Palaeoecology of the KBS member of the Koobi Fora Formation: Implications for Pleistocene hominin behaviour.

By

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in

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For Nathan,

Who would have been so proud.

Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

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Abstract

One of the defining features of our lineage is the manner in which we interact with landscape scale resource distributions. This pattern of landscape use distinguishes between modern humans and our closest living relatives. However, the nature of this development is poorly understood. The archaeology of human origins allows a rare insight into the use of resources by our remote ancestors. This study integrates landscape scale archaeological collections from the KBS Member of Areas 105, 108 and 130 in the Koobi Fora Formation with innovative methods of palaeoecological analysis to determine if palaeoecological changes are reflected in changes in hominin behaviour. This variation in hominin behaviour is indicated by increased levels of artefact reduction in Areas 108 and 130 and decreased levels of artefact reduction in Area 105. Both bovid ecomorphological analysis and an analysis of bovid tribal affiliations indicate significant palaeoenvironmental differences between Area 105, Area 108 and Area 130 (at the 0.05 significance level). These reconstructions place Areas 108 and 130 in open, dry environments and place Area 105 in a closed, wet environment. I propose that hominins in the Turkana basin were increasing the use-life of their artefacts by extensive reduction strategies in more open, dry environments as they were coming into contact with meat and marrow resources more often. These intensive reduction strategies would have been less crucial in closed, wet environments.

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Table of Contents

Table of Figures

Table of Tables

1. Introduction

1.1 Preface

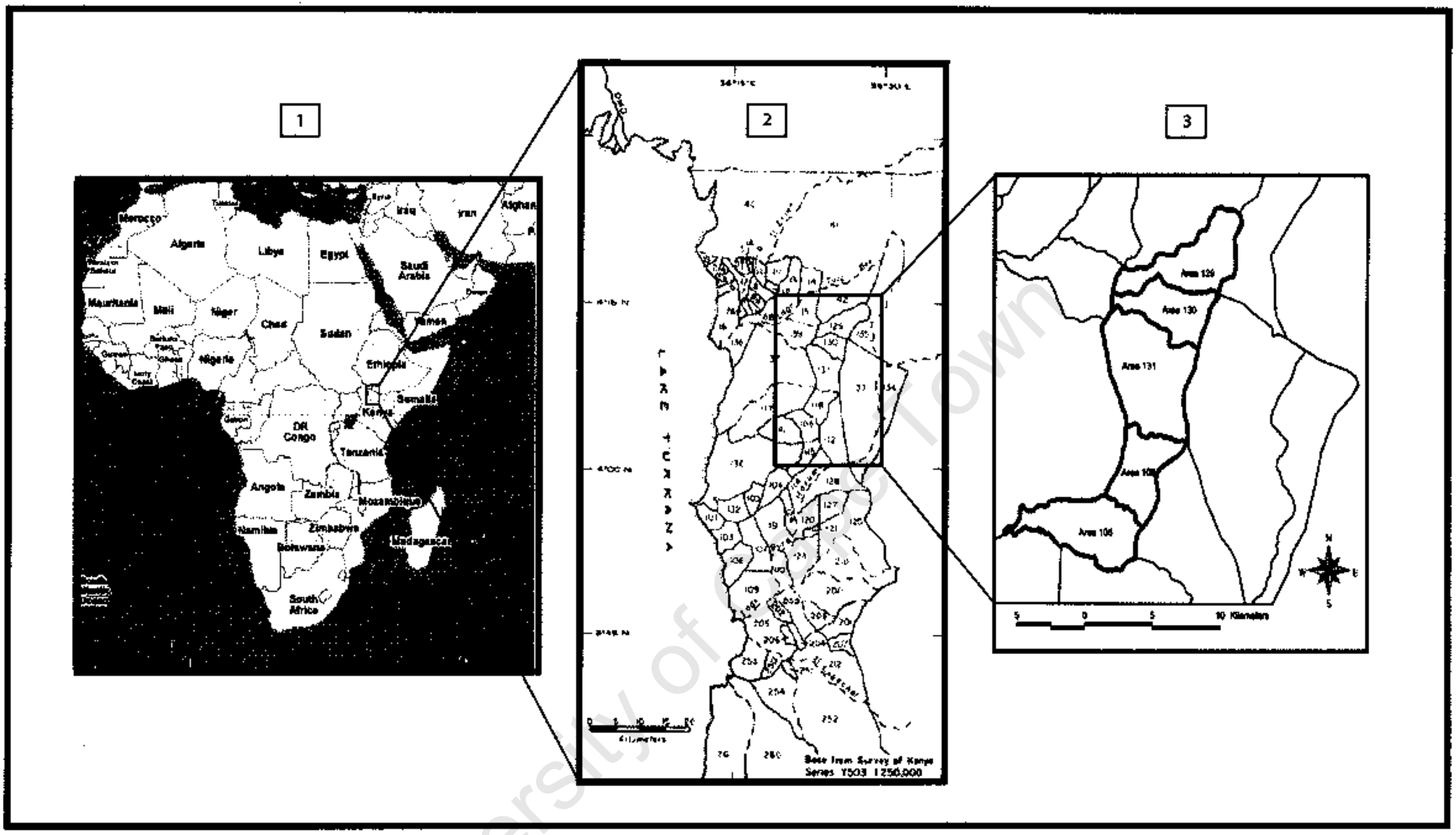


Figure 1.1 Geographic location of the Karari Ridge in the Turkana Basin [Map 1 (Google Maps), Map 2 (Isaac 1997 pp. 2), Map 3 (Isaac 1997 pp. 114)]

The eastern shores of Lake Turkana have long been of interest to the scientific community, with the first European explorers reaching the lake (initially named Lake Rudolf) in 1888 (Harris *et al.* 2006). Palaeontological interest was initiated in this region by the recovery of Plio-Pleistocene vertebrate fossils in the lower Omo Valley by the French expedition of Bourg de Bozas in 1902 and 1903 (Harris *et al.* 2006). The first archaeological site in Koobi Fora was discovered in 1969 and yielded *in situ* Oldowan-type artefacts from a volcanic ash in Area 105. This site was subsequently named the Kay Behrensmeyer Site (KBS) after the geologist on the project at the time (Leakey 1970). Today, this site is known as FxJj 1 and the volcanic tuff in which it is situated is known as the KBS tuff (Isaac 1997). From 1970 to 1974, work continued along the Karari escarpment, including the excavation of FxJj 3 (or the Hippo Artefact Site, HAS) also in Area 105, and the excavation of FxJj 10 in Area 108 (Isaac 1997). In 1973, two hominin

crania were discovered further north on the Karari escarpment in Area 130, KNM-ER 1805 and KNM-ER 1813. At present, numerous palaeoanthropological studies are situated in the Turkana basin as this region continues to provide valuable insight into the origins of early man.

The archaeological and palaeontological research focused on Lake Turkana over the last 50 years has provided tremendous insight into the origins of our species as well as contributing much to our understanding of its timing and context (Harris *et al.* 2006). Over 200 early hominin specimens representing at least 5 species have been collected from Koobi Fora, providing insight into the diversity of Plio-Pleistocene hominins in Africa (Harris *et al.* 2006). Most of the ungulates from Koobi Fora have been documented and described, with much attention given to the distribution of antelope species as a proxy for the Plio-Pleistocene habitats exploited by hominins (Shipman and Harris 1988; Bobe and Eck 2001). Two early stone tool industries were documented from archaeological work done in the Koobi Fora region; the KBS industry and the Karari industry (Isaac *et al.* 1976). The KBS industry describes artefact assemblages from the KBS Member of the Koobi Fora Formation that is defined by decreased amounts of small scraper forms. Further interpretation suggests that these assemblages are a local variant of the Oldowan industry (Isaac *et al.* 1997). The archaeological work done at Koobi Fora provides a basis from which to explore aspects of early hominin behaviour (Isaac and Isaac 1997) as indicated by the Oldowan Industrial complex. One of the most important aspects of the Koobi Fora Formation is the existence of large areas of lateral exposures so that archaeological inquiry can not only be investigated diachronically but also synchronically. The major focus of this project is to document variation across a single time horizon across an ancient landscape as opposed to variation through time.

The location of the Koobi Fora exposures with regard to their proximity to regions of great geological upheaval (tectonic plate boundary of the African plate and the Somali sub-plate) allow for large surfaces of exposed deposits to be linked chronologically through tephrostratigraphy (Feibel 1988; Brown *et al.* 2006; McDougall and Brown 2006). The Koobi Fora Formation in Northern Kenya is an ideal place to conduct this study because it is one of the most productive Plio-Pleistocene fossil localities in the world (Leakey 1978; Brown *et al.* 1985; Walker *et al.* 1986; Leakey *et al.* 1995). Hominin specimens as well as abundant mammalian vertebrate remains are known throughout the Koobi Fora Formation (Leakey 1982; Wood 1992; Wood 1992; Rightmire 1993; Leakey *et al.* 1995; Leakey *et al.* 1998). More importantly this excellent fossil record is associated with one of the most abundant Plio-Pleistocene archaeological collections in the world (Howell *et al.* 1987; Isaac *et al.* 1997). This includes abundant evidence of hominid activity in the form of cut-marked bone and associated lithic material (Isaac 1977;

Bunn *et al.* 1980; Toth 1982; Isaac 1983; Isaac 1984; Braun *et al.* 2003; Braun 2006; Braun *et al.* 2009). This project will investigate the bovid palaeoecology of the KBS Member of the Koobi Fora Formation dated at between 1.65 and 1.88 Ma (Brown and Feibel 1986; Brown *et al.* 2006; McDougall and Brown 2006) in an effort to better understand the context in which some of these lithic assemblages were created.

The application of palaeoecological models to understanding landscape scale variation in hominin behaviour has been a major focus of recent palaeoanthropological research [Olduvai Gorge: (Blumenschine and Masao 1991; Blumenschine *et al.* 2003); Olorgesailie: (Potts 1994; Potts *et al.* 1999)]. Previous research in the Turkana Basin has also identified behavioural variation in hominin behaviour on a landscape scale in the Okote Member (Rogers *et al.* 1994; Rogers 1997). However, many studies of landscape scale palaeoenvironmental variation suffer from a palaeoecological context which may be too coarse to be relevant to hominin behaviour (Potts 1998). This study will address this by applying new techniques to gain insights on finer scale palaeoecological variation in association with a large archaeological sample. Using bovid ecomorphology and other habitat affiliation techniques, palaeoecological reconstructions that are directly applicable to hominin behavioural variation are developed for three major areas of archaeological investigation. These areas are palaeontological survey Areas 105, 108 and 130 from the Koobi Fora Formation.

1.2 Context

The study of the Oldowan industry is more than just the study of stone artefacts, it has come to incorporate the land use and diet of hominins to explore why stone tools were made and discarded. Oldowan studies have begun to explore the variation evident within the temporal and geographic structure of this industry (Semaw *et al.* 1997; Delagnes and Roche 2005). Recent excavations of archaeological sites in the KBS Member of the Koobi Fora Formation suggest possible hypotheses that may explain variation across Oldowan landscapes, as these artefact collections represent hominin behaviours in diverse settings (Braun 2006; Braun and Harris In Press). The different factors that affect technological organization are well known from KBS Member times, such as raw material availability and quality (Braun *et al.* 2009). It is therefore possible to investigate the effects of different ecological settings on patterns of tool use and discard for this time period. Stone tool technology may represent a medium through which Oldowan hominins were able to increase the efficiency of their resource acquisition techniques (Bousman 1993; Bamforth and Bleed 1997; Braun and Harris In Press). One of the ways that hominins can increase the use-life of a core is to reduce it more extensively. Exhaustive reduction can be seen as a method of increasing the use-life of a flaked piece. The predicted stage in reduction sequence values of whole flakes (detached pieces with complete platforms and intact lateral and distal ends) have been used as a proxy for this behaviour of increasing use-life (Braun *et al.* 2008). Multiple linear regression models have been applied to the KBS assemblages in previous studies in an effort to model this behaviour. These models are based on a series of linear measurements of whole flakes and cores, and allow for a reasonably accurate description of the position of a whole flake in the reduction sequence (see Braun (2006) and Braun *et al.* (2008) for a complete description of the multiple regression model technique). These values record the intensity of core reduction at the time the detached piece was removed. Assemblages that exhibit higher frequencies of flakes that are predicted to be later in the reduction sequence represent cores that are near exhaustive reduction levels.

In the KBS Member there are significant differences in the extent of flaked piece reduction between earlier and later KBS Member assemblages. The whole flake assemblage at FxJj 3 (HAS) in Area 105 represents the least amount of reduction, whereas the flake assemblage from FxJj 82 in Area 130 exhibits patterns consistent with more exhaustive levels of reduction (Braun 2006; Braun and Harris In Press). One possible explanation for these increased levels of reduction may be variation in the requirement of stone artefacts in the behavioural repertoire of hominins across various ecological conditions in time and space. Although differences in raw material availability could explain the patterns seen in these assemblages, this is unlikely during KBS Member times (Braun *et al.* 2009). The basin margin drainage systems at this time would have been increasing in competence due to increased uplift in the Chew Bahir (previously known as Lake Stephanie) basin (Feibel 1988; Lepre 2001). The result would have been an increasingly higher incidence of clasts large enough from which to make artefacts. These clasts would have been available as raw material for artefact manufacture by hominids occupying the Aberegaiya and Karari escarpment regions during KBS Member times (Braun *et al.* 2009). In their ED-XRF analysis of samples of artefacts from excavations in the KBS Member Braun and colleagues showed that Asille Group basalts and pantellerites appear in all of the samples, regardless of their position in the basin (Braun *et al.* 2009). Another possible explanation for this variation may be ecological differences between different parts of the basin. During KBS Member times, available palaeoenvironmental data point to a trend towards more xeric conditions in the Turkana Basin (Feibel *et al.* 1991; Cerling 1992; deMenocal 2004). The general palaeoenvironment surrounding the basin, however, breaks down into a mosaic of local environmental situations, each with their own challenges and benefits to hominids (Bobe and Behrensmeyer 2004). This means that there is significant intra-basinal variation in the palaeoenvironments occupied by KBS Member hominins. In Africa, drier environments tend to have a

significant grassland component. In these types of environments the biomass available for hominid consumption is shifted toward large mammals (Leonard and Robertson 2000; Binford 2001). Binford (2001) has shown that medium sized ungulates are more common in savannah grassland areas (areas that are more arid). Binford (2001) also shows that where the biomass of these medium sized ungulates is greater, hunter-gatherers are exploiting them as sources of potential energy more often. Hominins that lived in environments dominated by an ecology with a lower bio-availability ratio (Figure 2.4) would have had access to a limited selection of resources (Binford 2001), where the 'bio-availability ratio' describes the relative abundance of leaves and grass for animals to eat (Binford 2001 pp. 83). It is therefore possible that hominin occupation of grassland environments required an increased reliance on mammal tissue as it does for modern hunter-gatherers, a resource for which access requires the use of sharp-edged stone tools (Blumenschine and Peters 1998). Experimental data from Pobiner and Braun (2005) and Braun *et al.* (2008) suggest that the skinning and disarticulation of even small sized mammals for tissue can drastically reduce the utility of stone edges. Thus it follows that the use life of tools at sites in more open and drier habitats would have been dramatically reduced. The result would have been a higher incidence of core reduction in these habitats. Drier grassland environments may have forced hominins to adopt more conservative tool-use strategies.

The increased levels of reduction found in the flake assemblages from FxJj 82 in Area 130 and FxJj 10 in Area 108 may represent a greater reliance on stone tool technology as a response to drier, more xeric environments. The lower levels of reduction found in the flake assemblages from FxJj 1 (KBS) and FxJj 3 (HAS) in Area 105 may indicate less intensive use of stone tools. This in turn may reflect the environment in Area 105. Palaeoenvironmental reconstructions of FxJj 1 and FxJj 3 in a back-delta swamp (Feibel 1988) indicate an abundance of resources such as fruiting trees that do not require intensive tool use to access. At FxJj 1, the sandy tuff silts that cover the concentration of artefacts and bone fragments also preserve numerous impressions of *Ficus* leaves that must have fallen from trees or large bushes (Isaac and Isaac 1997). It is therefore possible that sharp-edged stone tools were not a vital resource for hominins in this environment as the biomass available for hominid consumption may have been dominated by fruiting trees (Copeland 2009). The earliest record of hominin behaviour on the Eastern shores of Lake Turkana may therefore be more complex than originally modelled by Isaac and Harris (1997). The landscape scale variation observed in technological strategies between Area 105, Area 108 and Area 130 may be linked to variation in ancient environments. This variation in technological strategies allowed hominins to increase the use-life of their toolkit according to their requirements for stone tool mediated resources. This suggests that Oldowan technology may reflect differences in the

resources that hominins are acquiring, resources that are dependent on the palaeoenvironmental context of these assemblages.

1.3 Objectives

The archaeology of human origins allows a rare insight into the use of resources by our remote ancestors. This project integrates landscape scale archaeological collections from the KBS Member of the Koobi Fora Formation with innovative methods of palaeoecological analysis to develop an understanding of the variation in habitat use by Plio-Pleistocene hominins. The goals of this research are to collect palaeoecological data on geographic scales that are relevant to the landscape scale variation in hominin behaviour (Deocampo *et al.* 2002). This data will then be combined with a large archaeological sample of the KBS Member of the Koobi Fora Formation (Braun 2006; Braun *et al.* in press) outlined above to determine if palaeoecological changes are reflected in changes in hominin behaviour. This project will investigate palaeoenvironmental landscape scale variation by implementing bovid ecomorphological techniques established by Plummer and Bishop (1994; 2008), DeGusta and Vrba (2003; 2005) and others (Kappelman 1988; Kappelman *et al.* 1997; Kovarovic and Andrews 2007), bovid habitat tribal affiliation data as well as pedogenic carbonate data.

In summary, the aims of this research are

1 To investigate the potential forces acting to influence hominid tool-use behaviour in three separate areas in the KBS Member of the Koobi Fora Formation in Northern Kenya.

2 To collect palaeoecological data on geographic scales that are relevant to the landscape scale variation in hominin behaviour.

3 To combine this data with a large archaeological sample of the KBS Member of the Koobi Fora Formation (Braun 2006; Braun *et al.* in press) to determine if palaeoecological changes are reflected in changes in hominin behaviour.

1.4 Conclusion

This project aims to test the hypothesis that landscape scale variation in palaeoenvironments had an effect on the behaviour of KBS Member hominins. To do this, this project investigates the palaeoenvironments of the KBS Member of the Koobi Fora Formation on the Karari escarpment at a landscape scale. Previous palaeoenvironmental reconstructions for this palaeoanthropologically significant region have not always accessed palaeoecological data on a scale that is relevant to the individual hominin and its behaviour. This project utilises bovid ecomorphology, bovid tribal affiliation

data and pedogenic carbonate data in order to access palaeoenvironmental data on a landscape scale. This palaeoenvironmental data, combined with the archaeological data from the Koobi Fora Formation, indicates that KBS Member hominins were increasing the use-life of artefacts by extensive reduction strategies in more open, xeric environments, such as those reconstructed for Areas 108 and 130. These intensive reduction strategies would have been less crucial in closed, mesic environments, such as those reconstructed for Area 105. This is as hominins would have been coming into contact with resources that require stone tools (i.e. mammal carcasses) less often.

2. Background

2.1 Introduction

This chapter aims to inform on the background research upon which this project is based. The Karari region of the Koobi Fora Formation has been subject to much palaeoanthropological and palaeontological research since its discovery. This chapter provides a synthesis on the archaeological findings that are relevant to this project as well as on previous palaeoenvironmental reconstructions for this region.

2.2 Archaeology

Two archaeological sites within the KBS Member occur in Area 105, FxJj 1 and FxJj 3. The excavated archaeological collection from FxJj 1 consists primarily of many smaller detached pieces and many of these artefacts preserve evidence of the cortex of rounded river cobbles. FxJj 3 (or the Hippo Artefact Site, HAS) also in Area 105, was excavated from 1970 to 1974. The original surface finds from this excavation included only 64 artefacts and over 1000 fossils. The archaeological collection from this excavation is also dominated by relatively small detached pieces. Just as in FxJj 1, pebbles and cobbles greater than 4cm in maximum dimension were recovered. The initial excavations of another archaeological site from the KBS member, FxJj 10 in Area 108, took place from 1972 to 1973 (Harris and et al. 2006). Excavations at this site were reopened in 2003 (Braun 2006). The 1973 excavations at FxJj 10 recovered 564 artefacts and the 2003 excavations recovered a further 161 artefacts. Despite the great number of artefacts, only 6 fossils were recovered from FxJj 10 during the 1973 excavations, all of which were too weathered to determine taxonomic affiliation. No fossils were found at this site during the 2003 excavations. In 1973, two hominin crania were discovered further north on the Karari escarpment in the KBS Member of Area 130, KNM-ER 1805 and 1806. Survey near this area in 2001 resulted in the discovery of the archaeological site of FxJj 82. This locality is situated almost directly due east of the hominin localities of KNM-ER 1805 and 1806.

This combined sample of artefacts as well as extensive raw material sourcing (Braun *et al.* 2009) allow for a comprehensive study of the variation in technology of the KBS Member. In particular the diverse environmental context of the KBS Member in the Karari region provides insight into selective pressures acting on tool mediated behaviours (Braun and Harris In Press). Braun (2006) conducted three reduction assessment analyses on the archaeological collections from the KBS Member in Area 105, Area 108 and Area 130. Only basalt flakes and cores from these areas were analysed in these tests in

order to reduce the potential variability in the analysis derived from variability in raw materials. Variation in the reduction intensity across space under these circumstances is indicative of variation in hominin tool utilisation strategies.

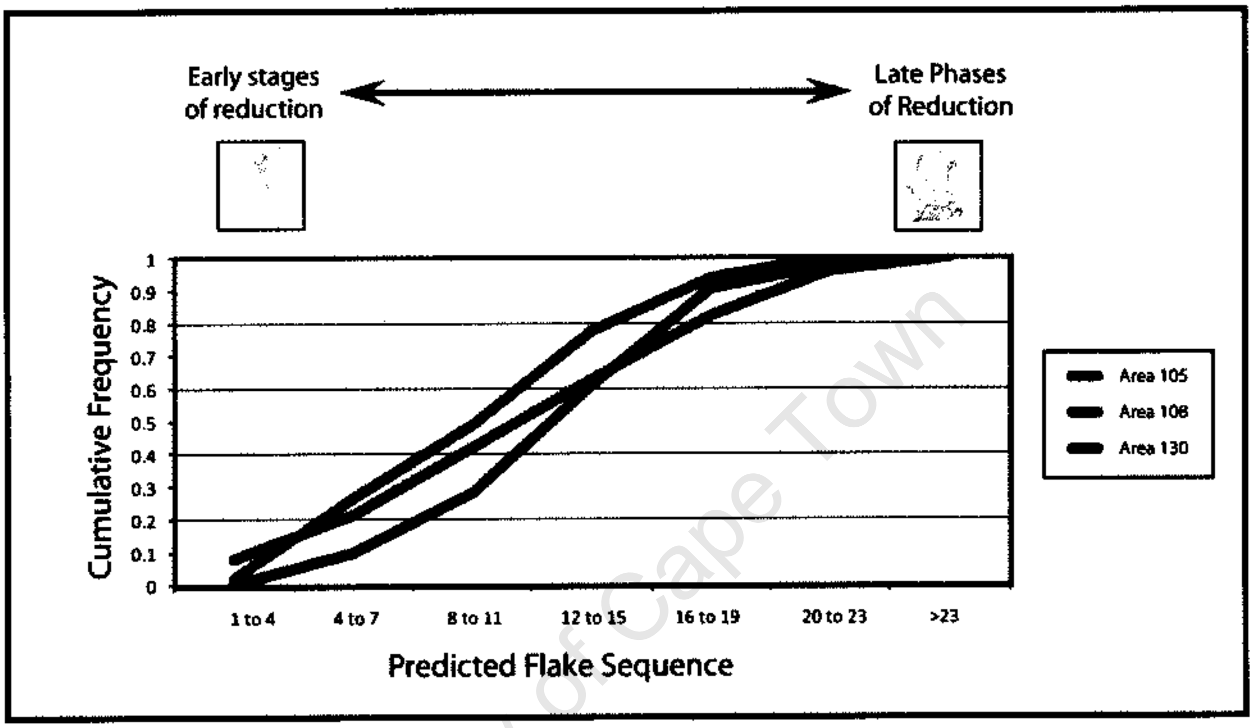


Figure 2.1 Cumulative frequency graph of the range of flake stages from an idealised reduction sequence found at Areas 105, 108 and 130 (Braun et al. 2008).

The first of the three analyses of reduction intensity conducted by Braun (2006) is the application of a multiple linear regression technique (Braun *et al.* 2008) to the archaeological collections from FxJj 1 (Area 105), 3 (Area 105), 10 (Area 108) and 82 (Area 130). For the following analyses, FxJj 1 and FxJj 3 were grouped due to their geographic proximity. This technique combines several variables and thus enables a reasonably accurate description of the position of a whole flake in an idealized reduction sequence [the system of the sequence of flake removals from a flaked piece]. In this case, the multiple linear regression produces values for the predicted stage of flakes in the reduction sequence for each assemblage by quantifying the correlation between flake attributes and reduction sequence order (Braun *et al.* 2008 pp. 2157). The results of this multiple linear regression (Figure 2.1) were tested for significance using the MWU Test (Null hypothesis: no significant difference at the 0.05 significance level). This significance test indicated that while the results from Area 105 are significantly different from the results from Area 130 (M-W U:1957, z = -2.388, p=0.017), the results from Area 108 are not significantly different from either Area 105 (M-W U:3640, z =-0.940, p=0.174) or Area 130 (M-W U:7473,

z = -1.751, p=0.08). A review of the cumulative distribution of values divided into evenly spaced sections of the reduction sequence (Figure 2.1) shows that assemblages from Area 108 and Area 130 show higher frequencies of flakes in later stages of an idealised reduction sequence. This indicates more extensive reduction in these regions.

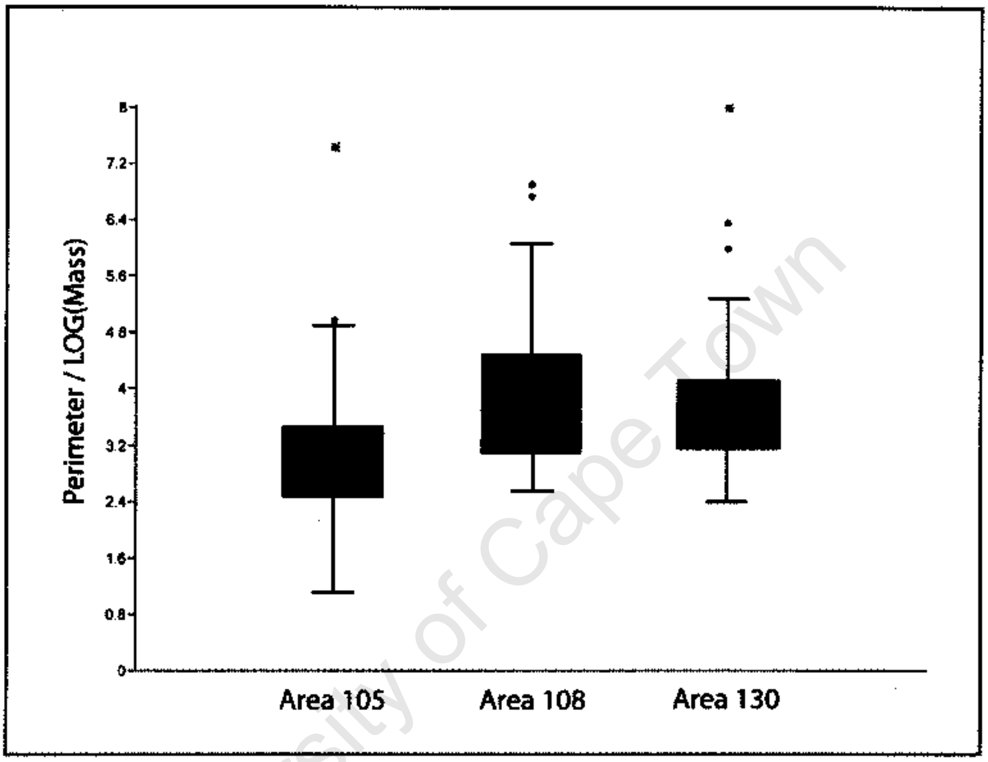


Figure 2.2 Box plot depicting the range of variation in flake utility (the perimeter to mass ratio) found at Areas 105, 108 and 130 (Braun and Harris 2003).

The second analysis applied to this archaeological data is an assessment of flake utility (flake utility = flake edge/log of flake mass) (Braun and Harris 2003 pp. 121). This perimeter to mass ratio (or flake utility) provides an "easy quantification of the meaning of a flake to an early hominid" (Braun and Harris 2003 pp. 121) as it is influenced by core reduction strategies that attempt to maximize the length of the cutting edge of a flake per volume of raw material (Braun and Harris 2003). The flake utility measures for Area 105, Area 108 and Area 130 (Figure 2.2) were tested for significance using the MWU Test (Null hypothesis: no significant difference at the 0.05 significance level). The ratio of perimeter to logged mass of flakes from Area 105 is lower than the same ratio in both Areas 108 (M-W U: 1143, z = 4.566, p<0.001) and 130 (M-W U: 1146, z=3.897, p<0.001). The flakes from Area 105 would therefore

have more mass than the flakes from Areas 108 and 130 (M-W U: 2756, z = -0.725, p<0.001), if the perimeter of each flake was kept constant.

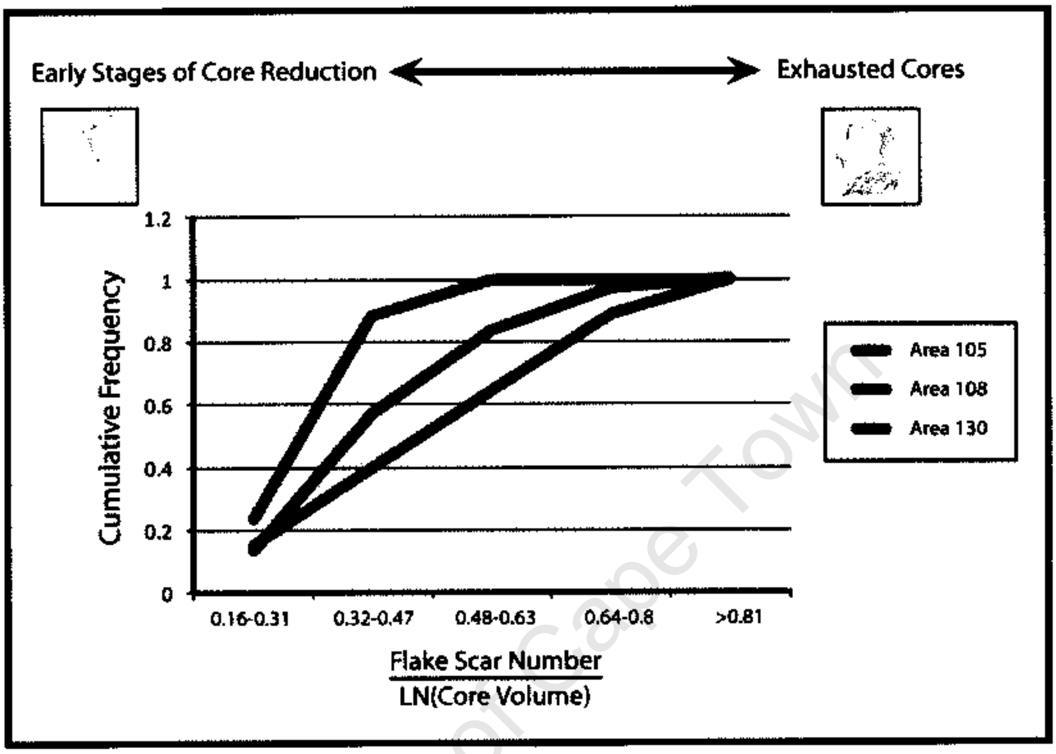


Figure 2.3 Cumulative frequency graph of flaked piece reduction calculated from the number of flake scars normalised by the natural log of the volume of the flaked piece (Braun et al. 2009 pp. 38).

The final analysis applied to this dataset by Braun (2006) measured core reduction from the flaked pieces themselves. In other analyses, flake scar counts have been used as a measure of core reduction intensity (Potts 1994), however some flake scars may be removed by the manufacture of subsequent flakes (Braun *et al.* 2005). A more appropriate measure of reduction intensity is therefore the number of flake scars normalised by the natural log of the volume of the flaked piece (Braun *et al.* 2009 pp. 38). The results for this measure of core reduction intensity (Figure 2.3) were tested for significance using the MWU Test (Null hypothesis: no significant difference at the 0.05 significance level). The results of this test indicate that the results from Area 105 are significantly different from the results from Area 108 (M-W U: 199, z = -2.459, p=0.013) and Area 130 (M-W U: 160, z = -1.826, p=0.035), as are the results from Area 108 significantly different from the results from Area 130 (M-W U: 477, z = -1.034, p=0.153).

Oldowan technology represents the first attempts by early hominins to culturally mediate their mode of resource acquisition. One of the possible methods hominins may use to increase efficiency is to

increase the use-life of an artefact by exhaustive reduction, thereby decreasing the time required to procure new sources of raw material (Braun *et al.* 2009). The extensive reduction of flaked pieces evident from Area 130 and Area 108 may be the result of an increased need for artefacts. Subsequently hominins may have preserved their sources of raw material by increasing the use-life of an artefact via extensive reduction. The less exhaustive reduction of flaked pieces from Area 105 may be the result of less hominin dependence on culturally mediated resources.

