B: 0.5 - 1 kg Included *Vormela peregusna* and *Erinaceus europaeus*.

C: 1 kg - 10 kg Included *Hypolagus beremendensis*, *Lutra simplicidens*, *Herpestes* sp., *Vulpes* sp., *Felis* cf. *chaus*, *Macaca sylvana*, *Pannonictis pilgrimi* and *Mellivora* sp.

D: 10 - 30 kg Included *Gazella* sp., *Canis mosbachensis*, *Lynx* sp. and *Hystrix indica*

E: 30 - 70 kg Included Antilopini gen. indet., *Capreolous* sp., *Megantereon* sp., *Theropithecus* cf. *oswaldi*, *Crocuta crocuta* and *Lycaon lycaonoides*.

F: 70-200 kg Included *Pseudodama* sp., *Oryx* sp., *Homo* sp., *Sus strozzi*, *Oryx* cf. *gazella* and *Panthera gombaszoegensis*.

G: 200-1000 kg Included *Praemegaceros verticornis* complex, *Leptobos* sp., *Equus* spp., *Kolpochoerus olduvaiensis* and *Ursus etruscus*.

H: 1000-2000 kg Included *Hippopotamus* spp., *Giraffa* cf. *camelopardis*, *Pelorovis oldowayensis*, *Stephanorhius etruscus etruscus* and *Camelus* sp.

I: $\geqslant$ 2000 kg Included *Mammuthus merdionalis*.

Fragments that could not be definitely assigned to one of the above categories were assigned intermediate body size groups i.e the category EF indicated specimens with body sizes intermediate between body size groups of both E and F size groups.

3.2.2 Choice of taxa for analysis

Tchernov (1986b) has suggested that the mammalian community is comprised of three distinct communities: The large terrestrial mammalian fauna, defined as taxa with live weight $\geqslant$ 3 kg which habitually exploit terrestrial habitats; the large aquatic mammalian fauna, defined as taxa with live weight $\geqslant$ 3 kg which require lakes or swamps (*Hippopotamus* spp.) and the micromammal community defined as taxa with live weight $\leqslant$ 3 kg. The latter include members of the orders Insectivora, Rodentia and Chiroptera (Tchernov, 1986b). This study concentrated on the analysis of the large mammalian community (i.e., excluding all Rodentia and Insectivora) in general and the terrestrial one in particular.

Micromammals are most commonly accumulated by raptors and carnivores and deposited in paleontological sites in pellet and scat remains respectively (Andrews, 1990). A preliminary study on the rodents of ‘Ubeidiya has suggested that they were deposited by diurnal raptors (Belmaker, 2005b). They are susceptible to very different biases than those which are exerted on the skeletal remains of mammals of larger sizes. Analysis of both micro and macro mammals in one assemblage thus confounds the problem of paleoecological fidelity. Thus, although useful for paleoecological reconstruction (Andrews, 1990; Reed, 1995), micromammals should be analyzed separately from the large mammals and hence are not included in this analysis.

Within the group of terrestrial large mammals, I have decided to exclude *Hippopotamus* spp., *Equus caballus* and *Homo* sp. from this analysis. The rational for the exclusion of each of the taxa is detailed in the following paragraphs.

Exclusion of *Hippopotamus* spp. is based on taphonomic, paleoecological and archaeological considerations.

The *Hippopotamus* spp. assemblage at ‘Ubeidiya probably represents an autochtonous assemblage. First, modern ecology of the genus *Hippopotamus* indicates that hippos require abundant quantities of water. They spend most of the day is the water but come out to land to graze at night (Oliver & Laurie, 1974). The presence of their remains in lakeshore and floodplain habitats is consistent with the working hypothesis that the hippos are a non-transported assemblage.

To test the working hypothesis presented above, body part distributions were compared to those expected from complete carcasses using the ratio diagram (Reitz & Wing, 1999). Comparison was done for two main taxonomic groups and body sizes. The first included the *Hippopotamus* spp. together with specimens belonging body size group, GH or H (see section 3.2 on page 26). The second included all ruminant taxa from small-medium body size groups (i.e., E and F). This included species identified to *Capreolous* sp., *Pseudodama* sp., *Gazella* sp., Antilopini gen. indet, *Oryx* cf. *gazella* and specimens belonging to body size groups E and F (see section 3.2 on page 26). Specimens removed from the analysis included antler fragments that included neither pedicle nor burr, horn core fragment that did not include an entire circumference, teeth fragments that were too small to identify to type and metapodials which could not be identified as either metacarpals or metatarsals.

Figure 9 on page 183 presents the ratio diagrams comparing skeletal portions based on the formula $D = \ln(\frac{X}{Y}) = \ln(X) - \ln(Y)$ where X is the percentage of each skeletal portion identified in the paleontological collection and Y is the percentage of the same portion in a complete skeleton (Reitz & Wing, 1999). Calculation were based on maximum quantification (Number of Identified Specimens or NISP) in which each element was counted as a separate individual.

Results presented indicate a different distribution for hippos compared to small-medium ruminants. The hippo indicate a relatively complete skeletal representation for all strata, consistent with autochtonous depositions. On the converse, small-medium ruminants indicate a pattern of under representation of axial elements and phalanges and an over representation of upper fore and hind limbs suggesting an assemblage modified by taphonomic processes. The difference in body portion representation suggests these groups of taxa were subjected to different taphonomic processes and thus should be treated differently in subsequent paleoecological analyses.

Another aspect to consider is the interaction both early hominins and carnivores had with the *Hippopotamus* and the large terrestrial mammal assemblage. Most comparative studies aimed at answering the question of human subsistence patterns focused on mammals of size D - G and excluded the larger one such as hippos (Domínguez-Rodrigo, 2002; Bunn & Kroll, 1986). The separation between the two size groups was based on the rational that due to the large proportion of fat tissue on very large ungulates (hippos or elephants), they are not diagnostic for hominin subsistence patterns. The cut-mark pattern produced on a carcass of very large ungulates by either hunting or scavenging are similar. Moreover, defleshing is possible without leaving many cut-marks, if any (Domínguez-Rodrigo, pers. com. 2005). Of course, this does not negate the fact that hippos were consumed by either hominins or carnivores (Gaudzinski, 2004a,b, 2005).

This is not to say that the hippopotamus assemblage does not warrant an independent analysis in the future nor that we can assume that their frequencies did or did not change through time. Rather, that their frequency is not necessarily indicative of the distribution of habitat types in the regions surrounding paleolake ‘Ubeidiya.

Exclusion of *Equus caballus* is based on taphonomic observations. Only one specimens was found (UB 2613 from stratum II 23) which is light in weight and color and which did not resemble the level of fossilization of the majority of specimens from stratum II 23-24. Moreover, it showed high taphonomic affinities to identified hominin specimens (UB 1700, 1701, 1703, 1704, 1705 and 1706) from the same stratum (Belmaker *et al.*, 2002) and which have been shown to be younger than the surrounding deposits (Molleson & Oakley, 1966). Thus, the specimen in question is probably an intrusive element and hence is not an integral part of the ‘Ubeidiya assemblage.

Exclusion of *Homo* sp. is based on the difficulty of assessing relative abundance of the taxon. While other taxon are quantified by ostoelogical remains only, hominin presence is estimated not only by actual remains but also by technological remains (lithics) and evidence of behavior (cutmarks). The two latter components cannot be quantified. Therefore, I elected to exclude the taxon altogether, in this study.

It is not the scope of this study to present a detailed paleontological taxonomic analysis of the fauna at the site (i.e., measurements, photographs, etc.) and they will be published elsewhere.

3.3 Quantification

3.3.1 Quantification of individuals per species

In order to analyze changes in community structure through-time, it is necessary to perform diversity analysis, which requires an estimate of number of individual per species. Two methods of quantification are used. The first is Number of Identified SPecimens (henceforth NISP) defined as “The number of identified specimens in a collection” (Lyman, 1994). It is the basic observational unit and highly replicable by different researchers (Davis, 1987; Klein & Cruz-Uribe, 1984; O’Connor, 2000; Reitz & Wing, 1999). The classification of each specimen as “identified” vs. “unidentified” depends on the level of taxonomic classification appropriate for each research question. Thus, for biodiversity questions, “identified” includes only specimens identified to species. However, for many taphonomic studies specimens do not need to be identified to the species level, and it is possible to suffice with identification of body element along with body size (Davis, 1987; Klein & Cruz-Uribe, 1984; O’Connor, 2000; Reitz & Wing, 1999).

In this thesis, “identified” specimens refer to those identified to low level taxon i.e., species or genus and “unidentified” refers to those identified to higher level taxon (i.e., family and order), element and body size.

It has been argued that NISP measures suffer from two inherent biases; difference in skeletal elements of different taxa and interdependence (Davis, 1987; Klein & Cruz-Uribe, 1984; O'Connor, 2000; Reitz & Wing, 1999). The first stems from the fact that different vertebrates have different numbers of elements (e.g., equids have one metapodial on each limb as opposed to two of ruminants) or specific elements such as horn or antler which may be highly fragmented and readily identifiable even as small fragments due to their unique internal structure. Thus, some taxa may have elevated NISP values as opposed to other taxa, based solely on their anatomy. The second bias, interdependence between specimens, originates from the fact that some of the specimens may belong to the same individual (Grayson, 1984).

The first bias is often resolved by comparing frequencies of taxa with similar skeletal elements (e.g., comparing ruminants among themselves and carnivores among themselves) or removing problematic elements from the analysis (e.g., antler or horn core fragments) (Davis, 1987; Klein & Cruz-Uribe, 1984; O'Connor, 2000; Reitz & Wing, 1999). The probably of interdependence (Grayson, 1984) is often naturally reduced in assemblages subjected to high levels of attrition (Gautier, 1984).

The second method of quantification, Minimum Number of Individuals (henceforth MNI) is defined as "minimum number of individual animals necessary to account for some analytical specified set of identified faunal specimens" (Lyman, 1994). The assumption is that some of the specimens found can be related to the same individual (White, 1953). For each taxon, the most abundant skeletal elements are sorted into left and right (when applicable), and the highest value per side is taken as the number of individuals of this taxon (Davis, 1987; Klein & Cruz-Uribe, 1984; O'Connor, 2000; Reitz & Wing, 1999).

MNI values may be increased if age, sex and overall size of each of the specimens are taken into consideration. Thus, as opposed to NISP counts, MNI values are an analytical derived unit and as such, different researchers can calculate it in different manners. This confounds the ability to use MNI values for inter-assemblage comparisons. Moreover, MNI values have been shown to usually underestimate the correct value in actualistic taphonomic studies (Davis, 1987; Klein & Cruz-Uribe, 1984; O'Connor, 2000; Reitz & Wing, 1999).

In this thesis, MNI are calculated for each species. MNI were estimated by including sex and age when possible into the equation.

3.3.2 Quantification of body elements

Quantification of taxa is required for biodiversity studies (dependent variables) and frequencies of skeletal portions provide insight into taphonomic processes (independent variables). Taphonomic processes include the accumulation agent (either hominins or carnivores), and density mediated processes such as trampling and carnivore ravaging.

The basic unit for quantification of body elements is the Minimum Number of Elements (henceforth MNE), defined as "the minimum number of skeletal element portion necessary to account for the specimens representing the portion" (Lyman, 1994). MNE can be calculated for complete elements (i.e., femur) or for portions thereof (i.e., proximal femur, distal femur).

There has been a detailed discussion in the literature as to the calculation of MNE. Klein & Cruz-Uribe (1984) advocated using the "overlapping fraction" method. For specimens which are not complete, an estimate is made of the size of the specimen found, as a fraction of a complete bone (i.e., one half, one quarter, one eighth etc.) The fractions are summed to produced the MNE value for each skeletal element. A modified method was suggested by Marean & Spencer (1991) and based on summing the percentage of complete circumferences represented by long bone shafts.

Due to density mediated processes and specifically, carnivore ravaging, axial elements and limb bone epiphyses tend to be removed from the assemblage. Early analyses primarily classified epiphyses (Davis, 1987; Speth, 1983). It has been shown that inclusion of shaft fragments (by refitting or use of anatomical markers) has the potential to alter previous conclusions derived from relative skeletal frequencies (Marean & Kim, 1998) although this has been shown to be case specific rather than the rule (Stiner, 2002).

MNE calculations were obtained for each identified species, as well as four higher level taxon of similar anatomical composition and body size; Ruminantia E, Ruminantia F, Ruminantia G and Equidae. Shaft fragments were identified whenever possible using refitting (Marean & Kim, 1998) and anatomical markers such as foramen and muscle attachments (Pickering, 2002).

MNE values are derived for each fragment type based on side and extent of overlap (Klein & Cruz-Uribe, 1984). Thus, a half medial fragment and a quarter lateral fragment of two left proximal radii would count as an MNE of one, on the other hand, two medial fragments, regardless of the fragment size, would count as two. Degree of ossification was used to separate juveniles from adults.

In order to estimate overlapping fraction, four levels of fragmentations were recorded for specimens:

1. *Limb portion* preserved; proximal end, proximal shaft, mid-shaft, distal shaft and distal end.

2. *Fragmentation* along the shaft; complete, $\frac{2}{3}$, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{4}$ and $\frac{1}{8}$.

3. *Fragment* of the portion preserved; distal, proximal, shaft, medial, lateral, anterior or posterior.

4. *Shaft circumference*; complete, $\frac{2}{3}$, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{4}$ and $\frac{1}{8}$.

Thus, a humerus specimen which scored $\frac{2}{3}$ on *fragmentation*, distal on *fragment* and complete on *shaft circumference* included the distal ephiphesis and nearly two thirds of the shaft. A femur which scored $\frac{1}{8}$ on *fragmentation*, shaft on *fragment* and $\frac{1}{2}$ on *shaft circumference* included a femur shaft fragment with approximately an eighth of a length of a shaft and a half of the circumference.

Following the method of Bunn & Kroll (1986), I have calculated MNE for epiphyses data "MNE ends" as well as those which include shafts "MNE complete". For the calculation of "MNE ends", if complete specimens were present, they were analyzed twice, once as a proximal epiphysis and once as a distal epiphysis. Similarly, MNE for skull and mandibles are calculated from bony elements separately from MNE derived for both upper and lower dentition (Stiner, 1995).

For the calculation of "MNE complete", estimation of the number of complete elements of each body element were calculated including shaft fragments lacking epiphyses which are excluded in the "MNE ends" calculation. Thus, a complete right tibia, left distal tibia and a left tibia mid-shaft fragment would count as a total MNE of two tibiae. MNE for skull and mandible include calculations for both bony specimens and dental specimens calculated together to estimate number of mandibles and cranial elements present.

Since different elements appear in different numbers in a vertebrate body (e.g., one atlas vs. five metatarsals and two humeri in a primate), MNE values are standardized to determine relative survival of elements. Minimum Anatomical Units (henceforth MAU) are derived from both left, right and un-sided MNE calculations (Klein & Cruz-Uribe, 1984). The total MNE is divided by the number of times the element appears in a single individual of a species. Thus, in the example outlined above, if the total complete MNE for the tibiae is two and there are two tibiae in a vertebrate body, the MAU is one. Percent MAU are normalized values which divide the MAU values per taxon by the highest MAU score per species found in the assemblage (Klein & Cruz-Uribe, 1984).

Aside from identification of element, fragmentation and side, each specimen was assigned two levels of anatomical units as explained below. This was useful in analyses of higher level skeletal element distribution.

First, an intermediate level of identification was applied to specimens with only a fragment of shaft circumferences preserved or lacking anatomical features. I followed the methodology suggested by Domínguez-Rodrigo (2002); shaft profiles and cross sections were used to identify shaft fragments to upper limb bones (femur and humerus), Intermediate limb bone (radius-ulna, tibia) and lower limb bone (metapodials).

Second, all identified body elements were assigned to eight anatomical body parts;

A: Head Horn/antler, cranial fragments, mandible and maxilla and dentition.

B: Axial All vertebrae and ribs.

B1: Axial Scapula

B2: Axial Pelvis

C1: Upper forelimbs Humerus, radius and ulna

C2: Lower forelimbs Carpals and metacarpals

D1: Upper hindlimbs Femur, tibia and fibula including patella and os mellolaire.

D2: Lower hindlimbs Tarsal and metatarsals.

E: Feet Phalanges, sesamoids and unknown metapodials.

Chapter 4

Identification of Pattern of Persistence or Change in the Large Mammalian Community throughout the ‘Ubeidiya Sequence

4.1 The statistical model

The main question at hand (i.e., can we observe a change in the large mammalian community throughout the ‘Ubeidiya sequence which can be related to climatic change), rests on our ability to remove taphonomic biases which may erroneously produce the appearance of change where one may not have existed. When performing reconstruction of the paleoenvironemental milieu, it is essential to control for taphonomic biases.

For example, given two strata, if one was accumulated by carnivores and the other not, the selectivity of prey by carnivores may increase the proportion of specific species in the fossil (death) assemblage compared to an assemblage accumulated by other factors. This would create the appearance that an increase in species proportion had occurred between strata where in fact it did not.

It is important to differentiate between the analysis of single assemblages and inter assemblage comparison studies as the one presented here. In single site analyses, the questions asked are: what are the taphonomic processes that have affected the assemblage and once they are determined, what is the paleoecological reconstruction of the catchment area of the assemblage? When several assemblages are compared, the question is not only what are the taphonomic biases exerted on the assemblages, but rather can we identify a *difference* in the taphonomic biases exerted on each of the assemblages.

If we compare assemblages which are isotaphonomic i.e., have similar taphonomic biases, we can infer that any change in species frequency is due to environmental and/or climatic factors (Belmaker, 2005b). On the other hand, although many potential taphonomic biases have been suggested, not all biases affect all assemblages all of the time or a given bias may not affect the relative frequency of a taxon in question. Thus, it is hard to assess whether the difference in species composition is due to differences in taphonomic biases, environment or a combination of the two. The problem is then, given the wide range of taphonomic biases, can we increase the fidelity of inter- assemblage comparison through time?

I used spatial autocorrelation (Legendre & Legendre, 1998; Manly, 1997) in the temporal scale as an approach to this problem. This test was developed to overcome some of the inherent problems in explaining species-environment relationships. The correlation of species distribution is space (or in time) is confounded by two main factors. The first, many of the predictors (i.e., dependent variables) are inter-correlated among themselves. Second, there is a likelihood that the spatial or temporal distribution of taxa may exhibit a patchiness (autocorrelation) due to biological processes such as dispersal (Legendre & Legendre, 1998). Mantel test approaches this problem by correlating two variables which are similarity matrices. Thus, the variable is the similarity in abundances of species between strata i and j rather than the abundance of species in strata i.

Each strata is characterized by several arrays of taphonomic and/or environmental parameters. Each array described a single taphonomic bias i.e., weathering, fluvial transport, carnivore ravaging etc. For example, the array which comprises the taphonomic bias “carnivore ravaging” includes the parameters: percent gnaw marks, percent bones cylinders, percent carnivore taxa and r_s of the correlation between skeletal element distribution (percent MAU) of fossils and the skeletal element distribution (percent MAU) of hyaena ravaged domestic sheep (Marean & Spencer, 1991). Similar arrays are defined for biodiversity data (species presence-absence, species abundance, diversity indices) for the seven ‘Ubeidiya ‘pooled strata’.

For each array we define the similarity between each pair of strata in respect to the variable and which includes all the parameters in the array. The similarity matrix is calculated using various similarity coefficient e.g., Gower asymmetrical similarity coefficient. For n strata, we obtain $\binom{n}{2}$ = $\frac{n(n-1)}{2}$ pairs. Similarity matrices derived from biodiversity data serve as the dependent variables (or the criterion) whereas the similarity matrices derived from the taphonomic and environmental data serve as the independent variable (or the descriptor). Each of the dependent and independent variables are correlated based on the hypotheses presented.

The rational when applying this method to paleoecology is that if a taphonomic bias, such as carnivore ravaging, affects the dependent variable (i.e., species composition), species which are similar to each other in the former similarity matrix will also be similar in the latter matrix, i.e., the distribution of variables in the two matrices is correlated. For example, if it is hypothesized that carnivore ravaging may have affected species frequency in the assemblage, then we expect that assemblages with similar levels of evidence for ravaging will also be similar in their species frequencies. On the converse, if such a correlation is not found, we can conclude that species proportion was not affected by the aforementioned bias.

The similarities in variables (dependent and independent) between all pair of assemblages may not be statistically independent. This precludes the use of commonly used correlations (e.g., Pearson's r coefficient of linear correlation or Spearman's r_s coefficient of rank correlation) in calculating P values. The Mantel test calculated all the possible permutations (or a sample of 10,000) and estimates the P value by the proportion of permutation in the simulation that obtained a value equal or larger than that which I obtained in my sample.

An additional advantage of using similarity matrices (as opposed to raw abundances) is that a single variable may be composed of as many parameters (both quantitative and qualitative) as we wish. For example, the variable "Weathering" may be calculated using the Gower similarity coefficient by combining data from many parameters such as percent of bones from weathering stage 1 as well as percent of bones from weathering stage 2 etc.

It would have been interesting to test the simultaneous affect of all independent variables on each of the dependent variables i.e., multiple regression analysis. The problem in this particular data set in that the numbers of cases is low ($n = 7$) compared to the number of descriptors ($n = 7$). The rule of thumb suggested is 5 to 10 data points for every variable tested. In a lower number of cases, as the one in this study, the power of the study is reduced and is not applicable.

I used a one tailed hypotheses calculated for positive test statistics. Two types of statistics were used; The standardized Mantel r_M statistic (henceforth r_M), is the same as the coefficient of linear correlation, Pearson's r statistic. The value on each of the similarity matrices in standardized before computing the Mantel statistic. The Mantel ρ_M statistic (henceforth ρ_M) is the same as Spearman's coefficient of rank correlation r_s. It measures monotonic but not necessarily linear relationships. The statistical significance of both types of statistics was determined by permutations. I used r_M statistic for continuous variable and ρ_M for ordinal variables.

A detailed account of the dependent and independent variables used in this study, their collection method and similarity coefficient used are presented in the following sections. For each variable, the similarity coefficient used is described as well as the parameters included in each variable.

Correlation between matrices was done using 10,000 permutation repetitions.

I am aware that multiple comparisons may increase the type I error of the statistics of significance for each comparison (adjusted critical P value using the Dunn - Šidák method for 6 multiple comparisons is calculated at 0.0174 for an experiment-wise error rate of 0.1). Feise (2002) has suggested that the use of adjusted P values should be reconsidered as it increases the chance of making type II errors and requires an increase in sample size. The latter point is of particular importance in paleontological studies. Following the suggestions described by Feise (2002), I present unadjusted P values and incorporate the study's statistical significance with the magnitude of effect, the quality of the study and with findings from other studies in lieu of adjusted P values.

Multivariate analysis was preformed using the Kovatch MVSP 3.12 computer program for the PC and JMP 5.1, Le Progiciel R and Aable 5.18 for the MAC.

4.2 Independent variables of the null hypotheses: The taphonomy of the ʻUbeidiya large mammal assemblages

One-tailed Mantel tests and partial Mantel tests (Legendre & Legendre, 1998; Manly, 1997) were used to test the six taphonomic null hypotheses (density mediated process, weathering, fluvial transport, hominins as primary agents of accumulation, carnivores as primary agents of accumulation and hyaena ravaging) and the alternative study hypothesis (local environmental change). The following sections describe in detail how the different taphonomic parameter chosen may effect the biodiversity of the fossil assemblage compared to the living assemblage and thus may present a potential bias for subsequent paleoecological analysis. Specific emphasis is placed on the issue of early hominin scavenging vs. hunting of large game. In the anthropological literature, there has been much discussion (see Domínguez-Rodrigo, 2002, and references therein) on the impact of early hominins on faunal assemblage. Thus, the presence of lithics in conjunction with faunal remains is often interpreted as a causal relationship between humans and the fauna. As ʻUbeidiya has been known primarily for the rich lithic assemblage, unravelling the relationship between the hominins which frequented the site and the faunal assemblages is a prerequisites to any subsequent paleoecological analysis and for the removal of one of the most influential taphonomic biases.

4.2.1 Weathering

Weathering is defined as the "process by which the original microscopic organic and inorganic components of bone are separated from each other and destroyed by physical and chemical agents operating on the bone *in situ*, either on the surface or within the surface zones" (Behrensmeyer, 1978, pg: 178).

Weathering of bone surfaces has been used as a rough ordinal measure of time of burial denoted as *taphonomic time* (Arribas & Palmqvist, 1998; Behrensmeyer, 1984, 1982, 1991, 1992; Behrensmeyer & Hill, 1980; Behrensmeyer & Dechant Boaz, 1980; Behrensmeyer *et al.*, 1992; Brain, 1981; Lyman, 1994).

It has been shown that two main factors, environmental and taxon variability, result in a different distribution of weathering stages. Environment affects weathering both on a small and large scale. The small scale is the microenvironment in which bones are deposited. The large scale is the vegetation habitat of the depositional area. Microenvironment includes the localized conditions which surround the bones e.g., shade, moisture and vegetation. Their present may exacerbate the rate of weathering.

Large scale environmental factors (vegetation habitat) differ in their degree of effect of weathering (Cutler *et al.*, 1999; Lyman, 1994). This may be attributed to differential mortality between the regions and to mixing (time and space averaging of habitat specific assemblages (Behrensmeyer, 1978; Cutler *et al.*, 1999).

The second factor is the taxa. If different taxa weather at different rates, due to either size (Behrensmeyer & Dechant Boaz, 1980) or taxonomy, weathering may lead to variable loss of identifiable elements due to splintering bones and cracking in advanced weathering stages. Thus, relative frequencies of a given taxon may be over represented in habitats that are susceptible to weathering. For example, if bovid are more susceptible to weathering than equids in humid environments, equid frequencies may be over represented.

A sample of bones both identified to taxon and unidentified shafts were analyzed for weathering stages. Analysis included quantification of the weathering stages of all specimens together, as well as analysis of the weathering stages separated for two body size groups; small-medium mammals (body sizes E and F) and large (body size G).

Weathering stages followed those set forth by Behrensmeyer (1978).

1 This category includes Behrensmeyer (1978) category 0 "Fresh, unaltered bone" together with category 1 "Fine cracks on bone surface, usually parallel to fiber structure".

2 "Flaking of outer bone layer, exposing inner layers. Crack edges are angular".

3 "Rough fibrous, cracked surface, with patches of fibrous texture. Cracked edges are rounded".

4 "Deep open cracks penetrate inner portions of bone, Portions of splintered surface may break off when bone is moved".

5 "Very deep cracks, with many splinters broken away, bone is extremely fragile and its original shape may be difficult to determine".

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices were calculated from an array which included the percent of bones assigned to each of the weathering categories (five parameters). The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used in correlation of whole community dependent variables, the second was used in correlation of individual taxa of small-medium size mammals (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

4.2.2 Fluvial transport

Degree of fluvial transport affects the formation of fossil assemblage. The degree of fluvial transported assemblages can be classified as follows (Lyman, 1994):

1. Not transported by water and in which all elements are retained as are found in ponds or lake beds.
2. Exposed to water and in which transportable objects are removed or depleted such as delta surfaces or floodplains.
3. Transported by water so that least transportable elements are left upstream such as crevasse splays and basins with internal drainage.
4. Exposed to water after transported from original site with transportable elements depleted such as channel bed or point bar.

The working hypothesis is that fluvial transport leads to space averaging of faunal assemblages i.e., mixing of fauna from different habitats into a single paleontological assemblage. For example, if the habitats surrounding a lake include two different habitats: close forest and open bush-land, a mixed paleontological assemblage may form on the delta surface as a result of carcasses transported from both habitats. Thus, different degrees of fluvial transport may lead to the appearance of different assemblages (Lyman, 1994).

Most of the study of fluvial transport stems from the study of sedimentology. In paleontology, bone fragments are effectively treated like stone particles and analyzed in the same manner. Fluvial transport differentially removes elements from assemblages depending on shape (Bates & Jackson, 1980; Henson, 1980; Voorhies, 1969) and density of bones (Behrensmeyer, 1975). The degree of fluvial transport can be discerned by several characteristics such as hydrodynamic grain shape (rod, blade, sphere or disk) or quantitative measurements based on the three perpendicular axes of a bone (Le Roux, 1996, 2004). Paleontological studies have used bone element and shape such as Voorhies group (Voorhies, 1969), settling groups (Korth, 1979) fluvial transport index (Behrensmeyer, 1975) to discern among assemblages based on different degree of transport.

Sphericity (ψ) is defined as “The relation to each other of the various diameters (length, width, thickness) of a particle; specifically the degree to which the shape of a sedimentary particle approaches that of a sphere” (Bates & Jackson, 1980). Sphericity could be thought of as the degree of equality of the three axes of a grain where in a perfect sphere the length, width and thickness are all equal. Although several equations have been suggested to approximate sphericity (Le Roux, 1996). Maximum Projection Sphericity (Sneed & Folk, 1958) has been widely adopted and considered a good estimate of settling rates and is calculated as $\psi_P = \sqrt[3]{\frac{S^2}{LI}}$.

Another approach is to use categorical classification of grain shape. Zingg (1935) proposed four classes of grain shape, namely bladed, oblate, prolate and equant, based on two axial ratios which represent the ratio of the different axes of a particle $\frac{S}{I}$ and $\frac{I}{L}$. If $\frac{S}{I} \leqslant 0.66$ and $\frac{I}{L} \geqslant 0.66$ the fragment is oblate, If $\frac{S}{I} \geqslant 0.66$ and $\frac{I}{L} \leqslant 0.66$ the fragment is prolate, If both axial ratios are $\geqslant 0.66$ the fragment is equate, and if both axial rations are $\leqslant 0.66$ the fragment is bladed.

The bladed shape is generally the least spherical of the four and the order of increasing sphericity proceeds first with the bladed shape, then with the oblate shape, then the prolate shape, and finally the equant shape (Sneed & Folk, 1958).

Another approach to categorical shapes was developed by Sneed & Folk (1958). They proposed a method which employs a triangular (ternary) diagram in which ratios of the three orthogonal axes of the particle are plotted. Particles are envisaged as lying in the continuum between blocks (equate), slabs (discs, oblate) and rods (prolate) which mark the corners of the diagram. It is worth noting that the axes in the Sneed and Folk diagram are arranged differently from the conventional triangular diagram, and the use of ratios results in the variables not summing to 1. The three axes of the ternary plot are $\frac{L-I}{L-S}$ (Disk - Rod Index or DRI), $\frac{I}{L}$ and $\frac{S}{L}$. Shape are defined as Compact, Plate like, Blade-like, Elongated and Very Elongated as well as combinations of all categories. The settling velocity of non-spherical grains is best represented by the axial ratio $\frac{S}{L}$, and not by the projection area of the grain normal to the direction of settling expressed by axial ratio $\frac{I}{L}$ (Le Roux, 2004).

There has been a discussion in the literature as to the better hydrodynamic classification of grain shapes (see Le Roux, 2004, and references therein). Zingg (1935) and Sneed & Folk (1958) classification methods are very similar and both suitable (Le Roux, 2004). It has been shown that the classification suggested by Zingg (1935) is better in discriminating between certain types of sedimentary deposits (Howard, 1992) and thus is used in this thesis.

All specimens (both identified to taxon and unidentified fragments) were analyzed for this parameter. Three orthogonal measurements were taken on each specimen with a digital caliper to an accuracy of two decimal points. The three dimensions (L = long, I = intermediate and S = short) were used to calculate three axial ratio per specimen and sphericity.

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices were calculated from an array which included the following parameters: maximum projection sphericity (mean and standard deviation), the three axial ratios: $\frac{S}{I}$,$\frac{I}{L}$ and $\frac{S}{L}$ (mean and standard deviation) and percent abundance of each grain shape (Zingg, 1935). The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used in correlations of whole community dependent variables, the second was used in correlations of individual taxa of small-medium size (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

4.2.3 Agents of accumulation

Predator activity is one of the most active forces which affects species distribution in paleontological assemblages. Since the Early Pliocene and the evolution of hominins, the presence of lithics in conjunction with faunal remains has lead to the question of the relationship between the two. Thus, the possibility of hominins as a possible active agent in bone assemblages as hunters or scavengers has become one of the main topics in Pleistocene anthropology (Bunn & Kroll, 1986).

Ivlev's Electivity Index (E) (Ivlev, 1961) was used to measure feeding selectivity, i.e., comparing the utilization of food with respect to its availability. Is the degree to which predators tend to select a given species in relation to its natural proportion and is given by the equation $E_i = \frac{(r_i - n_i)}{(r_i + n_i)}$, where r_i is the proportion of the species i consumed and n_i is the relative proportion of the species i available in the environment. The E values range from -1.0 to +1.0, with values between 0 and +1.0 indicating preference, values between 0 and -1.0 indicating avoidance and values equal 0 indicating no selection (Cooper *et al.*, 1999).

Intra species prey selection is oriented towards sex, age and the physical condition of the individuals. Inter species prey selection includes selectivity for species and prey size groups (Pole *et al.*, 2004). This selectivity is dependent on habitat and seasonality. The most important inter species selection is the size-based selection. For example, the spotted hyaena, *Crocuta crocuta*, has been shown to target medium to large ungulates. It is important to stress that the migratory pattern and the uneven temporal distribution of the wildebeest masks the month by month prey selection toward larger ungulate taxa (zebra, topi and wildebeest) over small ungulates (Thompson's gazelles). "Talek hyaenas proved themselves to be opportunistic predators, switching to feed on the most abundant prey species each time that relative prey densities change. However, superimposed on these opportunistic functional responses, was a clear set of food preferences exhibited by the hyaena" (Cooper *et al.*, 1999). Similarly, the diet of African wild dogs *Lycaon pictus* are ungulates ranging from 15 - 200 kg (Pole *et al.*, 2004). While they do not hunt selectively for the majority of taxa, they have been shown to selectively prefer kudu and hunt them in higher proportions than they appear in the environment.

Hominins as primary agent of accumulation

One of the main debates in evolutionary anthropology is the importance of big game hunting in the evolution of hominins (Domínguez-Rodrigo, 2002, and references therein). Four alternative modes of behavior have been suggested; active hunting, aggressive scavenging, where hominins seize nearly intact parts of the carcass while the predator is still in the process of consuming it, passive scavenging of carcasses abandoned by non human predators and passive scavenging of carcasses which dies by natural causes (O'Connell *et al.*, 2002).

Archaeological evidence distinguishing among the four patterns has relied mostly on body element representation, cut-mark and gnaw mark frequency. In this thesis I focus on three variables which indicate human activity as primary accumulators of the assemblages.

1. **Correlation of skeletal element distribution with food utility indices**

Skeletal element frequency has been widely used to uncover patterns of scavenging vs. hunting patterns of early hominins. This stems from zooarchaeological studies which focused on ethnographic data of human butchering and subsistence practices. White (1953) was one of the first to focus on the different elements brought to a camp site as opposed to those left at the kill site. This was later developed by Perkins & Daly (1968), who coined the term *Schlepp Effect* to describe the phenomenon in which a relationship exists between carcass size and distance between kill site and settlement. Thus, a larger animal, hunted further away from point of consumption, will have fewer of its bones brought back to the camp whereas a smaller animal may be brought back whole.

Borrowing from forging theory, Binford (1978) suggested correlating between skeletal element frequencies, measured by percent MAU, and the amount of meat, marrow and grease associated with each element combined into a single Modified General Utility Index (MGUI) or Food Utility Index (henceforth FUI). The rational is that different economic strategies would result in a different skeletal element distribution based on the underlying nutritional values of the elements i.e., bulk strategy, gourmet strategy and unbiased strategy (Speth, 1983).

Unfortunately, although widely used, skeletal element frequency present an equifinality problem. Results from numerous skeletal part profiles have provided inconclusive results and have lead to different interpretations for a given data base (Domínguez-Rodrigo, 2002). Since a negative correlation exists between bone mineral density and utility values of elements, it may be difficult to distinguish between the absence of elements due to density mediated destruction and those due to transport (Marean & Kim, 1998; Marean & Cleghorn, 2003). Thus the absence of elements such as ribs and vertebrae may be the results of either transport choice or fluvial transport or carnivore ravaging (Speth, 1983). Due to differences in bone mineral density between proximal and distal epiphysis, density mediated processes may also effected the distribution of the limb epiphyses in an assemblage. Additionally, in palimpsests archaeological sites, the accumulations of many butchering and/or scavenging events serves to even out the signal present in small sized single carcass kill/butchering stands (Lupo, 2001).

Two methodological steps were taken to try and improve the methodology. First, most studies used percent MAU calculated for proximal and distal ends separately (Speth, 1983). While this method is warranted in density studies, since proximal and distal end differ in their bone mineral density, the question at hand is which elements were transported by early hominins. Metcalfe & Jones (1988) have suggested using percent MAU based on whole elements under the assumption that hominins transported complete elements rather than fragments thereof. This issue is of particular methodological importance since using complete elements as opposed to proximal and distal epiphysis, we can control for correlations that stem from density mediated processes that differentially effect the epiphyses.

Second, Marean & Cleghorn (2003) suggested that better resolution is obtained if the correlations between percent MAU and FUI are done separately for high survival elements (i.e., cranial elements and long bones) and low survival elements (ribs and vertebrae). The latter may be represented in low quantities due to density mediated processes and hence may not reflect human transport choice.

Following both the suggestions outlined above, in this thesis all correlations between body part frequencies (percent MAU) and food utility indices used only high survival elements. These include cranial elements and long bones. Ruminant percent MAU for all body size groups (E, F and G) was correlated with FUI values for caribou *Rangifer tarandus* (Metcalfe & Jones, 1988). Equidae skeletal element frequency (percent MAU) was correlated with FUI values for horse, *Equus caballus* (Outram & Rowley-Conwy, 1998).

A positive correlation of high survival elements with food utility index is interpreted as evidence for a central place camp to which transported elements were brought, selected on the basis of their caloric gross return. A negative correlation of high survival elements with standardized utility index is interpreted as evidence for a near kill site in which the transported elements was removed from the site, selected on the basis of their caloric gross return.

An insignificant correlation between percent MAU and FUI may indicate a highly ravaged or lag assemblage (Lyman, 1994). Alternatively, it may indicates that if a carcass was utilized at the site, it is utilized completely such as in an unbiased strategy. This is possible when humans transport small ungulates, as expected from the schlepp effect, or when they scavenge a near complete carcass.

To distinguish between the two alternatives that can explain an insignificant correlation (human transporting a complete carcass or actively scavenging on one), further evidence must be obtained from cut-marks and percussion marks.

2. **Cut-mark distribution** The most direct and unambiguous evidence for human manipulation of carcasses is that of cut-marks. Unfortunately, they appear in rare percentages in the paleolithic record even when there is clear and independent evidence for human hunting. For example, in the Middle to Upper Paleolithic site of Grotte XVI (Dordogne, France), cut-mark percentage do not exceed ca. 10% for 6 strata and only a single stratum exhibits ca. 18% (Grayson & Delpech, 2003).

Most analyses, primarily from Middle and Upper Paleolithic sites, have focused on quantification of total percent of cut-marks as a measure of butchering intensity (Grayson & Delpech, 2003, and references therein). When trying to resolve the issue of primary vs. secondary access to carcasses, such an index retains the problem of equifinality, as they can be produced both when removing flesh from a hunted carcasses and from a scavenged one, thus not solving the main question at hand; what is the *primary* agent of accumulation (Domínguez-Rodrigo, 2002).

A novel approach suggested by Domínguez-Rodrigo (2002) uses actualistic taphonomic studies to distinguish between the two alternative hypotheses presented in the literature. The first hypothesis, hominin - carnivore, primary access to carcasses by hominins is followed by ravaging of the remains by carnivores, notably hyaenas. In the alternative hypothesis, carnivore-hominins-carnivore, carcasses are hunted by felids, which tend to leave a relatively high proportion of meat on the carcasses. Hominins can then scavenge the remains, only to leave bone to be ravaged by hyaenas in the final stage of the sequence.

In order to create a model to distinguish between the two scenarios, Domínguez-Rodrigo (2002) observed the number of cut-marks produced from carcasses which were originally butchered by humans and those first consumed by lions. The novelty of this research lies in the quantification methods used; rather than counting total cut-marks in the assemblage, he distinguished between the number of cut-marks which appear on the upper, intermediate and lower limb bones and on the proximal shaft, mid-shaft and distal shaft of the limbs.

Following his methodology, in the thesis, all limb bone ranging from size E to G were analyzed for the presence of cut-marks. All specimens from the sample analyzed were viewed under a light microscope with magnification up to X60. Distinction between cut-marks, chop marks, carnivore tooth marks and striae followed morphological criteria described in the literature (Fisher, 1995).

For each element, the presence and absence of cut-marks was recorded and their location on the bone: proximal shaft (epiphysis and shaft), mid-shaft and distal shaft (epiphysis and shaft). Figure 10 on page 184 presents a schematic representation of the five bone portions use for the four main limb bones. Each bone portion was recorded separately. Thus, bones which included more than one bone portion were recorded multiple times (Domínguez-Rodrigo, per. com.). Limb bones were divided according to upper limb bones (humerus and femur), Intermediate limb bones (radius-ulna, tibia) and lower limb bones (metapodials). Specimens which were highly abraded were not analyzed and marked as NA (not applicable).

Date obtained in this thesis for the 'Ubeidiya assemblages were compared to data acquired from experiments preformed to model hominin to carnivore vs. carnivore to hominin consumption sequences (Domínguez-Rodrigo, 1997). The two sequences: hominin to carnivore sequence and carnivore to hominin to carnivore sequence are labeled H1 and H2 respectively. In each sequence, several different experiments were done which included different sequences numbered from 1 to 3. In hypothesis H1, experiments included hominins only (H1S1), or both hominin and carnivore ravaging (H1S1/2). In hypothesis H2, experiments included carnivore and hominins (H2S1/2), carnivore - hominin sequence followed by hyaena scavenging as well (H2S1/2/3). Replicates of each sequence was designated by lowercase roman letters.

Following the model described by Domínguez-Rodrigo (1997) the alternative consumption sequences differ in the distribution of cut-marks. hominin to carnivore is characterized by a high proportion of cut-marks on upper limb bones and on the mid-shaft. Carnivore to hominin to carnivore is characterized by a high proportion of cut-marks on lower limb bones and on the distal ends.

3. **Percussion mark distribution**

Bones may be fragmented by many agents; trampling, carnivores or hominins. The two latter most often break bones to remove the marrow inside the cavity for consumption.

Distinction between agents of fragmentation rests on fracture shape and on the presence of an impact point. True spiral fractures are produced as a result of breaking fresh green bone i.e., by hominin or carnivore. Other fracture shapes such as perpendicular are produced by the breakage of dry bone as in the case of trampling. While the percent of spiral fractures is often used as an indicator for breakage of fresh bone, by itself, it cannot distinguish between carnivore and hominin breakage (Lyman, 1994) and thus will not be used here.

More indicative signs are unique marks found on the fracture surfaces associated with direct percussion. This creates a “point loading”, percussion pits and flake scars. These marks can be distinguished from conical fractures related to tooth marks from carnivores (Blumenschine *et al.*, 1996; Blumenschine, 1988, 1995; Capaldo & Blumenschine, 1994)

In this thesis, all limb bone specimens ranging from size E to G were analyzed for the presence or absence of percussion marks. All specimens from the sample analyzed were viewed under a light microscope with magnification up to X60. Distinction between human percussion marks and those made by carnivores followed morphological criteria described in the literature (Blumenschine *et al.*, 1996).

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices were calculated from an array which included the following parameters per ‘pooled stratum’: 1. Percent of cut-marks which appear of proximal shaft. 2. Percent of cut-marks which appear on mid-shaft. 3. Percent of cut-marks which appear on distal shaft. 4. Percent of cut-marks which appear on upper limb bones. 5. Percent of cut-marks which appear on intermediate limb bones. 6. Percent cut-marks which appear on lower limb bones. 7. Percent of upper limb bones with cut-marks. 8. Percent of intermediate limb bones with cut-marks. 9. Percent of lower limb bones with cut-marks. 10. Percent percussion marks. 11. Spearman’s coefficient of rank correlation r_s for the correlation between each taxon and utility indices (4 parameters). In the case that correlations are insignificant at the 0.1 significance level, r_s is given a value of 0.

The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used in correlation of whole community dependent variables, the second was used in correlation of individual taxa of small-medium size (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

Carnivores as primary agent of accumulation

While many factors are used to distinguish primary and secondary access to carcasses, carnivore surface modification (i.e., tooth marks) have been considered the most unequivocal evidence for carnivore modified assemblages. The advantage of such marks is that they are retained even on fragmented and unidentified splinters.

Since many assemblages may be accumulated by carnivores but then subjected to subsequent ravaging, distinguishing between the two processes may be difficult. The assumption is that most of the ravaging is caused by bone crushers i.e., hyaenas. Nonetheless, the amount of flesh remaining on carcasses consumed by hyaenas is little to none. Prey consumed by felids retain more flesh (to subsequently be consumed by scavenging hominins) than those originally consumed by other carnivores such as hyaenas (Domínguez-Rodrigo, 2002).

In order to distinguish among varying models of carnivore consumption, it has been suggested to look at the percent of carnivore gnaw marks on each of the five portions of limb bone.

In this thesis, all limb bone ranging from mammals of body size E to G were analyzed for the presence or absence of one or more of the carnivore modifications listed below. All specimens from the sample analyzed were viewed under a light microscope with magnification up to X60. Distinction between cut-marks, chop marks, carnivore tooth marks and striae followed morphological criteria described in the literature (Fisher, 1995).

For each element, the presence or absence of carnivore gnaw marks was recorded along with their location on the bone: proximal epiphysis, near epiphysis proximal shaft, mid-shaft, near epiphysis distal shaft and distal epiphysis. Figure 10 on page 184 depicts the five portions for the four main limb bones. Each bone portion was recorded separately. Thus, bones which included more than one bone portion were recorded multiple times. Specimens which were highly abraded were not analyzed and marked as NA (not applicable).

A specimens was considered to be subjected to carnivore modification if it included one or more of the following modifications (Lyman, 1994): 1. Ragged edge chewing 2. Crescent shaped fracture scars 3. Exposure of porous and cortical bone 4. Licking of chipped edges 5. Shallow pitting 6. Puncture 7. Tooth scratches/striation 8. Furrow 9. Scooping out 10. Digestion

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices were calculated from an array which including the following parameters per 'pooled stratum': 1. Percent of gnaw-marks which appear on proximal end. 2. Percent of gnaw-marks which appear on proximal shaft. 3. Percent of gnaw-marks which appear on mid-shaft. 4. Percent of gnaw-marks which appear on distal shaft. 5. Percent of gnaw-marks which appear on distal end.

The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used for correlations of whole community dependent variables, the second was used for correlations of individual taxa of small-medium size (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

4.2.4 Post depositional carnivore ravaging

Both hominins and hyaenas share the ability to crack open long bones of mammals to utilize the marrow within. Moreover, both species tend to accumulate bones in distinct locations. There has been a long discussion in the literature on the variables which can help us identify hyaena accumulation as opposed to hominin ones (Cruz-Uribe, 1991; Stiner, 1991). I followed the suggestions by Pickering (2002) and chose three variables to study, as well as an additional variable:

1. **Relative diversity of carnivores**

It has been shown in many faunal analysis of modern hyaena dens that hyaenas tend to have an eclectic diet. Specifically, brown hyaenas have been shown to have a preference for small mammals including small carnivores (Brain, 1981). Hyaena accumulation often have a high ($\geqslant 20$) percent of carnivore species of the total MNI (Cruz-Uribe, 1991).

For each ‘pooled strata’, I calculated the proportion of carnivores of the total number of individuals (MNI).

2. **Percent of shaft cylinders**

Based on actualistic studies, carnivores (and specifically hyaenas) have been observed to begin consumption of bones at the epiphyses, removing one or both completely but leaving the shaft resulting in limb bone cylinders which retain their original circumferences and their length (Pickering, 2002; Cruz-Uribe, 1991). On the other hand, human modified assemblages have been observed to contained a high percentage of fragmented bones due to bone marrow processing.

While the presence of cylinders is taken as a positive indicator for carnivore involvement in the assemblage formation, lack of such cylinders and the presence of smaller fragments is not a positive sign for hominin - faunal interaction. Thus, assemblages which have contained original carnivore produced cylinders, may have been subjected to various post depositional processes such as soil compaction, weathering and abrasion which lead to fragmentation patterns that mimic those produced by humans (Pickering, 2002; Cruz-Uribe, 1991).

In this thesis, for each ‘pooled strata’, I calculated the percentage of shaft fragments out of all limb bones for ungulates of small, medium and large size (body size group E, F, and G) and intermediate body sizes (body size groups EF and FG) as well as a sample of unidentified shaft fragments. Limb bones included humerus, radius - ulna, femur, tibia, fibula and metapodials with the exclusion of unfused epiphyses.

To quantify the percent of "bone cylinders" in the assemblages, limb elements were divided into three categories: (a) **Complete specimens** (b) **Fragments** which include all shaft fragments with *shaft circumferences* of less than 1 as well as the distal and proximal epiphyses with *fragmentation* $\leqslant 0.125$ or *shaft circumference* of less than 1. (c) "**bone cylinders"** which include all shaft fragments with *shaft circumferences* of 1 as well as proximal and distal fragments with *fragmentation* $\geqslant 0.25$ and *shaft circumference* of 1. The terminology is described in body element identification methodology described in section 3.3.2 on page 31.

3. **Surface modifications** Hyaena ravaged assemblages have been observed to have a minimum of 38% of bones which exhibit one or more carnivore modifications. This number usually ranges between 38 and 100 percent of observed modern assemblages (Cruz-Uribe, 1991; Klein & Cruz-Uribe, 1984; Pickering, 2002). Fossil assemblages may have lower percentages due to weathering and other post depositional processes which may destroy or mask the surface damage (Pickering, 2002).

Following the methodology described in the above section, "Carnivore as primary agents of accumulation" 4.2.3 on page 46, I calculated the total number of elements which exhibited one or more carnivore modifications.

In this thesis, all limb bone specimens ranging from mammals of body size E to G were analyzed for the presence or absence of one or more of the carnivore modifications listed below. All specimens from the sample analyzed were viewed under a light microscope with magnification up to X60. Distinction between cut-marks, chop marks, carnivore tooth marks and striae followed morphological criteria described in the literature (Fisher, 1995).

4. **Correlation with carnivore ravaging**

Skeletal element distribution, calculated as percent MAU, is effected both by the nutritional value of the elements for either hominins or carnivores and by its susceptibility to post depositional process and destruction. Actualistic studies in which domestic sheep bones have been fed to hyaenas to ravage upon have yielded typical patterns of destruction of bone epiphyses and shafts (Marean & Spencer, 1991).

Percent MAU was correlated with percent MAU of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991) for Ruminantia E, Ruminantia F, Ruminantia G and Equidae. Correlation used the Pearson's coefficient of correlation r.

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices were calculated from an array which including the following parameters per 'pooled stratum':

1. Percent of carnivore MNI of total assemblage MNI. 2. Percent of shaft fragments of total limb elements. 3. Percent of gnaw marks. 4. Pearsons's r coefficient of correlation between each taxon and percent MAU of hyaena ravaged domestic sheep bones (4 parameters). In the case that the correlation was insignificant at the 0.1 significance level, r is given a value of 0.

The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used in correlations of whole community dependent variables, the second was used in correlations of individual taxa of small-medium size (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

4.2.5 Density mediated processes

Skeletal element frequency has been shown to provide evidence on the taphonomic history of bone assemblages (Lyman, 1994). Bones, as well as regions within a single bone, differ in their structural density ($\frac{g}{cm^3}$). These differences affect the probability that skeletal elements (or parts thereof) survive in the paleontological record. A host of density mediating factors work to destroy less compact skeletal elements while leaving the more durable ones behind. Some of the main forces that shape skeletal element frequency are factors such as trampling, bone leaching and carnivore ravaging.

It has been suggested that species may differ in their Bone Mineral Density (henceforth BMD) and thus, sites which have been subjected to such processes may be biased towards the more durable species (Gifford-Gonzales, 1989)(but see Lam *et al.* (1999)).

To determine if density mediated factors have affected the bone assemblages in 'Ubeidiya strata, percent MAU values were correlated using average BMD values obtained for four taxonomic groups: Ruminantia E, Ruminantia F, Ruminantia G and Equidae. These comprise the majority of the 'Ubeidiya fauna. For each group, two different correlations were used: a correlation between percent MAU and BMD of traditional scan sites and a correlation between percent MAU and BMD of maximum scan site. Since BMD are only measured in the ordinal scale (Lyman, 1984), correlation were measured using the Spearman's coefficient of rank correlation (r_s).

Ruminant skeletal element frequency (percent MAU) was correlated with BMD values for deer *Odocoileus* spp. (Lyman, 1984). It has been shown that cofamilial taxa share similar BMD values

(Lyman, 1994). Since the majority of ruminants at ‘Ubeidiya are cervids, *Odocoileus* spp. are taxonomically close. Equidae skeletal element frequency (percent MAU) will be correlated with BMD values for *Equus* spp. (*Equus burchelli* and *Equus przewalkskii*) (Lam *et al.*, 1999).

For the one-tailed Mantel tests, results were transformed into three similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices was calculated from an array which including the following parameters per ‘pooled stratum’: Spearman’s coefficient of rank correlation (r_s) for the four taxa for both traditional and maximum scan site (total of eight parameters). If a correlation was insignificant, the value for r_s was given as 0.

The first matrix included all specimens, the second included small-medium mammals (body size E and F) and the third included large mammals (body size G). The first matrix was used in correlations of whole community dependent variables, the second was used in correlations of individual taxa of small-medium size (Ruminantia E and Ruminantia F) and the third was used in correlations of individual taxa of large size (Ruminantia G and Equidae).

4.3 Independent variables of the alternative hypothesis: The environmental proxy

An alternative variable which could explain the pattern of mammalian community structure observed is local environmental change. As a proxy for local environmental change I used the data obtained from the in-depth geomorphological analysis of the ‘Ubeidiya strata completed by Mallol (2004, 2006).

Mallol (2004, 2006) analyzed the sediments from different trenches as separate entities and characterize the specific microsedimentary environments represented by each of them using micromorphology. This was followed by a microstratigraphic comparison across the exposures in order to corroborate correlations traced in previous studies which resulted in a three-dimensional reconstruction of the tilted ‘Ubeidiya deposits.

Lakeshore deposits may represent various facies ranging from the actual shoreline or complex delta fan environments, in transition from fluvial to lacustrine conditions. The latter deposits contain a mixture of detrital components derived from the alluviation of ephemeral streams entering the lake (low-energy overbank deposits) and locally reworked lacustrine sediments accumulated during previous lake-level high stands. Micromorphological features are associated with depositional and post-depositional site formation processes. These include basic composition, pedogenesis, surface emersion and desiccation and may suggest stable vs. unstable climatic conditions i.e., alternating drier and humid period, associated with water-level fluctuations (Mallol, 2004, 2006).

Mallol (2004, 2006) identified an overall trend of desiccation throughout the Fi cycle. This is evident by several things: The onset of a deltaic style of sedimentation, documented by gross lithology in the field, from a coarsening-upwards trend of the gravel and sand-sized fractions. In thin section, these units show a high incidence of desiccation features and evaporates. Taken together with the evidence from trench III, which represents a zone of fluvial backswamps (III 22) and channels (III 23-24), this period of the Fi cycle seems to represent drier conditions in which the delta fan advanced towards the lake (with fluvial discharge in trenches I and II) (Mallol, 2004, 2006). In the end of the regressive cycle Mallol (2004, 2006) has inferred marked seasonality. A short series of successive inundations yielded an emerged mudflat in trench I (strata I 24-25) and swamps in trench II and III (strata II 33-35, and III 25-26). Also, stratum II 37 contains carbonate concretions (in the field) and in thin section, the gravel from that layer is coated with fibral calcite, which expresses strong aridity (Mallol, 2004, 2006).

The environmental data was supplemented by the data obtained from the diatoms analysis (Almogi Labin *et al.*, 1995; Siman-Tov *et al.*, 1993, 1994). Stratum III 20 was originally assigned to the Fi cycle (Picard & Baida, 1966a) and grouped in a the same environmental stage as II 23-25 by Mallol (2004, 2006). Diatom analysis suggested that stratum III 20 should be grouped with the diverse diatom assemblage of Li cycle (56 taxa) (see Figure 6 on page 180). This indicates a freshwater to oligosaline environment (salinity $< 5‰$). I attributed stratum III 20 to a stratigraphic level older than stratum II 23-25 and assign stratum III 20 to the Li cycle. Between the Li and Fi cycle (i.e., between III 20 and II 23-25), the gross sedimentology has been interpreted as a first order change corresponding to lake transgression and regressions. These most probably reflects climatic control on the basinal hyrographic budget (Feibel, 2004).

In this thesis, I developed a numerical ordinal scale which ranged from wet (5) to dry (0) based on the geomorphological and diatom analyses as follows:

5 Includes stratum III 20. Described by Mallol (2004, 2006) as a "a prolonged period of soil stability in a very wet environment". Diatom analysis suggests freshwater to oligosaline environment (salinity $< 5‰$) and shallow lake environments.

4 Includes stratum II 23-25. Described by Mallol (2004, 2006) "II 23-25 sediments have the characteristics of a marshy or swampy microenvironment; they were possibly waterlaid, and after a short time, dried and invaded by grassy plants".

3 Includes strata III 21-22, and II 26-27 (I 15-16). Described by Mallol (2004, 2006) "Drier conditions, Retreat of shorelines, advancement of the distal delta-fan and possible lateral shift of the main stream channel. No springs identified. Seasonal discharge from the streams brings pebbles to the shore and forms beach bars".

2 Includes strata III 23-25, I 17-I 20, II 28-31. Described by Mallol (2004, 2006) "The shoreline zone is drier, less swampy". "Similar conditions but with more lucastrine input; The shore was closer and the stream and delta continue to advance towards the shore".

1 Includes strata III 26-33, I 21-24, II 32-35. Described by Mallol (2004, 2006) "Similar conditions but drier. The shoreline continues to advance into the delta fan and the stream is more incised and active".

0 Includes strata III 34 and II 36-37. Described by Mallol (2004, 2006) "Similar conditions. Seasonal floods rework surface material, which gets redeposited near its original origin. The shoreline has been installed at this position and wave conditions also reworked surfaced material slightly".

There is no data from 'pooled stratum' III 11-13 for either geomorphology nor diatom analysis and hence it was not assigned an numerical ordinal value. Hence, this 'pooled stratum' was excluded from subsequent paleoecological analysis.

For the one-tailed Mantel tests, results were transformed to similarity matrices using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrices was calculated from an array which included the numerical ordinal value from wet to dry. Since this scale is ordinal, all correlations using this variable used Mantel's rank correlation (ρ_M).

There is a strong linear correlation between local climatic change and the stratigraphic sequence of the site (ρ_M = 0.86, P value = 0.012). Since the variable "local environmental change" does not include 'pooled stratum' III 11-13, these correlation include less cases and hence less degrees of freedom which may reduce the significance.

If there was a negative correlation between a given variable and "local environmental change", I also correlates the variable with the stratigraphic position of each 'pooled stratum' as a proxy for "local environmental change".

4.4 The dependent variables: The biodiversity of the ʿUbeidiya large mammal assemblages

One-tailed Mantel tests and partial Mantel tests (Legendre & Legendre, 1998) were used to test the affect of the taphonomic and environmental factors (independent variables described above) on the biodiversity of the large mammals in the ‘Ubeidiya assemblages (dependent variables). Biodiversity in measured both as presence-absence (faunal turnover) and as relative frequency of taxa.

4.4.1 Faunal turnover

Faunal turnover is the result of local extinction, immigration, evolution (anagenesis or cladogenesis). “First appearance” taxa are identified either as immigrating species i.e., species that dispersed from other regions or as in situ speciation occurring within the region (Barry *et al.*, 1995).

Following the methodology described by Barry *et al.* (1995), for each strata, I present two categories of faunal occurrences and nomenclature based on the presence or absence of species: FAD (First Appearance Datum) are species that appear for the first time in the sequence in a stratum, but continue to appear in subsequent strata. LAD (Last Appearance Datum) are species that were present in the sequence but were not found in subsequent strata. Species that appear only once in a sequence were calculated once as a FAD and once as a LAD. It was assumed that taxa occurring in older and younger strata, were also present in the intervening strata. Thus, FAD and LAD were calculated according to the “range through” method (Boltovsky, 1988).

Since species richness may differ between assemblage due to sampling bias, I used the rarefaction method to estimate the expected number of species for all assemblage in an equal sample size as described by Sanders (1968, 1969). This method was presented in detail in subsection 3.1.2 on page 25. For species richness estimation, a point by point rarefaction curve was not used, but rather an estimate was made of the number of species expected for an equal sample size for all strata (Hayek & Buzas, 1997). This study used an equal sample size based on the smallest sample size found in the ‘pooled strata’ $n = 135$. Error bars used variance based on the equation detailed in subsection 3.1.2 on page 25.

Turnover is expressed as the number FAD and LAD events adjusted for interval taxonomic richness or duration (Webb, 1969). The former is suitable for analysis of pairwise turnover between two assemblages and the latter is suitable for the analysis of cumulative turnover among sequences (Russel, 1998). At ‘Ubeidiya, correction for interval duration was not possible, however qualitative assessment of turnover was obtained using R (by strata) and Q (by species) mode clustering. Thus, the question asked is through the overall time span present at ‘Ubeidiya, can different communities be discerned based on species presence-absence only?

Clustering used the complete linkage method (Legendre & Legendre, 1998; Sneath & Sokal, 1973). The distance between two clusters is the maximum distance between an observation in one cluster and an observation in the other cluster. Similar results were obtained using other clustering methods (not presented here) suggesting that results obtained using this method were robust.

Analyses included two stages, the first was a multivariate analysis of taxa to determine the association of species into clusters and the second, correlation of the presence-absence of species with the independent variables (the taphonomic null hypotheses and the alternative environmental hypothesis).

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Dice-Sørenson asymmetrical similarity coefficient (Equation 5 on page 272). The similarity matrix was calculated from an array which including the species presence-absence per 'pooled stratum'.

4.4.2 Relative frequency of taxa

Analyses based on relative frequency of taxa includes several methods of analyses as described below:

Multi-species analyses

Multivariate analysis was used to test if strata differ among themselves based on relative abundance of taxa. Two methods were used. The first, correspondence analysis and the second, cluster analysis. R mode cluster analysis was used to group assemblages (i.e., 'pooled strata') into clusters containing similar faunal assemblages based on the relative frequency of the species. Q mode cluster analysis was used to group species into cluster based on their co-occurence in the same 'pooled strata'.

Analyses included two stages, the first was a multivariate analysis of taxa to determine the association of species into clusters and the second, correlation of the relative frequency of species with the independent variables (the taphonomic null hypotheses and the alternative environmental hypothesis).

Clustering used the complete linkage method (Legendre & Legendre, 1998; Sneath & Sokal, 1973). Similar cluster were obtained using other clustering methods (not presented here) suggesting that results obtained using this method were robust.

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which included the percent relative frequency of all taxa, calculated using the maximum quantification method (NISP) per 'pooled stratum'.

Analysis of individual species

Each of the species was tested for change or persistence through time. Following Bobe & Eck (2001), I used 95% confidence intervals (see Equation 4 on page 271) to tests for change between consecutive strata.

For those taxa that showed a significant shift in relative frequency throughout the sequence, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which included the percent relative frequency of each taxon individually, calculated using the maximum quantification method (NISP) per 'pooled stratum'.

Biodiversity

Different biodiversity indices have been suggested (Krebs, 2001; Magurran, 2005). I opted to present several indices for each parameter in order to provide robuscticity to the results. Thus, if several indices provide the same qualitative results (albeit with different absolute values), we can assume that they are resilient (Magurran, 2005). All indices were calculated using PAST - Paleontological Statistics, ver. 1.3 (Hammer *et al.*, 2001) using the NISP quantification method.

For all indices 95% confidence intervals were calculated using the bootstrap method. Approximate confidence intervals for the diversity indices were computed using a bootstrap procedure. 1000 random samples are produced, each with the same total number of individuals as in the original assemblage. The random samples are taken from the total combined data set (all 'pooled strata') (Hammer *et al.*, 2001).

