The Dietary Behaviour of Early Pleistocene Bovids from Cooper's Cave and Swartkrans, South Africa

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Declaration

I declare that this work is my own, unless indicated by author citations, and has not been submitted before for any other degree or examination at any other university. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg, South Africa.

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Abstract

There is ongoing speculation about how an increasingly arid environment contributed to the extinction of *Paranthropus robustus*, given that a mosaic landscape with a major part of the area consisting of predominantly open grassland environment accompanied by an escalating cooler drier climate remains the persistent palaeoecological reconstruction for this species. It has been suggested that *P. robustus*, a dietary specialist, was not able to adapt to an increasingly xeric habitat. This notion has been challenged by recent multi-disciplinary research on *P. robustus* remains, including stable light isotope and dental microwear analyses, which portray a more complex diet. *Paranthropus robustus* is present in a number of key fossil assemblages spanning the period ca. 1.8 to 1.0 Ma. Analysis of the stable carbon isotope composition of bioapatites and dental microwear texture analysis of different bovid taxa, associated with *P. robustus* remains from five discrete deposits, were used to reconstruct dietary behaviour and by inference availability of local resources.

The overall pattern emerging from the bovid data indicates a more mixed and varied diet than previously thought, suggesting a heterogeneous environment, and hence a less static ecological profile for *Paranthropus*. The significant occurrence of mixed diets and relatively few obligate C_4 grazers suggest that although C_4 grasses were available in a mosaic environment, a C_4-dominated ecosystem was not present. Swartkrans Member 2 (ca. 1.6 Ma) contains substantially more C_3 feeders than other *P. robustus* deposits, signifying a vegetation community structure that was more C_3-dominated than the other deposits. There is an apparent indication of shifting vegetation structure between

P. robustus deposits. Thus, despite its derived craniodental morphology, *P. robustus* seems to have thrived through a range of climatic and ecological shifts by selecting from a variety of available foods present on the landscape.

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Nomenclature Table

Aepyceros melampus (impala)	Ame
Antidorcas bondi	Ab
Antidorcas marsupialis (springbok)	Ama
Antidorcas recki	AR
Area scale of fractal complexity	*Asfc*
C_3 pathway (leaves, fruits, forbs, tubers, etc.)	C_3
C_4 pathway (grasses)	C_4
Connochaetes sp.	Csp
Connochaetes taurinus (blue wildebeest)	Ct
Cooper's D	CD
Damaliscus lunatus (tsessebe)	Dl
Damaliscus pygargus (blesbok)	Dp
Damaliscus sp.	Dsp
delta	δ
Dental microwear texture analysis	DMTA
Discriminant Function Analysis	DFA
Exact proportion length scale anisotropy of relief	*epLsar*
Fine texture fill volume	*Ftfv*
Gazella sp.	Gsp
Heterogeneity of area scale fractal complexity	*HAsfc*
Hippotragus niger (sable)	Hn
Hippotragus sp.	Hsp
Kobus leche (lechwe)	Kl
Kruger National Park	KNP
Litocranius walleri (gerenuk)	Lw
Makapania sp.	Masp
Makapansgat Member 3	MK M3
Megalotragus sp.	Mesp
Million years ago	Ma
Mixed feeder	Mixed C_3-C_4
Oreotragus oreotragus (klipspringer)	Oor
Oryx gazella (gemsbok)	Og
Ourebia ourebi (oribi)	Oou
Pelea capreolus (Grey rhebok)	Pc
per mil (parts per thousand)	‰
Principal Component Analysis	PCA
Rabaticeras porrocornutus	Rp
Raphicerus campestris (Steenbok)	Rc
Redunca arundinum (southern reedbuck)	Ra
Redunca fulvorufula (mountain reedbuck)	Rf

Scale of maximum complexity	*Smc*
Scale-sensitive fractal analysis	SSFA
Swartkrans Member 1 Hanging Remnant	SK HR
Swartkrans Member 1 Lower Bank	SK LB
Swartkrans Member 2	SK M2
Swartkrans Member 3	SK M3
Syncerus caffer (African buffalo)	Sc
Syncerus sp.	Ssp
Sterkfontein Member 4	ST M4
Texture fill volume	*Tfv*
Tragelaphus oryx (eland)	To
Tragelaphus sp.	Tsp
Tragelaphus strepsiceros (kudu)	Tst

Chapter 1. Introduction

Abundant and diverse faunal assemblages associated with *Paranthropus robustus* have been recovered from a series of dolomite-hosted caves in South Africa. These assemblages represent a broad time span between ca. 1.8 to 1.0 million years ago (Ma) (Vrba 1974, 1975, 1982; Brain 1993a; Brock et al. 1997; Delson 1988; Keyser et al. 2000; Thackeray et al. 2002; Herries et al. 2006; Adams et al. 2007; de Ruiter et al. 2009; Herries et al. 2009; Herries et al. 2010). Critical events in hominin evolution occur at this time: the appearance and extinction of *P. robustus*, geographic expansion of the genus *Homo* (Wood and Collard 1999, Wood and Richmond 2000); and behavioural complexity that is reflected in the development of Early Stone Age technology (Leakey 1970, 1971; Clark 1993; Kuman 1994; Plummer 2004; Roche et al. 2009), resource-specific bone tool utilization (Brain and Shipman 1993; Backwell and d'Errico 2008; d'Errico and Backwell 2009) and the first evidence of controlled use of fire in Swartkrans (Brain and Sillen 1988).