2.3 Interpretation

Differences in raw material availability could explain the patterns seen in these assemblages as raw material availability plays a dominant role in the technology of hominins. To this end, Braun *et al.* (2008) have constructed a model of raw material availability in the Turkana basin during KBS Member times. This model suggests that the two major river systems that were active on the eastern side of the Turkana basin during the Plio-Pleistocene, the basin-margin river system and the basin-axis river system (or Proto-Omo), provided distinct sources of raw material to hominins. Their results show that Plio-Pleistocene hominins used the igneous rocks (basalts and rhyolites) that form the eastern margin of the Turkana basin to make stone artefacts. In the KBS Member, these basalts and rhyolites appear in all archaeological samples found in the Turkana basin. Based on Feibel's (1988) reconstruction of the Turkana basin during KBS Member times, Braun *et al.* (2008) conclude that the presence of these basalts is a result of high velocity flow depositing coarse-grained deposits along the axial Proto-Omo river. The data from Braun *et al.* (2008) suggest that the Proto-Omo river was a major source of raw material for hominins during KBS Member times, with some influence from basin margin streams. The basin margin streams would have had higher competence during KBS Member times due to increased uplift in the basin (Feibel 1988; Lepre *et al.* 2007). The result of this uplift would have been a higher incidence of basalt clasts large enough from which to make stone artefacts (Braun *et al.* 2009 pp. 38). Similar types and amounts of raw material would therefore have been available to hominins at each site in Areas 105, 108 and 130. Raw material availability therefore does not adequately explain the patterns evident in the artefact assemblages from Area 105, Area 108 and Area 130.

Oldowan artefacts are the means by which Plio-Pleistocene hominins gained access to some of the resources, such as meat and marrow, which were vital to their survival (Braun and Harris 2003). Variation in the accessibility of these resources may have resulted in variation in the intensity of tool use and discard by Plio-Pleistocene hominins, in turn resulting in the kind of variation in the archaeological record outlined above. The question then becomes, what factors influence the accessibility of meat and

marrow resources by hominins? Binford (2001) has investigated this question with regard to modern hunter-gatherer populations. According to Binford (2001 pp. 73),

> ***"the amount of energy accessible from the biological components of habitats is strongly influenced by both sources of potential energy available for exploitation within the ecosystem and the tactics and strategies available for extracting that energy".***

In the case of hominins in Koobi Fora during KBS Member times, the "tactics and strategies available" for extracting the available energy are represented by the Oldowan artefacts recovered from the excavations in Areas 105, 108 and 130.

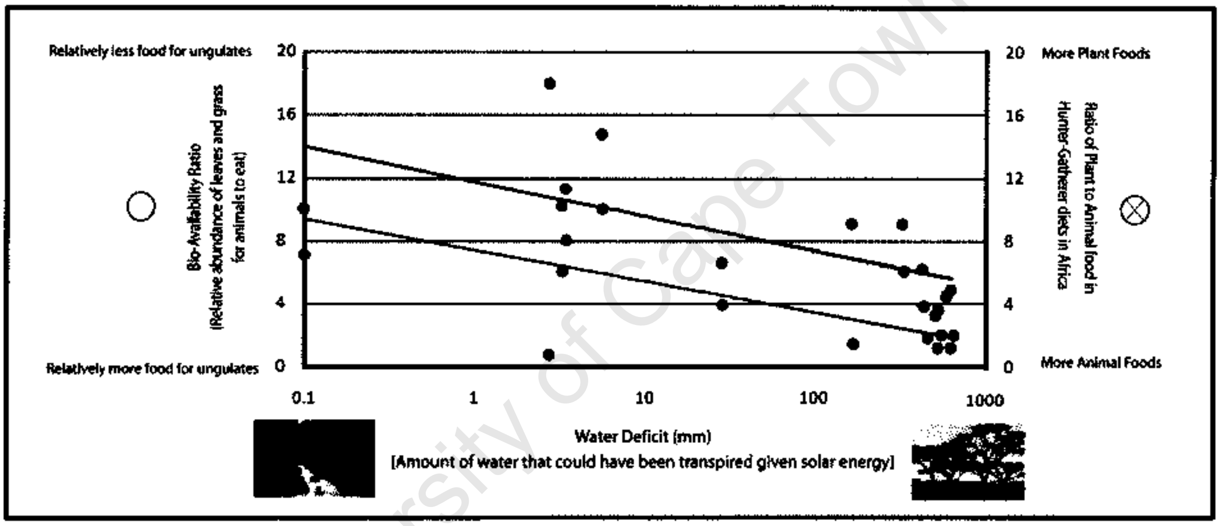


Figure 2.4 Graph indicating the correlation between Water Deficit (logarithmic scale) and Bio-availability (empty circles), as well as the correlation between Water Deficit and the ratio of plant to animal food consumed by hunter-gatherer populations (circles with a cross). Data from Tables 4.07, 4.09 and 5.01 in Binford (2001).

Binford (2001) has investigated the "potential energy available for exploitation" in various modern ecological settings. Binford's (2001) ecological settings are correlated with a measure of 'Water Deficit' (mm). This is a direct measure of the degree to which water limitation affects the production of new cells in a specific plant community and is calculated as the difference between 'Actual Evapotranspiration' and 'Potential Evapotranspiration' (Binford 2001 pp. 75). Binford's (2001) data supports the assertion that where water deficit is high, there is relatively more food available for ungulate consumption (Bio-availability; Figure 2.4). In other words, in drier, more open environments there is more primary production available for consumption by large to medium sized ungulates. On this same figure, Binford's (2001) data indicates that modern hunter-gatherer populations eat relatively more animal foods than plant foods when water deficit is high. When water deficit is low, in relatively

more mesic environments, hunter-gatherers eat relatively more plant foods (Binford 2001). Binford (2001) goes on to indicate that there is a correlation between the biomass of medium sized ungulates and the ratio of plant food to animal food in hunter-gatherer diets (Figure 2.5). This implies that where the biomass of medium sized ungulates is greater, hunter-gatherers are exploiting them as sources of potential energy more often, and where ungulate biomass is lower; hunter-gatherers are exploiting these resources less frequently. The biomass of medium-sized ungulates is in fact greatest in a savannah grassland type of environment (Binford 2001). In these environments medium sized ungulates are equal to or larger in size than impala and range up to and include giraffe (Figure 2.6). This evidence indicates that variation in ecological settings has a significant influence on the accessibility of resources by modern hunter-gatherers. Thus, variation in palaeoenvironmental settings may have had a significant influence on the accessibility of resources such as meat and marrow by hominins.

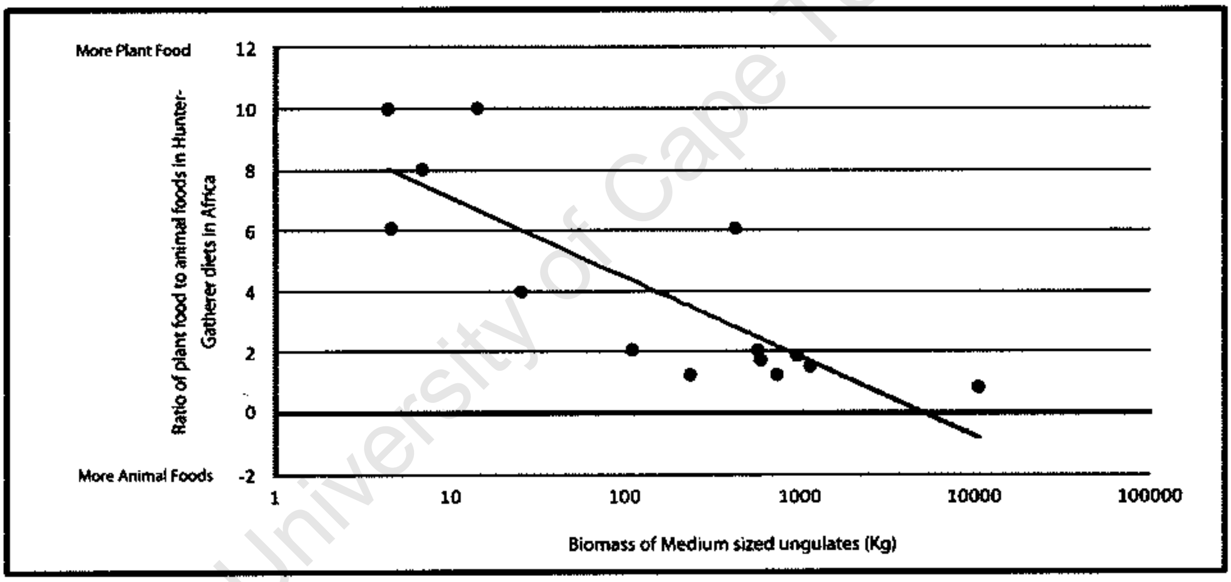


Figure 2.5 Graph depicting the correlation between the available biomass of medium-sized ungulates (logarithmic scale) and the amount of animal food in hunter-gatherer diets. Data from Tables 4.09 and 5.01 in Binford (2001).

It is possible that hominins in the Turkana Basin in KBS Member times were occupying a variety of environments, from more open, arid environments to more closed, mesic environments. According to Binford (2001), these environments may have been variable in the frequency of medium-sized ungulates. More medium-sized ungulates were accessible as resources to hominins in more open environments. Fewer medium-sized ungulates were accessible as resources in closed, swampy environments (Binford 2001). As a result, hominins may have been utilising different core reduction strategies according to the frequency with which they were coming into contact with these "meat and

marrow" resources. In more open environments such as Area 108 and Area 130, the archaeological record indicates a pattern of increased reduction whereas in more closed environments such as Area 105, the archaeological record indicates a less intensive core reduction strategy. It is therefore possible that KBS Member hominins were discerning the technological methods employed according to the environments they occupied, and the associated frequency of access to meat and marrow resources, mediated by stone artefacts.

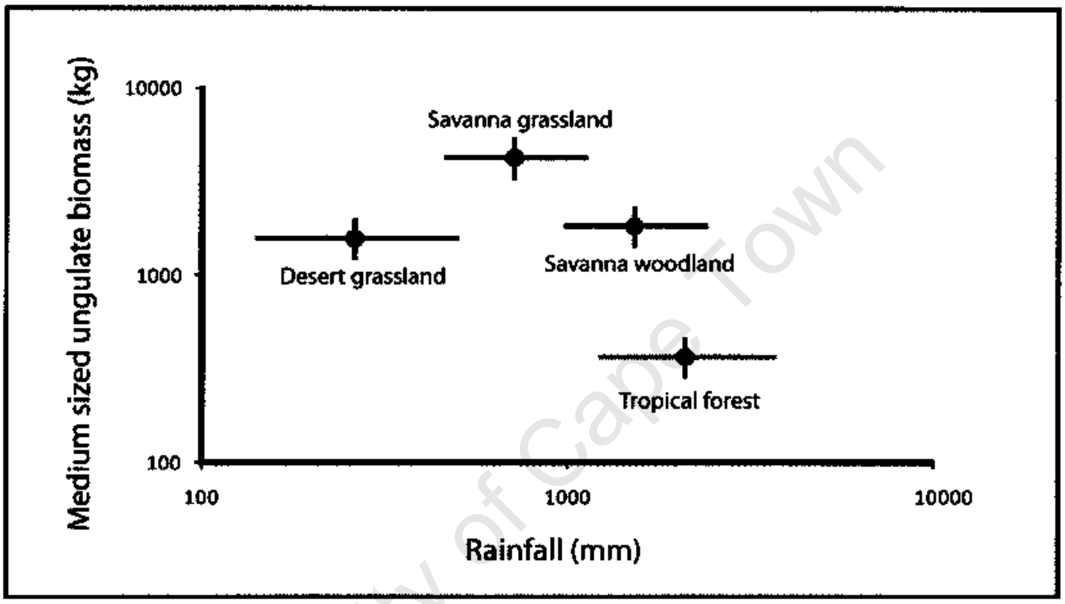


Figure 2.6 Graph depicting the abundance of medium-sized ungulates in various modern habitats from Binford (2001).

2.4 Previous Palaeoenvironmental Reconstructions

The archaeology from the KBS Member of the Karari Ridge indicates variation in hominin behaviour at a sub-basinal scale. One of the possible explanations for this variation in behaviour is provided by models developed by Binford (2001) described above. Palaeoenvironmental variation across the KBS Member landscape may have resulted in the variation in hominin behaviour indicated by the archaeology. A concise picture of landscape scale palaeoenvironmental variation is therefore required. Many previous palaeoenvironmental reconstructions of East Turkana are focused on reconstructing the palaeoenvironment for the entire basin (Feibel *et al.* 1991; Lepre *et al.* 2007; Quinn *et al.* 2007; Levin *et al.* 2009). A series of methods have been developed in order to interpret and measure the interactions and effects of climate forcing processes, as well as changes in climate on a shorter time scale, on the environments inhabited by early hominins. However it is unlikely that this scale is relevant for the daily to decadal scale variation in hominin behaviour that the archaeological record represents. Some of

these methods have been applied to Koobi Fora by other researchers. A selection of these is discussed below.

2.4.1 Geological Approaches

Geological approaches to palaeoenvironmental reconstruction include the analysis of ocean-dust records as well as the interpretation of lake sediments. These analyses provide a basinal to sub-continental scale perspective on palaeoenvironments. Ocean-dust records are applicable to palaeoenvironmental reconstructions on the principle that extended periods of aridity reduce vegetation cover leaving dry soil surfaces exposed to wind deflation which cause frequent dust storms as well as high levels of atmospheric dust-loading. Therefore, over geological timescales, variation in aridity is recorded stratigraphically as "variable quantities of aeolian detritus preserved in marine sediments" (deMenocal 1995 pp. 53). This approach is concerned with ecological change on a broader timescale. According to deMenocal (2004) "large scale shifts in climate alter the ecological composition of a landscape, which in turn present specific faunal adaptation or speciation pressures leading to genetic selection and innovation" (pp. 3). In his 2004 paper, deMenocal explores the African faunal and palaeoclimatic evidence which constrains the current environmental hypotheses of African faunal evolution described above. The analysis of marine sediments off the western and eastern margins of sub-tropical North Africa provided deMenocal with records documenting Plio-Pleistocene cooling at high latitudes occurring as a series of steps, starting after ca. 1.8 to 1.6 Ma.

Marine sediments recording Plio-Pleistocene aeolian transport from West and East sub-tropical Africa also reveal consistent patterns of variability. These records show that orbital-scale African climate variability (Milankovitch cycles: precession at 23 to 19 ka cycles, obliquity at 41ka cycles and eccentricity at 100ka cycles) persisted throughout the Plio-Pleistocene. These records also show that these orbital-scale, step-like shifts occurred at 2.8 Ma, 1.7 Ma and 1.0 Ma, and that aeolian concentration and supply increased gradually after 2.8 Ma. For East Africa and Arabia, deMenocal (2004) believes that this increase in aeolian supply likely reflects a real increase in source area aridity. These sites also indicate an interval of pronounced aridity between 1.8 and 1.6 Ma, a signal not pronounced at other locations. According to deMenocal (1995), these shifts in aeolian concentration indicate that after 2.8 Ma the African climate became sensitive to remote changes in high latitude climates, which were cooler and drier as a result of cold glacial sea-surface temperatures.

Ocean-dust records provide a unique perspective on palaeoenvironments; however, the continental scale of the data they provide is not much use with regard to questions that are more site specific, other than providing a continental-scale framework with which to contextualise finer-scale data. This finer-scale data can be provided by the sedimentological analysis of specific localities. This analysis includes describing major depositional environments or lithofacies. This site-specific analysis can be geographically extended in situations where the correlation of stratigraphic sections over several kilometres enables the reconstruction of palaeogeographic settings on a basin-wide scale, such as exists in the Turkana Basin.

Geologic investigation of the East Turkana basin was initiated by Kay Behrensmeyer in 1969. The Koobi Fora Formation consists of a series of beds of fluvially transported volcanic ashes or tuffs within archaeologically rich sediment. These tuffs, despite being discontinuous over the landscape, have been used as marker beds in the subdivision of local sequences as well as the basis for correlating between areas (Feibel *et al.* 1989; Brown and Feibel 1991; Isaac *et al.* 1997). The landscape scale nature of these tuffs has allowed for the synchronic investigation of numerous archaeological sites in this region, providing information on landscape scale variation (as opposed to chronological variation) in hominin behaviour. Well-dated and laterally extensive tuffs link the stratigraphy of the different formations within the Omo Group and permit basin-wide exposures of a single depositional system (Feibel *et al.* 1989). The KBS Member of the Koobi Fora Formation of the Omo Group (the member under investigation in this project) is stratigraphically bracketed by two of these well-dated volcanic tuffs. The KBS Member is situated between the base of the KBS tuff dated at 1.88 Ma and the base of the Okote tuff dated at 1.67 Ma (Brown *et al.* 2006; McDougall and Brown 2006). The KBS tuff was originally dated to 2.61 ± 0.26 Ma using the 40Ar/39Ar step-heating technique. However, this date did not agree with the available biostratigraphic indicators, leading to a debate on the validity of this age estimate (Behrensmeyer and Jolly 1978; McDougall 1981). Initially, age estimates for this tuff provided by palaeomagnetic stratigraphy seemed consistent with this early date, but were later shown to be incorrect. More attempts at refining the date for this tuff were carried out using conventional K/Ar dating techniques, as well as Ar^{40}/Ar^{39} dating techniques. These methods provided an age for the KBS tuff closer to 1.9 Ma, a date consistent with the available biostratigraphic indicator (White and Harris 1978). Fission track dating was also applied to what had become "the KBS problem", this technique provided dates that were consistent with the 1.8 — 1.9 Ma dates. Recent evidence has emerged indicating that the KBS tuff is in fact geochemically indistinguishable from tuff H2 in the lower Omo Valley, dated at 1.81 — 1.87 Ma (Brown *et al.* 2006). The final date provided for the KBS tuff, at 1.88 ± 0.2 Ma, is now one of the most reliable dates in palaeoanthropology (McDougall 1985; Isaac 1997).

Geologic analysis indicates that the lake that currently dominates the Turkana basin did not come into existence until the last several hundred thousand years (Feibel 1988). For most of the last 4 Ma, the ancestral Omo River flowed down into the Turkana Basin from the Ethiopian Highlands, and a second river, the Turkana River, flowed out from the basin to the Indian Ocean (Rogers *et al.* 1994). At 2.3 Ma, there was no lake present in the Turkana basin, instead, the Omo River ran through the basin along a course determined by structural control, such as uplift in the northeast of the basin (Rogers *et al.* 1994). By 1.8 — 1.9 Ma, the large lake which had been formed ca. 2 Ma was being filled with sediment by the delta of the Omo River along its eastern margin (Rogers *et al.* 1994 pp. 149). The sedimentary data associated with this early lake records a stable system. Starting at ca. 1.89 Ma, this sedimentary data indicates fluctuations and the lake level becomes unstable (Rogers *et al.* 1994). The archaeological sites from this period, found in the KBS Member, were formed on an alluvial delta plain. The fluvial sediments of the KBS and Okote Members show that the lake waters were more alkaline than they had been in the past, and that they fluctuated between relatively fresh and relatively alkaline conditions (Isaac and Behrensmeyer 1997). The bedding characteristics of the polymictic conglomerate lithofacies from the KBS and Okote Members in the Karari area of the Koobi Fora Formation are indicative of deposition in braided, ephemeral water courses rather than in meandering channels (Isaac and Behrensmeyer 1997).

Lepre *et al.* (2007) investigated the Koobi Fora ridge in the northeast Turkana Basin in order to determine what factors influenced the formation of the fossiliferous sediments at the lake margin. Sedimentological and stratigraphic analyses were used to determine the palaeoclimate for this region. This study identified four facies environments from the KBS Member at localities on the Koobi Fora Ridge. Lepre *et al.* (2007) interpreted these facies as lake level changes. Sedimentation rates and the stratigraphic distribution of facies environments suggest that lake-level changes occur with frequencies similar to the timescales of orbital precession and obliquity. This data indicates an orbital (glacial) climate control acting on the northeast Turkana Basin. While this study does investigate palaeoenvironments from a palaeoclimate perspective, the scale of the results from this study are such that they do not inform on what palaeoenvironmental factors are influencing a group of hominins on a scale that is likely to affect the technological variation seen within the KBS Member.

2.4.2 Isotopic Approaches

Isotopic approaches to environmental questions are informative on climatic as well as ecological variations. Methods using oxygen stable isotopes reflect the interaction between major water bodies, such as the ocean, and the atmosphere. This data is found both in deep sea cores as well as in ice cores, and is used as a proxy for both temperature and evaporation. During evaporation, ocean water is enriched in the heavier oxygen isotope, ^{18}0, as the lighter ^{16}0 is preferentially energized. Certain marine microorganisms absorb oxygen isotopes in the construction of their carbonate skeletons. In doing so, they preserve a record of the oxygen isotope ratio of the surrounding sea water (Prentice and Denton 1988; Potts 1998 pp. 96). However, this information only really pertains to variations in ocean temperature and ice volume. Because of its broad scale, this record does not necessarily provide information about palaeoenvironments on land at a scale relevant to the behaviour (and fitness) of an individual hominin. Herbivores incorporate 6^{18}0 values into their dental enamel through the consumption of environmental waters by drinking, eating and breathing. The 6 ^{18}0 data from extant animals compared with modern behavioural data provides an analogy for how 6^{18}0 values of fossil teeth can be used as indicators of aridity (an aridity index) and the composition of meteoric water, that is, water in the form of precipitation (Levin *et al.* 2006).

Another form of isotopic analysis that also provides information about terrestrial palaeoenvironments on a relevant scale is the analysis of the ratio between the carbon isotopes ^{13}C and ^{12}C. The distribution of 6^{13}C values across all plant species is bimodal in that it reflects two potential photosynthetic pathways used by plant species. Animals eating plants record this signal in their tissues such as dental enamel (Schoeninger *et al.* 2003). C3 plants, which include all trees, most shrubs and herbs, cool or moist climate grasses, and nearly all dicotyledonous plants, have low 6 ^{13}C values of around -26.5 ± 2%0 (Bocherens *et al.* 1996). C3 plants photosynthesize using the Calvin-Benson pathway which discriminates strongly against ^{13}C, producing plant tissues that have these low 6^{13}C values. C4 plants, which include warm or dry climate grasses and some herbs, have relatively higher 6^{13}C values of around -12.5 ± 1%0 (Bocherens *et al.* 1996). C4 plants photosynthesize using the Hatch-Slack pathway which discriminates less strongly against ^{13}C, resulting in plant tissue with these higher 6 ^{13}C values. CAM plants, or plants using Crassulacean Acid Metabolism, are capable of fixing carbon with either pathway and therefore display 6^{13}C values covering the range for C3 and C4 plants (Bocherens *et al.* 1996), however these plants are geographically restricted (Ségalen *et al.* 2007). Pedogenic carbonates reflecting the 6^{13}C signal of ancient plants are preserved in palaeosols as well as in the dental enamel of herbivores consuming these ancient plants. Analysis of these 6 ^{13}C values provides a proxy for palaeoenvironments. 6^{13}C values are, like 6^{18}0 values, expressed as 'parts per thousand' (%o) variation from a standard isotopic reference taken from a belemnite from the Pee Dee formation from the Cretaceous age in South Carolina. Stable carbon isotope records from pedogenic carbonates as well as from carbon isotopes in dental enamel are interpreted as reflecting the spread of C4 grasses in East Africa (Cerling 1992; Levin *et al.* 2008).

The signals provided by the carbon and oxygen isotopes can be extracted from both pedogenic carbonates and from the carbon isotopes recorded in dental enamel. Carbonate precipitation occurs in soils via soil dewatering by plants and evaporation. It is during these processes that the carbon and oxygen isotope composition of vegetation and soil water influence the isotopic composition of pedogenic carbonates (Levin *et al.* 2004). Unlike proxies of global climate from the marine realm, pedogenic carbonate isotopes offer direct, local environmental information from habitats of palaeoanthropological interest. East Africa is an ideal region for stable carbon isotope analysis as, in tropical regions, virtually all the C4 plants are grasses and in Kenya almost all grasses growing at an elevation below 2500m use the C4 photosynthetic pathway (Cerling *et al.* 2003). The oxygen isotope ratio from pedogenic carbonates can also be measured as a proxy for atmospheric temperature (Cerling 1992). The combined analysis of 6^{13}C and 6^{18}0 from palaeosols can therefore provide quite a specific palaeoenvironmental interpretation (Potts 1998 pp. 103).

Quinn *et al.* (2007) use pedogenic carbonates from the Koobi Fora Formation of the Turkana Basin to examine palaeoenvironmental change across the interval from 2.0 to 1.5 Ma. The results from the Quinn *et al.* (2007) study indicate that it is the unique proximity of the Karari Ridge to basin margin channel systems that point towards a different water availability regime. This explains the low $6\ ^{13}$C values in the results obtained from the Karari Ridge and the associated increase in heavy cover bushes and trees. According to Quinn *et al.* (2007), if preservational differences are negligible amongst the sampled regions, the Karari Ridge, as reconstructed by the $5\ ^{13}$C values of pedogenic carbonates, was a more wooded environment from 2.0 to 1.5 Ma than it is today. The regional scale used for this study gives a good indication of the general palaeoenvironmental conditions of the Karari Ridge in general during KBS Member times, however, the results from this study do not illuminate on the landscape scale changes in hominin behaviour that are of interest here. Although the results of the above study is relevant to this project, it does not provide data on a scale relevant to answering the questions associated with the possible influence of the palaeoenvironment on landscape scale variation in hominin behaviour.

Levin (2008) used pedogenic carbonate analysis of $6\ ^{13}$C and 6^{18}0 values to provide a basin-wide scale perspective on environmental variability within the Turkana Basin, as well as regionally in East Africa. This data indicates that there is only one basin-wide transition at ca. 1.9 Ma signalling the return

to fluvial deposition after the formation of a palaeolake known as Lake Lorenyang, which existed from 2.0 to ca. 1.7 Ma (Quinn *et al.* 2007). The compilation of palaeosol carbonate isotope data from this study make it clear that terrestrial environments in East Africa did not respond uniformly to climate change in the Pliocene and Pleistocene. Levin (2008) also investigated isotopes from tooth enamel as a proxy for the palaeoclimate of the Turkana Basin during the Plio-Pleistocene. Both carbon and oxygen isotope ratios are recorded in the enamel of herbivore teeth. The 6 ^{13}C values in enamel are reflective of diet and are offset by a diet-enamel enrichment factor that has been determined experimentally for domestic and laboratory animals and estimated for wild animals (Cerling and Harris 1999; Passey *et al.* 2005). Herbivores incorporate PO values into their enamel through the consumption of environmental waters by drinking, eating and breathing. The 6 ^{18}0 data from extant animals provides analogues for how fossil 5^{18}0 values can be used as indicators of aridity and the composition of meteoric water, that is, water in the form of precipitation. The tooth enamel of various East African mammalian taxa were classified according to their isotopic sensitivity to environmental aridity. The various mammalian taxa were divided into groups of evaporation sensitive (ES) mammals and evaporation insensitive (EI) mammals. ES animals consume mostly leaf water whereas EI animals mostly drink from large bodies of water. The PO values for ES mammals increase with aridity whereas the 6 ^{18}0 values for EI mammals track changes in local meteoric water. The difference between the 6 ^{18}0 values in the tooth enamel of ES and EI mammals therefore records the degree of ^{18}0 enrichment between ingested water and source water, which increases with environmental aridity (Levin *et al.* 2006).

For Levin's (2008) study, fossil teeth from various areas and time periods within the Turkana basin were sampled, including teeth from the archaeological collections of FxJj 1, FxJj 3 (Area 105) and FxJj 82 (Area 130). The aridity index from these data suggest that fossils were deposited in the Turkana basin during both mesic (humid) and xeric (arid) episodes, the timing of which agree with other records from the Turkana basin. The data also indicate that the deposition of the KBS tuff in particular at 1.87 Ma in the Koobi Fora Formation coincided with one of these mesic episodes. The results from this study also agree with other environmental indicators suggesting that long-term aridification of East Africa during the Pliocene was punctuated by intervals of more mesic conditions (Levin 2008). Pedogenic carbonate data, collected by N. Levin, from the KBS Member on the Karari Ridge are used as a comparative palaeoenvironmental proxy in this study, and are reported on in Chapter 6. By combining this information with the results from the present ecomorphological study and bovid tribe habitat affiliation data, a comprehensive reconstruction of the palaeoenvironments of the Karari Ridge in the Koobi Fora Formation can be created.

2.5 Conclusion

The archaeology from the KBS Member of the Koobi Fora Formation on the Karari Ridge reveals some interesting patterns in hominin behaviour that as yet have not been explained. One of the possible hypotheses explaining this pattern of behaviour requires information on landscape scale palaeoenvironmental variation. Previous palaeoenvironmental reconstructions have not accessed the landscape scale palaeoenvironmental data necessary to provide clarity on this hypothesis. This project aims to provide the landscape scale palaeoenvironmental data necessary to test the hypothesis in question.

3. Palaeoenvironments

3.1 Introduction

Palaeoecological analysis has become inseparable from palaeoanthropological investigations as the study of human evolution is intricately integrated with the models of environmentally mediated selection pressures operating on human ancestors (Kappelman *et al.* 1997; Reed 1997; Sponheimer *et al.* 1999; Bobe *et al.* 2002; Kovarovic and Andrews 2007; Plummer *et al.* 2009). Numerous hypotheses have been suggested in an attempt to explain the complex set of relationships that exist between hominins and their environments; such as the Savannah hypothesis (Dart 1925; Jolly 1970), the Variability Selection hypothesis (Potts 1998; Bobe and Behrensmeyer 2004) and the Turnover Pulse hypothesis (Vrba and Delson 1985). All of these hypotheses, however, rely on accurate palaeoecological reconstructions. This project utilizes palaeontological approaches in the reconstruction of the palaeoenvironment of the KBS Member of the Koobi Fora Formation and, therefore this chapter provides detail on palaeontological methods. This detail includes a review of taxon dependent versus taxon free methods as well as case studies for both approaches.

3.2 Palaeoecology

Palaeoecology is the study of ecological and environmental influences on fossil species. In the context of human evolution, many hypotheses have been described that attempt to explain the influence of palaeoecology on the emergence of hominin species. The most well-known and long-standing of these is known as the Savannah hypothesis (Dart 1925; Jolly 1970). This hypothesis dictates that humans emerged as a consequence of the spread of savannah grasslands across the African continent, with key hominin features such as bipedality, encephalisation and stone-tool making evolving as a response to life in such environments (Jolly 1970). Dart describes this as "For the production of man a different apprenticeship was needed to sharpen the wits and the higher manifestations of intellect — a more open veldt country where competition was keener between swiftness and stealth, and adroitness of thinking and movement played a preponderating role in the preservation of the species"(Dart 1925 pp. 199). Closely linked to this hypothesis is the concept that the expansion of savannah grasslands is tied to major pulses of faunal turnover in many mammalian taxa over wide geographical scales. This is known as the Turnover Pulse hypothesis described by Vrba (1985). The chronological correlation between the emergence of the genus *Homo* and major global and regional climate changes supports this hypothesis (Vrba 1985). This hypothesis, however, remains controversial when used with regard to human evolution (Bobe and Behrensmeyer 2004).

Recent palaeoenvironmental analyses, however, have changed some of the focus from the expansion of savannah environments toward more wooded and humid environments (Reed 1997) as the type of environments in which certain hominin characteristics evolved, even suggesting an arboreal origin for bipedality (Hunt 1996). This is known as the Woodland/Forest hypothesis which claims that Pliocene hominins had evolved in and were primarily attracted to closed habitats (Clarke and Tobias 1995; Berger and Tobias 1996). The most recent perspective on the question of palaeoenvironmental influence on hominin species is known as the Variability Selection hypothesis. This hypothesis suggests that increased palaeoenvironmental variability resulted in the selection of what are considered typical hominin adaptations (Bobe and Behrensmeyer 2004; Reed 2008). According to Potts (1998), early bipedality, stone transport, encephalisation, enhanced cognitive and social functioning as well as, most significantly for this project, diversification of artefact contexts all reflect adaptations to environmental novelty and highly variable selective contexts.

The various hypotheses submitted regarding the environmental conditions in which hominin characteristics evolved demonstrates the necessity to accurately contextualize evolutionary events (Soligo and Andrews 2005). Despite the proliferation of hypotheses regarding the environmental contexts of hominin evolution, "field projects are rarely designed specifically to recover high-resolution data on the ecological settings inhabited by early humans, thus there is a paucity of fine-scale spatial and temporal data that can be linked to in-situ evidence of hominins" (Potts 1998 pp. 94). This project utilises two faunal approaches to reconstruct past environments in an effort to mitigate this current gap in palaeoecological data. One, bovid tribal affiliation, is taxon dependent while the other, bovid ecomorphology, is perceived as a taxon free analysis. The following sections discuss these approaches.

3.2.1 Faunal Approaches

Taxon Dependent

Mammalian fossil assemblages are traditionally considered to be a suitable proxy for climatic and environmental reconstructions (Behrensmeyer *et al.* 1997; Kappelman *et al.* 1997; Potts 1998; Bobe and Behrensmeyer 2004; Behrensmeyer and Barry 2005). For this kind of analysis, it is assumed that the structure shown by a fossil assemblage is likely to afford a broadly reliable representation of an extinct community, that is, the relative abundance of different animal species informs on the general character of a habitat (Western and Behrensmeyer 2009), assuming that certain taxonomic groups correlate with specific habitats in both the past and the present (Reed 1997). This is known as taxonomic uniformatarianism. These kinds of analyses are useful for environmental reconstructions of hominin

localities as archaeological faunas provide an additional method of assessing the palaeoenvironmental context of hominin activities (Plummer *et al.* 2009). Species abundance data can utilize the full spectrum of available species (Bobe and Behrensmeyer 2004; Bobe 2006) in order to reconstruct past mammalian communities and the environments they were likely to inhabit (Klein *et al.* 2007). In these kinds of analyses, the structure of past mammalian communities in the form of species abundance data is compared with the structure of modern mammalian communities. Conclusions about the palaeoenvironments of these past mammalian communities are drawn from the ecological classification of the environments inhabited by modern mammalian communities exhibiting similar species abundance data (Fernandez and Vrba 2006).