(i) *Species richness*

Species richness has been shown to provide a useful measure of diversity in an assemblage. There are two basic measures of species richness: numerical species richness which is species richness for a specific number of individuals and species density, which is the species richness calculated for a specific collection area or unit (Magurran, 2005). All species richness indices given in this thesis are numerical species richness indices i.e., each stratum was considered a single sample and compared to all other strata.

Due to the inherent relationship between sample size and species richness, straight forward comparison among different assemblages of different sample size based on raw data will be biased (Magurran, 2005).

In order to avoid the bias described, the raw data (i.e., number of species) is normalized by total sample size to facilitate comparison between samples.

There are various indices that have been published and discussed in the literature (Magurran, 2005). Following Magurran (2005) and Hayek & Buzas (1997), I have chosen to use common and recommended indices of Margalef's richness index (see Equation 8 on page 272), Fisher's α (see Equation 2 on page 272) and rarefaction.

The Margalef's index D_{Mg}: This index corrects for sample size by dividing observed species richness with sample size but nonetheless it remains sensitive to sampling efforts (Magurran, 2005).

The log series α is the parameter of the log series model and may be used even when the log series distribution is not the best descriptor of the underlying species abundance pattern (Magurran, 2005). α represents an approximation of the number of species in an assemblage that are represented by a single individual. The parameter is relatively unaffected by sample size (Magurran, 2005).

Rarefaction is based on fitting to the log series abundance model. Using replication with replacement from the given samples, an estimation is obtained for the number of species we expect to find if the sample effort (sample size) is reduced to a specific level (Magurran, 2005).

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which including the following parameters per 'pooled stratum': Margalef's richness index D_{Mg}, Fisher's α diversity index and the estimated number of species obtained from rarefaction calculations for a sample size of $n = 135$ (the smallest sample size obtained for the 'pooled strata').

(ii) *Dominance*

Dominance indices measure abundance distribution of species and indicate to what degree few species are very common (dominant) as opposed to even communities, where species have similar abundances. Two assemblages which have an equal number of species and total number of individual (and hence equal richness) may differ greatly in their abundance indices; dominance and evenness.

Several dominance indices have been suggested over the years. The most widely used are the Simpson's D_s (see Equation 14 on page 274) and Berger-Parker d (see Equation 15 on page 274). Simpson's D_s gives the probability that two individuals drawn at random from a sample belong to the same species (Magurran, 2005). Berger-Parker index d expresses the proportional abundance of the most abundant species.

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which including the following parameters per 'pooled stratum': Simpson's D_s and Berger-Parker d indices.

(iii) *Evenness*

In an even community, all species share an equal abundance. The indices used are Equatability J' (see Equation 16 on page 274), Buzas and Gibson's evenness (see Equation 17 on page 274) and Simpson's evenness index.

Both Equatability J' and Buzas and Gibson's evenness are based on the calculation of the Shannon - Weaver index (H') (see Equation 18 on page 275 and described in detailed in the section below titled "Measurements of diversity based on information statistics") . Equatability J' uses the maximum diversity obtained when all species have equal abundances (i.e., the natural log of s) but since it is dependent on sample size, an alternative index, Buzas and Gibson's evenness, was developed, which is less sensitive to sample size (specifically for samples less than 10). Simpson's evenness index D is the complement of Simpson's D_s and is given by the equation $D = 1 - D_s$.

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which including the following parameters per 'pooled stratum': Equatability J', Buzas and Gibson evenness and Simpson's D diversity index values.

(iv) *Measurements of diversity based on information statistics*

A general diversity index is based on the rational that diversity in a natural system can be measured in a similar way to the data contained in a code.

The common indices used are the Shannon - Weaver index (H') of diversity (see Equation 18 on page 275) and the Brillouin index (HB) (see Equation 19 on page 275).

There has been a discussion in the literature as to the assumptions of each index and its applicability to paleontological assemblages. The Shannon - Weaver index (H') assumes that all individuals are randomly sampled from a infinitely large population and that all species are represented in the sample. The assumption that species are randomly sampled and that all species are represented in the sample may not hold true for all paleontological assemblages. Nonetheless, it is the common index used in paleontological research (e.g. Bonuso *et al.*, 2002a; Bar-Oz & Dayan, 2002, and references therein) and for sake of multisite comparison will be used here. Comparison between strata for the Shannon - Weaver index (H') used both the Bootstrap method (Section 4.4.2 on page 55) as well as Hutcheson's t - test for the Shannon - Weaver index (H') (Magurran, 2005).

Whereas the Shannon - Weaver index (H') of diversity can be used in very large data sets, a better index to use in finite populations is the Brillouin index (HB). The Brillouin Index (HB) is used when the randomness of the sample cannot be guaranteed or if the total population is analyzed. In paleontological samples the former clause is often the case. Thus, in the case of large mammals, the abundance of medium-small cervids may be increased due to predation. Since the Brillouin index measures the diversity of a collection (rather than a sample, as other indices), each value of HB is different with no measure of variance (Magurran, 2005).

For the one-tailed Mantel tests, results were transformed into a similarity matrix using the Gower asymmetrical similarity coefficient (see Equation 7 on page 272). The similarity matrix was calculated from an array which including the following parameters per 'pooled stratum': Shannon - Weaver H' and Brillouin HB diversity index values.

Chapter 5

Paleoecological Reconstruction

Large mammals have been widely used both for paleoecological reconstruction (Andrews *et al.*, 1979; Andrews, 1992, 1995, 1996; Reed, 1995, 1998; Reed & Fleagle, 1993) as well as for studies of changes through time (Alemseged, 2003; Behrensmeyer *et al.*, 1997; Bobe & Eck, 2001). The main premise underlying paleoecological reconstruction based on fauna is the unique niche requirements of the species. The presence of an indicative mammalian species and its relative abundance have been used as evidence for climatic change e.g., the finding of reindeer, present today in northern latitudes, in Plio-Pleistocene sites in the southern latitudes of Europe served to indicate the limits of glaciations during the Pleistocene (Delpech & Heintz, 1976).

Despite being widely used, the indicative taxon method has several shortcomings (Andrews, 1995). When inferring single species' adaptations there is a strong dependency on precise taxonomic identification, the association of the species to an ecomorphological characteristic and hence habitat. The presumed habitat associated with extinct species is usually based on similarities to extant related species. This premise, of resemblance in paleo and modern habitats between phylogentically close species, although probably true for most cases, should not be taken as an apriori assumption (Andrews, 1995). Another factor presents difficulties in the use of mammals as paleoecological indicators: relative species frequencies may be sensitive to taphonomic biases. These may be due to time and space averaging, depositional milieu, differential preservation, random effects or anthropogenic bias (Alemseged, 2003; Arribas & Palmqvist, 1998; Badgley, 1986; Behrensmeyer, 1984; Behrensmeyer *et al.*, 1986; Behrensmeyer, 1975, 1982, 1985, 1991, 1992; Behrensmeyer & Hill, 1980; Behrensmeyer *et al.*, 2000; Behrensmeyer & Dechant Boaz, 1980; Behrensmeyer, 1978, 1987; Fisher, 1995; Flessa, 2000; Lyman, 1994).

To overcome these problems, "taxon free" or "phylogeny free" methods have been developed. The first, ecomorphological diversity, was developed by Andrews *et al.* (1979). This method associates ecomorphological characteristics to a specimen regardless of its species taxonomic identification. For instance, some specimens may be identified to species level while other (due to fragmentation or anatomical position) cannot. Specimens can be classified by three ecomorphological characters (diet, size and locomotion) based on morphology (gross or micro) and measurements. Thus, a tooth fragment that can not be classified to species, can be classified as "grazer" based on the hypsodonty index. Size, locomotion and diet can thus be inferred from the specimens themselves and can include specimens that may be only identified to higher level taxa rather than those identified to species only. This allows for ecological comparison of sites that have no species in common due to spatial and temporal distances, but have similar ecomorphological diversities.

Andrews *et al.* (1979) compared four modern communities from various localities: lowland forest, montane forest, floodplain and woodland-bushland. Taxonomy at the ordinal level, size, locomotion and diet distributions were found to differ significantly among these habitats (Andrews *et al.*, 1979). Moreover when fossil assemblages were studied, they could be assigned to modern communities in a similar manner. Such analyses have since been done for many Neogene and Quaternary sites (Andrews, 1992, 1995, 1989, 1996; Andrews & Nesbit Evans, 1978; Cerling *et al.*, 1992; Fernandez-Jalvo *et al.*, 1998; Gagnon, 1997; Gunnell, 1995; Kay & Madden, 1997; Morgan *et al.*, 1995; Nesbit Evans *et al.*, 1981; Reed, 1996, 1995, 1998; Reed & Fleagle, 1993).

The second method is the cenogram graph developed by Valverde (1967) and later developed by Legendre (1986, 1987); Legendre *et al.* (1991). This method correlates mammalian species (all species sans chiroptera and carnivora) ranked by abundance against log estimated body weight. The slopes produced can be correlated with open vs. closed and humid vs. dry environments. This method has been applied to paleontological sites worldwide (Aguilar *et al.*, 1998; Gunnell, 1990; Legendre, 1986, 1987; Legendre *et al.*, 1991; Montuire, 1994, 1995, 1998, 1999; Montuire & Desclaux, 1997; Montuire & Girard, 1998; Morgan *et al.*, 1995; Valverde, 1967; Wilf *et al.*, 1998).

The use of models which emphasize presence-absence models has been useful in distinguishing between habitats which differ widely in vegetation cover such as tropical rain forest vs. woodland bush land and savanna grassland. On the converse, Belmaker (2002a) has shown that the Pleistocene site of 'Ubeidiya cannot be securely assigned to any of the comparative modern biomes. This may be a result of the unique habitat in 'Ubeidiya during the Lower Pleistocene or an analytical artifact of the model used.

Both African savanna woodland and Mediterranean woodland exhibit trees in low densities with grassland in between, but the two biomes differ in their seasonality and precipitation regime. From a faunal perspective, both include small-medium size ungulates, with both browsers, grazers and mixed feeders and thus similar ecomorphological histograms Andrews *et al.* (1979) are produced from both environments. Nonetheless, in African biomes the medium sized herbivores are commonly bovids, while in the Mediterranean region they are commonly cervids. In order to distinguish between the two habitats, new methods based on medium level taxonomy (i.e., family, tribe and genus) composition (presence-absence and abundance) should be used.

A method for paleoecological reconstruction, based on abundance rather than presence-absence data was developed by Vrba (1980) and by Greenarce & Vrba (1984). Using multivariate analysis of bovid tribes, the abundance of modern bovid tribes can be used to separate habitats based on vegetational cover (height and spacing of trees and bushes). Areas with higher proportions of bush and tree cover have a high abundance of Cephalopini, Tragelaphini and Reducini, without any members of the Antilopini tribe.

I applied a Correspondence Analysis (CA) (Legendre & Legendre, 1998) to both presence-absence and abundance values for mesoherbivores from various Plio-Pleistocene and modern assemblages. CA is a method of ordination in a reduced space. It consists of describing the trend or order of variation of the objects (e.g., sites) with respect to all descriptors (e.g., taxa abundances). The n descriptors are reduced to the most important variables, which explain the most variance in the data. The major axis is the direction of the maximum variance of the scatter of the points (Legendre & Legendre, 1998).

In this method of multivariate analysis (Vrba, 1980; Greenarce & Vrba, 1984), the focus was placed on the bovid tribes. To facilitate comparison among a wide range of habitats, both African and Eurasian, I opted to include tribes and genera of mesoherbivores i.e., Ruminantia, Suidae and Equidae following Alemseged (2003), as a community of trophically similar and sympatric species (Hubbell, 2001).

The fidelity given to presence-absence data as opposed to abundance data was based on the results obtained from the taphonomic analysis presented above. Thus, for example, if 'Ubeidiya biodiversity abundance variables were affected by one of the taphonomic independent variables (density mediated processes, weathering, fluvial transport, carnivore as primary accumulators, hominins as primary accumulators and carnivore ravaging), fidelity of paleoecological reconstructions based on abundance as interpreted as low. On the other hand, if biodiversity abundance variables correlated with the alternative hypothesis (local environment) but not with any of the null taphonomic hypotheses, the fidelity of abundance data was interpreted to be high.

I compared both the presence-absence and abundance data of mesoherbivore tribes and genera from 'Ubeidiya strata to Modern and Plio-Pleistocene sites from Africa and Europe as published in the literature. African Plio-Pleistocene sites were: Shungura (levels A through G) (Alemseged,

2003) and Konso (levels 4M, 4HA, 10L and 10M) (Suwa *et al.*, 2003). Modern African sites were: Serengeti grassland, Serengeti woodland, Manyara, Ngorongoro, Nairobi Park and Kruger Park (Schaller, 1972). Eurasian Plio-Pleistocene sites were: Poggio Rosso (Mazza *et al.*, 2004), Dmanisi (Gabunia *et al.*, 2000), Venta Micena (Palmqvist & Arribas, 2001) and Untermassfeld (Kahlke, 2000). Modern European sites were Rila National Park Bulgaria (Spasov, 1998) and the Province of Arezzo, Italy (Mattiolio *et al.*, 2004).

Part III

Results

Chapter 6

The Large Mammalian Fauna of ‘Ubeidiya

6.1 Overview of the large mammal fauna of ‘Ubeidiya

A total of 12098 specimens were analyzed during this study. The break down of identified taxa for this analysis is presented in Table 1 on page 232. Of the species analyzed, *Pseudodama* sp. is the most common taxon through out the sequence and comprises between 30 to 70% NISP of an assemblage. Other common taxa are the cervids *Capreolous* sp. and the *Praemegaceros verticornis* complex as well as *Equus tabeti*. The two most common bovids are *Pelorovis oldowayensis* and *Leptobos* sp. All other taxa i.e., proboscideans, carnivores and primates, are rare and do not exceed 5% of the assemblage in each strata. A complete list of species across the seven selected strata is presented in Table 2 on page 233 using NISP quantification and in Table 3 on page 236 using MNI quantification.

6.2 The biogeographic origins of the large mammals present in ‘Ubeidiya with emphasis on African taxa

It has been suggested that the high proportion of taxa of African origin in the Levant in general and in ‘Ubeidiya in particular, may be indicative of large scale ecological dispersal events. Thus, the identification of taxa of African origin and their ecological niche is fundamental for analysis of this hypothesis.

‘Ubeidiya is situated in the palaearctic zoogeographic province which includes both Eurasia and northern Africa. It has been suggested that dispersal of early hominin species from the Ethiopian zoogeographic province during the Lower Pleistocene is associated with the dispersal of other large mammals. The location of ‘Ubeidiya in the Levant (Figure 1 on page 175), a crossroad between

Africa and Eurasia and its date (ca. 1.6 - 1.2 Ma) in the Lower Pleistocene present a unique opportunity to test the hypothesis. The identification of the proportion of exotic African taxa in the assemblages of ‘Ubeidiya is of particular importance.

The majority of taxa present at ‘Ubeidiya are of Palaearctic biogeographic origin (Tchernov, 1988c,a, 1986a), including: *Capreolous* sp., *Pseudodama* sp. and *Praemegaceros verticornis* complex, *Sus strozzi*, Antilopini gen indet., *Leptobos* sp., *Equus* sp. (robust), *Stephanorhinus etruscus etruscus*, *Pannonictis pilgrimi*, *Vormela* cf. *peregusna*, *Hypolagus beremendesis*, *Panthera gombaszoegensis*, *Ursus etruscus*, *Mammuthus meridionalis*, *Canis mosbachensis*, *Lycon lyconoides*, *Vulpes* sp., *Lutra simplicidens*, *Lynx* sp. and *Felis* cf. *chaus*.

Several taxa of biogeographic African origin have been present in the region since before the Lower Pleistocene, thus their presence in the fossil record does not necessarily coincide with the Lower Pleistocene hominin dispersal event. These include taxa which have been identified in Eurasian fossil deposits in the Miocene or Pliocene such as: *Gazella* sp., *Macaca sylvana* and *Camelus* sp.

Eleven taxa found in one or more of ‘Ubeidiya strata can be associated with African biogeographic origins which may be temporally related to Lower Pleistocene dispersal events. They comprise 25 - 43% of the species composition of the ‘Ubeidiya strata (see Table 4 on page 239 and Table 5 on page 239). While including *Hippopotamus* spp. maintains high proportions of individuals of African origin in all strata, the percent of large terrestrial mammalian individuals of African origin is much lower. The following section presents a summary of the biogeography and ecology of the African taxa present at ‘Ubeidiya.

Pelorovis oldowaenyensis - This species was first described in Olduvai from middle and upper Bed II and Bed III (Gentry, 1978). *Pelorovis* was unknown outside of East Africa until the first record in ‘Ubeidiya (Geraads 1986), but since then it has been recorded as *P.* cf. *oldowayensis* at the site of Gesher Benot Ya‘aqov (Martìnez-Navarro, 2000). Moreover, it was found in the Early Pleistocene deposits of the An Nafud desert in the north of Saudi Arabia (Thomas *et al.*, 1998). In ‘Ubeidiya, it appears in all strata and comprises between 0.5 - 6% of the identified terrestrial large mammals specimens.

Oryx* cf. *gazella - This species has been identified in the Levant from only a few specimens in ‘Ubeidiya and is not known from other Levantine sites. *Oryx* species from East Africa, North Africa and Arabia have been assigned different taxonomic names. It has been suggested by Martìnez-Navarro *et al.* (n.d.) that together with the *Oryx* from ‘Ubeidiya, all should be assigned to the same species. These include the East African *Oryx* cf. *gazella* from Ternifine and Olduvai, the *Oryx* sp. from Koobi Fora and the *Oryx* el *eulmensis* described in Aïn Hanech.

Kolpochoerus oldoveinesis - The first appearance of the genus in Africa is during the Early Pliocene (Harris, 1983). This species begins a process of segregation from *K. limnetes* as early as Olduvai Bed I and persists through Bed IV. Although it is known from the Shungura Member G Formation, it becomes common in Member K. It also appears in other Middle Pleistocene African sites (Harris, 1983).

In the Levant, *Kolpochoerus oldoveinesis* is known from ‘Ubeidiya (Geraads *et al.*, 1986), where it comprised up to 2% of the assemblage. An endemic species *Kolpochoerus evronensis* (previously identified as *Metridiochoerus evronensis*) was found in Evron (Tchernov *et al.*, 1994).

Ecologically, despite a brachydont dentition, stable isotope analysis on *K. limnetes* from Koobi Fora suggest that it was a grazer although it was dependent on water (Harris & Cerling, 2002).

Equus tabeti - The gracile equid at ‘Ubeidiya was identified as *Equus* cf. *tabeti* by Eisenmann (1986) based on metapodial and tooth morphology. *E. tabeti* is known mostly from North African sites. It has been found in Aïn Hanech, Algeria (Arambourg, 1970) and Koobi Fora (Eisenmann, 1983). This species is very close to the African species *E. numadicus* and *E. oldowayensis* (Eisenmann, 1983).

Guérin *et al.* (1993) noted similarities between the ‘Ubeidiya specimens and those from Latamne. In ‘Ubeidiya, the abundance of *Equus tabeti* in various strata ranges from 5 - 24% per ‘pooled stratum’. Multivariate analysis has suggested similarities between the equids from the Levant, North African species (*E. numadicus* - *E. tabeti* lineage) and the specimens found in Venta Micena has which have been attributed to *Equus* cf. *altidens* and which have also been found in Spain (Orce, Cuúllar de Baza, Cueva Victoria, Huéscar-1), Italy (Pirro Nord, Selvella), France (Sainzelles) and Germany (Süssenborn) (Arribas & Palmqvist, 1999). This group is also similar to the modern *E. grevyi*.

In the Levant, the gracile equids were replaced by the true equids *E. caballus* and by the Asiatic onager *E. hemiones* and *E. hydruntinus* by the Middle Pleistocene and probably as early as 0.8 Ma at the site of Gesher Benot Ya‘aqov (Eisenmann *et al.*, 2002).

Theropithecus* cf. *oswaldi - This species was widely distribution in Africa during the Pleistocene (Jablonski, 1993). A single calcaneum from the oldest stratum (III 12) in ‘Ubeidiya has been identified as *Theropithecus* cf. *oswaldi* (Belmaker, 2002b). This taxon has also been also identified in Cueva Victoria (Spain) (Gilbert *et al.*, 1995) and in Pirro Nord (Italy) (Rook *et al.*, 2004). The genus, *T. atlanticus* is also found in the Pliocene of North African in the site of Ahl al Oughlam (Morocco) (Alemseged & Geraads, 1998) and the species *T. delsoni* in the Pleistocene of India, at the site Mirzapur (ca. 1.0 Ma) (Gupta & Sahni, 1981; Delson, 1993; Pikford, 1993).

Carbon isotope analyses indicates that δ^{13}C values for *T. oswaldi* from Swartkrans and Sterkfontein suggest a diet composed primarily of C_4 grasses, similar to the graminivorous diet of the living geladas (van der Merwe *et al.*, 2003). This is supported by cranial and tooth morphology (Leakey, 1993). On the other hand, microwear analysis suggest that its diet was more varied than modern *T. gelada* and that it may have consisted of grass and/or leaves and that it ingested more fruits compared to the living geladas (El-Zaatari *et al.*, 2005).

Hippopotamus behemoth* and *H. antiquus - *H. antiquus* has been described in the Pliocene deposits of Bethlehem (Hooijer, 1958). In ‘Ubeidiya, *H. behemoth* was described by Faure (1986) as an endemic species and is one of the most common species. This species has since been also identified in Latamne (Guérin *et al.*, 1993). The genus is present in all Levantine sites from the Lower Pleistocene: Evron (Tchernov *et al.*, 1994), Bizat Ruhama (Ronen *et al.*, 1998) and Gesher Benot Ya‘aqov (Martínez Navarro, 2004), but due to the preservation of the material it could not be securely identified to species. *H. amphibius* is known from Pliocene deposits in Africa (Coryndon, 1976). It first appears in Europe in the Villafranchian in MN 20 (as *H. antiquus*) (Martínez Navarro, 2004). In the Levant, it survived in the coastal rivers until the 4th century B.C.E. (Tchernov & Belmaker, 2004).

Hippopotamus gorgops - This species can be traced through the Early to Late Pleistocene deposits of Olduvai Gorge, Tanzania (Coryndon & Coppens, 1973; Coryndon, 1976). It is present at ‘Ubeidiya (Faure, 1986), although only three specimens have been found. This species had high crowned molars, small premolars, elevated orbits, large and strongly ridged canines (Coryndon & Coppens, 1973).

Giraffa* cf. *camelopardis - First appears in the Levant in the Bethlehem fauna (Middle Villafranchian), and has been identified in ‘Ubeidiya (Haas, 1966) and in Latamne (Guérin *et al.*, 1993). In ‘Ubeidiya it is rare and only three specimens were found throughout the entire sequence.

Crocuta crocuta has been found in Africa as early as Member B in Shungura Formation, in Omo and Olduvai (*C. crocuta ultra*) and is similar to ‘Ubeidiya specimens in size range (P_4 and M_1) (Petter, 1973). The species survived in the Levant until the Upper Paleolithic (Rabinovich, 2002). It first appeared in Europe in the Late Early Pleistocene and survived until the Late Pleistocene. ‘Ubeidiya is the only Eurasian site older than 1.0. Ma in which *C. crocuta* is present rather than *Pachycrocuta brevirostris* (Martìnez-Navarro, 1999).

***Mellivora* sp.** - A single large and robust Mustelidae ulna was found in ‘Ubeidiya. It exhibits morphology and size similar to the extant *Mellivora capensis*. *Mellivora capensis* morphological features present are the deep palmer sulcus and a dorsal notch.

Petter (1987) described a specimen of Mellivora of the size of the living species *M. capensis* from Laetoli. However, the material from Hadar and Koobi Fora is distinctly smaller and more similar in size to *M. benfieldi* from Langebaanweg (Hendley, 1978). It has been suggested that all the material from Laetoli onwards may represent a single highly plastic lineage (Petter, 1987; Werdelin & Lewis, 2005). In North African Plio-Pleistocene sites, *Mellivora* sp. has been found in Oum al Oghlam (Geraads, 1997), Ternifine and Boukendal Quarries (Michel, 1988). In the Levant, it is present today throughout Israel, Saudi Arabia, Kuwait and Iraq (Harrison & Bates, 1991). *Mellivora capensis* is rare in the Pleistocene and Holocene record. It has been recorded from the Upper Paleolithic from Erq el-Ahmar (Vaufrey, 1951) and two cranial fragments have been located in Nahal Hemar dated to 10,000 bp (Dayan, 1989).

***Herpestes* sp.** - Few specimens have been retrieved from ‘Ubeidiya. The genus *Herpestes* has a very patchy record in Africa (Werdelin & Lewis, 2005). The Egyptian mongoose, *H. ichneumon*, is first recorded at Laetoli (Petter, 1987), and with a possible later occurrence at Olduvai (Petter, 1973). In the Levant, it is present today in the north western Arabia peninsula, Israel and Southern Turkey (Harrison & Bates, 1991).

The taxonomic identification of the dirk tooth felid *Megantereon* is of particular importance. It has been suggested that the dispersal of African felids from Africa to Eurasia, was followed by hominins which utilized the meat left on the carcasses (Arribas & Palmqvist, 1999).

The dirk tooth felid, *Megantereon* sp. is represented at ‘Ubeidiya by a well preserved upper canine (UB 80) from stratum II 23 assigned by Haas (1966) to *Megantereon* cf. *megantereon*. Identification to the genus is based on the angle of the apex, striation and the anterior-posterior thickness. Ballesio (1986) reassigned the species to *Megantereon* cf. *cultridens* but stated that the scant material was insufficient to determine if the origin of the ‘Ubeidiya taxon was of Eurasian or African origin.

The question of the species level identification of the taxon has been widely debated and proves difficult since no complete mandibles nor cranial remains have been found. Turner (1997) is of the opinion that the Lower Pleistocene Marchidontids are a single taxon ranging through Eurasia and Africa, *Megantereon cultridens*. This species appears both in African and Eurasia as early as 3 Ma and survives as late as Untermassfeld around 0.9 Ma. If we accept his view, then it is a moot point whether the ‘Ubeidiya specimen is Eurasian or African in origin.

Martínez-Navarro & Palmqvist (1995) hold the opposite view, in that several distinct taxa existed during the Lower Pleistocene. According to this view, *M. cultridens* is the Eurasian species while *M. whitei* is the African species. *M. whitei* has been identified in the Lower Pleistocene sites of Venta Micena, Spain and Appolonia, Greece (Martínez-Navarro & Palmqvist, 1995; Martínez-Navarro & Palmqvist, 1996).

Following this paradigm, it was suggested by Martínez-Navarro & Palmqvist (1995) that the ‘Ubeidiya *Megantereon* is small of size and thus should also be identified as *M. whitei*. Large scale morphometrics do not appear to clearly distinguish between the European population *M. cultridens* and the African population *M. whitei* (and the asian species *M. cultridens nihowanesis* as well) (Hemmer, 2000; Turner, 1997). If this is so, both taxa should receive sub species designation rather than full species rank. I contend that given the current preservation of taxa at the site and equivocal taxonomic assignment of the African stock, this species cannot be definitively assigned to an African species.

An overview of the data suggest that the there are differences in community structure between the strata. These include species composition as well as relative frequency. The following three chapters will present results of data analysis. First, an in-depth taphonomic analysis of the independent factors which were discussed in depth in the methodology section is presented. The second analysis includes the analysis of change throughout the ‘Ubeidiya sequence followed by analysis aimed to correlate the pattern observed with several different factors which may explain the variance in species composition. The third chapter will first present a paleoecological reconstruction of ‘Ubeidiya strata. Each of the following chapters concludes with an interim summary and discussion.

Chapter 7

Taphonomic Analyses of ‘Ubeidiya Strata

The following chapter presents a detailed analysis of the taphonomic variables of the ‘Ubeidiya strata used as independent variables. Each section presents the results for an individual variable presented in the section 4.2 “Independent variables of the null hypotheses: The taphonomy of the ‘Ubeidiya large mammal assemblages” on page 37.

7.1 Weathering

1822 specimens from the seven ‘pooled strata’ were analyzed using the sample drawn as described in the “Methodology” Section, “Weathering“ Subsection 4.2.1 on page 37.

The majority of specimens in all strata can be assigned to weathering stage 1. This distribution is similar to that observed in a wide range Plio-Pleistocene sites in Olduvai Gorge in which up to 90% of the specimens can be assigned to weathering stages 0 - 2 (Potts, 1982).

Weathering stage percentages for all specimens are presented in Table 6 on page 240. The G^2 Likelihood Ratio Chi Square ($\chi^2_{18} = 57.318$ P value < 0.0001) test for independence between strata and distribution of weathering stages indicated that ‘pooled strata’ are not similar in their weathering stages distribution and thus may have biased the distribution of mammalian biodiversity across strata (dependent variables).

Correspondence analysis was performed to determine if some ‘pooled strata’ are more similar to each other based on weathering stages. Results show that the two first axes explain ca. 98% of the inertia. Two graphic presentations of correspondence analysis coordinates are given: a scattergram and dendrogram. A two dimensional scattergram is shown in Figure 11 on page 185 and the dendrogram using Euclidean distance and weighted pair-group with arithmetic averaging amalgamation is presented in Figure 12 on page 186 to visualize the clustering of the ‘pooled strata'.

Both analyses indicate that 'pooled stratum' II 37 is an outlier and distant from all others and is categorized by a high proportion of stage 3 weathering, 'pooled strata' III 21-22 and III 20 form a single cluster and are categorized by a high proportion of stage 2 weathering and all other 'pooled strata' III 11-13, II 23-25, II 26-27 and II 36 represent a third cluster categorized by a high proportion of stage 1 weathering.

Weathering stages were analyzed for different body groups. Results (Table 7 on page 240) suggest that for three 'pooled strata' (II 23-25, III 21-22 and II 26-27), large mammals are more heavily weathered (higher percentages of weathering stages 3 and 4) than small and medium mammals. There is no significant difference between large and small-medium mammals in 'pooled strata' III 11-13, III 20, II 36 and II 37.

The difference in weathering stages between the two body size groups may reflect a difference in the accumulation processes. Thus, most carnivore accumulators have been noted to collect bones in weathering stage 0 or 1 (Lyman, 1994). The higher stages of weathering of larger sized carcasses may suggest that other accumulating factors were involved. Further analysis of taphonomic biases is presented in the following section.

The question which arises from these results is: have the differences in the distribution of weathering stages among strata affect the biodiversity among strata 'Ubeidiya? The correlations between the independent variable "weathering stages" and the mammalian biodiversity dependent variables are presented in Chapter 8 "Identification of Patterns of Persistence or Change" on page 98.

7.2 Fluvial transport

7928 specimens were measured from seven 'pooled strata' using the sample drawn as described in the "Methodology" Section, "Fluvial Transport" Subsection 4.2.2 on page 39.

The distribution of grain shape is presented in Figure 13 on page 187. In all 'pooled strata', all grain shapes are present. This suggests that fluvial transport was not a major force in the formation of the assemblages. The majority of 'pooled strata' show a similar finding in which bladed and prolate specimens comprise the majority of the assemblages, with smaller fractions of oblate and equate specimens. The lower proportions of prolate and equate specimens in all 'pooled strata' suggests that these highly transportable fragments were removed from the assemblages, leaving behind a winnowed deposit enriched with blade and oblate specimens. These is consistent with delta surfaces and floodplains (Lyman, 1994).

The question is, within the generalized model suggested, are their observed differences between the different strata which may have affected the distribution of the mammalian community. Results show that strata differ significantly (G^2 Likelihood Ratio $\chi^2_{18} = 165.1$ P value = 0.0001) in the distribution of grain shape and thus may have biased the distribution of mammalian biodiversity across 'pooled strata' (dependent variables).

I preformed a correspondence analysis on grain shape percentages of each of the 'pooled strata'. The cumulative inertia of the two correspondence axis is 0.9548. Figure 14 on page 188 presents a scattergram for C1 and C2 axes. To clarify clustering of 'pooled strata' and grain shapes, a dendrogram using Euclidean distance and weighted pair-group with arithmetic averaging amalgamation for three factors is presented in Figure 15 on page 189.

Results for all specimens indicate two main clusters. The first, comprised of 'pooled strata' III 20 and III 21-22 is associated with bladed specimens. Bladed and elongated specimens have been shown to be associated with carnivore gnawing suggesting that the preponderance of bladed specimens in these strata may be explained by an increase in carnivore ravaging of the assemblage. Both 'pooled strata' III 20 and III 21-22 have the highest percent of total gnawed bones (Table 30 on page 254). The second main cluster includes four sub-clusters: 'pooled stratum' II 36 clusters with oblate specimens; 'pooled strata' II 37 and II 23-25 cluster with prolate specimens; 'pooled stratum' II 26-27 clusters with equate specimens and 'pooled stratum' III 11-13 forms a cluster of its own. The cluster of 'pooled stratum' II 26-27 with equate specimens can be explained by gross lithology. Since 'pooled stratum' II 26-27 is a conglomerate, the high proportion of spherical (equate) elements may be the result of mechanical weathering and fragmentation.

Quantitative analysis for the three axial ratios and sphericity presented similar results and clustering. Results for $\frac{S}{I}$ are presented in Table 8 on page 241. One way ANOVA for $\frac{S}{I}$, $F_{6,5692} = 31.9113$, P value < 0.0001. Post hoc comparisons using Tukey-Kramer HSD suggests three groups: group A includes 'pooled strata' II 26-27 ($\overline{x} = 0.65$) and III 11-13 ($\overline{x} = 0.64$), group B includes 'pooled strata' II 36 ($\overline{x} = 0.632$), II 37 ($\overline{x} = 0.626$) and II 23-25 ($\overline{x} = 0.623$) and group C includes 'pooled strata' III 20 ($\overline{x} = 0.588$) and III 21-22 ($\overline{x} = 0.588$).

Results for $\frac{I}{L}$ are presented in Table 9 on page 241. One way ANOVA for $\frac{I}{L}$, $F_{6,5692} = 41.5230$, P value < 0.0001. Post hoc comparisons using Tukey-Kramer HSD suggests three groups: group A includes 'pooled strata' II 36 ($\overline{x} = 0.63$) and II 26-27 ($\overline{x} = 0.62$), group B includes 'pooled strata' II 37 ($\overline{x} = 0.587$), II 23-25 ($\overline{x} = 0.583$) and III 11-13 ($\overline{x} = 0.52$) and group C includes 'pooled strata' III 20 ($\overline{x} = 0.52$) and III 21-22 ($\overline{x} = 0.493$).

Results for $\frac{S}{L}$ are presented in Table 10 on page 241. One way ANOVA for $\frac{S}{L}$, $F_{6,5693} = 33.8053$, P value < 0.0001. Post hoc comparisons using Tukey-Kramer HSD suggests three groups: group

A includes ‘pooled stratum’ II 26-27 ($\overline{x} = 0.43$), group B includes ‘pooled strata’ II 36 ($\overline{x} = 0.40$), III 11-13 ($\overline{x} = 0.398$), II 37 ($\overline{x} = 0.392$) and II 23-25 ($\overline{x} = 0.39$) and group C includes ‘pooled strata’ III 21-22 ($\overline{x} = 0.338$) and III 20 ($\overline{x} = 0.33$).

Results for maximum projection sphericity are presented in Table 11 in page 242. One way ANOVA for maximum projection sphericity, $F_{6,5692} = 31.9113$, P value < 0.0001. Post hoc comparisons using Tukey-Kramer HSD suggests three groups: group A includes ‘pooled stratum’ II 26-27 ($\overline{x} = 0.656$), group B includes ‘pooled strata’ III 11-13 ($\overline{x} = 0.64$), II 36 ($\overline{x} = 0.632$), II 37 ($\overline{x} = 0.62$) and II 23-25 ($\overline{x} = 0.623$) and group C includes ‘pooled strata’ III 20 ($\overline{x} = 0.588$) and III 21-22 ($\overline{x} = 0.581$).

To test if animals of different body sizes were subjected to a different degree of fluvial transport and hence subjected to different taphonomic processes, results for grain shape distribution are presented in table 12 on page 242 for body size E and F and in table 13 on page 242 for body size G. Cluster analysis on the percent abundance of grain shapes per ‘pooled stratum’ and animal size (Figure 16 on page 190) indicates that animal size does not affect clustering. The cluster analysis which takes into account body size does not differ significantly from cluster analysis for all specimens combined. Two main clusters can be discerned, which are similar to those obtained for both size groups combined: The first cluster includes ‘pooled strata’ III 11-13, II 26-27 and II 36, the second cluster includes ‘pooled strata’ III 20, II 23-25, III 21-22 and II 37.

Quantitative results for both size groups for $\frac{S}{I}$ are presented in Table 14 on page 243, for $\frac{I}{L}$ in Table 15 on page 244, for $\frac{S}{L}$ in Table 16 on page 245 and for sphericity in Table 17 on page 246.

There is no significant difference between sphericity means in all ‘pooled strata’ (P value > 0.05) between large mammals (body size G) and small-medium mammals (body size E and F). The exception is ‘pooled stratum’ II 36 in which large mammals have a higher sphericity mean than small-medium mammals (P value $= 0.03$).

Differences between the two size groups are insignificant for the three axial ratios for most ‘pooled strata’ (P value > 0.05). The few ‘pooled strata’ which exhibit significant differences between the two size groups indicate that the large size animals have higher values of axial ratio $\frac{I}{L}$ and $\frac{S}{I}$. Fluvial transport of specimens is influenced also by the weight of the specimens and their bone mineral density (Lyman, 1994). Thus, specimens derived from larger animals, even in a fragmented state, will be transported to a lesser extent than smaller animals.

The data of grain shape and sphericity in the ‘Ubeidiya assemblages suggests that although fluvial transport was not major factor in the formation of the assemblage, the assemblages may be winnowed as a results of their accumulation on delta floodplains.

The question which arises from these results is: have the differences in the distribution of grain shape and sphericity among strata affected the biodiversity among ‘pooled strata’ in ‘Ubeidiya? The correlations between the independent variable “fluvial transport” and the mammalian biodiversity dependent variables are presented in Chapter 8 “Identification of Patterns of Persistence or Change” on page 98.

7.3 Agents of accumulation

7.3.1 Body element representation

The overall pattern observed for both small, medium and large ungulates is a pattern dominated by head (mostly loose teeth), limb and feet bones. This distribution is common in many Plio-Pleistocene sites. Despite the overall similarities, G^2 Likelihood Ratio Chi Square ($\chi^2_{48} = 449.156$ P value < 0.0001) indicates that the body part distribution differ significantly among the ‘pooled strata’ and thus may indicate that the strata underwent different taphonomic processes which have biased the biodiversity of the assemblages.

Table 18 on page 247 presented the distribution of body part composition (percent NISP for all taxa) for ‘Ubeidiya ‘pooled strata’ with other Plio-Pleistocene sites for comparisons. The absence of elements with low bone mineral density is evident. Not only are ribs and vertebrae present in low proportions, but all cranial elements are represented by teeth and antler/horn fragments rather than by bone elements. This points to a high degree of post depositional fragmentation resulting from trampling and soil compaction.

Differences between the observed and expected proportion for Ruminantia F (the largest taxonomic group in ‘Ubeidiya) are significant for all ‘pooled strata’ (‘pooled stratum’ III 11-13 G$_{adj}, \chi^2_3 = 50.39$ P value < 0.0001 ; ‘pooled stratum’ III 20 G$_{adj}, \chi^2_3 = 124.53$ P value < 0.0001 ; ‘pooled stratum’ II 23-25 G$_{adj}, \chi^2_3 = 67.06$ P value < 0.0001 ; ‘pooled stratum’ III 21-22 G$_{adj}, \chi^2_3 = 83.28$ P value< 0.0001; ‘pooled stratum’ II 26-27 G$_{adj}, \chi^2_3 = 86.58$ P value < 0.0001 ; ‘pooled stratum’ II 36 G$_{adj}, \chi^2_3 = 101.09$ P value < 0.0001 ; ‘pooled stratum’ II 37 G$_{adj}, \chi^2_3 = 44.89$ P value < 0.0001). Table 19 on page 247 presents the observed vs. expected percent MNE for Ruminantia F.

Various factors may have produced such a pattern; hominin choice of skeletal elements for transport, selective destruction of elements high in nutrients by ravaging carnivores, selective destruction of low density elements by mechanical processes such as weathering and fluvial transport. Each of these processes may have affected the distribution or presence-absence of taxa at ‘Ubeidiya.

The following sections correlate body element distribution (measured as percent MAU) with various possible explanatory factors (density mediated factors, hominins and carnivores as primary accumulators and post depositional carnivore ravaging) to try and explain the discrepancy between observed and expected body element distribution and the differences among the strata.

7.3.2 Density mediated processes

The absence of axial elements (ribs, vertebrae, pelvises and scapulae) in conjunction with the absence of complete crania and near absence of complete mandibles suggests density mediated processes played a role in the formation of skeletal element distribution in ‘Ubeidiya. To test this hypothesis, percent MAU for the four main taxonomic groups (Ruminantia E, Ruminantia F, Ruminantia G and Equidae) were correlated with bone mineral density:

Ruminantia E Percent MAU distribution (presenting “MAU ends”) is presented in Figure 17 on page 191. Results for all strata suggest a similar overall pattern. Estimates for cranial and mandible elements based on dentition were often higher than those based on bony elements only. This is consistent with density mediated destruction of the less durable elements in the assemblages. Similarly, all strata have low or no axial elements (vertebrae and ribs) but higher proportions of limb and feet elements at varying frequencies.

In order to test whether density mediating factors (such as trampling or carnivore ravaging) have affected the skeletal element representation of size E ruminants, percent MAU was correlated with average deer bone mineral density (Lyman, 1984). Correlations are presented in Figure 18 on page 192 as scattergrams for both maximum and traditional scan sites with Spearman’s coefficient of rank correlation r_s and significance values.

Results suggests that all ‘pooled strata’, with the exception of ‘pooled stratum’ II 36, are positively and significantly (P value < 0.1) correlated with bone mineral density for both traditional and maximum scan sites and suggest that the skeletal element distribution of small ungulates is consistent with the pattern expected when an assemblage is subjected to density mediated processes. The correlation in ‘pooled stratum’ II 36 is positive yet insignificant for both traditional and maximum scan site values (P value > 0.1). The lack of correlation may suggest that other factors (i.e., utility based factors) may be involved in the formation of the skeletal element distribution, but it does not negate the possibility the density mediated processes have also affected the skeletal element distribution.

Ruminantia F Percent MAU distribution (presenting “MAU ends”) is presented in Figure 19 on page 193. The overall pattern for Ruminantia F is similar to that of Ruminantia E for all ‘pooled strata'. Cranial and mandible frequencies based on dentition are higher than those based on bony elements only. This is consistent with density mediated destruction of the less durable elements in the assemblages. Similarly, all strata have low or no axial elements (vertebrae and ribs) but higher proportions of limb and feet elements at varying frequencies.

In order to test whether density mediating factors have affected the skeletal element representation of size F ruminants, percent MAU was correlated with average deer bone mineral density values (Lyman, 1984). Correlations are presented in Figure 20 on page 194 as scattergrams for both maximum and traditional scan sites with Spearman's coefficient of rank correlation r_s and significance values.

Results indicate that for all 'pooled strata' percent MAU is positively and significantly (P value $\leqslant 0.05$) correlated with bone mineral density for both maximum and traditional scan sites suggesting that skeletal element frequency of Ruminantia F taxa is consistent with the distribution of body elements expected in an assemblage subjected to density mediated processes.

Ruminantia G Percent MAU distribution (presenting "MAU ends") are presented in Figure 21 on page 195. Results indicate a bimodal distribution with high frequencies of cranial elements, mostly the durable teeth and lower limb elements, metapodials and phalanges. Few limb bones are present.

In order to test for several factors which may have influenced the body element distribution, percent MAU was correlated with average deer bone mineral density values (Lyman, 1984). Correlations are presented in Figure 22 on page 196 as scattergrams for both maximum and traditional scan sites with Spearman's coefficient of rank correlation r_s and significance values.

For Ruminantia G, all 'pooled strata' indicate a positive correlation between between percent MAU and bone mineral density. The correlation between the two factors is insignificant for 'pooled strata' III 20, II 26-27 and II 36 (P value > 0.1) for both maximum and traditional scan sites. The correlation between the variables is significant for 'pooled stratum' III 11-13 (P value $= 0.0024$ traditional scan site), 'pooled stratum' II 23-25 (P value $= 0.0031$ maximum scan site) and 'pooled stratum' III 21-22 (P value $= 0.0284$ maximum scan site). The correlation is marginally significant for 'pooled stratum' II 37 (P value $= 0.0907$ traditional scan site). The lack of correlation for some of the 'pooled strata' may suggest that other factors (i.e., utility based factors) may be involved in the formation of the skeletal element distribution, but it does not negate the possibility the density mediated processes have also affected the skeletal element distribution.

Equidae Results for percent MAU distribution (presenting "MAU ends") are presented in Figure 23 on page 197. Results indicate a bimodal distribution with high frequencies of cranial elements, mostly the durable teeth, and lower limb elements, metapodials and phalanges. Very few limb bones are present.

In order to test for several factors which may have influenced the body element distribution, percent MAU was correlated with average Equidae bone mineral density values (Lam *et al.*, 1999). Correlations are presented in Figure 24 on page 198 as scattergrams for both maximum and traditional scan sites with Spearman's coefficient of rank correlation r_s and significant values. 'pooled strata' III 11-13 and III 20 are not shown due to very small sample sizes (less than three specimens per 'pooled stratum').

For Equidae, all 'pooled strata' indicate a positive correlation between between percent MAU and bone mineral density. The correlation between the two factors is insignificant for most 'pooled strata' i.e., 'pooled strata' III 21-22, II 26-27 and II 37 (P value$>$ 0.1) for both maximum and traditional scan sites. The correlation between the variables is significant for 'pooled stratum' II 23-25 (P value $=$ 0.0042 maximum scan site) and 'pooled stratum' II 36 (P value$=$ 0.0066 maximum scan site). The lack of correlation for some of the strata may suggest that other factors (i.e., utility based factors) may be involved in the formation of the skeletal element distribution, but it does not negate the possibility the density mediated processes have also affected the skeletal element distribution.

The skeletal element distribution of ungulates is highly affected by density mediated process. If no correlation exists between the two variables (i.e., body element distribution and bone mineral density) we would expect half of the correlations to be positive and have to be negative (regardless of statistical significance). Nonetheless, while not all 'pooled strata' exhibit a significant correlation, 26 of the 26 correlations are positive. This is highly significant (sign test P value $<$ 0.0001) and suggests that density mediated processes have affected all 'pooled strata' and all ungulate size groups. The lack of significance between the skeletal element distribution and bone mineral density in the larger ungulates, which is apparent in some of the 'pooled strata' may be an artifact of the small sample size available. The density mediated factors may include fluvial transport, soil compaction and leaching, trampling and carnivore ravaging.

The question which arises from these results is: did the intensity of density mediated process in each 'pooled strata' affect the biodiversity among 'pooled strata' in 'Ubeidiya? The correlations between the independent variable "density mediated process" and the mammalian biodiversity dependent variables are presented in Chapter 8 "Identification of Patterns of Persistence or Change" on page 98.

7.3.3 Evidence for hominin involvement in the accumulation of the ‘Ubeidiya large mammalian assemblages

Correlation of skeletal element frequency with food utility indices

Ruminantia E The percent MAU distribution (presenting “MAU complete”) for Ruminantia E is presented in Figure 25 on page 199. Inclusion of shaft fragments increased the relative proportion of limb bones, specifically intermediate limb bones, tibiae and radii, compared to the distribution obtained from epiphysis data (“MAU ends” see Figure 17 on page 191).

To test for utility based effects on skeletal element distribution, percent MAU for complete elements was correlated with FUI for caribou (Metcalfe & Jones, 1988). Correlations for high survival elements are presented in Figure 26 on page 200 as scattergrams with Spearman’s coefficient of rank correlation $r_s$and significance values.

Results indicate that caribou FUI correlations with Ruminantia E percent MAU are insignificant for all ‘pooled strata’ (P value > 0.05). Correlation coefficients are positive for ‘pooled strata’ III 11-13, III 20, II 23-25, III 21-22 and II 26-27 but negative for ‘pooled strata’ II 36 and II 37.

Since all the correlation are insignificant, this would suggest that utility was not an important factor in the distribution of Ruminantia E skeletal elements among the ‘pooled strata’ of ‘Ubeidiya.

Ruminantia F The percent MAU distribution (presenting “MAU complete”) for Ruminantia F is presented in Figure 27 on page 201. Inclusion of shaft fragments increased the relative proportion of limb bones, specifically intermediate limb bones, tibiae and radii, compared to the distribution obtained from epiphysis data (“MAU ends” see Figure 19 on page 193).

To test for utility based effects on skeletal element distribution, percent MAU for complete elements was correlated with caribou FUI (Metcalfe & Jones, 1988). Correlations for high survival elements are presented in Figure 28 on page 202 as scattergrams with Spearman’s coefficient of rank correlation $r_s$and significance values.

Results indicate that caribou FUI correlations with Ruminantia F percent MAU are insignificant (P value > 0.1) for most ‘pooled strata’. ‘Pooled stratum’ II 36 is negatively correlated and significant ($r_s = -0.79$, P value $= 0.0195$). Although insignificant, correlation coefficients are negative for ‘pooled strata’ III 20, II 23-25, II 26-27 and II 37 and positive for ‘pooled strata’ III 11-13 and III 21-22.

Since all the correlation are insignificant, this would suggest that utility was not an important factor in the distribution of Ruminantia F skeletal elements among the strata of ‘Ubeidiya. In strata II 36, results suggests that high utility elements were transport from the site for utilization elsewhere.

Ruminantia G The percent MAU distribution (presenting “MAU complete”) for Ruminantia

G is presented in Figure 29 on page 203. Inclusion of shaft fragments did not increased the relative proportion of limb bones, compared to the distribution obtained from epiphysis data ("MAU ends" see Figure 21 on page 195).

To test for utility based effects on skeletal element distribution, percent MAU for complete elements was correlated with caribou FUI (Metcalfe & Jones, 1988). Correlations for high survival elements are presented in Figure 30 on page 204 as scattergrams with Spearman's coefficient of rank coefficient of rank correlation r_s and significance values.

Results indicate that caribou FUI correlations with Ruminantia G percent MAU are insignificant (P value > 0.1) for all 'pooled strata'. 'pooled strata' III 20 is negative correlated and marginally significant ($r_s = -0.623$, P value $= 0.098$). Although insignificant, correlation coefficients are negative for 'pooled strata' III 11-13, II 23-25, III 21-22, II 36 and II 37 and positive for 'pooled strata' II 26-27.

Since all the correlation are insignificant, this would suggest that utility was not an important factor in the distribution of Ruminantia G skeletal elements among the strata of 'Ubeidiya. In 'pooled stratum' III 20, results suggests that high utility elements were transport from the site for utilization elsewhere.

Equidae The percent MAU distribution (presenting "MAU complete") for Equidae is presented in Figure 31 on page 205. Inclusion of shaft fragments did not increased the relative proportion of limb bones, compared to the distribution obtained from epiphysis data ("MAU ends" see Figure 23 on page 197).

To test for utility based effects on skeletal elements, percent MAU was correlated with Gross Utility Index (GUI) for horse (Outram & Rowley-Conwy, 1998). Correlations for high survival elements are presented in Figure 32 on page 206 as scattergrams with Spearman's coefficient of rank correlation r_s and significance values.

Correlations were not preformed for 'pooled strata' III 11-13 and III 20 due to small sample sizes. Results indicate that horse GUI correlations with Equidae percent MAU are insignificant (P value > 0.1) for all 'pooled strata'. Although insignificant correlation coefficients are negative for 'pooled strata' II 23-25, III 21-22, II 26-27 and II 37 and positive for 'pooled stratum' II 36.

Since all the correlation are insignificant, this would suggest that utility was not an important factor in the distribution of Equidae skeletal elements among the strata of 'Ubeidiya.

Data from all strata and for all size groups suggests that overall there is no correlation between FUI and skeletal element distributions. Nonetheless, for the two strata did indicate a significant negative correlation suggesting that high utility elements were removed from the site elsewhere.

According to the *Schlepp Effect*, it is expected that small to medium ungulates are transported/utilized in a near complete stage as opposed to large ungulates in which only choice elements are transported as a results of a number of functions such as the distance from the kill site to base site and mode of subsistence pattern (hunting vs. scavenging). According to this model, we would expect no correlation between skeletal element distribution and food utility indices of small-medium ungulates whereas there would be a negative (kill site) or positive (transport site) correlation obtained for large ungulates.

If there is no correlation between skeletal element distribution and food utility indices, given n correlations, we would expect (by chance), half to be positive and half to be negative, regardless of statistical significance. Results indicate that for all correlations (regardless of body size), 16 of the 26 correlation are negative (sign test P value = 0.327) confirming the null hypothesis. Moreover, of the small-medium ungulates 7 of the 14 correlations are negative (sign test P value = 1) and of the large ungulates 9 of the 12 correlations are negative (sign test P value = 0.146). Thus, there is no difference in pattern between large ungulates and small-medium ungulates.

This suggests that complete or nearly complete carcasses where originally present at the site, for both large and small-medium ungulates. Moreover, the lack of correlation may indicate that the assemblages are palimpsests, resulting from different accumulation processes and that time and space averaging processes have obliterated any correlations which may have been visible if the accumulations were more homogenous.

Cut-mark distribution

The presence of cut-marks on bones has been interpreted as evidence for human consumption of fully fleshed bones or as the removal of scraps of meat left on a carcass after carnivore consumption (Domínguez-Rodrigo, 1997).

A total of 18 cut-marks were observed among the strata overall (for example, see figure 33 on page 207), there were very few cut-marks on limb elements present in any of the ‘Ubeidiya strata, ranging from 1 to 5 cut-marks per ‘pooled stratum’ which are 1.51 - 5.71%. I compared the cut-mark distributions among the seven strata using a chi-square test for independence. Since the chi-square tests involve some rather small expected frequencies, the χ^2 distribution cannot be a reliable approximation. The P values (i.e., the probabilities of rejecting the null hypothesis that cut-mark frequencies are the same in all seven strata) were thus estimated by computer simulations. For each strata, 10,000 simulated samples were drawn under the assumption of the null hypothesis. The proportion of samples which had a χ^2 statistic larger than the observed χ^2 was taken as an estimate of the real P value. Pearson’s Chi Square ($\chi^2_6 = 5.525$ estimated P value (10,000 iterations)

$= 0.0001$) indicates that the cut-mark proportions differ significantly among the strata and thus may indicate that the intensity of butchering may have biased the biodiversity of the assemblages.

It is worth noting that other cut-marks observed on non limb elements i.e., mandible of *Equus* sp. (UB 2773) or axis of Ruminantia F (UB 2637) were not included in this analysis following the methodology outlined by Domínguez-Rodrigo (1997) and thus absolute number of cut-marks per 'pooled stratum' may be higher. It should be noted that taphonomic analysis which included all body elements did not result in high overall cut-mark frequencies (Gaudzinski, 2004a,b).

Since the distribution per 'pooled stratum' is scant, comparison with actualistic models is difficult and should be made with caution. Moreover, replicates of similar sequences in the actualistic studies result in a large variability (e.g., between 0 and 33.3%) which further hinders comparison. Nonetheless, in order to relate the pattern present in the different 'Ubeidiya strata to either one of the two alternative hypotheses, multivariate analysis was performed.

Table 20 on page 248 presents the number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for 'Ubeidiya strata and for experimental assemblages (Domínguez-Rodrigo, 1997). Table 21 on page 249 presents the number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for 'Ubeidiya strata and for experimental assemblages (Domínguez-Rodrigo, 1997). Table 22 on page 250 represents the number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for 'Ubeidiya strata and for experimental assemblages (Domínguez-Rodrigo, 1997).

Principle coordinate analysis was preformed. Results suggests that the two first principle axes comprise 80.94% of the variance. Figure 34 on page 208 presented a bivariate scattergram shows that most 'Ubeidiya 'pooled strata' cluster with the carnivore first actualistic models. 'pooled strata' II 36, II 23-25 and III 11-13 are equally distant from both carnivore first and hominin first actualistic models. No 'pooled strata' cluster with the hominin first models.

These results are further supported with cluster analysis. Results are presented in Figure 35 on page 209 which presents a dendrogram using squared Euclidean distances and minimum variance amalgamation for the cut-mark data from all seven of 'Ubeidiya strata and nine actualistic experiments (Domínguez-Rodrigo, 1997). The analysis was performed on other cluster methods (not shown here) and obtained similar results, suggesting that the clustering is robust.

Results indicate that the cut-mark data obtained for all of 'Ubeidiya 'pooled strata' cluster with data of H2 experiments (Domínguez-Rodrigo, 1997) suggesting that the cut-mark distribution is consistent with either the carnivore -hominin and carnivore-hominin-carnivore consumption sequence.

The cut-mark data is also presented for two major body size groups. Size E and F (small-medium) and body size G (large). Table 23 on page 251 presents the number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for ‘Ubeidiya strata for body size E and F and Table 24 on page 251 presents the number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for ‘Ubeidiya strata for body size G. Table 25 on page 252 presents the number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for ‘Ubeidiya strata for body size E and F and Table 26 on page 253 presents the number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for ‘Ubeidiya strata for body size G. Table 27 on page 253 presents the number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for ‘Ubeidiya strata for body size E and F and Table 28 on page 254 presents the number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for ‘Ubeidiya strata for body size G.

A larger percentage of cut-marks appears in the small-medium size groups than in the larger size group. All cut-marks of the large mammals appear in lower limb bones and in the distal region, which is more consistent with secondary access to carcasses than with primary access to carcasses. The pattern of small-medium mammals is more evenly distribution among upper, intermediate and lower limb bones as well as among proximal, mid-shaft and distal limb portions which may indicate access to more fleshed carcasses.

Principle coordinate analysis was preformed on the ‘Ubeidiya strata analyzed for the two size groups. The two first principle axis comprise 75.5% of the variance. Figure 36 on page 210 presents a scattergram for the two first principle axes. As in the data combined for the two size groups, none of the strata cluster with data from hominin first models. Most data of small-medium strata cluster with carnivore first models. Data from a large number of strata, large size mammals, is far from either models and emphasizes the low proportion of cut-marks in this group.

These results are further supported by cluster analysis. Figure 37 on page 211 presents a dendrogram using squared Euclidean distances and minimum variance amalgamation for cut-mark data split by size group. Results suggests that both size groups for all ‘pooled strata’ are equally distant from data obtained for either hominin first or carnivore first models. ‘pooled strata’ II 37, II 26-27 and III 20 for small-medium mammals cluster with the data for carnivore first models. None of the ‘pooled strata’ cluster with data consistent with the hominin first model.

The data presented here is more consistent with the carnivore model than with the hominin first model. It has been suggested that cut-marks data provide a more accurate reflection of Plio-

Pleistocene subsistence patterns compared to body part distribution. While body part distribution are highly affected by density mediated process and post depositional process, cut-marks are retained on small fragments (Domínguez-Rodrigo, 2002). Nonetheless, cut-mark data from Upper Paleolithic sites, where human hunting is not contested, often indicate low percentages of cut-marks, moreover, the distribution of the cut-marks may not always follow the models as predicted from actualistic models e.g., in the site of la grotte des Eglises, cut-marks appear in high frequencies on metapodials (Delpech & Villa, 1993).

Percussion mark distribution

Percussion mark percentages are presented in Table 29 on page 254. All 'pooled strata' have very low percentages of percussion marks, between 0 - 1.55$\%$. I compared the percussion mark distributions among the seven 'pooled strata' using a chi-square test for independence. Since the chi-square tests involve some rather small expected frequencies, the χ^2 distribution cannot be a reliable approximation. The P values (i.e., the probabilities of rejecting the null hypothesis that percussion mark frequencies are the same in all seven 'pooled strata') were thus estimated by computer simulations. For each 'pooled strata', 10,000 simulated samples were drawn under the assumption of the null hypothesis. The proportion of samples which had a χ^2 statistic larger than the observed χ^2 was taken as an estimate of the real P value. Pearson's Chi Square ($\chi^2_6 = 3.425$ P value (10,000 iterations) $= 0.0001$) indicates that percussion mark proportions differ significantly among the strata and thus may indicate that the intensity of bone marrow processing may have biased the biodiversity of the assemblages.

These values are much lower than expected for Plio-Pleistocene human subsistence strategies which include a higher intensity of bone marrow processing (Domínguez-Rodrigo, 2002; O'Connell *et al.*, 2002).

All percussion marks are found on specimens which have been identified as mammals of body size E and F and none on specimens identified as mammals of body size group G.

Although most 'pooled strata' exhibit an overall similar pattern (body part distribution, cut-marks, percussion marks), there are differences in the parameters used to define the interaction between early hominins among 'pooled strata' which may point to differences in pattern or intensity of this interaction. The question which arises from these results is: To what extent does the mode of hominin accumulation processes (primary or secondary) affect the biodiversity among 'pooled strata' in 'Ubeidiya? The correlations between the independent variable "hominins as primary accumulators" and the mammalian biodiversity dependent variables are presented in Chapter

8 “Identification of Patterns of Persistence or Change” on page 98.

7.3.4 Evidence for carnivore involvement in the accumulation of the ‘Ubeidiya large mammalian assemblages

To determine if an assemblage was a result of primary or secondary accumulation by carnivores, it has been suggested to analyze the pattern of gnawing and tooth marks along the limb bones portions as opposed to overall percentages (Blumenschine, 1988).

The percent of gnaw marks on limb bones in all ‘pooled strata’ is high ($\overline{x} = 45.27\%$, range 40 - 60%) and similar to the percent obtained from four actualistic experiments which model carnivore to hominin sequences (45 - 80%) (Blumenschine, 1988; O’Connell *et al.*, 2002). Percent gnaw marks did not differ significantly between ‘pooled strata’ for proximal epiphysis (G^2 Likelihood Ratio Chi Square, $\chi^2_6 = 10.438$ P value $= 0.1074$) and near epiphysis proximal shaft (G^2 Likelihood Ratio Chi Square, $\chi^2_6 = 8.364$ P value $= 0.2126$), but did differ significantly for distal epiphysis (G^2 Likelihood Ratio Chi Square, $\chi^2_6 = 18.311$ P value $= 0.0055$), near epiphysis distal shaft (G^2 Likelihood Ratio Chi Square, $\chi^2_6 = 12.625$ P value $= 0.0494$) and mid-shaft fragments (G^2 Likelihood Ratio Chi Square, $\chi^2_6 = 13.87$ P value $= 0.0311$). This suggests that the intensity or degree of carnivore accumulation may have biased the biodiversity of the assemblages.

Table 30 on page 254 presents the percentage of all limb specimens with tooth marks. Figure 38 on page 212 presents the distribution of carnivore tooth mark and gnaw marks for five bone portions (see Figure 10 on page 184 for bone portion representation); proximal epiphysis, proximal shaft, mid-shaft, distal shaft and distal epiphysis. Table 31 on page 255 presents the distribution of carnivore gnaw marks for three bone portions following Blumenschine (1988); epiphyses, near epiphyses and mid-shaft. Note that “epiphyses” include the “proximal epiphysis” and “distal epiphysis” in Figure 10 on page 184 and “near epiphyses” include the “proximal shaft” and “distal shaft” in Figure 10 on page 184.

While percent gnaw marks for both hominin first and carnivore first models are equally high on epiphyses and near epiphyses portions, the models differ in the percent gnaw marks on the mid-shaft fragment. Thus, carnivore first models have high ($78.2 \pm 6.16\%$) percent of gnaw marks on the mid-shaft while hominin first have low ($8.4 \pm 2.54\%$) proportions of gnaw marks on mid-shaft fragments (Blumenschine, 1988).

The percentages of gnaw marks on mid-shaft fragments from all ‘Ubeidiya strata is high ($\overline{x} = 54.54\%$, range 43 - 70%). Although results for all ‘pooled strata’ are lower that the 95% CI that is suggested experimentally for carnivore first model for most strata, they are much higher than the value suggested for hominin first models. They are also higher than other Plio-Pleistocene sites. Thus, gnaw marks appear on 19.2% of mid-shaft fragments in FxJj50 Site (Domínguez-Rodrigo, 2002) and 30% at Peninj (Domíguez-Rodrigo *et al.*, 2002).

Table 32 on page 256 presents the gnaw mark distribution for body size E and F (small-medium) specimens. Table 33 on page 257 presents the gnaw mark distribution for body size G (large) specimens.