Species abundance data is often used in conjunction with first and last appearance dates (FADs and LADs) of particular species (Bobe and Eck 2001; Bobe and Behrensmeyer 2004; Bobe 2006). This information has been used extensively to test Vrba's Turnover Pulse hypothesis (1985), in which climate change results in brief periods of significant evolutionary change resulting in the emergence of numerous new species of African mammals, including hominins. According to Vrba, significant habitat changes are causally associated with significant evolutionary changes and nearly constant habitats are associated with stable evolutionary lineages. In Vrba's Turnover Pulse hypothesis, it is predicted that physical environmental changes initiate most speciations, extinctions and migrations. Species turnover involving different kinds of organisms should then be concentrated non-randomly in time and in predictable association with the climatic record for that area (Vrba 1999). In their analysis of the African record for bovid species, Vrba (1999) identifies 147 species that show a strong pulse of first appearances between 2.8 and 2.5 Ma, and smaller pulses at 1.9 to 1.8 Ma and 0.9 to 0.6 Ma. However, Behrensmeyer and colleagues (1997) as well as subsequent studies (Bobe 1997; Bobe *et al.* 2002) provide evidence that the proposed faunal turnover between 2.5 and 1.8 Ma was a prolonged rather than pulsed response to late Pliocene climate change in East Africa. Although significant species turnover occurred during the 4.0 to 1.8 Ma interval (Bobe and Behrensmeyer 2004), there is no marked pulse affecting different taxonomic groups between 2.8 and 2.5 Ma. Rather, Bobe and Behrensmeyer (2004) found that intervals of higher than average turnover occur from 3.4 to 3.2 Ma, 2.8 to 2.6 Ma, 2.4 to 2.2 Ma and 2.0 to 2.8. Ma. Bobe and Behrensmeyer (2004) concede that the Turnover Pulse hypothesis (Vrba 1995) may be able to link critical events in human evolution to broader pulses of faunal change driven by climate. However, this "link" is not simple, nor is it direct, as some of these "critical events" are not correlated in time with specific episodes of faunal turnover or global climate change.

A more specific version of species abundance analyses focuses on the abundance of certain bovid taxa in fossil assemblages. Bovid taxa are useful for palaeoenvironmental analysis as the remains of these animals are relatively abundant at sites significant to questions pertaining to hominid evolution, as they are speciose and inhabit a wide range of environments (Kappelman *et al.* 1997). A great number of bovid species exist in Africa today, and manage to coexist, avoiding competition through a complex system of resource partitioning (Kovarovic and Andrews 2007). Extant bovid species are taxonomically divided at the sub-family level into tribes. These bovid tribes are associated with specific environments as many related bovids share habitat preferences at the tribal level (Kappelman *et al.* 1997 pp. 230). Tribal distinctions can be viewed as different suites of shared characters which represent adaptations to specific adaptive zones (Kappelman 1984) such as alcelaphines and antilopines. Vrba (1980) surveyed the bovid tribes from sixteen game reserves and parks in summer rainfall habitats in Africa in order to determine if certain tribes of modern bovids had preferences for a particular habitat. She found that in the areas classified as closed habitats, or areas with a higher percentage of bush and tree cover, the total number of individuals belonging to the Alcelaphini and Antilopini bovid tribes was usually below 40% of the total bovid population. In open habitats, or areas with a lower percentage of bush and tree cover, the percentage of alcelaphines and antilopines of the bovid total is usually greater than 60% (Vrba 1980). This calculation is known as the alcelaphine plus antilopine criterion (AAC). According to Vrba (1980), the adaptations for grassland habitats in alcelaphine and antilopine species arose by the early Pleistocene, therefore the use of the AAC should be restricted to late Pliocene and early Pleistocene assemblages.

Vrba's AAC method (1980) was elaborated on by Shipman and Harris (1988) in their study on the habitat preference and palaeoecology of *Australopithecus boisei* in East Africa. Shipman and Harris (1988) noted that alcelaphines and antilopines are not the only bovid tribes that demonstrate a preference for specific habitats. The bovid tribes Tragelaphini and Aepycerotini (TA) show a marked preference for bush or closed habitats that are dry and the tribes Reduncini and Bovini (RB) are usually found near standing water and generally prefer wetter closed environments. This observation allowed increased resolution to be applied to Vrba's AAC method in that the closed environments indicated by low percentages of antilopines and alcelaphines could be further interpreted as either mesic or xeric depending on the preponderance of tragelaphines and aepycerotines, or reduncines and bovines (Shipman and Harris 1988).

Taxon Free

The assumption that underlies the taxonomic uniformitarian approaches described above is that the habitat specificity exhibited by modern day fauna is also meaningful in the past (Kappelman 1984). One critique of this assumption is that uniformitarianism masks the differences between the past and present and makes it difficult to identify unique adaptations to past environments (Bishop *et al.* 1999).

Rather than relying on the habitat preference of modern bovid tribes to interpret palaeoenvironments as in both Vrba's (1980) and Shipman and Harris's (1988) methods, Spencer (1997) interprets palaeobehaviours, and thus palaeohabitats, from bovid cranial and dental morphology. A quantitative morphometric study was performed on the skull and mandible of bovids (Spencer 1997). These are the skeletal elements most directly associated with the acquisition and processing of food, and are therefore indicative of plant food preference and, consequently, habitat preference. This study provided evidence that nearest living ancestors do not always share the palaeohabitats of their Plio-Pleistocene relatives. This is indicates that the habitat specificity exhibited by modern day fauna is not necessarily meaningful in the past. Spencer (1997) found evidence for a habitat type with no modern analogue in *Menelikia lyrocera,* a reduncine found at Koobi Fora from 2 to 1.6 Ma. Spencer also found that the habitat occupied by *Antidorcas recki* is different to that of its nearest living descendant, *Antidorcas marsupialis* (the southern African springbok). This study highlights some of the problems in solely using bovid tribal associations to reconstruct palaeoenvironments. The extension of the habitat preferences of modern bovid tribes into the Plio-Pleistocene relies heavily on the principle of taxonomic uniformitarianism. Therefore, as noted by Kappelman *et al.* (1997), this taxonomic-affinity approach relies upon a formal analogy *[sensu* (Binford 1981)]. Approaches to palaeoenvironmental reconstruction that are independent of taxonomic affinity circumvent these issues. A combination of taxon free and taxon dependent palaeoenvironmental proxies provides a more reliable indication of past environments.

3.3 Ecomorphology

One taxon-free approach relies on functional morphology as a means to understanding dietary and locomotor adaptations and the way that these adaptations are associated with specific ecologies and habitats. These associations are investigated and tested among living taxa and extended to the fossil record (Kappelman *et al.* 1997). This approach is known as ecomorphology. Ecomorphology is useful because it circumvents the assumption that ancient bovids preferred the same habitats as their closest living relatives. It also simplifies habitat reconstruction as the identification of specimens below family level is not a requirement (although see alternative views by Klein *et al.* (2010) discussed below).

Bock (1994) describes the concepts and methods of ecomorphology with two possible definitions. The first of these was described by Bock (1990) as "ecomorphology is primarily concerned with analyses of the adaptiveness of morphological features and all dependent, correlated topics such as the comparisons of adaptations in different organisms, modifications of adaptive features due to competition and other causes, structure of ecological communities and diversity within taxa" (Bock 1990 pp. 262). The second possible definition was described by Winckler (1988) as "Ecomorphology deals with the covariation of morphology and ecology" (Winckler 1988 pp. 2246), a definition that Bock (1994)elaborates on when he highlights two potential approaches for ecomorphological studies. The first of these approaches comes from the morphological tradition and its basic aim is to determine the adaptiveness of complex morphological features and systems in individual species. This is followed by comparative analyses of these adaptations in different organisms. The second of these approaches to ecomorphology comes from the ecological tradition and it aims to determine the pattern of adaptive features in taxa as well as to determine the composition of communities and niche structures. Plummer *et al.* (2008) describe ecomorphological studies as being implicitly about fitness and adaptation. The design of an organism provides limits on what an animal can and cannot do successfully. Plummer and colleagues (2008) believe that functional morphology should be viewed as a tool providing baseline information for many ecomorphological analyses which are concerned with higher order issues of community structure and palaeoenvironmental reconstruction. Thus Bock's (1994) second definition of ecomorphology can be applied to the reconstruction of palaeoenvironments.

Both metric and non-metric approaches have been applied to bovid ecomorphology in the pursuit of palaeoenvironmental reconstructions. DeGusta and Vrba (2005) investigated the non-metric, discrete traits suggested by Gentry (1970) and Kohler (1993) for use in the prediction of habitat preference for bovids. Gentry (1970) and Kohler (1993) each describe characters of bovid post-cranial material and their various states, as well as how these character states correspond to a different habitat preference. DeGusta and Vrba (2005) used a modern bovid sample consisting of adult, wild-caught, non-pathological post-crania to test the utility of these character states in palaeoenvironmental reconstructions. DeGusta and Vrba's study (2005) incorporated 37 characters from Gentry's analysis (1970) and 37 from Kohler's (1993). There were only two characters that appeared in both Gentry and Kohler's analyses. A further ten characters were identified by DeGusta and Vrba for their study, thus a total of 86 characters were analyzed. The four category habitat system described by Kappelman, Plummer *et al.* (1997) was implemented by DeGusta and Vrba (2005). However, DeGusta and Vrba (2005) performed their own assignment of bovid taxa to habitat categories. The association of characters to habitat preference was considered a "best fit" designation to the arbitrary division of a continuous range of habitat categories. The association between these discrete traits and habitat preference was evaluated using the correspondence coefficient, Cramers V. The accuracy of this procedure was established by testing the results of the correspondence coefficient for the modern bovid sample against known habitat preferences. The procedure was 88% accurate for the proximal phalanx, 85% accurate for the intermediate phalanx and 97% accurate for the distal phalanx. However, the definition and scoring of non-metric traits is inherently subjective. Despite this subjectivity and lack of resolution regarding bovid habitat preference (closed versus open), the non-metric analysis of bovid post-cranial material allows for habitat predictions even if the remains are not sufficiently complete for metric analysis (Degusta and Vrba 2005). The fossils utilised in this study, however, were often preserved such that non-metric analysis was not viable option for determining habitat preference as the necessary detail had often been eroded.

Kappelman (1988) pioneered the use of the metric analysis of bovid post-crania in the reconstruction of palaeoenvironments. Kappelman (1988) chose to investigate the ecomorphology of the bovid femur as femoral morphology relates to different patterns of locomotion and thus can be associated with different substrates across the habitat spectrum. Kappelman (1988) designed a series of measurements to investigate the relationship between the functional morphology of the femur and habitat. Kappelman (1988) took the measurements of four features in his analysis of bovid femoral morphology that correlated with habitat preference. These are the femoral head shape score (FHSS) which quantifies the sphericity of the head of the femur; the proximal shaft ratio (PSR) which measures the antero-posterior shaft diameter against the medio-lateral shaft diameter; the medial patellar lip ratio (MPLR) which is larger for bovids from open environments and smaller for bovids from closed environments; and the patellar groove ratio (PGR) which measures the symmetry of the distal femoral epiphysis. Discriminant function analysis was used to test the strength with which these different features of the bovid femur can be used to sort extant species among three habitat categories. These features were shown to have high discriminating power ($p>0.05$) (Kappelman 1988). Thus, the data collected by Kappelman (1988) support a statistically significant separation of the different morphological complexes present in bovids into different habitat categories.

In a separate study, Kappelman and colleagues (1997) applied the information from Kappelman (1988) regarding femoral ecomorphology as an indication of the palaeoenvironments at the fossil localities of Koobi Fora and Olduvai Gorge. Out of a total sample size of 27 fossils, 22 are from Olduvai Gorge and only 5 are from Koobi Fora. Of the 27 fossils, 9 are examples of complete femora and 18 are fragmentary, therefore two kinds of analyses were tested in this study. The first discriminant function analysis run by Kappelman *et aL* (1997) is a reworked version of Kappelman's (1988) analysis, using features of the entire femur. This analysis produced a correct habitat classification for 85% of the extant bovids studied. The second discriminant function analysis was conducted using four features of the proximal femur only in order to expand the sample by including fragmentary femora (from 9 to 18). This restricted discriminant function analysis correctly classified 81% of extant bovid individuals to habitat. These results indicate that although the habitat classification from the analysis of a complete element is more reliable, complete elements are rare in the fossil record. The small sample sizes that come as a result of an incomplete fossil record are problematic and are not addressed in Kappelman's study, other than by the inclusion of the fragmentary femora sample. Despite these small sample sizes, Kappelman *et al.* (1997) conclude from the ecomorphological analysis that the palaeoenvironments at Koobi Fora tended* to be more closed while the palaeoenvironments at Olduvai Gorge tended to be more open. However, Kappelman *et al.* (1997) fail to include the age of these fossils and this, coupled with small sample sizes, casts doubt on the significance of these results for smaller scale changes in palaeoenvironments *within* East African basins.

In their investigation into the palaeoecology of Olduvai Gorge, Plummer and Bishop (1994) use the ecomorphology of modern bovid metapodials. Metapodials were chosen for three reasons. Firstly, their morphology is linked to locomotor adaptations. Secondly, they are among the most durable of bovid long bones. Finally, metapodials are very well presented at Olduvai fossil localities. Plummer and Bishop (1994) measured a total of 306 metacarpals and 301 metatarsals of 37 species of extant African bovids. Discriminant function analysis was used to generate three separate models, one analyzing the complete metapodial, one just the proximal end and one just the distal end. This is similar to the two kinds of analyses performed by Kappelman *et al.* (1997). From these analyses, the best predictor for bovid habitat preference is the complete metatarsal with a classification rate of 89%. The complete metacarpal has a classification rate of 84%. The success rates for partial metapodials are lower at around 60% for the proximal ends and 70% for the distal ends. Fossil bovid metapodials from Bed 1 of Olduvai Gorge were analyzed using these results. All three models were used in an effort to boost the sample size of the fossil material. The palaeoenvironmental data provided by these analyses are not

conclusive. The metapodials from each of the sampled localities in Olduvai Gorge span the range of morphologies in modern antelopes, from open to closed habitats, with no emphasis on a particular environment. In a modern setting, it would be unusual to find bovids with such diverse habitat preferences naturally accumulating in one habitat zone. Plummer and Bishop (1994) explain that this is likely to be due to the influence of carnivores on the accumulation of the Bed 1 assemblage.

Another study done using ecomorphological analyses to interpret palaeoenvironments was done by Kovarovic and Andrews (2007) at Laetoli, Tanzania. Instead of using relationships already established between the morphology of certain bovid post-cranial elements and their preferred habitats (see above), Kovarovic and Andrews (2007) performed their own ecomorphological analysis of the entire post-cranial skeleton, except for the pelvis, scapula and vertebrae. Kovarovic and Andrews (2007) collected data on the post-crania of 224 individuals from 70 species representing 11 bovid tribes, as well as tragulids and cervids from a variety of global habitats. These individuals were all modern and wild-caught. A total of 209 measurements were taken on each individual by one person, some of which are standard measurements but most which were devised specifically for this study. Discriminant function analysis was performed to determine which post-cranial elements are the best indicators of habitat. The results show that the top six elements for habitat reconstruction are the humerus at 68% accuracy, the femur at 66.7% accuracy, the metatarsal at 66.5% accuracy, the radius at 58% accuracy, the proximal phalanx at 57.1% accuracy and the distal phalanx at 55.6% accuracy. These results were then extended to the fossil bovid specimens from the Laetoli locality. The sample sizes for the fossil specimens were small, consisting of only two metatarsals and one radius that were complete from the Laetolil beds and one humerus and one radius that were complete from the Ndolanya beds. The largest sample sizes consisted of 74 proximal and 62 intermediate phalanges from the Laetolil beds and 49 proximal radii from the Ndolanya beds. The most abundant elements in the Laetolil beds are also the elements with the lowest predictive accuracy (phalanges). Most of the specimens from the Laetolil beds (112 out of a total of 310) were indicative of a "heavy woodland-bushland" palaeoenvironment whereas most of the specimens from the Ndolanya beds (65 out of a total of 170) were indicative of a "wooded-bushed grassland" palaeoenvironment (Kovarovic and Andrews 2007).

The most recent study applying bovid ecomorphology to the reconstruction of palaeoenvironments was completed in conjunction with numerous other palaeoenvironmental reconstruction methods in order to determine the palaeoenvironment of the hominid species *Ardipithecus ramidus* at the locality of Aramis, Ethiopia at 4.4 Ma (White *et al.* 2009). The measurements and methodology used in this study were taken from DeGusta and Vrba (2003). Only astragali were measured as metapodials and femora, other elements that can be informative regarding ecomorphology, were not preserved in sufficient numbers. Eleven astragali predicted palaeoenvironments from the discriminant function analysis with statistically significant results (accuracy >95%), ten of which were classified as "forest" and one of which was classified as heavy cover. This study also made use of the non-metric analysis of bovid phalanges (Degusta and Vrba 2005) which provided similar results. The results from these ecomorphological studies were combined with the results from other methods for palaeoenvironmental reconstruction such as dental wear, taxonomic abundance and others. The strength of the results from this study, which describe the habitats occupied by *Ardipithecus ramidus* as woodland with forest patches, (White *et al* 2009) rest on the range of independent methods used to infer the type of habitat occupied by *Ardipithecus ramidus* at Aramis.

3.4 Limitations

There are numerous issues to consider with regard to ecomorphology. Is ecomorphology really taxon-independent as it claims? How does the classification and division of a continuous range of habitats affect the assignment of specimens to a particular environment? As with all palaeontological studies, how do small sample sizes affect the data? How is the statistical accuracy of the habitat assignments determined? Each of these issues will be discussed in turn below.

In an effort to determine whether Discriminant Function Analysis (DFA) is capable of determining bovid genus from post-cranial measurements, the results from Klein *et al.* (2010) have implications for palaeoenvironmental reconstruction using bovid ecomorphology. Klein and colleagues (2010) assert that ecomorphology is in fact taxon-dependent even though it "circumvent[s] the assumption that ancient bovids preferred the same habitats as their closest living relatives" (pp. 390). In their analysis, Klein *et al.* (2010) focus on the genus attributions of metacarpals and metatarsals, using the ecomorphological measurements for these elements from Plummer and Bishop (1994). However, Klein *et al.* (2010) omit the following measurements MGAP, MGML, PRONGAP, PRONGML, L and TMLMAX (see Methods Appendix). Klein *et al.* (2010) then calculated three derived variables from the raw measurements taken, the first being the log of each measurement on each specimen, the second being the mean of the logs for each specimen (or the geometric mean) and the third being the subtraction of the geometric mean from each logged measurement on each specimen. The log variables describing size and shape as well as the log shape variables were subjected to a Principal Components

Analysis (PCA). The results of the PCA indicated that 96.34% of the variation in the sample is attributable to size (PC 1) and 2.12% to shape (PC 2).

Klein *et a!.* (2010) therefore found that a combination of size (and to a lesser extent, shape) separate most genera from others when PC 1 is plotted against PC 2. The most conspicuous overlapping occurs with bovid size classes 1, 2 and 3 and the more that two genera overlap with regard to size and shape, the more likely it is that a DFA will attribute an incorrect genus. Klein and colleagues (2010) thus conclude that differences in metapodial length are reflected in differences in metapodial shape in like-sized taxa. Thus a DFA based on size and shape variables will also allow the accurate assignment of bovid metapodials to genus. Klein *et a!.* (2010) conclude that size discriminates more than shape and that shape alone does not contribute to the identification of bovid genus. The intention of Klein *et al.'s* (2010) paper is to test the utility of DFA in the attribution of bovid post-crania to genus. Despite this intention, Klein *et al* (2010) determine that the DFA will calculate different habitat assignments based on the species chosen to represent a particular habitat category and on the relative abundance of each species in the analysed sample. As a result, Klein and colleagues (2010) conclude that habitat reconstruction founded in DFA is actually taxon-dependent and not taxon-free. Although these results are quite compelling, and do seem to signify that ecomorphology is in fact more dependent on taxonomy than indicated in previous studies, Klein *et al.* (2010) do not succeed in making the case that ecomorphology is powerless with regard to palaeoenvironmental reconstructions. It remains a valid argument that a DFA based on taxon-free data (such as the metapodial measurements used in (Klein *et a!.* 2010)) will still accurately assign bovid post-cranial elements to habitat 84% to 89% of the time (Plummer and Bishop 1994).

One of the concerns inherent in applying an ecomorphological analysis to palaeoenvironmental reconstruction emerged in the studies described above, that of habitat division and classification. Modern bovid species inhabit environments that fall along a continuous range of habitats. Methods such as Vrba's AAC index divide this continuum into open habitats versus closed habitats (Vrba 1980). Earlier ecomorphological studies used a 3 part habitat scheme consisting of environments classified as either open (grassland), intermediate (bushland, woodland, swamp or ecotone) or closed (continuous canopy, including forests) (Kappelman 1988; Plummer and Bishop 1994). Although this division produces a high number of correct assignments in a DFA, its utility is questionable as so many varying habitats are encompassed by the intermediate category (Kappelman *et a!.* 1997). In order to account for this lack of resolution in their study, Kappelman *et a!.* (1997) used a four part division of modern habitat categories

into forest, heavy cover, light cover and open plains. These habitat categories reflect a gradient of decreasing vegetative cover and ground level obstacles, but environmental resolution is still lost in the intermediate categories. As these categories are an arbitrary division of a continuous range, the assignments of bovid species to habitat is a "best-fit" designation. In their study, Kovarovic and Andrews (2007) used a seven part habitat scheme in order to "refine the habitat distinctions that apply to Africa ... and to encompass a broader spectrum of global habitats that have not previously been included in any dataset" (pp. 666). These seven categories consist of grassland/treeless habitats, wooded-bushed grassland (as well as semi-desert) habitats, forest habitats, light woodland-bushland habitats, heavy woodland-bushland habitats, montane light-cover habitats and montane heavy-cover habitats. The assignment of modern bovids to these habitat categories was based on published ecological literature. While the intentions for this detailed habitat classification scheme were noble, its utility for palaeoanthropological studies is also questionable. The differences between the intermediate habitat categories in this seven part scheme are slight and thus may not represent distinctions that are relevant to hominin habitat preference. In their analysis of the bovids from Laetoli, the classifications of the Laetolil beds as heavy woodland-bushland and the Ndolanya beds as wooded-bushed grassland are an example of this kind of unhelpful detail. It seems that a delicate balance must be found between "descriptive reality and analytical utility" with regard to habitat division and classification, and therefore some resolution of habitat categories must be sacrificed in order to obtain significant results (Plummer *et al.* 2008 pp. 3018).

A third issue inherent in ecomorphology, as with all palaeontological work, is the tendency to draw conclusions from small sample sizes. Small sample sizes may not be representative of real patterns and may only represent a small portion of the variation that exists in a population. The smallest sample of bovid material that has been analysed in an ecomorphological context is from Kappelman's (1991) investigation into the palaeoenvironments of the Miocene localities of Fort Ternan in Kenya and the Chinji Formation in Pakistan. In this study, Kappelman (1991) used just 4 complete femora and 8 proximal femora to interpret the palaeoenvironments of these localities. The same ecomorphological model was applied to 22 complete femora from Olduvai Gorge and just 5 complete femora from Koobi Fora for palaeoenvironmental reconstructions (Kappelman *et al.* 1997). In the analysis of metapodials from Bed 1 at Olduvai Gorge, a total of 49 complete metacarpals and 30 complete metatarsals were used (Plummer and Bishop 1994). In an effort to augment these sample sizes, Plummer and Bishop (1994) had to consider proximal and distal metapodial fragments in their analysis. The palaeoenvironmental signal that emerges from these analyses (Kappelman 1991; Plummer and Bishop

1994; Kappelman *et al.* 1997) is interpreted as the habitat to which the highest proportion of specimens was assigned. In each of these studies, only one element was used for this palaeoenvironmental reconstruction, the femur in Kappelman (1991) and Kappelman *et al.* (1997) and the metapodials in Plummer and Bishop (1994). Kovarovic and Andrews (2007) attempt to ameliorate the small sample sizes associated with palaeontological studies by sampling numerous bovid post-cranial elements in their research. In their study, sample sizes are increased, and comparisons are allowed between elements to ensure that they are providing the same signal. The results from different elements can be combined to show trends more clearly.

One of the most disputed issues in ecomorphology is over how best to determine the accuracy of the models achieved in a DFA. If the accuracy of a model developed with modern specimens is not high, the utility of this model in its application to ecology of extinct taxa will be limited (Plummer *et al.* 2008). Many ecomorphological studies use resubstitution analysis to assess model accuracy (Kappelman 1991; Plummer and Bishop 1994; Kappelman *et al.* 1997). Resubstitution analysis tests the predictive accuracy of the model with the same data used to generate it, in other words, accuracy is described as the percentage of the modern sample that is correctly classified by the discriminant function. As this procedure tests the function on the same sample used to generate it, the resulting estimate of accuracy is likely a maxima (Degusta and Vrba 2003). More conservative estimates of accuracy are achieved using a subset of data that was not used in the generation of the discriminant function model (Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007; Plummer *et al.* 2008). This is known as a jack knife analysis. In this analysis, one specimen is removed from the sample, and a discriminant function is derived from this 'n-1' sample. This function is then applied to the removed specimen to predict habitat. The accuracy of the model is then described as the percentage of cases for which habitat was correctly predicted for the removed specimens. In DeGusta and Vrba's (2003) investigation into the bovid astragalus as a habitat predictor, they performed this jack knife analysis 39 times. The results of this analysis confirmed the accuracy of their resubstitution analysis at 67% (146 out of 218 bovids). Jack knife analysis was also performed in DeGusta and Vrba's (2005) investigation into the use of phalanges as habitat predictors, in which it too confirmed the percentage accuracy established by the resubstitution analysis (71%). In Plummer and Bishop's (2008) investigation into bovid astragalus morphology as a habitat predictor, they performed the jack knife analysis 286 times, once for every specimen in the sample. Their results indicated that the overall accuracy of the model dropped from 92.7% from the resubstitution analysis to 87.1% from the jack knife analysis. These three studies (Degusta and Vrba 2003; Degusta and Vrba 2005) also make use of a third method for assessing

accuracy. In this method, "test samples" are created by removing one specimen per bovid species from the data sample in order to assess the effects of withholding large numbers of specimens from the generator dataset simultaneously (Degusta and Vrba 2003; Plummer *et al.* 2008). A discriminant function is then generated using the remaining specimens and applied to the "test sample". Accuracy is described as the percentage of the "test sample" correctly assigned to habitat. This method resulted in an accuracy of 79.5% for DeGusta and Vrba's (2003) astragalus data. Plummer and Bishop (2008) carried out this procedure twice, using two unique "test samples". This resulted in an accuracy of 91.7% and 94.4% for their astragalus data. Plummer and Bishop (2008) attribute this difference in accuracy in bovid astragalus ecomorphology to the limited measurement scheme (nine measurements) and smaller bovid sample (n=218) used in DeGusta and Vrba's (2003) work versus the 23 measurements and 286 bovid astragali used in their work (Plummer *et al.* 2008).

Despite these assessments of model accuracy, all predictions generated by a discriminant function are not equal (Degusta and Vrba 2003). Each specimen put into the DFA is assigned to each habitat group with an associated percentage probability. These probabilities represent the likelihood that a particular specimen belongs to each of the four habitat categories. The habitat category with the highest probability is the one used in the reconstruction of past environments (Plummer *et al.* 2008). Therefore, different predictions have different probabilities of being accurate (Degusta and Vrba 2003). To take these probabilities into account, DeGusta and Vrba (2003) suggest a "confidence threshold" approach, which argues that as all habitat predictions are not equal, specimens accorded with high probability habitat predictions should be given the most weight in an analysis. For their astragalus dataset, this "confidence threshold" was set at 75%. This means that habitat predictions with associated probability values of less than 75% were considered to be indeterminate. This resulted in a reduction in the total number of misclassifications from 72 out of 218 (33%) to 11 out of 218 (5%). DeGusta and Vrba (2003; 2005) equate this to a p-value of 0.05 (assuming a of 0.05), and thus give their results statistical significance. However, Plummer and Bishop (2008) critique this approach, stating that it is misleading as including the 'indeterminate' specimens in the total number of specimens used to calculate the error rate leads to a winnowing of the data and an inappropriately low error rate. In order to test this "confidence threshold" approach, Plummer and Bishop (2008) used their proxies of the DeGusta and Vrba (2003) astragalus variables to generate a DFA model for comparison. This model has a similar accuracy to the DeGusta and Vrba (2003) model at 67%. The "confidence threshold" for this data was set at 80%, therefore all habitats assigned with an associated probability of less than 80% were considered indeterminate to habitat. Only 69 out of the 286 specimens used in this analysis had

confidence values greater than or equal to 80%. Of these, 94.2% were classified correctly. The remaining 217 had habitat probabilities less than 80%. Of these, 60.4% were, in fact, classified correctly. Plummer and Bishop (2008) used the "test sample" approach to determine the accuracy of this model, and as before, carried out this procedure twice. In both test samples, the proportion representation of the predicted habitat preferences that passed through the filter provided by the 80% confidence threshold deviated considerably from the actual habitat preferences of the test samples in question. From these results, Plummer and Bishop (2008) establish that this approach, when applied strictly, may distort the proportional representation of ecomorphological variation in an assemblage. "Eliminating specimens with lower confidence of attribution may create more, rather than less, bias in the overall frequency of habitats represented" (Plummer *et al.* 2008 pp. 19).

3.5 Conclusion

This section provided a concise but detailed review of the literature relevant to the core themes of palaeoenvironmental reconstruction and its implications for hominin behaviour. The hypotheses put forward to explain the relationship between hominins and their environments have each influenced the direction of palaeoanthropological research in their own way, however, it remains important to understand the environmental context of significant events in human evolution.

This study incorporates a range of proxies looking at palaeoenvironments, stable isotope analysis, bovid tribal affiliation analysis as well as ecomorphology. Ecomorphology is a relatively new method for looking at palaeoenvironments. Relatively few applications of this methodology have been used to assess palaeoanthropologically significant sites (Kappelman 1991; Plummer and Bishop 1994; Kappelman *et al.* 1997; White *et al.* 2009). However, with further investigations into the use of more bovid post-cranial elements for palaeoenvironmental reconstruction (Degusta and Vrba 2003; Degusta and Vrba 2005; Plummer *et al.* 2008), this method has great potential for providing data on hominin habitats that has not yet been accessible. Faunal analysis of medium sized mammals is able to provide data for palaeoenvironmental reconstruction on a scale that is broader than that provided by micromammalian, isotopic, geological and sedimentological analysis and more detailed than that provided by deep sea and ice core records as well as other globally-climatic relevant data. In combining the results of ecomorphological analysis with more established methods of palaeoenvironmental reconstruction, such as isotope analysis and tribal affiliation analysis, a detailed picture of past hominin habitats is assembled.

4. Materials and Methods

4.1 Introduction

The chief objective in this study is to investigate the interaction between palaeoenvironment and hominin behaviour in three separate areas in the KBS Member of the Koobi Fora Formation in Northern Kenya. The archaeology from these areas indicates that hominins from 1.65 to 1.87 Ma are using different artefact reduction strategies, in different geographic areas. This thesis tests the hypothesis that the decision to employ different stone artefact reduction strategies in geographic regions is mediated by the palaeoenvironment in which these artefacts were used. This chapter describes the methodology used to collect and analyze palaeoecological data on geographic scales that are relevant to the landscape scale variation in this kind of hominin behaviour, including collection strategy and statistical analysis. Here I outline statistical approaches including multivariate and univariate analyses in order to provide a methodological background for the palaeoenvironmental reconstructions used in this study.

4.2 Research Strategy

The purpose of this study is to determine the level of palaeoenvironmental variation across three specific geographic areas located in the KBS Member in the Karari region of the Koobi Fora Formation in East Turkana, Northern Kenya. The null hypothesis is that there is no association between the palaeoecologies of these three areas and the associated technological strategies employed by hominins. The areas under investigation are Areas 105, 108 and 130 (see Figure 3.1). These are collecting areas marked by previous research in this region and are delimited by geographic features such as roads and rivers. The fossils incorporated into this study were found in sediments of the KBS Member of the Koobi Fora Formation in these collecting areas (Feibel 1988; Feibel *et a!.* 1989). This provided a strict chronological bracket for the data collected, from 1.65 to 1.87 Ma (Brown *et a!.* 2006; McDougall and Brown 2006). To allow comparison of the palaeoecological data with the variation already isolated in the archaeological record (Braun 2006; Braun *et a!.* 2008) the fossils selected for analysis were restricted to the areas associated with archaeological sites in the KBS Member. The sites within the KBS Member sediments that have been excavated include FxJj 1, FxJj 3, FxJj 10 and FxJj 82. The fossils used in this analysis were identifiable to the family Bovidae (also referred to as the non-Linnean term "bovid") and had to be suitable for both ecomorphological and taxon-based analyses. There are some post-cranial elements for which a reasonable modern standard as well as a developed ecomorphological model exists. These include bovid humeri, metapodials, astragali and phalanges

(Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007). Previous studies have shown that these elements are indicative of specific locomotor adaptations and are thus linked with specific ecological or habitat parameters (Kappelman *et al.* 1997). There is a strong, tested relationship between the functional anatomy of modern bovid species and their ecological preference (Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007). Teeth and horn cores are suitable for identification to the taxonomic category of tribe, (e.g. Alcelaphini) and thus are also suitable for palaeoenvironmental reconstructions as the comparative frequency of different bovid tribes has long been used as a palaeoenvironmental indicator (Vrba 1980; Kappelman 1984).

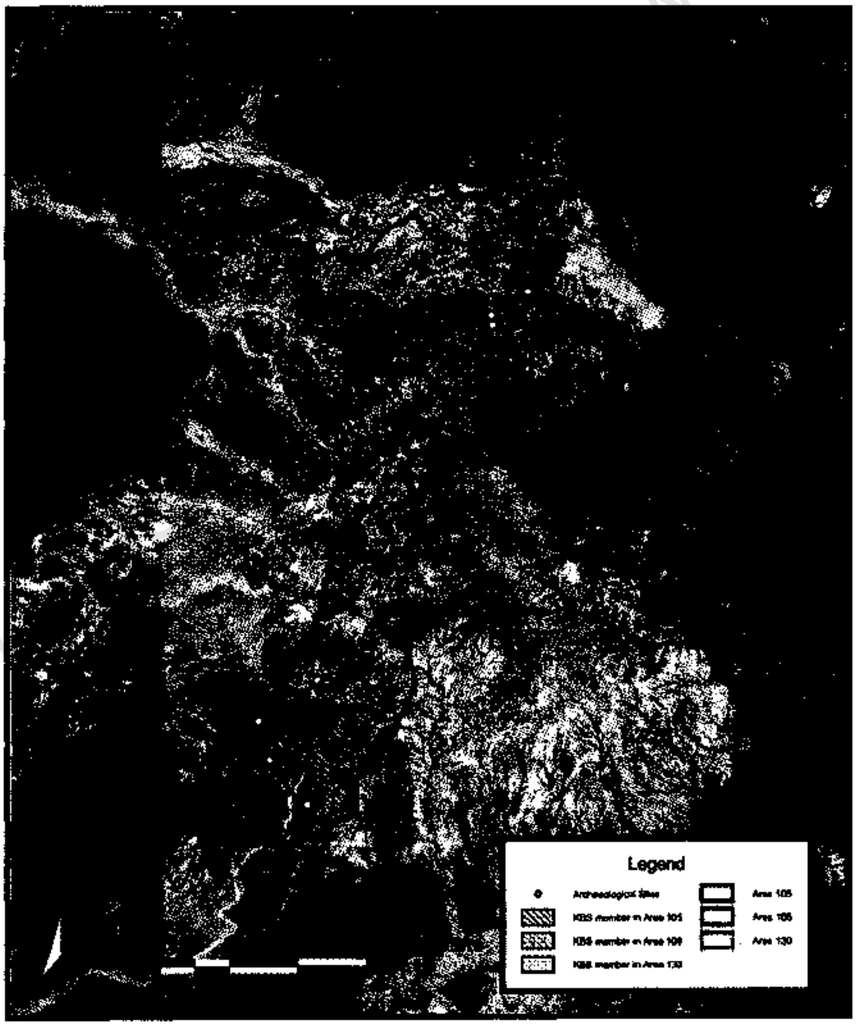


Figure 4.1 A detailed map of the Karari Ridge region of the Koobi Fora Formation showing the location of each of the areas under investigation.

4.3 Data Collection

In this investigation, the family Bovidae was used as they are abundant in the fossil record and bovid tribes have well developed habitat preferences that can be traced back through to the Pleistocene. Bovids generally die where they live, as do most mammals (Western and Behrensmeyer 2009). The proportions of bovid tribes indicated by remains closely resemble the living communities they represent. However, it is apparent that fossilization depends on the proximity of the community to water. To link palaeoecological indicators to aspects of early hominin behaviour requires investigation of the variation in habitats on a relatively small scale (i.e. sub-basinal). One of the methods chosen to access this small-scale ecological_ information is Functional Ecomorphology as described by Plummer and Bishop(1994), Plummer *et a!.* (2008), DeGusta and Vrba (2003; 2005) and others (Kappelman 1988; Kappelman 1991; Kappelman *et a!.* 1997).

Data collected for this study come from two separate datasets. The first was collected during a period of two months spent at the National Museums of Kenya in Nairobi in 2008. During this time, both the archaeological and palaeontological collections from the KBS Member of the Koobi Fora Formation were systematically investigated for fossil specimens that could be used for the ecomorphological or taxon based tribal analysis (i.e. conformed to the criteria described above). The second dataset was collected from specimens found in the Karari Ridge region of the Koobi Fora Formation of the Turkana Basin in Northern Kenya in 2008 and 2009. During this fieldwork, a surface survey of previously described palaeontological Areas (Areas 105, 108 and 130) was conducted in order to develop a spatial database of fossil localities. High precision geological provenience for the specimens was obtained as digital maps from previous geological surveys of the areas under investigation (Burggraf 1976; Frank 1976). This allowed for precise location in relation to the documented tuff exposures. These digital maps were linked to a Global Positioning System (GPS) in mobile based Geographic Information System (GIS) programs, such as Cybertracker and TierraMapper, designed for a handheld, ruggedized computer (such as the TDS JunoTM) that was used during fieldwork. This allowed for the real-time tracking of the position using GPS coordinates in decimal degrees, based on the World Geodetic Survey of 1984 (WGS84) datum. Using these GIS programs, we were able to determine our position relative to mapped sedimentary units that define the base and the top of the KBS Member in each area of interest. Each area was surveyed for at least one week by a team comprising of between 5 and 30 undergraduate and graduate students as well as local assistants trained in fossil identification, led by Dr. D. R. Braun. This field season took place as part of the Koobi Fora Field School of 2008 run by Rutgers University, co-directed by Dr. J.W.K. Harris of Rutgers University, Dr. D.R. Braun of the University of Cape Town and Dr. P. Kuira of the

National Museums of Kenya. As has been shown by Western and Behrensmeyer (2009), the relative abundance and habitat distribution of species of modern herbivore communities is accurately reflected in the changes in composition of modern bone assemblages. According to Western and Behrensmeyer (2009), it is therefore appropriate to use the same "framework for inferring the ecological properties of both contemporary and palaeontological bone assemblages" (pp. 1063). Thus, the fossils surveyed for this study from the exposed surfaces of the KBS Member represent the ecological properties of the surveyed areas during KBS Member times.

Ecomorphological measurements were taken of 125 bovid post-cranial elements (see Tables in the Appendix to the Methods Section) by a single analyst (JCL) using digital callipers accurate to 1/1000 cm. These elements were categorized according to their geographical position (i.e. the survey area in which they were found) as well as by element type (i.e. humerus, metacarpal, metatarsal, astragalus, proximal phalanx, intermediate phalanx and distal phalanx). The ecomorphological measurements used for humeri, metapodials and astragali were taken from Plummer and Bishop (1994; 2008). Those used for the phalanges were taken from DeGusta and Vrba (2005). The specific data regarding the measurements taken from the astragali, the metapodials and the humeri were analyzed using a discriminant function analysis (DFA) (Plummer and Bishop 1994; Plummer *et al.* 2008).

Table 4.1 Table identifying the elements used for this study from each survey area.

Element	105	108	130	Total
Teeth	70	18	46	134
Horn cores	31	1	13	45
Humeri	7	1	10	18
Metacarpals	12	6	22	40
Metatarsals	7	3	18	28
Astragali	6	1	4	11
Proximal Phalanges	3	2	11	16
Intermediate Phalanges	8	0	7	15
Distal Phalanges	1	0	1	2

The dental and horn core elements of bovids were identified to tribe in an effort to establish a taxon-based palaeoenvironmental signal, independent of the signal provided by the ecomorphological

data. Bovid tribal affiliation studies utilise the frequency of specimens within specific tribal level groups of bovids that are associated with specific habitat types in order to infer palaeoenvironments. This methodology has been previously applied to Kanjera, Olduvai Gorge as well as the Omo Shungura Formation sites by Plummer *et al.* (2009) building upon an analytical technique originally described by Vrba (1980) and modified by Shipman and Harris (1988). The identified teeth and horn core elements were then divided into counts of tribal groupings of Alcelaphini and Antilopini, Reduncini and Bovini as well as Tragelaphini and Aepycerotini.

4.4 Data Analysis

Most ecomorphological analyses focus on one post-cranial element (Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005), applying the modern ecomorphological model for this single element to the same element in the fossil record. In this study, however, the different habitat associations of different elements will be combined in a multivariate dataset. Both discriminant function analyses as well as correspondence analyses will be used to investigate the ecological patterns in this multivariate dataset.

4.4.1 Discriminant Function Analysis

In previous ecomorphological studies (Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007), DFA has been employed as a statistical tool to relate post-cranial element morphometrics to habitat preference in modern bovids. DFA works on the principle that certain observations can be divided into groups based on a particular characteristic of the data such as habitat. DFA then attempts to find ways in which to distinguish those same groups based on "some independent criterion derived from the data" (Baxter 1994 pp. 186). DFA can be used to confirm that identified groups in a population are indeed distinct, to identify observations that do not belong to their presumed group and to identify variables that are able to discriminate between groups (Baxter 1994 pp. 186). In the context of ecomorphological studies, however, DFA provides a criterion for allocating unclassified individuals to a group based on post-cranial element morphometrics (Kappelman 1984; Kappelman 1988; Solounias and Dawson-Saunders 1988; Kappelman 1991; Degusta and Vrba 2003; Kovarovic and Andrews 2007; Plummer *et al.* 2008). Discriminant analyses presume that there already exists an inherent structure in the data based on existing groups (e.g. habitat assignment), and is therefore not an exploratory technique like Principal Components Analysis (PCA). Where a PCA enhances patterns in a multivariate dataset, "discriminant

analysis identifies a single linear combination of variables (a function) that maximizes the existing difference between predefined groups" (Baxter 1994 pp. 186). DFA requires the following assumptions;

- **it is better if the data is normally distributed, however this is not essential,**
- **existing groups in the data need to be of a similar size and shape in multivariate space and**
- **the spread of 'scores' around the group mean must be similar in all groups.**

However, DFA is not negatively affected by the violation of these assumptions (Baxter 1994). In a population consisting of groups whose members are identifiable, DFA uses the characteristics of these groups to obtain a linear function for each group. Unknown individuals are then given a probability value based on these functions. These individuals are then allocated to the group with the highest probability value (Baxter 1994 pp. 191).

Table 4.2 Table identifying the average probabilities of the accepted habitat assignments from the results of the DFA.

	Astragalus	**Humerus**	**Metacarpal**	**Metatarsal**	**Proximal Phalanx**	**Intermediate Phalanx**
Area 105	0.93	0.97	0.78	0.51	0.58	0.82
Area 108	No data	No data	0.82	0.64	0.99	No data
Area 130	0.86	0.89	0.84	0.47	0.87	0.99

The present study makes use of DFAs already reported in the works of Plummer and Bishop (1994) and Plummer *et al.* (2008). Plummer and colleagues (2008) have produced DFA models using a four category habitat scheme (open, light cover, heavy cover and closed) for complete and partial bovid humeri, radii, ulnae, tibiae, calcanei, astragali and phalanges. Plummer *et al.* (2008) recently updated the metapodial models first described in Plummer and Bishop (1994). In these previous bovid ecomorphological studies (Plummer and Bishop 1994; Plummer *et al.* 2008) DFA was used to test whether a certain post-cranial element morphology could distinguish between bovids from different habitats. In this procedure, a function (or equation) is derived using the metrics and indices from the modern bovid elements that best discriminate among known, contemporary habitat preference groups. These habitat preference groups are based on modern behavioural observations of bovid taxa in the wild. As implied by the term "preference", these assignments to habitat are not exclusive and certain bovid taxa may be found in more than one of these categories in a given time period. For example, certain alcelaphines (with a preference for open habitats) will travel long distances, often through variable habitats, to access water (e.g. *Connochaetes gnu).* However, it has been shown that the modern bone assemblages associated with a certain region accurately reflect the modern herbivore community

occupying that region (Western and Behrensmeyer 2009). The environments inhabited by modern bovid species fall along a continuous range of habitats. However, not all of these habitats can be taken into account with regard to statistical analyses. At times the resolution with which the analysis will assign a specimen to specific habitat category is sacrificed in order to obtain results that are relevant for palaeoecological analysis. "Ecomorphological analysis attempts to achieve a balance between descriptive reality and analytical utility" (Plummer *et al.* 2008 pp. 3018), thus, the distinction of habitats into open, light, heavy and closed habitat preference groups provides a simple framework in which to interpret environmentally relevant data (Plummer *et al.* 2008).

Using a discriminant function, individual specimens can be assigned probabilities of membership to predetermined categories, in this case, habitat preference groups. There are several different approaches to interpreting the DFA output for ecomorphological analysis. The most appropriate of these for this study, and the approach adopted by Plummer and Bishop (1994) and Plummer *et al.* (2008), has been to ensure that the derived model has a good predictive power. It is therefore plausible to accept the DFAs habitat assignment for fossil specimens based on this model. In the development of these models, the intention is to achieve high overall success rates (over 80% of unknown individuals assigned correctly) so that there is a greater probability that fossil unknowns will be assigned to the correct habitat preference group (Plummer *et al.* 2008 pp. 3022). The success of the derived model was tested by assessing the significance of differences between group means as well as by testing how well the discriminant function classified specimens of known habitat (Plummer *et al.* 2008 pp. 3019). As explained above, the outcome of a DFA is a formula for classifying unknown individuals into a group. The accuracy of this function needs to be assessed in order to determine whether it is successful (Baxter 1994 pp. 201). Typically, two methods are employed to determine the success of a discriminant function, both of which employ individuals belonging to a known group. The results of these methods (i.e. the group to which the discriminant function allocates these individuals) are then compared to what is already known about the groups to which these individuals belong. Accuracy is then determined by the number of correct assignments made by the discriminant function. These methods are resubstitution and jack-knifing (also known as cross-validation). In the resubstitution method, the same individuals used to define a function are allocated to a group based on that function (Baxter 1994 pp. 201). In other words, the individuals testing the resulting discriminant function for accuracy are the individuals used to create the discriminant function. As a result, this method usually produces an over-optimistic assessment of the success of the function. In the jack-knifing or cross-validation method, each individual is classified to a group based on observations that omit that particular individual (Baxter 1994 pp. 201). In this method, each individual testing for accuracy is treated as an unknown and therefore this method provides a more realistic assessment of the accuracy of a discriminant function. Only successful models for astragali, humeri, metapodials and phalanges were used in this study, where over 80% of unknown individuals were correctly assigned to habitat using the jack-knifing method described above.

4.4.2 Correspondence Analysis

Correspondence Analysis (CA) has largely been used in other studies for the "reduction and interpretation of large, multivariate, ecological datasets with environmental or other gradients" (Hammer *et al.* 2009 pp. 27). According to Hammer *et al* (2009), CA is the appropriate algorithm for comparing the association of datasets containing counts or percentages. CA is used in the present study to interpret the ecological differences in each of the sampled areas as indicated by the palaeoenvironmental signals identified in the DFA. CA uses chi-squared distances as a measure of variance in the data and subsequently approximates these distances as accurately as possible on a two-dimensional plot in which the rows (or columns) of the chi-squared contingency table are represented as points (Baxter 1994). The chi-squared statistic is used to measure the departure of a contingency table from the hypothesis of no association between the data in rows and the data in columns (Baxter 1994). In other words, the chi-squared statistic measures the departure of data from an expected behaviour. The CA is an attempt to explain as much of this statistic as possible in a 2 dimensional plot. The chi-squared statistic is defined as the equation

$$\chi^2= \Sigma(O-E)^2/E$$

where x is the chi-squared statistic, O is the observed value for this statistic and E is the expected value for this statistic. Thus, Baxter (1994) notes that a CA can be viewed as a form of PCA of chi-squared residuals as defined by the equation

$$\chi =(O-E)/\sqrt{E}.$$

PCA aims to find hypothetical variables which account for as much variance in a multi-dimensional dataset as possible (Hammer *et al.* 2009). In a similar fashion, CA attempts to explain as much of the variation as possible in a given dataset using chi-squared distances (Baxter 1994).

Baxter (1994) provides a detailed explanation of the steps required to obtain a CA plot describing the correspondence between the rows of a contingency table. The same steps are used to obtain a plot describing the correspondence between the columns of a contingency table:

1 Define the row profiles by dividing each value by the row total. Each of the values is now a percentage of the row total. This places each of the rows on an equal footing and eliminates the effect of sample size (i.e. number of observations in a row). The resultant analysis is thus a comparison of row shapes.

2 Define the chi-squared distances between the rows, for all pairs of rows (as opposed to the Euclidian or Mahalanobis distances used in a PCA).

3 These distances are then reproduced as accurately as possible in a 2 dimensional plot. This kind of analysis tends to give more weight to rows with a greater number of observations.

The distances between the points on the CA plot approximate their chi-squared distances. The resultant CA plot therefore indicates which rows differ from the average or expected row profile and how. The axes on which these points are plotted can be interpreted as explaining the most variation in the data matrix, thus they perform the same role as the Principal Components in a PCA. The eigenvalue sum (or the sum of weighted distances) in a PCA of a data matrix is interpreted as the total amount of departure from the average of that dataset (Shennan 1997). In a CA, this quantity is called the Total Inertia. The individual eigenvalues that are obtained in a CA (or a PCA) are interpreted as the proportion of inertia (or variation) explained by the associated axis (Baxter 1994).

The resultant plot output therefore consists of two axes. The first axis (the *x* axis in a Cartesian system) explains the most inertia (or variation) in the given contingency table. The second axis (the y axis in a Cartesian system) explains the second greatest proportion of inertia in the contingency table. The (0:0) co-ordinate in this Cartesian plot represents the average row profile, therefore locations away from this point are representative of departures from the average. The location of each of the variables on this plot is determined by the proportion counts associated with that row (or column) in question. The true power of the CA lies in its ability to display both row and column data on the same Cartesian system (Baxter 1994), as this allows for an examination of the relationship between rows and columns. However, interpretation of these plots requires vigilance as, although the distances between row data points can be interpreted as indicative of the similarity between row profiles, the distance between row data points and column data points on the same plot does not have this kind of interpretation (Baxter 1994). As such, in the analysis of the data for testing the hypothesis at hand, only the row data was plotted (i.e. only the Areas) and the associated differences in ecology interpreted.

4.4.3 Ternary Plots

The ternary plot (or Tripolar Graph) method used in the analysis of the tribal affiliations of the bovid teeth and horn cores was adapted from Plummer *et al.* (2008). This methodology is a modified version of the method described in Shipman and Harris (1988). This methodology makes use of a ternary plot in the display of data describing a tripartite system of palaeoecological reconstruction via the relative frequencies of three groups of bovid tribes. High Alcelaphini and Antilopini frequencies indicate open, dry habitats. High Tragelaphini and Aepycerotini frequencies indicate environments that are closed but dry. High Reduncini and Bovini frequencies indicate closed, wet environments. Ternary plots describe the same kind of data as CA, that is, counts or percentages, but is limited in the number of variables it is able to display. The display is in the form of an equilateral triangle (hence the name "ternary" or "tripolar"). In the case of three variables, percentages and proportions are closed scales because if two of the values are known, the third is fixed. Each side of the output ternary plot represents a percentage scale and the variables are displayed on this plot according to their percentage composition of each of these variables.

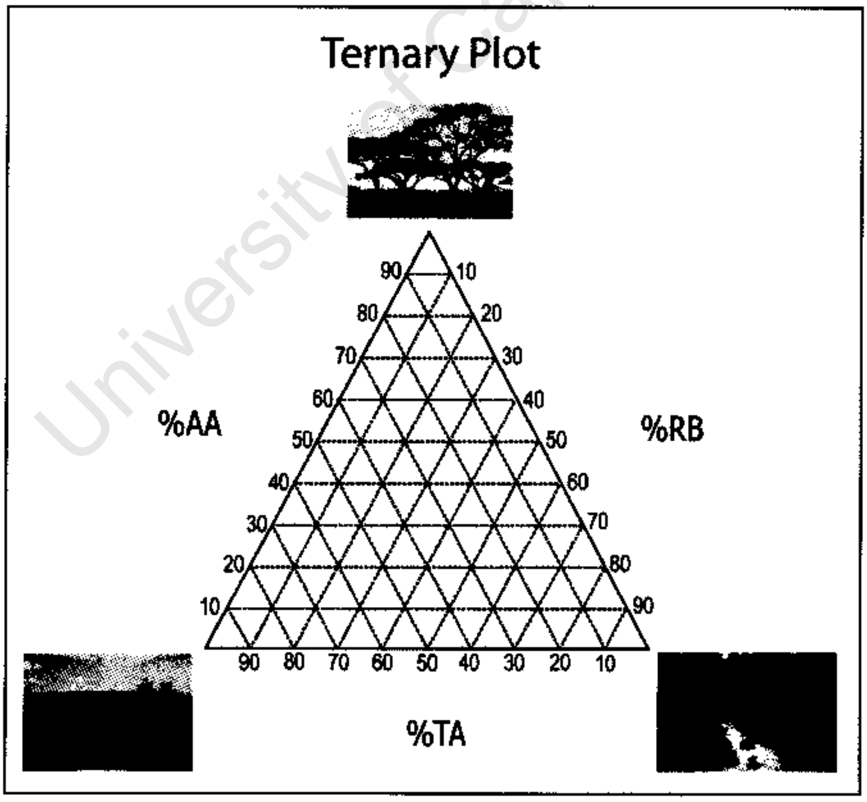


Figure 4.2 A ternary plot showing the relative frequencies of three sets of bovid tribes from modern wildlife areas. High Alcelaphini and Antilopini frequencies signal high proportions of open, arid environments, high Bovini and Reduncini frequencies signal closed, frequently moist environments and high Tragelaphini and Aepycerotini frequencies signal closed, frequently dry environments (Shipman and Harris 1988).

4.4.4 Significance Testing

Significance testing is generally used in statistics to test the hypothesis that two samples were drawn from different populations. Non-parametric statistics were run as these tests are widely used for studying data at the ordinal scale and do not require the data to be normally distributed. These methods are applicable when data have a ranking (such as open, light, heavy or closed cover) but no clear numerical interpretation. Two significance tests utilized in this project are the Kolmogorov-Smirnov (KS) test and the Wald-Wolfowitz Runs (WW) test, as both of these tests are appropriate for comparing two sets of independent samples measured at the ordinal scale (Shennan 1997). The KS test is based on the difference between two cumulative distributions of interest whereas the WW test indicates whether the number of "runs" (i.e. the order of the data) in a particular case is less than what would be expected if the two distributions were randomly intermixed (Shennan 1997). The WW test compares the number of runs in a distribution to a statistical table based on the number of observations in each sample. This test is based on the randomization of the data, questioning whether the order of the data is significantly different from a random pattern. The KS test is based on an assessment of the largest difference between two distributions of cumulative proportions. This observed difference, be it positive or negative, is then compared with an expected distribution of differences derived theoretically. These tests are used to determine whether any observed difference between samples from the investigated areas is significant. In the WW as well as in the KS test, the null hypothesis is one of no significant difference between the samples from each of the survey areas at the 0.05 significance level.

4.5 Conclusion

Although ecomorphology has been used in the past for the reconstruction of palaeoenvironments (Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007), these analyses have often relied on the signal from just one type of bovid post-cranial element (Kappelman 1988; Plummer and Bishop 1994; Kappelman *et al.* 1997; Degusta and Vrba 2003; Degusta and Vrba 2005; Kovarovic and Andrews 2007). In combining the signals from numerous bovid post-cranial elements, an increased sample as well as a more robust description of associated habitats is achieved. The more traditional method of using bovid tribal affiliation data for habitat reconstruction is based on data from teeth and horn cores. These elements are persistent in the archaeological record and as a result, this analysis is based on generally much larger sample sizes than ecomorphological analysis. When the data from these kinds of analysis are combined, a more complete picture of past environments is obtained.

5. Results

5.1 Introduction

In the following discussion I will describe the results of statistical comparisons between the areas under study. This to determine if the palaeoenvironments described for these areas provide sufficient evidence to reject the null hypothesis that there is no association between the palaeoecology of the three areas and the associated reduction strategies employed by hominins.

The results of the discriminant function analysis (DFA) provide an assignment of habitat group to each specimen. These habitat associations are either open, light cover, heavy cover or closed. These groups describe an arbitrary division of a continuous range of habitats occupied by modern bovid species as defined by previous studies (Kappelman *et al.* 1997; Plummer *et al.* 2008). For ease of reference, I have provided a graphic description of each of these generalised habitat groups (see Figure 5.1). The results of the tribal affiliation analyses initially describe the bovid family to which the specimens belong (e.g. Alcelaphini, Antelopini, Reduncini, Bovini, Tragelaphini, Aepycerotini). Of the 10 existing bovid tribes, the tribes used in this study have well developed habitat associations and are therefore good indicators of palaeoenvironments (Vrba 1980; Shipman and Harris 1988).

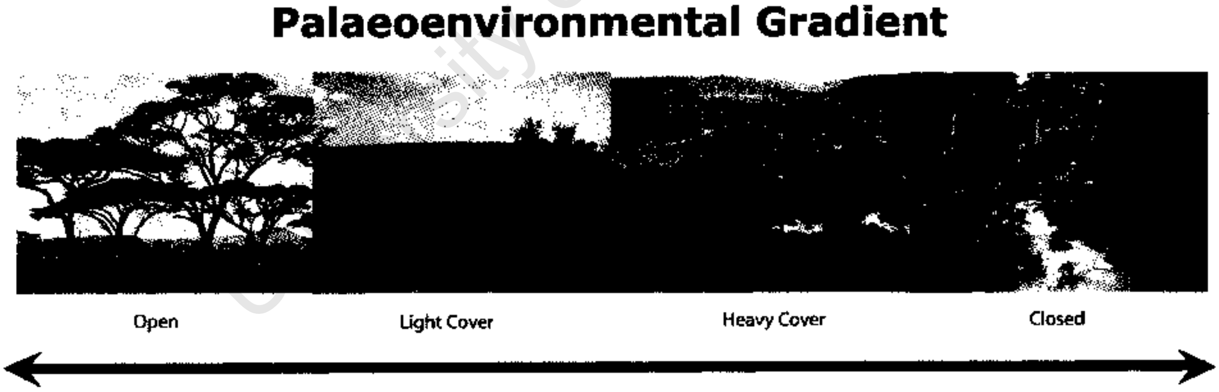


Figure 5.1 Graphic description of the palaeoenvironmental gradient ranging from open to closed environments.

5.2 Site Descriptions

5.2.1 Area 105

The results from the DFA for Area 105 are listed in Table 5.1. The pie chart for Area 105 in Figure 5.2 indicates that 70% of the habitat group assignments from the DFA are heavy cover or closed environments. The results from the tribal affiliation analysis indicate that although the area is dominated by Antilopini and Alcelaphini (57.3%), bovid tribes associated with open environments, the

next most dominant tribal groups are Reduncini and Bovini (30.3%), bovid tribes associated with closed and wet environments (see Figure 5.3).

Table 5.1 Results of the DFA for Area 105. The "Probability" column refers to the probability of assignment to this specific habitat class (see page 51).

Area 105			
ID	**Element**	**Prediction**	**Probability**
FW.105.AS.02	Astragalus	Heavy Cover	0.924
FW.105.AS.03	Astragalus	Open	0.973
FW.105.AS.04	Astragalus	Closed	0.907
FW.105.HM.01	Humerus	Closed	0.968
FW.105.MC.02	Metacarpal	Heavy Cover	0.785
FW.105.MC.06	Metacarpal	Heavy Cover	0.789
FW.105.MC.05	Metacarpal	Heavy Cover	0.969
FW.105.MC.03	Metacarpal	Open	0.535
FW.105.MC.01	Metacarpal	Closed	0.985
FW.105.MC.08	Metacarpal	Light Cover	0.626
FW.105.MT.02	Metatarsal	Light Cover	0.511
NMK.105.PP.01	Proximal Phalanx	Closed	0.395
NMK.105.PP.02	Proximal Phalanx	Heavy Cover	0.374
NMK.105.PP.03	Proximal Phalanx	Open	0.971
NMK.105.IP.01	Intermediate Phalanx	Closed	0.858
NMK.105.IP.02	Intermediate Phalanx	Closed	0.753
NMK.105.IP.03	Intermediate Phalanx	Heavy Cover	0.974
FW.105.IP.01	Intermediate Phalanx	Closed	0.781
FW.105.IP.02	Intermediate Phalanx	Heavy Cover	0.999
FW.105.IP.03	Intermediate Phalanx	Open	0.569

5.2.2 Area 108

The fossils from the KBS Member in this area are not as well preserved as those from Area 105 and Area 130. As a result, the analyses for this area are based on a particularly small sample size. Only the metatarsals, metacarpals and the proximal phalanges from Area 108 were successfully assessed in the DFA. As is indicated in Table 5.2, every element assessed in the DFA was assigned to the open habitat category (see Figure 5.2). The astragali, humeri and intermediate phalanges from this area were also subjected to DFA, however they could not be assigned to a specific habitat. The results from the tribal affiliation analysis indicate that although the area consists mostly of Antilopini and Alcelaphini (63.2%), bovid tribes associated with open environments, the next most dominant tribal groups are Tragelaphini and Aepycerotini (26.3%), bovid tribes associated with closed and dry environments (see figure 5.3).

Table 5.2 Results of the DFA for Area 108. The "Probability" column refers to the probability of assignment to this specific habitat class (see page 51).

ID	Element	Prediction	Probability
FW.108.MC.02	Metacarpal	Open	0.852
FW.108.MC.01	Metacarpal	Open	0.759
FW.108.MC.05	Metacarpal	Open	0.858
FW.108.MT.07	Metatarsal	Open	0.640
FW.108.PP.01	Proximal Phalanx	Open	0.986
FW.108.PP.02	Proximal Phalanx	Open	0.999

Table 5.3 Results of the DFA for Area 130. The "Probability" column refers to the probability of assignment to this specific habitat class (see page 51).

Area 130			
ID	**Element**	**Prediction**	**Probability**
NMK.130.AS.01	Astragalus	Closed	0.757
FW.130.AS.03	Astragalus	Open	0.955
NMK.130.HM.01	Humerus	Closed	0.799
NMK.130.HM.03	Humerus	Open	0.828
NMK.130.HM.04	Humerus	Heavy Cover	0.805
NMK.130.HM.05	Humerus	Heavy Cover	0.999
FW.130.HM.03	Humerus	Heavy Cover	0.997
FW.130.MC.05	Metacarpal	Open	0.904
NMK.130.MC.0	Metacarpal	Light Cover	0.721
FW.130.MC.04	Metacarpal	Light Cover	0.862
FW.130.MC.09	Metacarpal	Open	0.988
FW.130.MC.10	Metacarpal	Closed	0.617
FW.130.MC.11	Metacarpal	Closed	0.777
NMK.130.MC.0	Metacarpal	Closed	0.994
NMK.130.MT.04	Metatarsal	Open	0.482
FW.130.MT.01	Metatarsal	Closed	0.405
FW.130.MT.02	Metatarsal	Light Cover	0.659
FW.130.MT.04	Metatarsal	Light Cover	0.345
NMK.130.PP.01	Proximal Phalanx	Light Cover	0.996
NMK.130.PP.03	Proximal Phalanx	Heavy Cover	0.492
FW.130.PP.04	Proximal Phalanx	Open	0.999
FW.130.PP.05	Proximal Phalanx	Open	0.999
NMK.130.IP.01	Intermediate Phalanx	Light Cover	0.991
NMK.130.IP.03	Intermediate Phalanx	Light Cover	0.972
NMK.130.IP.05	Intermediate Phalanx	Heavy Cover	0.993

S.2.3 Area 130

The results from the DFA for this area yielded somewhat more assignments to light cover and open environments than to heavy cover and closed environments (see Table 5.3). The pie chart for Area 130 in Figure 5.2 combines the habitat group assignments for all the elements assessed by the DFA from this region. The pie chart indicates that 56% of the habitat group assignments are open or light cover environments. The results from the tribal affiliation analysis indicate that the area is overwhelmingly dominated by Antilopini and Alcelaphini (80.8%), bovid tribes associated with open environments, with only limited numbers of Reduncini and Bovini (9.6%), and Tragelaphini and Aepycerotini (9.6%), bovid tribes associated with closed environments (see Figure 5.3).

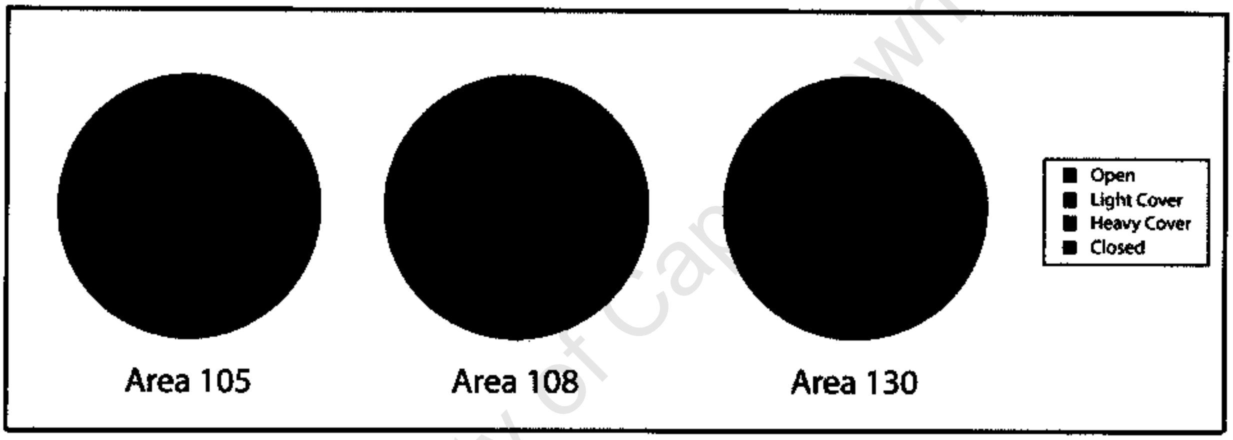


Figure 5.2 Pie chart describing the relative frequencies of open, light cover, heavy cover and closed environments for Areas 105 (n=20), 108 (n=6) and 130 (n=25).