Results analyzed according to body size are similar to those obtained for the complete assemblage. Results for small-medium herbivores suggests that the proportion of mid-shaft fragments with gnaw marks is high ($\overline{x} = 52.12\%$, range 40 - 73%) and consistent with a carnivore first model. Results for large herbivores suggest that the proportion of mid-shaft fragments with gnaw marks is high ($\overline{x} = 46\%$, range 0 - 75%). 'Pooled stratum' II 26-27 forms an outlier with no gnaw marks on mid-shaft specimens. Data calculated with the exclusion of 'pooled stratum' II 26-27 ($\overline{x} = 53.57\%$, range 33.33 - 75%) suggest that the data is consistent with the carnivore first model.

The absence of gnaw marks in mid-shaft fragments may suggest that 'pooled stratum' II 26-27 is the result of hominin primary access to large mammals. However, specimens from this strata exhibit no cut-marks for this size group. Moreover, the sample size for limb mid-shafts is very small ($n = 2$) suggesting that this anomalous pattern may be attributed to the small sample size.

These results suggests that for the data for all is consist with carnivore first access to 'Ubeidiya specimens. Nonetheless, there are differences in the proportion of carnivore gnaw-marks which may suggest a difference in intensity or degree in which each of the strata were accumulated by carnivores. The question which arises from these results is: To what extent does the mode of carnivore accumulation processes (primary or secondary) affect the biodiversity among 'pooled strata' in 'Ubeidiya? The correlation between the independent variable "carnivores as primary agent of accumulation" and the mammalian biodiversity dependent variables is presented in Chapter 8 "Identification of Patterns of Persistence or Change" on page 98.

7.4 Evidence for post depositional carnivore ravaging

Evidence for further scavenging or ravaging by carnivores, after consumption of the carcasses by the predator (carnivore or hominin), is common in many archaeological and paleontological sites. Of the known carnivores which accumulated bones, hyaenas are the most prominent (Cruz-Uribe, 1991).

7.4.1 Tooth marks

Table 30 on page 254 shows the percent of bones with carnivore modifications. All ‘pooled strata’ have a proportion higher than 38% which is the minimum present in modern hyaena dens (Pickering, 2002) indicating that the ‘pooled strata’ were probably ravaged by carnivores. It is important to stress that ravaging may occur before hominins had accesses to the carcasses (primary or secondary), after or include a combination of both. The ‘pooled strata’ differ significantly in percent bones with carnivore modifications (G^2 Likelihood Ratio Chi Square ($\chi^2_6 = 30.260$ P value $< .0001$) suggesting that the intensity of carnivore ravaging may have biased the biodiversity of the assemblages.

Table 34 on page 258 presents the percent of total carnivore modification and for body size E and F (small-medium) and G (large). Results suggest that most strata exhibit high proportions (>40%) of tooth marks, suggesting assemblages highly ravaged by carnivores. ‘pooled strata’ with lower proportion of tooth marks are ‘pooled stratum’ III 20 (large mammals) and ‘pooled stratum’ II 23-25 (small-medium mammals) with ca. 30%. These results may indicate a lower intensity of post depositional ravaging,

7.4.2 Proportion of carnivores of total assemblage

Table 35 on page 258 presents the results of relative abundance of carnivore taxa for the seven selected ‘pooled strata’ in ‘Ubeidiya for both MNI and NISP quantification.

Proportion of carnivores above 20% using MNI quantification is interpreted as indicative of hyaena accumulated assemblages whereas assemblages accumulated by humans usually have less then 10% of carnivores and never more than 13% (Cruz-Uribe, 1991; Klein & Cruz-Uribe, 1984). All ‘pooled strata’ exhibit low proportion of carnivores <15% using NISP quantification.

Results suggests that the two oldest ‘pooled strata’ from the Li cycle III 11-13 and III 20 have a low proportion of carnivores ca. 10% for MNI quantification. Of the Fi cycle, the majority of the ‘pooled strata’ exhibit high carnivore proportions, above 20%, with the exception of ‘pooled stratum’ III 21-22 with a carnivore proportion of ca. 15%. The two ‘pooled strata’ from the Fi cycle are similar in carnivore ungulate ratio to those obtained for archaeological assemblages, all other strata values falls above the 10% cut off limit suggested by Klein & Cruz-Uribe (1984) for hominin accumulated assemblages. On the contrary, all ‘pooled strata’ exhibit low proportions of carnivores using NISP quantifications consistent with archaeological assemblages.

The apparent contradicting results obtained for the MNI and NISP quantifications suggests that this criterion may not be as indicative as suggested. Specifically, it is important to note that this values were obtained for the brown hyaena and that comparative values for the spotted hyaena may be different.

7.4.3 Proportions of "bone cylinders" shaft fragments

936 specimens from the seven 'pooled strata' were analyzed using the sample drawn as described in the "Methodology" Section, "Agents of accumulations" Subsection 4.2.3 on page 41. Results are presented in Table 36 on page 258 and presented in Figure 39 on page 213.

Results indicate that most 'pooled strata' do not differ in the proportion of "bone cylinder" shaft fragments (within 95% CI). All 'pooled strata' have high percentages, with a median of 24.8% and average of 26.15%, suggesting modification by carnivores. 'Pooled stratum' II 26-27, is the only one that falls below the 95% CI and which has a lower proportion of "bone cylinder" shaft fragments. The high percentage of fragments in this 'pooled stratum' as opposed to complete bones and "bone cylinder" shaft fragments, may be attributed to either anthropogenic bone marrow processing or a relative increase in post depositional taphonomic biases such as soil compaction, abrasion and weathering (Cruz-Uribe, 1991; Pickering, 2002).

Subsistence patterns (either human or carnivores) often vary with different body size groups. Thus, to test if this phenomenon is taxon specific or a general phenomenon of the 'pooled strata', percent of limb fragments was measured for two main size groups; E and F (small-medium) and G (large). Table 37 on page 259 presents the percent limb fragments for body size E and F (small and medium). Table 38 on page 259 presents the percent limb fragments for body size G (large).

Results indicate that the proportion of cylinders in 'pooled stratum' II 26-27 is lower for both small-medium and large mammals than is other strata, suggesting that the phenomenon is not taxon specific but rather a generalized characteristic of 'pooled strata'.

Further analysis supports the latter hypothesis. I hypothesize that post depositional fragmentation may have eliminated cylinder fragments thus reducing their original frequency. 'Pooled stratum' II 26-27 does not exhibit a lower percentage of overall carnivore tooth marks as would be expected if fragmentation is due to anthropogenic bone marrow processing (see Table 30 on page 254 on bones and Table 31 on page 255). 44.7% of specimens in 'pooled stratum' II 26-27 exhibit one or more of the diagnostic carnivore modification, which is similar to the average of the majority of strata with an average of 45.36% and a range of 37 - 60%. Moreover, 'pooled stratum' II 26-27 is characterized by a gross lithology of conglomerates interpreted as shoreline (Picard & Baida, 1966a). This lithology may have contributed to post depositional fragmentation compared to strata of silt and clay matrices.

A short methodological issue should be considered in light of the results present here. The percent of bone cylinders may be affected by post depositional processes. Thus, strata may have been subjected to post depositional processes such as these which may break cylinders present in the assemblage. Two assemblages with originally similar proportions of cylinders, may have very different proportions as a result of trampling. Thus, the low proportion of cylinder fragments in 'pooled stratum' II 26-27 may be attributed to the fact that II 26-27 is overall a conglomerate 'pooled stratum' (Picard & Baida, 1966a). As a result of the taphonomic analysis, I have decided to exclude the parameter "percent bone cylinder" from the calculation of the independent variable "carnivore ravaging".

7.4.4 The effect of carnivore ravaging on body part distribution

To test for the effect of carnivore ravaging, percent MAU of high survival elements was correlated with skeletal element distribution of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991).

Ruminantia E Percent MAU for proximal and distal elements of Ruminantia E was correlated with skeletal element distribution of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991). Correlations for high survival elements are presented in Figure 40 on page 214 as scattergrams with Pearson's coefficient of correlation r and significance values.

Results indicate that Ruminantia E percent MAU positively correlates with the skeletal element distribution of hyaena ravaged domestic sheep bones (P value < 0.1) for 'pooled strata' III 11-13, III 20, II 23-25, III 21-22 and II 37. Correlations of the variables in two 'pooled strata', II 26-27 and II 36 are insignificant (P value > 0.1).

Ruminantia F Percent MAU for proximal and distal elements of Ruminantia F was correlated with the skeletal element distribution of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991). Correlations for high survival elements are presented in Figure 41 on page 215 as scattergrams with Pearson's coefficient of correlation r and significance values.

Results indicate that Ruminantia F percent MAU positively correlates with skeletal element distribution of hyaena ravaged domestic sheep bones (P value < 0.1) for 'pooled strata' III 11-13, III 20, II 23-25, III 21-22 and II 36. Correlations of the variables in two 'pooled strata', II 26-27 and II 37 are insignificant (P value > 0.1).

Ruminantia G Percent MAU for proximal and distal elements of Ruminantia G was correlated with skeletal element distribution of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991). Correlations for high survival elements are presented in Figure 42 on page 216 as scatter-

grams with Pearson's coefficient of correlation r and significance values.
Results indicate that Ruminantia G percent MAU positively correlates with skeletal element distribution of hyaena ravaged domestic sheep bones (P value < 0.1) for 'pooled strata' II 23-25, II 36 and II 37. Correlations of the variables in four 'pooled strata', III 11-13, III 20, III 21-22 and II 26-27 are insignificant (P value> 0.1).

Equidae Percent MAU for proximal and distal elements of Equidae was correlated with skeletal element distribution of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991). Correlations for high survival elements are presented in Figure 43 on page 217 as scattergrams with Pearson's coefficient of correlation r and significance values.
Results are not presented for 'pooled strata' III 11-13 and III 20 due to a very low sample size. Results indicate that although Equidae percent MAU positively correlates ($r > 0.5$) with skeletal element distribution of hyaena ravaged domestic sheep bones, all correlations are insignificant (P value > 0.1).

These results suggest that carnivore ravaging was a significant density meditating factor. This is evidence in percent surface modification, bone cylinder fragments and the high proportion of carnivores in the assemblages. Moreover, most 'pooled strata' show a significant correlation between the distribution of skeletal elements and the skeletal distribution of hyaena ravaged domestic sheep bones.

All correlation are positive although some are insignificant. If there was no correlation between skeletal element distribution (percent MAU) and skeletal element distribution of hyaena ravaged domestic sheep bones, we would expect that half of the 26 correlations to be positive and half to be negative, regardless of their significance. Of the 26 correlations preformed, 24 were positive (sign test P value < 0.0001) indicating that there is an overall positive significant correlation between the two variables. The lack of significance observed in specific 'pooled strata' and body sizes may be attributed to sample size. For example, Ruminantia E and G as well as Equidae which have smaller samples sizes, also have fewer significant correlations. These results suggest that the assemblages at 'Ubeidiya were highly affected by hyaena ravaging.

These conclusions are further confirmed by the distribution of skeletal elements. Table 39 on page 260 presents the distribution of body element frequency calculated as percent NISP and compared to several modern and Plio-Pleistocene assemblages. Cranial elements do not include loose teeth or antler fragments. Modern comparative data includes surface remains from Amboseli Natural Park (Behrensmeyer & Dechant Boaz, 1980), bones partially buried in Amboseli Natural park (Behrensmeyer & Dechant Boaz, 1980), Spotted Hyaena *Crocuta crocuta* den (Behrensmeyer

& Dechant Boaz, 1980), stripped hyaena *Hyaena hyaena* den (Martínez Navarro & Palmqvist, 1999), Porcupine *Hystrix indica* den (Martínez Navarro & Palmqvist, 1999), Magugu which is a Hadza kill size (Lupo, 2001) and Tsipitibe which is a Hadza camp site (Lupo, 2001). The Plio - Pleistocene comparative sites include Venta Micena, Spain which has been interpreted as a short faced hyaena *Pachycrocuta brevirostris* den (Martínez Navarro & Palmqvist, 1999). Figure 44 on page 218 presents a dendrogram using Euclidean distances and weighted pair-group with arithmetic averaging amalgamation for ‘Ubeidiya and modern and Pleistocene comparative data. Results indicate that all ‘Ubeidiya strata cluster with hyaena den accumulations.

Differences between ‘pooled strata’ indicate possible difference in the intensity of carnivore ravaging between strata. The question which arises from these results is: Did the intensity of carnivore post depositional ravaging affect the biodiversity among strata in ‘Ubeidiya? The correlation between the independent variable “carnivore ravaging” and the mammalian biodiversity dependent variables is presented in Chapter 8 “Identification of Patterns of Persistence or Change” on page 98.

7.5 Interim summary and discussion: Taphonomy and the accumulation of the large mammalian fauna of ‘Ubeidiya

As common in many archaeological and paleontological assemblage, the taphonomic processes which may be observed in the ‘Ubeidiya ‘pooled strata’ suggest an amalgamations of processes and the presence of palimpsests rather than single processes assemblages. Although there are subtle differences between the ‘pooled strata’ in ‘Ubeidiya, they can all be characterized by similar taphonomic parameters: The assemblages are largely unweathered. Assemblages are enriched with a high proportion of bladed and oblate specimens. The large ungulates are dominated by head and feet and are similar in distribution to that found in hyaena accumulated assemblages. The assemblages are positively correlated with bone mineral density suggesting destruction of low survivorship elements by post depositional process. By in large, the body part distributions do not correlate with food utility indices, although two strata exhibit negative correlations. The faunal assemblage exhibit a low percentage of cut-marks but a high percentage of gnaw marks, specifically on mid-shaft fragments.

Neither weathering nor fluvial transport were found to be a main factor in the accumulation of the large mammalian fauna of ‘Ubeidiya. The preponderance of specimens assigned to weathering stage 1 suggests that most specimens were buried quickly. The presence of bones of all grain shapes attests to the minimal role played by fluvial transport in the formation of the assemblages. Nonetheless, the preponderance of bladed and oblate specimens suggests that the more spherical elements may have been winnowed out, such as suggested by models of fluvial transport in floodplains. The highly fragmented state of the cranial elements usually not consumed by carnivores points to a high degree of post depositional mechanical fragmentation as a results of trampling and soil compaction.

The overall low proportion of cut-marks, absence of bone marrow processing and lack of correlation between high survival skeletal element frequency and food utility indices suggests that hominins were not a major factor in the accumulation of the bones at the site.

All the assemblages in ‘Ubeidiya were subjected to a high degree of post depositional ravaging by hyaenas. This is supported by the body part distribution, high proportion of gnaw marks and modified bones and a high proportion of cylinder type shaft fragments.

Despite the apparent low impact of hominins on the accumulation of the bones in the assemblage, the understanding of the role of hominins in the accumulation of a fossil assemblage is pertinent to our ability to interpret taphonomic processes and hence infer paleoecological phenomena. The degree of taphonomic bias exerted by hominins is a function of their subsistence pattern i.e., hunting or scavenging.

In the following discussion, I will first address the evidence for primary vs. secondary accumulation by hominins of the ‘Ubeidiya assemblages and then discuss the evidence for post depositional carnivore ravaging as possible taphonomic processes in the formation of the fossil assemblages of ‘Ubeidiya.

There are two main groups of hypotheses presented in the literature to describe Plio-Pleistocene hominin subsistence patterns: The first main hypothesis uggests that hominins scavenged the bone and flesh remains from carcasses hunted by carnivores, notably large felids. These leave largely defleshed but skeletally intact carcasses. According to this hypothesis, hominins transported limb and head elements to be utilized for marrow and brain content. A low proportion of cut-marks may have been produced by scraping flesh remains off the carcasses. The literature describes that archaeological sites created this way are dominated by head and limb elements, with a high proportion of gnaw marks ($> 70\%$) on mid-shaft fragments, a high proportion of cut-marks on lower limb bones (metapodials) and on distal ends and evidence for bone marrow processing as indicated by percussion marks (Blumenschine, 1986, 1987, 1988; Blumenschine & Cavallo, 1992; Blumenschine *et al.*, 1994; Shipman, 1983).

The second main hypothesis in the literature suggests that hominins practiced active scavenging or hunting. Thus, primary access to fleshed carcasses would result in a high proportion of cut-marks, primarily on upper limb bones (femur and humerus) and on mid-shaft fragments. If the assemblages were ravaged by carnivores after the remains had been discarded, a low proportion of gnaw marks may be apparent on the mid-shaft (ca. 15%). It has further been suggested that such carcasses may have only been partially utilized by hominins, thereby resulting in a medium proportion of carnivore gnaw-marks on the mid-shaft and a larger proportion of complete limb bones. The latter fact suggests that bone marrow was not processed (Domínguez-Rodrigo, 2002, 1997; Domínguez-Rodrigo & Pickering, 2003) as primary access to largely fleshed mammals would have reduced the necessity for consumption of bone marrow.

In both scenarios, body element distribution is highly affected by post depositional ravaging by carnivores, which results in a depletion of axial elements. This would manifest in a positive correlation between skeletal element distribution (percent MAU) with bone mineral density (BMD) and with skeletal element distribution of an hyaena ravaged domestic sheep (Lyman, 1994; Marean & Spencer, 1991).

These two extremes presents the end case scenarios for a continuum which range from active hunting of large animal, active scavenging of near complete carcasses to passive scavenging rather than a dichotomy. Moreover, as common in archaeological and paleontological sites, most assemblages are palimpsests and one can envision an assemblage which results from several independent accumulation processes and from different hominin subsistence strategies in particular.

The data presented in this thesis suggested that the faunal assemblage from ‘Ubeidiya confirm to the carnivore - hominin - carnivore model of Blumenschine *et al.* (1994). Several lines of evidence support this model: cut-mark data, gnaw mark data and skeletal element frequency.

The cut-mark data from ‘Ubeidiya indicates that overall frequencies are low and range between 1.5 - 5.7% per ‘pooled stratum’, the percent of cut-marks in upper limb bones ranges from 0 - 10% per ‘pooled stratum’. All ‘pooled strata’ cluster together with the experimental data based on a carnivore - hominin model (Domínguez-Rodrigo, 1997). The overall proportion of cut-marks at ‘Ubeidiya are much lower than that of many of the Plio-Pleistocene sites in Africa. At FLK Zinj, cut-mark counts on upper limb shafts are 30% (Bunn & Kroll, 1986), 19% at FxJj 50 (Domínguez-Rodrigo, 2002) and 30% at Peninj (Domíguez-Rodrigo *et al.*, 2002). All these sites have been interpreted as consistent with a hominin first model. On the other hand, sites which have been interpreted as carnivore first models have a percent of cut-marks that are more similar to that found in ‘Ubeidiya. At BK, percent of cut-marks is 9% while at MNK it is 6% (O’Connell *et al.*, 2002).

The gnaw marks of various ‘Ubeidiya ‘pooled strata’ ranged from 44 - 70% on mid-shaft fragments. The range for five sets of hominin first experiments suggests 5 - 30% gnaw marks on limb bones on opposed to 45 - 80% for four carnivore first experiments (O’Connell *et al.*, 2002). All of the ‘Ubeidiya ‘pooled strata’ fall within the range of variability of carnivore first models and are much higher than hammer stone to carnivore model (O’Connell *et al.*, 2002). The percent of gnaw marks on mid-shaft fragments of ‘Ubeidiya is higher than most African Plio-Pleistocene sites. Tooth mark frequency at FxJj 50 are 20% (Domínguez-Rodrigo, 2002) and 5% for Peninj (Domíguez-Rodrigo *et al.*, 2002). The low frequencies at FxJj 50 and Peninj have been interpreted as consistent with the hominin first model as supported by the cut-mark data for both sites. Overall tooth mark cuts for FLK Zinj are 60%, suggestive of a carnivore first model. This does not confirm to the results of the cut-mark data from the site which suggest a hominin first model. Interestingly, both BK and MNK, exhibit low frequencies of tooth marks (5% and 1% respectively), supporting a hominin first model although the cut-mark date from these two sites have been interpreted as supporting the carnivore first model (O’Connell *et al.*, 2002).

Evidence for bone marrow processing would be expected in a carnivore-hominin-carnivore model. If hominins were transporting defleshed head and limb elements for their marrow contents, there should be evidence in the form of multiple bone fragments with percussion marks. The very low proportions of percussion marks in all ‘Ubeidiya strata as well as relatively high proportion of complete elements attests to the fact that bone marrow processing was not practiced at the site. It has been suggested that in hominin first models, the high quality and quantity of protein obtained from the fleshed carcasses reduces the necessity for the fat and nutrients in bone marrow (Domínguez-Rodrigo & Pickering, 2003; Gaudzinski, 2004a,b, 2005). According to this model, carcasses and parts of carcasses were transported to archaeological sites but only a portion of the total assemblage were demarrowed (Domínguez-Rodrigo & Pickering, 2003). This partial utilization hominin first model has been used to explain both moderate (ca. 30 - 50%) gnaw mark frequency on mid-shaft fragments as well as a high proportion of complete limbs with no evidence of bone marrow processing. This pattern has been suggested for sites such as FLK North 6 (Olduvai Gorge, Tanzania) and GaJi 5 (Koobi Fora, Kenya). At these sites, complete bones exhibit cut-marks since they were defleshed but were not processed for bone marrow (Domínguez-Rodrigo & Pickering, 2003).

By contrast at ‘Ubeidiya, the complete bones found at the site do not exhibit any cut-marks but do exhibit gnaw marks on the epiphyseal regions. This would suggest that the complete bones represent natural background fauna that were killed by carnivores and do not support the hominin first model. The skeletal elements frequency at ‘Ubeidiya is head, limb (especially lower limb) and feet dominated. Overall, the correlation of skeletal element frequencies and food utility indices are insignificant. This would suggest that originally, the entire or nearly complete skeleton were present at the site. Contrary to the expectations from the *Schlepp Effect*, results suggests that nearly complete skeletons of both small-medium as well as large ungulates are present at the site. Nonetheless, for two 'pooled strata', the proportion of high survival skeletal elements is negative and suggests that the elements were transported from the site to be processes elsewhere.

Given the evidence present (low proportion of cut-marks, absence of bone marrow utilization, lack of correlation with food utility indices), how can the apparent low utilization of animal protein/fat by early hominins at 'Ubeidiya be explained?

First, subsequent loss of low survival elements may be attributed to carnivore ravaging as attested by the positive correlation with bone mineral density and specifically with the survivorship of ungulate bone post hyaena ravaging survivorship. Are there methodological biases which may explain the pattern observed? It has been suggested by Marean & Kim (1998) that the exclusion of shaft fragment in MNE and MAU calculations may artificially reduce limb bones and over represent feet and teeth. I used shaft fragments in both small, medium and large ungulate identification so the apparent under-representation of limb bones compared to feet bones in the larger ungulates is real. Moreover, the near absence of percussion marks suggests that bone marrow processing cannot explain the low frequency of upper limb bones.

Second, 'Ubeidiya assemblages undoubtedly represents palimpsests accumulations. Thus, some elements may be the result of kill animals that were not scavenged by hominins but only ravaged by carnivores. This is manifested by complete elements which do not have cut-marks but do exhibit carnivore gnaw marks.

Third, as suggested by the two 'pooled strata' which indicate a negative correlation, specimens may be the results of carcasses which were scavenged by hominins and in which high utility elements where removed off the site. Lack of correlation between the two variables would have been accentuated by post depositional processes may have altered the original assemblage as attested by the positive correlation with bone mineral density. Another aspect which may explain the lack of significant correlation with food utility indices is the fact that a wide range of factors may affect transport of carcasses. O'Connell *et al.* (2002) has shown that transport of elements vs. discard in near kill sites is dependent on size of animal, its anatomy, distance from residential base and the number of people that can assist in the butchery and transport processes. Other cultural factors may include group size and sharing considerations (Tappen *et al.*, 2002a). Ecological factors may include degree of competition from other carnivores (Tappen *et al.*, 2002a). It is interesting to note that bone accumulations of the Hadza did not show the expected significant correlation with food utility indices (Lupo, 2001). Thus, bone marrow processing may have been practiced off the site rather than excluded as a subsistence pattern altogether.

Fourth, Speth (1987) proposed that during periods of resource stress (usually low levels of precipitation), ungulates become depleted in fat. During such periods, hominin reliance on animal food source is reduced or even avoided in favor of carbohydrate rich plants. If this is the case, ‘Ubeidiya assemblages may represent low resource seasonal sites reflecting the dry period. Thus the accumulation of carcasses may be primarily attributed to a wide variety of causes rather than predation such as starvation, exposure and other natural causes (DeVault *et al.*, 2003).

The data presented here is consistent with the interpretation of the ‘Ubeidiya as a carnivore kill site with secondary low level hominin utilization of the remains. According to this interpretation, small to medium ungulates were hunted and killed by large carnivores. Hominins scavenged the remains, perhaps removing high utility limb elements to be processed elsewhere. It is important to note that due to the high degree of post depositional attrition present at the site, it is difficult to ascertain if the scavenging was active, passive or a combination of the two. The surface modification (both cut-mark and gnaw-marks) do not support an active hunting or primary access but the possibility that this subsistence pattern did occur in some frequency, cannot be excluded. Similarly, the absence of bone marrow processes would appear to represent a local phenomenon i.e., the limb bones were removed elsewhere rather than indicate a particular subsistence pattern i.e., a preference of flesh over marrow.

It has been suggested that the absence of evidence for bone marrow processing in the site would have required the acquisition of protein and fat from other sources. Such a source may have been the large quantities of flesh removed from carcasses in the process of active scavenging or perhaps even hunting (Gaudzinski, 2004a,b, 2005). I contend that the evidence presented in this thesis for the assemblages at ‘Ubeidiya do not warrant this conclusion. First, there is evidence (‘pooled strata’ III 20 and II 36) that high utility elements were removed off the site. If this is the case, we would not expect to find evidence for bone marrow processing on site. If this is so, bone marrow was utilized by early hominins elsewhere.

Second, large ungulates such as hippos are common in ‘Ubeidiya as well as in African Plio-Pleistocene and in Europe. Nonetheless, they are often not included in subsistence pattern analysis (Domínguez-Rodrigo, 2002). Even in a scavenging model, the quantities of proteins obtained from such a carcass may be sufficient to account for the dietary requirements of early hominins in ‘Ubeidiya.

O’Connell *et al.* (2002) have suggested a model for archaeological sites termed multiple carcass butchering stands or near kill sites. These localities, observed at the Hadza, are located around perennial water points and in stream channels. When large animals frequent the site, Hadza hunters have been observed to monitor the area, waiting for a scavenging opportunity from fresh kills. Once a carcass is located, it is removed to a spot close to the water for further processing. Thus, these localities normally contain the refuse of stripped bones as well as bone processed for marrow. Transport of elements from the site is utility based and is determined by body size of carcasses, distance to camp site and number of butchers.

Although it is important not to jump to conclusion based on comparisons between modern ethnographic studies and paleolithic assemblages, the format suggested by O'Connell *et al.* (2002) is intriguing in the possibilities it presents for the interpretation of the 'Ubeidiya fauna.

O'Connell *et al.* (2002) mention four characteristics indicative of such sites:

1. Sites are found near perennial water points were Hadza never camp. 2. They contain the remains of many individuals. 3. They contain taxa often identified as markers of diverse habitats. 4. They are dominated by head and limb elements.

All four criteria can be found in 'Ubeidiya: The site is located near a water point; it has many individuals; it contains taxa representing many habitats; the assemblages are dominated by head and limb. The main difference between the pattern observed in the Hadza and that in 'Ubeidiya is that in the Hadza near-kill sites, much of the processing of the scavenged carcasses involves the consumption of meat and marrow on site as well as preparation of elements for further transport and as such produces areas with discarded bone and specifically bone marrow processing refuse. Nonetheless, I do not think that this precludes using near kill sites as a generalized model for the 'Ubeidiya assemblages. Moreover, the distance between the actual kill site and near kill site among the Hadza is ca. 100 - 200 m. (O'Connell *et al.*, 2002). Thus, we may imagine that given both time and space averaging, an assemblage such as that found in 'Ubeidiya may include a mixture of carcasses from the two site types i.e., both a kill sites and near-kill sites and will include a mixture of carcasses utilized both to a high and to a lower degree by hominins.

This model is consistent with that proposed by Shea (1999). Based on the abrasion patterns of the lithics from 'Ubeidiya he suggested that the "living floors" reflect the abandonment of stone tool and the site is thought to be a resource procurement site. Thus, after simple flake tools were used in carcass processing, they were discarded on site. This model was based particularly on the reconstruction of the 'Ubeidiya shoreline as a dangerous place, in which hominins were poor competitors compared to other large carnivores, crocodiles and hippos. If this model is correct, the absence of evidence for bone marrow processing is not evidence of absence but rather absence of evidence and we cannot conclude if early hominin in 'Ubeidiya did or did not process bones for marrow in this location.

This may be similar to the described "Lake Margin Foraging" subsistence pattern which included brief foraging visits for carcasses within marshy or shallow floodplains (Bunn, 1994) and similar to that described by Blumenschine (1991) for Olduvai and by Potts (1989) for Olorgasailie.

This model was based on the findings at Koobi Fora ridge, where several complete pygmy hippo femora that exhibit cut-marks were found (Bunn, 1994).

This research indicates that ‘Ubeidiya assemblages do not represent camp sites but rather regions which hominins frequented in order to scavenge carcasses killed by large carnivores. This was phrased by Shea (1999, pg. 203) “ ...Unless we can envision early hominins camping, flint-knapping, and dividing up animal carcasses while ankle-deep in mud, all while being exposed to both aquatic and terrestrial predators, it is exceedingly improbable that the lithic assemblage from these levels are residues of habitation sites, or “living floors”...”.

This model does not negate the possibility that some individual specimens were acquired by active scavenging or even by hunting, probably some of the animals in the smaller end of the scale, but it does suggest that this was not the common modus operandi practiced by the early hominins in ‘Ubeidiya.

Following the accumulation of bones in near-kill sites, the assemblages was further ravaged by carnivores and specifically hyaenas. The criteria used to identify hyaena accumulated assemblage has been widely discussed in the literature. The data from ‘Ubeidiya suggests that the overall gnaw mark frequency is high ($> 38\%$) and consistent with carnivore ravaged assemblages (Pickering, 2002). Also, there is a positive correlation between body element distribution and skeletal elements frequency post hyaena ravaging (Marean & Spencer, 1991). Body elements distribution from ‘Ubeidiya clusters with modern and Pleistocene body elements distribution data from hyaena dens.

All ‘Ubeidiya ‘pooled strata’ have a high proportion of bone cylinders indicative of carnivore ravaging (26.15%). The low proportion of bone cylinders in ‘pooled stratum’ II 26-27 has been attributed to post depositional fragmentation which may have decreased the original proportion of shaft cylinder fragments.

The proportion of carnivore MNI of the total species is over 20% and consistent with a hyaena accumulated assemblage. The finding of two ‘pooled strata’ with a lower percentage of carnivore MNI may be an analytical artifact.

The preference for carnivores has been noted specifically for the brown hyaena rather than the spotted hyaena present in ‘Ubeidiya (Cruz-Uribe, 1991). Since this criteria is based on a species not found at ‘Ubeidiya, this criteria may be inapplicable for determining whether hyaenas were active in the accumulation of the large mammalian fauna at ‘Ubeidiya.

Support for this hypothesis may be found if we look at the data set obtained for NISP quantification. Klein & Cruz-Uribe (1984) have noted that a high proportion of carnivores species in hyaena dens using either NISP or MNI quantification methods. Thus, we would expect similar carnivore proportion in an assemblage using either quantification methods. But this is not the case in ‘Ubeidiya. While the MNI method has indicated ‘pooled strata’ with carnivore proportion of over 20%, suggestive of carnivore modifications, the NISP method has yielded only low proportions, all well below 20%. This can be explained by the fact the the carnivore remains are most often represented by a single bone per ‘pooled stratum’. Thus, while they indicate a low NISP, MNI calculations artificially inflate the abundance of rare taxa. A skeletal element distribution of a single bone is more representative of background fauna, incorporated into the assemblage via fluvial transport.

It is interesting to note that the accumulation of small carnivores has been observed specifically in dens and in feeding of young cubs. In ‘Ubeidiya, none of the ‘pooled strata’ exhibit juvenile specimens as might be expected from a hyaena den. This would suggest that while evidence indicates a that the ‘Ubeidiya strata were subjected to carnivore ravaging, the evidence for denning activity and the rearing of young is inconclusive.

One of the main points which arises from the issue in our absence in models of subsistence pattern of very large mammals i.e, hippos. These common ungulates are often found in many Plio-Pleistocene sites but are excluded from taphonomic analysis. Future studies which can model the surface modification left by human and other carnivores after primary and secondary access to carcasses of such size will be of valuable information.

In summary, the evidence presented here suggests that all ‘Ubeidiya assemblage, represent kill or near kill sites of large carnivores. The carcasses were subsequently scavenged by hominins which transported limb bones elsewhere. The remaining bones were ravaged by carnivores and further altered by density mediated processes.

Chapter 8 “Identification of Patterns of Persistence or Change” on page 98 will present statistical analysis aimed at testing the degree to which the various taphonomic independent variables (i.e., weathering, fluvial transport, hominins as primary accumulators, carnivores as primary accumulators and carnivore ravaging) may be correlated with biodiversity indices (dependent variables) of the large mammalian community of ‘Ubeidiya. Positive correlations would suggest that taphonomic processes may have biased the distribution of large mammal species across ‘pooled strata’ at ‘Ubeidiya (the taphonomic null hypotheses).

Chapter 8

Identification of Patterns of Persistence or Change

8.1 Faunal turnover

Table 40 on page 261 presence the distribution of presence-absence of taxa among strata in ‘Ubeidiya. Table 41 on page 262 presents the FAD’s and LAD’s for the ‘Ubeidiya strata. Results indicate that there is a significant increase in number of species following ‘pooled stratum’ III 20. There is no significant difference in species richness in subsequent ‘pooled strata’. This would suggests that there is a change in species presence-absence through time (faunal turnover) within the ‘Ubeidiya sequence.

In order to qualify possible turnover, correspondence analysis (CA) was preformed. Total inertia (total CA variance) = 0.4125. Figure 45 on page 219 presents the a scattergrams for the three first axes (cumulative variance = 75.28%). Results indicate that ‘pooled strata’ III 11-13 and III 20 are distant from the main cluster formed by the majority of ‘pooled strata’. Within the large cluster, two clusters can be observed. The first includes ‘pooled strata’ II 23-25, III 21-22 and II 26-27 and the second includes ‘pooled strata’ II 36 and II 37.

These results are further exemplified using double cluster Q and R mode analysis. Results are presented in Figure 46 on page 220.

R mode clustering suggests that taxa cluster based on their frequency in different ‘pooled strata’ along the sequence. Taxa that appear once or twice in the sequence form a cluster while common taxa which appear throughout the sequence form another cluster.

Q mode clustering indicates that the strata cluster according to stratigraphic sequence and suggest two main faunal units. The first, faunal unit A, comprised of ‘pooled strata’ in the Li cycle:

III 11-13 and III 20, the second, faunal unit B comprised of the ‘pooled strata’ in the Fi cycle II 23-25, III 21-22, II 26-27, II 36 and II 37. There is a difference between the faunal composition of the older ‘pooled strata’ in the Fi cycle: II 23-25, III 21-22 and II 26-27 which form a single cluster (sub-faunal unit B1) and the younger ‘pooled strata’ in the Fi cycle: II 36 and II 37 which form another cluster (sub-faunal unit B2). Although most species appear in both groups, only a few appear exclusively in faunal group A and B. Table 42 on page 263 show the taxa present in each faunal unit.

To test possible factors which may have influenced the distribution of taxa, I correlated the presence-absence data with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) for the entire sequence. One-tailed Mantel tests were performed using the Dice-Sørenson asymmetrical similarity coefficient.

No correlation is found between faunal composition (presence-absence data) and taphonomic null hypotheses. These include: density mediated processes (r_M = 0.35, P value = 0.402), fluvial transport (r_M = 0.384, P value = 0.1), weathering (r_M = 0.1151, P value = 0.346), hominins as agents of accumulation (r_M = 0.330, P value = 0.108), carnivores as agents of accumulation (r_M = -0.3, P value = 0.88) and carnivore ravaging (r_M = 0.0293, P value = 0.19).

The alternative hypothesis, local environmental change, was found to be positively and significantly correlated with faunal composition (ρ_M = 0.477, P value = 0.0174). This correlation may be related to the stratigraphic sequence rather than environment per se. Since local environmental change and stratigraphy are positively and significantly correlated (ρ_M = 0.86, P value = 0.012), the correlation of faunal composition with local environmental change may be in part, an artifact of the autocorrelation above.

To tests for factors which may affect faunal changes within a faunal unit, I correlated the presence-absence data of faunal unit B only with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental (the alternative hypothesis) with the exclusion of ‘pooled strata’ III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Dice-Sørenson asymmetrical similarity coefficient.

No correlation were found between faunal composition within faunal unit B and most of the taphonomic independent variables. These include: fluvial transport (r_M = -0.03, P value = 0.6549), weathering (r_M = 0.52, P value = 0.09), hominins as agents of accumulation (r_M = -0.168, P value = 0.446), carnivores as agents of accumulation (r_M = -0.04, P value = 0.6167). Moreover, the alternative hypothesis, local environmental change, was found not to correlate with presence-absence of taxa (ρ_M = 0.448, P value = 0.136).

There was a positive marginal significant correlation between faunal composition and carnivore ravaging (r_M = 0.444, P value = 0.068) and between faunal composition and density mediated processes (r_M = 0.422, P value = 0.0964).

Since there is a positive correlation between carnivore ravaging and local environmental change within the Fi cycle (ρ_M = 0.959, P value = 0.034), I ran partial Mantel tests to test the hypothesis presented above. There is no correlation between faunal composition and carnivore ravaging when controlling for local environmental change (ρ_M = 0.343, P value = 0.257) but there is a positive and significant correlation between faunal composition and density mediated process when controlling for local environmental change (ρ_M = 0.542, P value = 0.047).

The latter is probably a result of carnivore ravaging. Carnivores are known to ravage elements in accordance to their bone mineral density (Lyman, 1994). This is supported by the lack of correlation between faunal composition and density mediated processes when controlling for carnivore ravaging (r_M = 0.374, P value = 0.168).

Thus, the main factor which affects the change in faunal composition is local environmental change. This correlation reflects the difference between faunal unit A and B. It is important to remember that this may reflect the affect of stratigraphy or a combination of stratigraphy and the environment. Local environmental change nor stratigraphy cannot account for the difference between the two sub-faunal units in the Fi cycle: B1 and B2. None of the taphonomic independent variables tested have been shown to have affected the change in faunal composition. Apparent correlation between faunal compositions and taphonomic variables (i.e., carnivore ravaging, density mediated processes) have been shown to be an artifact of autocorrelations.

8.2 Relative frequency analysis of taxa

8.2.1 Multi-species analysis

Table 2 on page 233 presents the distribution of species across strata using NISP quantification and Table 3 on page 236 presents the distribution of species across strata using MNI quantification. I compared the species distribution (NISP quantification) among the seven 'pooled strata' using a chi-square test for independence. Since the chi-square tests involve some rather small expected frequencies, the χ^2 distribution cannot be a reliable approximation. The P values (i.e., the probabilities of rejecting the null hypothesis that species frequencies are the same in all seven 'pooled strata') were thus estimated by computer simulations. For each 'pooled strata', 10,000 simulated samples were drawn under the assumption of the null hypothesis. The proportion of samples which had a χ^2 statistic larger than the observed χ^2 was taken as an estimate of the real P value. Pearson's

Chi square test ($\chi^2_{192} = 867$ P value (10,000 iterations) = 0.001) suggests that there are differences in the distribution of taxa across 'pooled strata' using NISP quantification.

I preformed correspondence analysis (CA) on percent NISP data for all 'pooled strata'. Total inertia (total CA variance) = 0.6783. Figure 47 on page 221 presents a scattergram represented the first three CA axes (total cumulative variance = 79.66%). Results indicate three main clusters: 'Pooled stratum' III 11-13, forms an out-group, 'pooled strata' II 36 and II 37 form another and all other 'pooled strata' (III 20, II 23-25, III 21-22 and II 26-27) form a third. This grouping is similar to the grouping developed based on the presence-absence data: faunal units A, B1 and B2. The main difference is the position of 'pooled stratum' III 20. Based on presence-absence data analysis it is grouped in faunal unit A, whereas according to relative abundance data analysis it should be grouped with faunal unit B1.

Within the group analogous to faunal unit B1, we can distinguish two sub clusters: 'pooled strata' III 20 and II 26-27 form one cluster and 'pooled strata' II 23-25 and III 21-22 form another cluster. This suggests that factors other than environment (which has been found to affect presence-absence distribution) may have affected the distribution of taxa abundances.

Figure 48 on page 222 presents a double cluster for both Q and R mode analysis. R mode analyses (clustering by species) suggests that species cluster into three groups based on abundance; *Pseudodama* sp. is the most abundant taxa in all strata and this forms a group of its own. The second cluster is formed by the moderately abundant taxa: *Capreolous* sp, *Praemegaceros verticornis* complex and *Equus tabeti*. All other taxa formed the third group and included taxa with low frequencies.

Cluster analysis results in slightly different clustering than suggested by correspondence analysis. 'Pooled stratum' III 11-13 formed an out group, consistent with its position within faunal unit A. The other strata form two clusters. The first include 'pooled strata' III 20, III 21-22 and II 26 and the second includes 'pooled strata' II 23-25, II 36 and II 37.

In order to test the specific factors that influence the relative frequency of large mammalian fauna across strata, I correlated the relative frequency data (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental (the alternative hypothesis). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

Results for all taxa indicate that none of the taphonomic independent variables correlate with similarity of taxa relative frequency between strata (the taphonomic null hypotheses). These include: density mediated factors (r_M = 0.1194, P value = 0.312), weathering (r_M = 0.076, P value = 0.397), fluvial transport (r_M = 0.05, P value = 0.429), hominins as agents of accumulation (r_M = 0.166, P value = 0.3), carnivores as agents of accumulation (r_M = -0.245, P value = 0.779) and carnivore ravaging (r_M = 0.080, P value = 0.374).

A significant positive correlation was found between local environmental change and taxa relative frequency (ρ_M = 0.456, P value = 0.036). These results suggests that the null hypotheses can be rejected and that local environmental change has an affect on the faunal abundance through the 'Ubeidiya sequence. This correlation may be related to the stratigraphy rather than environment per se. Since local environmental change and stratigraphy are positively and significantly correlated (ρ_M = 0.86, P value = 0.012), the correlation of faunal composition with local environmental change may be in part, an artifact of the autocorrelation above.

To test which factors may control changes in faunal abundances in the Fi cycle only, I correlated the relative frequency (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of 'pooled strata' III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found for most of the taphonomic independent variable and taxa relative frequency (the taphonomic null hypotheses). These include: density mediated factors (r_M = 0.30, P value = 0.236), weathering (r_M = 0.09, P value = 0.429), fluvial transport (r_M = -0.555, P value = 0.8583), hominins as agents of accumulation (r_M = -0.254, P value = 0.31) and carnivores as agents of accumulation (r_M = 0.147, P value = 0.257).

A positive but marginally significant correlation was found between taxa relative frequency and local environmental change (the alternative hypothesis) (ρ_M = 0.467, P value = 0.068) and between taxa relative frequency and carnivore ravaging (r_M = 0.423, P value= 0.068).

Since there is a positive and significant correlation between local environmental change and carnivore ravaging within the Fi cycle (ρ_M = 0.959, P value = 0.0341), the correlations above may be related to the autocorrelations between them.

No correlation was found between relative taxa abundance and local environmental change when controlled for carnivore ravaging (ρ_M = 0.431, P value = 0.197) and between relative taxa abundance and carnivore ravaging when controlled for local environmental change (ρ_M = -0.317, P value = 0.7624). This would indicate that both variables, local environmental change and carnivore ravaging, have only a weak affect on taxa abundance.

Results suggests that relative frequency is controlled primarily by the affect of first order environmental changes (between the Li and Fi cycles). Within the Fi cycle, there is a weak affect second order environmental changes (the continued desiccation of the sequence) and of carnivore ravaging.

This taphonomic bias may explain the difference in clustering between presence-absence data and that which is apparent with relative frequency data. Specifically, the similarity between 'pooled strata' II 23-25, II 36 and II 37 and the similarity between 'pooled strata' III 21-22 and II 26-27.

8.2.2 Individual taxa analysis

The change in the relative frequency of individual taxa across strata was tested for each of the 33 taxa using 95% confidence intervals. Only four taxa were observed to differ significantly across the sequence; these correspond to the four taxa which formed the second cluster in the relative frequency R mode analysis: *Pseudodama* sp., *Capreolous* sp., *Praemegaceros verticornis* complex and *Equus tabeti*.

These taxa can be divided into two ecological groups. Thus, *Pseudodama* sp. and *Capreolous* sp. are identified as sclerophyllous woodland taxa while *Praemegaceros verticornis* complex and *Equus tabeti* are identified as shrubland and grassland taxa.

I grouped each of the two pairs according to their habitat preference. Figure 49 on page 223 presents the distribution of the four taxa in NISP and MNI quantifications. Figure 50 on page 224 presents the distribution of forest taxa and open habitat taxa using NISP quantification.

To test for the possible factors which may have influenced the change in relative frequency of each of the taxa, a similarity matrix was created using the Gower asymmetrical similarity coefficient based on the relative frequency for each of the two pairs of taxa as presented in the subsections below:

Forest taxa

The distribution of forest taxa can be observed in Figure 50 on page 224. The overall proportions of forest taxa are high with an average of ca. 50%. 'Pooled stratum' III 20 has the highest abundance with nearly 90% of the terrestrial taxa assigned to these two taxa: *Pseudodama* sp. and *Capreolous* sp. Following the high abundance in 'pooled stratum' III 20, there is a sharp decrease in 'pooled stratum' II 23-25. There is only a slight and insignificant increase in abundance between 'pooled strata' II 23-25 and II 26-27. Following 'pooled stratum' II 26-27, there is a sharp decrease in abundance in 'pooled stratum' II 36 which is maintained in 'pooled stratum' II 37.

A naive analysis of this distribution may attribute all of the change in abundance as a proxy to change in forest cover. If this is the case, the decrease between 'pooled strata' III 20 and II 23-25 would reflect a period of climatic shift from highly forested area to a more open area. The subsequent increase in 'pooled stratum' II 26-27 would be interpreted as an increase in forest habitat again.

In order to test the specific factors that influence the distribution of taxa among the 'pooled strata', I correlated the relative frequency data (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. Since both taxa which comprised this dependent variable were assigned body sizes E and F, all taphonomic independent variables were calculated using specimens assigned body sizes E and F and the intermediate body size EF.

No correlations were found between taphonomic independent variables and forest taxa abundance (the taphonomic null hypotheses). These include: density mediated factors (r_M = 0.302, P value = 0.140), weathering (r_M = -0.156, P value = 0.7345), fluvial transport (r_M = 0.173, P value = 0.120), hominins as agents of accumulation (r_M = -0.09, P value = 0.379) and carnivores as agents of accumulation (r_M = 0.1888, P value = 0.221).

A correlation of marginal statistical significance was found between local environmental change and forest taxa abundance (ρ_M = 0.362, P value = 0.098) and between carnivore ravaging and forest taxa abundance (r_M = 0.308, P value = 0.1).

I ran partial Mantel tests to correlate between each variable and forest taxa abundances controlling for local environment change and carnivore ravaging. Under the working hypothesis, the significant effect of local environmental change or carnivore ravaging may have masked the effect of other taphonomic variables.

Results indicate that despite controlling for carnivore ravaging, no correlation was found between the taphonomic independent variables and forest taxa abundances. These include density mediated processes (r_M = 0.251, P value = 0.148), fluvial transport (r_M = 0.14, P value = 0.351), weathering (r_M = -0.137, P value = 0.717), hominins as agents of accumulation (r_M = 0.086, P value = 0.339), carnivores as agents of accumulation (r_M = 0.057, P value = 0.392). Moreover, no correlation was found between forest taxa abundance and local environment change (ρ_M = 0.318, P value = 0.126).

Despite controlling for local environmental change, no correlation was found between forest taxa abundances and the taphonomic independent variables. These include: Density mediated factors (ρ_M = 0.250, P value = 0.216), weathering (ρ_M = 0.235, P value = 0.187), fluvial transport (ρ_M = -0.074, P value = 0.5356), hominins as agents of accumulation (ρ_M = -0.353, P value = 0.8216), carnivores as agents of accumulation (ρ_M = 0.381, P value = 0.116) and carnivore ravaging (ρ_M = 0.107, P value = 0.322). Thus, there is only a weak effect of both local environmental change and carnivore ravaging on forest taxa abundance.

To tests which factors may affect changes in faunal abundances in the Fi cycle only, I correlated the relative frequency (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of ‘pooled strata’ III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found between the taphonomic independent variables and forest taxa abundance within the Fi cycle (the taphonomic null hypotheses). These include: density mediated factors (r_M = 0.428, P value = 0.153), weathering (r_M = 0.149, P value = 0.338), fluvial transport (r_M = 0.184, P value = 0.302), hominins as agents of accumulation (r_M = -0.263, P value = 0.277), carnivores as agents of accumulation (r_M = 0.292, P value = 0.196) and carnivore ravaging (r_M = -0.36, P value= 0.8546). Moreover, no correlation is found between local environmental change and forest taxa abundance (ρ_M = 0.138, P value = 0.339).

Results suggests that forest taxa abundance is weakly controlled by the affect of first order environmental changes (between the Li and Fi cycles). This is confounded by the taphonomic bias of carnivore ravaging. ‘pooled strata’ with high proportions of forest taxa (III 20) reflect periods of greater humidity and thus, greater forest coverage. This phenomenon is accentuated by the fact that strata will high proportions of forest taxa, ‘pooled strata’ III 20 and II 26-27 were subjected to higher intensities of carnivore ravaging. Within the Fi cycle, the change in relative frequency of forest taxa cannot be attributed statistically either to any of the taphonomic null hypotheses nor to the alternative hypothesis.

Open habitat taxa

The distribution of forest taxa can be observed in Figure 50 on page 224. The overall proportions of open habitat taxa are lower than forest taxa with an average of 10%. ‘Pooled stratum’ III 11-13 has the highest abundance with nearly 25% of the terrestrial taxa assigned to these two taxa: *Praemegaceros verticornis* complex and *Equus tabeti*. Following the high abundance in ‘pooled stratum’ III 11-13, there is a shape decrease in ‘pooled stratum’ III 20. This is followed by an increase in ‘pooled stratum’ II 23-25. There is no significant change between ‘pooled strata’ II 23-25 and III 21-22. There is a significant decrease in abundance in ‘pooled stratum’ II 26-27 followed by an increase in ‘pooled stratum’ II 36, which is maintain in ‘pooled stratum’ II 37.

Similar to that described for the forest taxa, a naive analysis of this distribution may attribute all of the change in abundance as a proxy to change in forest cover. If this is the case, the increase between ‘pooled strata’ III 20 and II 23-25 would reflect a period of climatic shift from highly forested area to a more open area. The subsequent decrease in ‘pooled stratum’ II 26-27 would be interpreted as an increase in forest habitat again.

In order to test the specific factors that influence the distribution of open habitat taxa, I correlated the relative frequency data (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. Since both taxa which comprise this dependent variable were assigned to body size G, all independent variables were calculated using specimens assigned to body size G only.

No correlation was found between the taphonomic independent variables and open habitat taxa abundance (the taphonomic null hypotheses). These include: density mediated factors (r_M = -0.238, P value = 0.8512), weathering (r_M = -0.347, P value = 0.9405), fluvial transport (r_M = -0.299, P value = 0.8593), hominins as agents of accumulation (r_M = 0.3, P value = 0.139), carnivores as agents of accumulation (r_M = 0.026, P value = 0.385) and carnivore ravaging (r_M = -0.05, P value = 0.6497). Moreover, no correlation was found between local environmental change and open habitat taxa abundance (ρ_M = -0.03, P value = 0.6659). There is no correlation between open habitat taxa abundance and stratigraphy suggesting that latter is not an artifact of the lower number of cases (ρ_M = 0.174, P value = 0.222).

To test which factors may affect changes in faunal abundances in the Fi cycle only, I correlated the relative frequency (NISP) with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of ‘pooled strata’ III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found between the taphonomic independent variables and open habitat taxa abundance (the taphonomic null hypotheses). These include: weathering (r_M = 0.54, P value = 0.149), fluvial transport (r_M = -0.266, P value = 0.7814), hominins as agents of accumulation (r_M = 0.32, P value = 0.246), and carnivore ravaging (r_M = -0.294, P value = 0.8003). Moreover no correlation is found between local environmental change and taxa relative frequency (ρ_M = -0.075, P value = 0.6).

There was a significant correlation between open habitat taxa abundance and carnivores as agents of accumulation (r_M = 0.786, P value = 0.0395) and between open habitat taxa abundance and density mediated factors (r_M = 0.414, P value = 0.038).

When controlling for carnivores as agent of accumulation, no correlation was found between abundance of open habitat taxa and the taphonomic variables. These include: density mediated factors (r_M = 0.05, P value = 0.396), weathering (r_M = 0.506, P value = 0.145), fluvial transport (r_M = -0.299, P value = 0.8182), hominins as agents of accumulation (r_M = -0.087, P value = 0.4865), and carnivore ravaging (r_M = -0.252, P value = 0.7337). Moreover no correlation is found between local environmental change and taxa relative frequency (ρ_M = 0.207, P value = 0.235).

When controlling for density mediated processes, no correlation was found between abundance of open habitat taxa and the taphonomic variables. These include: weathering (r_M = 0.555, P value = 0.151), fluvial transport (r_M = -0.116, P value = 0.6028), hominins as agents of accumulation (r_M = 0.377, P value = 0.2), and carnivore ravaging (r_M = -0.285 P value= 0.7412). Moreover no correlation is found between local environmental change and taxa relative frequency (ρ_M = -0.08, P value = 0.6478).

There is a positive a marginal significant correlation between open forest habitat taxa abundance and carnivores as agents of accumulation (r_M = 0.734, P value = 0.07).

There was no correlation between the taphonomic variables nor the environmental variable and with open habitat taxa abundance. Within the Fi cycle, there is only a weak affect of density mediated process. ‘Pooled stratum’ II 26-27 with a lower abundance of open habitat taxa also does not exhibit positive correlation of skeletal element distribution for both Ruminantia G and Equidae with bone mineral density. Since this ‘pooled stratum’ is a conglomerate, post depositional fragmentation may have reduced the specimens to a levels beyond identification. Mammals of larger size group posses less anatomical markers per size then smaller mammals, thus fragmentation renders more fragments as unidentifiable (Bartram & Marean, 1999).

Within the Fi cycle, there is also a weak affect if carnivores as primary accumulators on open taxa habitat abundance. This is primarily a reflection of the absence of cylinder shaft fragments in stratum II 26-27. Since the sample size was very low ($n = 2$). These results should be regarded as suspect.

8.2.3 Diversity indices

Species richness

Results for three different indices (Marglef’s, Fisher’s α and rarefaction) are presented in Figure 51 on page 225 and in Table 43 on page 264. Species richness values, unadjusted for sample size, are presented for comparison.

A similar pattern is apparent for all three indices, indicating robusticity of the results. ‘Pooled stratum’ III 11-13 and III 20 appear to have a lower richness per sample size than the other strata, which do not differ among them. ‘Pooled stratum’ II 36 and II 37 are slightly higher in species richness than expected.

Stratum by stratum P value comparison for Marglef’s index and Fisher’s α are presented in

Table 44 on page 264. P values are estimated by bootstrapping. Results indicate a significant difference for both the Margalef and Fisher's α index at the 0.05 significance level between III 20 and II 23-25. There is difference between 'pooled strata' II 26-27 and II 36 significant at the 0.1 significance level.

These results suggest an increase in species richness over time throughout the 'Ubeidiya sequence, although it is not monotonous and may be related to two or three stages. The main distinction is between 'pooled strata' III 11-13 and III 20 and all others. The 'pooled strata' are assigned to the Li cycle whereas all other 'pooled strata' are assigned to the Fi cycle. Within the Fi cycle, there is a slight distinction between older (II 23-25 to II 26-27) and younger (II 36-II 37) 'pooled strata' i.e., faunal sub-unit B1 and B2 respectively.

One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. No correlation was found between any of the taphonomic independent variables and species richness. These include: density mediated processes (r_M = -0.075, P value = 0.443), fluvial transport (r_M = 0.0275, P value = 0.403), weathering (r_M = 0.0275, P value = 0.403), hominins as agents of accumulation (r_M = 0.085, P value = 0.352), carnivores as agents of accumulation (r_M = -0.278, P value = 0.9668) and carnivore ravaging (r_M = 0.0042, P value = 0.5). Moreover, species richness does not correlate with the alternative hypothesis of local environment change (ρ_M = 0.172, P value = 0.273). Species richness is marginally significantly correlated with stratigraphy (ρ_M = 0.410, P value = 0.062) reflecting the increase in species richness over time. These results may be related to the change in faunal composition indicated by a significant change between faunal unit A and B.

To test which factors may control changes in faunal abundances in the Fi cycle only, I correlated richness with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of 'pooled strata' III 11-13 and III 20 (faunal unit A). Correlations were performed using the asymmetrical Gower similarity matrix.

Within the Fi cycle, no correlation was found between any of the taphonomic independent variables and species richness. These include: density mediated processes (r_M = 0.325, P value = 0.231), fluvial transport (r_M = 0.288, P value = 0.199) , weathering (r_M = -0.104, P value = 0.5797), carnivores as agents of accumulation (r_M = -0.08, P value = 0.5551) and carnivore ravaging (r_M = 0.035, P value= 0.294). Moreover, species richness does not correlate with the alternative hypothesis of local environment change (ρ_M = -0.328, P value = 0.8976). However, there is a positive and marginal significant correlation between richness and hominins as agents of accumulation (r_M = 0.375, P value = 0.09).

The latter result is surprising. Within the Fi cycle, most strata exhibit similar richness values which do not differ significantly from one another. Thus, this would appear to represent an artifact of the slight differences in the absolute values of richness between strata. Nonetheless, future studies and perhaps an increase in sample size may indicate whether this correlation is meaningful or simply reflects a sampling bias.

Evenness

Results for three evenness indices (Equitability J', Simpson's $1 - D_s$ and Buzas and Gibson's evenness) are presented in Figure 52 on page 226 and in Table 45 on page 264. P values for consecutive 'pooled strata' are presented in Table 46 on page 265.

The trend across 'pooled strata' is similar for all three indices, albeit with different absolute values. A significant decrease in evenness is observed between 'pooled strata' III 11-13 and III 20. This is followed by a significant increase in evenness between 'pooled strata' III 20 and II 23-25. Although there is a slight decrease between 'pooled strata' II 23-25 and III 21-22, the over all pattern between 'pooled strata' II 23-25, III 21-22 and II 26-27 is of similar evenness values. Finally, a significant increase in evenness is observed between 'pooled strata' II 26-27 and II 36. There is no change in evenness between 'pooled strata' II 36 and II 37.

One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. No correlation was found between any of the following taphonomic independent variables and evenness. These include: density mediated factors (r_M = 0.201, P value = 0.189), fluvial transport (r_M = 0.031, P value = 0.443), hominins as agents of accumulation (r_M = -0.037, P value = 0.491) and carnivores as agents of accumulation (r_M = 0.025, P value = 0.412).

Evenness is positively and significantly correlated with carnivore ravaging (r_M = 0.625, P value = 0.0042). Evenness is positively and marginally significant correlated with weathering (r_M = 0.396, P value = 0.06) and with the alternative hypothesis of local environment change (ρ_M = 0.516, P value = 0.03).

I ran partial Mantel tests between each variable and evenness controlling for environment, carnivore ravaging and weathering. Under the working hypothesis, the significant effect of the environment, carnivore ravaging or weathering may have masked the effect of other taphonomic variables.

Results indicate that despite controlling for carnivore ravaging no correlation was found between the following taphonomic variables and evenness: fluvial transport (r_M = -0.186, P value = 0.7623), weathering (r_M = 0.235, P value = 0.154), hominins as agents of accumulation (r_M = -0.164, P value = 0.33) and carnivores as agents of accumulation (r_M = 0.209, P value = 0.233).

Controlling for carnivore ravaging resulted in a positive marginally significant correlation between evenness and density mediated processes (r_M = 0.364, P value = 0.057) and positive significant correlation between evenness and local environmental change (ρ_M = 0.493, P value = 0.041).

Despite controlling for weathering no correlation was found between evenness and the following taphonomic variables. These include: density mediated factors (r_M = 0.136, P value = 0.299), fluvial transport (r_M = -0.075, P value = 0.5948), hominins as agents of accumulation (r_M = -0.136, P value = 0.334) and carnivore as agents of accumulation (r_M = 0.127, P value = 0.35).

Controlling for weathering resulted in a positive significant correlation between evenness and carnivore ravaging (r_M = 0.563, P value = 0.005) and between evenness and local environment change (ρ_M = 0.516, P value = 0.0292)

Despite controlling for local environment change no correlation was found between evenness and the following taphonomic variables. These include: Density mediated factors (ρ_M = 0.251, P value = 0.205), weathering (ρ_M = 0.307, P value = 0.136), fluvial transport (ρ_M = -0.138, P value = 0.6674), hominins as agents of accumulation (ρ_M = -0.36, P value = 0.14) and carnivores as agents of accumulation (ρ_M = 0.170, P value = 0.274).

Controlling for local environmental change resulted in a positive marginally significant correlation between evenness and carnivore ravaging (ρ_M = 0.421, P value = 0.078).

These results suggests that evenness is affected primarily by carnivore ravaging and to a lesser extent by local environment change. The effect of weathering is eliminated by controlling for either local environment change or carnivore ravaging, suggesting that this correlation is an artifact of either factor or a combination of both. The effect of density mediated processes which is apparent when controlling for carnivore ravaging may be a result of the correlation between carnivore ravaging and density mediated factors.

To test which factors may control changes in faunal abundances in the Fi cycle only, I correlated evenness with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of ‘pooled strata’ III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found between most of the taphonomic independent variables and evenness. These include: fluvial transport (r_M = -0.377, P value = 0.7844), hominins as agents of accumulation (r_M = -0.41, P value = 0.7961), carnivore as agents of accumulation (r_M = -0.002, P value = 0.591) and carnivore ravaging (r_M = 0.473, P value = 0.192). Moreover, results indicate that there is no correlation between evenness and local environmental change (ρ_M = 0.366, P value =

0.139).

A positive and marginal significant correlation is present between evenness and density mediated processes (r_M = 0.507, P value = 0.074). The latter is probably a reflection of the correlation between carnivore ravaging and density mediated processes. Thus when evenness is correlated with density mediated processes while controlling for carnivore ravaging (r_M = 0.688, P value = 0.043). Moreover, a positive and significant correlation is found when evenness is correlated with carnivore ravaging while controlling for density mediated processes (r_M = 0.671, P value = 0.032).

Evenness is highly effected by carnivore ravaging. This taphonomic variable is correlated both with the difference in evenness between faunal units A and B and within faunal unit B. There is a weak affect of local environmental change on the change in evenness between faunal unit A and B.

Dominance

Results for dominance indices (Simpson D_s and Berger-Parker d) are presented in Figure 53 on page 227 and in Table 47 on page 265. P values for consecutive 'pooled strata' are presented in Table 48 on page 265.

The trend is similar to that observed for evenness (but reversed as expected). There is a significant increase in dominance between 'pooled strata' III 11-13 and III 20, followed by a decrease between 'pooled strata' III 20 and II 23-25 followed by an increase between 'pooled strata' II 23-25 and III 21-22. There is no increase between 'pooled strata' III 21-22 and II 26-27 followed by a decrease in 'pooled stratum' II 36. There in no difference in dominance between 'pooled strata' II 36 and II 37.

One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. No correlation was found between dominance and most of the taphonomic independent variables. These include density mediated processes (r_M = 0.07, P value = 0.355), fluvial transport (r_M = 0.141, P value = 0.342), hominins as agents of accumulations (r_M = 0.066, P value = 0.36) and carnivores as agent of accumulation (r_M = 0.098, P value = 0.256).

There is a positive and significant correlation between dominance and carnivore ravaging (r_M = 0.483, P value = 0.0188). There is also a positive and marginally significant correlation between dominance and the alternative hypothesis of local environment change (ρ_M = 0.395, P value = 0.083) and between dominance and weathering (r_M = 0.338, P value = 0.078).

I ran partial Mantel tests between each variable and dominance controlling for environment, carnivore ravaging and weathering. Under the working hypothesis, the significant effect of the environment, carnivore ravaging or weathering may have masked any effect of the taphonomic variables.

Despite controlling for carnivore ravaging, no correlation was found between the the taphonomic variables and dominance. These include: density mediated factors (r_M = 0.152, P value = 0.249), weathering (r_M = 0.2, P value = 0.2), fluvial transport (r_M = 0.011, P value = 0.515), hominins as agents of accumulation (r_M = -0.01, P value = 0.467) and carnivores as agents of accumulation (r_M = 0.236, P value = 0.187). Moreover, no correlation was found between local environment change and dominance when controlling for carnivore ravaging (ρ_M = 0.357, P value = 0.115).

When controlling for weathering, no correlation was found between any taphonomic variables and species dominance. These include: density mediated processes (r_M = 0.004, P value = 0.460), fluvial transport (r_M = 0.068, P value = 0.468), hominins as agents of accumulation (r_M = -0.006, P value = 0.534), carnivores as agents of accumulation (r_M = 0.189, P value = 0.234). There was a highly significant correlation between dominance and carnivore ravaging (ρ_M = 0.774, P value = 0.003) and a marginally significant correlation between dominance and local environmental change (ρ_M = 0.387, P value = 0.081).

Despite controlling for local environment change, no correlation was found between all taphonomic variables and species dominance. These include: density mediated processes (ρ_M = -0.089, P value = 0. 5815), fluvial transport (ρ_M = 0.062, P value = 0.258), weathering (ρ_M = 0.145, P value = 0.296), hominins as agents of accumulation (ρ_M = -0.3, P value = 0.167), carnivores as agents of accumulation (ρ_M = -0.006, P value = 0.4120) and carnivore ravaging (ρ_M = 0.354, P value = 0.1244).

Results suggests that carnivore ravaging and local environment change affect the species dominance of the assemblages.

To test which factors may control changes in faunal abundances in the Fi cycle only, I correlated dominance with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of 'pooled strata' III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found between dominance and any of the variables tested. These include: fluvial transport (r_M = -0.309, P value = 0.8109), weathering (r_M = -0.05, P value = 0.5149) hominins as agents of accumulation (r_M = -0.428, P value = 0.9066), carnivore as agents of accumulation (r_M = 0.183, P value = 0.282) and carnivore ravaging (r_M = 0.275, P value = 0.183). Moreover, results indicate that there is no correlation between evenness and local environmental change (Mantel ρ statistic = 0.113, P value = 0.139).

A positive marginal significance correlation was found between dominance and density mediated processes (r_M = 0.380, P value = 0.095).

The latter is probably a reflection of the correlation between carnivore ravaging and density mediated processes. No correlation is found either when dominance is correlated with density mediated processes while controlling for carnivore ravaging (r_M = 0.419, P value = 0.121), nor when evenness is correlated with carnivore ravaging while controlling for density mediated processes (r_M = 0.239, P value = 0.194). This would suggest that the effect of density mediated processes is very weak and is related to carnivore ravaging.

There is a weak affect of local environmental change on dominance of the assemblages. Specifically, in more humid environments, assemblages are less dominant. This affect can be observed between faunal units A and B and not within faunal unit B. Moreover, there is a weak affect of carnivore ravaging. ‘pooled strata’ that are high in carnivore ravaging are low in dominance. Within faunal unit B, this is manifested by a correlation with density mediated processes.

Diversity

Results for diversity indices (Shannon - Weaver index (H') and Brillouin (HB)) are presented in Figure 54 on page 228 and in Table 49 on page 266. P values for Shannon - Weaver index (H') for consecutive strata are using t-test are presented in Table 50 on page 266 and using the bootstrap method are presented in Table 51 on page 266.

Results indicate that there is a significant difference between each of the consecutive strata with the exclusion of ‘pooled strata’ III 21-22 and II 26-27 which do not differ significantly from one another. ‘pooled strata’ II 36 and II 37 do not differ from one another at the 0.05 significance level but do differ at the 0.1 significance level. Similar results are obtained for t-test comparison a well as for bootstrap comparisons.

One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient. No correlation was found between any of the following taphonomic independent variables and species diversity: density mediated processes (r_M = -0.11, P value = 0.304), fluvial transport (r_M = 0.234, P value = 0.212), hominins as agents of accumulation (r_M = 0.002, P value = 0.433) and carnivores as agents of accumulation (r_M = -0.106, P value = 0.487).

Diversity is correlated with weathering (r_M = 0.440, P value = 0.038), carnivore ravaging (r_M = 0.397, P value = 0.056) and the alternative hypothesis of local environment change (ρ_M = 0.436, P value = 0.053).

I ran partial Mantel tests between each variable and diversity controlling for environment, carnivore ravaging and weathering. Under the working hypothesis, the significant effect of the environment, carnivore ravaging or weathering may have masked any effect of the taphonomic variables.

Despite controlling for carnivore ravaging no correlation was found between the following taphonomic variables and diversity: density mediated processes (r_M = -0.06, P value = 0.363), fluvial transport (r_M = 0.152, P value = 0.337), hominins as agents of accumulation (r_M = -0.077, P value = 0.383), carnivores as agents of accumulation (r_M = -0.024, P value = 0.556).

When controlling for carnivore ravaging a positive a correlation of marginal statistical significance was found between diversity and weathering (r_M = 0.347, P value = 0.061) and between diversity and local environment change (ρ_M = 0.442, P value = 0.053).

When controlling for weathering no correlation was found between the following taphonomic variables and diversity: density mediated processes (r_M = -0.224, P value = 0.165), fluvial transport (r_M = 0.153, P value = 0.337), hominins as agents of accumulation (r_M = -0.104, P value = 0.397), carnivores as agents of accumulation (r_M = -0.009, P value = 0.575) and carnivore ravaging (r_M = 0.284, P value = 0.113). However, a significant correlation was found between diversity and local environment change (ρ_M = 0.431, P value = 0.049).

When controlling for local environmental change no correlation was found between the following taphonomic variables and diversity: density mediated processes (ρ_M = -0.182, P value = 0.6761), weathering (ρ_M = 0.296, P value = 0.123), hominins as agents of accumulation (ρ_M = -0.213, P value = 0.293 and carnivores as agents of accumulation (ρ_M = -0.221, P value = 0.7211). However, a positive correlation of marginal statistical significance was found between diversity and carnivore ravaging (ρ_M = 0.442, P value = 0.057) as well as between diversity and fluvial transport (ρ_M = 0.448, P value = 0.089)

These results suggests that local environment change and carnivore ravaging affect the diversity. The affect of fluvial transport is related to carnivore ravaging. Since fluvial transport is measured by grain shape, it may reflect carnivore ravaging in addition to fluvial transport as carnivores tend to produce blade shape fragments. The lower diversity values for ‘pooled strata’ III 20 and III 21-22 are also correlated with high proportions of bladed elements. The correlation with weathering is probably related to the correlation local environmental change. The ‘pooled stratum’ with the highest proportion of weathered specimens, ‘pooled stratum’ II 37, is also the driest.

To test which factors may control changes in faunal abundances in the Fi cycle only, I correlated diversity with various taphonomic independent variables (the taphonomic null hypotheses) and the environmental variable (the alternative hypothesis) with the exclusion of ‘pooled strata’ III 11-13 and III 20 (faunal unit A). One-tailed Mantel tests were performed using the Gower asymmetrical similarity coefficient.

No correlation was found between diversity and the taphonomic variables. These include: density mediated factors (r_M = 0.462, P value = 0.121), weathering (r_M = 0.008, P value = 0.289), fluvial transport (ρ_M = -0.122, P value = 0.6818), hominins as agents of accumulation ($r_M = -0.312$, P value = 0.8293), carnivore as agents of accumulation (r_M = -0.006, P value = 0.5647), carnivore ravaging (r_M = 0.262, P value = 0.187). Moreover, no correlation was found between diversity and the alternative hypothesis local environmental change (ρ_M = 0.167, P value = 0.305)

Diversity is affect by local environmental change and by carnivore ravaging. Both these variables affect the distribution of diversity between faunal unit A and B. Within faunal unit B there is no correlation with either taphonomic null hypotheses or the alternative hypothesis.

8.3 Interim summary and discussion : Can persistence or change in the large mammalian community be discerned throughout the ʿUbeidiya sequence?

Two research questions were presented relating to the change in mammalian community structure throughout the temporal sequence. The first; can any change in the large mammal community be observed and second, can this change be related to taphonomic factors, environmental factors or both? If the accumulation of fauna at the site is correlated only with taphonomic factors, subsequent paleoecological reconstructions should be interpreted with caution.

Results from the analyses of the large mammalian fauna of ‘Ubeidiya suggests that both an evolutionary (species composition) and ecological (species abundance) change can be observed throughout the sequence. These changes may be related to first order changes (between the Li and Fi cycles) and second order changes within the Fi cycle as well. The faunal assemblage composition is also affected by carnivore activity which alters the relative abundance of herbivores in different ‘pooled strata’.

Evolutionary change can be identified throughout the ‘Ubeidiya sequence. Change can be observed based on species composition and indices of species richness. Species composition (presence-absence) and indices of species richness cannot be related to any of the taphonomic variables tested: density mediated processes, weathering, fluvial transport, carnivores as primary accumulators, hominins as primary accumulators and carnivore ravaging. This would suggest that this change represents a biological phenomenon rather than a taphonomic artifact. Species composition was correlated with first order environmental change (between the Li and Fi cycle) but not with second order change (within the Fi cycle).

Based on the data analysis presented in this thesis, I suggest dividing the 'Ubeidiya sequence into two faunal units. Faunal unit A comprise 'pooled strata' from the Li cycle III 11-13 and III 20 and Faunal unit B comprise the 'pooled strata' from the Fi cycle: II 23-25, III 21-22, II 26-27, II 36 and II 37. There is a significant increase in species richness between faunal unit A and B. Faunal unit A is characterized by low species richness, while there was an increase in species richness in faunal unit B. A difference in faunal composition between sub faunal unit B1 and B2 cannot be related to environmental change and is apparently a result of a smaller sample size in 'pooled strata' II 36 and II 37.

The increase in species richness between the two faunal units may be attributed to several factors relating to the different structures of the communities. The species - area curve hypothesis (Rosenzweig, 1995) suggests that the larger the area, the high the species richness. If this were the case, we would expect faunal unit B to be from a larger catchment area than faunal unit A. Species accumulating from a larger catchment area would probably have to be transported further and thus differ in their measurements of grain shape and sphericity than those transported from a smaller catchment area. The lack of correlation between species richness and fluvial transport variables suggests that this is not the case.

Most taxa which occur in faunal unit B and are absent from faunal unit A are rare taxa. This suggests that their absence should be attributed in some part to sampling bias. From an environmental aspect, with the exception of *Giraffa* cf. *camelopardis* and *Camelus* sp., most taxa are ubiquitous rather than specific to open habitats and are not good indicators of the environmental shift as observed in the geological sequence.

It stands to reason that the difference between the two faunal units may be related to stratigraphy. Recent paleomagnetic analysis on the Fi cycle (strata II 24 - II 50) has indicated a R-N-R-N-R sequence (Sagi, 2005). The first normal episode is in the lower part of stratum II 24 and the second normal episode is located in stratum II 33-34 (Figure 4 on page 178). The total accumulation between the two normal episodes is 30 m. These have been attributed to the Gilsa (1.575 - 1.567 Ma) to Cobb Mt. (1.215 - 1.190 Ma), a duration of accumulation of ca. 352 Ka (Sagi, 2005)(but consider that Feibel (2004) has suggested a shorted duration of ca. 41 Ka).

There is no knowledge of the absolute dating of earlier strata i.e., strata III 11-13 and III 20. Thus, they may be stratigraphically (and hence biochronologically) more temporally distant than the majority of the 'Ubeidiya strata. However, none of the taxa which appear for the first time in the Fi cycle can be distinctly assigned to a specific chronological horizon or to a biochronological zone younger than those which appear first in the Li cycle. Thus, the faunal assemblage indicative of the Fi cycle and that of the Li cycle can both be correlated with the Italian Farenta faunal unit (the sites of Selvella and Pieterfitta, Italy) which has been dated to ca. 1.6 - 1.2 Ma (Calio & Palombo, 1997, and references therein).

The main factor which affects the change in faunal composition (presence-absence) is local environmental change. This correlation reflects the difference between faunal unit A and B. It is important to remember that this may reflect the affect of stratigraphy or a combination of stratigraphy and the environment. Local environmental change nor stratigraphy cannot account for the difference between the faunal composition of the two sub-faunal units in the Fi cycle: B1 and B2.

Species abundance change through time cannot be related to most of the taphonomic variables tested: density mediated processes, weathering, fluvial transport, carnivores as primary accumulators and hominins as primary accumulators. Results suggests that relative frequency is controlled primarily by the affect of first order environmental changes (between the Li and Fi cycles).

Within each faunal unit, A and B, we can observe changes in the relative frequency of taxa. Community level analysis of abundances suggests that 'pooled strata' III 11-13 is different from other strata. Thus, although it is similar to 'pooled stratum' III 20 in faunal composition, it differs in the relative frequency of the taxa. This may suggest a different climatic or environment period within the larger Li cycle. Unfortunately, no independent climatic data is available to test this hypothesis. Analysis of biodiversity parameters within the Fi cycle (faunal unit B) indicates that there is a weak affect second order environmental changes (the continued desiccation of the sequence) and of carnivore ravaging.

Analysis of change in relative frequency using 95% CI of taxa indicates that most of the majority of taxa present at 'Ubeidiya maintain a statistical persistence throughout the entire sequence studied. Nonetheless, analysis focused on the entire community as a whole, rather than in individual species, reveals difference based on only on presence-absence (between the Li and Fi cycles), but based on abundance as well i.e., ecological evolution sensu Rahel (1990). Thus, although individual taxa may not change significantly in frequency throughout the cycle, a trend can be observe. Arid taxa, *Camelus* sp. and *Gazella* sp. are more abundant in the youngest 'pooled strata' II 36 and II 37.

Detailed analysis of individual taxa suggests that the community pattern observed may be related to the abundance of forest taxa. Most taxa do not exhibit change throughout the sequence with the exception of the four common taxa; *Pseudodama* sp. *Capreolous* sp., *Praemegaceros verticornis* complex and *Equus tabeti*. The large herbivores associated with the evergreen oak forest are the small-medium cervids; these are *Pseudodama* sp. and *Capreolous* sp. Herbivores associated with open habitats (batha and grassland) are *Praemegaceros verticornis* complex and *Equus tabeti*. The pattern of change of both groups mirror each other; there is a large increase in forest herbivores in ‘pooled stratum’ III 20, followed by a sharp decrease in relative proportion. A second peak in forest taxa is present in ‘pooled stratum’ II 26-27 followed by a decrease in ‘pooled strata’ II 36 and II 37.

Forest taxa (*Capreolous* sp. and *Pseudodama* sp.) abundance is weakly controlled by the affect of first order environmental changes (between the Li and Fi cycles). ‘pooled strata’ with high proportions of forest taxa (III 20) reflect periods of greater humidity and thus, greater forest coverage. This is confounded by the taphonomic bias of carnivore ravaging. Strata with high proportions of forest taxa, ‘pooled strata’ III 20 and II 26-27 were subjected to higher intensities of carnivore ravaging. Within the Fi cycle, the change in relative frequency of forest taxa cannot be attributed statistically either to any of the taphonomic null hypotheses nor to the alternative hypothesis.

Both evenness and dominance can be correlated primarily with carnivore ravaging and with local environment change. Both can be correlated with first order environmental change between the Li and Fi cycles as well. In ‘Ubeidiya, high evenness is associated with drier environments and low evenness is associated with wet environments. This can be related to the high proportion of cervids, specifically *Pseudodama* sp., present in stratum III 20. This species, indicative of woodlands, is the most dominant taxon in ‘pooled stratum’ III 20. In a fossil assemblage a homogenous environment of oak forest will be associated with a low evenness assemblage, highly dominated with small-medium cervids. Following an increase in aridity, a more heterogeneous area would develop with more open scrubland patches. The opening of niches allows the habitation of more species and hence an increase in evenness. Thus, the high evenness in ‘pooled stratum’ III 11-13 may suggests that it represented a local event of drier conditions within the Li cycle, although the cycle is considered by Picard & Baida (1966b) and Bar-Yosef & Tchernov (1972) to be dominated by high water lake stand and interpreted as a more humid environment than in the Li cycle.

The high proportion of cervids in ‘pooled stratum’ III 20 may also be related to the high degree of hyaena ravaging as measured by overall carnivore surface modifications and conical fractures. Thus, strata with high levels of carnivore ravaging also have low evenness values. Carnivore ravaging affects evenness by the electivity of hyaena towards specific species. Thus, the preference of *Crocuta crocuta* to accumulate taxa in proportions above their abundance in the environment will increase their percent in the assemblage. If the hyaena will tend to accumulate a taxa which is normally rare it will increase the evenness of the fossil assemblage; if the hyaena accumulates the most dominate taxa, it will decrease the evenness of the fossil assemblage.

Modern studies of the spotted hyaena from the Masai Mara National Reserve, Kenya and Timbavati, Uganda suggest a positive selectivity for Wildebeest regardless of seasonality. On the other hand, Thompson's gazelles were consistently consumed in proportions less than their natural occurrence (Cooper *et al.*, 1999; Bearder, 1977). Seasonal variation was observed and depended on the migration of wildebeest in the dry season.

The effect of carnivore ravaging is also observed within faunal unit B, as attested by the positive correlation between relative frequency of taxa and carnivore ravaging. There is a gradual increase in cervid proportion from 'pooled strata' II 23-25 to II 26-27. These results would suggest that this increase should not be interpreted as an increase in dense forest habitat but rather as an increase in the degree of carnivore ravaging.

This research emphasizes three points: The stratigraphy and paleoecology of 'Ubeidiya, the fidelity of paleoecological reconstructions and the issue of persistence in the ecological record.

Picard & Baida (1966a) have suggested to assign 'pooled strata' III 20 to the Fi cycle. This has been since supported by Bar-Yosef & Tchernov (1972) and by Mallol (2004, 2006). On the converse, diatom analysis (Almogi Labin *et al.*, 1995; Siman-Tov *et al.*, 1993, 1994) have suggested to assign the strata to the Li cycle based on similarities with earlier assemblages. The results presented in this thesis support the stratigraphic interpretation based on diatom analysis. There is a clear distinction in the faunal composition between 'pooled strata' III 20 and II 23-25 and not between 'pooled strata' III 11-13 and III 20 as would be expected from the geological interpretation. Both 'pooled strata' III 11-13 and III 20 may represent more terrestrial periods or localities within the overall higher lake stand. Further in-depth geological and faunal analysis is needed to resolve this issue.

The environmental sequence at 'Ubeidiya can be interpreted at a slow decrease in forest habitat and increase in open habitat. The main decrease can be related to first order environmental change between the Li and Fi cycle (i.e., between 'pooled strata' III 20 and II 23-25). This change can be observed in species composition, abundance as well as various diversity indices: richness, evenness and dominance. Throughout the Fi cycle, there is only a weak affect of the environment and in general a period of ecological and evolutionary stasis. The increase in cervid proportions in 'pooled stratum' II 26-27 is related to carnivore ravaging rather to the environment and as such reflects a taphonomic bias.

The duration of the Fi cycle is roughly estimated at ca. 325 Ka according to recent paleomagnetic studies (but see detailed discussion and possibility for a shorter duration of ca. 41 Ka in Section 2.2 "Dating of the 'Ubeidiya Formation" on page 10). During this period, there is an overall persistence in the large mammalian community structure. The change in species presence-absence is related to sampling bias and the change in evenness and dominance indices can be related to carnivore ravaging. There is a weak affect of local environmental change that can be observed only when the entire community is analyzed as a single unit, but is not visible when individual taxa are analyzed. This extenuates the affect of rare taxa indicative of arid and open environments (such as *Camelus* sp. and *Gazella* sp.) which appear in higher abundances in the younger strata.

The second issue is a methodological issue pertaining to paleoecological reconstruction. The correct interpretation of relative frequency of indicative taxa (i.e., cervids as forest dwellers) may be masked when the assemblage has been subjected to carnivore ravaging which may increase the proportion of cervids in a fossil assemblage in relation to their natural abundance. Thus, analysis of proportion of taxa is not only a reflection of the habitat but also of the intensity of the carnivore ravaging during the time period. This reduces the fidelity of our paleoecological reconstruction. Thus, strata with a high proportion of small-medium cervids may be erroneously interpreted to represent an environment of dense forest where is fact, the environment is actually more open but the assemblage was subjected to a high intensity of carnivore ravaging. Of course, the case presented for ‘Ubeidiya is only a singular case. Each site may have its own biases and warrants it own study. Nonetheless, this study cautions against naive interpretation of relative frequency of taxa as straight forward proxies of environmental change.

Another factor to consider is the importance of the response of fauna to varying intensities and amplitudes of climatic change. This phenomenon not only has implications for ecological and paleoecological theory but also further confounds our limits of paleoecological reconstructions.

Modern ecological studies have suggested that taxa respond individualistically to directional environmental change (Barnosky *et al.*, 2003). These has been shown for a wide range of taxa and in a wide range of habitats. In the young paleontological record, on a scale of $10^3 - 10^5$ years, a wide range of evidence of Quaternary and Holocene studies from a wide range of taxa suggest that distribution change is the most frequent response to climatic change followed by local extinction and then morphological evolution of a species (Bennett, 1997; Dayton, 1989; Overpeck *et al.*, 1991; Shugart, 1998)(but see Pandolfi (1996)). These studies suggest that assemblages of taxa in the past were “disharmonious” i.e. comprised of species different of those than today. This has been interpreted as been formed by climatic changed which operated on species in an individualistic manner, in accordance with the Gleasonian community model rather than the Cleamentsian one (Graham *et al.*, 1996; Jablonski & Sepkoski, 1996).

On the converse, in paleontological assemblages, on the scale of $10^6 - 10^7$ years many studies have described various patterns of recurring fossil assemblages (Miller, 1993). The most well documented and known pattern is “coordinated stasis” which describes an empirical pattern of community level stasis coupled with an abrupt change in community structure of fossil assemblages. The coordinated stasis pattern illuminates an apparent discrepancy in the faunal response between the pre-Quaternary (Phanerzoic) pattern of coordinated stasis and the Neoecological and Quaternary pattern (Holterhoff, 1996; Pandolfi, 1996; Jackson *et al.*, 1996; Miller, 1996). This phenomenon was coined "Pleistocene Paradox" (Boucot, 1990; Sterelny, 2001) or "Macroecological Breakpoint" (Jackson *et al.*, 1996).

The site of ʻUbeidiya is dated within the period of the "Macroecological Breakpoint" or "Pleistocene paradox". It is younger than most sites which exhibit coordinated stasis (ca. $>$100 Ma) yet older than the glacial Pleistocene sites ($>$ 0.8 Ma). The data presented in this thesis which suggest a period of stasis over ca. 300 Ka despite independent evidence for second order environmental change. Such patterns of stasis in Lower and Middle Pleistocene assemblages are rare. Nonetheless, Rodríguez (2004) has indicated stasis in ecological structure in Atapuerca (Spain) and Pandolfi (1996) has described faunal turnover stasis in reef assemblages.

The pattern which emerges from the analysis of the ʻUbeidiya fauna are in accordance with the "recurrent assemblages" model suggested by (Miller, 1993, 1996; Barnosky *et al.*, 2003) for paleontological assemblage and supported for modern ecological communities (Rahel, 1990). I present a modified gradualist climatic faunal-response model based on the intensity of the environmental shift and the response of the faunal community. Four levels can be distinguished:

1. I - Very low amplitude environmental change, this would result in no faunal change
2. II - Low amplitude environmental change - change in abundance
3. III - Moderate amplitude environmental change - faunal turnover with no change in ecological structure
4. IV - High amplitude environmental change - faunal turnover with a change in ecological structure

During the low and medium amplitudes of environmental shift, taxa may be able to tolerate the change or slightly change their behavior. Thus, despite independent evidence for a climatic shift, no change is observed in the fossil record. In higher amplitudes of environmental shift, taxa will first shift their range. This is often observed in the fossil record as a change in abundance. In very high amplitudes of climatic shift, taxa will become extinct. This may be observed in the fossil record as faunal turnover.

This the change within the Fi cycle may be attributed between stages I and II, i.e., during periods of low environmental change, the faunal assemblage does not respond. The change between the Li and Fi cycles in ʻUbeidiya may be attributed to the stage between stages II and III. There is a clear change in abundance but also a change in presence-absence of species. Nonetheless, this did not include speciation and may represent local immigration rather than faunal turnover. The study from Atapuerca (Spain) (Rodríguez, 2004), may be attributed to stage III. Full faunal turnover, stage IV, is represented in the faunal assemblages during the Middle Paleolithic Europe and the alternations between steppe fauna and temperate woodland fauna during glacial and interglacial periods (Lister, 2004).

It is important to stress, that the tolerance to climatic change in also taxa specific and some taxa will respond to very low amplitudes of climatic shifts while others will be tolerant of a wide range of environments. In 'Ubeidiya, most of the taxa did not show any change in abundance between the Li and Fi cycle, where as the small-medium cervids were more susceptible to the first order changes recorded at the site.

Early hominins during the Lower Pleistocene are part of the large mammalian community. Their presence it attested to throughout the 'Ubeidiya sequence by lithics (Bar-Yosef & Goren-Inbar, 1993; Goren, 1981), cut-marks (Gaudzinski, 2004a,b, 2005) and a single incisor (Belmaker *et al.*, 2002). Unfortunately, we cannot quantify the proportion of *Homo ergaster* at 'Ubeidiya and test if early hominins responded to the climatic shift present between the Li and Fi cycles or throughout the Fi cycle by a change in their relative abundance or speciation. Nonetheless, the lack of correlation between the independent variable "hominins as agents of accumulation" and the dependent biodiversity parameters suggests that there is no significant observable shift in pattern in correlation with the climatic shift. Moreover, analysis of the lithic assemblages has suggested a uniform assemblage throughout the sequence (Bar-Yosef & Goren-Inbar, 1993; Goren, 1981).

These results emphasize the high level of tolerance of early hominins to environment variability. Within a range of low to medium environmental change (i.e., stage I or II in the gradualist climatic faunal-response model presented above) there is no evidence for behavioral (technology, subsistence pattern) change.

The different forms of ecological response (abundance, ecological structure, faunal turnover) in relation to climatic change intensity has implication for the fidelity of paleoecological reconstructions. In areas of high latitudes (Europe and North America), the amplitude of climatic change and specifically during glacial and interglacial periods is high. Thus, faunal response often includes speciation and turnover. Faunal analysis of strata from glacial and interglacial period exhibit a different suit of taxa. Even in cases where taphonomic biases are extreme, they cannot obliterate the affects of the environmental change on the faunal community.

On the other hand, in areas of medium latitude as in the Levant, climatic shifts are often of lower and of medium amplitudes. In these scenarios, faunal response may be nil or confined to abundance changes rather than faunal turnover. Thus, sites subjected to a myriad of taphonomic biases, may show a pattern of change, where one did not exist (as in the Fi cycle in ‘Ubeidiya). Thus, the presence of change through time in the faunal record should not be taken as a priori evidence for an environment shift. Only site specific taphonomic analysis can determine whether a shift of abundances of taxa is a reflection of the environment, taphonomy or both.

The analysis presented here suggests that in ‘Ubeidiya, the fidelity of presence-absence data to environmental reconstructions is high, whereas that based on abundance data is weak, albeit present. The following chapter 9 “Paleoecological Reconstruction of ‘Ubeidiya” on page 124 presents a general paleoecological reconstruction of the ‘Ubeidiya environment.

Chapter 9

Paleoecological Reconstruction of ʻUbeidiya

9.1 Multivariate analysis of the mesoherbivore community

Paleoecological reconstruction are based on the premise that the fossil taxa are derived, albeit through a variety of taphonomic biases, from the living community. Thus, while the presence of taxa may be useful for paleoecological reconstruction as they were also present in the living assemblage, the absence of taxa is not taken as evidence of absence. In this respect, it is important to understand the relationship between the interpretation of the ʻUbeidiya assemblages as effected by carnivore ravaging and our subsequent ability to use these strata for paleoecological reconstruction. Thus, the previous chapter has shown that carnivore ravaging has weakly effected the relative frequency of taxa but not their presence-absence. This would suggest that the latter may be used for paleoecological reconstructions with higher fidelity than the former. Moreover, this is further supported by the correlations with climate. Climate does have an effect on the presence absence of taxa and a weak effect on relative abundance of taxa. Thus, while we do need to account for the effects of taphonomy, specifically in the analysis of variation between strata, the assemblages may be used for paleoecological reconstructions.

Using the methodology developed by Vrba (1980) and Greenarce & Vrba (1984). I present two correspondence analyses. The first based on presence-absence data and the second based on abundance data. The taphonomic analysis and identification of patterns of change throughout the ʻUbeidiya sequence have suggested that the fidelity of presence-absence data is higher in this site than abundance data. Nonetheless, the environment does have an affect on the environment, albeit a weak one.

Table 52 on page 267 presents the abundance data for mesoherbivores from ʻUbeidiya strata and various modern and Plio-Pleistocene sites.

Results for correspondence analysis based on presence-absence data indicate that the two first axes explain 62.93% of the variance and that total inertia (total CA variance) = 1.3712. Figure 55 on page 229 indicates that all ‘Ubeidiya strata are more similar to the Plio-Pleistocene and modern Eurasian sites than to African modern and Plio-Pleistocene sites. All the former have negative values of Axis 1 while the latter have positive values. All European sites cluster between the values obtained for cervids and equids.

Results for the correspondence analysis for abundance data suggests that the two first CA axes explain 42.26% of the variance and inertia (total CA variance) = 3.2961. Figure 56 on page 230 presents a two way scattergram for the two main CA axes. Results on two way cluster analysis suggests similar qualitative results to that obtained from the presence-absence data and that the meso-herbivore community of ‘Ubeidiya is more similar to the modern European Mediterranean and Plio-Pleistocene communities than to any of the African communities (recent or Plio-Pleistocene) and have low negative values on CA axis I (< -0.5) while all African communities (modern and Plio-Pleistocene) have positive values. All European communities cluster together with the taxa cervids, suids and caprines of palaearctic origins. All African (modern and Plio-Pleistocene) communities cluster with taxa of African biogeographic origin: the bovid tribes Antilopini, Alcelaphini, Hippotragini, Reduncini and Aepycerotini and the suid genera Metridiochoerus and Phachocoereous. The position of *Equus* and Bovini tribe in the center of the diagram between European and African localities emphasizes their joint distribution on both continents.

Axis II distinguishes between two African habitats: Serengeti Woodland, Manyara and Kruger park (Group A) all with negative values while Nagorgorno, Savanna grassland and Nairobi Park (Group B) have positive values of CA axis II. This is similar to the classification found by Vrba (1980) and which she interpreted as a difference in rainfall. Thus, Group B have a lower rainfall and thus attain a more open vegetation pattern than Group A. Group B can be classified based on the presence of Antilopini, Alcelaphini, Hippotragini and Phachocoereous. The Plio-Pleistocene sites of Konoso 10 L and Konso 10 M may also be included in the classification. Group A can be classified based on the presence of Metridiochoerus, Reduncini and Aepycerotini. The Pliocene sites of Shungura and Konso 4M and 4HA can also be grouped here. The clustering of the European modern and Plio-Pleistocene sites with values of CA axis II similar to African woodland (0.5 to -0.5), as opposed to the open grassland (1.00 - 1.50), strengthens the identification as a closed forest habitats within the Mediterranean region.

Thus, while Africa taxa are present at ‘Ubeidiya, they do not warrant identification of the habitats in ‘Ubeidiya as Africa savanna or as African woodland but rather as a Mediterranean woodland or shrubland.

The Mediterranean maquis and forest in the Levant are dominated by *Quercus calliprinus*. The density, shape and composition of floral elements is largely dependent on the local lithology, fire regime and grazing which create a mosaic habitat with herbaceous communities, semi shrub, taller shrubs and trees. In lower levels of precipitation, a park forest (tree canopies which are far away from each other) is formed which is dominated by *Quercus ithaburensis* (Danin, 1995).

It is important to note that all 'Ubeidiya 'pooled strata' clustered in a similar biome. The gradient which is apparent may be related to the taphonomic biases discussed in the previous chapter and hence will not be addressed here.

9.2 Interim summary and discussion: The paleoecological milieu of 'Ubeidiya

Results of the CA analysis of the mesoherbivore community have suggested that 'Ubeidiya is more similar to European Plio-Pleistocene sites and to modern European Mediterranean sites than to African modern savanna and woodland habitats and African Plio-Pleistocene sites. Nonetheless, 'Ubeidiya exhibit a significant proportion of African taxa. How can their presence be explained in light of the paleoecological reconstruction of the region as a Mediterranean woodland - scrubland?

I suggest incorporating an ecological model of long distance dispersal (LDD) (Nathan, 2001; Nathan *et al.*, 2003) coupled with biotic interactions such as competition and predation to explain the existence of exotic African taxa in Plio-Pleistocene Mediterranean sites in the Levant.

Dispersal is defined as the movements of organisms (in any stage of its life cycle) away from their parents' source location to a new location defined as an end location (Nathan, 2001). Long distance dispersal (LDD) is the rare occasion in which species shift their range by moving over long distances. We define an exotic species as a species from a different biogeographic origin than the location in which it is present, suggesting long distance dispersal.

In order to expand its range, a species must be able to complete all of the following three processes: 1. Travel to a new area 2. Withstand potential unfavorable conditions during its passage. 3. Establish a viable population upon its arrival (post depositional establishment).

If any one of the three processes is not completed, long term colonization may not occur. Thus, an organism may travel successfully to a new area only to find it too harsh for its own existence or the niche may be occupied by a superior competitor and the dispersing species will die out (Nathan, 2001). It might survive in the new region, but if there is not a large enough colonizing population of both sexes, a viable population will not be able to colonize the new region. Only if all three conditions occur, can colonization be observed in the paleontological record.

Diffusion (dispersal over several generations), is a complex yet distinctive pattern. Early waves of dispersal (invasion and range expansion) are slow, intermittent and may require repeated dispersal events. Following adaptation to the new environment and successful colonization, the geographic range increases at an exponential rate (Brown & Lomolino, 1998). Post depositional establishment is dependent on the ecological condition at the site and traits specific to the biotic community i.e., the presence or absence of competitors or predators (Nathan, 2001). Thus, if the dispersing species is adapted to the ecological conditions and is not excluded by biotic interaction such as competition with native taxa or predation, it will successfully establish itself, its abundance will increase, its range will expand or both. If either of these conditions will not occur, it will remain in low abundance and low geographic range until it will become extinct in the end location.

If we analyze the African fauna found in ‘Ubeidiya in relation to their relative frequency i.e., rarity and their adaptive niche compared to other taxa at the site, we may evaluate their colonization success in light of the LDD model. I hypothesize that new comer African taxa consistent with the early waves of dispersal will be rare in the fossil record and will be less adapted to the Mediterranean biome, either in their dietary niche or due to the presence of well adapted and abundant competitors. The subsequent adaptation of the African taxa and their adaptation or colonization to the Mediterranean environment may be measured via their spatial and temporal distribution. Thus, successful colonizers will be geographically wide spread and geologically long lived taxa while unsuccessful colonizers will be confined to a small geographic region and time period.

The exotic African fauna in ‘Ubeidiya can be divided into main three ecological groups: herbivore grazers, aquatics and carnivores (for a detailed ecological summary of the African taxa see Section 6.2 on page 63). The exotic grazer taxa in the Levant are: *Pelorovis oldowaenyensis*, *Kolpochoerus oldoveinesis* and *Oryx* cf. *gazella*. Skeleton remains of these taxa are observed in ‘Ubeidiya (ca. 1.6 - 1.2 Ma) and they are not present in the region later than Gesher Benot Ya‘aqov (0.78 Ma). Possible changes in species between the *Pelorovis* and *Kolpochoerus* may signify regional in situ evolution or an additional dispersal wave ca. 1.0 Ma.

The distribution of exotic African grazers in the Levant suggest a small geographic range and that they did not expand their range past their primary dispersal event. This pattern is consistent with the first stage of dispersal; low level and intermittent. Moreover, since this group is rare in abundance, their distribution in out-of-African sites during the Lower Pleistocene indicates that they were probably poor adaptors to the new habitats. This may have resulted from two phenomenon; the first, the climate and habitat were not suitable for the newly arriving taxa and second, the habitat included competing species or predators which prevented successful establishment.

African savanna grasslands contain widely scattered trees or shrubs. These may grade into tree savanna, shrub savanna, or savanna woodland. This forms mosaic landscapes in which clumps, groves of woody plants are dispersed throughout a grassy matrix. Thus, savanna landscape denotes areas where savanna vegetation is dominant but may be interspersed with riparian or gallery forest, or patches of woodland, swamps, or marshes (Scholes & Archer, 1997). Stable isotopic analyses of pedogenic carbonates from the East Africa sites of Turkana and Olduvai indicates a gradual replacement of closed forest woodland by open savanna grasslands between 3 Ma and 1 Ma, with sharp increases in savanna vegetation near 1.8 Ma, 1.2 Ma and 0.6 Ma (Cerling, 1992). However, at no point in the record is there evidence for soils supporting pure C_4 biomass (positive δ^{13}C values), which would indicate the presence of typical savanna grassland habitats. The stable carbon isotopic values are more characteristic of mixed tree - grass savanna habitats such as savanna woodlands, low tree-shrub savannas, and savanna parklands (Wynn, 2004)

Mediterranean woodlands are dominated by sclerophyllous evergreen shrubs and trees. Different communities are recognized based on gradients of moisture and temperature which results in a range of ground coverage of various heights and density. Thus, woodland refers to regions with dense forest coverage ($> 80\%$) and maquis, garrige and batha refer to decreasing levels of ground coverage as well as decreasing density and height of vegetation (Allen, 2001). Tree density is also dependent on the presence of nutrients. For example, regions with high levels of phosphate in the soil may result in low tree density (0 - 20%) (Rabinovich-Vin, 1986) producing is a “savanna-like” or “savannoid” habitat rather than a true savanna. Savanna grassland around the Mediterranean basin is regarded as anthropogenic (rather than climatic) in origin and is considered to be the result of the clearing of trees and shrubs for grazing pasture (Allen, 2001).

Superficial similarities exist between woodland parks in East Africa and a park forest in the Mediterranean region. Both exhibit sparse trees with grassland in between. Both regions are a mosaic environment which include woodland and grassland. The extend of woodland is usually dependent on precipitation and natural fires. Despite superficially similarities between a savanna woodland and a mediterranean woodland (i.e., low tree density with grassland between), there are differences in the precipitation regime and seasonality between the two biomes as well as differences in geographic distribution of sub-habitats which affect the success of grazers in each biome.

The East African savanna is largely dominated by two wet periods and two dry periods (Delany & Happold, 1979). In the wet season (defined as one whose mean rainfall exceeds the mean for all months), there is a dietary overlap between grazer species that is mitigated by the abundance of the vegetation growth. During the dry season and decrease in graze, competition is reduced primarily by "migration" between wet season range on the open plains and the dry season range in the woodland (Maddock, 1979; Eltringham, 1979). Migration patterns differ among taxa in order to minimize competition (Maddock, 1979).

In the Mediterranean region, there is only one dry season which is long and is correlated with the hot season (Blondel & Aronson, 1999). The Mediterranean landscape in constricted between the sea and the mountain ranges that encircle the basin and dissect it (Blondel & Aronson, 1999). Due to the highly fragmented landscape, reduction of competition during the dry season is more difficult by migration and many taxa, specifically cervids, are mixed feeders which consume the browse of the sclerophyllous evergreen shrubs and trees during the dry seasons.

Poor adaptation of exotic African grazers to the Mediterranean habitat may have been caused by their inability to adapt to the relative absence of graze in the dry season coupled with a high level of competition from the large local mixed feeders such as *Praemegaceros verticornis* complex. Using mesowear analysis on *Praemegaceros obscurus* specimens from Ceyssaguet, France it was suggested that it is a mixed-feeder closer to the browse-dominated range of the browse-graze spectrum (Kaiser & Croitor, 2004).

Thus, while grazing ungulates are indeed present in the region in the Lower Pleistocene, their low abundances and restricted geographic range suggest that they are not indicative of the habitat in their region of origin i.e, savanna, but rather point to a period of many small intermittent dispersal events, each of which may have ended in local extinction due to inadequate adaptation and poor competition with the local taxa. Thus, the presence of savanna and savanna woodland grazing herbivores taxa in the Plio-Pleistocene of the Levant is not inconsistent with the multivariate analysis which suggest association with a Mediterranean woodland and scrubland.

Aquatic African fauna in the Levant include the hippopotamus species *Hippopotamus gorgops* and the endemic *Hippopotamus behemoth*. Hippos are dependent on the existence of perennial waters and thus are less sensitive to the differences in seasonalities and precipitation such as defined the differences between the African savanna and the Mediterranean region. The dispersal of *H. antiquus* to Europe in the Pliocene was mitigated by favorable climatic conditions and local habitats (i.e., the presence of water), and promoted by an unoccupied ecological niche.

The dispersal of hippos in the Plio - Pleistocene into the Levant was dependent on a chain of freshwater lakes. Three paleolakes: Kuntila, Zihor and Hiyyon were present in northeastern Sinai and along the margins of the Arava Valley in the Dead Sea Rift. Ostracod composition suggests freshwater lakes (Rosenfeld *et al.*, 2002). In the Southern Jordan Valley, ostracod samples from the the Mazar Formation (2.0 - 1.8 Ma) suggested a salinity of fresh to brackish waters (Almogi Labin *et al.*, 1995). In the Central Jordan Valley, ostracod analysis has suggested that the salinity of paleolake ‘Ubeidiya was fresh to brackish (Almogi Labin *et al.*, 1995). The hydrogeographical connection between the Nile Valley and the Sea of Galilee, is also evident by recent genetic studies of the cichlid *Astatotilapia flaviijosephi* which suggest that it separated from the other haplochromines during the Middle to Late Pliocene (2.5 - 3.3 Ma) and probably dispersed from Africa to the Levant via the Nile (Werner & Mokady, 2004).

The in situ evolution of the local Pliocene *Hippopotamus* population into *H. behemoth* in the Lower Pleistocene of the Levant suggests a fragmentations of habitat into smaller lake basins (specifically between Europe and the Levant) promoting local speciation. The evolution of a wide spread taxa (*H. amphibius* - *H. antiquus* lineage) into endemic local species such as *H. behemoth* emphasizes the geographic position of the Levant as an evolutionary cul-de-sac. Species which dispersed could not maintained sufficient gene flow with their ancestral populations. The continued presence of *H. amphibius* in the region as late as the Holocene indicate later dispersal events probably through the Nile (Tchernov & Belmaker, 2004).

Since local populations of *H. behemoth* (or its evolutionary precursor) inhabited the paleolakes of the Levant, the new dispersing *H. gorgops* would have encountered a higher level of competition, hindering its ecological success in the region. Based on the morphology and distribution of *Hippopotamus* species in Plio-Pleistocene African lakes, it has been suggested that *H. gorgops* was an aquatic grazer which preferred lacustrine environments (Coryndon, 1976). The ecological relationship with other tetraprotodonts (such as *H. Behemoth* or *H. antiquus*) remains to be studied, but isotope analysis on Pleistocene hippopotamids from Africa (Bocherens *et al.*, 1996) and *H. antiquus* from Venta Micena, Spain (Palmqvist *et al.*, 2003) suggests that they fed predominantly on aquatic vegetation instead of on C_4 grasses as in the case of modern *H. amphibius*. This would suggest increased competition between the two species. The large size difference between the two taxa may have allowed some degree of niche exclusion but it should be remembered that the overall carrying capacity in the tropical latitudes is larger than in northern ones (the latitudinal gradient) and is also a function of area (the species - area curve) (Rosenzweig, 1995). Thus large lake systems (as present in East Africa in the Plio-Pleistocene) may have been able to carry two close species of *Hippopotamus* while the smaller lake systems of the Levant may have not.

Three species of African carnivores were recorded in the Levant during the Lower Pleistocene: *Herpestes* sp., *Mellivora* sp. and *Crocuta crocuta*. Since carnivores as secondary and tertiary consumers are high on the food chain, we expect them to have relatively low abundances compared to primary consumers (Krebs, 2001) but their adaptation to the new habitat can be evaluated by an analysis of their continued habitation and range expansion. Thus, all three carnivore taxa, have expanded their range in the Levant since the Lower Pleistocene. *Herpestes* cf *ichenuemon* and *Mellivora capensis* continue to survive in the region today and have highly variable habitats. *M. capensis* is observed both in the Arava desert, the Galilee, Judea as well as the coastal plain (Mendelssohn & Yom-Tov, 1999). *H. ichenuemon* is common in the Mediterranean region but it is also found in the arid regions of the Negev and the Arava (Mendelssohn & Yom-Tov, 1999). This modern distribution suggest that these species have successfully adapted to the Mediterranean woodland, maquis and shrub-land as well as more arid habitats (Harrison & Bates, 1991). *Crocuta crocuta* originally occupied a wide range of open habitats in Africa including both dry acacia plains, open savanna and rocky country (Kingdon, 1974). It persisted in temperate and glacial Europe as late as the Upper Paleolithic paleolithic period (Rabinovich, 2002) suggesting a tolerance to a wide range of habitats.

To date, no taxa have been found in the Lower Pleistocene sites in the Levant that may be inferred to occupy niches similar to those of the these three carnivores. This suggests that their ecological success may be attributed to two facts. First, they are ecological generalists and have the ability to adapt to a wide range of environments and second, the ecological niches occupied by the three taxa were presumably not occupied by local taxa in the Lower Pleistocene and thus potential competition would have been reduced.

Several species cannot be classified as one of the three groups described above and are discussed individually. Two species which have been assigned as grazers have attained a wider geographic distribution which was circum - Mediterranean rather than confined to the eastern region: *Theropithecus* cf. *oswaldi* and *Equus tabeti*.

Success of the *Theropithecus* cf. *oswaldi* may be partially explained by the absence of competitors in the new region. New evidence based on morphology of the limb bones has suggested that the locomotion of *Theropithecus oswaldi* was assigned to ‘open mixed’ rather than ‘open terrestrial’ as modern geladas. This is similar to modern *Papio anunbis* and required some arboreal substrate (Elton, 2002). Thus, they may have been pre-adapted to utilize the woodlands present in the Mediterranean region. Moreover, this further strengthens the reconstruction of the Mediterranean regions as a more wooded environment as opposed to a more open one.

Analysis of the biogeographic distribution of equids is confounded by difficulties in taxonomic assignment of fossil forms and identification of the relationship to modern ones (Eisenmann, 2004). If we accept a conservative splitting taxonomy, the presence of *E. tabeti* sensu stricto in ‘Ubeidiya represented a dispersal of small geographic range, which did not persist in the region past 1.0 Ma. Although they are recorded with moderate abundance ($> 25\%$) in ‘Ubeidiya, their overall pattern of ecological success in the Mediterranean region is similar to the pattern described above for other herbivore grazers. The dispersal of *E. altidens* into Spain and Europe, would be viewed as a different dispersal event, perhaps via a different route.

On the other hand, if we accept a lumping taxonomy, that all circum - Mediterranean gracile equids belong to a single lineage, a "simplicidens" group (sensu Guerreo-Alba & Palmqvist (1997)) and which includes *E. numadicus*, *E. tabeti* and *E. altidens*, we can infer that upon dispersal from Africa ca. 2 Ma. this taxa did attain ecological success in Eurasia. Current ecomorphological reconstruction of this group suggests similarities to the modern *E. grevyi*. Nonetheless, in both taxonomic scenarios, these forms were replaced by Eurasian forms as early as the onset of the Middle Pleistocene.

Paleoecological reconstruction of this taxon from Aïn Hanech, Algeria, based on ecomorphological analysis of limb bone measurements, suggest that *E. tabeti* was adapted to an open country with a flat and hard ground (Eisenmann, 1984). Analysis of two subspecies of *E. stenonsis* based on the same methodology have indicated that they occupy a different habitat. Thus, the *E. stenonsis* from Saint - Vallier were inferred to occupy a not too open, humid and soft ground habitat while *E. stenonsis* from le Puebla de Valverde occupied open, dry and hard ground (Eisenmann & Guérin, 1984). Moreover, although equids as a family are classified as grazers, based on gross dental morphology, mesowear analysis has suggested that *E. capensis* from South Africa was a mixed feeder rather than a grazer (Kaiser & Franz-Odendaal, 2004). This suggests that further analysis is needed to work out both the taxonomic issues as well as the ecomorphological characteristics of *local* populations to discern preferred habitat.

A single herbivore browser, *Giraffa* cf. *camelopardis*, is found among the Africa exotic species in the Levant. The *Giraffa* cf. *camelopardis* is part of an earlier Pliocene dispersal event as attested by the distribution of giraffids in Eurasian sites (Spain, Greece and Romania) (Martínez Navarro, 2004). The presence of this taxon in the lower Pleistocene is probably a straggler from earlier periods (Tchernov, 1984) and as such has little bearing on the Lower Pleistocene dispersal event.

Evidence from the correspondence analysis has shown that although African taxa are present in the Levant in the Lower Pleistocene, the presence of cervids and *Sus* suggest that the environment was a Mediterranean biome rather than an African one. The presence of African taxa in the region for most taxa is rare in abundance and restricted to a small geographic range. This is in accordance with the early stages of dispersal, which are characterized by intermittent dispersal events. Colonization of most taxa was not successful, probably due to a combination of environmental conditions and competition with native taxa. Taxa which did succeed in surviving in the new region were ecological generalists which could tolerate a wide range of environments and presumably did not have competitors from the local taxa. Thus, the present of African taxa in the Levant and specifically in ‘Ubeidiya does not contradict the reconstruction of the habitat as Mediterranean woodland - scrubland.

Part IV

Discussion and Conclusions

Chapter 10

Discussion

Potts (1998) distinguished between two groups of hypotheses to explain patterns of hominin evolution and its association with environment change; habitat specific hypotheses and the Variablity Selection (VS) hypothesis. Habitat specific hypotheses emphasize adaptations that arise as a response to the selection demands of a specific habitat. The savanna hypothesis suggests that early hominins evolved as a response to the increased aridity and open savanna environments (Vrba, 1988, 1995; Wynn, 2004). According to this hypothesis, the progressive increase in aridity throughout the Pliocene and Early Pleistocene (Cooke, 1978), was the main selective force for the major morphological (bipedalism, large brains) and behavior (tool making, meat eating) characteristics associated with more developed hominins (Klein, 2000). The alternative Variablity Selection (VS) hypothesis promotes the idea that hominin adaptation was more influenced by an increase in different types of environments in long temporal time scales. Thus, hominin adaptation is primarily geared towards novelty and the ability to adapt to a variety of environment (Potts, 1998).

If hominins are adapted to an open savanna environment as suggested by the savanna hypothesis, the success of their dispersal is dependent on the presence of such habitats in the new region, specifically in the early stages of the dispersal in the Lower Pleistocene. Thus, during periods of increased aridification, the spatial extent of the savanna may have increased, resulting in a range increase of many species, including hominins (observed as dispersal in the paleontological record), all adapted to open savanna environment. Dennell (2003) has suggested that one of the basic assumptions we should consider when discussing hominin dispersal events is "The earliest Eurasians preferentially occupied grasslands and open scrub and wood-lands, as in East Africa" as they were adapted to hot and dry conditions and open grasslands. On the other hand, if hominins are pre-adapted to a wider range of habitats as suggested by the Variablity Selection hypothesis, their ability to disperse is not dependent on the presence or absence of their native habitat (savanna woodland). This suggests that other factors, unique to hominins, may have been effective in promoting the dispersal events. Moreover, upon arrival to a new environment, pre-adaptation to variability increases the probability of survival.

Analysis of the paleoecology of the Lower Pleistocene site of ‘Ubeidiya was chosen to illuminate the issues presented here. All seven ‘pooled strata’ analyzed (III 11-13, III 20, II 23-25, III 21-22, II 26-27, II 36 and II 37) show similar taphonomic attributed (albeit with minor differences between them). These include weathering, fluvial transport, density mediated processes, agent of accumulation and carnivore ravaging.

Taphonomic analysis suggested that weathering and fluvial transport were not found to be a main factor in the accumulation of the large mammalian fauna of ‘Ubeidiya. The high abundance of specimens assigned to weathering stage 1 and 2 suggests that most specimens were buried quickly.

The presence of bones of all grain shapes attests to the minimal role played by fluvial transport in the formation of the assemblages. Nonetheless, preponderance of bladed and oblate specimens suggests that spherical elements may have been winnowed out, as suggested by models of fluvial transport in floodplains. The absence of fluvial transport modification has also been noted by Gaudzinski (2004b, 2005) for stratum II 24.

The highly fragmented state of the cranial elements usually not consumed by carnivores points to a high degree of post depositional mechanical fragmentation as a results of trampling and soil compaction. Gaudzinski (2004b, 2005) has pointed out that in stratum I 15-16, most fragments are rectangular and she has attributed them to sediment compression associated with the shoreline lithology.

All the assemblages in ‘Ubeidiya were subjected to a high degree of post depositional ravaging by hyaenas. This is supported by the body part distribution, high proportion of gnaw marks and modified bones, high proportion of carnivores in the assemblages and a high proportion of cylinder type shaft fragments. The preferences of hyaena to small-medium cervids resulted in an increase in their proportion in strata subjected to a high intensity of carnivore ravaging (‘pooled strata’ III 20 and II 26-27). In these strata, the high proportion of cervids, did not only reflect an environment of dense forest habitat, but also the taphonomic attributes of the strata.

Evidence for hominin presence is indicated throughout the sequence. This research indicates that ‘Ubeidiya assemblages do not represent camp sites but rather regions which hominins frequented in order to scavenge carcasses killed by large carnivores. Evidence suggests that hominins subsistence patterns practiced by early hominins at ‘Ubeidiya is more consistent with scavenging from large carnivores, such as large felids, rather than hunting. This is evidence by the low proportion of cut-marks and their distribution among the limb bones and the high proportion of gnaw-marks on mid-shaft fragments. Absence of bone marrow processes may be attributed to a reverse utility and processing off site. This model does not negate the possibility that some individual specimens were acquired by active scavenging or even by hunting, but it does suggest that this was not the common modus operandi practiced by the early hominins in ‘Ubeidiya.

Of the six taphonomic independent variables tested, I rejected the five taphonomic null hypotheses (density mediated processes, weathering, fluvial transport, carnivores as primary accumulator and hominins as primary accumulators) for all dependent biodiversity variables tested. I could not reject the null hypothesis of carnivore ravaging for relative frequency data but could reject this variable for presence-absence data. This suggested that the intensity of carnivore ravaging was shown to have an affect of the distribution of abundance of large terrestrial mammals among the strata. Moreover, local environmental change was shown to have a strong affect on presence-absence data and a weak affect on abundance data. Thus, the fidelity of paleoecological reconstructions of ‘Ubeidiya strata using presence-absence data is high but low using abundance data.

It has been proposed that the presence of East African taxa can be interpreted as indicating the presence of savanna and savanna woodland habitats in northern latitudes. Several studies have suggested that the paleoecological reconstruction of ‘Ubeidiya in particular was ”open and semi - arid” (Dennell, 2003). This is based on the presence of Africa species and specifically *Oryx* sp., *Kolpochoerus olduvaiensis*, *Hippopotamus gorgops*, *Pelorovis oldowayensis* and *Crocuta crocuta*. Recently, it has been suggested that that the *Megantereon* found at the site should be identified as the African species *M. whitei*, further increasing the proportion of African species at the site (Martínez Navarro, 2004). Similarly, reconstruction of the paleoenvironment of the site of Dmanisi, Georgia was interpreted by Palmqvist (2002) as “African savanna with tall grasses, shrubs and low bush/tree cover”. Ecomorphological analysis of Venta Micena, Spain has indicated that “Orce at Venta Micena was very similar to that represented in modern African savannas with tall grass and low bush/tree cover, suggesting that the countryside in the Guadix-Baza basin was relatively un-forested during early Pleistocene times, as happens today” (Palmqvist *et al.*, 2003). These reconstructions are inconsistent with the conclusions presented here.

Results for paleoecological reconstruction based on presence -absence data and abundance data resulted in similar results. These suggested that the large mammalian fauna from all strata from the Lower Pleistocene site of ‘Ubeidiya are indicative of the Mediterranean biome and are similar in faunal distribution to other Plio-Pleistocene sites in Eurasia. Despite the presence of some African taxa and specifically savanna type herbivores, a paleoecological reconstruction of an African type savanna is not warranted. This would suggest that the early hominin population that dispersed to the Levant, had to adapt to a new environment.

Support for the reconstruction presented in this paper is presented by Tchernov (1980). Analysis of the avifauna of ‘Ubeidiya indicated that the Palaearctic groups predominate the assemblages and only a few are tropical (Oriental or Ethiopic). The development of the Mediterranean endemic elements from Asian species took place shortly after the Messinian crisis (ca. 5.0 Ma) but increased during the Pliocene and Early Pleistocene around the humid Mediterranean basin and resulted in an high proportion of endemic species in ‘Ubeidiya (Tchernov, 1980).

Further support can be obtained from pollen spectra obtained from Plio-Pleistocene sites in the Mediterranean region. Pollen analysis of the site of Dmanisi suggested a Mediterranean type climate analogous to modern Mediterranean woodlands (Gabunia *et al.*, 2000). Macrofloral remains of fossilized leaves (Lorch, 1966) and pollen spectra (Bar-Yosef & Tchernov, 1972) retrieved from ‘Ubeidiya suggested a Mediterranean park-forest with rocky and steppe terrain. The botanical remains of Gesher Benot Ya‘aqov suggest the presence of Mediterranean wood and plant species and that the climate pattern in the Hula valley at the time of deposition resembled the seasonal Mediterranean pattern seen today (Goren Inbar *et al.*, 2004).

While superficial similarities exist between the vegetation forms in the savanna woodland and the Mediterranean woodland, they are not the same environment. Both have mosaic open grassland and shrubland with trees of varying densities but the main differences lay in the the seasonality and precipitation regime (Allen, 2001; Blondel & Aronson, 1999).

While Mediterranean vegetation is dominated by evergreen sclerophyllous shrubland of oaks (*Quercus* spp.), olives (*Olea*) and *Pistacia*, different communities occur depending on environmental gradients such as moisture, nutrients and temperatures (Allen, 2001). The matorral can be classified into high matorral $>$ 2m and includes evergreen low trees, very dense and impenetrable, middle matorral (garrigue) $0.6 - 0.2$m, lower height of scrub, with calcareous substrata and low matorral (batha) < 0.2m.

Differences in the large mammalian community among different sites and specifically the meso-herbivore community may help distinguish between the sub-habitats within the Mediterranean biome. Thus, the small faunal assemblage in Bizat Ruhama (1.0 Ma) has revealed only an unidentified bovid, equids and hippo remains (Ronen *et al.*, 1998). In Evron (1.0), the cervid sample comprises only 4 specimens of 36 (11%) identified specimens, and bovids are represented by 11 specimens (30%) (Tchernov *et al.*, 1994), whereas in ‘Ubeidiya (ca. 1.6 - 1.2 Ma) cervids are 30 - 60% of the assemblage. The absence or low proportion of cervids in Bizat Ruhama and Evron may be the result of the small sample size, taphonomic bias or may indicate a regional (or chronological) shift from more humid regions, where the forest cover would have been higher, supporting a high cervid population, to drier regions with a more open forest and batha habitat represented by a high equid frequency.

Evidence from ‘Ubeidiya suggests that early hominins, dispersing from East African savanna type habitats, would have adapted to a a wide range of novel environments, both in space and in time. Their ability to successfully utilize this novel environments suggests that they had a pre-adaptation to environmental variability as hypothesized by the Variablity Selection (VS) hypothesis (Potts, 1998).

All seven ‘pooled strata’ of ‘Ubeidiya can be related to the Mediterranean biome. Within the temporal span of the ‘Ubeidiya sequence, there is evidence for both evolutionary (faunal turnover) and ecological (relative frequency) change, which can be attributed to both first and second order climatic changes. Throughout the sequence, the large mammal community reflects the slow process of desiccation indicated by a decrease in forest dwelling taxa and an increase in open habitat taxa. This would suggest a shift from a more homogenous dense forest landscape to a more open mosaic one.

Throughout the ‘Ubeidiya sequence there is evidence for two faunal units, which differ in species composition, richness and abundance. The latter may be related to two factors; local environment change (both first order change and second order change) and carnivore ravaging.

Faunal unit A - The large mammal assemblage from faunal unit A is one with low diversity of large mammals, with high dominance of cervid taxa. There are two strata that have been assigned to this faunal unit based on presence-absence data: ‘pooled strata’ III 11-13 and III 20. However, within this faunal unit, when relative frequency of large mammals is analyzed, they are not similar in their community structure. Thus, ‘pooled stratum’ III 11-13 has high evenness and diversity and exhibits a low proportion of forest dwelling cervids. ‘Pooled stratum’ III 20 has low evenness and diversity and a very high proportion of forest dwelling cervids. This is indicative of a high proportion of woodlands and, as shown in this thesis, also an increased activity of carnivore selectivity. Thus, partial dominance of the high cervid taxa in ‘pooled strata’ III 20, compared to ‘pooled stratum’ III 11-13, may be attributed to carnivore ravaging as well as a reflection of habitat preference.

Low evenness in the Mediterranean region is indicative of a closed environment whereas a high evenness is indicative of a more mosaic region which encompasses a wider range of sub-habitats.

The high evenness of ‘pooled stratum’ III 11-13 may be interpreted as a drier interlude within the Li cycle, as supported by the low proportions of cervids. These results are supported by other methods of paleoecological reconstructions. Montuire (1994) and Montuire & Girard (1998) applied the cenogram graph to the large mammals and micromammal faunal list published by Tchernov (1986a). Their results indicate that stratum III 12 (included in ‘pooled stratum’ III 11-13) was an open environment. Additionally, diatom analysis has suggested that this stratum was affected by high turbidity. If this is so, the high evenness of III 12 may be a results of the taphonomic origin of the strata; a mixed assemblage, ‘pooled stratum’ III 11-13 also is an outlier in the fluvial transport, with the highest sphericity value of all strata ($\overline{\psi} = 0.666$).

Faunal unit B - The large mammals of this faunal units are characterized by a lower proportion of forest dwelling cervids than in ‘pooled stratum’ III 20. Throughout the faunal unit, there is a gradual increase in the proportion of forest dwelling cervids. Since the geomorphological data had suggested some degree of desiccation between ‘pooled strata’ II 23-25 and II 26-27, the apparent increase in forest dwelling cervids and a decrease in equid proportion appear to represent an opposite one to that expected from ecomorphological reconstruction of the taxa. Thus, it would be expected that the more humid phases would correlate with higher proportions of cervids and drier phases with higher proportions of equids. Correlation of the relative frequency suggested that the distribution may be related to the taphonomic null hypothesis; carnivore ravaging. Thus, although it is possible that a wetter phase was present in ‘pooled stratum’ II 26-27 (a significant decrease in equids and peak in cervids), the results show that I cannot reject the taphonomic null hypotheses of carnivore ravaging and carnivore as primary accumulators. The cenogram analysis by Montuire (1994) and Montuire & Girard (1998) has suggested that stratum II 23-24 (included in ‘pooled stratum’ II 23-25) is a closed environment compared to stratum III 12 (included in ‘pooled stratum’ III 11-13).

The youngest ‘pooled strata’ of this faunal unit, II 36 and II 37 may be distinguished as a sub faunal unit (B2) characterized by a shift in the relative frequency of the species despite the stasis in faunal composition (presence-absence). The sharp decline in relative proportion of forest dwelling cervids and increase in relative frequency of equids and gazelles is consistent with the continued desiccation of the unit compared to B1. The phase may be related to the weak correlation with local environmental change and relative frequency of taxa and of forest habitat taxa in particular. Cenogram analysis has indicated that stratum II 36 was indicative of an open environment (Montuire, 1994; Montuire & Girard, 1998).

Of the 33 large mammalian species present at ‘Ubeidiya, not all show a significant change through time despite evidence for both first order and second order environmental change, whereas other taxa, such as small and medium cervids and equids, responds to first order environmental change.