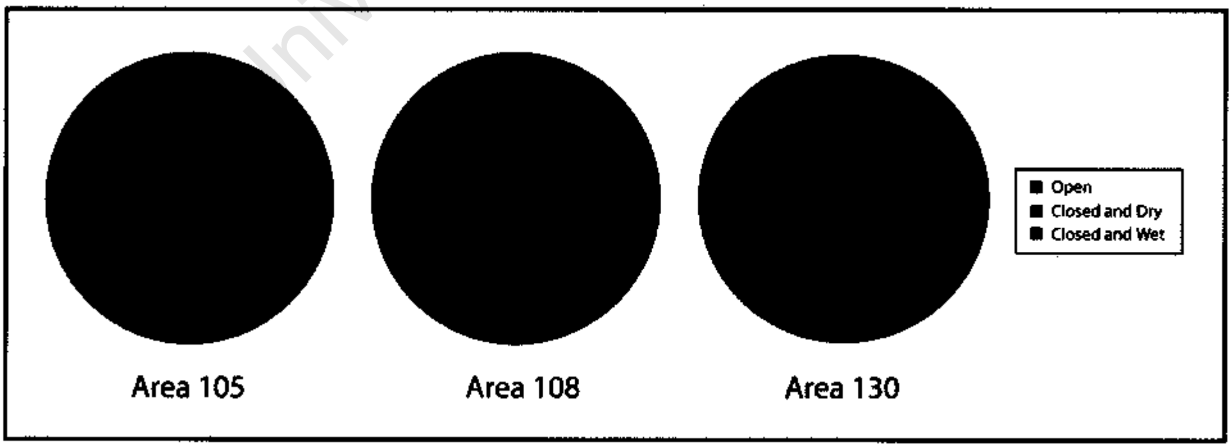


Figure 5.3 Pie chart describing the relative frequencies of bovid tribes and the palaeoenvironments they prefer for Areas 105 (n=101), 108 (n=19) and 130 (n=59).

5.3 Comparisons between Areas 105, 108 and 130.

5.3.1 Correspondence Analysis

Correspondence analysis (CA) was used to interpret the ecological differences in each of the sampled areas as indicated by the frequency of habitat associations identified in the DFA (i.e. open, light cover, heavy cover and closed). A CA was performed on the classifications to habitat derived from the DFA of each of the elements used in this study. The results from the CA for the metacarpal data (Figure 5.4), the metatarsal data (Figure 5.5) and the proximal phalanx data (Figure 5.6) are displayed below.

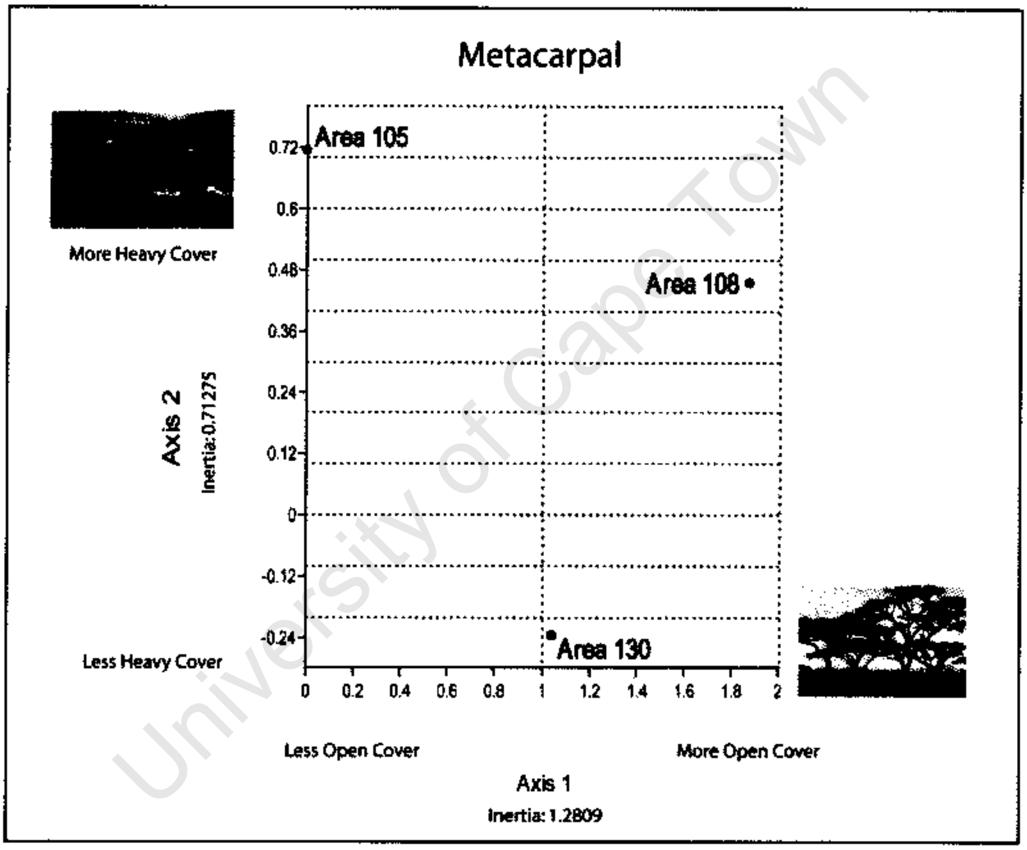


Figure 5.4 Output graph for the CA performed on the metacarpal data from Areas 105, 108 and 130.

In the graph of the metacarpal data (Figure 5.4), axis 1 is most closely associated with the amount of open cover in an environment. This axis therefore explains 43.7% of the inertia or variance in the metacarpal dataset (inertia for axis 1 = 1.28). Of the variance in axis 1, 59.7% is explained by open cover (eigenvalue = 0.44). Axis 2 of this graph is most closely associated with the amount of heavy cover in an environment. This axis explains a remaining 0.25% of the inertia in the metacarpal dataset (inertia for axis 2 = 0.71). Of the variance in axis 2, 40.3% is explained by heavy cover (eigenvalue = 0.29).

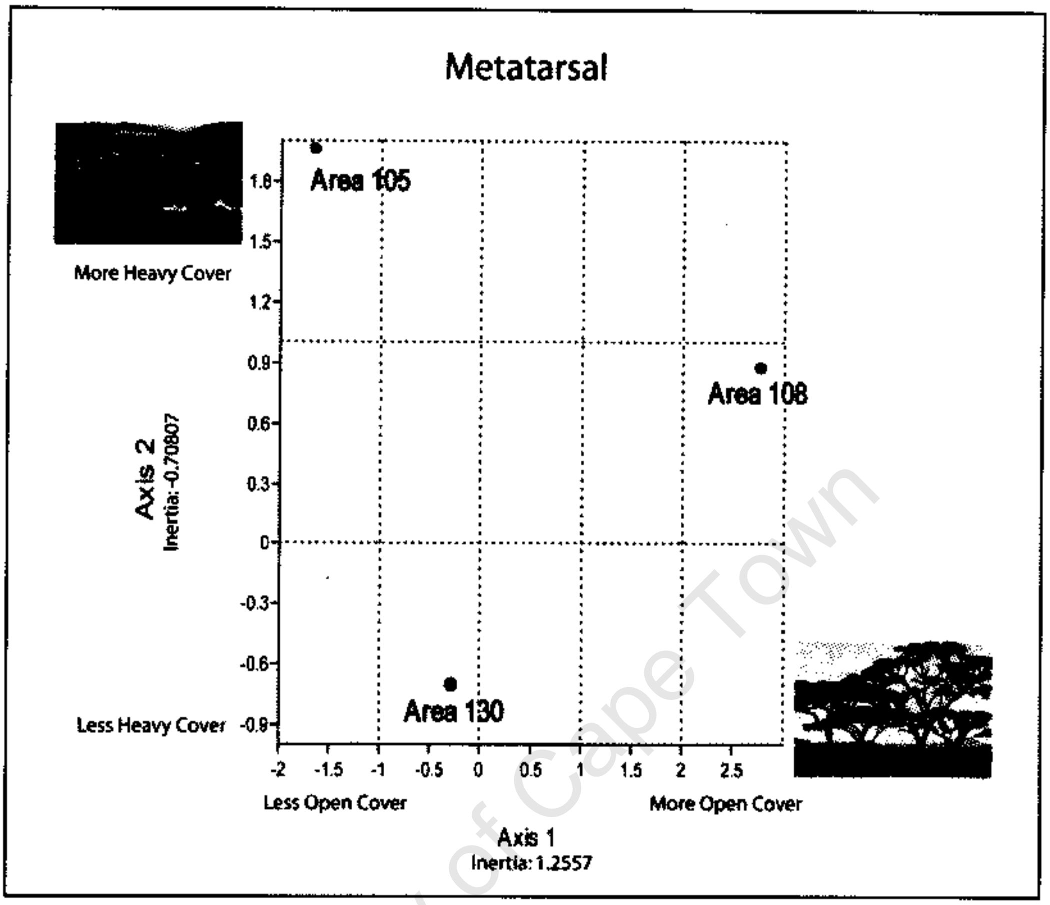


Figure 5.5 Output graph for the CA performed on the metatarsal data from Areas 105, 108 and 130.

In the graph of the metatarsal data (Figure 5.5), axis 1 is also most closely associated with the amount of open cover in an environment. This axis explains 44.8% of the inertia in the metatarsal dataset (inertia for axis 1= 1.26). Of the variance in axis 1, 82.9% is explained by open cover (eigenvalue = 0.45). Axis 2 of this graph is most closely associated with the amount of heavy cover in an environment. This axis explains a remaining 9.3% of the inertia in the metatarsal dataset (inertia for axis 2 = -0.71). Of the variance in axis 2, 17.1% is explained by heavy cover (eigenvalue = 0.09). Both of these graphs indicate that Area 105 consists of more heavy cover than both Areas 108 and 130; however, Area 130 consists of less heavy cover than Area 108. The metacarpal and metatarsal data also indicates that Area 108 consists of more open cover than both Areas 105 and 130; however, Area 130 consists of slightly more open cover than Area 105.

In the graph of the data yielded by the proximal phalanges (Figure 5.6); axis 1 is most closely associated with the amount of closed cover in an environment. This axis explains 35.3% of the inertia in the proximal phalanx dataset (inertia for axis 1 = 1.75). Of the variance in axis 1, 65.1% is explained by

closed cover (eigenvalue = 0.35). Axis 2 is most closely associated with the amount of light cover in an environment, explaining a remaining 5.1% of the inertia in this dataset (inertia for axis 2 = -1.05). Of the variance in axis 2, 34.9% is explained by light cover (eigenvalue = 0.19). The results of the CA on the proximal phalanx data indicate that Area 105 consists of more closed cover than both Areas 108 and 130; however, Area 130 consists of slightly more closed cover than Area 108. This graph also indicates that Area 108 consists of more light cover than both Areas 105 and 130; however, Area 105 consists of more light cover than Area 130.

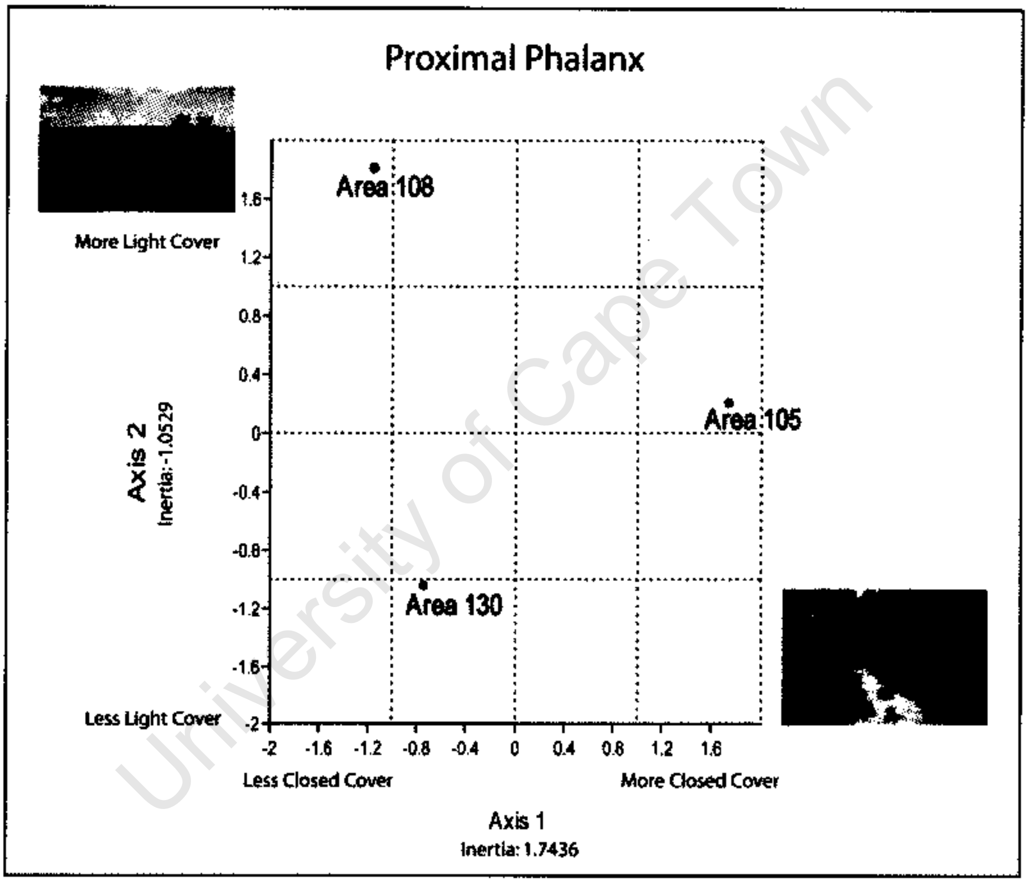


Figure 5.6 Output graph for the CA performed on the proximal phalange data from Areas 105, 108 and 130.

A CA was conducted on a combined dataset of all the elements that could be assigned to habitat type from all of the areas. The results of this analysis are displayed below in Figure 5.7. The results from this analysis indicate that Area 105 consists of more heavy cover and less open cover than both Areas 108 and 130; however Area 108 consists of more heavy cover than Area 130. In this graph, axis 1 is most closely associated with the amount of open cover in an environment. This axis represents 27.5% of the inertia in this combined dataset (inertia for axis 1= 0.84). Of the variance in axis 1, 80.4% is explained by

open cover (eigenvalue = 0.28). Axis 2 on this graph is most closely associated with the amount of heavy cover in an environment and explains a remaining 0.08% of the inertia in the combined dataset (inertia for axis 2 = 0.51). Of the variance in axis 2, 19.6% is explained by heavy cover (eigenvalue = 0.07). Area 108 consists of more open cover than both Areas 105 and 130; however Area 130 consists of more open cover than Area 105. Overall, these four graphs seem to indicate that Area 105 consists of more closed, heavy cover environments, Area 108 consists of more open environments and Area 130 consists of a mosaic of environments.

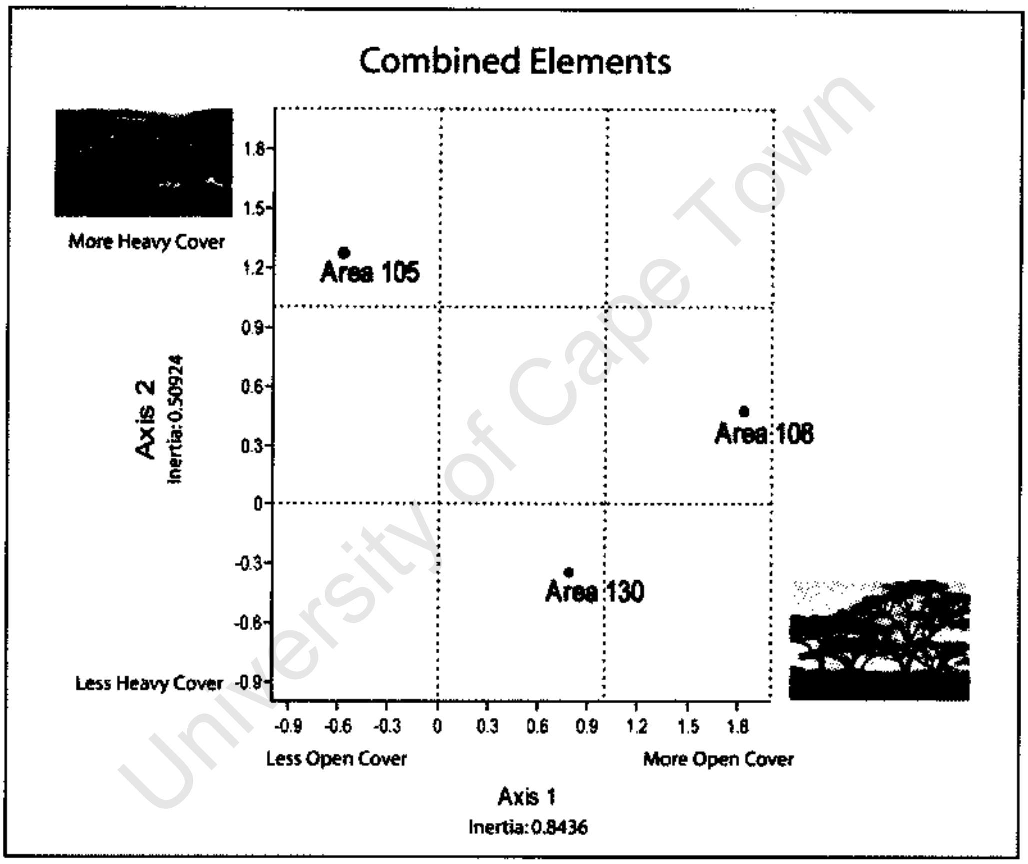


Figure 5.7 Output graph for the CA performed on all of the elements assessed by the DFA from Areas 105, 108 and 130.

In order to determine whether the differences between Areas 105, 108 and 130 indicated by the CA are significant, non-parametric statistical analyses comparing two independent samples were run on these data. In both the Kolmogorov-Smirnov (KS) Test and the Wald-Wolfowitz Runs (WW) Test, the null hypothesis is one of no significant difference between the samples from each of the survey areas at the 0.05 significance level. The results of the KS Test for significance found significant differences between Area 108 and Area 105 (KS: 0.8, $p<0.01$) as well as between Area 108 and Area 130 (KS: -0.72, $p<0.025$)

at the 0.05 significance level; however, no significant difference was reported between Areas 105 and 130 (KS: 0.26, p>0.1). This test for significance reported statistically significant differences between Area 108 and Area 130 (p=0.005) at the 0.05 significance level. However, this test did not report any statistically significant differences between Area 105 and Area 108 (p=0.201) or between Area 105 and Area 130 (p=0.709) at the 0.05 significance level.

Table 5.4 A summary table of all of the palaeoenvironmental assignments from the DFA

	Open	Light Cover	Heavy Cover	Closed
Area 105	4	2	7	7
Area 108	6	0	0	0
Area 130	7	7	5	6

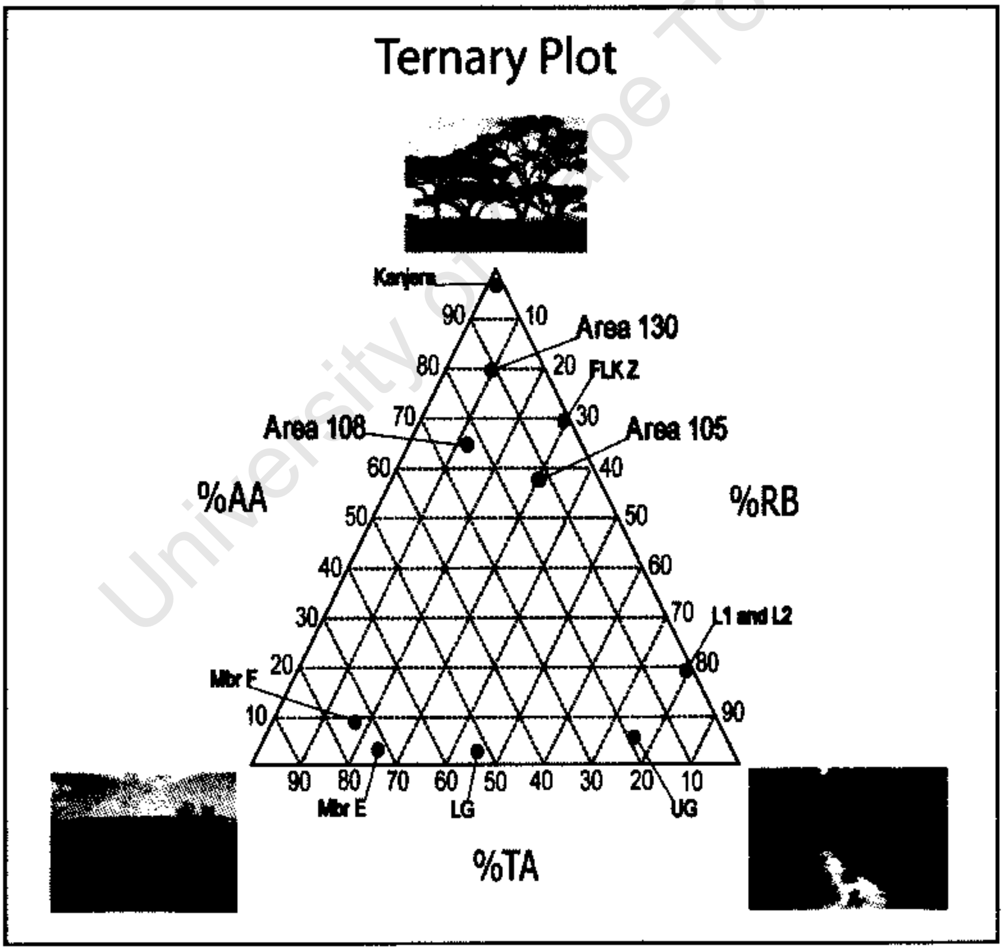


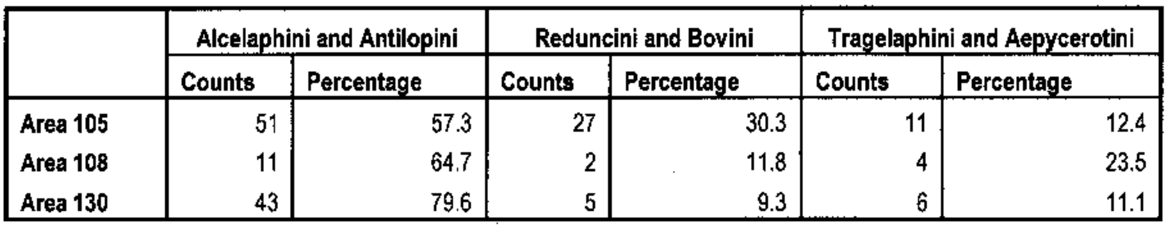
Figure 5.8 Ternary plot describing the relative abundance of Alcelaphini and Antilopini (%AA), Reduncini and Bovini (%RB) and Tragelaphini and Aepyceratini (%TA) for Areas 105, 108 and 130. The same data is provided from Kanjera (Plummer *et al.* 2009), from Olduvai (KLK Z, Zinjanthropus, and L1 and L2) and from the Shungura formation (Lower member G (LG), Upper member G (UG), Member E and Member F) for comparison (Shipman and Harris 1988). Redrawn from Shipman and Harris (1988).

5.3.2 *Tribal Affiliation Data*

The ternary plot describing palaeoenvironmental differences between Areas 105, 108 and 130 as indicated by the tribal affiliation of bovid teeth and horn cores is displayed below (Figure 5.8). This ternary plot is a relative assessment of the habitats from Areas 105, 108 and 130 compared to other habitats in the past. As signified by the ternary plot, the tribal affiliation of bovid teeth and horn cores from the KBS Member in Area 105 are indicative of more closed, and often wet environments. The tribal affiliation of bovid teeth and horn cores from the KBS Member in Area 130 are indicative of more open, often dry environments and the tribal affiliation data from Area 108 indicate that this area is somewhat intermediate, consisting of slightly more closed but dry environments. To determine whether the differences between Areas 105, 108 and 130 as indicated by the tribal affiliation data are significant, non-parametric statistical analyses comparing two independent samples were run on these data. Non-parametric statistics were run as these tests are widely used for studying data at the ordinal scale.

The results of the WW Test indicate that there is a significant difference between the data from each of the survey areas under investigation at the 0.05 significance level. The null hypothesis of no significant difference between the samples from each of the survey areas at the 0.05 significance level can therefore be rejected for Area 105 compared to Area 108 (p=0.000), Area 105 compared to Area 130 (p=0.000) and Area 108 compared to Area 130 (p=0.003), with the most significant differences found between the data from Areas 105 and 130. The results of the KS Test, however, indicate that there is no significant difference between the data from Areas 105 and 108 (p>0.1), and between the data from Areas 108 and 130 (p>0.1). The null hypothesis can therefore not be rejected at the 0.05 significance level for the data from these Area 105 and Area 108, and Area 108 and Area 130. However, the results of the KS Test indicate that there is a significant difference between the data from Areas 105 and 130 (p<0.025) at the 0.05 significance level. In this case, the null hypothesis can be rejected for the data from Areas 105 and 130.

Table 5.5 A summary table of the bovid tribal affiliation data.



	Alcelaphini and Antilopini		Reduncini and Bovini		Tragelaphini and Aepycerotini	
	Counts	Percentage	Counts	Percentage	Counts	Percentage
Area 105	51	57.3	27	30.3	11	12.4
Area 108	11	64.7	2	11.8	4	23.5
Area 130	43	79.6	5	9.3	6	11.1

6. Faunal Patterns and Associations

6.1 Introduction

In the previous chapter, the palaeoenvironments of three survey areas in the Koobi Fora Formation were investigated by means of bovid ecomorphological analysis as well as by means of bovid tribal affiliations. This chapter provides a synthesis of the main results from these analyses and combines these results with other palaeoenvironmental data (pedogenic carbonates; data from Levin (2008) with comparative data from Plummer *et al.* (2009)) in order to provide a comprehensive account of landscape scale palaeoenvironmental variation in the Turkana basin. The KBS Member is of particular interest to palaeoanthropology as it is during this time period that the hominin lineage undergoes a major radiation, with the emergence of *Homo ergaster* (Rogers *et al.* 1994). The palaeoenvironments investigated in the previous chapter are directly associated with these archaeological sites as the data used in the reported analyses come from the excavations from these sites, or from surveys done in the immediate vicinity of these excavations.

6.2 Palaeoenvironments

Despite the small samples sizes utilized in the bovid ecomorphological analysis, trends in palaeoenvironmental variation between the investigated areas at 1.67 to 1.88 Ma are apparent. The results of the ecomorphological analysis of specimens from Area 105 indicate relatively more closed and heavy cover environments than Areas 108 and 130. The results of the ecomorphological analysis from Area 108 indicate relatively open environments whereas the results from Area 130 indicate relatively more light cover environments than either Area 105 or Area 108. The results of the ecomorphological analysis from Area 105 and Area 108 indicate that Area 105 has relatively more closed environments whereas Area 108 consists largely of open environments. The results of the ecomorphological analysis from Area 130, however, appear to indicate a more mosaic palaeoenvironment relative to Area 105 and Area 108. The results from the bovid tribal affiliation analysis for Area 130 vary slightly from the results of the ecomorphological analysis and instead indicate that Area 130 consists of by far the most open and dry environment of Area 105, Area 108 and Area 130. This variation in the results for the same area may be accounted for by differences in sample size. Of the 25 bovid post-cranial elements used in the bovid ecomorphological analysis for Area 130, 14 (56%) elements were indicative of open/light cover habitats and 11 (44%) were indicative of heavy cover/closed habitats. Of the 54 bovid teeth and horn cores used in the bovid tribal affiliation analysis for Area 130, however, only 11 (20.4%) specimens belonged to bovid tribes affiliated with closed environments (both wet and dry) while 43 (79.6%) specimens were

attributed to bovid tribes affiliated with open environments. The bovid tribal affiliation data for Area 130 are clear in indicating that this Area is best described as consisting of open and dry habitats. The bovid tribal affiliation data for Area 105 and 108 are indicative of palaeoenvironments dominated by bovid tribes affiliated with open habitats; however, the data from these two areas are significantly different from each other. These areas are different in that more specimens attributed to bovid tribes associated with closed, often dry habitats were found in Area 108 whereas more specimens attributed to bovid tribes associated with closed, often wet habitats were found in Area 105. Based on the palaeoenvironmental data collected in this study, Areas 130 and 108 are reconstructed as more open and dry compared to Area 105 during KBS Member times.

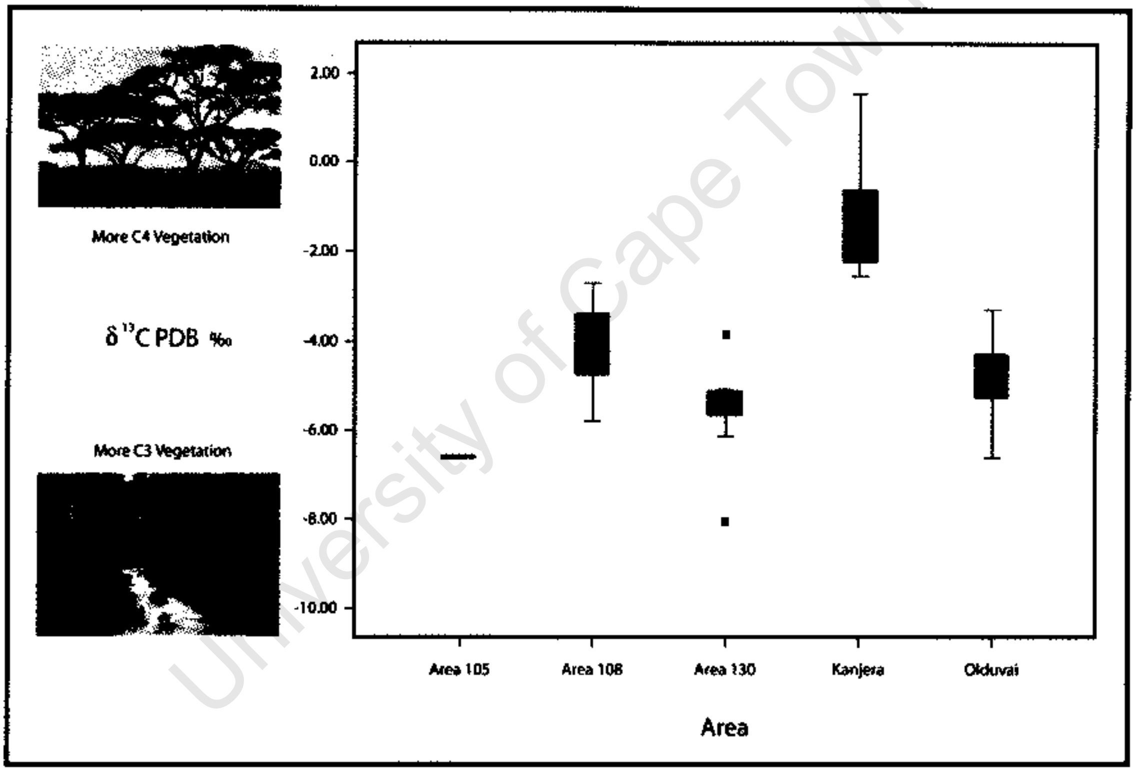


Figure 6.1 Box plot depicting the range of variation in carbon isotopes from Areas 105, 108 and 130. Results from Kanjera and Olduvai are included as a reference (Levin 2008; Plummer *et al.* 2009).

The pedogenic carbonate data from Levin (2008) broadly reflect the patterns identified above. Both carbon and oxygen isotopic data indicate more closed and wet palaeoenvironments associated with Area 105 and more open and dry palaeoenvironments associated with Areas 108 and 130. The carbon isotope results from the pedogenic carbonates indicate lower median 6 ^{13}C values for Area 105 (-6.5%o) than for either Area 108 (-3.5%o) or Area 130 (-5.5%o, see Figure 6.1). The carbon isotope results from Kanjera and Olduvai are included in this box-plot to provide comparative examples of other palaeoanthropological sites dated to a similar period. This graph indicates that Area 105 consists of relatively more C3 vegetation (bushes and trees), whereas Areas 108 and 130 consist of relatively more C4 vegetation (possibly grasses and sedges). The oxygen isotope results from the pedogenic carbonates sampled by Levin (2008) also indicate lower PO values for Area 105 (-5.0%0) than for either Area 108 (-2.0%0) or Area 130 (-2.5‰, see Figure 6.2).