Of specific interest, is the apparent lack of response of hominins to this change. The relative abundance of hominins cannot be directly measured but evidence for behavior patterns i.e., subsistence patterns. Thus, throughout the sequence, there is no apparent change in subsistence pattern in relation to both first and second order environmental change. This data is further augmented by the lack of change in the lithic assemblage throughout the sequence (Bar-Yosef & Goren-Inbar, 1993; Goren, 1981). These results indicate that early at ‘Ubeidiya hominins posses a higher threshold for environmental change and can endure low and moderate levels of environmental variability without changing their behavior. This adaptation is in accordance with the Variablity Selection hypothesis (Potts, 1998, 2002).

The dispersal pattern of large mammals in the Levant can shed light on hypotheses that have been suggested to explain the impetus for hominin dispersal. The first group of hypotheses are intrinsic hypotheses which perceive the dispersal event as uniquely human and resulted from technological innovation or an increase in population size (Larick & Ciochon, 1996). The hunting hypothesis suggests that hominins evolved to become active hunters and hence needed larger territories (Walker & Shipman, 1996). Thus, hominins became better competitors for meat, allowing them to occupy new niches. The second group are extrinsic hypotheses and suggest that the dispersal event was part of a large ecological phenomenon driven by climatic change, and thus associated with the dispersal of several species of large mammals. It has been suggested that the Aullan dispersal event (ca. 1.8 Ma) which was associated with the new appearance of African faunas in Eurasia, may have also included the African genus *Homo* (Martínez-Navarro & Palmqvist, 1995).

Following the paradigm described above, we can see that although African taxa were present in the dispersal event together with other hominins, the ecological success of hominin, compared to that of many of the taxa that dispersed with them, raises the question of their unique biological and behavioral traits and their pre-adaptation compared to other dispersing taxa. As with all other species, the dispersal of early hominins required three distinct phases; first, the impetus for dispersal and ability to disperse, second, physical access and crossing of the barrier and third, the post depositional establishment.

Since hominins are large mammals, we can assume that the pattern of dispersal in similar to that followed by large mammals (Brown & Lomolino, 1998). The early dispersal events were presumed to have been sporadic and intermittent (Dennell, 2004). Following adaptation to the new region, dispersal continued at a faster rate. The adaptational requirements for successful post-dispersal establishment are habitat dependent. It has been suggested that the relative high proportion of African fauna at the site of ‘Ubeidiya indicated that the hominin presence at the site should not be viewed as a dispersal event but rather as a range expansion into part of the greater African milieu (Klein, 2000). If this indeed is the case, hominins would have not required any biological or behavioral adaptation to their new habitat in the Levant. This study has indicated that this is not the case and that the Levant was a Mediterranean habitat during the Plio-Pleistocene.

All exotic African taxa which are recorded in the Levant would have had to cross the Saharo - Arabian barrier. In northern Sahara and Arabia, the Pliocene grasslands which developed around 3 mya were still present and formed the majority of the vegetation in Southwest and South Asia ca. 2 Ma during onset of hominin dispersal events. The Plio-Pleistocene boundary was characterized by a relatively moist climate supporting the growth of conifers and the formation of carbonate sediments (Dennell, 2004). Moreover, for much of the Plio-Pleistocene, the main part of the Nile draining northern Ethiopia and eastern Sudan flowed eastward to the Red Sea, and was thus less of a barrier to faunal migrations between Africa and Asia (Dennell, 2004).

A case in point is the site of Al Nafud in Arabia (Thomas *et al.*, 1998). This site exhibits many of the African taxa present in the Levant (*Crocuta crocuta*; *Pelorovis* cf. *oldowayensis*; *Oryx* sp.) as well additional African alcelephines, bovids, and camelids, whereas the palaearctic species such as cervid are notably absent. Carbonate analyses of herbivore teeth indicate a diet of C_4 plants typical of open grassland (Thomas *et al.*, 1998).

Thus, Al Nafud is representative of the barrier or filter region between East Africa (from which the dispersal originated) whereas the Levant sensu stricto is the end location. The difference in the faunal composition between the Al Nafud and the contemporaneous Levantine site of ‘Ubeidiya i.e., presence of cervids and *Sus* in ‘Ubeidiya and the higher proportion of bovids in Al Nafud reiterate the paleoecological reconstruction of the Levant as Mediterranean rather than savanna grassland.

Campbell (1972) has suggested that hominin dispersal followed two broad categories which were followed by biological and cultural adaptation: tropical to temperate dispersal and a much later temperate to arctic dispersal. These two phases represent an increase in ability to cope and exploit harsh environments (Dennell, 2004; Turner, 1984). While the conditions in the Mediterranean are not as harsh as more northern latitudes, they do have a wider range of annual temperatures than tropical African habitats and thus may represent adaptational “stepping stones” which facilitated further adaptation to the more temperate conditions at a later period. Such adaptation may include the controlled use of fire at Gesher Benot Ya‘aqov (Goren Inbar *et al.*, 2004) and changes in subsistence patterns.

Taphonomic data from ‘Ubeidiya indicates that the assemblages are kill sites and near-kill site which were scavenged by hominins for further processing. The bone refuses were ravaged and further accumulated by carnivores, notable hyaenas. Similarly, no cut-marks were found in Evron, but this may be attributed to the small sample size (Tchernov *et al.*, 1994). This may be suggestive also of a subsistence pattern oriented towards the savaging end of the spectrum.

Plio-Pleistocene African sites indicate a variability in human subsistence patterns that is strongly dependent on local environment conditions. Research in Plio-Pleistocene sites of comparable age in Africa has provided evidence for both secondary access (passive scavenging) (Blumenschine, 1986, 1987; Blumenschine & Cavallo, 1992; Shipman, 1983, 1986) as well as primary access (hunting or active scavenging) to carcasses (Domínguez-Rodrigo, 1997, 2002) and have suggested that early hominins have practiced some formed of mixed hunting - scavenging strategy (Blumenschine, 1986). Similarly, some sites indicate a high degree of bone marrow processing (Domínguez-Rodrigo, 2002) while others do not (Bunn, 1994).

Although the causes which determine the choice of one subsistence pattern over another are not yet clear, we can assume that different parameters were at play in the Mediterranean woodland compared to the African savanna. The differences in carnivore guilds between East and South Africa has been postulated as a possible difference for different scavenging opportunities between the two regions (Lewis, 1997). Thus, ecological differences between East Africa and the Mediterranean may account for the variability in subsistence patterns between the two regions.

The quality of scavenging opportunity provided by a carcasses in measured by the amount of edible remaining on the carcass after consumption by the primary predator and length of time a carcass persists as edible food (Blumenschine, 1987). Two main ecological factors can be considers: first, the carnivore guild and the quantity of carcasses produced and second, the persistence of carcasses.

It has been shown that quantity of carcasses after consumption by large felids differs in open habitats compared to closed riparian habitats in East Africa (Blumenschine, 1987). This is primarily due to the absence of hyaenas in the closed habitats compared to more open habitats. Carcass persistence is also decreased in the presence of the short-faced hyaena *Pachycrocuta brevirostris* compared to the spotted hyaena *Crocuta crocuta* (Lewis, 1997). In ‘Ubeidiya the hyaena present is *Crocuta crocuta*. Thus, together with the presence of the felids *Megantereon* sp. and *Panthera gombaszoegensis* the carnivore guild found at the site suggests the presence of the opportunity for carcasses of large taxa.

Thus, in closed environments, such as those present in Mediterranean woodlands, carcasses may remain untouched by hyaenas until they putrefy (Blumenschine, 1987). The rate of putrefaction is dependent on temperature and humidity as well the community of decomposing invertebrates (Richardson & Lee Goff, 2001; Watson & Carlton, 2005). For example, it has been observed that rabbit carcasses in Pubjab, India remained fresh for up to 22 hours in the summer compared to up to 117 hours in the winter. The average recorded temperature in the summer was 31.3 °C compared to an average of 16°C during the winter (Bharti & Singh, 2003). Since the distribution of both temperatures and humidity are lower in the Mediterranean region than in the sub-tropical region, specifically in the winter time, rates of decomposition may be lower, suggesting that carcasses may have persisted slightly longer than in warmer regions thereby providing more opportunities for scavenging. Observation of a carcass decomposition in the Jordan Valley, Israel has suggested a persisted for 4 days in 35°C (Lotan, 2000) compared to two and one half days persistence of medium size carcasses in margins of riparian woodlands of East Africa (Blumenschine, 1987).

Another intriguing issue to consider is the issue of the taxa consumed. The ungulates in Africa are bovids, whereas in ‘Ubeidiya, the common ungulates are cervids. If hominin subsistence patterns differs according to the stress level of their prey and its nutritional level in the different seasons (Speth, 1987, 1991), it is important to assess the fat depletion response of different taxa to the specific level of resource stress present in different latitudes. For example, the average fat content of African herbivores is lower than that of North American ungulates (Speth & Spielmann, 1983) and in Europe (Włodzimeriez *et al.*, 2002). It stands to reason the the specific levels and pattern of body composition and fat depletion for Mediterranean cervids (Weber & Thompson, 1998) would differ from those of semi-arid savanna bovids, providing for a new array of hominin subsistence patterns.

Moreover, it has been shown that there are differences in the fatty acid composition, in the distribution between muscle, fat, marrow and brain and in quantity, between antelopes, deer and elk (Cordain *et al.*, 2002). Thus, optimal subsistence patterns may differ slightly depending on micro-nuterientinal availability (Cordain *et al.*, 2000, 2001).

Another issue to consider is the consumption patterns of very large mammals during the Lower Pleistocene. Most of the taphonomic modeling includes mammals of small to large size and specifically did not include hippos and elephants (see Domínguez-Rodrigo, 2002, and references therein). This problem is further confounded because as more studies are included, these taxa are continued to be excluded in order to facilitate comparisons. Nonetheless, we can assume that these taxa provide a large quantity of protein, bone marrow and fat. The possibility to remove muscle from a carcasses without leaving cut-marks required that detailed actualistic for both primary and secondary access models.

Thus, the Plio-Pleistocene appears to be a period of high variability in subsistence patterns. While some sites indicate primary access of hominins to fleshed carcasses, other sites are more indicate of active or passive scavenging. Dispersal to new regions i.e., Mediterranean may have facilitated the preference of one of the several modes of subsistence patterns utilized by early hominins in East Africa in accordance with the availability of carcasses and their nutritional value.

Hominin dispersal from an East African Savanna type biome would have had to adapt to a novel environment of closed Mediterranean type woodland. Thus, while the ability to cross the Saharo-Arabian barrier was facilitated by Upper Pliocene and Lower Pleistocene climatic change (Dennell, 2004), the post dispersal establishment requires other processes that may be unique to humans. If hominins were selected for variable environments as predicted by the Variability Selection hypothesis (Potts, 1998), they would have possessed the necessary pre-adaptation to facilitate the successful colonization in the Mediterranean biome which they would have encountered in their dispersal.

Chapter 11

Conclusions

The pattern present at ‘Ubeidiya indicates a clear evolutionary and ecological change between the Li and Fi cycle, suggesting that ‘Ubeidiya should be divided into two faunal units A and B, which can be the basis of further analysis of the large mammalian fauna in ‘Ubeidiya be based on the two faunal units. ‘Ubeidiya faunal unit A includes the LI cycle ‘pooled strata’ III 12 and III 20, while faunal unit B include ‘pooled strata’ II 23-25, III 21-22, II 26-27, II 36, II 37.

Taphonomic analysis suggests that all ‘Ubeidiya assemblages are palimpsests comprised of faunal elements from kill or near kill sites, from which hominins scavenged carcass remains from large carnivore kills and transported high utility limb bones elsewhere. These sites were augmented by natural back ground fauna, probably the results of carnivore kills. The assemblage was subjected to post depositional attritional processes and specifically hyaena ravaging and accumulation.

‘Ubeidiya was situated within the Mediterranean biome and similar to other Eurasian Plio-Pleistocene sites. The change in the large mammal fauna throughout the ‘Ubeidiya sequence reflects the general trend in desiccation. This is indicated by a decrease in closed woodland and an increase in open grassland habitats. Increased carnivore ravaging in ‘pooled stratum’ III 20 and II 26-27 increased the relative frequency of forest dwelling small and medium cervids in the fossil assemblage creating the the appearance of a more humid climate than was actually present. Nonetheless, the taphonomic overprint does not negate the effect of the local environmental change on the large mammalian community.

Hominin dispersal into the Levant in the Lower Pleistocene included adaptation to a novel environment. The pattern found in the site of ‘Ubeidiya lends support to the Variability Selection (VS) hypothesis Potts (1998) rather than the habitat specific hypotheses.

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Community Structure through Time: ‘Ubeidiya, a Lower Pleistocene Site as a Case Study

Thesis submitted for the degree of
“Doctor of Philosophy”
by
Miriam Belmaker

Submitted to the Senate of the Hebrew University
March 2006

APPENDICES

Part V

Appendices

Appendix A

Figures

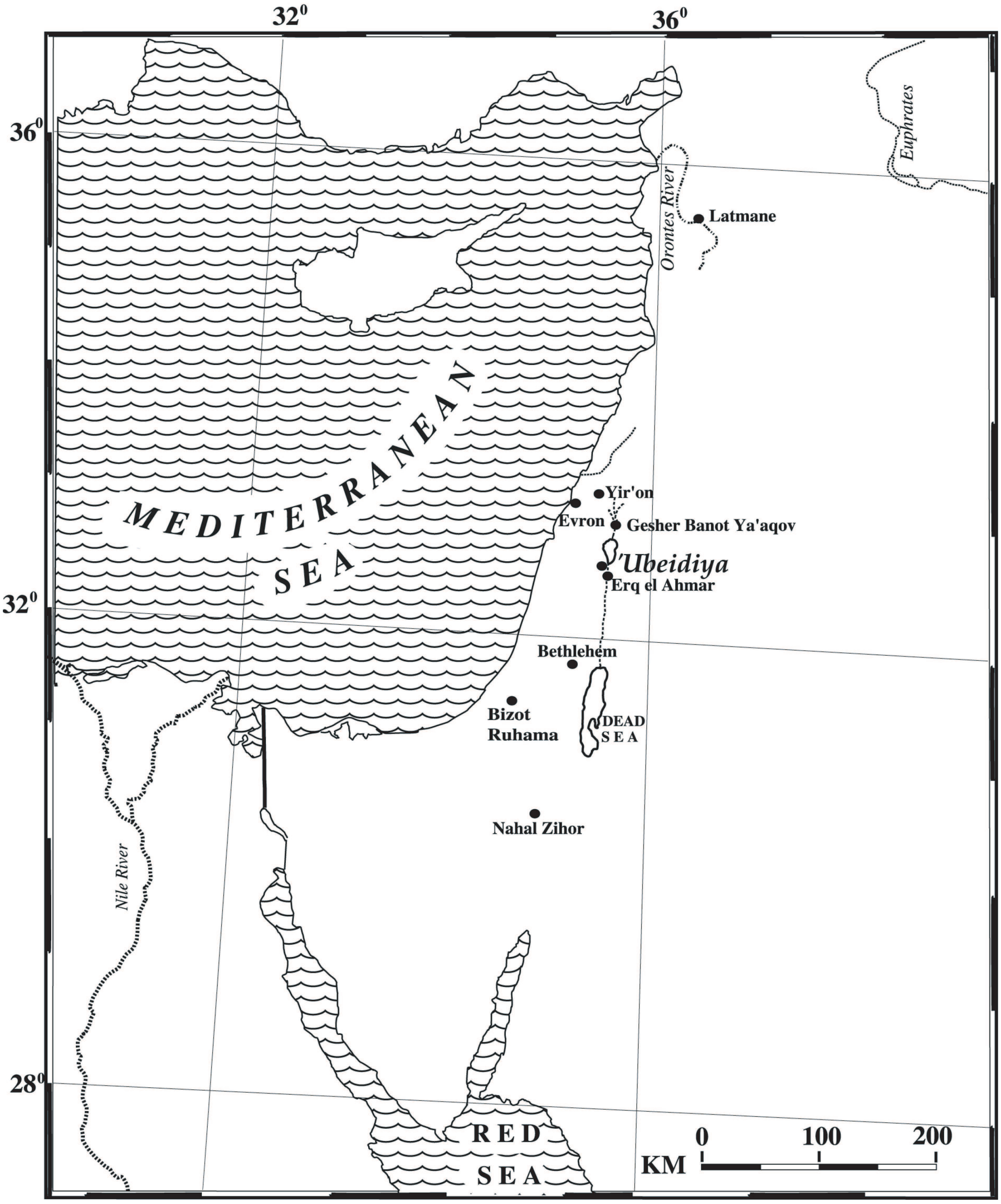


Figure 1: The Levant and the location of Plio-Pleistocene sites mentioned in the text

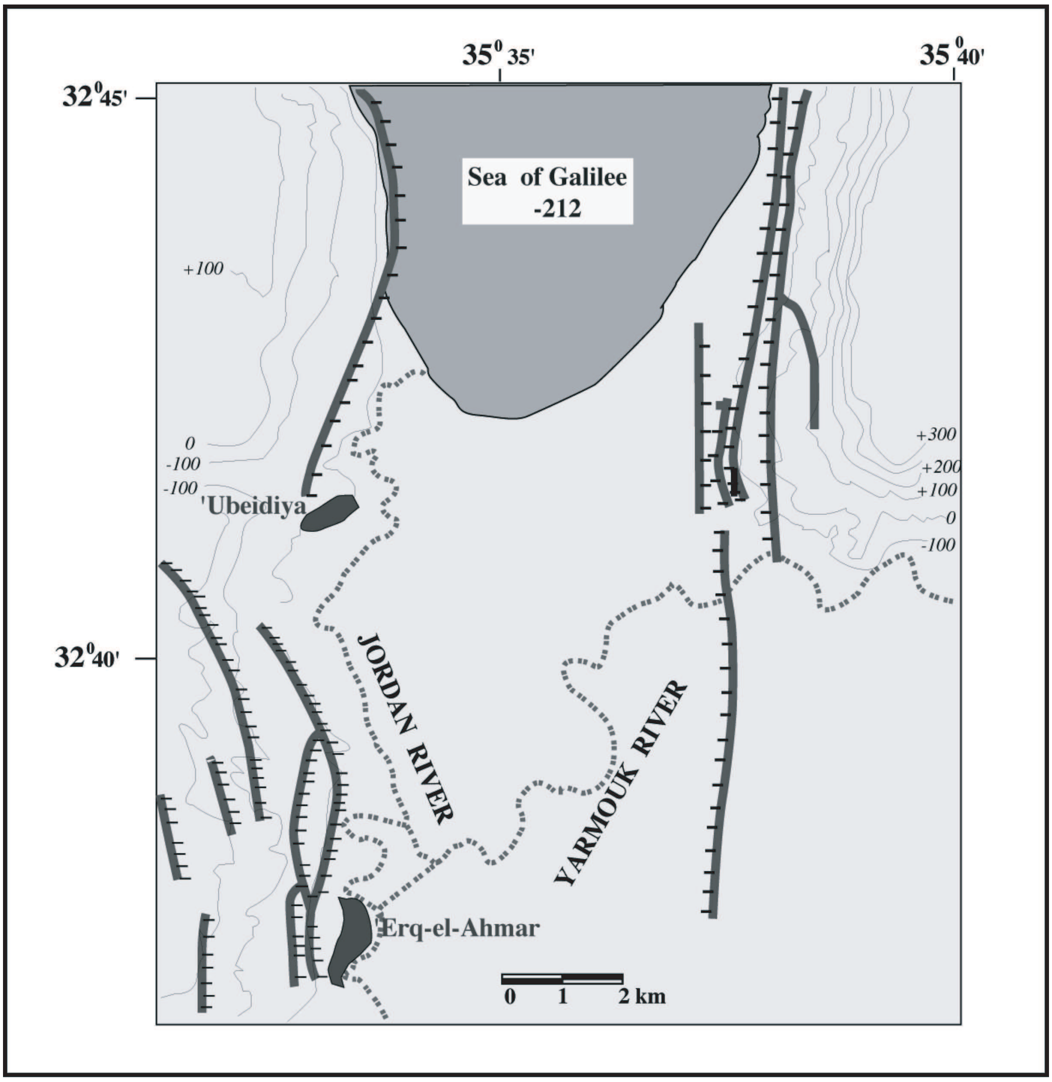


Figure 2: The location of the ‘Ubeidiya Formation main outcrop in the central Jordan Valley

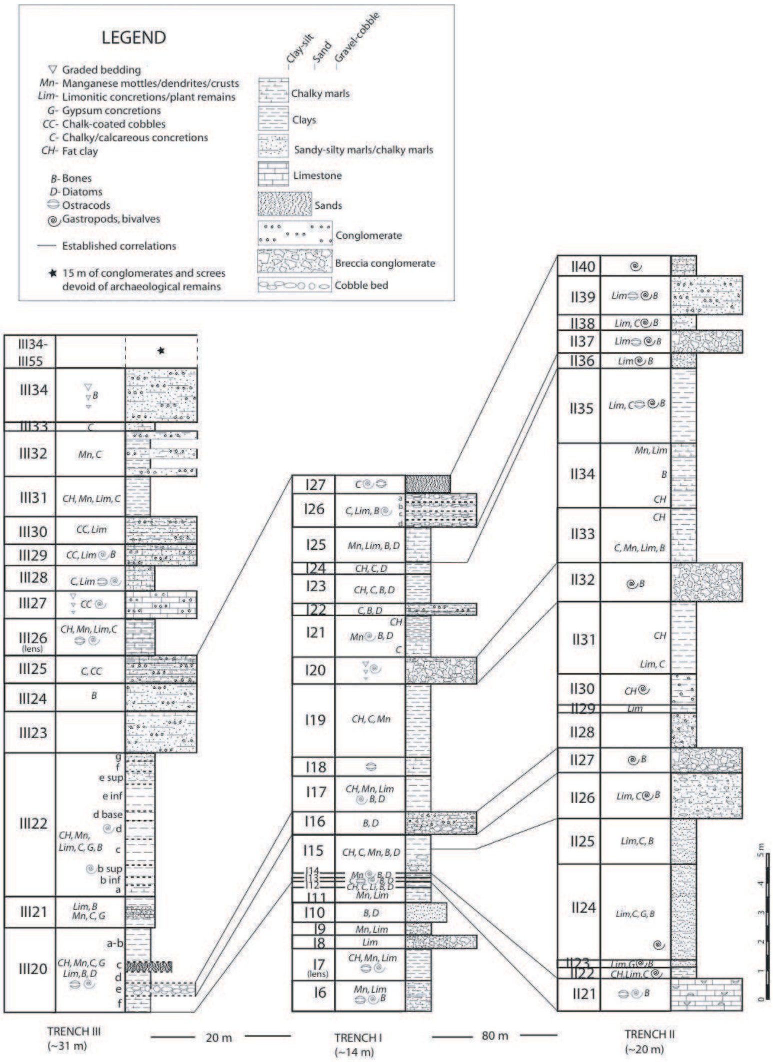


Figure 3: Stratigraphy and lithology of the Fi cycle (Mallol, 2006)

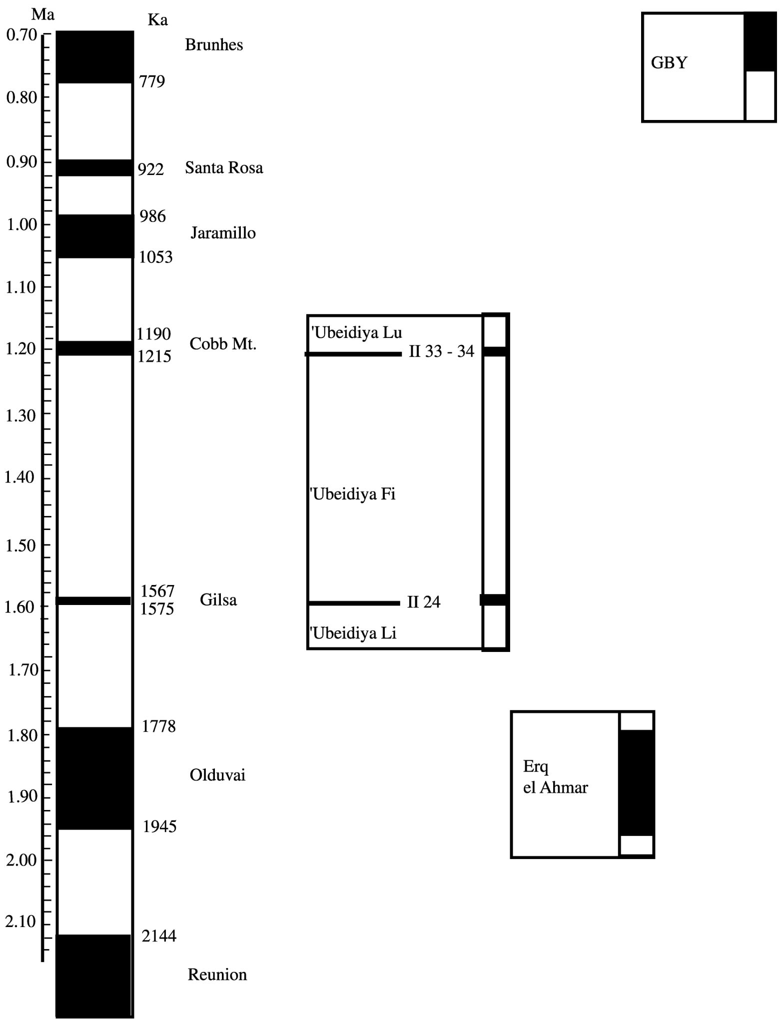


Figure 4: Schematic representation of the position of ‘Ubeidiya within the GPTS

Data for ‘Ubeidiya from Sagi (2005), data form Erq el Ahmar from Ron & Levi (2001) and data for Gesher Benot Ya‘aqov (GBY) from Goren Inbar *et al.* (2000).

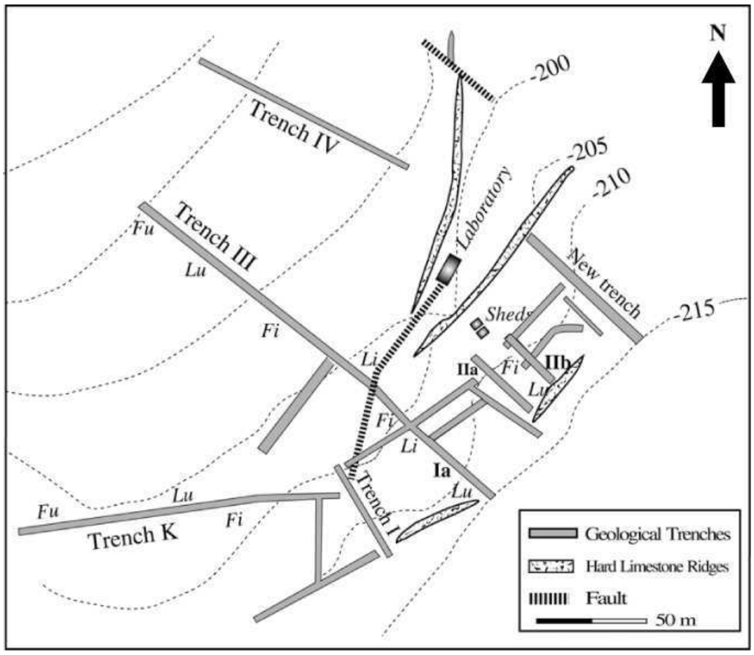
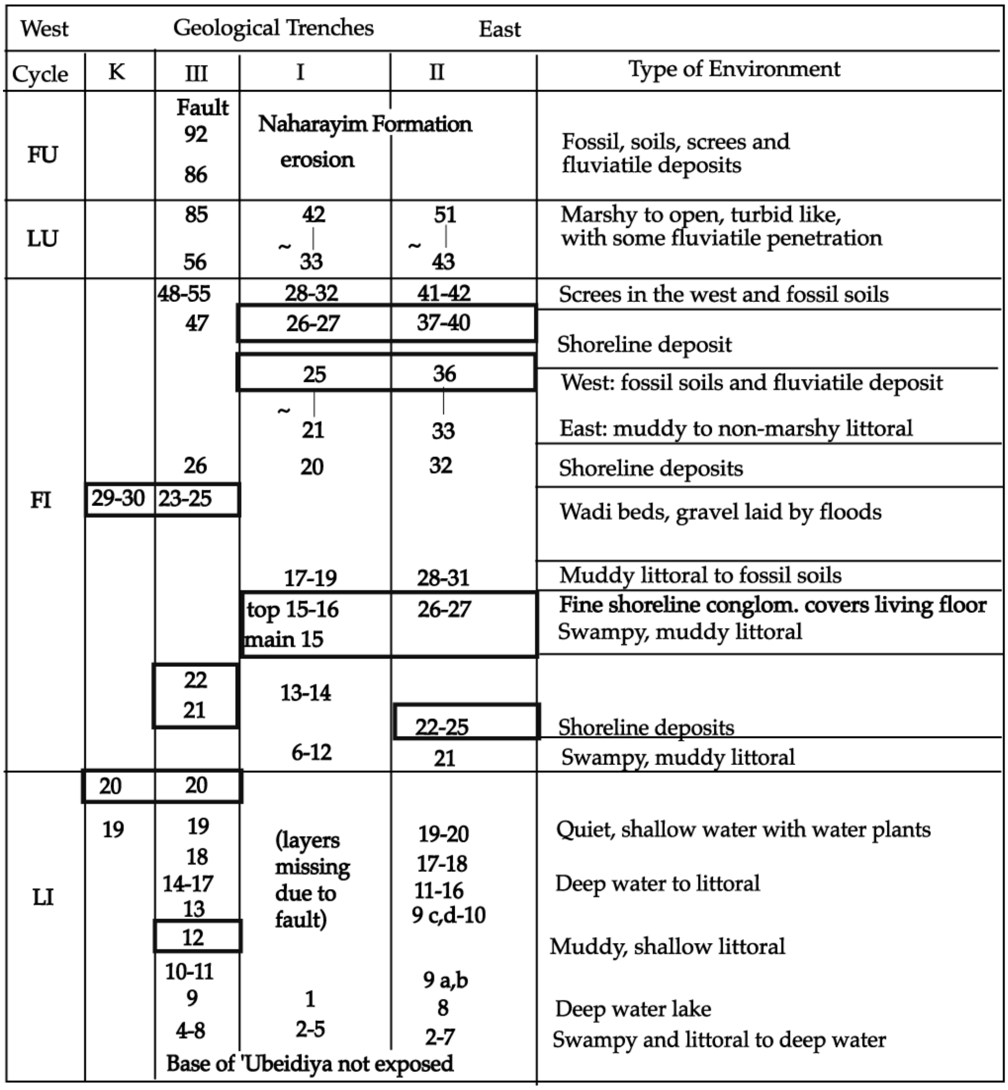


Figure 5: The plan of ‘Ubeidiya excavations 1960-1999

West		Geological Trenches		East	
Cycle	K	III	I	II	Type of Environment
FU		Fault 92 86	Naharayim Formation erosion		Fossil, soils, screes and fluviatile deposits
LU		85 56	42 ~ 33	51 ~ 43	Marshy to open, turbid like, with some fluviatile penetration
FI		48-55	28-32	41-42	Screes in the west and fossil soils
		47	26-27	37-40	Shoreline deposit
			25 ~ 21	36 33	West: fossil soils and fluviatile deposit East: muddy to non-marshy littoral
		26	20	32	Shoreline deposits
	29-30	23-25			Wadi beds, gravel laid by floods
			17-19	28-31	Muddy littoral to fossil soils
			top 15-16 main 15	26-27	Fine shoreline conglom. covers living floor Swampy, muddy littoral
		22 21	13-14	22-25	Shoreline deposits
			6-12	21	Swampy, muddy littoral
LI	20	20			
	19	19	(layers missing due to fault)	19-20	Quiet, shallow water with water plants
		18		17-18	
		14-17		11-16	Deep water to littoral
		13		9 c,d-10	
		12			Muddy, shallow littoral
		10-11		9 a,b	
		9	1	8	Deep water lake
		4-8	2-5	2-7	Swampy and littoral to deep water
		Base of 'Ubeidiya not exposed			

Figure 6: The stratigraphic sequence of ‘Ubeidiya strata



West		Geological Trenches		East	
Cycle	K	III	I	II	Type of Environment
FU		Fault 92 86	Naharayim Formation erosion		Fossil, soils, screes and fluviatile deposits
LU		85 56	42 ~ 33	51 ~ 43	Marshy to open, turbid like, with some fluviatile penetration
FI		48-55	28-32	41-42	Screes in the west and fossil soils
		47	26-27	37-40	Shoreline deposit
			25	36	West: fossil soils and fluviatile deposit
			~ 21	33	East: muddy to non-marshy littoral
		26	20	32	Shoreline deposits
	29-30	23-25			Wadi beds, gravel laid by floods
			17-19	28-31	Muddy littoral to fossil soils
			top 15-16 main 15	26-27	Fine shoreline conglom. covers living floor Swampy, muddy littoral
		22 21	13-14	22-25	Shoreline deposits
			6-12	21	Swampy, muddy littoral
LI	20	20			
	19	19	(layers missing due to fault)	19-20	Quiet, shallow water with water plants
		18		17-18	
		14-17		11-16	Deep water to littoral
		13		9 c,d-10	
		12			Muddy, shallow littoral
		10-11		9 a,b	
		9	1	8	Deep water lake
		4-8	2-5	2-7	Swampy and littoral to deep water
		Base of 'Ubeidiya not exposed			

Figure 7: The stratigraphic sequence of 'Ubeidiya strata depicting 'pooled strata'

'Pooled strata' III 23-25 and K 29-25 presented here were subsequently not included in the final analysis as a result of small sample size.

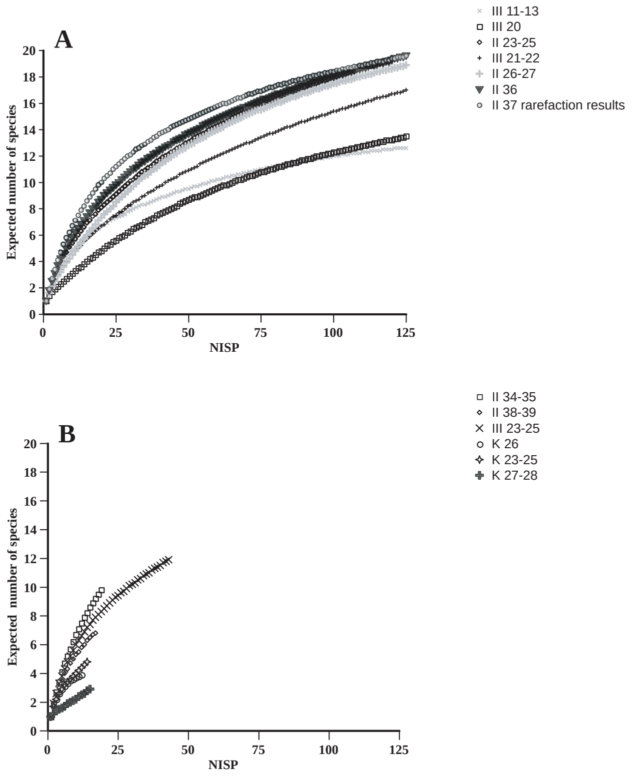


Figure 8: Point by point rarefaction curves for ‘Ubeidiya ‘pooled strata’ using large terrestrial mammal specimens

Rarefaction curves were calculated using NISP data. Subfigure A represents the ‘pooled strata’ which reached an asymptote and were included in subsequent analyses. Subfigure B represents ‘pooled strata’ which did not reach and asymptote and were not included in subsequent analyses.

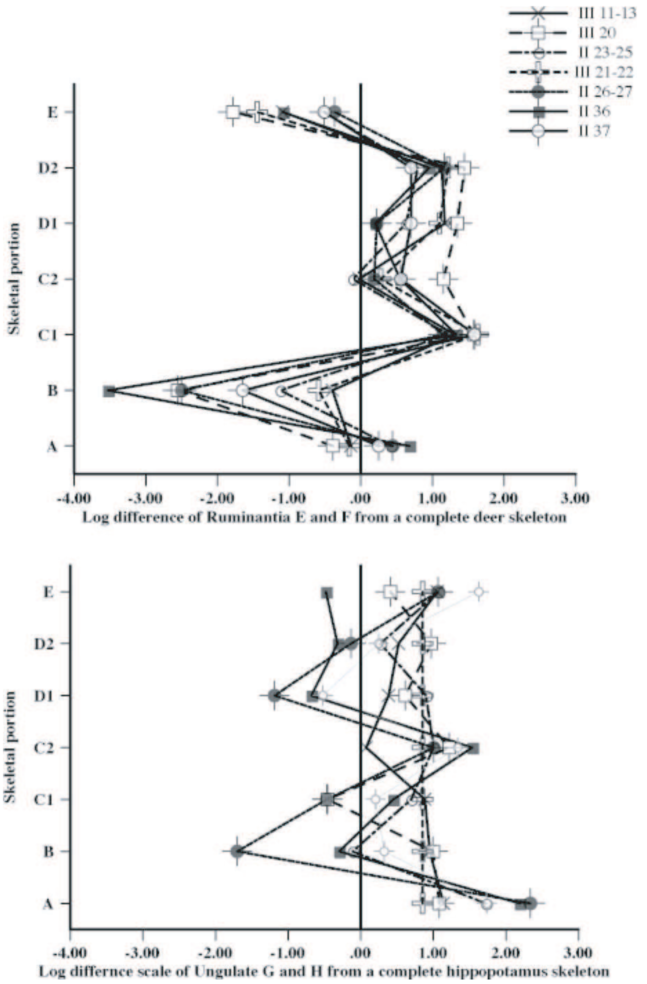


Figure 9: Ratio diagram for ‘Ubeidiya Ruminantia E and F compared with ratio diagram for ‘Ubeidiya Ungulata G and H per ‘pooled stratum’

‘Ubeidiya Ruminantia size E and F skeletal proportions are compared with those of complete deer *Dama mesopotamica* (upper figure) and ‘Ubeidiya Ruminantia G and H skeletal proportions are compared with those of a complete *Hippopotamus amphibius* (lower figure).

Skeletal portions are denoted as follows: A - cranial elements including teeth fragments; B - rib and vertebra; C1 - upper forelimb (humerus, radius and ulna); C2 - Lower forelimb (carpals and metacarpals); D1 - Upper hindlimb (femur and tibia); D2 - Lower hindlimb (tarsals and metatarsals) and E - phalanges, sesamoids and undetermined metapodials.

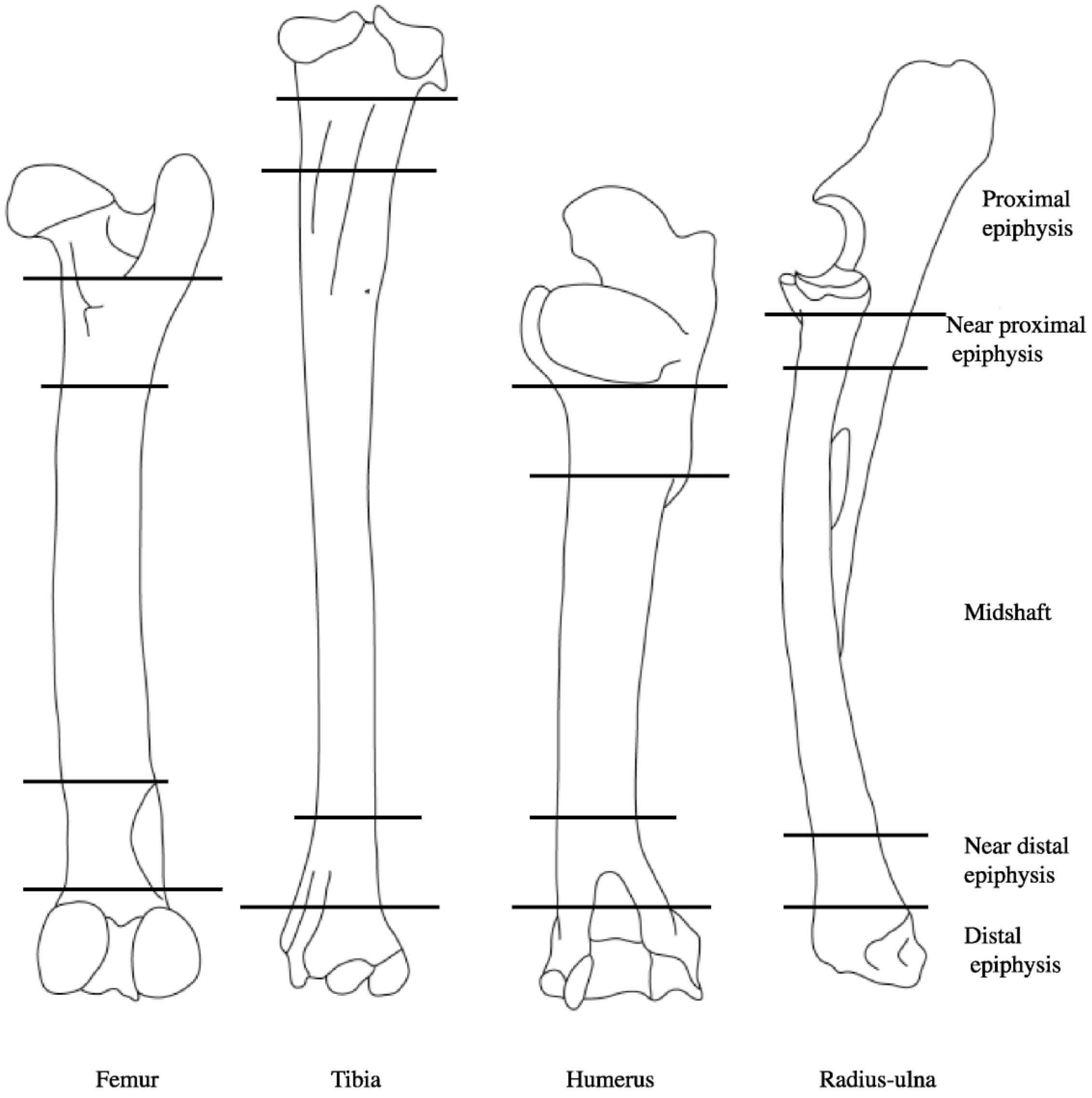


Figure 10: Schematic depiction of five portions for four major limb bones arithmetic

The limb figures are based on outlines downloaded from Popkin (2004).

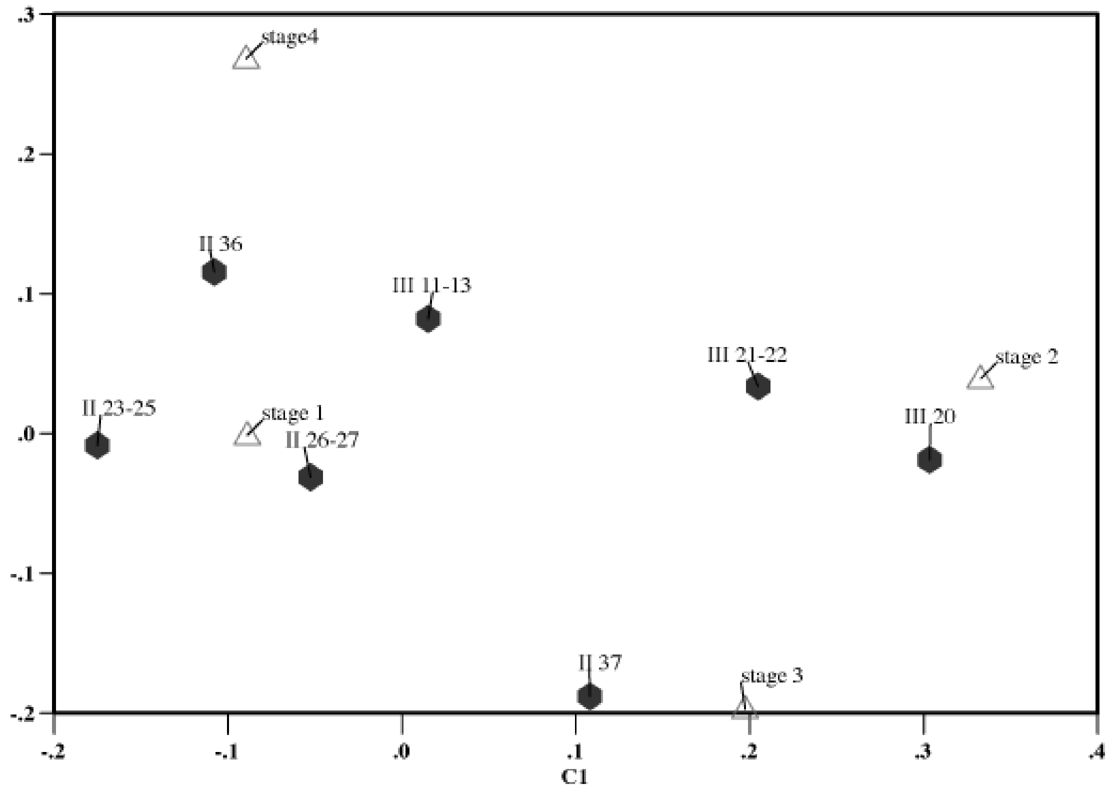


Figure 11: Scattergram of correspondence analysis axes for weathering stages of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

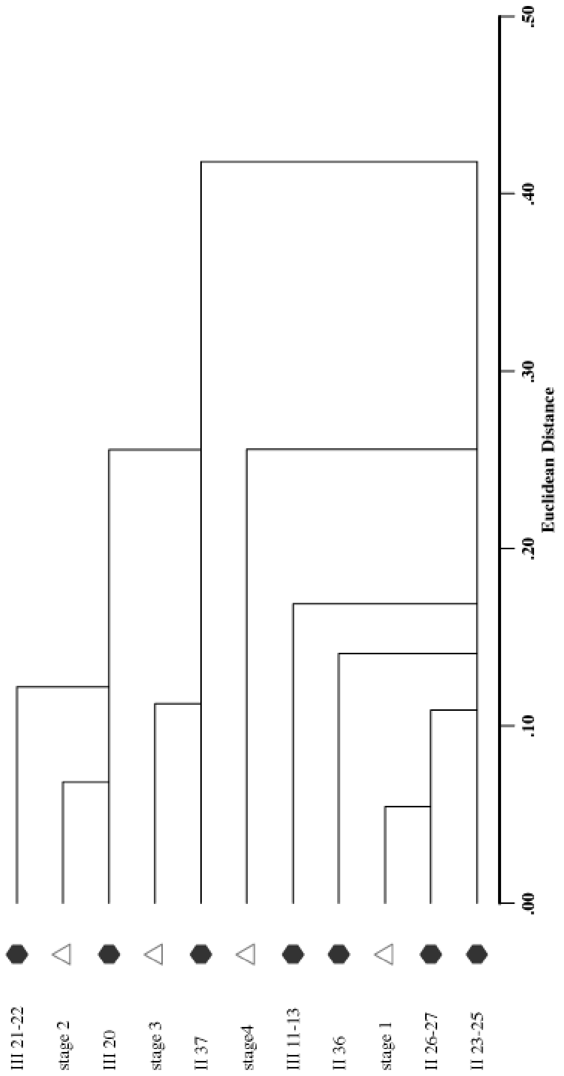


Figure 12: Dendrogram using Euclidian distance and weighted pair-group with arithmetic averaging amalgamation for correspondence analysis axes for weathering stages of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

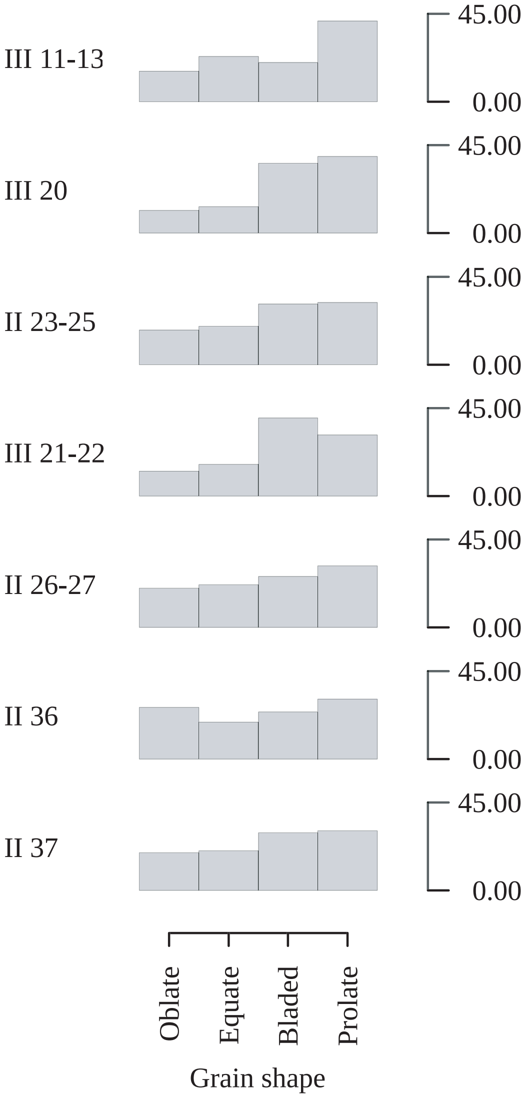


Figure 13: Grain shape percentage of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

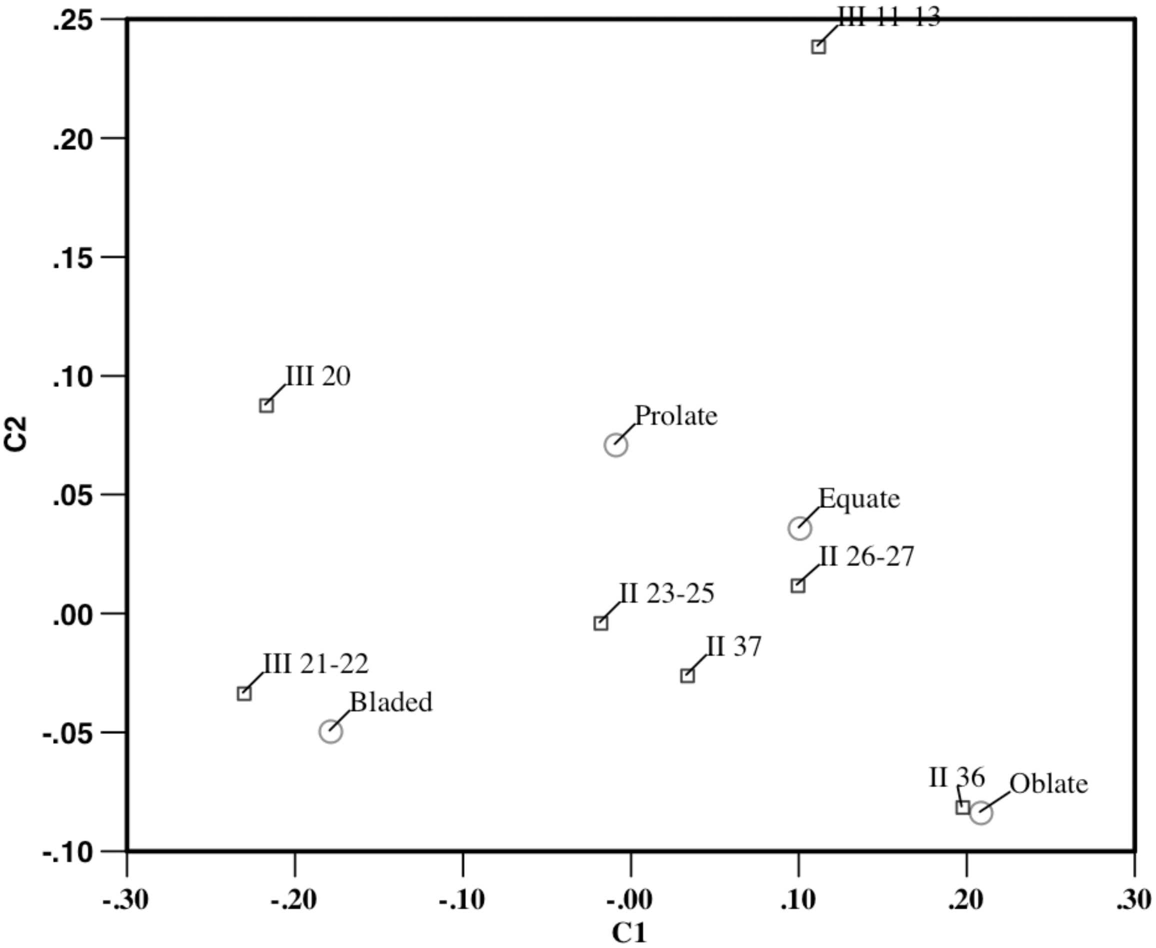


Figure 14: Scattergram of correspondence analysis axes for grain shape frequencies of the large terrestrial mammals of 'Ubeidiya per 'pooled stratum'

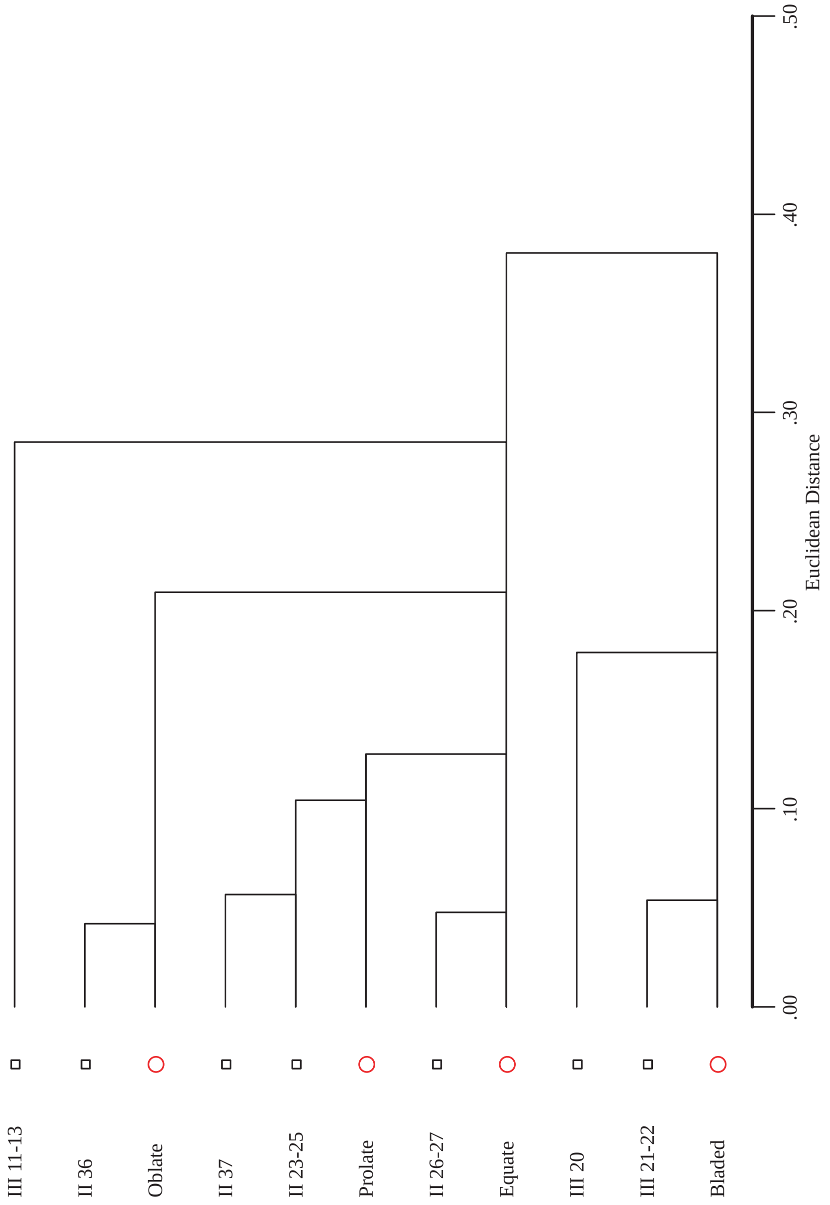


Figure 15: Dendrogram using Euclidian distance and weighted pair-group with arithmetic averaging amalgamation for correspondence analysis (C1-C3 axes) for grain shape frequencies (Zingg, 1935) of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

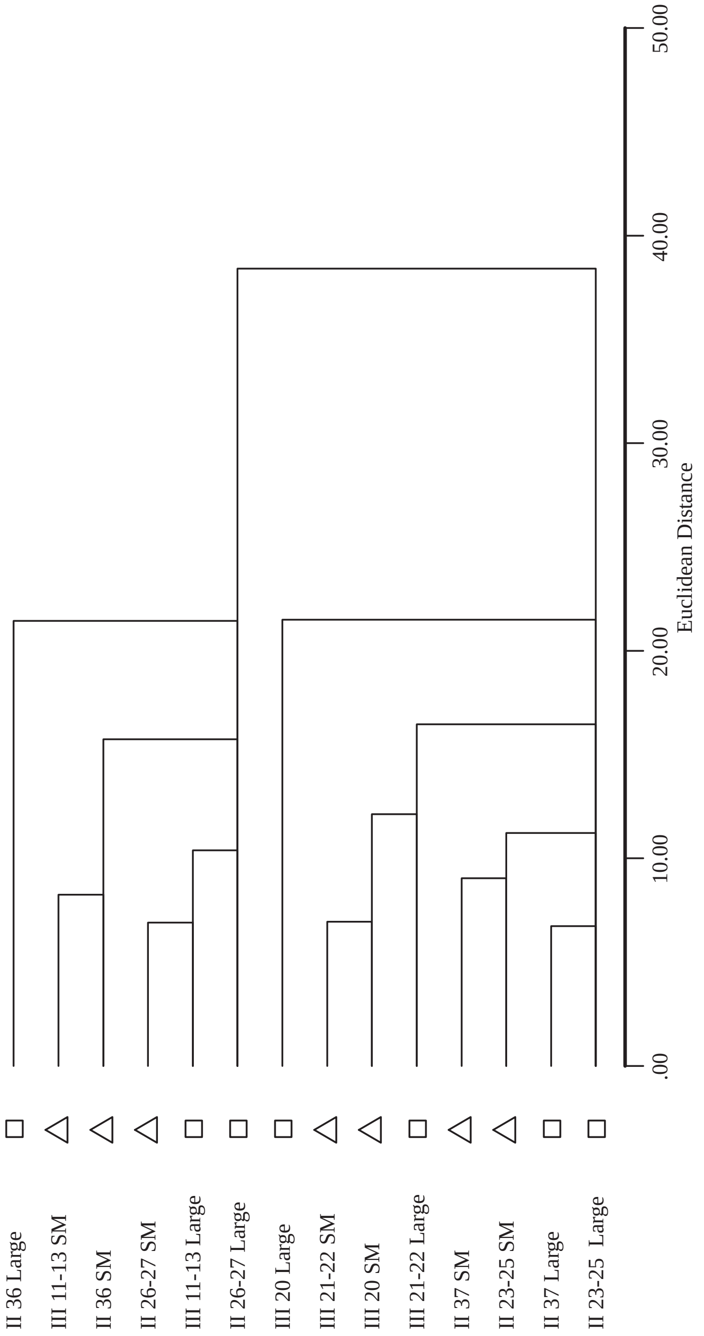


Figure 16: Dendrogram using Euclidian distance and weighted pair-group with arithmetic averaging amalgamation for grain shape percentages (Zingg, 1935) of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’ and by body size. Small-medium mammals of body size E and F are denoted as SM and large mammal of body size G are denoted as Large

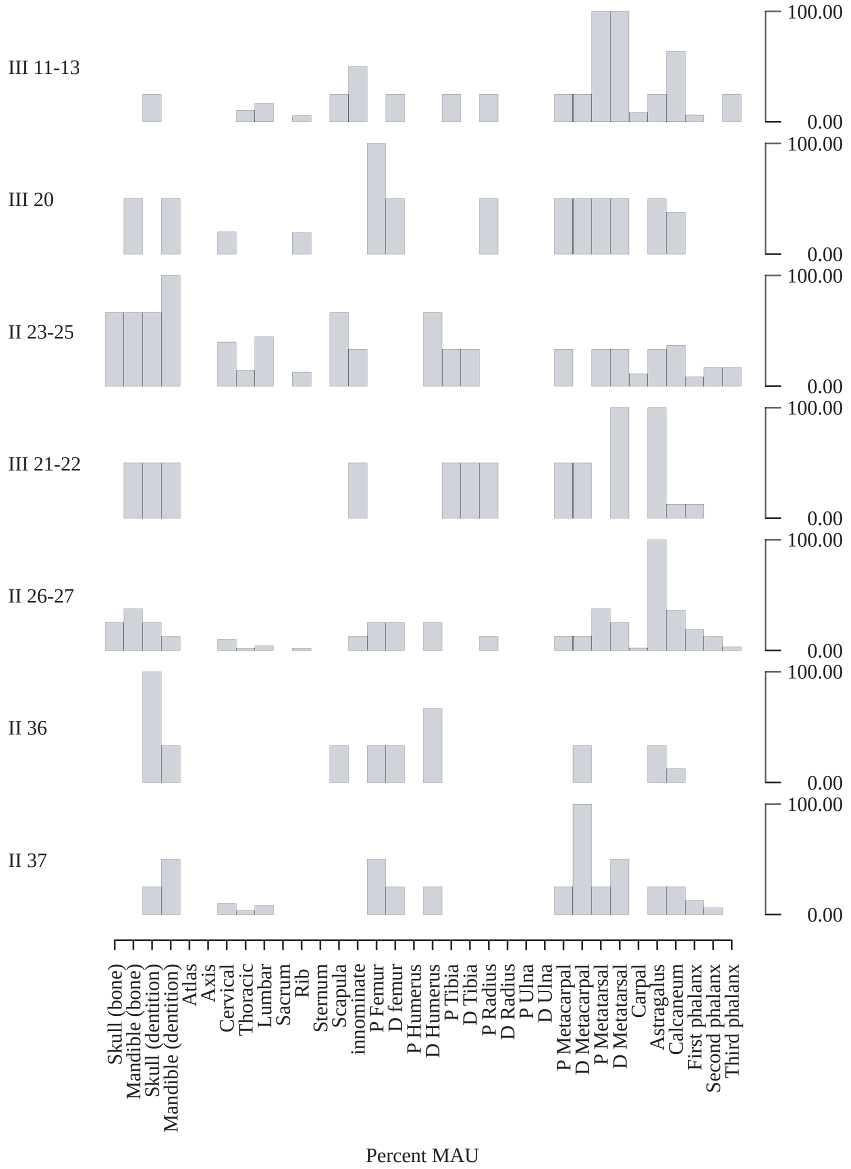


Figure 17: Percent MAU distribution for ‘Ubeidiya Ruminantia body size E per ‘pooled stratum’, epiphyseal data

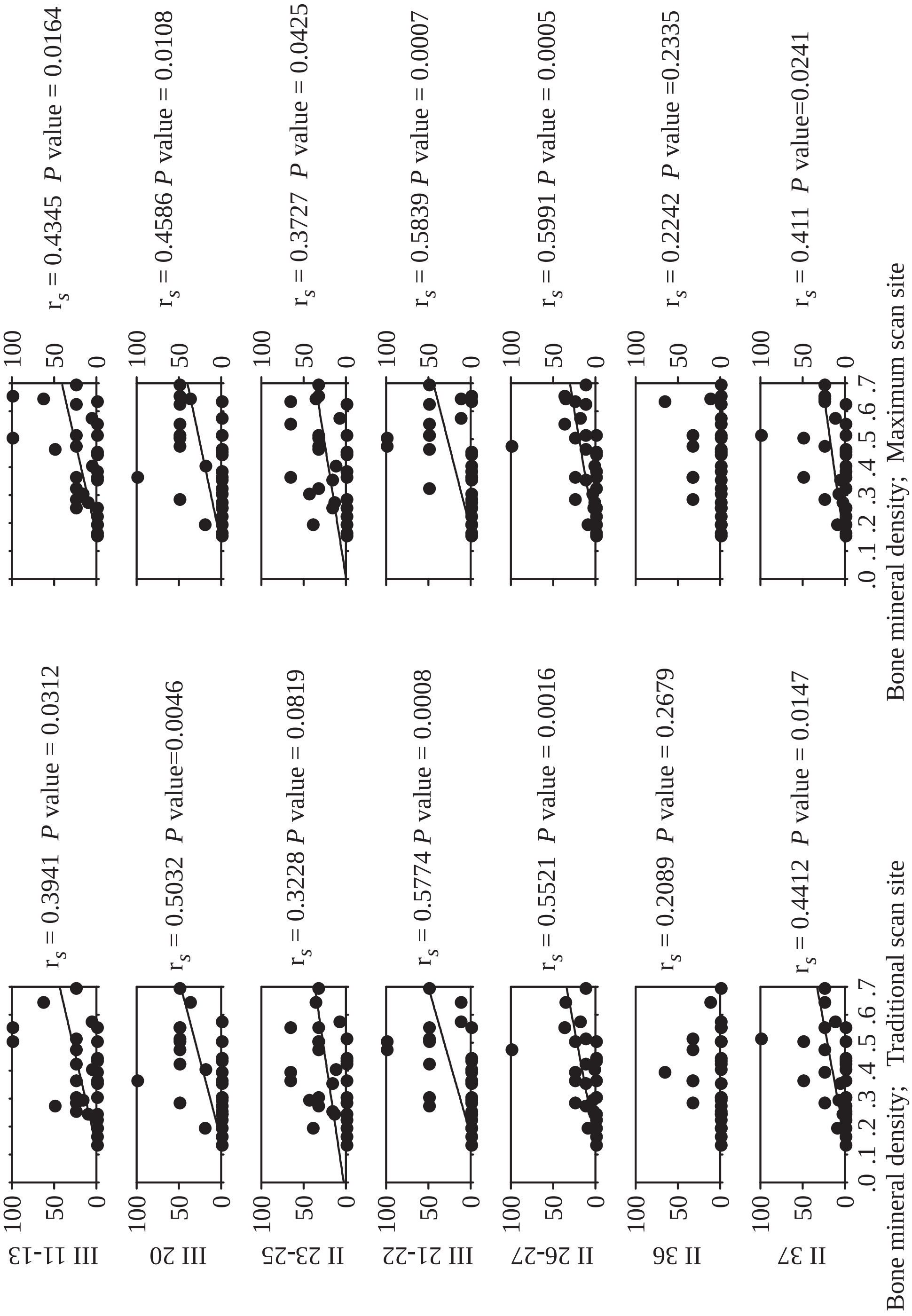


Figure 18: Percent MAU for ‘Ubeidiya Ruminantia body size E correlated with bone mineral density, per ‘pooled stratum’

Bone mineral densities are of deer *Odocoileus* spp. (Lyman, 1994). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value < 0.1).