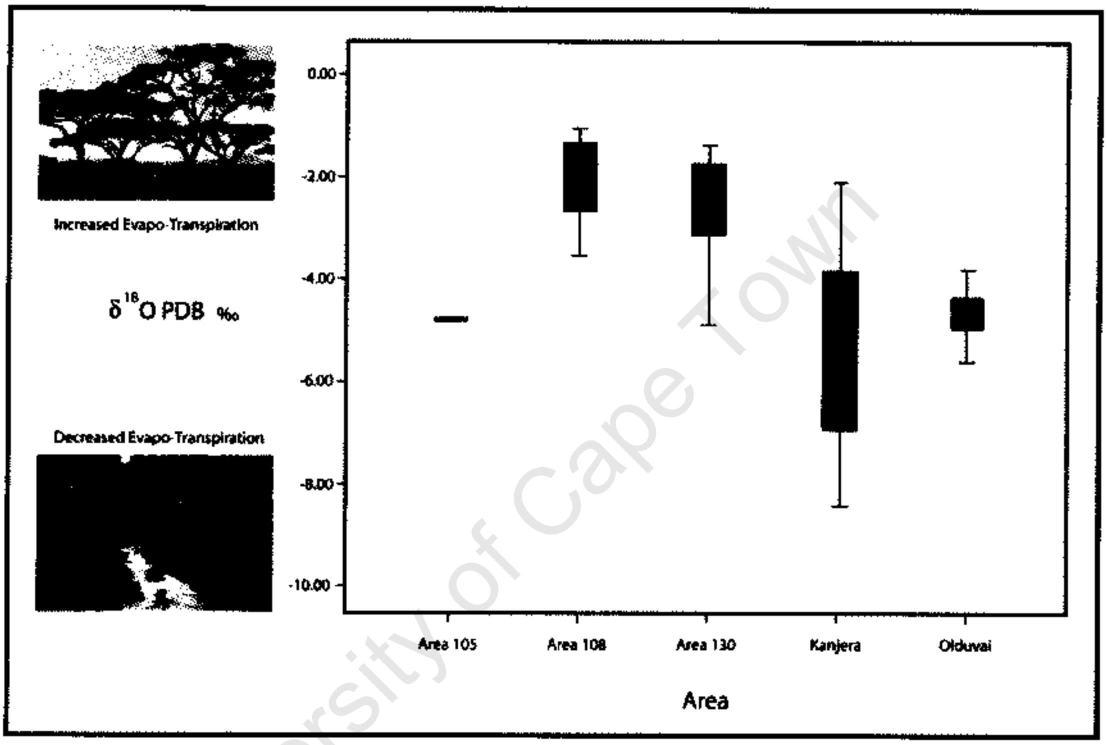


Figure 6.2 Box plot depicting the range of variation in oxygen isotopes from Areas 105, 108 and 130. Results from Kanjera and Olduvai are included as a reference (Levin 2008; Plummer *et al.* 2009).

The oxygen isotope results from Kanjera and from Olduvai are included in this box-plot to provide comparative examples of other palaeoanthropological sites dated to a similar period. This graph indicates that Area 105 has relatively more $^{16}0$ in the water found in the KBS Member soils, whereas Areas 108 and 130 have relatively more $^{18}0$ in the water found in their soils. The soils that formed in Area 105 were therefore more likely to have had more readily available ground water than Areas 108 and 130. In her thesis, Levin (2008) collected oxygen isotope samples from the enamel of Giraffids and Hippopotamids from the KBS Member to apply Levin *et al.'s* (2006) aridity index. However, only Area 105 had a suitable sample from the Karari region to calculate this index. The Giraffids from FxJj 1 and FxJj 3 yielded 5$^{18}0$ values of -2.5%0 (VPDB) and the Hippopotamids from FxJj 1 and FxJj 3 yielded 6 $^{18}0$ values of -6.1‰ (VPDB). The calculated aridity index from these values is -3.6. This index represents

mesic conditions, similar to the environment in modern day Nairobi, where WD (water deficit) is 600 — 800mm (Levin 2008).

In summary, the palaeoenvironmental data for Area 105 indicate more closed, wet habitats during KBS Member times whereas the palaeoenvironmental data for Areas 108 and 130 indicate more open and light cover, often dry habitats during KBS Member times. Although significance testing of the bovid ecomorphological data from Areas 108 and 130 indicate that these survey areas are significantly different from one another, the nature of this difference is obscured by small sample sizes. However, the bovid tribal affiliation data points to the presence of more closed but dry habitats in Area 108 as a possible explanation for this difference. These results indicate significant landscape scale variation of the habitats available to hominins at 1.65 to 1.87 Ma in the Turkana basin.

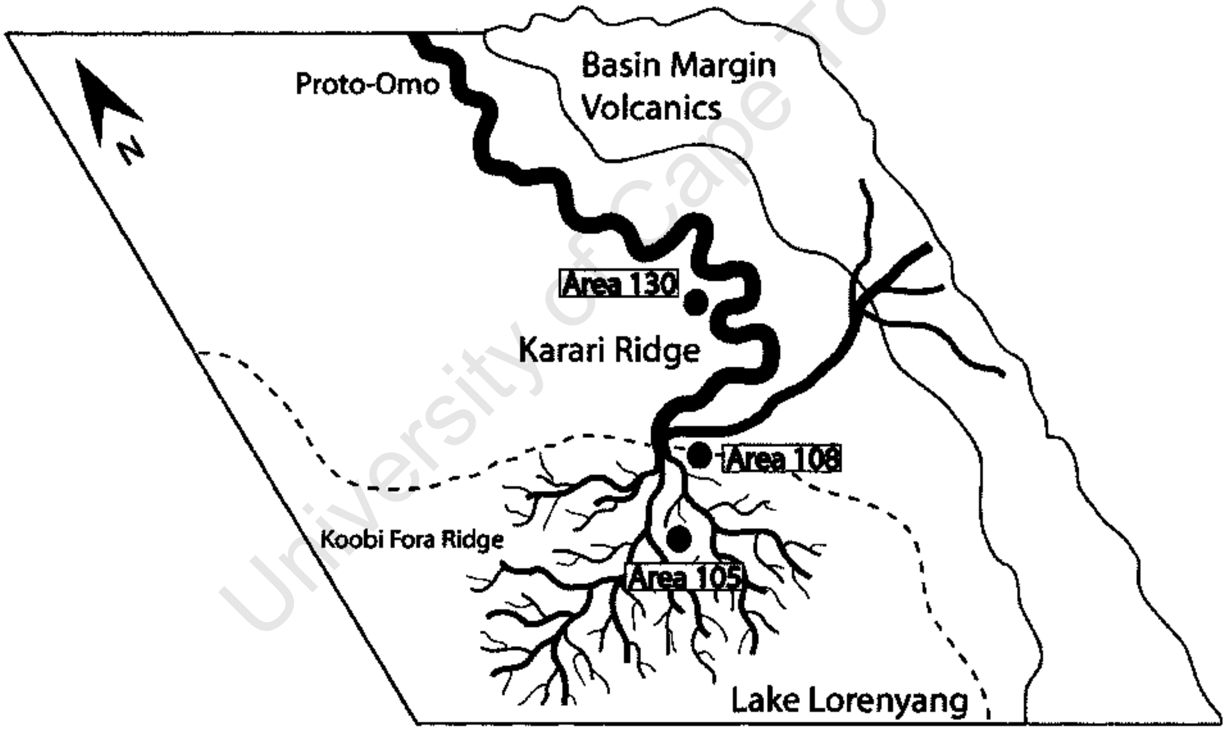


Figure 6.3 A palaeoenvironmental reconstruction of the Karari Ridge during KBS Member times and the relative positions of Areas 105, 108 and 130 based on the reconstruction from Quinn *et al.* (2007).

Quinn *et al.* (2007) provide a concise description of the geological changes that occur in the Turkana basin during KBS Member times. Figure 6.3 provides a reconstruction of the Karari region in the Koobi Fora Formation during KBS Member times, including the relative positions of Areas 105, 108 and 130. Lake Lorenyang, the precursor to Lake Turkana, is estimated to have formed 2 Ma and extended to –9000 km^2. This lake was fed primarily by the ancestral form of the Omo River, known as the Proto-Omo

(Feibel 1988; Rogers *et al.* 1994; Quinn *et al.* 2007). The fluvial channel and floodplain facies that occur just above the stratigraphic level of the KBS tuff indicate the course followed by the Proto-Omo on its route through the Koobi Fora region (Quinn *et al.* 2007). More extensive channel and floodplain deposits in the upper part of the Olduvai Subchron indicate an increase in the prevalence of Proto-Omo river environments at Koobi Fora in KBS Member times (Quinn *et al.* 2007). In addition to the Proto-Omo, channel systems originating in the basin margin volcanics along the north eastern basin margin emptied into the shallows at the edge of Lake Lorenyang over which there were frequent transgressions and regressions (Feibel *et al.* 1991; Quinn *et al.* 2007).

Taking into account the geographic position as well as the palaeoenvironmental reconstruction for Area 105 as consisting largely of closed, wet environments; it can be established that the palaeoenvironmental context for Area 105 occurs at the back swamp delta at the interface of the Proto-Omo with Lake Lorenyang (Rogers *et al* 1994; Isaac 1997). Area 108, best described as open, with light cover and dry environments, was situated along the banks of the Proto-Omo and along the Lake Lorenyang margin in a much more open palaeoenvironmental setting. The sedimentology from FxJj 10 is described as tuffaceous sand, deposited as the floodplain facies of sedimentation by an aggrading channel system (Isaac 1997 pp. 108). It is possible that the deposit from FxJj 10 represents a point bar or bank that was periodically submerged by high water flow from this channel system (Isaac 1997 pp. 108). Area 130, occurring further north along the banks of the Proto-Omo, was substantially dominated by open, dry environments. The archaeological sites found in Area 130 represent occupation of this dissected landscape during a time when a major meandering river was flowing through a broad floodplain.

6.3 Implications

As demonstrated in this chapter, various lines of evidence; including ecomorphological data, tribal affiliation data and pedogenic carbonate data; indicate significant variation in the palaeoenvironments of the KBS Member in Areas 105, 108 and 130 in the Koobi Fora Formation. Analysis of the excavated material from KBS Member archaeological sites within these areas is also indicative of significant differences in the patterns of artefact reduction used at these sites as discussed in Chapter 2. These lines of evidence demonstrate that in Area 105, where palaeoenvironmental indicators suggest more closed and heavy cover, wet environments; most of the recovered artefacts fall within the early stages of an idealized reduction sequence. Also, detached pieces from FxJj 1 and FxJj 3 in Area 105 have a much greater ratio of mass to perimeter indicating a technological system that is less

conservative in the production of whole flakes. In Area 108 and Area 130, where palaeoenvironmental indicators suggest more open and light cover, arid environments; most of the recovered artefacts fall within the later, more reduced stages of an idealized reduction sequence. The detached pieces from these areas have a lower ratio of mass to perimeter indicating an attempt by hominins to attain maximum utility from their stone resources. Hominins from Area 105 produced fewer flakes from the same amount of raw material than their counterparts in Areas 108 and 130. This evidence seems to support the hypothesis that hominids had more reason to conserve raw material for artefacts in more arid areas such as in Areas 108 and 130 than in more closed and wet areas such as Area 105. The extensive reduction evident from Area 130 and Area 108 may be the result of an increased need for artefacts and a subsequent attempt by early hominins to preserve their sources of raw material by increasing the use-life of an artefact through extensive reduction.

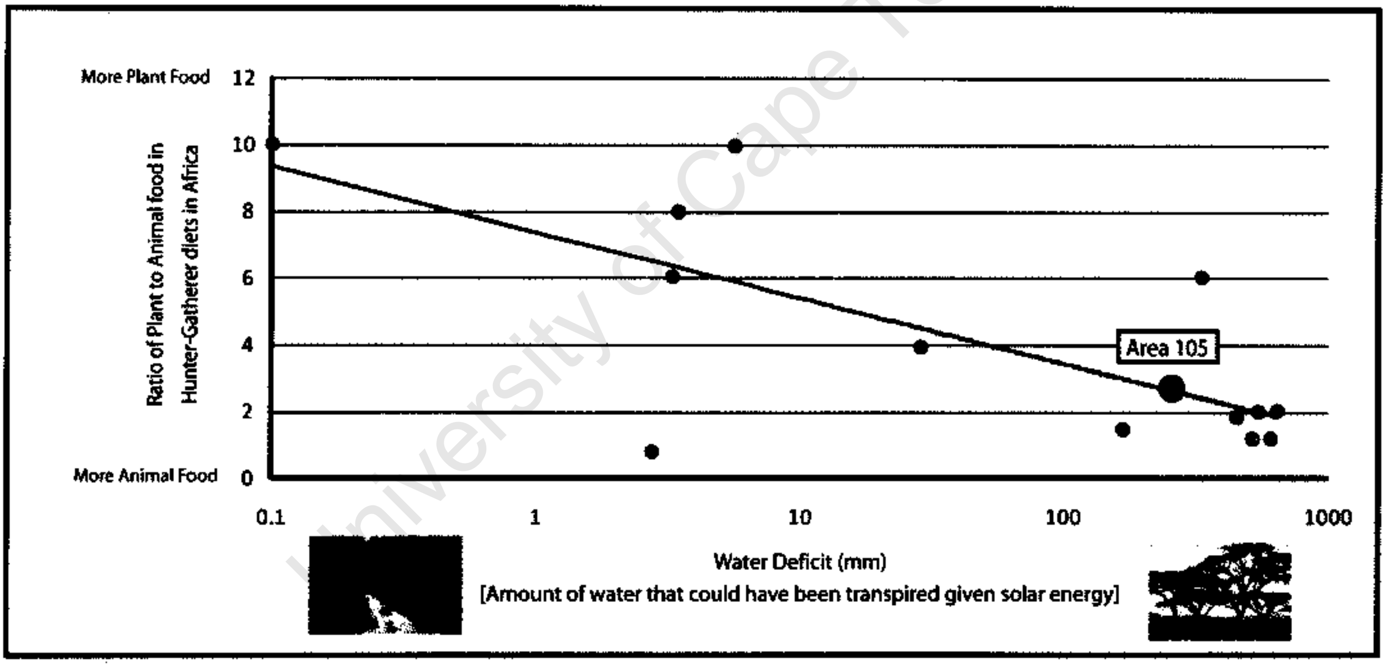


Figure 6.4 Graph indicating the correlation between Water Deficit (logarithmic scale) and the ratio of plant to animal food consumed by modern hunter-gatherer populations using data from Binford (2001). The Water Deficit calculated for Area 105 (400mm) is included.

Raw material availability has been demonstrated by others (e.g.: Braun *et al.* 2008) as not variable enough between Areas 105, 108 and 130 to result in the observed variation in artefact reduction. Instead, Binford's (2001) assertion on the correlation between Water Deficit, the diets of modern hunter-gatherers in Africa, provides a working hypothesis that can be used to explain the patterns of variation in the behaviour of KBS Member hominins. Binford (2001) convincingly demonstrates that in areas with a high water deficit (more open, arid regions), the biomass of medium

sized ungulates is at its greatest and hunter-gatherer populations are consuming more animals relative to plants than they would in areas with a lower water deficit (more closed, wet regions). Using the aridity index data from Levin (2008) for FxJj 1 and FxJj 3, a Water Deficit value was calculated for Area 105 (Figure 6.4). Clearly there are numerous differences between KBS Member hominins and modern hunter-gatherers as described in Binford (2001). However, the ecological pattern of increasing abundance of large to medium sized ungulates in areas of high Water Deficit provides a compelling relational analogy for explaining the patterns described in the KBS Member. Modern hunter-gatherers occupying environments more arid than Area 105 were consuming a ratio of plant to animal food that is close to 1:1 (Figure 6.4). It is extremely unlikely that hominins during KBS Member times were consuming similar amounts of animal tissue in their diet. However, it is plausible that this ecological pattern explains the increased energy investment in artefact production exhibited in Areas 108 and 130.

6.4 Conclusion

I propose that hominins occupying the Koobi Fora landscape during KBS Member times were coming into contact with the carcasses of medium sized ungulates more often in Areas 108 and 130, due to the generally greater biomass of medium sized ungulates in open, arid environments (i.e. those with greater Water Deficit). These hominins would therefore be using artefacts to gain access to resources, such as meat and marrow, more often in the environments that have been modelled for Area 108 and Area 130. Increased access to these protein resources would result in an increase in the intensity with which tools were used and discarded by Plio-Pleistocene hominins. This in turn would result in the necessity for hominins to conserve their sources of raw material by increasing the use-life of artefacts via extensive reduction. The converse would be true for Area 105. Plio-Pleistocene hominins would be coming into contact with medium sized ungulates less often in more closed, wet environments such as Area 105, due to the decreased biomass of medium sized ungulates in these environments. There would therefore be less necessity for hominins to conserve their sources of raw material in Area 105, resulting in flaked pieces that are less reduced.

7. Conclusion

7.1 Summary of Results

The archaeology from three different areas in the Karari region of the Koobi Fora Formation indicates different patterns of tool use by KBS Member hominins. The artefacts from Area 105 are less reduced than the artefacts from Area 108, which are in turn less reduced than the artefacts from Area 130. Two hypotheses are presented to explain this landscape scale variation in hominin behaviour. Variation in raw material availability between these areas may result in increased levels of reduction associated with well known distance to source scenarios. Increased reduction of artefacts with distance from raw material source has been documented in many archaeological settings (Renfrew 1969; Roth and Dibble 1998). However, reconstructions of raw material availability in the Turkana basin during KBS Member times indicate that each of the survey areas in question (Areas 105, 108 and 130) had similar access to raw material sources from the Proto-Omo river as well as basin margin drainages (Braun *et al* 2009).

This project investigates a second hypothesis. Oldowan artefacts were primarily used by hominins to access valuable food resources such as meat and marrow. Variation in the availability of these meat and marrow resources would have affected the patterns of tool use and, more importantly, discard by hominins. Increased levels of artefact reduction are expected from areas with a greater likelihood of encountering meat and marrow resources. Decreased levels of artefact reduction are expected from areas where meat and marrow are less common or at least are a less important aspect of hominin foraging practices. The meat and marrow resources that are most utilised by modern hunter-gatherer populations are those of medium sized ungulates (Binford 2001). Access to the carcasses of medium sized ungulates occurs more frequently in open, grassland environments. Increased levels of artefact reduction are therefore expected from areas exhibiting open, dry, grassland environments during KBS Member times and decreased levels of artefact reduction are expected from areas exhibiting closed, wet palaeoenvironments.

Ecomorphological techniques, bovid tribal affiliation data as well as pedogenic carbonate data were used to test this hypothesis. The results generally indicate that Area 105 consisted of a palaeoenvironment that was more closed and wet, while Areas 108 and 130 consisted of palaeoenvironments that were more open and dry.

7.2 Implications

The results from the investigations into the palaeoenvironment of the KBS Member of the Karari region support the hypothesis that more reduced artefacts are found in areas that consist of more open, arid palaeoenvironments and less reduced artefacts are found in areas that consist of more closed and wet palaeoenvironments. KBS Member hominins would have been coming into increased contact with medium sized ungulates in open, arid environments more often than in closed wet environments. As a result of this increased contact, KBS Member hominins had more opportunities to access valuable meat and marrow resources in these open, arid environments. Copeland (2009) states that more closed, mesic environments are assumed to have more fruiting trees available for hominin consumption than more open, arid, savannah environments. Without available fruiting trees in open, arid environments, hominins may have employed an increased focus on animal foods in order to survive (Copeland 2009).

KBS Member hominins were therefore utilising raw materials more intensely in these open areas to access these resources resulting in increased levels of artefact reduction. KBS Member hominins therefore seem to have altered their behaviour according to the environment in which they found themselves. The landscape scale approach to answering this question has provided insight into how hominins managed palaeoenvironmental variation at 1.67 to 1.88 Ma.

7.3 Limitations

In attempting to reconstruct the lifeways of hominins occupying the landscape during the Plio-Pleistocene, palaeoanthropologists have to make use of "all possible avenues for obtaining information" (Rogers *et al* 1994 pp. 139). This is because, relative to the archaeological studies of more recent populations, little evidence is preserved that can inform palaeoanthropologists of hominin lifeways.

This project was hampered by small sample sizes. Although the preservation of fossil fauna in the Koobi Fora Formation is generally very good, it still does not provide the numbers of fossils necessary for strong statistical analysis. The largest sample sizes used in this analysis come from Area 105 (bovid teeth and horn cores = 101), and the smallest sample sizes from Area 108 (bovid post-crania = 15). This is despite the assertion that medium sized ungulates occur more frequently in Area 108. Increased opportunities for preservation can be found in closed, wet environments that are ideal for fossilisation, such as Area 105. Taphonomic factors therefore play a large role in the preservation of evidence from KBS Member times on the Karari Ridge. This combined with the limited time spent in the field due to its remote nature resulted in particularly small sample sizes for the bovid ecomorphological analysis. In an effort to mitigate the effect of small sample sizes in the data, the DFA results from

numerous bovid post cranial elements were combined in order to provide a stronger palaeoenvironmental signal for each survey area.

The nature of palaeoenvironmental reconstruction requires that a limit to the boundless variation in habitat type be adopted. In this project, only four bovid habitat types were used in the analysis — open, light cover, heavy cover and closed habitats. The full spectrum of available environments was therefore not taken into consideration, and only a superficial division of this variety was considered. While this resulted in the loss of considerable resolution with regard to the palaeoenvironmental reconstruction of the KBS Member, it did allow for the coherent and useful analysis of the palaeoenvironments on a landscape scale.

7.4 Future Research

According to Copeland (2007 pp. 147), too many palaeoecological techniques consider palaeoenvironments as though they are homogenous over large regions. Much of the local variation in palaeoenvironments that is relevant to hominin behaviour is therefore lost. According to Delagnes and Roche (2005 pp. 468), "variations in available resources or in the way resources are processed can result in different patterns of site occupation". This project indicates that some of the palaeoenvironmental variation evident in the Turkana basin may explain at least some of the variation that is evident in the Oldowan archaeological assemblages found there. The results of this project open up space for enquiry into hominin behavioural variation in a landscape, local habitat context at other locations, such as at Lokalalei 1 and 2c (Delagnes and Roche 2005). Most importantly, however, this project provides a different way in which to interpret landscape scale variation in hominin artefact production that will perhaps provide insight into the great variability found within one technological industry, within one region at one time.

8. References

Bamforth, D. B. and P. Bleed (1997). "Technology, flaked stone technology, and risk." Archeological Papers of the American Anthropological Association 7: 109-139.

Baxter, M. J. (1994). Exploratory multivariate analysis in archaeology. Edinburgh University Press.

Behrensmeyer, A. K. and J. C. Barry (2005). "Biostrategraphic surveys in the Siwaliks of Pakistan: A method for standardised surface sampling of the vertebrate fossil record." Palaeontologica Electronica 8.

Behrensmeyer, A. K. (1978). The habitat of Plio-Pleistocene hominids in East Africa: Taphonomic and microstratigraphic evidence. Early hominids of Africa. C. J. Jolly, London, Duckworth: 165-165.

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

Berger, L. R. and P. V. Tobias (1996). "A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in Australopithecus africanus." Journal of Human Evolution 30: 343-348.

Binford, L. R. (1981). Bones: ancient men and modern myths. Orlando, Academic Press.

Binford, L. R. (2001). Constructing frames of reference: an analytical method for archaeological theory building using hunter-gatherer and environmental data sets. California, University of California Press.

Bishop, L. C. (1999). Suid palaeoecology and habitat preferences at African Pliocene and Pleistocene hominid localities. African biogeography, climate change and human evolution. T. G. Bromage and F. Schrenk, Oxford, Oxford University Press: 216.

Blumenschine, R. J. and F. T. Masao (1991). "Living sites at Olduvai Gorge, Tanzania?: preliminary landscape archaeology results in the basal Bed II lake margin zone." Journal of Human Evolution 21: 451-462.

Blumenschine, R. J. and C. R. Peters (1998). "Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times." Journal of Human Evolution 34: 565-607.

Blumenschine, R. J., C. R. Peters, F. T. Masao, R. J. Clarke, A. L. Deino, R. L. Hay, C. C. Swisher, I. G. Stanistreet, G. M. Ashley, L. J. McHenry, N. E. Sikes, N. J. van der Merwe, J. C. Tactikos, A. E. Cushing, D. M. Deocampo, J. K. Njau and J. I. Ebert (2003). "Late pliocene Homo and hominid land use from western Olduvai Gorge, Tanzania." Science 299: 1217-1221.

Bobe, R. (1997). "Hominid Environments in the Pliocene: An Analysis of Fossil Mammals from the Omo Valley, Ethiopia." University of Washington, Seattle. Doctoral Thesis.

Bobe, R. (2006). "The evolution of arid ecosystems in eastern Africa." Journal of Arid Environments 66: 564-584.

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

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

Bobe, R. and G. G. Eck (2001). "Responses of African Bovids to Pliocene Climatic Change." Paleobiology 27: 1-47.

Bocherens, H., G. Pacaud, P. A. Lazarev and A. Mariotti (1996). "Stable isotope abundances (^ 1^ 3C,^ 1^ 5N) in collagen and soft tissues from Pleistocene mammals from Yakutia: Implications for the palaeobiology of the Mammoth Steppe." Palaeogeography Palaeoclimatology Palaeoecology 126: 31-44.

Bock, W. J. (1990). "From Biologische Anatomic to Ecomorphology." Netherlands Journal of Zoology 40: 254 - 277.

Bock, W. J. (1994). "Concepts and methods in Ecomorphology." Journal of Bioscience 19(4): 403-413.

Bousman, C. B. (1993). "Hunter-gatherer adaptations, economic risk and tool design." Lithic Technology 18: 59-86.

Braun, D. R. (2006). "The ecology of Oldowan technology: Perspectives from Koobi Fora and Kanjera South (Kenya)". Rutgers University, New Jersey. Doctoral Thesis.

Braun, D. R., S. L. Arnow, J. Ferraro and J. Tactikos (2003). "Quantifying Oldowan Lithic Reduction sequences: Theoretical and Methodological considerations." PaleoAnthropology 1: 4-5.

Braun, D. R. and J. W. K. Harris (2003). Technological developments in the Oldowan of Koobi Fora: Innovative techniques of artifact analysis. Oldowan: Rather more than smashing stones. **J. M. Moreno, R. M. Torcal and I. de la Torre Sainz, First Hominid Technology Workshop, Bellaterra, Treballs d'Arqueologia. 117-144.**

Braun, D. R. and J. W. K. Harris (In Press). Plio-Pleistocene technological variation: A view from the KBS Mbr., Koobi Fora Formation. Approaches to Early Stone Age Technology. **N. Toth and K. Schick. Indiana, Stone Age Institute.**

Braun, D. R., J. W. K. Harris and D. N. Maina (2009). "Oldowan raw material procurement and use: evidence from the Koobi Fora Formation." Archaeometry **51: 26-42.**

Braun, D. R., B. L. Pobiner and J. C. Thompson (2008). "An experimental investigation of cut mark production and stone tool attrition." Journal of Archaeological Science **35: 1216-1223.**

Braun, D. R., M. J. Rogers, J. W. K. Harris and S. J. Walker (2008). "Landscape-scale variation in hominin tool use: Evidence from the Developed Oldowan." Journal of Human Evolution **55: 1053-1063.**

Braun, D. R., J. C. Tactikos, J. V. Ferraro, S. L. Arnow and J. W. K. Harris (2008). "Oldowan reduction sequences: methodological considerations." Journal of Archaeological Science: **2153-2163.**

Braun, D. R., J. C. Tactikos, J. V. Ferraro and J. W. K. Harris (2005). "Flake recovery rates and inferences of Oldowan hominin behavior: a response to." Journal of Human Evolution **48: 525-531.**

Brown, F., J. Harris, R. Leakey and A. Walker (1985). "Early Homo erectus skeleton from west Lake Turkana, Kenya." Nature **316: 788-792.**

Brown, F. H. and C. S. Feibel (1986). "Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya." Journal of the Geological Society **143: 297.**

Brown, F. H. and C. S. Feibel (1991). "Stratigraphy, depositional environments and palaeogeography of the Koobi Fora Formation." Koobi Fora Research Project, Volume 3 The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments. **J. M. Harris, Oxford, Clarendon Press: 1-29.**

Brown, F. H., B. Haileab and I. McDougall (2006). "Sequence of tuffs between the KBS Tuff and the Chari Tuff in the Turkana Basin, Kenya and Ethiopia." Journal of the Geological Society **163: 185-204.**

Bunn, H., J. W. K. Harris, G. Isaac, Z. Kaufulu, E. Kroll, K. D. Schick, N. Toth and A. K. Behrensmeyer (1980). "FxJj50: an early pleistocene site in northern Kenya." World Archaeology 12: 109-36.

Burggraf, D. R. (1976). Stratigraphy of the Upper Member Koobi Fora Formation, Southern Karari Escarpment, East Turkana Basin, Kenya., Iowa State University, Ames.

Cerling, T. and J. M. Harris (1999). "Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and palaeoecological studies." Oecologia 120: 347-363.

Cerling, T. E. (1992). "Development of grasslands and savannas in East Africa during the Neogene." Global and Planetary Change 5: 241-247.

Cerling, T. E., J. M. Harris and B. H. Passey (2003). "Diets of East African Bovidae based on stable isotope analysis." Journal of Mammalogy 84: 456-470.

Clarke, R. J. and P. V. Tobias (1995). "Sterkfontein member 2 foot bones of the oldest South African hominid." Science 269: 521.

Copeland, S. R. (2007). "Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs." Journal of Human Evolution 53: 146-175.

Copeland, S. R. (2009). "Potential hominin plant foods in northern Tanzania: semi-arid savannas versus savanna chimpanzee sites." Journal of Human Evolution 57: 365-378.

Dart, R. A. (1925). "Australopithecus africanus: The ape-man of South Africa." Nature 115: 195-197.

Degusta, D. and E. S. Vrba (2003). "A method for inferring palaeohabitats from the functional morphology of bovid astragali." Journal of Archaeological Science 30: 1009-1022.

Degusta, D. and E. S. Vrba (2005). "Methods for inferring palaeohabitats from discrete traits of the bovid postcranial skeleton." Journal of Archaeological Science 32: 1115-1123.

Degusta, D. and E. S. Vrba (2005). "Methods for inferring palaeohabitats from the functional morphology of bovid phalanges." Journal of Archaeological Science 32: 1099-1113.

Delagnes, A. and H. Roche (2005). "Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya." Journal of Human Evolution 48: 435-472.

deMenocal, P. B. (1995). "Plio-Pleistocene African climate." Science 270: 53-59.

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

Deocampo, D. M., R. J. Blumenschine and G. M. Ashley (2002). "Wetland Diagenesis and Traces of Early Hominids, Olduvai Gorge, Tanzania." Quaternary Research 57: 271-281.

Feibel, C. S. (1988). Palaeoenvironments from the Koobi Fora formation, Turkana Basin, northern Kenya. University of Utah. Doctoral Thesis.

Feibel, C. S., F. H. Brown and I. McDougall (1989). "Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia." American Journal of Physical Anthropology 78: 595-622.

Feibel, C. S., J. M. Harris and F. H. Brown (1991). "Palaeoenvironmental context for the late Neogene of the Turkana Basin." Koobi Fora Research Project, Volume 3 The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments. J. M. Harris, Oxford, Clarendon Press: 321-370.

Fernandez, M. H. and E. S. Vrba (2006). "Plio-Pleistocene climatic change in the Turkana Basin (East Africa): Evidence from large mammal faunas." Journal of Human Evolution 50: 595-626.

Frank, H. J. (1976). Stratigraphy of the Upper Member, Koobi Fora Formation, northern Karari Escarpment, East Turkana Basin, Kenya., Iowa State University, Ames.

Gentry, A. W., L. S. B. Leakey and R. J. G. Savage (1970). The Bovidae (Mammalia) of the Fort Ternan fossil fauna. Fossil vertebrates of Africa. R. J. G. Savage and S. C. Coryndon, London, Academic Press. 2: 569.

Hammer, Oyvind, D. A. T. Harper and P. D. Ryan (2009). PAST - PAlaeontological STatistcs, ver. 1.89.

Harris, J. M., M. G. Leakey and F. H. Brown (2006). "A Brief History of Research at Koobi Fora, Northern Kenya." Ethnohistory 53: 35.

Howell, F. C., P. Haesaerts and J. De Heinzelin (1987). "Depositional environments, archeological occurrences and hominids from Members E and F of the Shungura Formation (Omo basin, Ethiopia)." Journal of Human Evolution 16: 665-700.

Hunt, K. D. (1996). "The postural feeding hypothesis: an ecological model for the evolution of bipedalism." South African Journal of Science 92: 77-90.

Isaac, G. and A. K. Behrensmeyer (1997). "Geological context and palaeoenvironments". Koobi Fora Research Project Volume 5: Plio-Pleistocene Archaeology. G. a. I. Isaac and B. Isaac, Oxford, Oxford University Press: 12-70.

Isaac, G. L. (1977). Early stone tools - an adaptive threshold? Problems in economic prehistory and social archaeology. G. d. G. Sievking, I. H. Longworth and K. E. Wilson. London, Duckworth: 39-47.

Isaac, G. L. (1983). "Early stages in the evolution of human behavior: the adaptive significance of stone tools." Zesdekroon-voordraft gehouden voor die Stichting Nederlands Museum voor anthropologie en praehistorie(22 April): 5-43.

Isaac, G. L. (1984). "Archaeology of human origins: studies of the lower Pleistocene in East Africa 1971-1981." Advances in World Archaeology 3: 1-87.

Isaac, G. L. (1997). Koobi Fora Research Project Volume 5: Plio-Pleistocene Archaeology. New York, Oxford University Press.

Isaac, G. L., J. W. K. Harris and D. Crader (1976). Archaeological evidence from the Koobi Fora formation. Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Palaeoecology and Evolution. Y. Coppens, F. Clark Howell and R. E. F. Leakey, Chicago, University of Chicago Press: 533.

Isaac, G. L., J. W. K. Harris and E. M. Kroll (1997). "The stone artefact assemblages: a comparative study". Koobi Fora Research Project Volume 5: Plio-Pleistocene Archaeology. G. a. I. Isaac, B. Oxford, Oxford University Press: 262-362.

Isaac, G. L. and B. Isaac (1997). Koobi Fora Research Project Volume 5: Plio-Pleistocene Archaeology. Clarendon Press.

Jolly, C. J. (1970). "The seed-eaters: a new model of hominid differentiation based on a baboon analogy." Man 5: 5-26.

Kappelman, J. (1984). "Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania." Palaeogeography, Palaeoclimatology, Palaeoecology 48: 171-196.

Kappelman, J. (1988). "Morphology and locomotor adaptations of the bovid femur in relation to habitat." Journal of Morphology 198: 119-130.