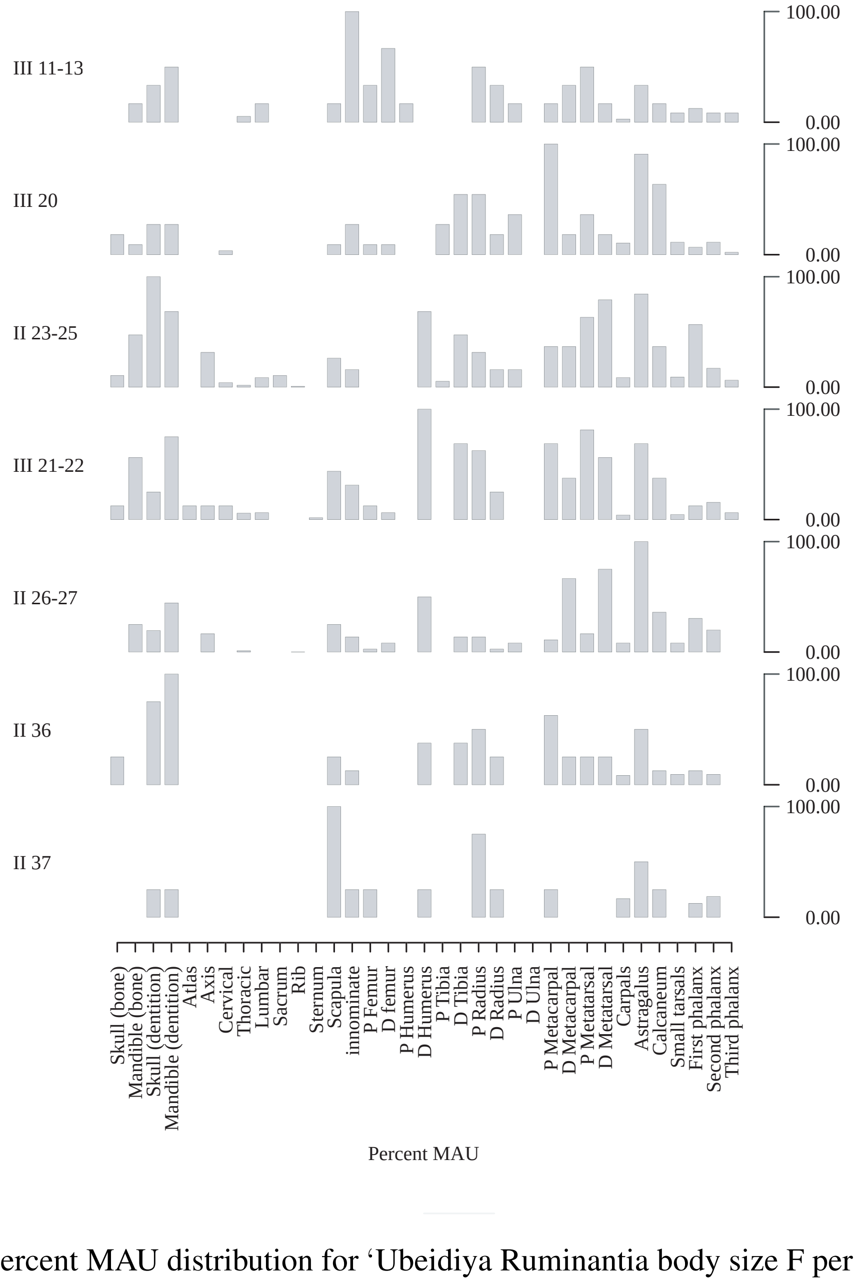


Figure 19: Percent MAU distribution for ‘Ubeidiya Ruminantia body size F per ‘pooled stratum’, epiphyseal data

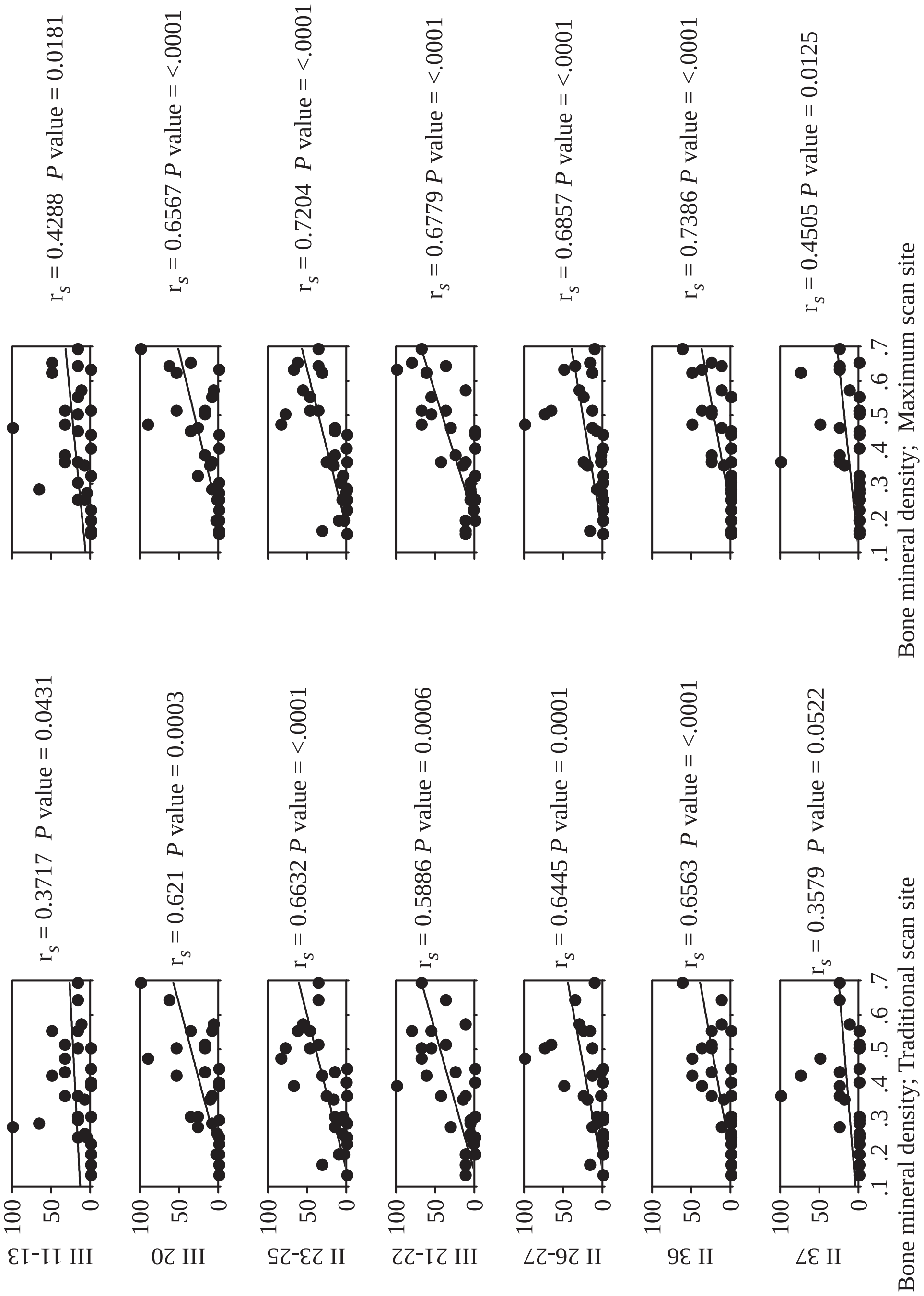


Figure 20: Percent MAU for 'Ubeidiya Ruminantia body size F correlated with bone mineral density, per 'pooled stratum'

Bone mineral densities are of deer *Odocoileus* spp. (Lyman, 1994). Spearman's coefficient of rank correlation r_s and P values are presented for significant correlation (P value < 0.1).

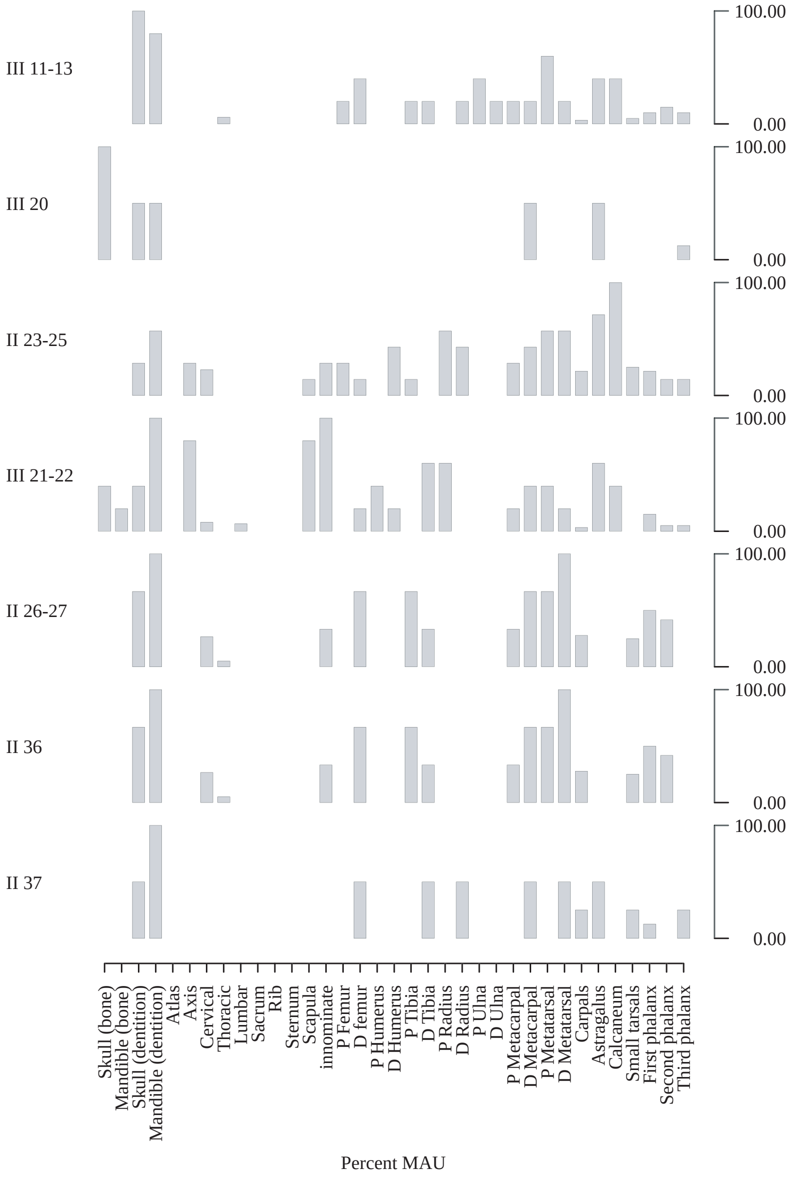


Figure 21: Percent MAU distribution for 'Ubeidiya Ruminantia body size G per 'pooled stratum', epiphyseal data

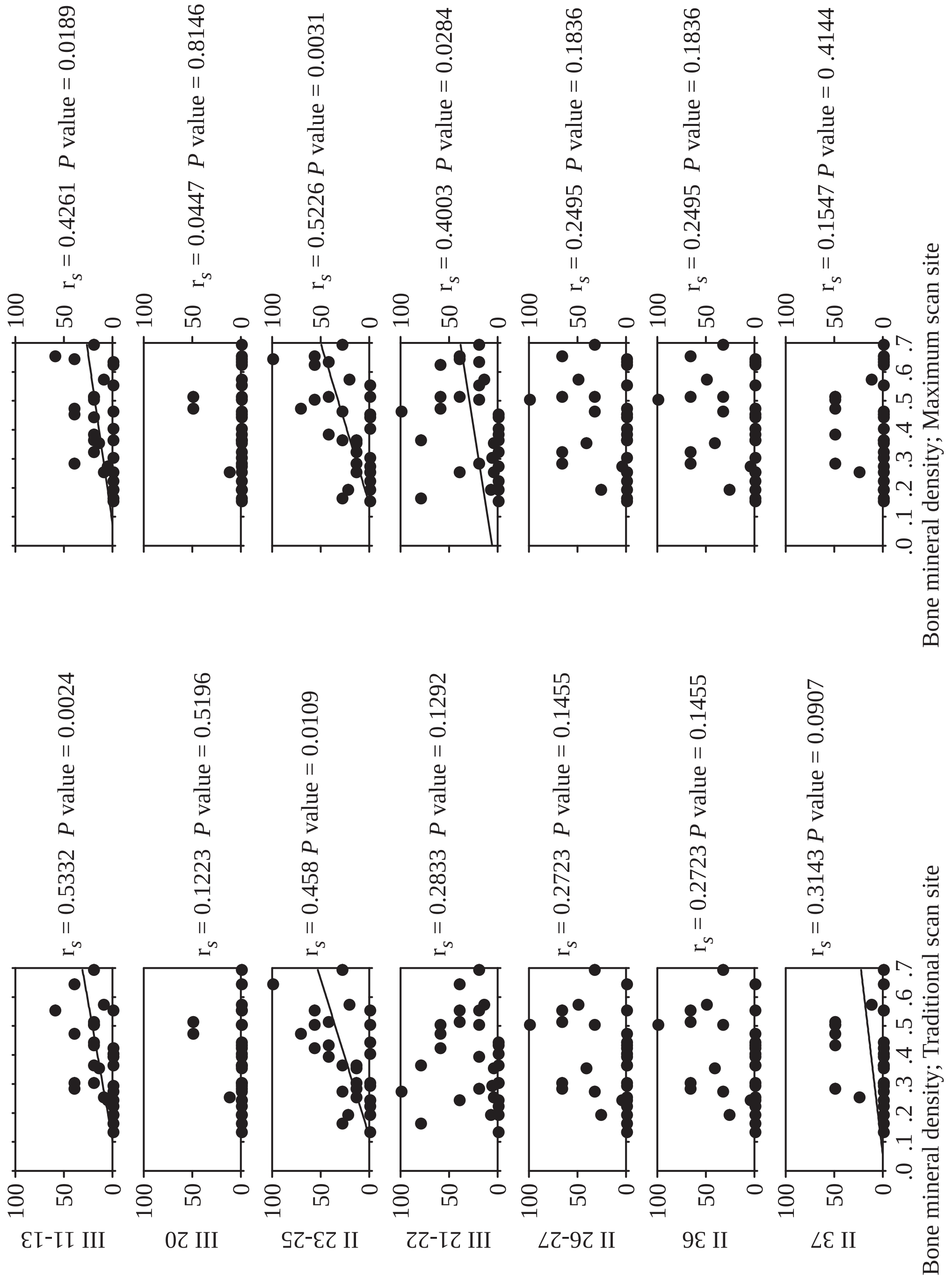


Figure 22: Percent MAU for ‘Ubeidiya Ruminantia body size G correlated with bone mineral density, per ‘pooled stratum’

Bone mineral densities are of deer *Odocoileus* spp. (Lyman, 1994). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value < 0.1).

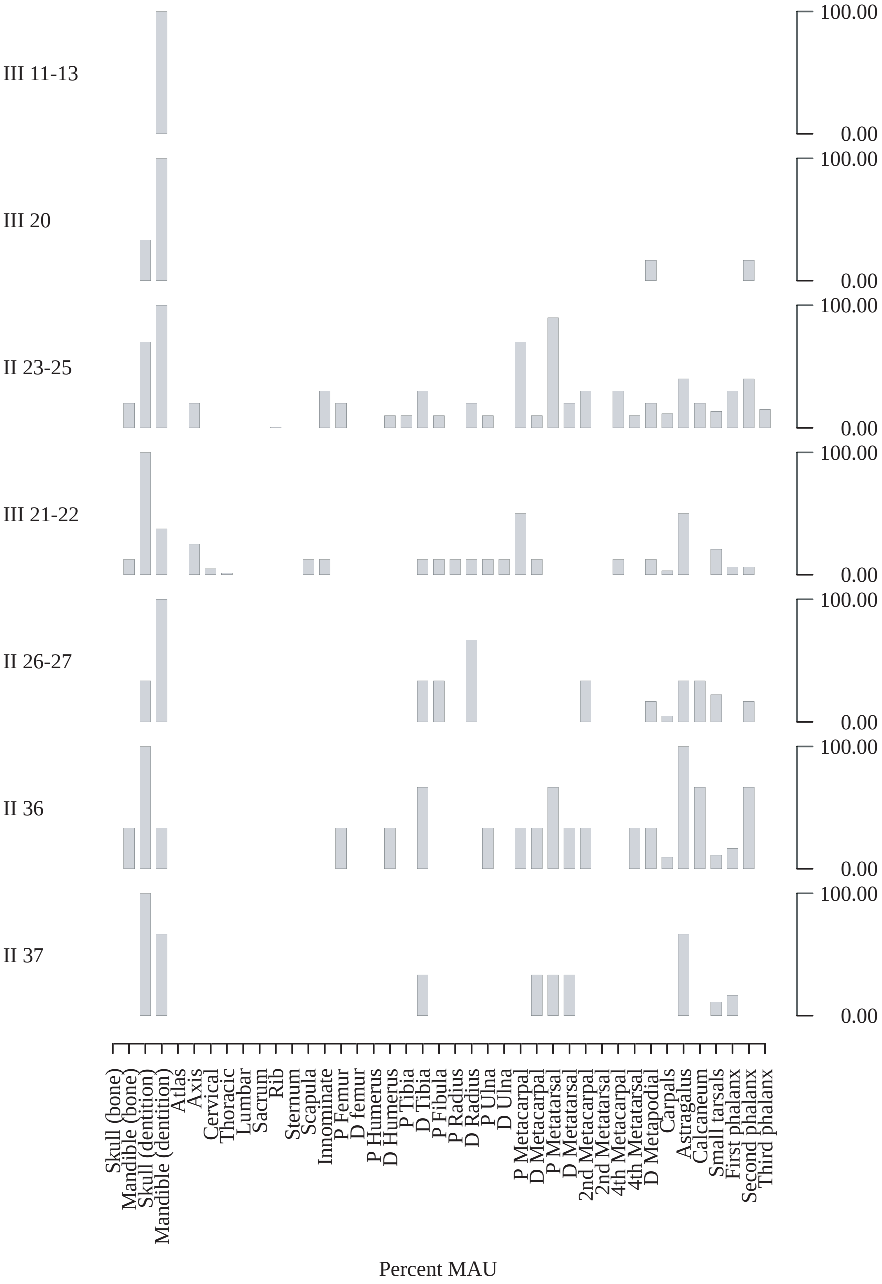


Figure 23: Percent MAU distribution for 'Ubeidiya Equidae per 'pooled stratum', epiphyseal data

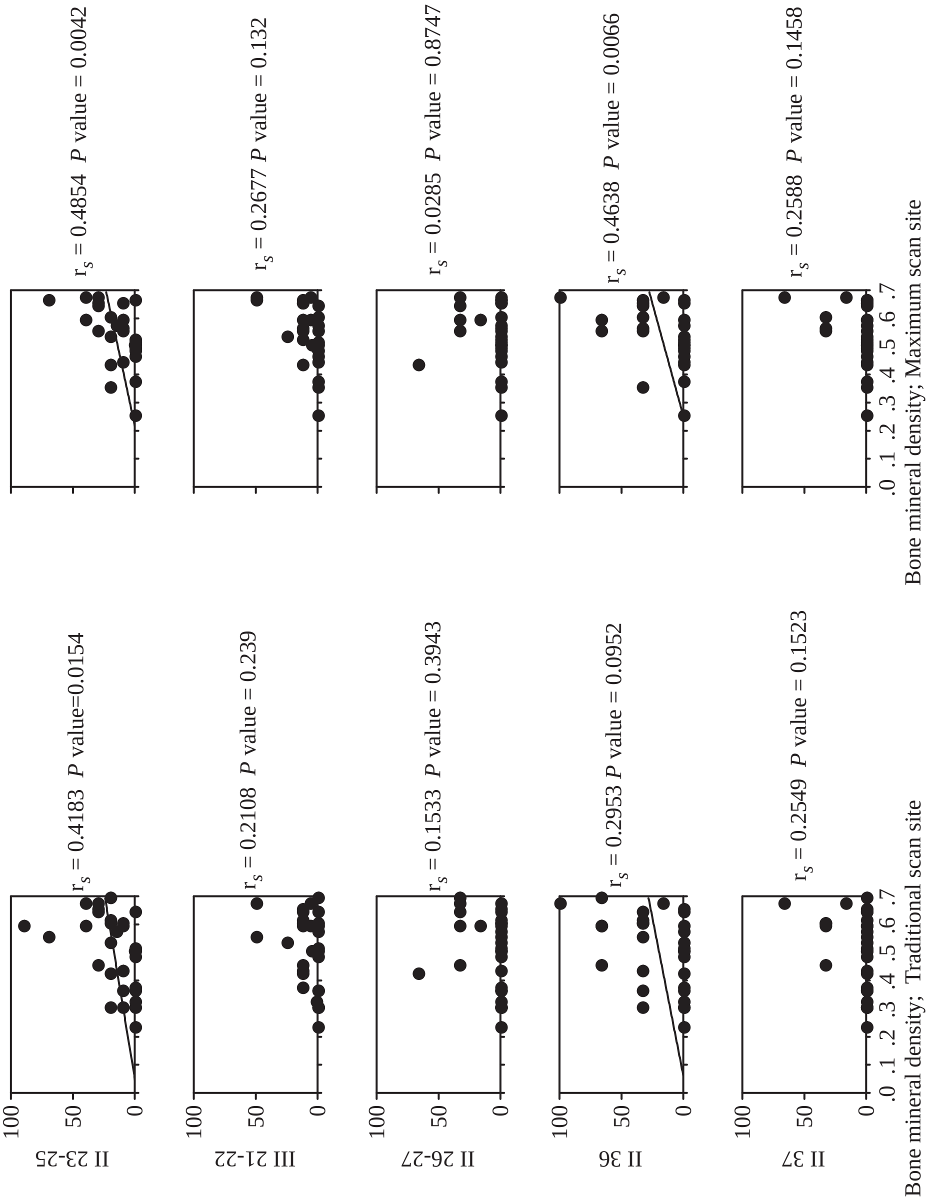


Figure 24: Percent MAU for ‘Ubeidiya Equidae correlated with bone mineral density, per ‘pooled stratum’

Bone mineral densities are of horse *Equus caballus* (Lam *et al.*, 1999). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value < 0.1). ‘Pooled stratum’ III 11-13 and III 20 are not presented due to small sample size.

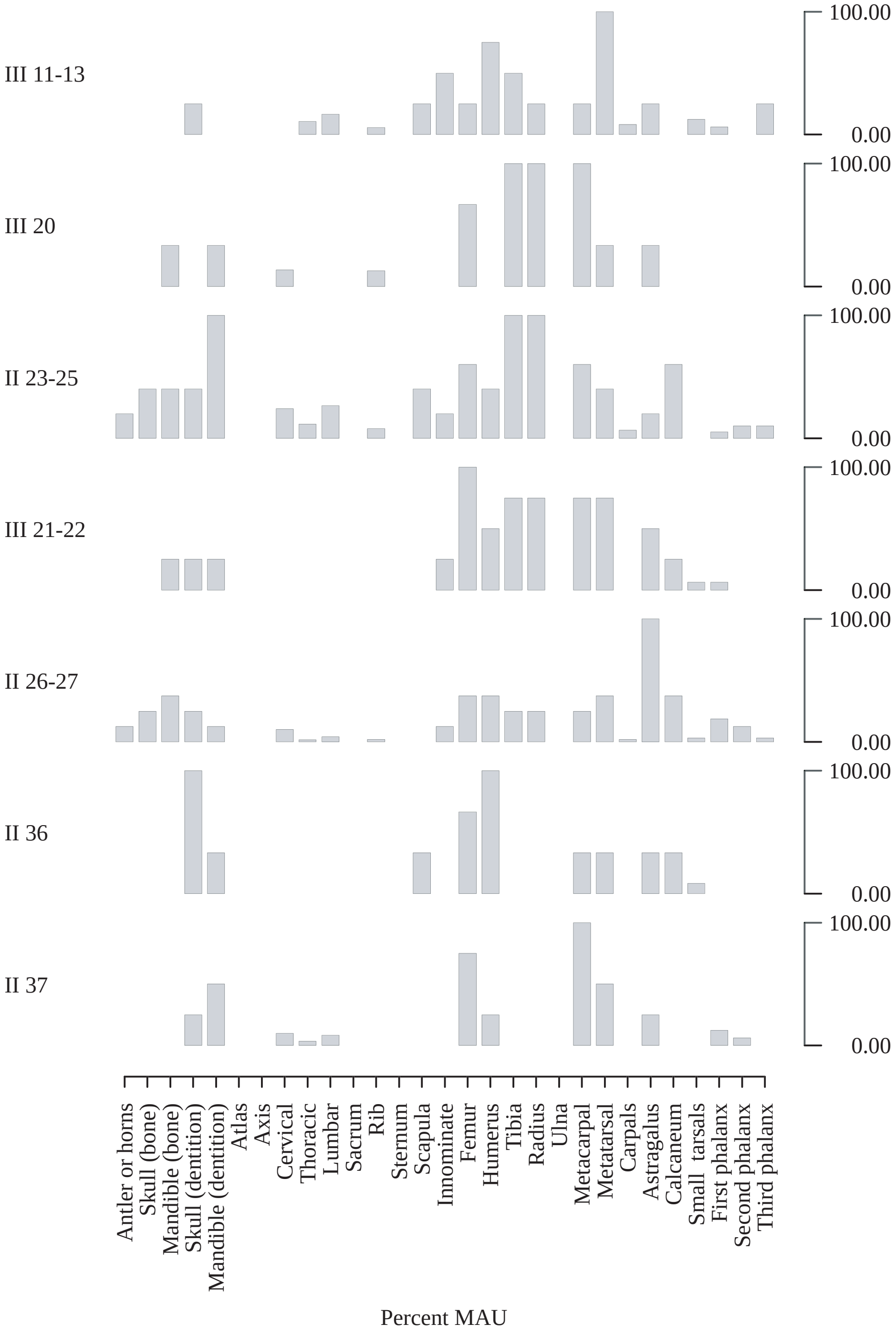


Figure 25: Percent MAU distribution for ‘Ubeidiya Ruminantia body size E per ‘pooled stratum’, complete limbs

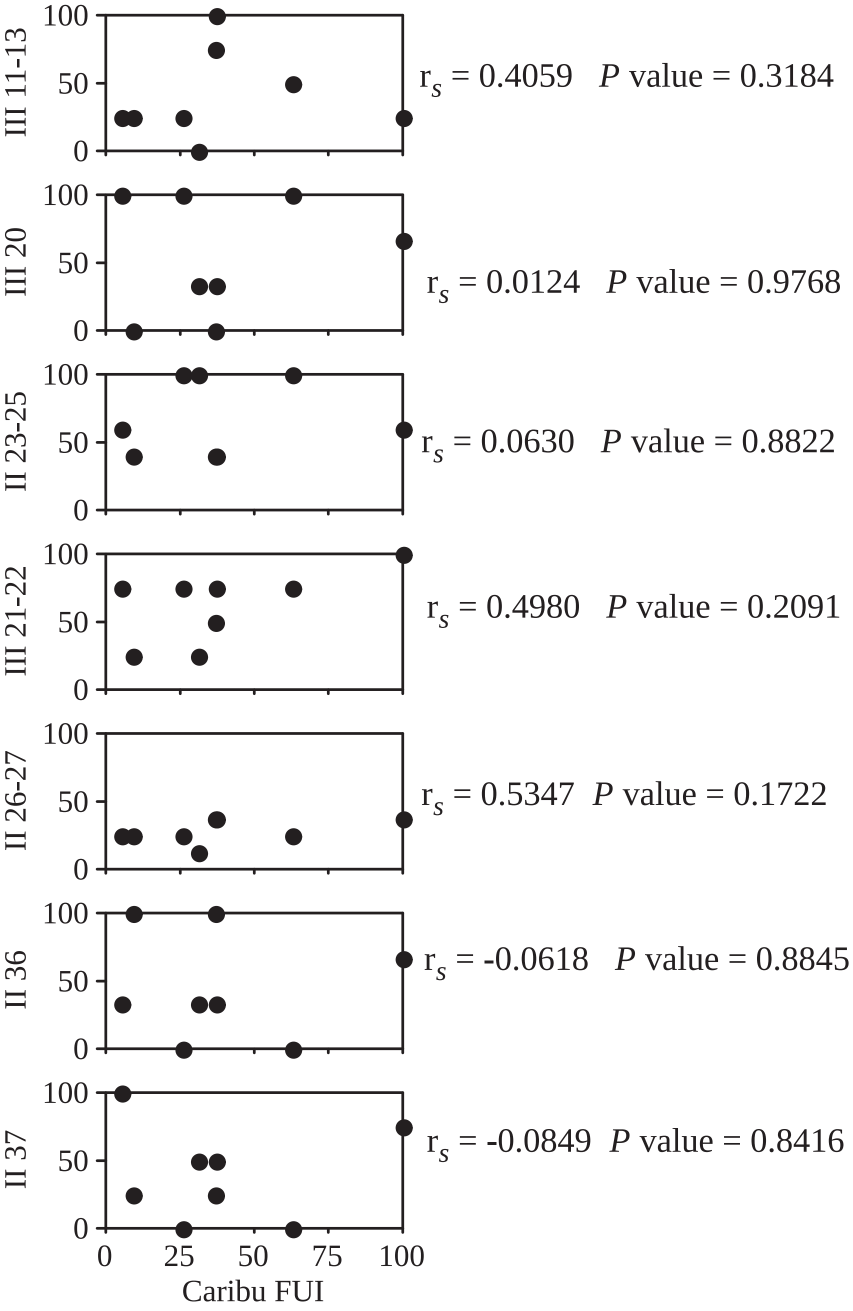


Figure 26: Percent MAU for ‘Ubeidiya Ruminantia body size E correlated with FUI for high survival elements, per ‘pooled stratum’

FUI are calculated for Caribou *Rangifer tarandus* (Metcalfe & Jones, 1988). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value $<$ 0.1).

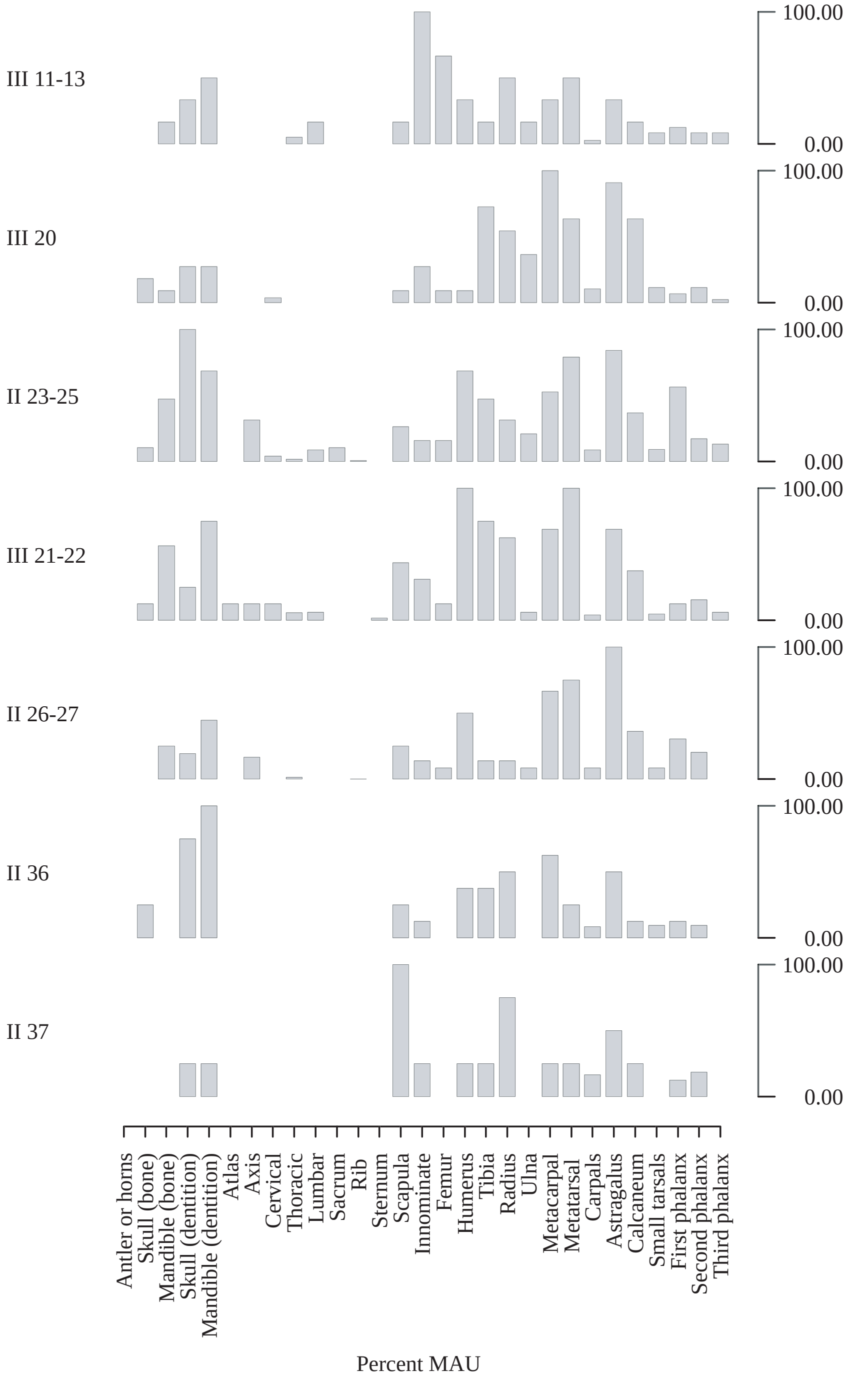


Figure 27: Percent MAU distribution for ‘Ubeidiya Ruminantia body size F per ‘pooled stratum’, complete limbs

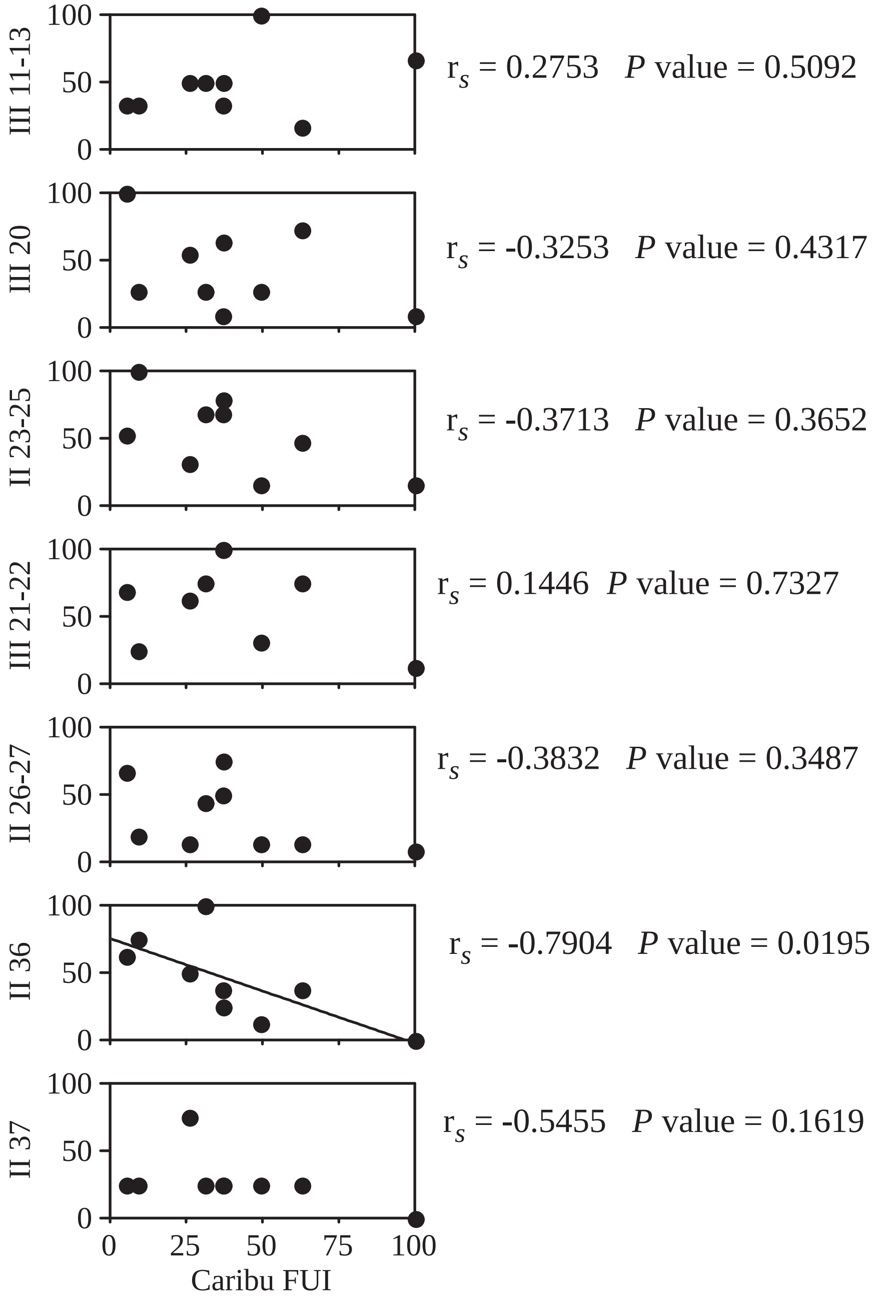


Figure 28: Percent MAU for ‘Ubeidiya Ruminantia body size F correlated FUI for high survival elements, per ‘pooled stratum’

FUI are calculated for Caribou *Rangifer tarandus* (Metcalfe & Jones, 1988). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value $<$ 0.1).

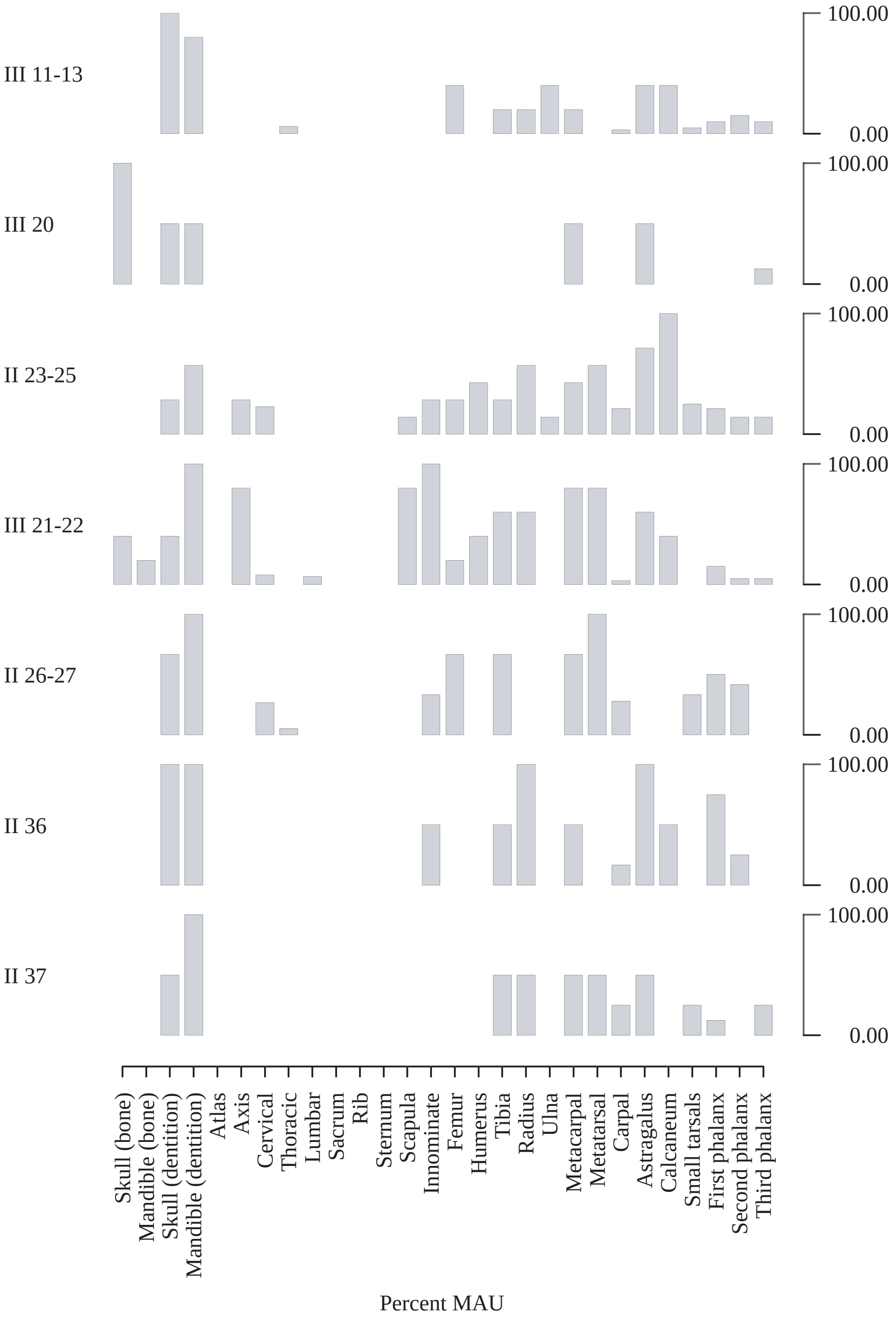


Figure 29: Percent MAU distribution for 'Ubeidiya Ruminantia body size G per 'pooled stratum', complete limbs

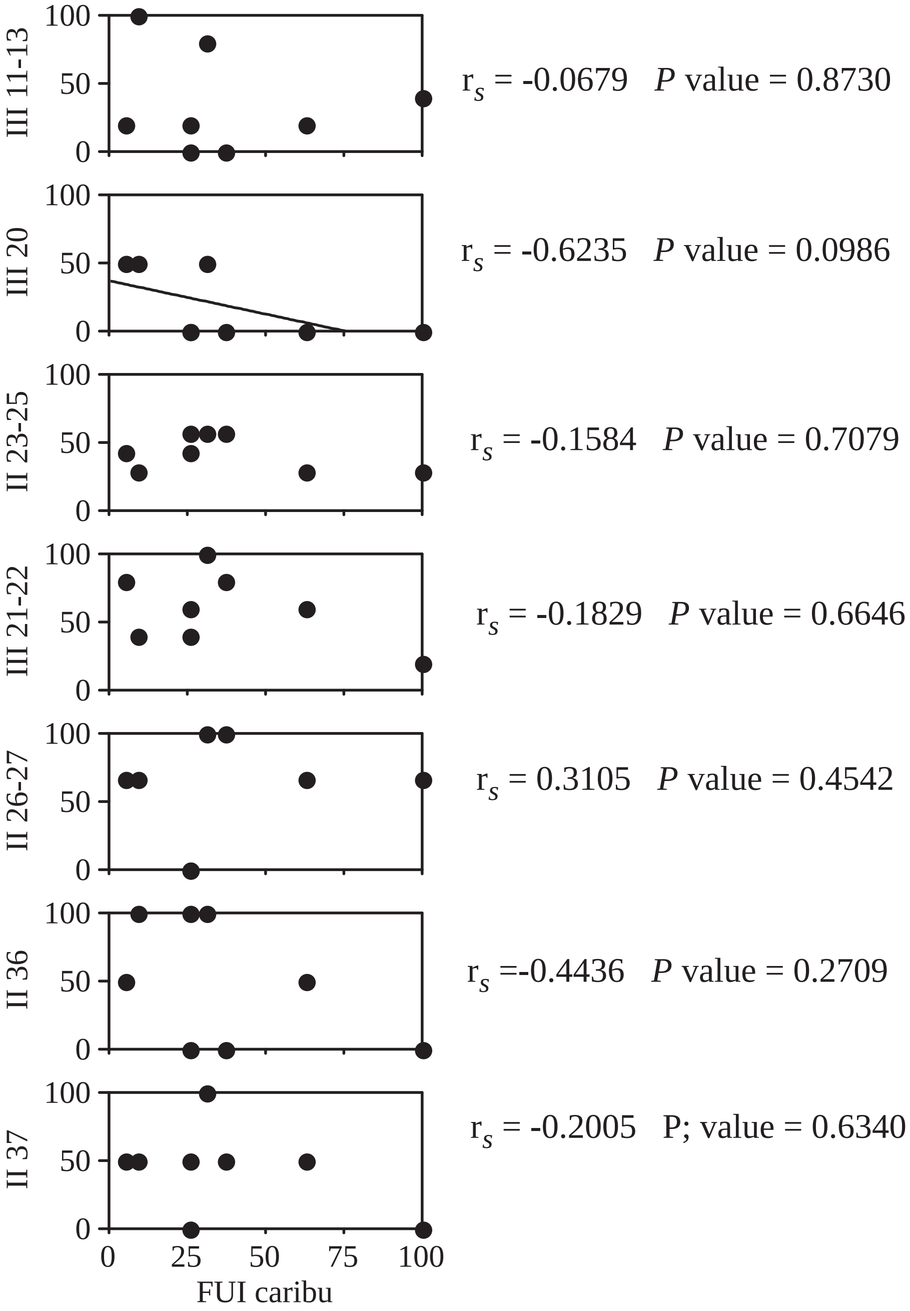


Figure 30: Percent MAU for ‘Ubeidiya Ruminantia body size G correlated with FUI for high survival elements, per ‘pooled stratum’

FUI are calculated for Caribou *Rangifer tarandus* (Metcalfe & Jones, 1988). Spearman’s coefficient of rank correlation r_s and P values are presented for significant correlation (P value $<$ 0.1).

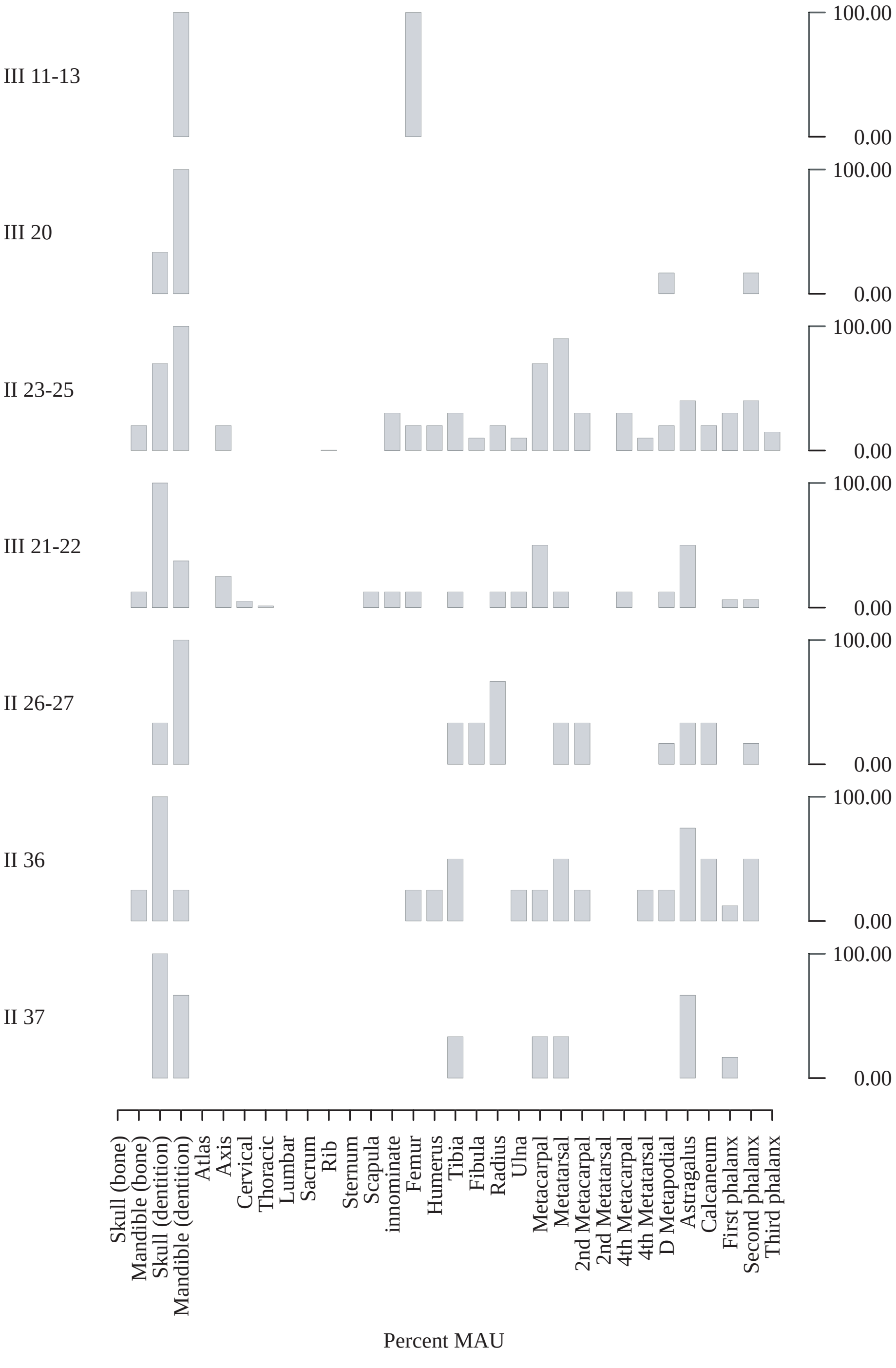
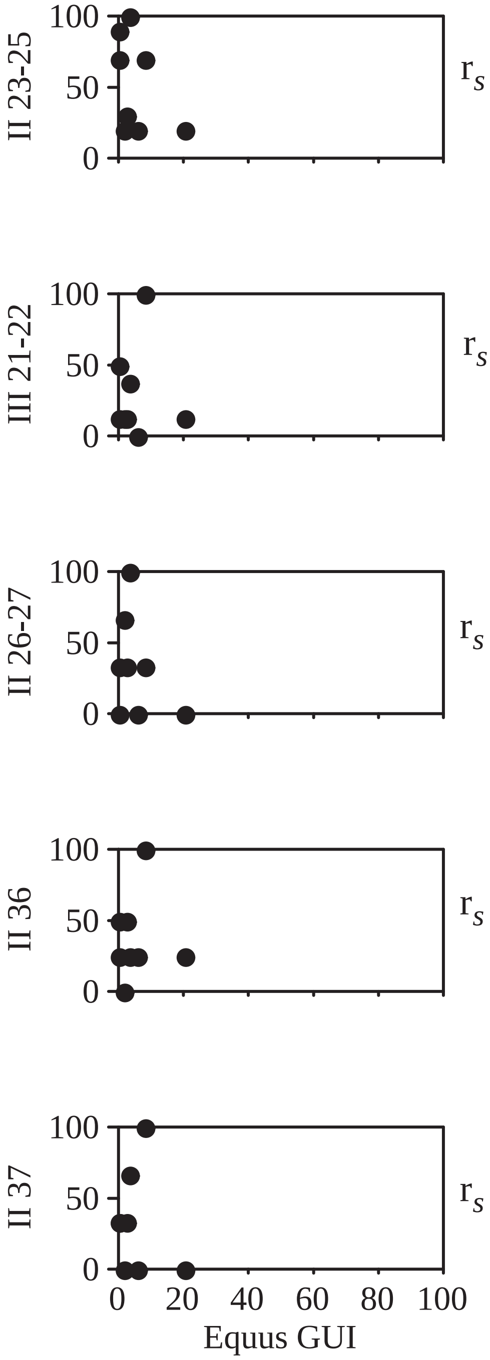


Figure 31: Percent MAU distribution for ‘Ubeidiya Equidae per ‘pooled stratum’, complete limbs



r_s = -0.3805 *P* value = 0.3524

r_s = 0.0000 *P* value = 1.0000

r_s = -0.2253 *P* value =0.5917

r_s = 0.0766 *P* value = 0.8569

r_s = -0.0501 *P* value = 0.9063

Figure 32: Percent MAU for 'Ubeidiya Equidae correlated with GUI for high survival elements, per 'pooled stratum'

GUI are calculated for Equidae *Equus caballus* (Outram & Rowley-Conwy, 1998). Spearman's coefficient of rank correlation r_s and P values are presented for significant correlation (P value $<$ 0.1).

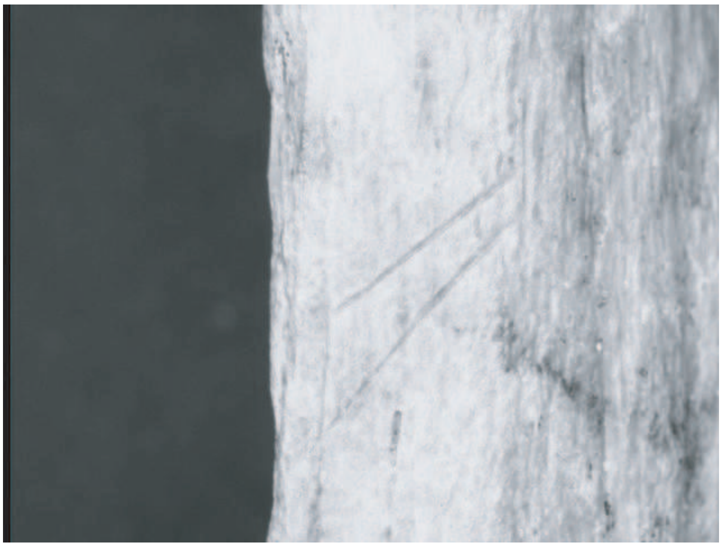


Figure 33: Cutmark on specimen UB 6227 (magnification X6.7)

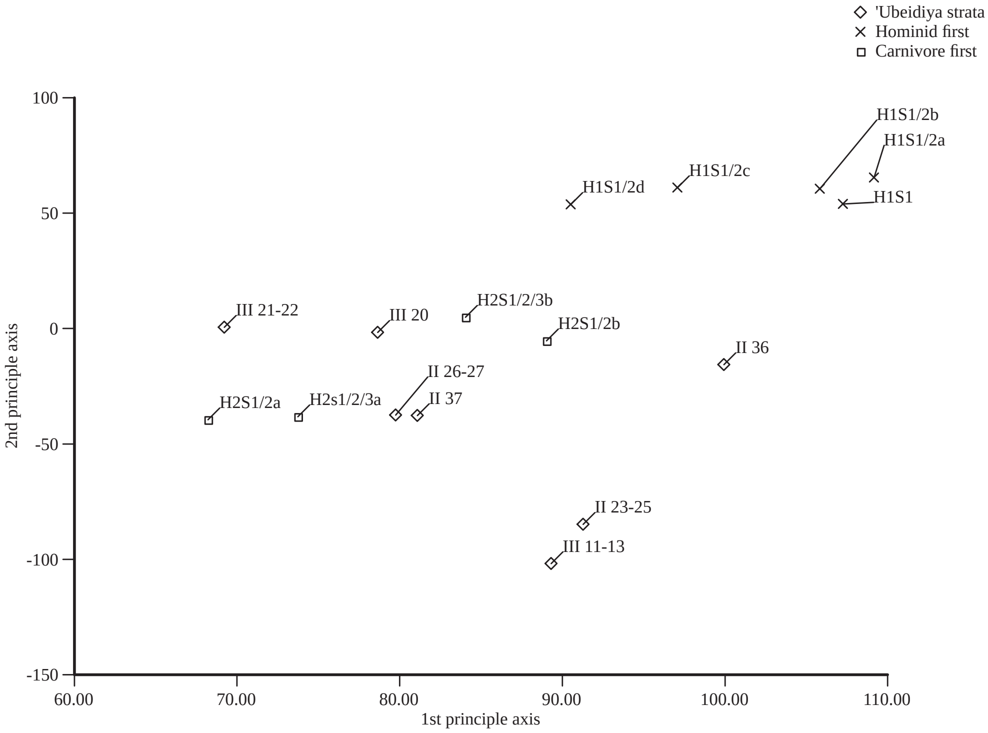


Figure 34: Principle component analysis scattergram for cut-mark distribution of the large terrestrial mammals from 'Ubeidiya per 'pooled stratum' and nine actualistic experiments

Principle component analysis for cut-mark distribution and nine actualistic experiments. Comparative data obtained from Domínguez-Rodrigo (1997). The two sequences: hominin to carnivore sequence and carnivore to hominin to carnivore sequence are labeled H1 and H2 respectively. In each sequence, several different experiments were done which included different sequences numbered from 1 to 3. In hypothesis H1, experiments included hominins only (H1S1), or both hominin and carnivore ravaging (H1S1/2). In hypothesis H2, experiments included carnivore and hominins (H2S1/2), carnivore - hominin sequence followed by hyaena scavenging as well (H2S1/2/3). Replicates of each sequence was designated by lowercase roman letters.

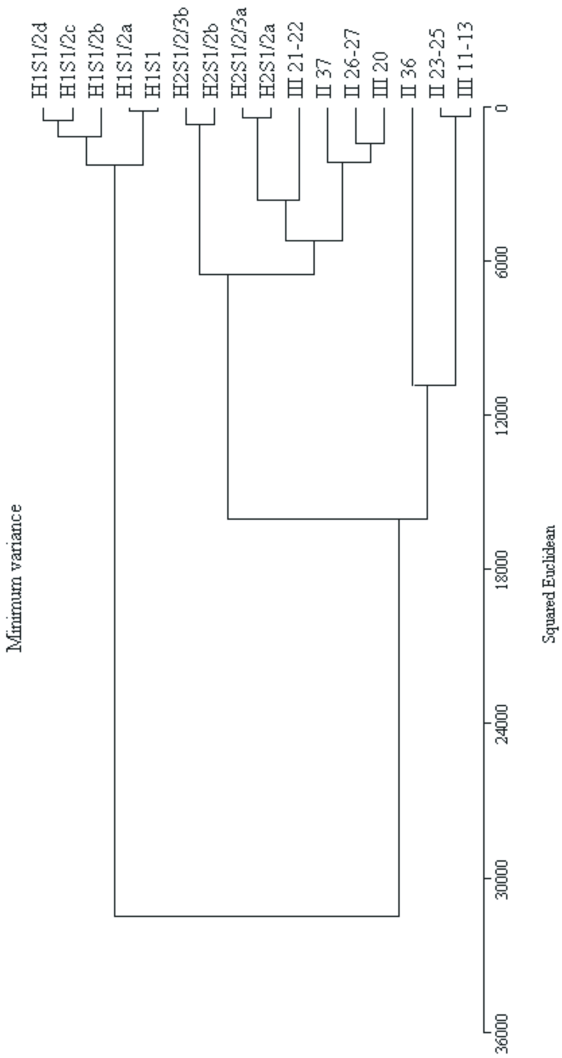


Figure 35: Dendrogram using squared Euclidian distance and minimum variance amalgamation for cut-mark frequencies from of the large terrestrial mammals from ‘Ubeidiya per ‘pooled stratum’ and nine actualistic experiments

Comparative data obtained from Domínguez-Rodrigo (1997). The two sequences: hominin to carnivore sequence and carnivore to hominin to carnivore sequence are labeled H1 and H2 respectively. In each sequence, several different experiments were done which included different sequences numbered from 1 to 3. In hypothesis H1, experiments included hominins only (H1S1), or both hominin and carnivore ravaging (H1S1/2). In hypothesis H2, experiments included carnivore and hominins (H2S1/2), carnivore - hominin sequence followed by hyaena scavenging as well (H2S1/2/3). Replicates of each sequence was designated by lowercase roman letters.

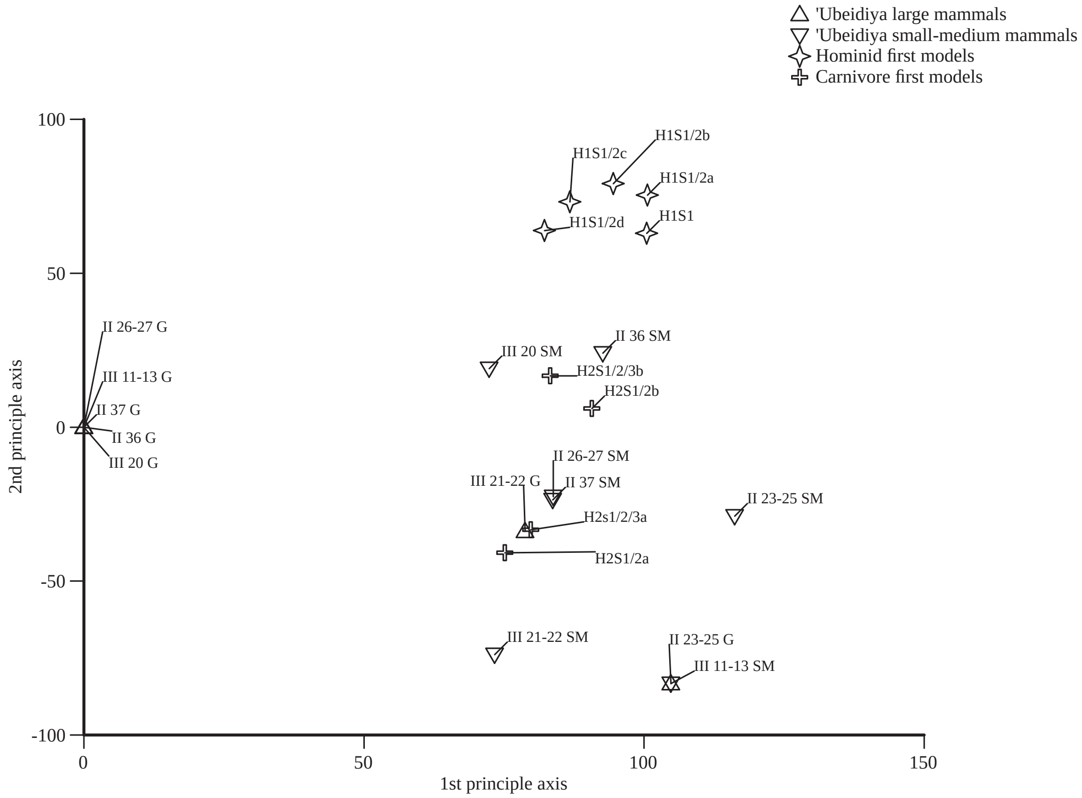


Figure 36: Principle component analysis scattergram for cut-mark distribution of the large terrestrial mammals from 'Ubeidiya per 'pooled stratum' and by body size and nine actualistic experiments. Mammals of body size E and F are denoted by the suffix SM after the name of the strata and mammals of body size G are denoted with the suffix G after the name of the strata.

Principle component analysis for cut-mark distribution and nine actualistic experiments. Comparative data obtained from Domínguez-Rodrigo (1997). The two sequences: hominin to carnivore sequence and carnivore to hominin to carnivore sequence are labeled H1 and H2 respectively. In each sequence, several different experiments were done which included different sequences numbered from 1 to 3. In hypothesis H1, experiments included hominins only (H1S1), or both hominin and carnivore ravaging (H1S1/2). In hypothesis H2, experiments included carnivore and hominins (H2S1/2), carnivore - hominin sequence followed by hyaena scavenging as well (H2S1/2/3). Replicates of each sequence was designated by lowercase roman letters.

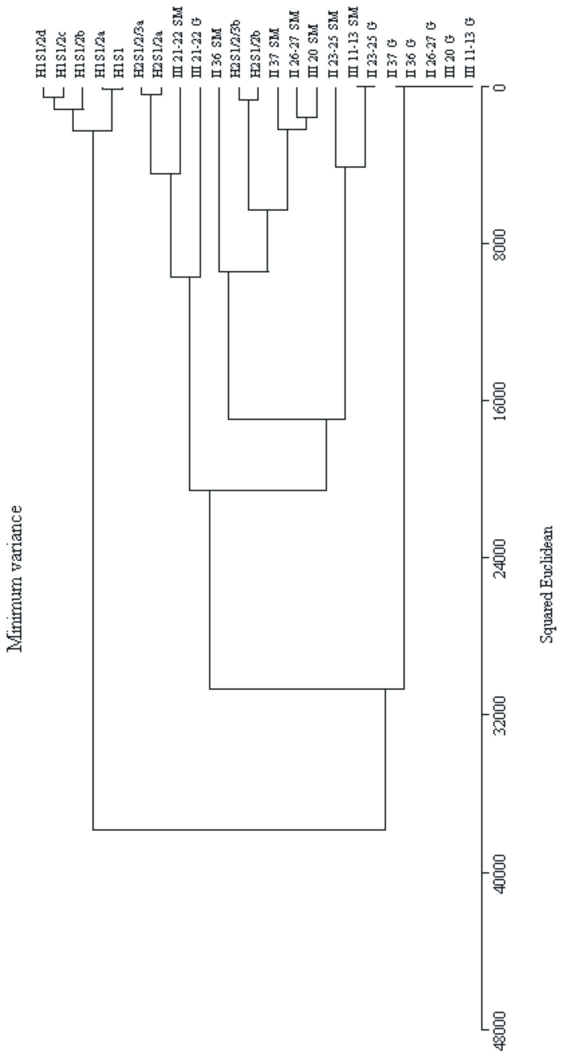


Figure 37: Dendrogram using squared Euclidian distance and minimum variance amalgamation for cut-mark frequencies of the large terrestrial mammals from ‘Ubeidiya per ‘pooled stratum’ and size and nine actualistic experiments. Mammals of body size E and F are denoted by the suffix SM after the name of the strata and mammals of body size G are denoted with the suffix G after the name of the strata

Body size of ‘Ubeidiya fauna is analyzed as Ruminantia G (L) and Ruminantia E and F (SM). Comparative data obtained from Domínguez-Rodrigo (1997). The two sequences: hominin to carnivore sequence and carnivore to hominin to carnivore sequence are labeled H1 and H2 respectively. In each sequence, several different experiments were done which included different sequences numbered from 1 to 3. In hypothesis H1, experiments included hominins only (H1S1), or both hominin and carnivore ravaging (H1S1/2). In hypothesis H2, experiments included carnivore and hominins (H2S1/2), carnivore - hominin sequence followed by hyaena scavenging as well (H2S1/2/3). Replicates of each sequence was designated by lowercase roman letters.

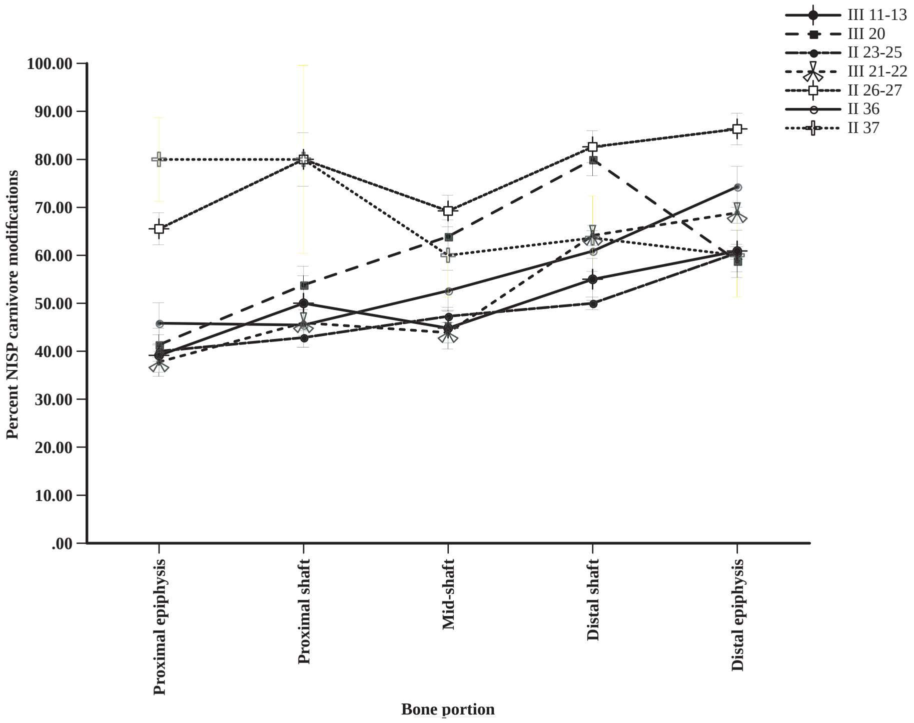


Figure 38: Percent limb portions with carnivore modifications of the ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

Error bars represent 95% confidence intervals.

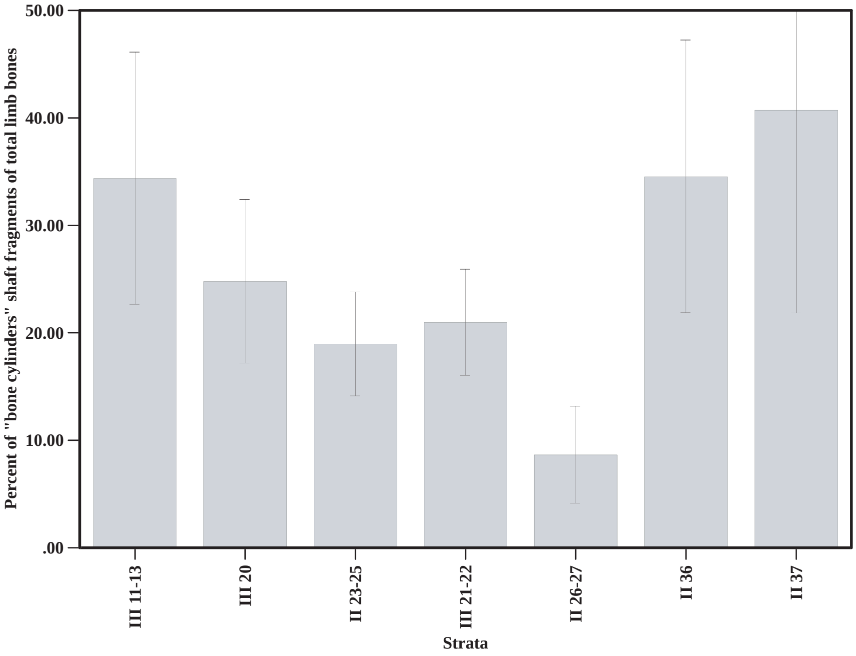


Figure 39: Percent of “bone cylinder” shaft fragments of all limb specimens of the ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

Error bars represent 95% confidence intervals.

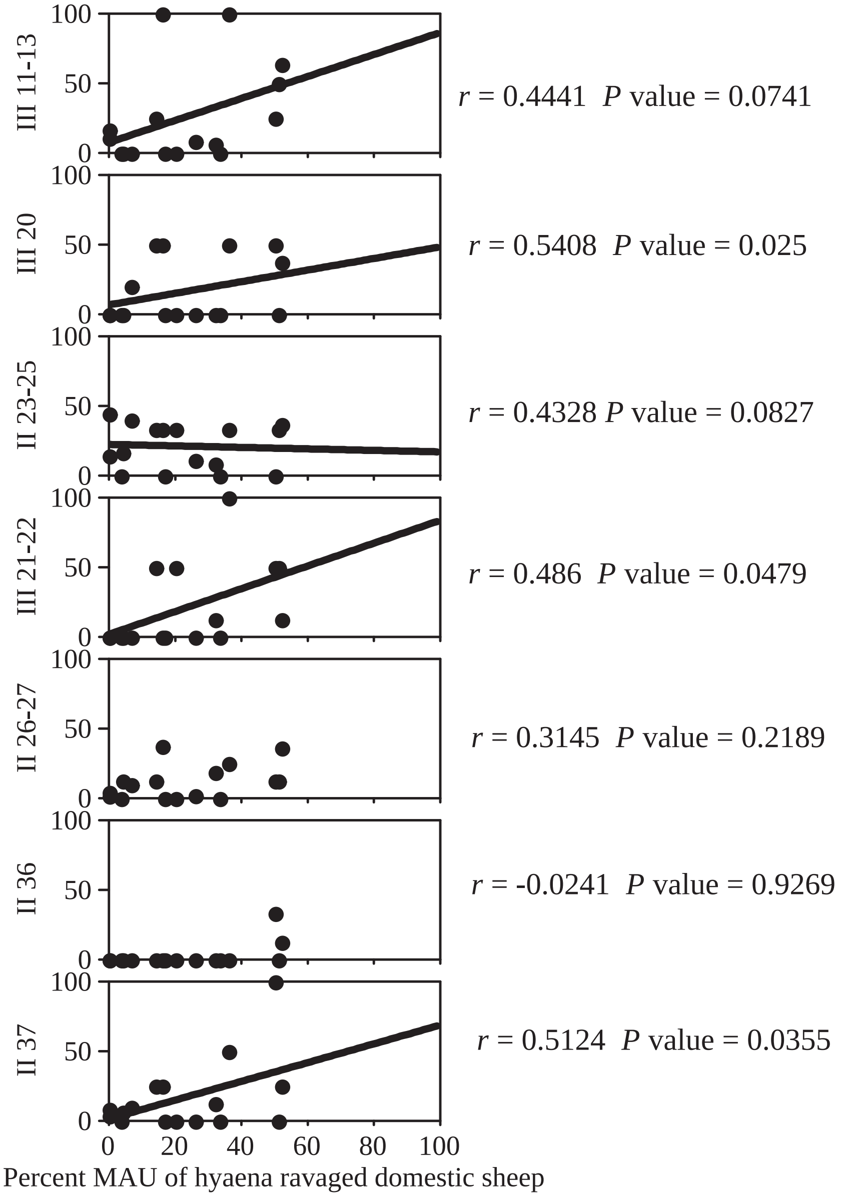


Figure 40: Percent MAU for 'Ubeidiya Ruminantia body size E correlated with percent MAU of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991)

Pearson's coefficient of correlation r and *P* values are presented for significant correlation (P value < 0.1).

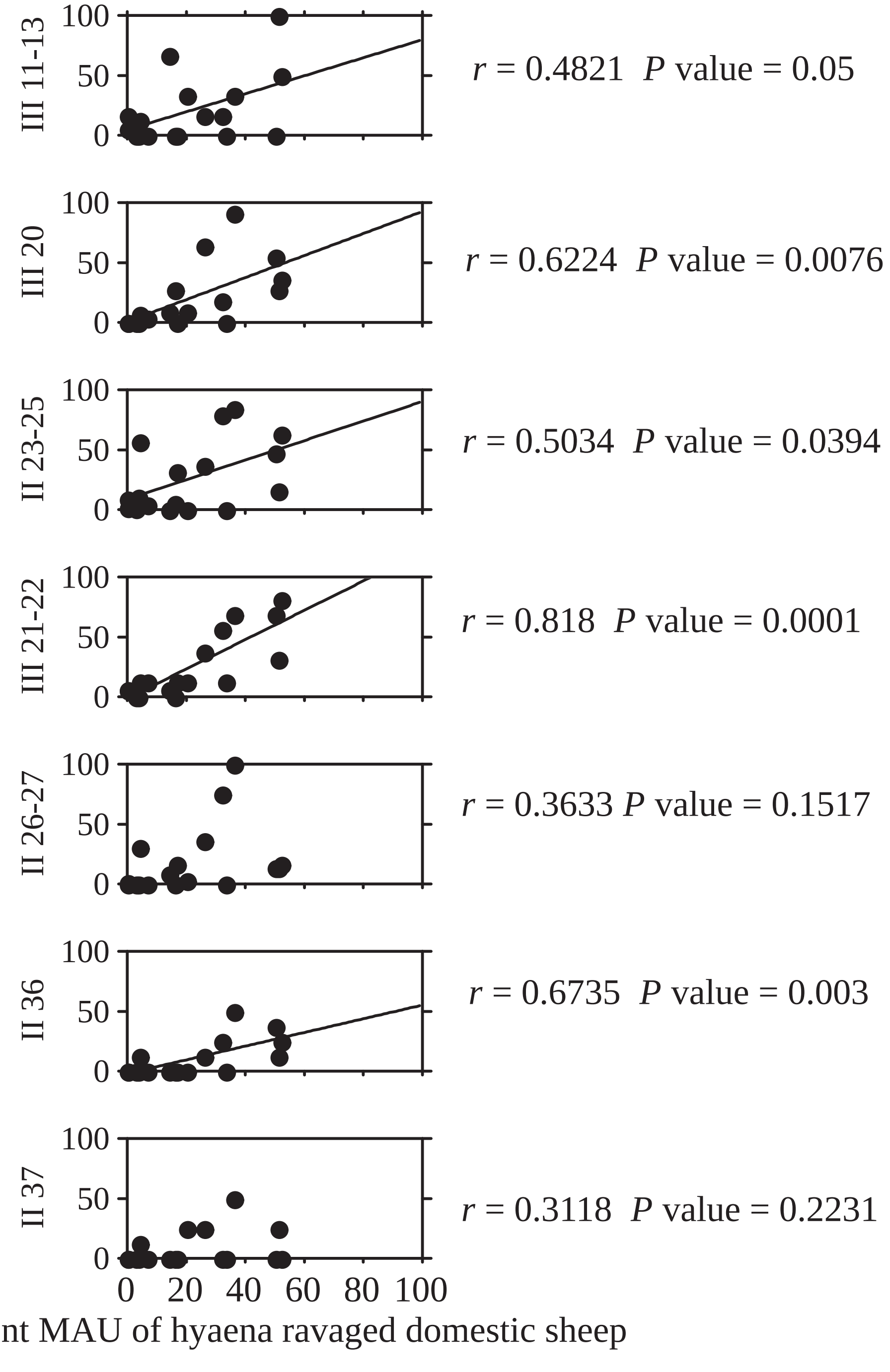


Figure 41: Percent MAU for ‘Ubeidiya Ruminantia body size F correlated with percent MAU of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991)

Pearson’s coefficient of correlation r and P values are presented for significant correlation (P value < 0.1).

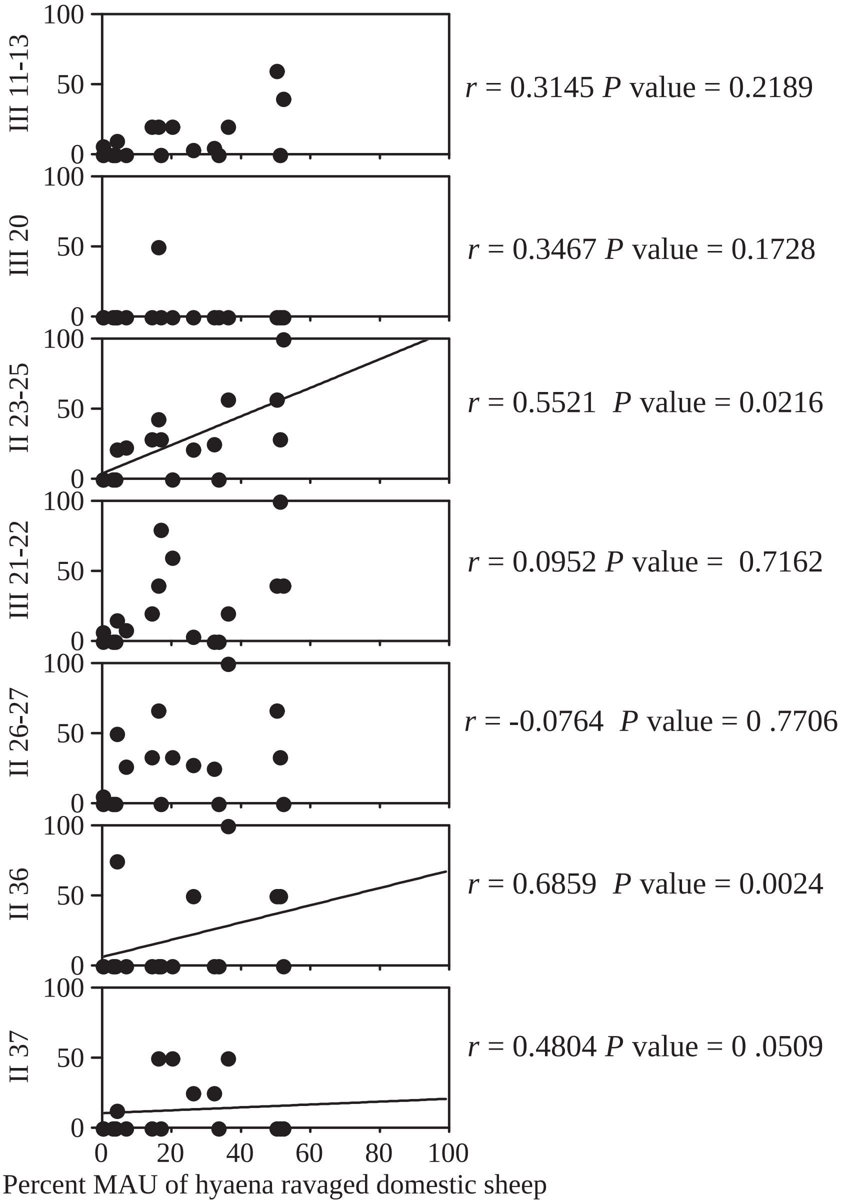
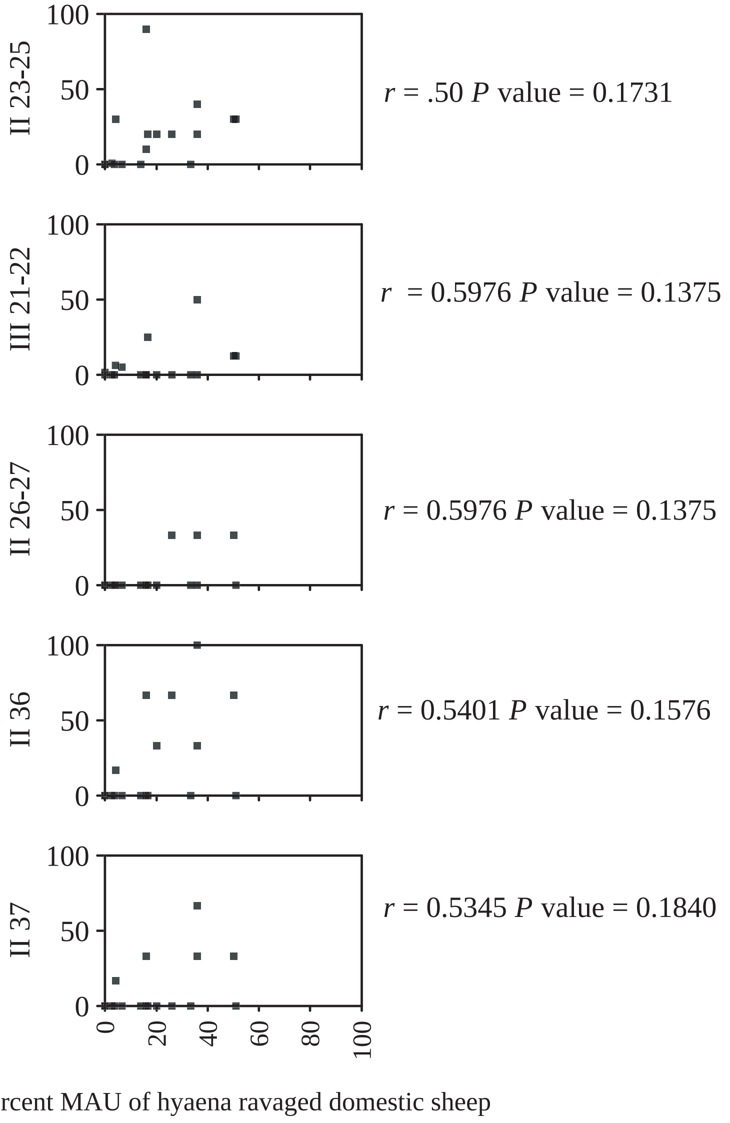


Figure 42: Percent MAU for ‘Ubeidiya Ruminantia body size G correlated with percent MAU of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991)

Pearson’s coefficient of correlation r and P values are presented for significant correlation (P value < 0.1).



r = .50 *P* value = 0.1731

r = 0.5976 *P* value = 0.1375

r = 0.5976 *P* value = 0.1375

r = 0.5401 *P* value = 0.1576

r = 0.5345 *P* value = 0.1840

Figure 43: Percent MAU for ‘Ubeidiya Equidae correlated with percent MAU of hyaena ravaged domestic sheep bones (Marean & Spencer, 1991)

Pearson’s coefficient of correlation r and *P* values are presented for significant correlation (P value < 0.1).

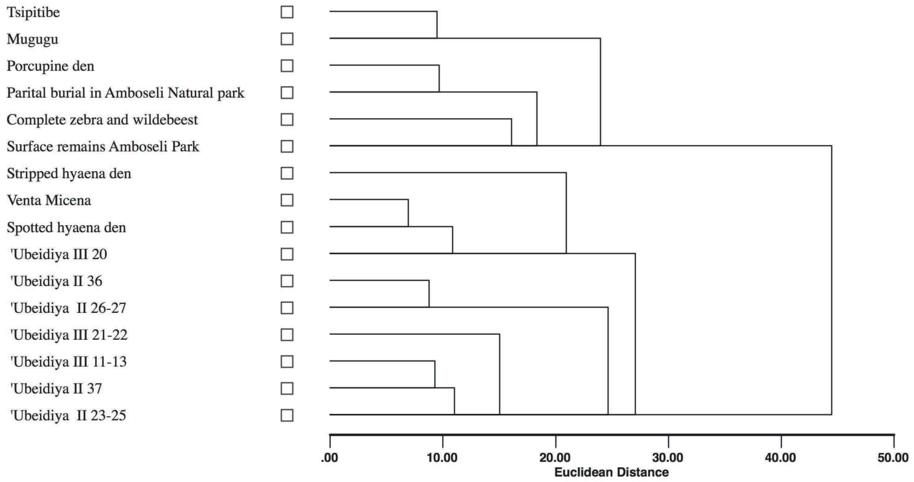


Figure 44: Dendrogram using Euclidian distance and weighted pair-group with arithmetic averaging amalgamation for body part distribution of the large terrestrial mammals of 'Ubeidiya per 'pooled stratum' and comparative ethnographic and taphonomic assemblages

Cranial elements do not include loose teeth or antler fragments. Modern comparative data includes surface remains from Amboseli Natural Park (Behrensmeyer & Dechant Boaz, 1980), bones partially buried in Amboseli Natural park (Behrensmeyer & Dechant Boaz, 1980), Spotted Hyaena *Crocuta crocuta* den (Behrensmeyer & Dechant Boaz, 1980), stripped hyaena *Hyaena hyaena* den (Martínez Navarro & Palmqvist, 1999), Porcupine *Hystrix indica* den (Martínez Navarro & Palmqvist, 1999), Magugu which is a Hadza kill size (Lupo, 2001) and Tsipitibe which is a Hadza camp site (Lupo, 2001). The Plio - Pleistocene comparative sites include Venta Micena, Spain which has been interpreted as a short faced hyaena *Pachycrocuta brevirostris* den (Martínez Navarro & Palmqvist, 1999).

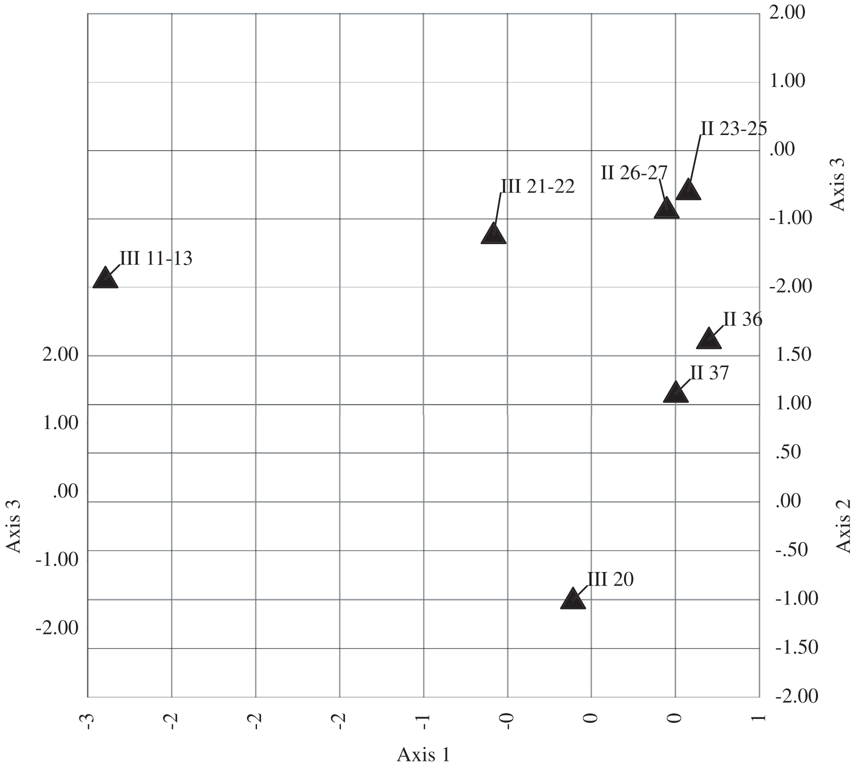


Figure 45: Scattergram for correspondence analysis axes using presence-absence of large terrestrial mammals among ‘Ubeidiya strata

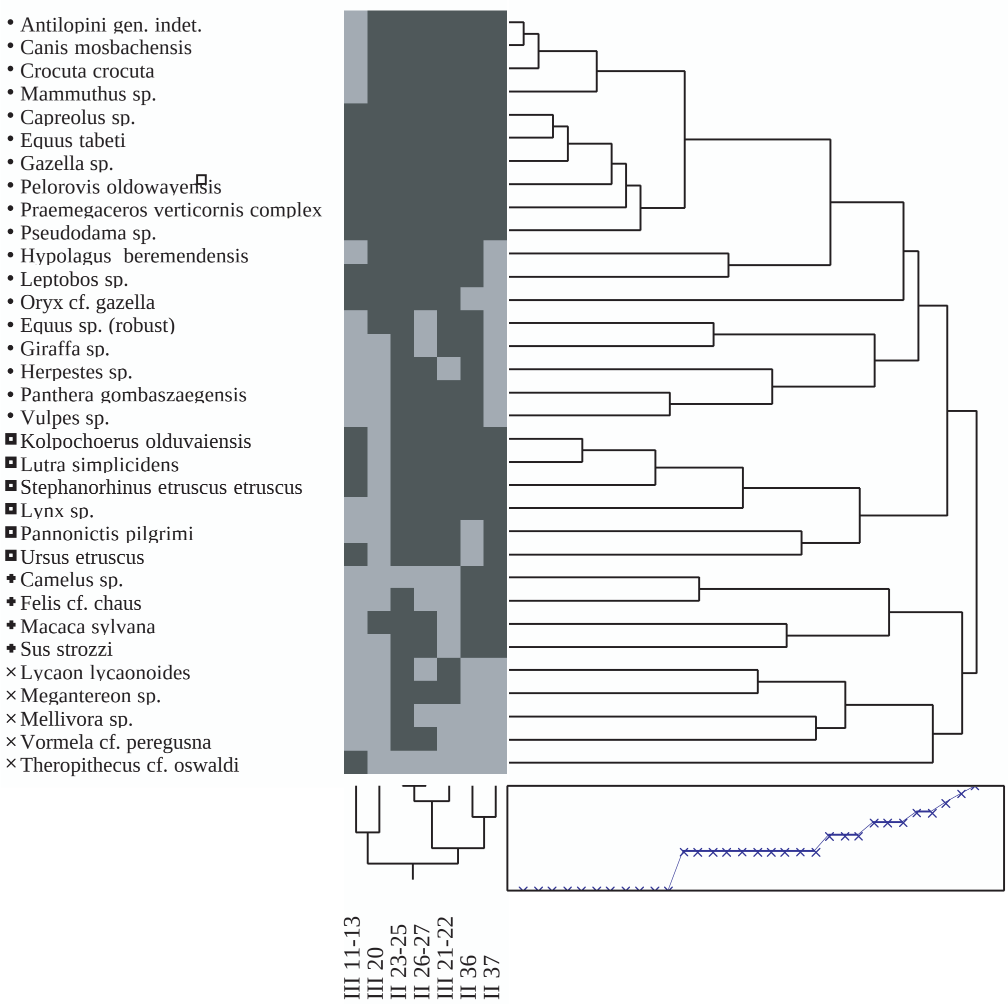


Figure 46: Q and R mode clustering for presence-absence distribution of large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

Hierarchical clustering of presence-absence of species per ‘pooled stratum’ using maximum distance method on unstandardized data. Dark squares denote presence and light squares denote absence. Species are marked according to cluster affiliation.

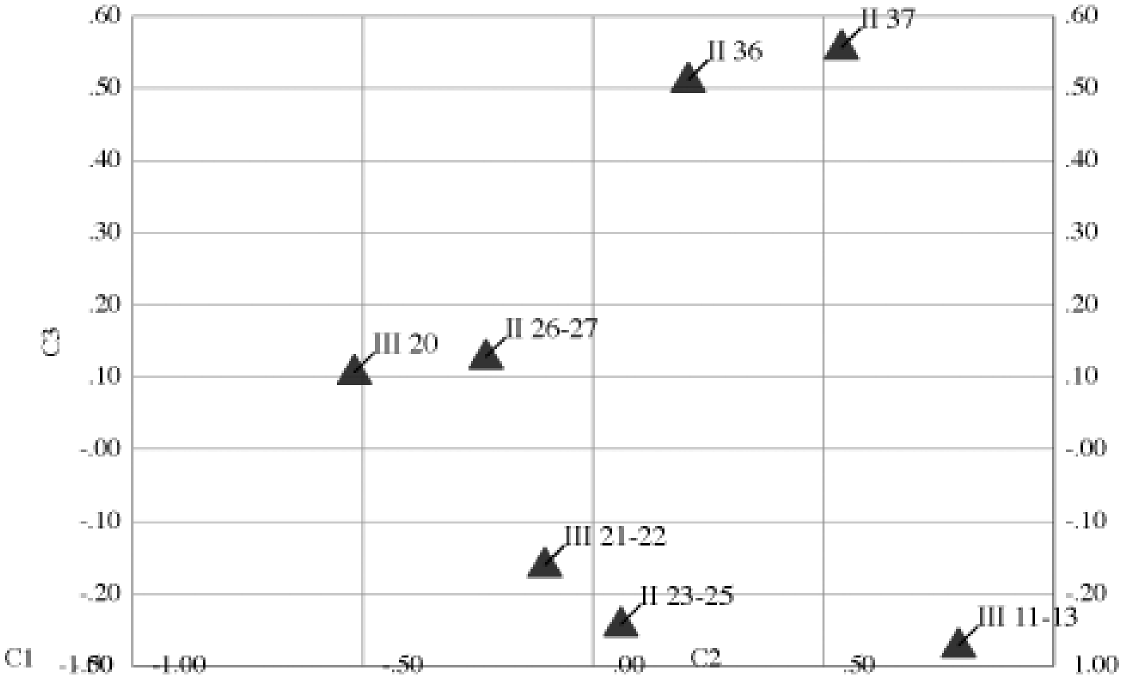


Figure 47: Scattergram for correspondence analysis axes using NISP frequencies of large terrestrial mammals among ‘Ubeidiya strata

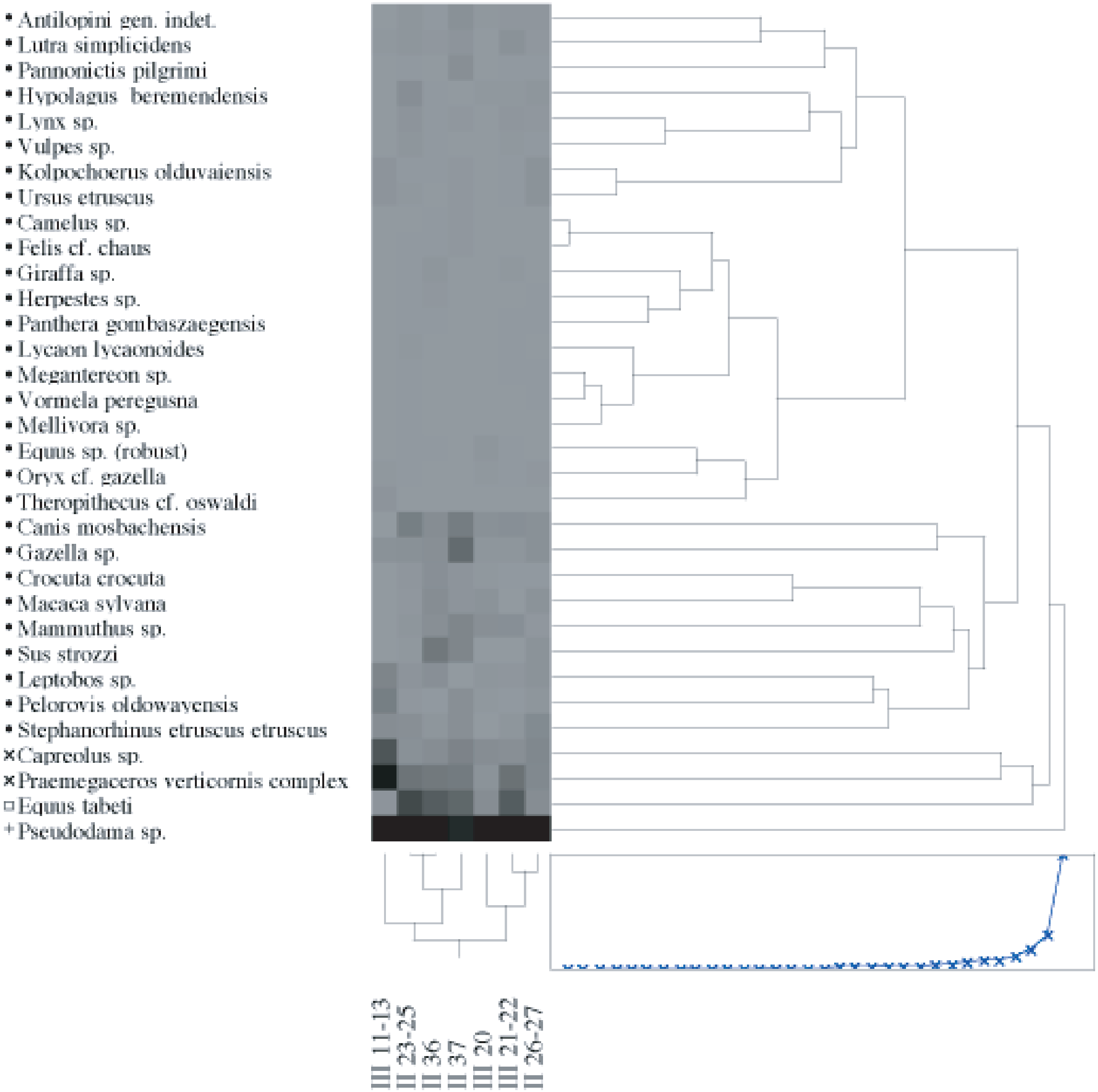


Figure 48: R and Q mode double cluster for NISP frequencies of the large terrestrial mammals of ‘Ubeidiya per ‘pooled stratum’

Hierarchical clustering of NISP frequencies per ‘pooled stratum’ using ward method on unstandardized data. Dark squares denote high abundance. Deceasing color denotes decreasing abundance. White denotes absence.

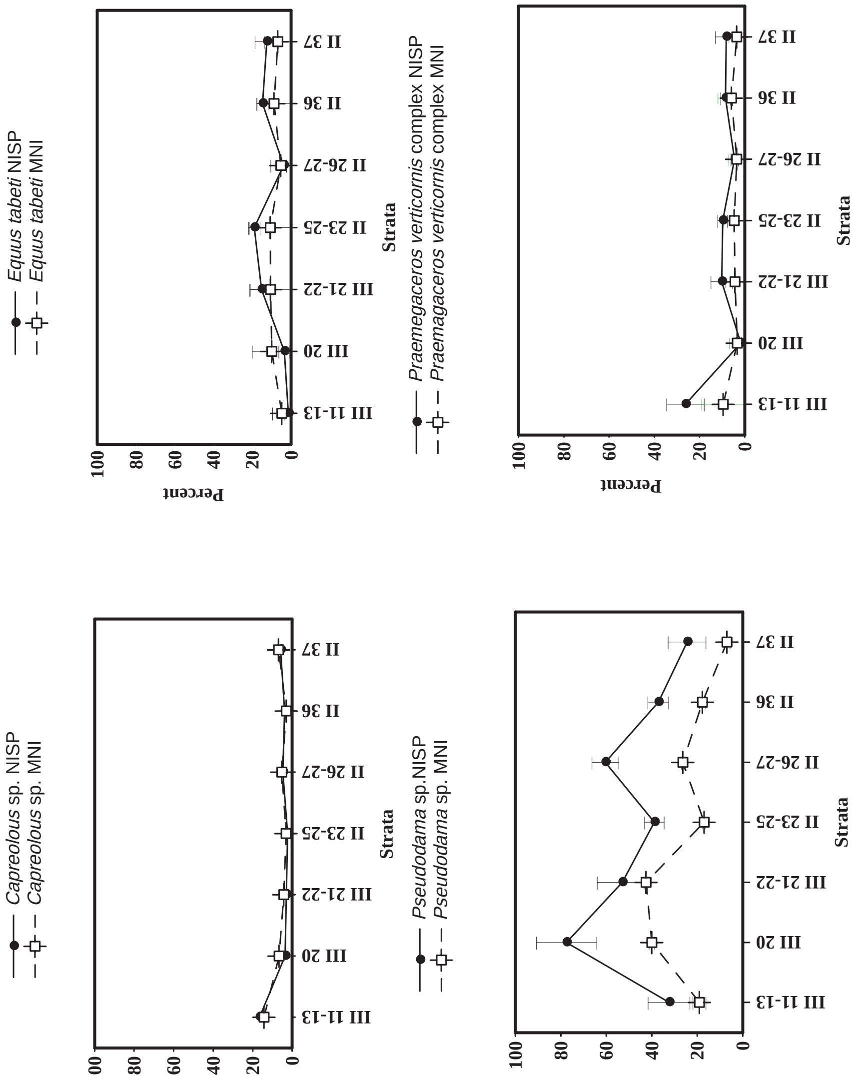


Figure 49: Distribution of four common taxa in ‘Ubeidiya through time using NISP and MNI quantification

Error bars represent 95% CI.

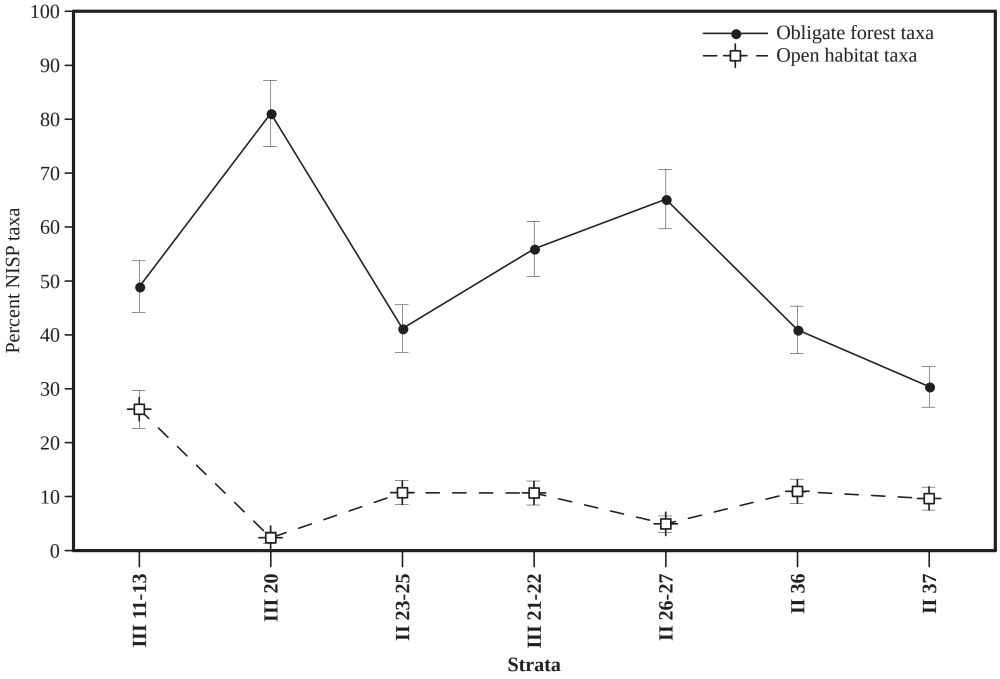


Figure 50: Distribution of two groups of habitat specific taxa in ‘Ubeidiya using NISP quantification

Error bars represent 95% CI.

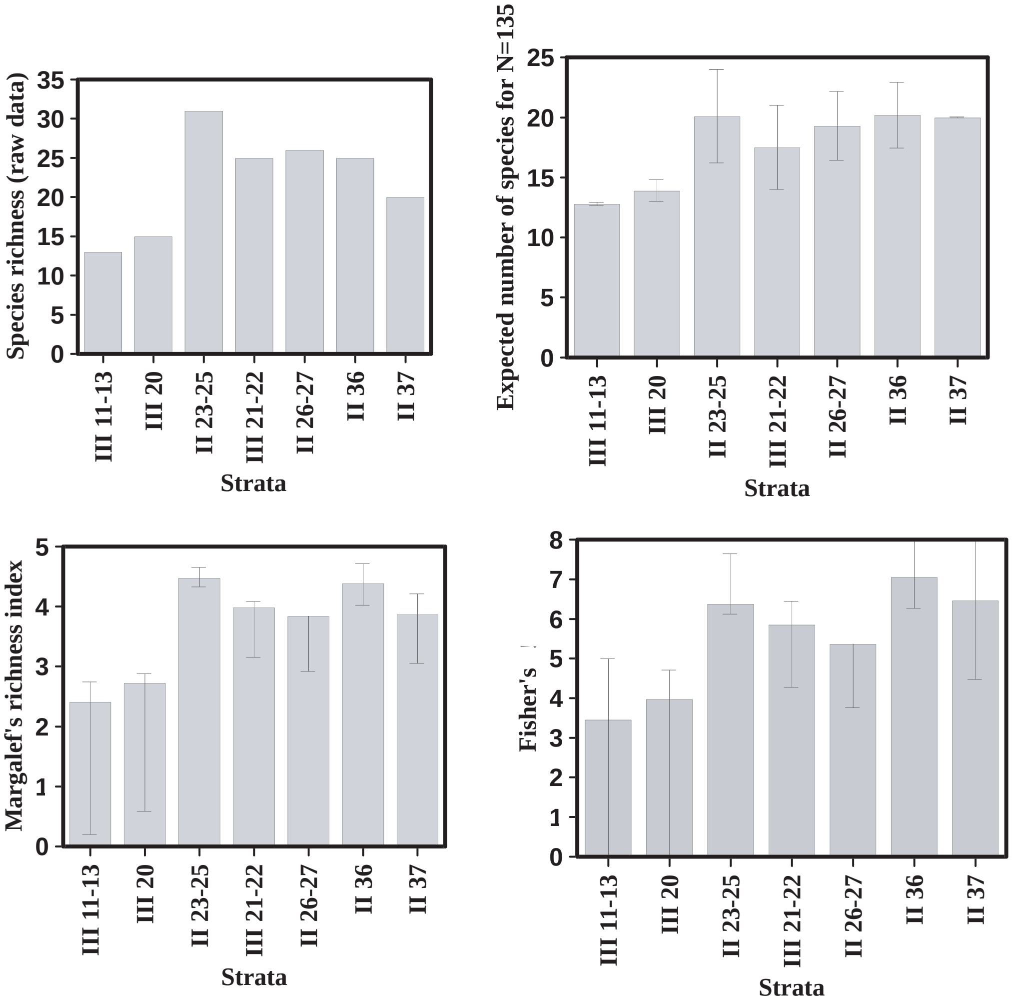


Figure 51: Species richness indices for ‘Ubeidiya strata

Rarefaction calculated for estimated number of species for $n = 135$; error bars represent rarefaction variance. Margalef’s richness index and Fisher’s α error bars represent pooled strata 95% bootstrapped confidence intervals.

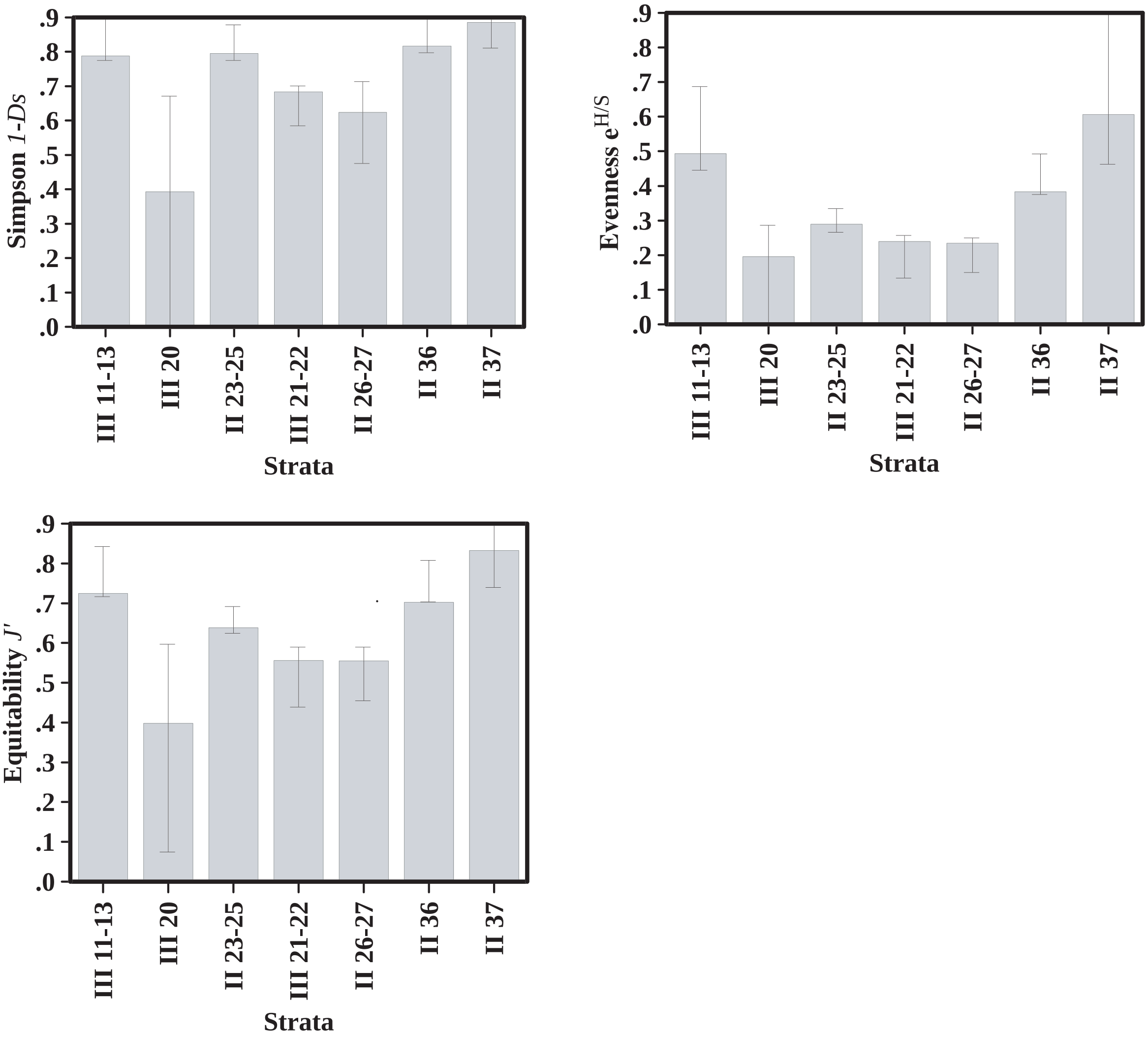
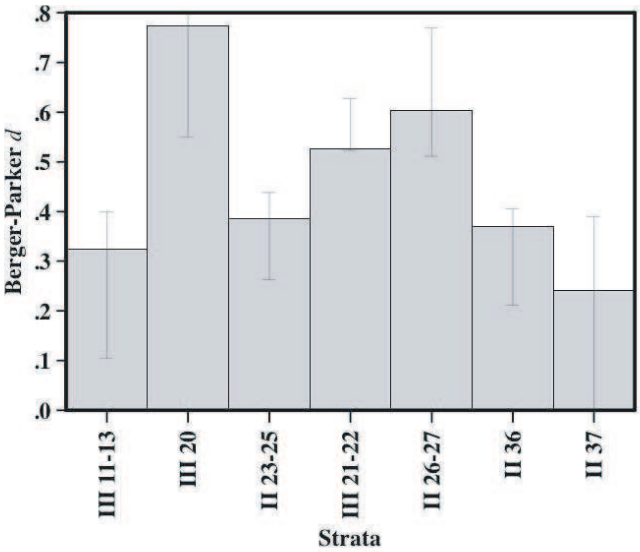


Figure 52: Evenness diversity indices for ‘Ubeidiya strata

Error bars represent 95% confidence intervals.



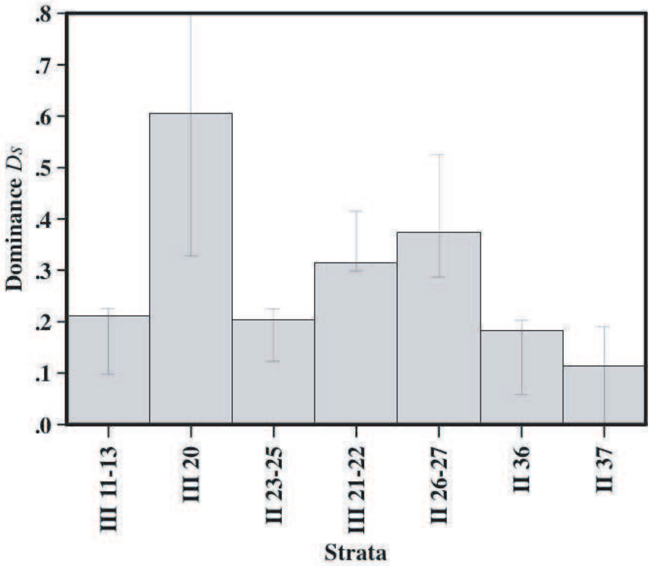
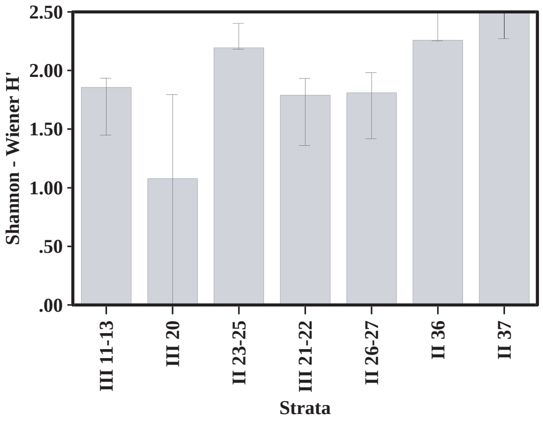


Figure 53: Dominance diversity indices for ‘Ubeidiya strata

Error bars represent 95% confidence intervals.



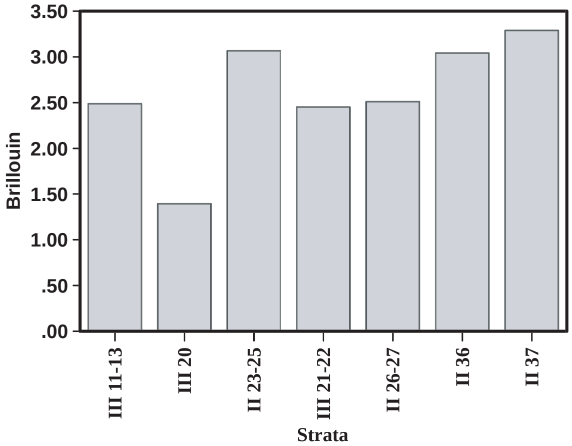


Figure 54: Diversity indices for ‘Ubeidiya strata

Error bars represent 95% confidence intervals.

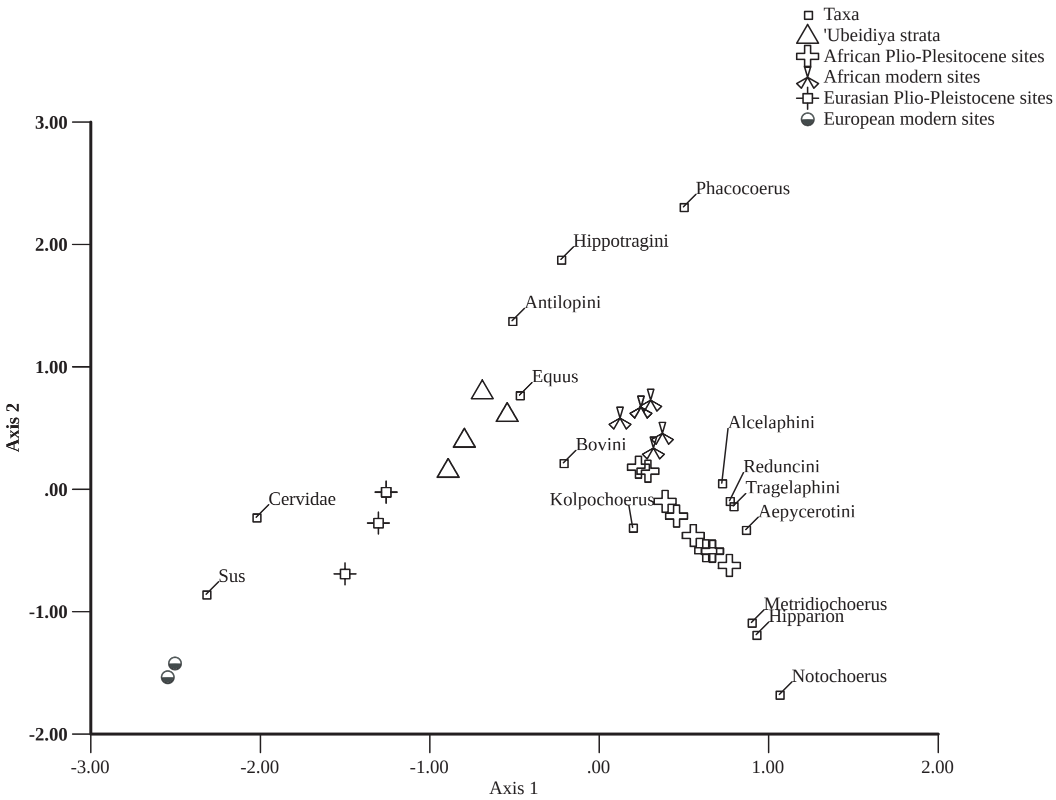


Figure 55: Scattergram for correspondence analysis axes based on presence-absence of mesoherbivores from 'Ubeidiya strata and comparative sites

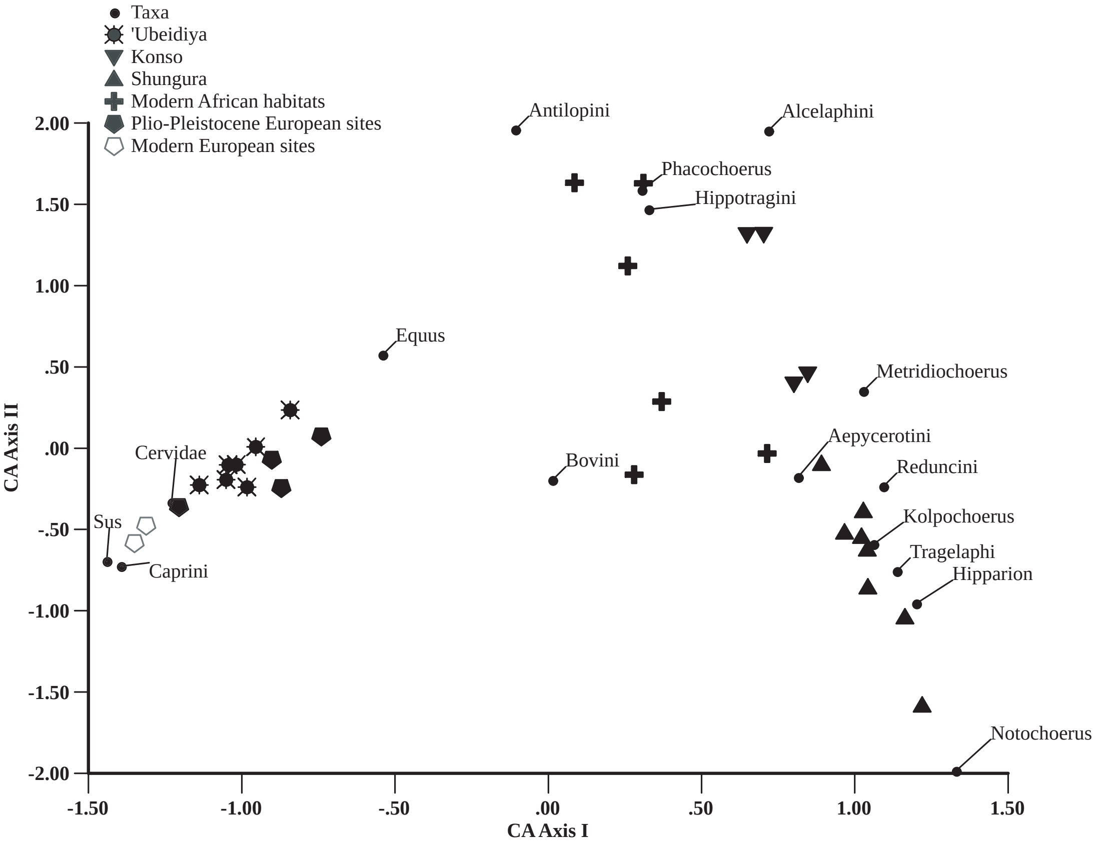


Figure 56: Scattergram for correspondence analysis axes based on relative frequencies of meso-herbivores from ‘Ubeidiya strata and comparative sites

Appendix B

Tables

Table 1: Distribution of identified specimens from ‘Ubeidiya

Fraction	n	**Percent of total large mammals**	**Percent of total specimens**
Identified to large terrestrial mammal species	2582	29.02	21.34
Identified to *Hippopotamus* spp.	947	10.64	7.82
Identified to *Homo* sp.	7	0.078	0.057
Identified to *Equus* cf. *caballus*	1	0.01	0.008
Total identified to large mammal species	3537	39.75	31.68
Identified to skeletal element and/or higher level taxon	3833	43.08	31.68
Unidentified large mammal fragments	539	6.058	4.455
Total large mammals assigned to strata	7909	88.89	65.37
Large mammals not assigned to strata	799	8.98	6.6
Total large mammals	8897	100	73.54
Conjoined mammal fragments	46	NA	0.38
Other taxa	3155	NA	26.07
TOTAL SPECIMENS ANALYZED	12098	NA	100

Subtotals in boldface.