Kappelman, J. (1991). "The palaeoenvironment of Kenyapithecus at Fort Ternan." Journal of Human Evolution 20: 95-129.

Kappelman, J., T. W. Plummer, L. C. Bishop, A. Duncan and S. Appleton (1997). "Bovids as indicators of Plio-Pleistocene palaeoenvironments in East Africa." Journal of Human Evolution 32: 229-256.

Klein, R. G., G. Avery, K. Cruz-Uribe and T. E. Steele (2007). "The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa." Journal of Human Evolution 52: 164-186.

Klein, R. G., R. G. Franciscus and T. E. Steele (2010). "Morphometric identification of bovid metapodials to genus and implications for taxon-free habitat reconstruction." Journal of Archaeological Science. 37: 389-401.

Ohler, M. (1993). Skeleton and habitat of recent and fossil ruminants, Verlag Friedrich Pfeil.

Kovarovic, K. and P. Andrews (2007). "Bovid postcranial ecomorphological survey of the Laetoli palaeoenvironment." Journal of Human Evolution 52: 663-680.

Leakey, M. G. and Leakey, R. E. (1978). The fossil hominids and an introduction to their context 1968 - 1974. Koobi Fora research project. 1. Oxford, Clarendon Press.

Leakey, M. G. (1982). Extinct large colobines from the Plio-Pleistocene of Africa. American Journal of Physical Anthropology. 58: 153-172.

Leakey, M. G., C. S. Feibel, I. McDougall and A. Walker (1995). "New four-million-year old hominid species from Kanapoi and Allia Bay, Kenya." Nature 376: 565-571.

Leakey, M. G., C. S. Feibel, I. McDougall, C. Ward and A. Walker (1998). "New specimens and confirmation of an early ape for Australopithecus anamensis." Nature 393: 62-66.

Leakey, M. G., A. Walker and P. S. Ungar (1995). "New genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya." Journal of Human Evolution 28: 519-531.

Leakey, R. E. (1970). "Fauna and artefacts from a new plio-pleistocene locality near Lake Rudolf in Kenya." Nature **226: 223.**

Leonard, W. R. and M. L. Robertson, Eds. (2000). "Ecological correlates of home range variation in primates: implications for hominid evolution". On the Move: How and Why Animals Travel in Groups. **S. Boinski and P. A. Garber, Chicago, University of Chicago Press: 628-648.**

Lepre, C. J. (2001). "Home bases, raw material and sedimentology from the Okote Member, Koobi Fora Formation, northern Kenya: A geoarchaeological study." Journal of Human Evolution **40: A13-A14.**

Lepre, C. J., R. L. Quinn, J. C. A. Joordens, C. C. Swisher and C. S. Feibel (2007). "Plio-Pleistocene facies environments from the KBS member, Koobi Fora Formation: implications for climate controls on the development of lake-margin hominin habitats in the northeast Turkana Basin (northwest Kenya)." Journal of Human Evolution **53: 504-514.**

Levin, E. N. (2008). "Isotopic records of Plio-Pleistocene climate and environments." The University of **Utah.Doctoral Thesis.**

Levin, N. E., T. E. Cerling, B. H. Passey, J. M. Harris and J. R. Ehleringer (2006). "A stable isotope aridity index for terrestrial environments." PNAS USA **103: 11201-11205.**

Levin, N. E., J. Quade, S. W. Simpson, S. Semaw and M. Rogers (2004). "Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia." Earth and Planetary Science Letters **219: 93-110.**

Levin, N. E., S. W. Simpson, J. Quade, T. E. Cerling and S. R. Frost (2008). Herbivore enamel carbon isotopic composition and the environmental context of Ardipithecus at Gona, Ethiopia. The Geology of Early Humans in the Horn of Africa: Geological Society of America Special Paper. **J. Quade and J. G. Wynn. 446: 215 - 234.**

McDougall, I. (1981). "Argon-40/argon-39 age spectra from the KBS Tuff, Koobi Fora Formation." Nature **294: 120-124.**

McDougall, I. (1985). "K-Ar and 40Ar/39Ar dating of the hominid-bearing Pliocene-Pleistocene sequence at Koobi Fora, Lake Turkana, northern Kenya." Bulletin of the Geological Society of America **96: 159.**

McDougall, I. and F. H. Brown (2006). "Precise 40Ar/39Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya." Journal of the Geological Society **163: 205.**

Passey, B. H., T. F. Robinson, L. K. Ayliffe, T. E. Cerling, M. Sponheimer, M. D. Dearing, B. L. Roeder and J. R. Ehleringer (2005). "Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals." Journal of Archaeological Science **32: 1459-1470.**

Plummer, T. W. and L. C. Bishop (1994). "Hominid palaeoecology at Olduvai Gorge, Tanzania as indicated by antelope remains." Journal of Human Evolution **27: 47-75.**

Plummer, T. W., L. C. Bishop, P. W. Ditchfield, J. V. Ferraro, J. D. Kingston, F. Hertel and D. R. Braun (2009). "The environmental context of Oldowan hominin activities in Kanjera South, Kenya." Interdisciplinary Approaches to the Oldowan. **E. Hovers and D. R. Braun, Springer, Dordrecht: 149-160.**

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

Plummer, T. W., P. W. Ditchfield, L. C. Bishop, J. D. Kingston and J. V. Ferraro (2009). "Oldest Evidence of Toolmaking Hominins in a Grassland-Dominated Ecosystem." PLoS ONE **4: e7199.**

Pobiner, B. L. and D. R. Braun (2005). "Strengthening the inferential link between cutmark frequency data and Oldowan hominid behavior: results from modern butchery experiments." Journal of Taphonomy **3: 18-26.**

Potts, R. (1994). "Variables Versus Models of Early Pleistocene Hominid Land-Use." Journal of Human Evolution **27: 7-24.**

Potts, R. (1998). "Environmental hypotheses of hominin evolution." Yearbook of Physical Anthropology **41: 93-136.**

Potts, R. (1998). "Variability selection in hominid evolution." Evolutionary Anthropology **7: 81-96.**

Potts, R., A. K. Behrensmeyer and P. Ditchfield (1999). "Paleolandscape variation and Early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation, Kenya." Journal of Human Evolution **37: 747-788.**

Prentice, M. L. and G. H. Denton (1988). "The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution". Evolutionary History of the" Robust" Australopithecines. **F. E. Grine. New York, Aldine de Gruyter: 383-403.**

Quinn, R. L., C. J. Lepre, J. D. Wright and C. S. Feibel (2007). "Paleogeographic variations of pedogenic carbonate 13C values from Koobi Fora, Kenya: implications for floral compositions of Plio-Pleistocene hominin environments." Journal of Human Evolution 53: 560-573.

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

Reed, K. E. (2008). "Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia." Journal of Human Evolution 54: 743-768.

Renfrew, C. (1969). "Trade and culture process in European prehistory." Current Anthropology 10: 151-169.

Rightmire, G. P. (1993). "Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region." American Journal of Physical Anthropology 90: 1-33.

Rogers, M. J. (1997). "A Landscape Archaeological Study at East Turkana, Kenya". Rutgers University, New Brunswick. Doctoral Thesis.

Rogers, M. J., J. W. K. Harris and C. S. Feibel (1994). "Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin." Journal of Human Evolution 27: 139-158.

Roth, B. J. and H. L. Dibble (1998). "Production and transport of blanks and tools at the French Middle Paleolithic site of Combe-Capelle Bas." American Antiquity: 47-62.

Schoeninger, M. J., K. Hallin, H. Reeser, J. W. Valley and J. Fournelle (2003). "Isotopic alteration of mammalian tooth enamel." International Journal of Osteoarchaeology 13: 11-19.

Ségalen, L., J. A. Lee-Thorp and T. Cerling (2007). "Timing of C4 grass expansion across sub-Saharan Africa." Journal of Human Evolution 53: 549-559.

Semaw, S., P. Renne, J. W. Harris, C. S. Feibel, R. L. Bernor, N. Fesseha and K. Mowbray (1997). "2.5-million-year-old stone tools from Gona, Ethiopia." Nature 385: 333-336.

Shennan, S. (1997). Quantifying archaeology. Edinburgh University Press, Edinburgh.

Shipman, P. and J. M. Harris (1988). Habitat preference and paleoecology of Australopithecus boisei in Eastern Africa. Evolutionary history of the "Robust" Australopithecines. **F. E. Grine, Transaction Publishers, New Brunswick: 343-381.**

Soligo, C. and P. Andrews (2005). "Taphonomic bias, taxonomic bias and historical non-equivalence of faunal structure in early hominin localities." Journal of Human Evolution **49: 206-229.**

Solounias, N. and B. Dawson-Saunders (1988). "Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece." Palaeogeography, Palaeoclimatology, Palaeoecology **65: 149-172.**

Spencer, L. M. (1997). "Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use." Journal of Human Evolution **32: 201-228.**

Sponheimer, M., K. E. Reed and J. A. Lee-Thorp (1999). "Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality." Journal of Human Evolution **36: 705-718.**

Toth, N. (1982). The Stone Age Technology of Early Hominids at Koobi Fora, Kenya: an experimental approach. Anthropology. **Berkeley, University of California.**

Vrba, E. S. (1980). The significance of bovid remains as indicators of environment and predation patterns. Fossils in the Making: Vertebrate taphonomy and palaeoecology. **A. K. Behrensmeyer and A. P. Hill, University of Chicago Press, Chicago: 247-271.**

Vrba, E. S. (1999). Habitat theory in relation to the evolution in African Neogene Biota and Hominids. African biogeography, climate change and human evolution. **T. G. Bromage and F. Schrenk, New York, Oxford University Press: 19-39.**

Vrba, E. S. (1985). "Ecological and adaptive changes associated with early hominid evolution". Ancestors: The Hard Evidence. **E. Delson, New York, Alan R. Liss Inc: 63-71.**

Vrba, E. S. (1995). "On the connection between palaeoclimate and evolution". Palaeoclimate and evolution with emphasis on human origins. **E. S. Vrba, G. H. Denton, T. C. Partridge and L. H. Burkle, New Haven, Yale University Press: 24-48.**

Walker, A., R. E. Leakey, J. M. Harris and F. H. Brown (1986). "2.5-Myr Australopithecus boisei from west of Lake Turkana, Kenya." Nature 322: 517-522.

Western, D. and A. K. Behrensmeyer (2009). "Bone Assemblages Track Animal Community Structure over 40 Years in an African Savanna Ecosystem." Science 324: 1061.

White, T. and J. M. Harris (1978). "Stratigraphic interpretation of the Omo Shungura and Lake Turkana fossil suid record." Science 202: 1309.

White, T. D., S. H. Ambrose, G. Suwa, D. F. Su, D. DeGusta, R. L. Bernor, J. R. Boisserie, M. Brunet, E. Delson and S. Frost (2009). "Macrovertebrate Paleontology and the Pliocene Habitat of Ardipithecus ramidus." Science 326: 67.

Winckler, H. (1988). An examination of concepts and methods in ecomorphology. Acta XIX Congr. International Ornithological Congress. H. Ouellet, National Museum of Natural Sciences, Ottawa: 2246 - 2243.

Wood, B. (1992). "Early hominid species and speciation." Journal of Human Evolution 22: 351-365.

Wood, B. (1992). "Origin and evolution of the genus *Homo.*" Nature 355: 783-790.

9. Materials and Methods - Appendix

Figures below illustrate the measurements used in the ecomorphological analysis of the data collected from the Karari region of the Koobi Fora Formation. The post-cranial elements of a bontebok *(Damaliscus dorcas)* are used to illustrate the measurements used. (Certain humeral measurements are not illustrated due to their awkward position on the element. These measurements are described with the others below.)

Humerus:

FUNLEN:	**Functional length**
MAXLEN:	**Maximum length**
MAP:	**Midshaft antero-posterior measurement**
MML:	**Midshaft medio-lateral measurement**
PROXAP:	**Proximal epiphysis, maximum antero-posterior measurement**
PROXML:	**Proximal epiphysis, maximum medio-lateral measurement**
TUBTUB:	**Length of tuberosity**
BICGMXL:	**Maximum closure of head of humerus and tuberosity**
BICG:	**Width of groove between head of humerus and tuberosity**
BTUBAP:	**Base of tuberosity on shaft, antero-posterior measurement**
BTUBML:	**Base of tuberosity on shaft, medio-lateral measurement**
DISTMAP:	**Distal epiphysis, medial side anter-posterior maximum measurement**
DISTLAP:	**Distal epiphysis, lateral side antero-posterior maximum measurement**
DISTLML:	**Distal epiphysis, maximum medio-lateral measurement**
TSIM:	**Distal medial trochlear, superior-inferior measurement**
TSIMI:	**Distal medial-intermediate trochlear, superior-inferior measurement**

TSIC:	**Distal centre trochlear, superior-inferior measurement**
TSILI:	**Distal lateral-intermediate trochlear, superior-inferior measurement**
TSIL:	**Distal lateral trochlear, superior-inferior measurement**
TM LLC:	**Distal trochlear, medio-lateral measurement from the lateral to the centre spool**
TMLII:	**Distal trochlear, medio-lateral measurement from the lateral-intermediate to the medial intermediate spool**
TMLCM:	**Distal trochlear, medio-lateral measurement from the centre to the medial spool**
TMLCI:	**Distal trochlear, medio-lateral measurement from the centre to the medial-intermediate spool**
TMLIM:	**Distal trochlear, medio-lateral measurement from the medial-intermediate to the medial spool**
TMLT:	**Distal trochlear, medio-lateral total measurement**
TROAPMIN:	**Distal trochlear, antero-posterior minimum**
GRTUBSI:	**Greater tuberosity on the proximal epiphysis, maximum superior-inferior measurement**
SD:	**Minimum shaft dimension**
HEADAP:	**Antero-posterior measurement of the head of the humerus**
HEADML:	**Medio-lateral measurement of the head of the humerus**
FOFO:	**Fossa to fossa measurement on the distal trochlear**

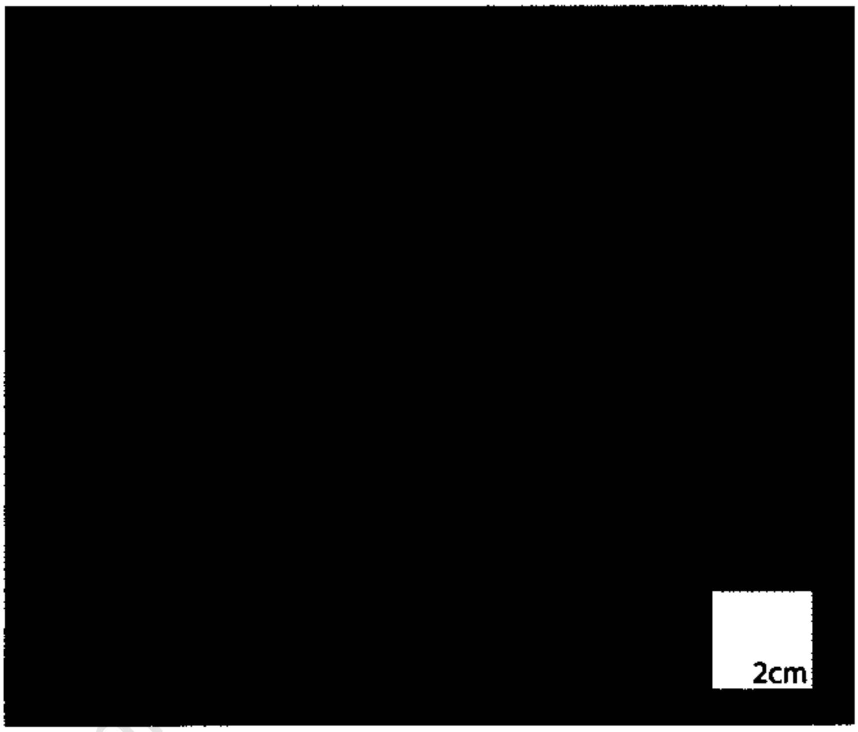


Figure 9.1: Proximal bovid humerus of a bontebok (*Damaliscus dorcas*).

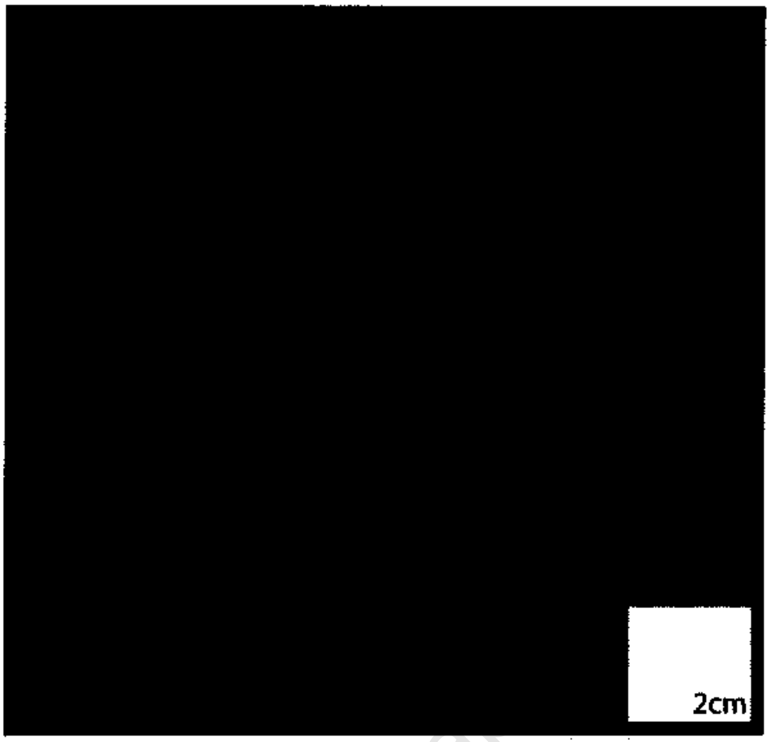


Figure 9.2: Distal bovid humerus of a bontebok (*Damaliscus dorcas*).

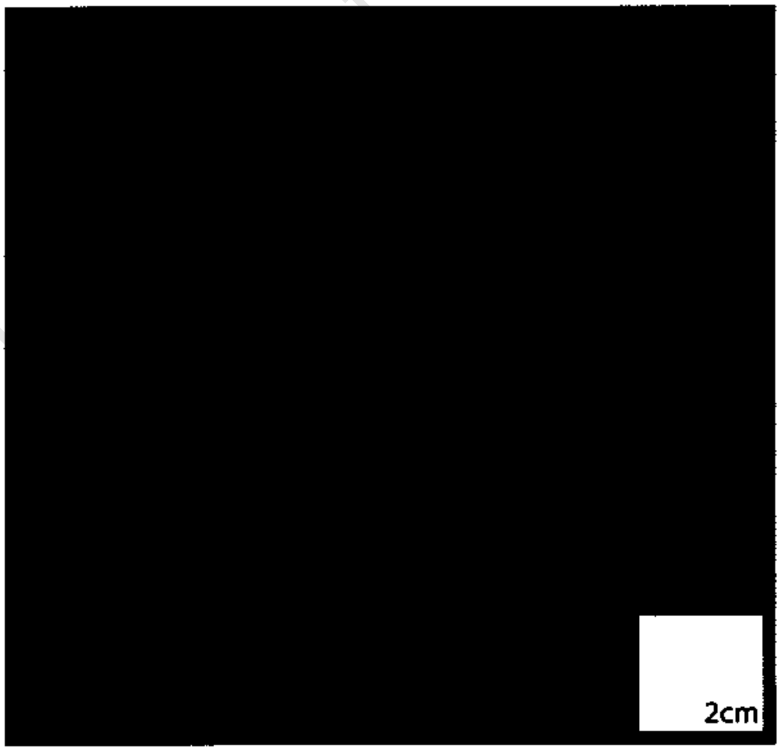


Figure 9.3: Distal bovid humerus of a bontebok (*Damaliscus dorcas*).

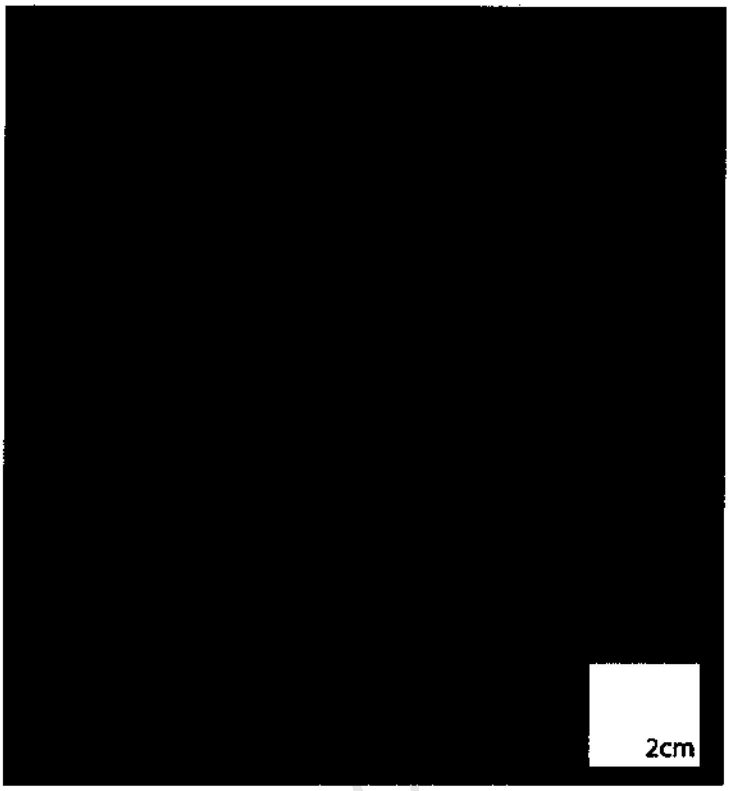


Figure 9.4: Distal bovid humerus of a bontebok (*Damaliscus dorcas*).

Figure 9.5: Ventral view of the humerus of a bontebok (*Damaliscus dorcas*).

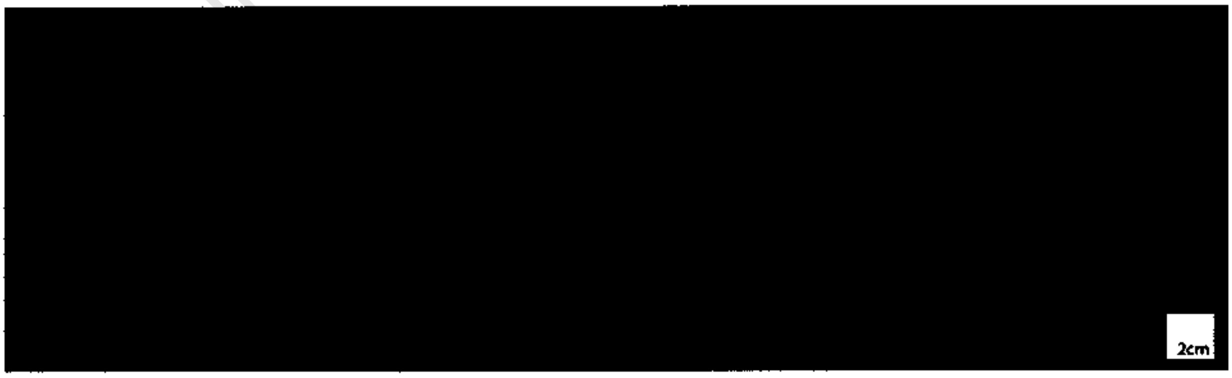


Figure 9.6: Ventral view of a bontebok metapodial (Damaliscus dorcas).

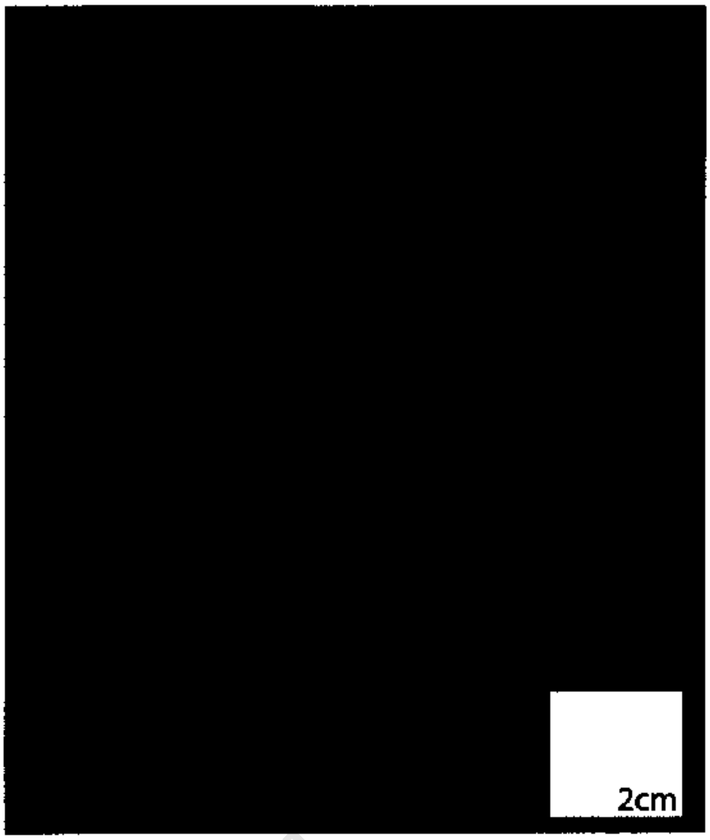


Figure 9.7: Ventral view of the distal end of a bontebok metapodial (*Damaliscus dorcas*).

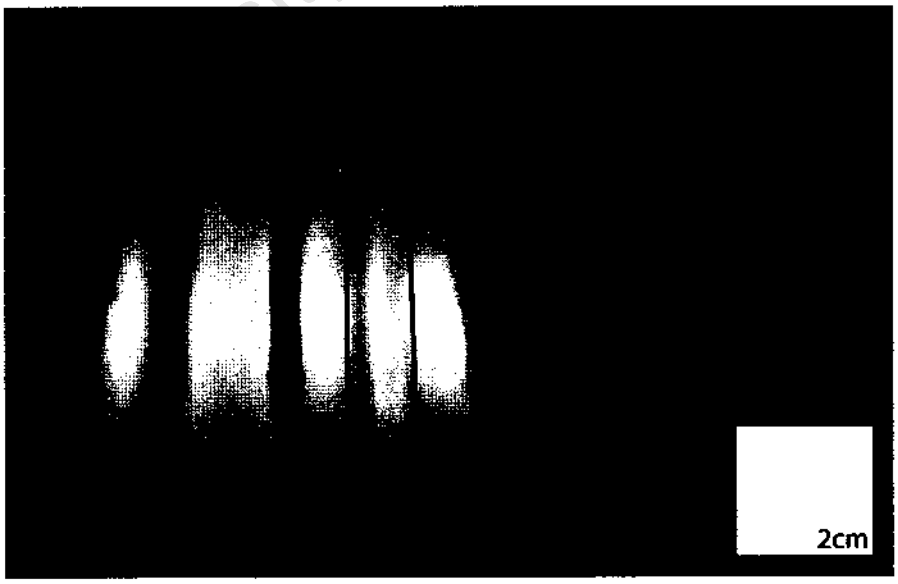


Figure 9.8: Distal view of trochlear on a bontebok metapodial (*Damaliscus dorcas*).

Metacarpal

MGAP: Proximal epiphysis, magnum facet antero-posterior measurement

MGML: Proximal epiphysis, magnum facet medio-lateral measurement

Figure 9.9: Proximal view of a bontebok metacarpal (*Damaliscus dorcas*).

Metatarsal

PRONGAP:	**Proximal epiphysis, antero-posterior measurement of prong**
PRONGML:	**Proximal epiphysis, medio-lateral measurement of prong**

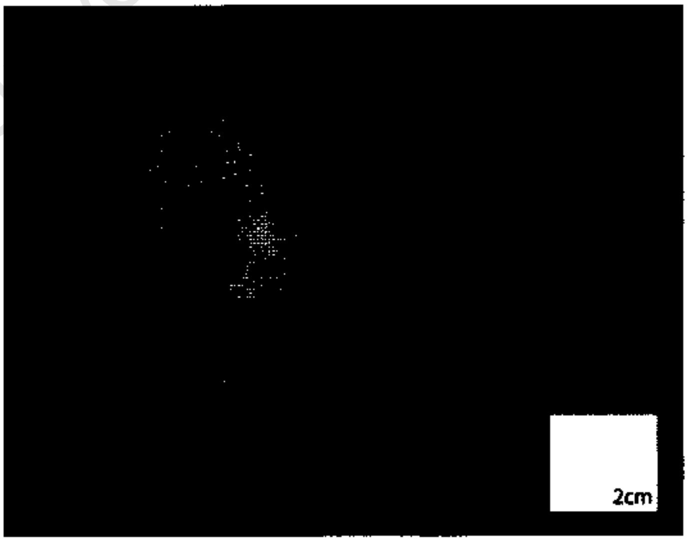


Figure 9.10: Proximal view of a bontebok metatarsal (*Damaliscus dorcas*).

Astragalus:

LATLEN: Maximum lateral length

MEDLEN: Maximum medial length

TIRTMLT: Tibial articulation, medio-lateral total measurement

TUBML: Tuberosity, medio-lateral total measurement

FLANGML: Medio-lateral total across the flange

TARSMLT: Tarsal articulation, medio-lateral total measurement

TARSMLL: Tarsal articulation, medio-lateral measurement of lateral side

TARSMLM: Tarsal articulation, medio-lateral measurement of medial side

TALAP: Tarsal articulation, lateral side antero-posterior measurement

TAMAP: Tarsal articulation, medial side antero-posterior measurement

TIMAP: Tibial articulation, medial side antero-posterior measurement

TILAP: Tibial articulation, lateral side antero-posterior measurement

TICAP: Tibial articulation, centre antero-posterior measurement

PCFLAP: Posterior calcaneum facet, lateral side, proximal-distal measurement

PCFMLP: Posterior calcaneum facet, medio-lateral measurement of the proximal end

PCFMLD: Posterior calcaneum facet, medio-lateral measurement of the distal end

MAXSI: Maximum medial side superior-inferior measurement

MINLEN: Minimum length

LCFDAP: Lateral calcaneum facet, distal antero-posterior measurement

LCFDSI: Lateral calcaneum facet, distal superior-inferior measurement

TUBTIBA: **Maximum measurement from tuberosity to top of tibial articulation on the lateral side**

HOLLOW: **Hollow to hollow measurement**

FOFO: **Fossa to fossa measurement**

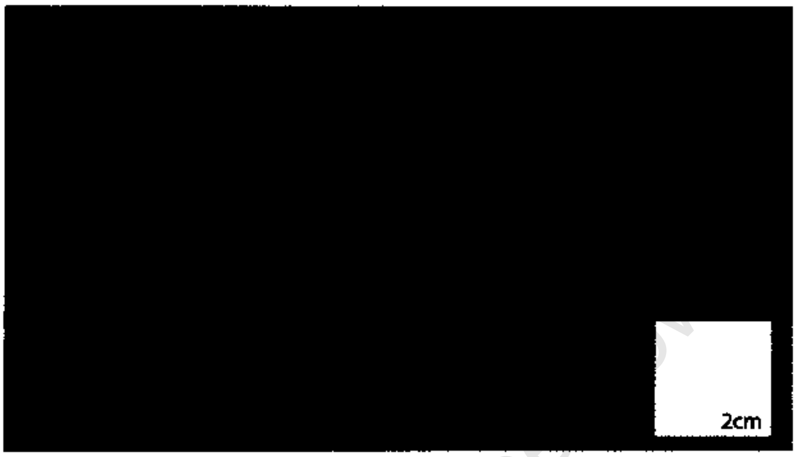


Figure 9.11: Medial view of a bontebok astragalus (*Damaliscus dorcas*).

Figure 9.12: Ventral view of a bontebok astragalus (*Damaliscus dorcas*).

Figure 9.13: Proximal view of a bontebok astragalus (*Damaliscus dorcas*).

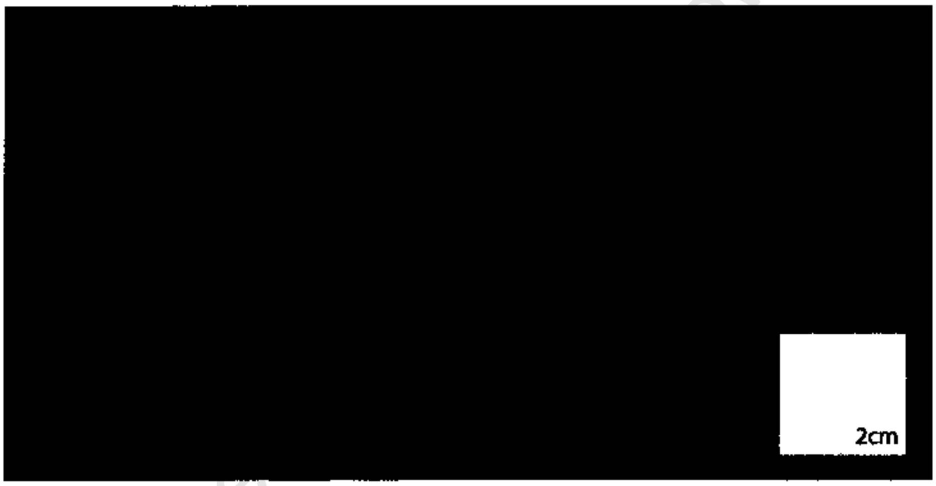


Figure 9.14: Lateral view of a bontebok astragalus (*Damaliscus dorcas*).

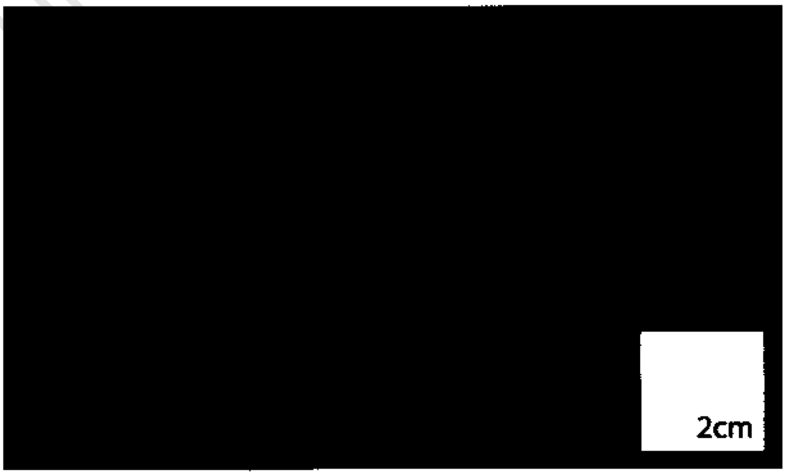


Figure 9.15: Dorsal view of a bontebok astragalus (*Damaliscus dorcas*).

Proximal Phalanx:

PROXWID:	**Proximal width**
MIDLEN:	**Midline length**
INTWID:	**Intermediate width**
DISTWID:	**Distal width**
INTHGT:	**Intermediate height**
DISTHGT:	**Distal height**
PROXHGT:	**Proximal height**

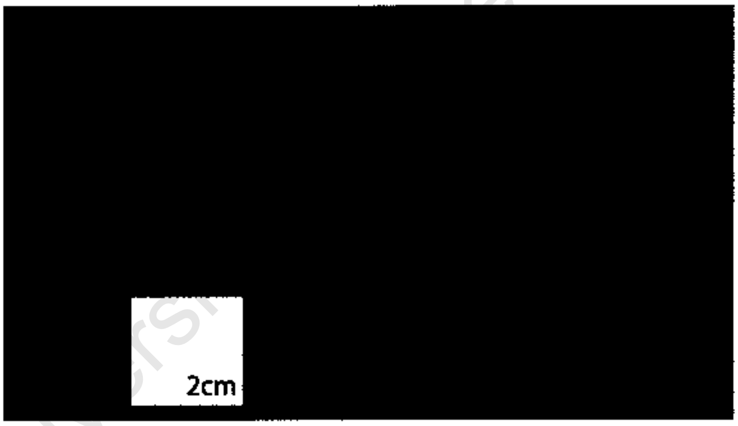


Figure 9.16: Proximal phalanx of a bontebok (*Damaliscus dorcas*).

Figure 9.17: Dorsal view of a proximal phalanx from a bontebok (*Damaliscus dorcas*).

Intermediate Phalanx:

PROXWID:	**Proximal width**
DISTWID:	**Distal width**
SUPLEN:	**Superior length**
INFLEN:	**Inferior length**
DISTHGT:	**Distal height**
LATHGT:	**Lateral height**
MEDHGT:	**Medial height**

Figure 9.18: Intermediate phalanx of a bontebok (*Damaliscus dorcas*)

Figure 9.19: Ventral view of the intermediate phalanx of a bontebok (*Damaliscus dorcas*).

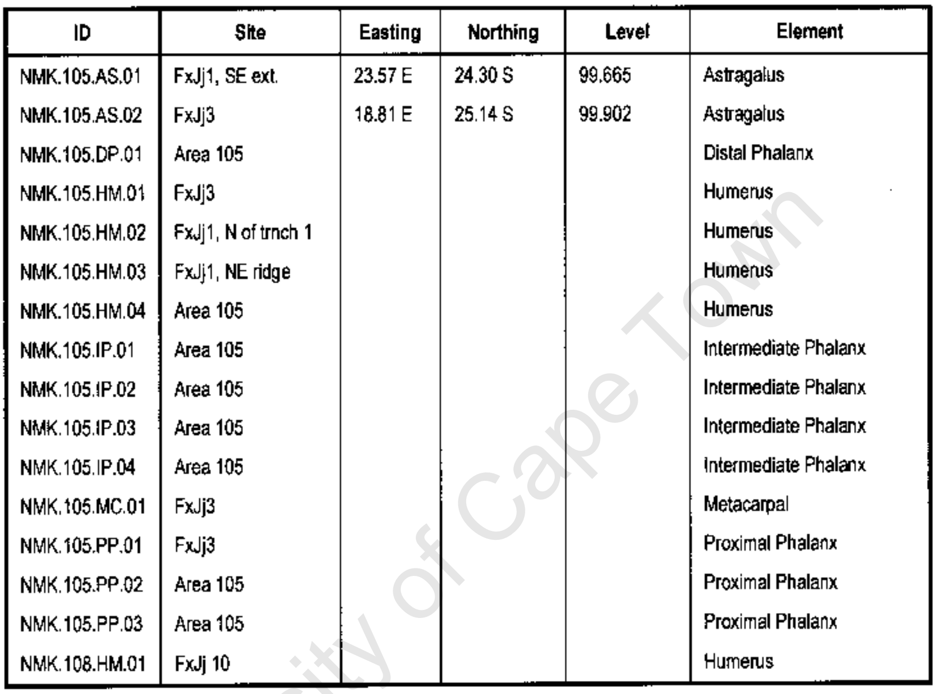
Distal Phalanx:

SUPLEN:	**Superior length**
INFLEN:	**Inferior length**
BASWID:	**Basal width**
TOTHGT:	**Total height**
AFHGT:	**Articular facet height**

Figure 9.20: Distal phalanx of a bontebok (*Damaliscus dorcas*).

Bovid Post-crania from the National Museums of Kenya

Table 9.1: Available location data for all specimens housed at the National Museums of Kenya Archaeology and Palaeontology Department in Nairobi from Area 105 and Area 108. The ID number consists of the origin of the fossil (the National Museum of Kenya in this case), the area in which it was found, which element it is (AS-Astragalus; HM-Humerus; MC-Metacarpal; MT-Metatarsal; PP-Proximal Phalanx; IP-Intermediate Phalanx and DP-Distal phalanx) as well as a unique identity number.



ID	Site	Easting	Northing	Level	Element
NMK.105.AS.01	FxJj1, SE ext.	23.57 E	24.30 S	99.665	Astragalus
NMK.105.AS.02	FxJj3	18.81 E	25.14 S	99.902	Astragalus
NMK.105.DP.01	Area 105				Distal Phalanx
NMK.105.HM.01	FxJj3				Humerus
NMK.105.HM.02	FxJj1, N of trnch 1				Humerus
NMK.105.HM.03	FxJj1, NE ridge				Humerus
NMK.105.HM.04	Area 105				Humerus
NMK.105.IP.01	Area 105				Intermediate Phalanx
NMK.105.IP.02	Area 105				Intermediate Phalanx
NMK.105.IP.03	Area 105				Intermediate Phalanx
NMK.105.IP.04	Area 105				Intermediate Phalanx
NMK.105.MC.01	FxJj3				Metacarpal
NMK.105.PP.01	FxJj3				Proximal Phalanx
NMK.105.PP.02	Area 105				Proximal Phalanx
NMK.105.PP.03	Area 105				Proximal Phalanx
NMK.108.HM.01	FxJj 10				Humerus

Table 9.2: Available location data for all specimens housed at the National Museums of Kenya Archaeology and Palaeontology Department in Nairobi from Area 130. The ID number consists of the origin of the fossil (the National Museum of Kenya in this case), the area in which it was found, which element it is (AS-Astragalus; HM-Humerus; MC-Metacarpal; MT-Metatarsal; PP-Proximal Phalanx; IP-Intermediate Phalanx and DP-Distal phalanx) as well as a unique identity number.

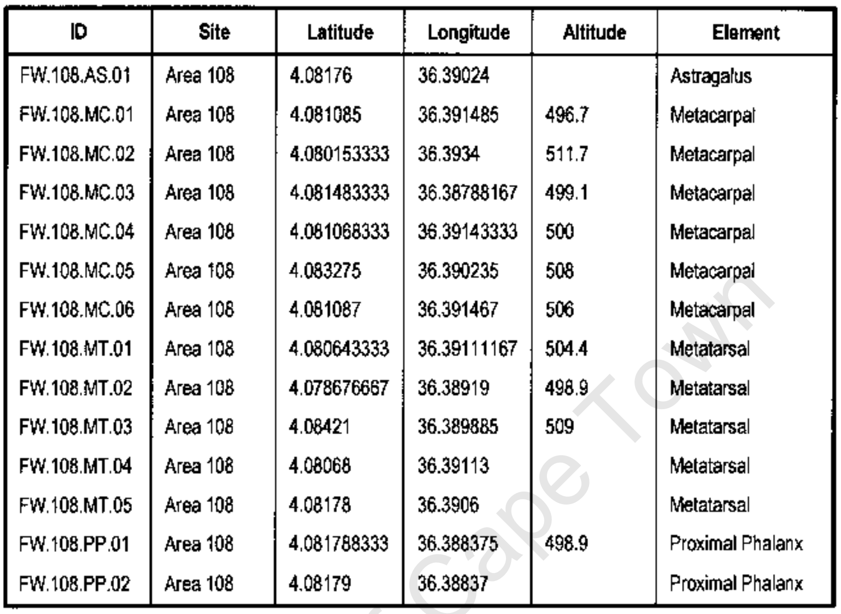
ID	Site	Easting	Northing	Level	Element
NMK.130.AS.01	FxJj38 SE				Astragalus
NMK.130.DP.01	FxJj38 SE				Distal Phalanx
NMK.130.HM.01	FxJj38 SE	102-103 E	101-102 S	99.60-99.55	Humerus
NMK.130.HM.02	FxJj38 SE	101-102 E	91-92 S	99.50-99.60	Humerus
NMK.130.HM.03	FxJj38 SE				Humerus
NMK.130.HM.04	FxJj82	1011.95 X	1000.88 Y	100.33	Humerus
NMK.130.HM.05	FxJj82	1001.612 E	1005.487 N	1001.125	Humerus
NMK.130.HM.06	FxJj82	1005.20 X	1000.42 Y	99.98	Humerus
NMK.130.IP.01	FxJj38 SE				Intermediate Phalanx
NMK.130.IP.02	FxJj38 SE				Intermediate Phalanx
NMK.130.IP.03	FxJj38 SE				Intermediate Phalanx
NMK.130.IP.04	FxJj38 SE				Intermediate Phalanx
NMK.130.IP.05	FxJj38 SE				Intermediate Phalanx
NMK.130.IP.06	FxJj38 F	36-37 E	99-100 S	99.80-99.75	Intermediate Phalanx
NMK.130.MC.01	FxJj38 SE				Metacarpal
NMK.130.MC.02	FxJj38 SE				Metacarpal
NMK.130.MC.03	FxJj38 SE				Metacarpal
NMK.130.MC.04	FxJj82	1002.413 X	1009.855 Y	100.23	Metacarpal
NMK.130.MC.05	FxJj82	1002.479 X	1009.746 Y	100.231	Metacarpal
NMK.130.MC.06	FxJj82	1001.492 E	1005.343 N	100.126	Metacarpal
NMK.130.MC.07	FxJj82	1000-1001 E	1005 - 1006 N	SFCE	Metacarpal
NMK.130.MC.08	FxJj82	1001.766 E	1005.55 N	100.136	Metacarpal
NMK.130.MC.09	FxJj82	1005.77 X	1000.30 Y	99.9	Metacarpal
NMK.130.MC.10	FxJj82	1005.71 X	999.94 Y	99.9	Metacarpal
NMK.130.MT.01	FxJj38 SE				Metatarsal
NMK.130.MT.02	FxJj38 SE				Metatarsal
NMK.130.MT.03	FxJj82	1001.477 E	1005.548 N	100.127	Metatarsal
NMK.130.MT.04	FxJj82	1001.862 E	1005.256 N	100.142	Metatarsal
NMK.130.MT.05	FxJj82	1013.39 X	998.32 Y	100.34	Metatarsal
NMK.130.MT.06	FxJj82				Metatarsal
NMK.130.PP.01	FxJj38 SE				Proximal Phalanx
NMK.130.PP.02	FxJj38 SE				Proximal Phalanx
NMK.130.PP.03	FxJj38 SE				Proximal Phalanx
NMK.130.PP.03	FxJj82				Proximal Phalanx
NMK.130.PP.04	FxJj82				Proximal Phalanx
NMK.130.PP.05	FxJj82				Proximal Phalanx

Bovid Post-crania from Fieldwork in Koobi Fora

Table 9.3: Available location data for all specimens measured from Area 105 during the 2008 and 2009 field seasons in the Turkana Basin. The ID number consists of the origin of the fossil (field work), the area in which it was found, which element it is (AS-Astragalus; HM-Humerus; MC-Metacarpal; MT-Metatarsal; PP-Proximal Phalanx; IP-Intermediate Phalanx and DP-Distal Phalanx) as well as a unique identity number.

ID	Site	Latitude	Longitude	Altitude	Element
FW.105.AS.01	Area 105	4.063018333	36.36202833	509	Astragalus
FW.105.AS.02	Area 105	4.07144	36.36151833	507.2	Astragalus
FW.105.AS.03	Area 105	4.073093333	36.36388333	494	Astragalus
FW.105.AS.04	Area 105	4.07255	36.36412	497.8	Astragalus
FW.105.HM.01	Area 105	4.073383333	36.35829	484.3	Humerus
FW.105.HM.02	Area 105	4.071983333	36.35894167	482.6	Humerus
FW.105.HM.03	Area 105	4.070693333	36.36187667	495.6	Humerus
FW.105.IP.01	Area 105	4.070158333	36.36090833	482.5	Intermediate Phalanx
FW.105.IP.02	Area 105	4.070168333	36.360885	478.7	Intermediate Phalanx
FW.105.IP.03	Area 105	4.070133333	36.360865	487.7	Intermediate Phalanx
FW.105.IP.04	Area 105	4.062621667	36.367825	484.4	Intermediate Phalanx
FW.105.MC.01	Area 105	4.072958333	36.35841667	487.5	Metacarpal
FW.105.MC.02	Area 105	4.072863333	36.360415	476.5	Metacarpal
FW.105.MC.03	Area 105	4.071976667	36.35881	483.7	Metacarpal
FW.105.MC.04	Area 105	4.070206667	36.360495	490.5	Metacarpal
FW.105.MC.05	Area 105	4.071568333	36.36156667	493.1	Metacarpal
FW.105.MC.06	Area 105	4.073258333	36.36421667	485.9	Metacarpal
FW.105.MC.07	Area 105	4.06261	36.36784833	494.8	Metacarpal
FW.105.MC.08	Area 105	4.06913	36.36150167	492.9	Metacarpal
FW.105.MC.09	Area 105	4.073315	36.36426833	485.9	Metacarpal
FW.105.MC.10	Area 105	4.073058333	36.36398167	467.8	Metacarpal
FW.105.MC.11	Area 105	4.067661667	36.36353833	498.4	Metacarpal
FW.105.MT.01	Area 105	4.07063	36.35681833	467.1	Metatarsal
FW.105.MT.02	Area 105	4.061175	36.368775	498.2	Metatarsal
FW.105.MT.03	Area 105	4.0743	36.358955	475.3	Metatarsal
FW.105.MT.04	Area 105	4.073228333	36.359595	480.6	Metatarsal
FW.105.MT.05	Area 105	4.071516667	36.35848333	485.1	Metatarsal
FW.105.MT.06	Area 105	4.070168333	36.36046167	486.3	Metatarsal
FW.105.MT.07	Area 105	4.070276667	36.36066833	488.1	Metatarsal

Table 9.4: Available location data for all specimens measured from Area 108 during the 2008 and 2009 field seasons in the Turkana Basin. The ID number consists of the origin of the fossil (field work), the area in which it was found, which element it is (AS-Astragalus; HM-Humerus; MC-Metacarpal; MT-Metatarsal; PP-Proximal Phalanx; IP-Intermediate Phalanx and DP-Distal Phalanx) as well as a unique identity number.



ID	Site	Latitude	Longitude	Altitude	Element
FW.108.AS.01	Area 108	4.08176	36.39024		Astragalus
FW.108.MC.01	Area 108	4.081085	36.391485	496.7	Metacarpal
FW.108.MC.02	Area 108	4.080153333	36.3934	511.7	Metacarpal
FW.108.MC.03	Area 108	4.081483333	36.38788167	499.1	Metacarpal
FW.108.MC.04	Area 108	4.081068333	36.39143333	500	Metacarpal
FW.108.MC.05	Area 108	4.083275	36.390235	508	Metacarpal
FW.108.MC.06	Area 108	4.081087	36.391467	506	Metacarpal
FW.108.MT.01	Area 108	4.080643333	36.39111167	504.4	Metatarsal
FW.108.MT.02	Area 108	4.078676667	36.38919	498.9	Metatarsal
FW.108.MT.03	Area 108	4.08421	36.389885	509	Metatarsal
FW.108.MT.04	Area 108	4.08068	36.39113		Metatarsal
FW.108.MT.05	Area 108	4.08178	36.3906		Metatarsal
FW.108.PP.01	Area 108	4.081788333	36.388375	498.9	Proximal Phalanx
FW.108.PP.02	Area 108	4.08179	36.38837		Proximal Phalanx

Table 9.5: Available location data for all specimens measured from Area 130 during the 2008 and 2009 field seasons in the Turkana Basin. The ID number is as above.

ID	Site	Latitude	Longitude	Altitude	Element
FW.130.AS.01	Area 130	4.179918333	36.4271	516.8	Astragalus
FW.130.AS.02	Area 130	4.176721667	36.42623167	535.9	Astragalus
FW.130.AS.03	Area 130	4.181781667	36.424295	516	Astragalus
FW.130.HM.01	Area 130	4.176293333	36.42683667	538.7	Humerus
FW.130.HM.02	Area 130	4.175671667	36.42502	527	Humerus
FW.130.HM.03	Area 130	4.177001667	36.41965333	508.1	Humerus
FW.130.HM.04	Area 130	4.176255	36.42685167	527.6	Humerus
FW.130.IP.01	Area 130	4.176675	36.42612833	521.6	Intermediate Phalanx
FW.130.MC.01	Area 130	4.175793333	36.42486	528.7	Metacarpal
FW.130.MC.02	Area 130	4.175713333	36.42505833	529.8	Metacarpal
FW.130.MC.03	Area 130	4.175783333	36.424455	526.9	Metacarpal
FW.130.MC.04	Area 130	4.176633333	36.42607667	532.6	Metacarpal
FW.130.MC.05	Area 130	4.17652	36.426455	526.8	Metacarpal
FW.130.MC.06	Area 130	4.184031667	36.43427333	526.5	Metacarpal
FW.130.MC.07	Area 130	4.176546667	36.42595667	517.1	Metacarpal
FW.130.MC.08	Area 130	4.176695	36.42614667	528.6	Metacarpal
FW.130.MC.09	Area 130	4.176666667	36.42614833	519.2	Metacarpal
FW.130.MC.10	Area 130	4.176511667	36.42644667	527.3	Metacarpal
FW.130.MC.11	Area 130	4.176485	36.42649	525.2	Metacarpal
FW.130.MC.12	Area 130	4.176213333	36.42657167	529.8	Metacarpal
FW.130.MT.01	Area 130	4.184731667	36.42575333	498.9	Metatarsal
FW.130.MT.02	Area 130	4.179946667	36.42708167	517.1	Metatarsal
FW.130.MT.03	Area 130	4.176676667	36.42613167	516.1	Metatarsal
FW.130.MT.04	Area 130	4.1765	36.42683667	521.1	Metatarsal
FW.130.MT.05	Area 130	4.17651	36.42641	529	Metatarsal
FW.130.MT.06	Area 130	4.1765	36.42644667	531.9	Metatarsal
FW.130.MT.07	Area 130	4.17644	36.42591167	530.4	Metatarsal
FW.130.MT.08	Area 130	4.176433333	36.42592167	532	Metatarsal
FW.130.MT.09	Area 130	4.175636667	36.42476	544.7	Metatarsal
FW.130.MT.10	Area 130	4.175633333	36.424745	536.1	Metatarsal
FW.130.MT.11	Area 130	4.175756667	36.42427167	503.8	Metatarsal
FW.130.MT.12	Area 130	4.175798333	36.424435	526.8	Metatarsal
FW.130.PP.01	Area 130	4.175745	36.42431167	528.9	Proximal Phalanx
FW.130.PP.02	Area 130	4.175761667	36.42434333	542.4	Proximal Phalanx
FW.130.PP.03	Area 130	4.175753333	36.42432167	516.8	Proximal Phalanx
FW.130.PP.04	Area 130	4.18198	36.42429833	513	Proximal Phalanx
FW.130.PP.05	Area 130	4.181801667	36.42425667	516.6	Proximal Phalanx

Tribal Affiliation data

ID	Specimen Number	Site	Tribe Allocation
NMK.105.T.47	2154	FxJj3	Alcelaphini
NMK.105.T.46	2140	FxJj3	Hippotragini
NMK.105.T.45	469	FxJj3	Reduncini
NMK.105.T.44	174	FxJj3	Bovini
NMK.105.T.43	610	FxJj1	Reduncini
NMK.105.T.42	357	FxJj1	Reduncini
NMK.105.T.41	493	FxJj1	Reduncini
NMK.105.T.40	460	FxJj1	Neotragini
NMK.105.T.39	395	FxJj1	Antilopini
NMK.105.T.38	141	FxJj1	Antilopini
NMK.105.T.37	69	FxJj1	Bovini
NMK.105.T.36	22	FxJj13	Hippotragini
NMK.105.T.35	2169	FxJj3	Alcelaphini
NMK.105.T.34	2152	FxJj3	Alcelaphini
NMK.105.T.33	2135	FxJj3	Alcelaphini
NMK.105.T.32	2172	FxJj3	Alcelaphini
NMK.105.T.31	2163	FxJj3	Alcelaphini
NMK.105.T.30	2156	FxJj3	Hippotragini
NMK.105.T.29	2180	FxJj3	Alcelaphini
NMK.105.T.28	2136	FxJj3	Alcelaphini
NMK.105.T.27	2	FxJj3	Alcelaphini
NMK.105.T.26	433	FxJj3	Alcelaphini
NMK.105.T.25	357	FxJj3	Antilopini
NMK.105.T.24	440	FxJj3	Alcelaphini
NMK.105.T.23	141 G	FxJj3	Alcelaphini
NMK.105.T.22	105 D	FxJj3	Reduncini
NMK.105.T.21	432	FxJj1	Reduncini
NMK.105.T.20	540	FxJj3	Reduncini
NMK.105.T.19	526	FxJj3	Reduncini
NMK.105.T.18	555	FxJj3	Reduncini
NMK.105.T.17	1047	FxJj1	Reduncini
NMK.105.T.16	375	FxJj1	Reduncini
NMK.105.T.15	406	FxJj1	Reduncini
NMK.105.T.14	2069	FxJj1	Reduncini
NMK.105.T.13	64	FxJj1	Reduncini
NMK.105.T.12	48	FxJj1	Reduncini
NMK.105.T.11	616	FxJj1	Reduncini
NMK.105.T.10	62	FxJj1	Alcelaphini
NMK.105.T.09	28	FxJj1	Antilopini
NMK.105.T.08	807	FxJj1	Reduncini
NMK.105.T.07	487	FxJj1	Bovini
NMK.105.T.06	609	FxJj1	Alcelaphini
NMK.105.T.05	528	FxJj1	Antilopini
NMK.105.T.04	815	FxJj1	Antilopini
NMK.105.T.03	366	FxJj1	Antilopini
NMK.105.T.02	567	FxJj1	Alcelaphini
NMK.105.T.01	2029	FxJj3	Alcelaphini

Table 9.6: Table of teeth (T) and horn cores (HC) from Area 105 that have been allocated to one of 13 bovid tribes, from the National Museum of Kenya (NMK).

ID	Specimen Number	Site	Tribe Allocation
NMK.105.HC.28	ER 75 FS 913	Area 105	Reduncini
NMK.105.HC.27	ER 75 FS 915	Area 105	Reduncini
NMK.105.HC.26	ER 74 FS 364	Area 105	Reduncini
NMK.105.HC.25	ER 71 FS 637	Area 105	Antilopini
NMK.105.HC.24	ER 75 FS 762	Area 105	Antilopini
NMK.105.HC.23	ER 75 FS 997	Area 105	Reduncini
NMK.105.HC.22	ER 74 FS 354	Area 105	Reduncini
NMK.105.HC.21	ER 71 FS 304	Area 105	Reduncini
NMK.105.HC.20		Area 105	Reduncini
NMK.105.HC.19	ER 75 FS 918	Area 105	Reduncini
NMK.105.HC.18	ER 72 FS 238	Area 105	Neotragini
NMK.105.HC.17	ER 73 FS 650	Area 105	Alcelaphini
NMK.105.HC.16	ER 71 FS 305	Area 105	Alcelaphini
NMK.105.HC.15	ER 69 FS 145	Area 105	Alcelaphini
NMK.105.HC.14	ER 75 FS 841	Area 105	Alcelaphini
NMK.105.HC.13	ER 75 FS 784	Area 105	Alcelaphini
NMK.105.HC.12	DF 1479	Area 105	Alcelaphini
NMK.105.HC.11	ER 75 FS 777	Area 105	Alcelaphini
NMK.105.HC.10	ER 73 FS 650	Area 105	Alcelaphini
NMK.105.HC.09	ER 80 FS 550	Area 105	Alcelaphini
NMK.105.HC.08	DF 1447	Area 105	Bovini
NMK.105.HC.07	ER 74 FS 365	Area 105	Bovini
NMK.105.HC.06	DF 1450	Area 105	Bovini
NMK.105.HC.05	ER 80 FS 556	Area 105	Tragelaphini
NMK.105.HC.04	ER 73 FS 399	Area 105	Tragelaphini
NMK.105.HC.03	ER 74 FS 376	Area 105	Tragelaphini
NMK.105.HC.02	ER 73 FS 648	Area 105	Tragelaphini
NMK.105.HC.01	ER 74 FS 342	Area 105	Tragelaphini

Table 9.7: Table of teeth (T) and horn cores (HC) from Area 105 that have been allocated to one of 13 bovid tribes, from fieldwork (FW) in the Turkana basin.

ID	Specimen Number	Site	Tribe Allocation
FW.105.T.23	FW 2008	Area 105	Antilopini
FW.105.T.22	FW 2008	Area 105	Antilopini
FW.105.T.21	FW 2008	Area 105	Alcelaphini
FW.105.T.20	FW 2008	Area 105	Alcelaphini
FW.105.T.19	FW 2008	Area 105	Alcelaphini
FW.105.T.18	FW 2008	Area 105	Tragelaphini
FW.105.T.17	FW 2008	Area 105	Reduncini
FW.105.T.16	FW 2008	Area 105	Tragelaphini
FW.105.T.15	FW 2008	Area 105	Alcelaphini
FW.105.T.14	FW 2008	Area 105	Antilopini
FW.105.T.13	FW 2008	Area 105	Antilopini
FW.105.T.12	FW 2008	Area 105	Alcelaphini
FW.105.T.11	FW 2008	Area 105	Alcelaphini
FW.105.T.10	FW 2008	Area 105	Alcelaphini
FW.105.T.09	FW 2008	Area 105	Bovini
FW.105.T.08	FW 2008	Area 105	Tragelaphini
FW.105.T.07	FW 2008	Area 105	Alcelaphini
FW.105.T.06	FW 2008	Area 105	Alcelaphini
FW.105.T.05	FW 2008	Area 105	Alcelaphini
FW.105.T.04	FW 2008	Area 105	Alcelaphini
FW.105.T.03	FW 2008	Area 105	Alcelaphini
FW.105.T.02	FW 2008	Area 105	Tragelaphini
FW.105.T.01	FW 2008	Area 105	Alcelaphini
FW.105.HC.03	FW 2008	Area 105	Reduncini
FW.105.HC.02	FW 2008	Area 105	Tragelaphini
FW.105.HC.01	FW 2008	Area 105	Tragelaphini

Table 9.8: Table of teeth (T) and horn cores (HC) from Area 108 that have been allocated to one of 13 bovid tribes, from both the National Museum of Kenya (NMK) and fieldwork (FW).

ID	Specimen Number	Site	Tribe Allocation
NMK.108.T.01	2119	FxJj10	Tragelaphini
NMK.108.T.02		FxJj10	Alcelaphini
FW.108.T.01	FW 2008	Area 108	Tragelaphini
FW.108.T.02	FW 2008	Area 108	Alcelaphini
FW.108.T.03	FW 2008	Area 108	Tragelaphini
FW.108.T.04	FW 2008	Area 108	Bovini
FW.108.T.05	FW 2008	Area 108	Alcelaphini
FW.108.T.06	FW 2008	Area 108	Reduncini
FW.108.T.07	FW 2008	Area 108	Alcelaphini
FW.108.T.08	FW 2008	Area 108	Alcelaphini
FW.108.T.09	FW 2008	Area 108	Alcelaphini
FW.108.T.10	FW 2008	Area 108	Alcelaphini
FW.108.T.11	Fw 2009	Area 108	Alcelaphini
FW.108.T.12	Fw 2009	Area 108	Antilopini
FW.108.T.13	Fw 2009	Area 108	Alcelaphini
FW.108.T.14	Fw 2009	Area 108	Alcelaphini
FW.108.H.01	FW 2009	Area 108	Tragelaphini

Table 9.9: Table of teeth (T) and horn cores (HC) from Area 130 that have been allocated to one of 13 bovid tribes, from the National Museum of Kenya (NMK).

ID	Specimen Number	Site	Tribe Allocation
NMK.130.T.01	183	FxJj83	Alcelaphini
NMK.130.T.02	25	FxJj38 SE	Antilopini
NMK.130.T.03	129	FxJj38 SE	Antilopini
NMK.130.T.04	4	FxJj38	Alcelaphini
NMK.130.T.05	10	FxJj38	Antilopini
NMK.130.T.06	17	FxJj38 F	Tragelaphini
NMK.130.T.07	122	FxJj81	Cephalophini
NMK.130.T.08	1315	FxJj82	Alcelaphini
NMK.130.T.09	182	FxJj82	Alcelaphini
NMK.130.T.10	1737	FxJj82	Alcelaphini
NMK.130.T.11	1305	FxJj82	Bovini
NMK.130.T.12	1609	FxJj82	Alcelaphini
NMK.130.T.13	1733	FxJj82	Hippotragini
NMK.130.T.14		FxJj 15	Tragelaphini
NMK.130.T.15		FxJj 15	Alcelaphini
NMK.130.HC.01		Area 130	Tragelaphini
NMK.130.HC.02	ER 74 FS 336	Area 130	Tragelaphini
NMK.130.HC.03	ER 73 FS 523	Area 131	Tragelaphini
NMK.130.HC.04	DF 924	Area 130	Bovini
NMK.130.HC.05	ER 73 FS 525	Area 131	Bovini
NMK.130.HC.06	ER 73 FS 48	Area 130	Alcelaphini
NMK.130.HC.07	DF 959	Area 130	Alcelaphini
NMK.130.HC.08	ER 75 FS 1198	Area 130	Alcelaphini
NMK.130.HC.09	ER 74 FS 633	Area 130	Alcelaphini
NMK.130.HC.10		Area 130	Neotragini
NMK.130.HC.11	DF 960	Area 130	Reduncini
NMK.130.HC.12	ER 74 FS 307	Area 131	Reduncini
NMK.130.HC.13	ER 74 FS 312	Area 130	Antilopini

Table 9.10: Table of teeth (T) from Area 130 that have been allocated to one of 13 bovid tribes, from fieldwork (FW) in the Turkana basin.

ID	Specimen Number	Site	Tribe Allocation
FW.130.T.01	FW 2008	Area 130	Antilopini
FW.130.T.02	FW 2008	Area 130	Antilopini
FW.130.T.03	FW 2008	Area 130	Antilopini
FW.130.T.04	FW 2008	Area 130	Antilopini
FW.130.T.05	FW 2008	Area 130	Alcelaphini
FW.130.T.06	FW 2008	Area 130	Alcelaphini
FW.130.T.07	FW 2008	Area 130	Alcelaphini
FW.130.T.08	FW 2008	Area 130	Alcelaphini
FW.130.T.09	FW 2008	Area 130	Alcelaphini
FW.130.T.10	FW 2008	Area 130	Alcelaphini
FW.130.T.11	FW 2008	Area 130	Alcelaphini
FW.130.T.12	FW 2008	Area 130	Alcelaphini
FW.130.T.13	FW 2008	Area 130	Alcelaphini
FW.130.T.14	FW 2008	Area 130	Alcelaphini
FW.130.T.15	FW 2008	Area 130	Alcelaphini
FW.130.T.16	FW 2008	Area 130	Alcelaphini
FW.130.T.17	FW 2008	Area 130	Hippotragini
FW.130.T.18	FW 2008	Area 130	Hippotragini
FW.130.T.19	FW 2008	Area 130	Alcelaphini
FW.130.T.20	FW 2008	Area 130	Antilopini
FW.130.T.21	FW 2008	Area 130	Alcelaphini
FW.130.T.22	FW 2008	Area 130	Alcelaphini
FW.130.T.23	FW 2008	Area 130	Alcelaphini
FW.130.T.24	FW 2008	Area 130	Antilopini
FW.130.T.25	FW 2008	Area 130	Alcelaphini
FW.130.T.26	FW 2008	Area 130	Alcelaphini
FW.130.T.27	FW 2008	Area 130	Hippotragini
FW.130.T.28	FW 2008	Area 130	Hippotragini
FW.130.T.29	FW 2008	Area 130	Alcelaphini
FW.130.T.30	FW 2008	Area 130	Alcelaphini
FW.130.T.31	FW 2008	Area 130	Tragelaphini
FW.130.T.32	FW 2008	Area 130	Alcelaphini
FW.130.T.33	FW 2008	Area 130	Alcelaphini