Table 2: Large terrestrial mammal distribution among ‘Ubeidiya strata using NISP quantification, percentages in parentheses

Species	III 11-13	III 20	II 23-25	III 21-22	II 26-27	II 36	II 37	TOTAL
Antilopini gen. indet.	0 (0.00)	1 (0.59)	11 (1.35)	4 (0.97)	7 (1.04)	1 (0.42)	3 (2.21)	28
Camelus sp.	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.42)	1 (0.74)	3
Canis mosbachensis	0 (0.00)	4 (2.37)	57 (7.00)	11 (2.66)	15 (2.23)	9 (3.80)	10 (7.35)	108
Capreolous sp.	24 (16.55)	6 (3.55)	19(2.33)	13 (3.15)	32 (4.75)	9 (3.80)	9 (6.62)	115
Crocuta crocuta	0 (0.00)	1 (0.59)	8 (0.98)	2 (0.48)	3 (0.45)	6 (2.53)	2 (1.47)	23
Equus sp. (robust)	0 (0.00)	2 (1.18)	2 (0.25)	1 (0.24)	0 (0.00)	1 (0.42)	0 (0.00)	6
Equus tabeti	2 (1.38)	6 (3.55)	154 (18.92)	63 (15.25)	26 (3.86)	35 (14.77)	17 (12.50)	326
Felis cf. *chaus*	0 (0.00)	0 (0.00)	1 (0.12)	0 (0.00)	0 (0.00)	1 (0.42)	1 (0.74)	3
Gazella sp.	3 (2.07)	2 (1.18)	18 (2.21)	5 (1.21)	15 (2.23)	7 (2.95)	16 (11.76)	70
Giraffa sp.	0 (0.00)	0 (0.00)	1 (0.12)	3 (0.73)	0 (0.00)	3 (1.27)	0 (0.00)	8
Herpestes sp.	0 (0.00)	0 (0.00)	3 (0.37)	0 (0.00)	1 (0.15)	2 (0.84)	0 (0.00)	6
Hypolagus beremendensis	0 (0.00)	1(0.59	25 (3.07)	3 (0.73)	9 (1.34)	1 (0.42)	0 (0.00)	40
Kolpochoerus olduvaiensis	2 (1.38)	0 (0.00)	2 (0.25)	1 (0.24)	12 (1.78)	1 (0.42)	1(0.74)	20
Leptobos sp.	8 (5.52)	2 (1.18)	13 (1.60)	4 (0.97)	12 (1.78)	6 (2.53)	0 (0.00)	49
Lutra simplicidens	1 (0.69)	0 (0.00)	10 (1.23)	9 (2.18)	6 (0.89)	2 (0.84)	2 (1.47)	32
Lycaon lycaonoides	0 (0.00)	0 (0.00)	5 (0.61)	2 (0.48)	0 (0.00)	0 (0.00)	0 (0.00)	8
Lynx sp.	0 (0.00)	0 (0.00)	12 (1.47)	4 (0.97)	5 (0.74)	1 (0.42)	1 (0.74)	25

Table 2: con't

Species	III 11-13	III 20	II 23-25	III 21-22	II 26-27	II 36	II 37	TOTAL
Macaca sylvana	0 (0.00)	3 (1.78)	6 (0.74)	0 (0.00)	12 (1.78)	9 (3.80)	2 (1.47)	32
Mammuthus sp.	0 (0.00)	5 (2.96)	10 (1.23)	11 (2.66)	5 (0.74)	7 (2.95)	7 (5.15)	62
Megantereon sp.	0 (0.00)	0 (0.00)	3 (0.37)	1 (0.24)	1 (0.15)	0 (0.00)	0 (0.00)	5
Mellivora sp.	0 (0.00)	0 (0.00)	1 (0.12)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1
Oryx cf. *gazella*	1 (0.69)	1 (0.59)	3 (0.37)	1 (0.24)	5 (0.74)	0 (0.00)	0 (0.00)	12
Pannonictis pilgrimi	0 (0.00)	0 (0.00)	1 (0.12)	2 (0.48)	3 (0.45)	0 (0.00)	4 (2.94)	10
Panthera gombaszoegensis	0 (0.00)	0 (0.00)	1 (0.12)	2 (0.48)	2 (0.30)	1 (0.42)	0 (0.00)	6
Pelorovis oldowayensis	10 (6.90)	1 (0.59)	7 (0.86)	2 (0.48)	9 (1.34)	1 (0.42)	4 (2.94)	40
Praemegaceros verticornis complex	38 (26.21)	3 (1.78)	79 (9.71)	42 (10.17)	30 (4.46)	20 (8.44)	11 (8.09)	238
Pseudodama sp.	47 (32.41)	131 (77.51)	315 (38.70)	218 (52.78)	406 (60.33)	88 (37.13)	33 (24.26)	1298
Stephanorhinus etruscus etruscus	5 (3.45)	0 (0.00)	24 (2.95)	5 (1.21)	28 (4.16)	3 (1.27)	4 (2.94)	72
Sus strozzi	0 (0.00)	0 (0.00)	5 (0.61)	0 (0.00)	13 (1.93)	21 (8.86)	7 (5.15)	51
Theropithecus cf. *oswaldi*	2 (1.38)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2
Ursus etruscus	2 (1.38)	0 (0.00)	5 (0.61)	1 (0.24)	12 (1.78)	0 (0.00)	1 (0.74)	22
Vormela cf. *peregusna*	0 (0.00)	0(0.00	3 (0.37)	0 (0.00)	1 (0.15)	0 (0.00)	0 (0.00)	4
Vulpes sp.	0 (0.00)	0 (0.00)	10 (1.23)	3 (0.73)	3 (0.45)	1(0.42)	0(0.00	18
n	145	169	814	413	673	237	136	2743

Table 3: Large terrestrial mammal distribution among ‘Ubeidiya ‘pooled strata’ using MNI quantification

Species	III 11-13		III 20		II 23-25		III 21-22		II 26-27		II 36		II 37	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Gazella sp.	1	4.76	1	3.33	2	3.08	1	2.13	2	3.51	1	2.94	1	3.45
Antilopini gen. indet.	0	0.00	1	3.33	2	3.08	1	2.13	2	3.51	1	2.94	1	3.45
Oryx cf. *gazella*	1	4.76	1	3.33	2	3.08	1	2.13	2	3.51	0	0.00	0	0.00
Leptobos sp.	1	4.76	1	3.33	1	1.54	1	2.13	2	3.51	1	2.94	0	0.00
Pelorovis oldowayensis	2	9.52	1	3.33	1	1.54	1	2.13	1	1.75	1	2.94	2	6.90
Capreolous sp.	3	14.29	2	6.67	2	3.08	2	4.26	3	5.26	1	2.94	2	6.90
Pseudodama sp.	4	19.05	12	40.00	11	16.92	20	42.55	15	26.32	6	17.65	2	6.90
Praemegaceros verticornis complex	2	9.52	1	3.33	3	4.62	2	4.26	2	3.51	2	5.88	1	3.45
Camelus sp.	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	2.94	1	3.45
Giraffa sp.	0	0.00	0	0.00	1	1.54	1	2.13	0	0.00	1	2.94	1	3.45
Sus strozzi	0	0.00	0	0.00	2	3.08	0	0.00	3	5.26	1	2.94	2	6.90
Kolpochoerus olduvaiensis	1	4.76	0	0.00	2	3.08	1	2.13	1	1.75	1	2.94	1	3.45
Equus tabeti	1	4.76	3	10.00	7	10.77	5	10.64	3	5.26	3	8.82	2	6.90
Equus sp. robust	0	0.00	1	3.33	1	1.54	1	2.13	0	0.00	1	2.94	0	0.00
Stepahnorhinus etruscus etruscus	2	9.52	0	0.00	2	3.08	1	2.13	2	3.51	1	2.94	1	3.45
Hypolagus beremendensis	0	0.00	1	3.33	3	4.62	1	2.13	1	1.75	0	0.00	0	0.00

Table 3: con't

Species	III 11-13		III 20		II 23-25		III 21-22		II 26-27		II 36		II 37	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Macaca sylvana	0	0.00	1	3.33	1	1.54	0	0.00	3	5.26	2	5.88	1	3.45
Theropithecus cf. *oswaldi*	1	4.76	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Mammuthus merdionalis	0	0.00	1	3.33	1	1.54	1	2.13	1	1.75	2	5.88	1	3.45
Ursus etruscus	1	4.76	1	3.33	1	1.54	0	0.00	2	3.51	0	0.00	1	3.45
Crocuta crocuta	0	0.00	1	3.33	2	3.08	1	2.13	1	1.75	1	2.94	1	3.45
Megantereon sp.	0	0.00	0	0.00	1	1.54	0	0.00	1	1.75	0	0.00	0	0.00
Panthera gombaszoegensis	0	0.00	0	0.00	1	1.54	1	2.13	1	1.75	1	2.94	1	3.45
Lynx sp.	0	0.00	0	0.00	1	1.54	1	2.13	1	1.75	1	2.94	1	3.45
Felis	0	0.00	0	0.00	1	1.54	0	0.00	0	0.00	1	2.94	1	3.45
Lycaon lycaonoides	0	0.00	0	0.00	1	1.54	1	2.13	0	0.00	0	0.00	0	0.00
Canis mosbachensis	0	0.00	1	3.33	4	6.15	1	2.13	2	3.51	1	2.94	2	6.90
Vulpes sp.	0	0.00	0	0.00	3	4.62	1	2.13	1	1.75	1	2.94	0	0.00
Mellivora sp.	0	0.00	0	0.00	1	1.54	0	0.00	0	0.00	0	0.00	0	0.00
Lutra simplicidens	1	4.76	0	0.00	2	3.08	0	0.00	2	3.51	1	2.94	1	3.45
Pannonictis pilgrimi	0	0.00	0	0.00	1	1.54	1	2.13	1	1.75	0	0.00	2	6.90
Vormela cf. *peregusna*	0	0.00	0	0.00	1	1.54	0	0.00	1	1.75	0	0.00	0	0.00

Table 3: con't

Species	III 11-13		III 20		II 23-25		III 21-22		II 26-27		II 36		II 37	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Herpestes sp.	0	0.00	0	0.00	1	1.54	0	0.00	1	1.75	1	2.94	0	0.00
n	21	100.00	30	100.00	65	100.00	47.000	100.00	57	100.00	34	100.00	29	100.00

Table 4: Percent of taxa of Africa biogeographic origin of total number of species across ‘Ubeidiya ‘pooled strata’

‘Pooled stratum’	Percent Africa species	Number of species in ‘pooled strata’
III 11-13	42.8	14
III 20	29.4	17
II 23-25	27.2	33
III 21-22	26	23
II 26-27	25.9	27
II 36	22.2	27
II 37	21.7	23

African taxa do not include taxa which have been found in Eurasia during the Miocene and Pliocene: *Gazella* sp., *Camelus* sp. and *Macaca sylvana*.

Table 5: Percent of individuals of African biogeographic origin of total large mammals of ‘Ubeidiya per ‘pooled stratum’

‘Pooled stratum’	Percent of African taxa	n	Percent African taxa without *Hippopotamus* spp.	n without *Hippopotamus* spp.
III 11-13	22.89	166	11.72	145
III 20	18.27	197	5.29	170
II 23-25	43.89	1137	21.72	815
III 21-22	49.11	676	16.71	413
II 26-27	57.3	1445	8.46	674
II 36	40.37	322	18.64	236
II 37	63.12	301	17.78	135
Total	2053	4244	397	2588

African taxa do not include taxa which have been found in Eurasia during the Miocene and Pliocene: *Gazella* sp., *Camelus* sp. and *Macaca sylvana*.

Table 6: Percentage of weathering stages of ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

	Weathering stage				
‘Pooled stratum’	1	2	3	4	n
III 11-13	74.07	18.52	4.63	2.78	108
III 20	63.35	27.95	7.45	1.24	161
II 23-25	83.06	11.42	4.05	1.47	543
III 21-22	67.69	25.35	5.57	1.39	359
II 26-27	77.60	15.16	5.66	1.58	442
II 36	80.15	15.27	2.29	2.29	131
II 37	71.79	19.23	8.97	0.00	78
N	1380	320	94	28	1822

Table 7: Percent weathering stage of ‘Ubeidiya large terrestrial mammals by body size groups and per ‘pooled stratum’

‘Pooled stratum’	1		2		3		4		n	Significance
	SM	L	SM	L	SM	L	SM	L		
III 11-13	71.62	78.79	21.62	12.12	4.05	6.06	2.7	3.03	107	0.699
III 20	61.74	77.78	29.53	11.11	7.38	11.11	1.34	0	158	0.576
II 23-25	83.87	80.43	12.02	10.87	2.35	7.61	1.76	7.61	525	0.0468
III 21-22	67.19	66.32	27.34	22.11	3.91	10.53	1.56	1.05	351	0.061
II 26-27	79.95	52.38	14.65	23.81	4.11	19.05	1.29	4.76	431	0.0003
II 36	79.31	85.37	13.79	14.63	3.45	0	3.45	0	128	0.1758
II 37	64	82.61	26	8.7	10	8.7	0	0	73	1

Body size group SM is equivalent to body sizes E and F. body size group L is equivalent to body size G. Significance is determined using Fisher’s exact test. Since more than 20% of cells had an expected value of less than 5, weathering stages 1 and 2 as well as 3 and 4 for combined for statistical analysis.

Table 8: Distribution of $\frac{S}{I}$ of 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Number	Mean	Std Dev	Std Err Mean	Lower 95%	Upper 95%
III 11-13	289	0.716123	0.173005	0.01018	0.69609	0.73615
III 20	326	0.676247	0.172298	0.00954	0.65747	0.69502
II 23-25	1889	0.664721	0.185456	0.00427	0.65635	0.67309
III 21-22	1173	0.645976	0.191535	0.00559	0.63500	0.65695
II 26-27	1807	0.669877	0.180898	0.00426	0.66153	0.67822
II 36	776	0.655438	0.180517	0.00648	0.64272	0.66816
II 37	422	0.666045	0.181687	0.00884	0.64866	0.68343

Table 9: Distribution of $\frac{I}{L}$ of 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Number	Mean	Std Dev	Std Err Mean	Lower 95%	Upper 95%
III 11-13	289	0.565896	0.230543	0.01356	0.53920	0.59259
III 20	326	0.495270	0.228907	0.01268	0.47033	0.52021
II 23-25	1889	0.586538	0.207418	0.00477	0.57718	0.59590
III 21-22	1173	0.524598	0.220950	0.00645	0.51194	0.53726
II 26-27	1808	0.624531	0.192493	0.00453	0.61565	0.63341
II 36	776	0.629008	0.185507	0.00666	0.61594	0.64208
II 37	422	0.600226	0.192556	0.00937	0.58180	0.61865

Table 10: Distribution of $\frac{S}{L}$ of 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Number	Mean	Std Dev	Std Err Mean	Lower 95%	Upper 95%
III 11-13	289	0.399813	0.184993	0.01088	0.37839	0.42123
III 20	326	0.335040	0.183718	0.01018	0.31502	0.35506
II 23-25	1889	0.388866	0.182926	0.00421	0.38061	0.39712
III 21-22	1173	0.341557	0.187674	0.00548	0.33081	0.35231
II 26-27	1808	0.415987	0.170746	0.00402	0.40811	0.42386
II 36	776	0.404371	0.154941	0.00556	0.39345	0.41529
II 37	422	0.399584	0.176116	0.00857	0.38273	0.41644

Table 11: Distribution of maximum projection sphericity of 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Number	Mean	Std Dev	Std Err Mean	Lower 95%	Upper 95%
III 11-13	288	0.666736	0.215796	0.01272	0.64171	0.69176
III 20	326	0.596024	0.149463	0.00828	0.57974	0.61231
II 23-25	1883	0.628804	0.168210	0.00388	0.62120	0.63641
III 21-22	1168	0.593295	0.168800	0.00494	0.58360	0.60299
II 26-27	1806	0.646362	0.149197	0.00351	0.63948	0.65325
II 36	776	0.637570	0.141047	0.00506	0.62763	0.64751
II 37	421	0.641229	0.201778	0.00983	0.62190	0.66056

Table 12: Distribution of grain shape frequencies for 'Ubeidiya large terrestrial mammals for body size E and F (small-medium) per 'pooled stratum'

'Pooled stratum'	Bladed	Equate	Oblate	Prolate
III 11-13	18.31	23.24	14.79	43.66
III 20	34.62	14.53	8.97	41.88
II 23-25	32.34	25	13.93	28.73
III 21-22	36.61	16.94	10.56	35.88
II 26-27	20.03	33.58	14.61	31.78
II 36	14.1	26.28	19.87	39.74
II 37	26.52	24.24	13.64	35.61

Table 13: Distribution of grain shape frequencies for 'Ubeidiya large terrestrial mammals body size G (large) per 'pooled stratum'

'Pooled stratum'	Bladed	Equate	Oblate	Prolate
III 11-13	18.39	28.74	18.39	34.48
III 20	46.88	9.38	18.75	25
II 23-25	27.01	20.78	22.08	30.13
III 21-22	40.21	19.59	11.68	28.52
II 26-27	14.84	39.06	17.19	28.91
II 36	8.06	41.94	6.45	43.55
II 37	26	26	22	26

Table 14: Distribution of axial ratio $\frac{S}{I}$ for 'Ubeidiya large terrestrial mammals body size E-F (small-medium) and body size G (large) per 'pooled stratum'

'Pooled stratum'	Small-medium mean	Small-medium n	Large mean	Large n	Difference	t ratio	DF	P value
III 11-13	0.729	138	0.714	87	-0.01551	-0.663	177.5	0.508
III 20	0.694	230	0.579	32	-0.11584	-3.684	40.31	0.0007
II 23-25	0.683	746	0.67	385	-0.01	-1.17	779	0.24
III 21-22	0.663	536	0.65	291	-0.01367	-0.97	574	0.332
II 26-27	0.7229	653	0.725	128	0.002	0.165	178	0.868
II 36	0.723	156	0.773	62	0.05	2.53	144	0.01
II 37	0.703	129	0.691	50	-0.011	-0.389	87.69	0.697

Table 15: Distribution of axial ratio $\frac{I}{L}$ for ‘Ubeidiya large terrestrial mammals body size E-F (small-medium) and body size G (large) per ‘pooled stratum’

‘Pooled stratum’	Small-medium mean	Small-medium n	Large mean	Large n	Difference	t ratio	DF	P value
III 11-13	0.548	138	0.616	87	0.068	2.134	188.89	0.034
III 20	0.469	230	0.586	32	0.116	3.349	47.9	0.0016
II 23-25	0.5965	746	0.609	385	0.0134	0.998	779	0.318
III 21-22	0.51	536	0.556	291	0.046	2.89	627.1	0.0039
II 26-27	0.649	653	0.683	128	0.034	1.849	195.7	0.06
II 36	0.615	156	0.642	62	0.027	0.748	101	0.456
II 37	0.585	129	0.628	50	0.042	1.298	92	0.197

Table 16: Distribution of axial ratio $\frac{S}{L}$ for ‘Ubeidiya large terrestrial mammals body size E-F (small-medium) and body size G (large) per ‘pooled stratum’

‘Pooled stratum’	Small-medium mean	Small-medium n	Large mean	Large n	Difference	t ratio	DF	P value
III 11-13	0.3945	138	0.435	87	0.0414	1.6	184.47	0.1108
III 20	0.327	230	0.341	32	0.0138	0.489	48.044	0.627
II 23-25	0.414	746	0.407	385	-0.007	-0.6	856	0.547
III 21-22	0.34	536	0.368	291	0.0278	1.973	579	0.0489
II 26-27	0.472	653	0.4968	128	0.02475	1.422	188.8	0.156
II 36	0.438	156	0.4979	62	0.059	1.96	99.79	0.052
II 37	0.414	129	0.436	50	0.022	0.728	93.53	0.46

Table 17: Distribution of maximum projection sphericity for ‘Ubeidiya large terrestrial mammals body size E-F (small-medium) and body size G (large) per ‘pooled stratum’

‘Pooled stratum’	Small-medium mean	Small-medium n	Large mean	Large n	Difference	t ratio	DF	P value
III 11-13	0.6409	138	0.661	87	0.02	1.1	101.56	0.27
III 20	0.588	230	0.571	32	-0.174	-0.70282	42.22	0.486
II 23-25	0.639	746	0.633	385	-0.0059	-0.644	852	0.519
III 21-22	0.588	536	0.602	291	0.01432	1.252	575.5	0.211
II 26-27	0.6844	653	0.7	128	0.0156	1.198	185	0.2324
II 36	0.667	156	0.71	62	0.043	2.16	105	0.03
II 37	0.6485	129	0.656	50	0.008	0.363	89.11	0.7168

Table 18: Body part distribution for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’ and for selected comparative Plio-Pleistocene sites

‘Pooled stratum’	Skull	Vertebra	Scapula/pelvis	Limbs	Manus/Pes	n
III 11-13	22.96	18.21	3.17	22.69	16.37	379
III 20	24.64	10	2.5	23.57	31.43	280
II 23-25	42.82	15.64	3.31	14.11	15.46	1630
III 21-22	25.7	23.32	5.86	20.61	21.91	922
II 26-27	55.72	3.32	1.49	8.45	15	1206
II 36	79.87	0.93	0.66	5.2	8.26	750
II 37	49.26	8.31	2.08	12.46	11.57	337
FxJj I	68	10	2	19	2	235
FxJj 3	64	3	0	29	4	75
FxJj 20E	50	4	1	31	14	381
FxJj 20M	62	10	1	22	6	391
Bk	33	16	3	40	8	1444
Fxjj 50	13	45	1	39	3	739
Fxjj 64	14	73	0	11	3	107
FLK Zinj	28	23	2	36	12	3513
MNK	34	14	5	36	12	842
FLNK 6	38	18	4	17	22	402
GgJj 5	20	22	22	32	4	76

Data for percent NISP. Skull includes crania, mandibles and loose teeth. Data for comparative Plio-Pleistocene sites from O’Connell *et al.* (2002).

Table 19: Percent MNE of ‘Ubeidiya Ruminantia F body portions compared to complete ruminant skeleton

‘Pooled stratum’	Cranium	Axial	Limbs	Feet	n
III 11-13	6.82	27.27	36.36	29.55	56.00
III 20	3.53	5.88	44.71	45.88	90.00
II 23-25	9.09	11.00	28.71	51.20	232.00
III 21-22	7.74	18.71	43.87	29.68	184.00
II 26-27	5.80	7.61	30.80	55.80	297.00
II 36	17.02	6.38	36.17	40.43	50.00
II 37	4.00	20.00	28.00	48.00	30.00
Expected	7.91	46.04	10.07	35.97	

Cranial elements include two hemi-mandibles, two hemi-maxillae and 7 cranial bones. Axial elements includes vertebrae, sternum, ribs, scapulae and pelvises. Limbs include femurs, humeri, tibiae, radii - ulnae and metapodials, feet include carpals, tarsal and phalanges.

Table 20: Number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Upper limb bone	Intermediate limb bone	Lower limb bone
III 11-13	0/1 (0)	0/1 (0)	1/1 (100)
III 20	1/2 (50)	1/2 (50	0/2 (0)
II 23-25	1/5 (20)	0/5 (0)	4/5 (80)
III 21-22	1/2(50)	0/2 (0)	1/2 (50)
II 26-27	1/5 (20)	2/5 (40)	2/5 (40)
II 36	1/1 (100)	0/1 (0)	0/1 (0)
II 37	1/2(50)	0/2 (0)	1/2 (50)
H1S1	19/42 (45.2)	15/42 (35.7)	8/42 (19)
H1S1/2a	11/22 (50)	8/22 (36.3)	3/22 (13.6)
H1S1/2b	10/13 (76.9)	3/13 (23.1)	0/13 (0)
H1S1/2c	8/13 (61.6)	5/13 (38.4)	0/13 (0)
H1S1/2d	7/14 (50)	6/14 (42.8)	1/14 (7.1)
H2S1/2a	1/30 (3.3)	8/30 (26.6)	21/30 (70)
H2S1/2b	2/12 (16.6)	5/12 (41.6)	5/12 (41.6)
H2s1/2/3a	0/5 (0)	2/5 (40)	3/5 (60)
H2S1/2/3b	1/13 (7.7)	9/13 (69.2)	3/13 (23.1)

Experimental assemblages (Domínguez-Rodrigo, 1997) for specimens body size E through G. H1S1 denotes hominin only sequence, H1S1/2 denotes hominin - carnivore sequence, H2S2 1/2 denotes carnivore-hominin sequence and H2S2 1/2/3 denotes carnivore-hominin-carnivore sequence. Alphabetical subscript indicates replicas of similar sequences. For full description see Domínguez-Rodrigo (1997, table 1).

Table 21: Number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for ‘Ubeidiya large terrestrial mammals

‘Pooled stratum’	Upper limb bone	Intermediate limb bone	Lower limb bone
III 11-13	0/24 (0)	0/16 (0)	1/26 (3.85)
III 20	1/18 (5.56)	1/41 (2.44)	0/54 (0)
II 23-25	1/71 (1.41)	0/75 (0)	4/107 (3.74)
III 21-22	1/65 (1.54)	0/81(0)	1/104 (0.96)
II 26-27	1/42 (2.38)	2/31 (6.45)	2/87 (2.30)
II 36	1/10 (10)	0/14 (0)	0/35 (0)
II 37	1/14 (7.14)	0/6 (0)	1/15 (6.67)
H1S1	19/29 (65.5)	15/23 (65.2)	N.D.
H1S1/2a	11/15 (73.3)	8/13 (61.5)	N.D.
H1S1/2b	9/14 (64.2)	3/9 (33.3)	N.D.
H1S1/2c	8/17 (47)	5/12 (41.6)	N.D.
H1S1/2d	7/21 (33.3)	5/16 (31.2)	N.D.
H2S1/2a	0	0	N.D.
H2S1/2b	2/15 (13.3)	5/15 (33.3)	N.D.
H2s1/2/3a	0/29 (0)	2/25 (8)	N.D.
H2S1/2/3b	1/28 (3.5)	9/24 (37.5)	N.D.

Experimental assemblages (Domínguez-Rodrigo, 1997) for specimens body size E through G. H1S1 denotes hominin only sequence, H1S1/2 denotes hominin - carnivore sequence, H2S2 1/2 denotes carnivore-hominin sequence and H2S2 1/2/3 denotes carnivore-hominin-carnivore sequence. Alphabetical subscript indicates replicas of similar sequences. For full description see Domínguez-Rodrigo (1997, table 1).

Table 22: Number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Proximal shaft	mid-shaft	Distal shaft
III 11-13	0/1 (0)	0/1 (0)	1/1 (100)
III 20	0/2 (0)	1/2 (50)	1/2 (50)
II 23-25	0/5 (0)	0/5 (0)	5/5 (100)
III 21-22	1/2 (50)	1/2 (50)	0/2 (0)
II 26-27	0/5 (0)	2/5 (40)	3/5 (60)
II 36	0/1 (0)	0/1 (0)	1/1 (100)
II 37	0/2 (0)	1/2 (50)	1/2 (50)
H1S1	18/42 (43)	12/42 (28.5)	12/42 (28.5)
H1S1/2a	12/22 (54.5)	4/22 (18.1)	6/22 (27.2)
H1S1/2b	7/13 (53.8)	1/13 (7.7)	5/13 (38.4)
H1S1/2c	7/13 (53.8)	3/13 (23.1)	3/13 (23.1)
H1S1/2d	10/14 (71.4)	1/14 (7.1)	3/14 (21.4)
H2S1/2a	7/30 (23.3)	16/30 (53.3)	7/30 (23.3)
H2S1/2b	5/12 (41.6)	1/12 (8.3)	6/12 (50)
H2s1/2/3a	1/5 (20)	2/5 (40)	2/5 (40)
H2S1/2/3b	5/13 (38.4)	2/13 (15.4)	6/13 (41.6)

Experimental assemblages (Domínguez-Rodrigo, 1997) for specimens body size E through G.
Proximal and distal shafts includes both proximal epiphysis and shaft.
H1S1 denotes hominin only sequence, H1S1/2 denotes hominin - carnivore sequence, H2S2 1/2 denotes carnivore-hominin sequence and H2S2 1/2/3 denotes carnivore-hominin-carnivore sequence. Alphabetical subscript indicates replicas of similar sequences. For full description see Domínguez-Rodrigo (1997, table 1).

Table 23: Number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for ‘Ubeidiya body size E and F (small-medium) specimens per ‘pooled stratum’

‘Pooled stratum’	Upper Limb Bone	Intermediate Limb Bone	Lower Limb Bone
III 11-13	0/1 (0)	0/1 (0)	1/1 (100)
III 20	1/2 (50)	1/2 (50)	0/2 (0)
II 23-25	1/3 (33)	0/3 (0)	2/3 (66)
III 21-22	0/1 (0)	0/1 (0)	1/1 (100)
II 26-27	1/5 (20)	2/5 (40)	2/5 (20)
II 36	1/1 (100)	0/1 (0)	0/1 (0)
II 37	1/2 (50)	0/2 (0)	1/2 (50)

Table 24: Number of cut-marked specimens of each skeletal part in relation to the total number of cut-marked specimens for ‘Ubeidiya body size G (large) specimens per ‘pooled stratum’

‘Pooled stratum’	Upper Limb Bone	Intermediate Limb Bone	Lower Limb Bone
III 11-13	0/0 (0)	0/0 (0)	0/0 (0)
III 20	0/0 (0)	0/0 (0)	0/0 (0)
II 23-25	0/2 (0)	0/2 (0)	2/2 (100)
III 21-22	0/1 (0)	0/1 (0)	1/1 (100)
II 26-27	0/0 (0)	0/0 (0)	0/0 (0)
II 36	0/0 (0)	0/0 (0)	0/0 (0)
II 37	0/0 (0)	0/0 (0)	0/0 (0)

Table 25: Number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for ‘Ubeidiya large terrestrial mammals body size E and F (small-medium) specimens per ‘pooled stratum’

‘Pooled stratum’	Proximal epiphysis	Mid-shaft	Distal epiphysis
III 11-13	0/1 (0)	0/1 (0)	1/1 (100)
III 20	0/2 (0)	1/2 (50)	1/2 (50)
II 23-25	0/3 (0)	0/3 (0)	3/3 (100)
III 21-22	0/1 (0)	1/1 (100)	0/1 (0)
II 26-27	0/6 (0)	2/6 (33)	4/6 (66)
II 36	0/1 (0)	0/1 (0)	1/1 (100)
II 37	0/2 (0)	1/2 (50)	1/2 (50)

Table 26: Number of cut-marked specimens of each limb bone portion in relation to the total number of cut-marked specimens for ‘Ubeidiya large terrestrial mammals body size G (large) specimens per ‘pooled stratum’

‘Pooled stratum’	Proximal epiphysis	Mid-shaft	Distal epiphysis
III 11-13	0/0 (0)	0/0 (0)	0/0 (0)
III 20	0/0 (0)	0/0 (0)	0/0 (0)
II 23-25	0/2 (0)	0/2 (0)	2/2 (100)
III 21-22	1/1 (100)	0/1 (0)	0/1 (0)
II 26-27	0/0 (0)	0/0 (0)	0/0 (0)
II 36	0/0 (0)	0/0 (0)	0/0 (0)
II 37	0/0 (0)	0/0 (0)	0/0 (0)

Table 27: Number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for ‘Ubeidiya large terrestrial mammals body size E and F (small- medium) specimens per ‘pooled stratum’

‘Pooled stratum’	Upper Limb Bone	Intermediate Limb Bone	Lower Limb Bone
III 11-13	0/21 (0)	0/17 (0)	1/43 (2.32)
III 20	1/17 (5.88)	1/63 (1.58)	0/64 (0)
II 23-25	1/44 (2.272)	0/63 (0)	2/101 (1.98)
III 21-22	1/54 (1.85)	0/77(0)	0/114 (0)
II 26-27	1/46 (2.17)	2/36 (5.55)	3/91(3.29)
II 36	1/15 (6.66)	0/19 (0)	0/41 (0)
II 37	1/13 (7.69)	0/6 (0)	1/14 (7.14)

Table 28: Number of cut-marked specimens of each limb bone portion in relation to the total number of specimens of the same skeletal part for ‘Ubeidiya large terrestrial mammals body size G (large) specimens per ‘pooled stratum’

‘Pooled stratum’	Upper Limb Bone	Intermediate Limb Bone	Lower Limb Bone
III 11-13	0/13	0/9	0/9
III 20	0/3	0/0	0/7
II 23-25	0/45	0/25(0)	2/39 (5.12)
III 21-22	0/23	0/33 (0)	1/29 (3.44)
II 26-27	0/4	0/8	0/9
II 36	0/3	0/12	0/24
II 37	0/5	0/2	0/9

Table 29: Number and percent of percussion marks for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	percussion marks	n	Percent
III 11-13	0	71	0
III 20	2	129	1.55
II 23-25	2	264	0.758
III 21-22	4	270	1.49
II 26-27	1	166	0.6
II 36	0	61	0
II 37	0	40	0

Table 30: Percent bones gnawed by carnivores for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Percent	Std Dev	n
III 11-13	42.86	9.51	105
III 20	59.87	7.69	157
II 23-25	36.98	4.01	557
III 21-22	46.35	5.187	356
II 26-27	44.7	4.635	443
II 36	42.54	8.43	134
II 37	43.59	11.076	78

Table 31: Percent of carnivore gnaw marks on different limb portions for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Epiphyses	Near epiphyses	Mid-shaft	References
III 11-13	23/42 (54.76)	16/30 (53.33)	13/29 (44.83)	this study
III 20	22/43 (51.16)	33/47 (70.21)	39/61 (63.93)	this study
II 23-25	78/142 (54.93)	44/87 (50.57)	52/109 (47.71)	this study
III 21-22	59/103(57.28)	46/77 (59.74)	60/138 (43.48)	this study
II 26-27	100/122 (81.97)	25/32 (78.12)	27/39 (69.23)	this study
II 36	33/49 (67.35)	20/34 (58.82)	10/19 (52.63)	this study
II 37	16/22 (72.73)	10/14 (71.43)	6/10 (60)	this study
Carnivore only model	6/6 (100)	47/51 (92.2)	136/174 (78.2)	Blumenschine (1988)
Hammer stone to carnivore	3/4 (75)	40/75 (53.3)	39/462 (8.4)	Blumenschine (1988)
FxJj50	12/17 (70.5)	18/31 (58)	45/126 (35.7)	Domínguez-Rodrigo (2002)

Table 32: Percent of carnivore gnaw marks on different limb portions for ‘Ubeidiya large terrestrial mammals body size E and F (small-medium) per ‘pooled stratum’

‘Pooled stratum’	Epiphyses	Near epiphyses	Mid-shaft	References
III 11-13	11/27 (40.74)	12/24 (50)	9/21 (42.86)	this study
III 20	20/20 (50)	33/46 (71.74)	38/58 (65.52)	this study
II 23-25	45/85 (52.94)	23/45 (51.11)	29/67 (43.28)	this study
III 21-22	46/79 (58.23)	38/64 (59.38)	39/97 (40.21)	this study
II 26-27	89/109 (81.65)	21/28 (75)	27/37 (72.97)	this study
II 36	23/31 (74.19)	16/23 (69.57)	6/12(50)	this study
II 37	11/16 (68.75)	7/11 (63.64)	3/6 (50)	this study
Carnivore only model	2/2 (100)	7/9 (77.7)	55/80 (60.8)	Blumenschine (1988)
Hammer stone - carnivore model	2/3 (66.7)	17/34 (50)	25/250 (10)	Blumenschine (1988)
FxJj50	12/17 (70.5)	18/31 (58)	45/126 (35.7)	Domínguez-Rodrigo (2002)

Table 33: Percent of carnivore gnaw marks on different limb portions for ‘Ubeidiya large terrestrial mammals body size G (large) per ‘pooled stratum’

‘Pooled stratum’	Epiphyses	Near epiphyses	Mid-shaft	Reference
III 11-13	12/15 (80)	4/6 (66.67)	4/8 (50)	this study
III 20	2/3 (66.67)	0/1 (100)	1/3 (33.33)	this study
II 23-25	33/57(57.89)	21/42 (50)	23/43 (54.76)	this study
III 21-22	13/24 (54.17)	8/13 (61.54)	21/41 (51.22)	this study
II 26-27	11/13 (84.62)	4/4 (100)	0/2 (0)	this study
II 36	10 (55.56)	4/11 (36.36)	4/7 (57.14)	this study
II 37	5/6 (83.33)	3/3 (100)	3/4 (75)	this study
Carnivore only model	4/4 (100)	40/42 (95.2)	81/91 (86.2)	Blumenschine (1988)
Hammer stone to carnivore	1/1 (100)	40/42 (95.2)	14/212 (6.6)	Blumenschine (1988)
FxJj50	12/17 (70.5)	18/31 (58)	45/126 (35.7)	Domínguez-Rodrigo (2002)

Table 34: Percent of carnivore gnaw marks for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’ for body size E and F (small-medium) and G (large) per ‘pooled stratum’

‘Pooled stratum’	Large percent	Large n	Small-medium percent	Small-medium n
III 11-13	53.12	32	37.5	72
III 20	30	10	62.94	143
II 23-25	45.26	190	32.47	348
III 21-22	44.21	95	48.22	253
II 26-27	47.62	42	45.27	391
II 36	48.84	43	40.23	87
II 37	45.45	22	46.15	52

Table 35: Percent carnivores of total ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

	MNI		NISP	
‘Pooled stratum’	n	Percent	n	Percent
III 11-13	21	9.52	3	2.07
III 20	30	10	5	2.96
II 23-25	65	32.3	102	12.57
III 21-22	47	14.9	32	7.73
II 26-37	57	24.56	45	6.71
II 36	34	23.53	22	9.27
II 37	29	34.48	20	14.81

Table 36: Distribution of fracture type for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Complete	Cylinder	Fragment	n
III 11-13	4.69	34.38	60.94	64
III 20	2.40	24.80	72.80	126
II 23-25	4.35	18.97	76.68	253
III 21-22	2.67	20.99	76.34	262
II 26-27	0.67	8.67	90.67	150
II 36	16.36	34.55	49.09	55
II 37	3.70	40.74	55.56	27
Total	35	199	702	936

Table 37: Percent of limb bone fragments for ‘Ubeidiya large terrestrial mammals body size E and F (small-medium) per ‘pooled stratum’

‘Pooled stratum’	Complete	Cylinder	Fragment	n
III 11-13	6.98	39.53	53.49	43
III 20	1.67	25.83	72.5	120
II 23-25	4.61	14.47	80.92	152
III 21-22	2.6	23.44	73.96	192
II 26-27	0	9.3	90.7	129
II 36	10.53	36.84	52.63	38
II 37	0	40	60	20

Table 38: Percent of limb bone fragments for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’ body size G (large) per ‘pooled stratum’

‘Pooled stratum’	Complete	Cylinder	Fragment	n
III 11-13	0	23.81	76.19	21
III 20	20	0	80	5
II 23-25	3.96	25.74	70.3	101
III 21-22	2.86	14.29	82.86	70
II 26-27	4.76	4.76	90.48	21
II 36	29.41	29.41	41.18	17
II 37	14.29	42.86	42.86	7

Table 39: Body element distribution for 'Ubeidiya large terrestrial mammals per 'pooled stratum' and for comparative assemblages

'Pooled stratum'	Cranial	Axial	Limbs	Manus/Pes	References
III 11-13	13.10	20.54	51.78	14.58	This study
III 20	12.45	11.62	70.54	5.39	This study
II 23-25	20.21	21.83	46.05	11.90	This study
III 21-22	12.77	27.46	54.27	5.49	This study
II 26-27	25.04	5.63	49.22	20.11	This study
II 36	29.11	3.29	53.52	14.08	This study
II 37	16.59	13.66	50.24	19.51	This study
Surface remains Amboseli Park	6.10	55.80	32.60	5.50	Behrensmeyer & Dechant Boaz (1980)
Partial burial in Amboseli Natural park	5.20	45.90	40.00	9.00	Behrensmeyer & Dechant Boaz (1980)
Spotted hyaena den	4.70	22.20	67.00	6.10	Behrensmeyer & Dechant Boaz (1980)
Stripped hyaena den	25.40	3.30	69.50	1.80	Martínez Navarro & Palmqvist (1999)
Porcupine den	5.10	39.70	47.30	7.80	Martínez Navarro & Palmqvist (1999)
Venta Micena	6.80	16.20	68.50	8.40	Martínez Navarro & Palmqvist (1999)
Complete zebra and wildebeest	2.00	43.00	25.00	10.00	Behrensmeyer & Dechant Boaz (1980)
Mugugu	21.46	34.14	32.20	12.20	Lupo (2001)
Tsipitibe	24.00	40.63	27.85	7.45	Lupo (2001)

Crania does not include loose teeth. Magugu is a Hadza near kill site and Tsipitibe is a Hadza camp. Values for both Hadza sites includes specimens from Impala, Alcelaphine and Zebra.

Table 40: Presence-absence distribution of ‘Ubeidiya large terrestrial mammals across ‘pooled strata’

Species	III 11-13	III 20	II 23-25	III 21-22	II 26-27	II 36	II 37
Antilopini gen. indet.	0	1	1	1	1	1	1
Camelus sp.	0	0	0	0	0	1	1
Canis mosbachensis	0	1	1	1	1	1	1
Capreolous sp.	1	1	1	1	1	1	1
Crocuta crocuta	0	1	1	1	1	1	1
Equus sp. (robust)	0	1	1	1	0	1	0
Equus tabeti	1	1	1	1	1	1	1
Felis cf. *chaus*	0	0	1	0	0	1	1
Gazella sp.	1	1	1	1	1	1	1
Giraffa sp.	1	0	1	1	0	1	0
Herpestes sp.	0	0	1	0	1	1	0
Hypolagus beremendensis	0	1	1	1	1	1	0
Kolpochoerus olduvaiensis	1	0	1	1	1	1	1
Leptobos sp.	1	1	1	1	1	1	0
Lutra simplicidens	1	0	1	1	1	1	1
Lycaon lycaonoides	0	0	1	1	1	1	0
Lynx sp.	0	0	1	1	1	1	1
Macaca sylvana	0	1	1	0	1	1	1
*Mammuthus*sp.	0	1	1	1	1	1	1
Megantereon sp.	0	0	1	1	1	0	0
Mellivora sp.	0	0	1	0	0	0	0
Oryx cf. *gazella*	1	1	1	1	1	0	0
Pannonictis pilgrimi	0	0	1	1	1	0	1
Panthera gombaszoegensis	0	0	1	1	1	1	0
Pelorovis oldowayensis	1	1	1	1	1	1	1
Praemegaceros verticornis complex	1	1	1	1	1	1	1
Pseudodama sp.	1	1	1	1	1	1	1
Stephanorhinus etruscus etruscus	1	0	1	1	1	1	1
Sus strozzi	0	0	1	1	1	1	1
Theropithecus cf. *oswaldi*	1	0	0	1	0	0	0
Ursus etruscus	1	0	1	1	1	0	1
Vormela peregusna	0	0	1	0	1	0	0
*Vulpes*sp.	0	0	1	1	1	1	0

1 denotes presence and 0 denotes absence

Table 41: FAD and LAD for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Total number of species	Upper 95% CI	Lower 95% CI	FAD	LAD
III 11-13	13	13.59	12.1		1
III 20	19	15.72	12	7	0
II 23-25	30	24.02	16.28	11	1
III 21-22	29	21.18	13.85	0	1
II 26-27	28	22.66	16.01	0	2
II 36	27	23.4	16.9	1	7
II 37	20	20.33	19.59	0	

Upper and lower 95% CI presents 95% confidence intervals for expected number of species for $n = 135$

Table 42: Presence-absence of ‘Ubeidiya large terrestrial mammals for the three faunal units

Species	A	B1	B2
Theropithecus cf. *oswaldi*	1	0	0
Oryx cf. *gazella*	1	1	0
Antilopini gen. indet.	1	1	1
Canis mosbachensis	1	1	1
Capreolous sp.	1	1	1
Crocuta crocuta	1	1	1
Equus sp. (robust)	1	1	1
Equus tabeti	1	1	1
Gazella sp.	1	1	1
Ursus etruscus	1	1	1
Hypolagus beremendensis	1	1	1
Kolpochoerus olduvaiensis	1	1	1
Leptobos sp.	1	1	1
Lutra simplicidens	1	1	1
Macaca sylvana	1	1	1
Mammuthus sp.	1	1	1
Pelorovis oldowayensis	1	1	1
Praemegaceros verticornis complex	1	1	1
Pseudodama sp.	1	1	1
Stephanorhinus etruscus etruscus	1	1	1
Ursus etruscus	1	1	1
Vulpes sp.	0	1	1
Felis cf. *chaus*	0	1	1
Sus strozzi	0	1	1
Pannonictis pilgrimi	0	1	1
Panthera gombaszoegensis	0	1	1
Lynx sp.	0	1	1
Giraffa sp.	0	1	1
Herpestes sp.	0	1	1
Megantereon sp.	0	1	0
Mellivora sp.	0	1	0
Lycaon lycaonoides	0	1	0
Camelus sp.	0	0	1

Faunal unit A includes ‘pooled strata’ III 11-13 and III 20, faunal unit B1 includes ‘pooled strata’ II 23-25, III 21-22 and II 26-26 and faunal unit B2 includes ‘pooled strata’ II 36 and II 37. 1 indicates presence and 0 indicates absence.

Table 43: Species richness for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Index			n
	Number of species	Margalef	Fisher’s α	
III 11-13	13	2.14	3.46	145
III 20	15	2.73	3.98	169
II 23-25	31	4.48	6.38	814
III 21-22	25	3.98	5.85	413
II 26-27	26	3.84	5.37	673
II 36	25	4.39	7.05	237
II 37	20	3.87	6.47	136

Table 44: P values for ‘Pooled stratum’ by ‘Pooled stratum’ comparison for ‘Ubeidiya large terrestrial mammals richness indices

‘Pooled stratum’	Index	
	Margalef	Fisher’s α
III 11-13 and III 20	0.36	0.529
III 20 and II 23-25	0.000	0.018
II 23-25 and III 21-22	0.161	0.538
III 21-22 and II 26-27	0.667	0.463
II 26-27 and II 36	0.108	0.081
II 37 and II 37	0.305	0.597

Table 45: Evenness indices for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Index			n
	Evenness	Simpson $1 - D_s$	Equitability J'	
III 11-13	.49	.79	.72	145
III 20	.20	.39	.40	169
II 23-25	.29	.80	.64	814
III 21-22	.24	.68	.56	413
II 26-27	.24	.63	.56	673
II 36	.38	.82	.70	237
II 37	.61	.89	.83	136

Table 46: P values for 'Pooled stratum' by 'Pooled stratum' comparison for 'Ubeidiya large terrestrial mammals evenness indices

'Pooled stratum'	Index		
	Evenness	Simpson $1 - D_s$	Equitability J'
III 11-13 and III 20	0	0	0
III 20 and II 23-25	0.379	0	0
II 23-25 and III 21-22	0.174	0	0.002
III 21-22 and II 26-27	0.885	0.077	0.986
II 26-27 and II 36	0.004	0	0
II 37 and II 37	0.001	0.018	0

Table 47: Dominance indices for 'Ubeidiya large terrestrial mammals per 'pooled stratum'

'Pooled stratum'	Index		
	Berger-Parker d	Dominance D_s	n
III 11-13	0.32	0.21	145
III 20	0.78	0.61	169
II 23-25	0.39	0.2	814
III 21-22	0.53	0.32	413
II 26-27	0.60	0.37	673
II 36	0.37	0.18	237
II 37	0.24	0.11	136

Table 48: P values for stratum by stratum comparison for 'Ubeidiya large terrestrial mammals dominance indices

'Pooled stratum'	Index	
	Berger-Parker d	Dominance D_s
III 11-13 and III 20	0	0
III 20 and II 23-25	0	0
II 23-25 and III 21-22	0	0
III 21-22 and II 26-27	0.021	0
II 26-27 and II 36	0	0
II 37 and II 37	0.012	0.018

Table 49: Diversity indices for ‘Ubeidiya large terrestrial mammals per ‘pooled stratum’

‘Pooled stratum’	Shannon - Weaver index (H')	Brillouin (HB)	n
III 11-13	1.86	2.492	125
III 20	1.08	1.397	169
II 23-25	2.20	3.069	814
III 21-22	1.79	2.453	413
II 26-27	1.81	2.513	673
II 36	2.26	3.044	237
II 37	2.5	3.293	136

Table 50: P values (t test) for stratum by stratum comparison for ‘Ubeidiya large terrestrial mammals Shannon - Weaver index (H')

‘Pooled stratum’	t	P value
III 11-13 and III 20	5.3057	0.000
III 20 and II 23-25	-8.7334	0.000
II 23-25 and III 21-22	4.6707	0.000
III 21-22 and II 26-27	-0.30492	0.76049
II 26-27 and II 36	-3967	0.000
II 36 and II 37	-1.8607	0.063618

Table 51: P values (bootstrap) for ‘Pooled stratum’ by ‘Pooled stratum’ comparison for ‘Ubeidiya large terrestrial mammals Shannon - Weaver index (H')

‘Pooled stratum’	Shannon - Weaver index (H')
III 11-13 and III 20	0
III 20 and II 23-25	0
II 23-25 and III 21-22	0
III 21-22 and II 26-27	0.857
II 26-27 and II 36	0.002
II 37 and II 37	0.08

Table 52: Distribution of relative frequency (NISP) of mesoherbivores in ‘Ubeidiya ‘Pooled stratum’ and comparative sites

‘Pooled stratum’	Cerv	Alce	Anti	Redu	Bovi	Capr	Trag	Aepy	Hippo	Kolp	Metr	Noto	Phac	Sus	Equu	Hippa
III 11-13	80.74	0	2.22	0	13.33	0	0	0	0.74	1.48	0	0	0	0	1.48	0
III 20	90.32	0	1.94	0	1.94	0	0	0	0.65	0	0	0	0	0	5.16	0
II 23-25	65.76	0	4.62	0	3.18	0	0	0	0.48	0.32	0	0	0	0.8	24.84	0
III 21-22	77.12	0	2.54	0	1.69	0	0	0	0.28	0.28	0	0	0	0	18.08	0
II 26-27	82.54	0	3.88	0	3.7	0	0	0	0.88	2.12	0	0	0	2.29	4.59	0
II 36	61.58	0	4.21	0	3.68	0	0	0	0	0.53	0	0	0	11.05	18.95	0
II 37	52	0	19	0	4	0	0	0	0	1	0	0	0	7	17	0
Konso 4M	0	29.4	2.7	30	6.76	0	3.86	2.5	0	16	0.96	1.54	0	0	4.26	1.74
Konso 4HA	0	34.14	0	42.68	6.09	0	4.87	0	0	7.31	0	0	0	0	3.65	3
Konso 10 L	0	63.33	1.25	14.58	0	0	0	0	5.83	5.83	0.48	0	0	0	5.23	1.66
Konso 10 M	0	63.97	3.13	9.15	0.84	0	0.84	0	0.24	3.86	8.43	0	0	0	9.63	1.32
Shungura Upper G	0	10.01	0	39.23	0.66	0	4	14.69	0	16.19	1.84	4	0	0	7.51	1.84
Shungura Lower G	0	1.51	0	45.99	1.65	0	17.23	13.2	0	9.83	3.14	5.12	0	0	1.25	1.01
Shungura F	0	6.01	0	19.08	6.36	0	16.96	10.6	0	10.6	5.3	16.96	0	0	0	8.13
Shungura E	0	0.84	0	16.46	4.22	0	23.63	10.13	0	31.65	0.84	9.28	0	0	0	2.95
Shungura D	0	0	0	21.05	0	0	10.53	10.53	0	10.53	0	36.84	0	0	0	10.53
Shungura C	0	1.6	0	17.95	8.65	0	15.38	18.91	0	20.51	1.28	7.37	0	0	0	8.33

Table 52: con't

'Pooled stratum'	Cerv.	Alce	Anti	Redu	Bovi	Capr	Trag	Aepy	Hippo	Kolp	Metr	Noto	Phac	Sus	Equu	Hippa
Shungura B	0	1.11	0	26.94	9.17	0	7.22	11.11	0	5	2.22	33.61	0	0	0	3.61
Shungura A	0	0	0	5.31	3.54	0	1.77	3.54	0	8.85	0	73.45	0	0	0	3.54
Serengeti grassland	0	21.3	56.74	0.18	2.19	0	0.42	4.32	2.66	0	0	0	0.98	0	11.13	0
Serengeti woodland	0	0.01	3.35	1.16	35	0	1.65	33.04	22.67	0	0	0	1.23	0	1.81	0
Manyara	0	0	0	2.33	63.69	0	1.06	29.72	0	0	0	0	1.06	0	2.12	0
Ngorongoro	0	57.06	21.08	0.51	0.25	0	1.69	0	0.42	0	0	0	0	0	18.98	0
Nairobi Park	0	6.94	23.16	2.8	0	0	2.14	17.35	30.02	0	0	0	4.22	0	13.38	0
Kruger Park	0	5.32	0	2.05	4.11	0	3.25	79.06	0.61	0	0	0	0	0	5.57	0
Dmanisi	55.72	0	1.96	0	11.62	5.97	0	0	0	0	0	0	0	0	24.7	0
Untermassfeld	64.08	0	0	0	25.4	0	0	0	0	0	0	0	0	3.31	7.18	0
Poggo rosso	68.53	0	0	0	2.79	0	0	0	0	0	0	0	0	23	5.59	0
Venta Micena	25.71	0	0	0	14.45	12.04	0	0	0	0	0	0	0	0	47.78	0
Arezzo Italy	60.65	0	0	0	0	0.84	0	0	0	0	0	0	0	38.5	0	0
Rila	33.98	0	0	0	0	40.12	0	0	0	0	0	0	0	25.88	0	0

Table 52: con't

cerv. = cervidae, Alce.= Alcelphini, Anti. = Antilopini, Redu. = Reduncini, Bovi. = Bovini, Cape. = Caprini, Trag. = Tragelaphini, Aepy.

=Aepycerotini, Hippo. = Hippotragini, Kolp. = Kolpochoerus, Metr. = Metridiochoerus, Noto. = Notochoerus, Phac. = Phacocoerus, Sus. = Sus, Equu. = Equus, Hippa. =Hipparion. Data for modern African habitats from Schaller (1972), data for Poggo Rossio Mazza *et al.* (2004), data for Dmanisi from Gabunia *et al.* (2000), data for Venta Micena from Palmqvist & Arribas (2001), data for Untermassfeld from Kahlke (2000) (MNI quantification), data for Arezzo, Italy from (Mattiolio *et al.*, 2004), and data for Rila National park, Bulgaria from Spasov (1998). Data for Shungura from Alemseged (2003) and for Konso from Suwa *et al.* (2003).

Appendix C

Statistical Equations

General notation

S is used to denote the total number of species in the population while s is used to denote the number of species in a sample. As all paleontological assemblages are samples of the true population, thus their observed number of species is considered a sample. An estimate of S is denoted as $\hat{S}$.

N is used to denote the total number of individuals in the population while n is used to denote the number of individuals in a sample. As all paleontological assemblages are in fact samples of the true population, their observed number of individuals is considered a sample. An estimate of N is denoted as $\hat{N}$.

Rarefaction

Rarefaction is used to compare species richness between two samples in paleontological and archaeological assemblages of unequal size by estimating the species richness expected based on random sub-samples of individuals (Gotelli & Graves, 1996). The rarefaction equation is based on a modification of the original equation by Sanders (1968) as developed by Hulbert (1971) and is based on hypergeometric distribution sub-sampling without replacement from a parent distribution (the observed assemblage). Under this equation, the parent assemblage is considered the population (and denoted in large cap letters) and the sub samples is considered a sample thereof (and denoted in small cap letters)

The equation of rarefaction is:

$$\hat{S}_n = \sum_{i=1}^{s} \left[1 - \frac{\binom{N-m_i}{n}}{\binom{N}{n}} \right] \tag{1}$$

Where $\hat{S}_n$ is the estimated number of species for the sub-sample. N is the total number of individuals in the observed sample, $\hat{S}$ is the estimated number of species in the assemblage, m_i is the number of individuals of species i in the collection, s is the number of species in the sub sample and n is the number of individuals in the sub-sample, where $n < N$.

Rarefaction was calculated using the freeware program analytic rarefaction 1.3 by Steve Holland http: //www.uga.edu/$\sim$strata/.

The variance is calculated as

$$\begin{gathered} \sigma^2(S_n) = \binom{N}{n}^{-1} \left[\sum_{i=1}^{S} \binom{N-m_i}{n} \left\{ 1 - \frac{\binom{N-m_i}{n}}{\binom{N}{n}} \right\} + \right. \\ \left. 2\sum_{i=1}^{S-1} \sum_{j=2}^{S} \left\{ \binom{N-m_i-m_j}{n} - \frac{\binom{N-m_i}{n}\binom{N-m_j}{n}}{\binom{N}{n}} \right\} \right. \end{gathered} \tag{2}$$

The increment of the rarefaction curve

The increment of the rarefaction curve of the second is calculated using the following equation:

$$\triangle_n = \frac{\hat{S}_n(n+1) - \hat{S}_n(n)}{(n+1) - n} = \hat{S}_n(n+1) - \hat{S}_n(n) \tag{3}$$

Where is $\hat{S}_n$ is the expected number of species as calculated by the rarefaction curve and n is the number of identified specimens (NISP quantification) in each assemblage.

Confidence intervals

A 95$\%$ confidence intervals (CI) for the unknown parameter p (the percentage of a certain character in a population), was calculated using the equation

$$\hat{p} \pm t_{n-1} * \sqrt{\frac{\hat{p}\hat{q}}{n-1}} \tag{4}$$

Where $\hat{p}$ is the percent of the taxon in the strata and $\hat{q}$ is the percent of all other taxa. n is the number of individuals in the strata. For large n, t_{n-1} is replaced by 1.96.

Similarity indices

The similarity equation used are

1. Dice-Sørenson asymmetrical similarity coefficient. Asymmetrical refers to the exclusion of double zeros (i.e., absence in both assemblages).

$$\frac{2a}{2a+b+c} \tag{5}$$

   Where a is the species common to both assemblages, b is the number of species unique to the first assemblage and c is the number of species unique to the second assemblage.

2. The Gower asymmetrical similarity coefficient. Asymmetrical refers to the exclusion of double zeros (i.e., absence in both assemblages).

$$\frac{S(w_i) \times Si}{\sum S(w_i)} \tag{6}$$

   where S_i is the similarity calculated as

$$S_i = \frac{|y_i - y_j|}{R} \tag{7}$$

   Where y_i and y_j is the character states for object y, R is the max distance between the objects and $S(w_i)$ is the relative weight assigned to each descriptor. In all cases, equal weight was given to each of the taxa.

Richness indices

1. Margalef's richness index

$$D_{Mg} = \frac{s-1}{\ln(n)} \tag{8}$$

where s is the number of taxa and n is the number of individuals.

2. Fisher's α

The log series takes the form

$$-\alpha \ln(1-x) = \alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \cdots, \frac{\alpha x^n}{n} \tag{9}$$

where αx is the number of species predicted to have one individual, $\frac{\alpha x^2}{2}$ is the number of species predicted to have two individuals and so on.

In order to calculate α from a known sample with a n and s, Fisher provided an iterative equation based in both parameters which also serves as a diversity index:

$$\frac{n}{s} = \frac{e^{\frac{s}{\alpha}} - 1}{\frac{s}{\alpha}} \tag{10}$$

with variance calculated as

$$var_{\alpha} = \frac{0.693174\alpha}{\left[\ln \frac{x}{(1-x)} - 1\right]^2} \tag{11}$$

After α is estimated by iteration, x can be calculated by a substitution into the equation

$$x = \frac{n}{n+\alpha} \tag{12}$$

The estimated total number of species can be derived from the following equation

$$\hat{S} = \alpha\left[-\ln(1-x)\right] \tag{13}$$

Dominance indices

Dominance indices include

1. Simpson's index D_s provides the probability the any two individuals drawn at random will

belong to the same species as is given by the following equation

$$D_s = \sum(\frac{n_i}{n})^2 \tag{14}$$

Where n_i is the number of individual in the ith species and n is the total number of individuals in the assemblage. This index ranges from $\frac{1}{n}$ where all taxa are equally present to 1 where one taxon dominates the community completely.

2. Berger-Parker index d

$$d = \frac{n_{max}}{n} \tag{15}$$

Where n_{Max} is the number of individuals in the most abundant species and n is the total number of individuals.

Evenness indices

Evenness indices include

1. Equatability J' is the ratio of observed maximum Shannon - Weaver index (H') to maximum diversity possible. This occurs when all species are equality abundant i.e., $H' = H_{max} = \ln(s)$. Therefore the Equatability index is given by the equation

$$J' = \frac{H'}{H_{max}} = \frac{H'}{\ln(s)} \tag{16}$$

Where H' is the Shannon - Weaver index of diversity and s is the number of species in the assemblage.

2. Buzas and Gibson's evenness is a slightly different way of looking at the equatability equation and is given by the following equation

$$Evenness = \frac{e^{H'}}{s} \tag{17}$$

Where H' is the Shannon - Weaver index and s is the number of species in the assemblage.

3. Simpson's $1 - D_s$ is the complement of the Simpson's dominance index and is a measure of evenness. It is measured as $1 - D_s$. It ranges from 0 were one taxon dominates the community

completely to $1 - \frac{1}{n}$ where all taxa are equally present. Other studies in the literature have used the reciprocal $\frac{1}{D_s}$ as measure of evenness in lieu of the complement (Magurran, 2005).

Diversity indices

The most common diversity index is that of Shannon - Weaver. It is also cited as Shannon - Wiener in honor of Norbert Wiener, the effective founder of cybernetics, with which information theory is closely linked (Magurran, 2005).

1. The Shannon - Weaver index (H') is calculated as:

$$H' = -\sum p_i \ln(p_i) \tag{18}$$

Where p_i is the proportion of the ith species in the sample calculated as $\frac{n_i}{n}$. Where n_i is the number of individuals in the i species and n is the total number of individuals. This is an index of entropy and varies from 0 in communities with only a single taxon to high values in communities with many taxa, but each with only a few individuals.

2. The Brillouin index is similar to the Shannon - Weaver index (H') but is better suited for finite populations. It is calculated as:

$$HB = \frac{\ln n! - \sum \ln n_i!}{n} \tag{19}$$

Where n is the total number of individuals in an assemblage and n_i is the number of individuals in the i species.

Appendix D

Names of Museum Collections Visited

1. HUJI The Hebrew University of Jerusalem, Jerusalem, Israel - paleontology and comparative mammalian collection.
2. TAU The Tel Aviv University, Tel Aviv, Israel - comparative mammalian collection.
3. AMNH American Museum of Natural History, NY. - comparative mammalian collection.
4. FMNH Field Musuem of Natural History, Chicago, Ill. - comparative mammalian collection.
5. UCMP University of California Musuem of Paleontology, Berkeley, Cal.
6. USNM United States National Museum of Natural History, Smithsonian. Washington D.C. - Comparative mammalian collection and Vertebrate Paleontology collection.
7. BMNH British Museum of Natural History, London, UK - Comparative mammalian collection and Vertebrate Paleontology collection.
8. UNIFI Florence Natural History Museum, Florence, Italy. - Paleontology collection.
9. MCZ Museum of Comparative Zoology, Cambridge, Mass.
10. UMICH University of Michigan Museum of Paleontology, Ann Arbor, Mich.
11. ASM Arizona State Museum Comparative Vertebrate Collection, Tucson, Az.
12. ZMT Georgian State Museum, Tbilisi, Georgia. - Paleontology collection.
13. OM Orce Museum, Granada, Spain. - Paleontology collection.

Appendix E

Grouping of Substrata into Strata

During the work on the thesis, the original notation on boxes, actual specimens and notes attached to specimens was noted. The stratigraphic information was then converted into the Trench - Layer system i.e. II 23.

Due to small sample sizes, it was not possible to discuss the differences between substrata, and all substrata were grouped into single stratum. Similarly, consecutive strata with small sample size and similar depositional environment were also joined.

The following strata were grouped into 'pooled strata' together. For the sake of brevity only fossilforous strata are described.

I 29 Includes specimens from I 29.

I 38 Includes specimens from I 38.

II 15 Includes specimens from II 15, II 15?.

II 22

II 23-25 Includes specimens from II 23, II 23-24, II 23?, II 23-25, II 24, II 24?, II 24a, II 25, layers 5, 6, 7.

II 26-27 Includes specimens from I 15, I 15?, I 15 LF, I 15 LF?, I 15?, I 15 - I 15b, I 15b, I 15-16, I 15-16?, I 15-16 LF, I 15-16? LF, I 16, I 16b, I 16c, I 16 LF, I 16a, I 16b, I 16c and I 16 d, VII, VII 12, VII 13, VII 15, VII 15 LF. This strata was pooled with strata II 26-27 which includes specimens from II 26, II 26?, II 26a, II 26b, II 26c, II 27 and layer 8 - 9.

II 28 Includes specimens from II 28.

II 33-34 Includes specimens from II 33-34 and II 33.

II 34-35 Includes specimens from II 34-35, II 35, II 34, II 34a and II 35b.

II 36 Includes specimens from II 36, II 36 LF, II 36?.

II 37 Includes specimens from I 26, I 26 LF, I 26a, I 26b, I 26b_1, I 26b_2, I 26b_2 base, I 26b-c, I 26c, I 26c_2, I 26c-d, I 26d, I 26d bottom. This grouping was based on the fact that the lithic analysis did not show any change between the strata, note that the geomorphological analysis indicated a difference between the substrata. This strata was pooled with strata II 37 which includes specimens from II 37, II 37?.

II 38-39 Includes specimens from II 38 and II 39.

III 11-13 Includes specimens from III 11, III 11-12, III 12, III 12-13, III 12b, III 12e, III 12f, III 13.

III 19 Includes specimens from III 19.

III 20 Includes specimens from III 20, III 20b, III 20c, III 20d and was pooled with strata K 20.

III 21-22 Includes specimens from III 21, III 21-22, III 21, 22a, III 21a inf, III 22f, III 22,III 22 inf, III 22 sup, III 22a, III 22a bottom, III 22a inf, III 22a?, III 22a-b, III 22b, III 22b inf, III 22b sup, III 22b-c, III 22c, III 22c-d, III22d, III 22d base, III22d base?, III 22d-e inf, III 22d-e, III 22e, III 22e$*$, III 22e arg, III 22e inf, III 22e sup, III 22e-f, III 22f, III 22f inf, III 22g.

III 23-25 Includes specimens from III 23, III 23-24, III 23-25, III 23-25?, III 24, III 24?, III 25, III 25 inf. and was pooled with strata K 29-30 which includes specimens from K 29, K 29-30, K 30, Vineyard, and K5-K6 (from the early seasons).

III 34 Includes specimens from III 34, III 34c, III 34d.

K 22 Includes specimens from K 22.

K 23-25 Includes specimens from K 24-25, K 25a, K 24, K 25b and K 25.

K 26 Includes specimens from K 26 and K 26b.

K 27-28 Includes specimens from K 27, K 28 and K1 from the early seasons.

K 39-42 Includes specimens from K 39, K 40, K 41, K 42.

K 57 Includes specimens from K 57.

Strata that were dropped from the analyses III 1, II 21-24, II 22-23, II 23 or I 26, II 24 or II 36, II 25-26, II 35 - 37, III 17-22, III 19-20, III 20-21, III 20-22, III 20-23, III 22-23, Trench I, Trench III, top soil and specimens with no stratigraphic information at all.

A total of 22 specimens (all belonging to ruminants) were assigned strata III 1. Since the geology of this strata is entirely limnic, the finds of terrestrial mammalian fauna was very puzzling. Moreover, some of the specimens were also assigned (by numbers on the bones) to other strata as well: VII 15, II 34, K 24, K 26, K 27 or K 25. Since none of these could be reconciled with the known stratigraphy of the site, they were omitted from the analysis altogether.