There is speculation concerning how much an increasingly arid habitat contributed to the extinction of *P. robustus* (Robinson 1963; Wood and Strait 2004; de Ruiter et al. 2008). The unique craniodental morphology of *P. robustus* and Scanning Electron Microscopy based microwear studies indicates a hominin specialized in consuming hard, brittle foods (Grine and Kay 1988). It has been suggested that as the environment became more xeric, *P. robustus,* a dietary specialist, was not able to adapt its behaviour to cope with the changing conditions (Robinson 1954, 1963). This has been challenged by Wood and Strait

(2004), who suggest that *P. robustus* exploited a wide variety of foods. Research on *P. robustus* dentition, including stable light isotopes (e.g. Lee-Thorp et al. 1994; 2000; Lee-Thorp and van der Merwe 1993; Sponheimer et al. 2005 a, b, 2006; Lee-Thorp et al. 2010), and microwear studies (Ungar and Grine 1991; Ungar et al. 2008; Scott et al. 2005), reveals a more complex and flexible diet than previously thought. A critical question thus remains –did the environment shape the behavioural adaptations of *P. robustus*? To begin addressing this question, I will use information from the species rich and abundant Bovidae assemblages associated with *P. robustus* in order to establish the environmental context. Reconstruction of past environments is based on the animals that inhabited them as they provide the most informative ecological clues. Since bovids are primary consumers, they are strongly linked to their habitats and their foraging behaviours may accordingly yield ecological insights. Specifically, their diets reflect resource availability, which in turn reflects types of vegetation on the landscape. Elucidation of bovid foraging behaviour and its inferred ecological characteristics can provide the interpretative framework in which to link possible evolutionary events. Reconstructing past ecosystems can provide a context in which to identify potential selective pressures placed on hominin morphology and behavioural adaptations.

1.1 Palaeodietary analyses

The importance of bovid dietary behaviour in the interpretation of palaeoecology has been established in numerous studies, and includes research on taxonomic (species) abundance (Vrba 1980, 1984, 1985, 1995, 2000; Bobe and Eck 2001;

Bobe et al. 2002; Alemseged 2003; Bobe and Behrensmeyer 2004; de Ruiter et al. 2008) and body mass (Demment and Van Soest 1985; Underwood 1983; Van Soest 1994, 1996; Reynolds 2007). These reconstructions rely heavily on taxonomic uniformitarianism. This method examines habitat characteristics based on the most closely related living taxon (Vrba 1977; Gentry 1978, 1985; Harris 1991) and resulting interpretations are based mainly on this analogy. Problems associated with this method are: (1) extinct forms may not have a modern counterpart; (2) some species are behaviourally flexible and may occupy a wide range of ecosystems; and (3) a species may change their habitat and dietary preferences through time (Sponheimer and Lee-Thorp 2003; Codron 2006).

Ecological morphology (Fortelius 1985; Janis 1988; Janis and Fortelius 1988; Kappelman 1984; Plummer and Bishop 1994; Solounias et al. 1995; Spencer 1995, 1997; Kappelman et al. 1997) and ecological diversity (Reed 1996, 1997, 1998, 2008, Reed and Rector 2007; Assefa et al. 2008) use a taxon-free approach. However, this approach requires standardization of modern ecosystems and their associated faunal community as well as assuming continuity in the composition of fossil communities (Kingston and Harrison 2007). Ultimately, these approaches involve weak chains of inferences. For example, ecomorphology is a product of behavioural adaptation and phylogeny, and when examined in a phylogenetic context, morphology may misrepresent behaviour (Sponheimer et al. 1999; Klein et al. 2010).

Another approach to interpreting dietary behaviour is mesowear. Mesowear is the result of attrition and abrasion on the tooth. This is based on the degree of wear observed on the buccal cutting edge of postcanine dentition

(Fortelius and Solounias 2000). For example, a diet high in abrasives results in low, rounded or blunt cusps, whereas less abrasion results in sharper cusps. Many studies have utilized this approach to reconstruct modern and palaeodiets of various bovid taxa (Fortelius and Solounias 2000; Franz-Odendaal 2002; Franz-Odendaal and Kaiser 2003; Schubert 2007). There are several concerns about the use of mesowear. It is subjective and may produce high interobserver errors, limiting its usefulness when comparisons are made between various researchers. Even within this kind of analysis, accuracy in diet classification is only as high as 75% (Fortelius and Solounias 2000).

Stable carbon isotope composition ($\delta^{13}C$) of bovid bioapatites provides direct dietary evidence, indicating the relative amounts of C_3 plants (trees, shrubs, forbs[1], temperate grasses) and C_4 plants (tropical grasses) consumed. The distinct carbon isotope difference between C_3 and C_4 plants is significant, and has been widely used for reconstructing dietary preference of and resource availability for both modern bovids (Vogel 1978; Cerling et al. 2003; Sponheimer et al. 2003; Codron 2006; Codron et al. 2007a, b) and fossil bovids (Lee-Thorp and van der Merwe 1993; Lee-Thorp 2000; Lee-Thorp et al. 2007; Sponheimer and Lee-Thorp 1999a; van der Merwe et al. 2003; Sponheimer and Lee-Thorp 2003; Sponheimer et al. 2003; Cerling et al. 1997a; Cerling and Harris 1999; Luyt 2001; Luyt and Lee-Thorp 2003; Codron 2006; Kingston and Harrison 2007; Plummer et al. 2009; White et al. 2009).

Though the use of stable isotopes is unbiased, and directly based on diet, its limitation is twofold. In the short term, small dietary changes (>20%

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[1] A broad-leaf herb that is not grass and is frequently associated with grasslands.

proportion of grass or browse) are dampened in signals from body tissues that integrate information over several months (Tieszen et al. 1983, Tieszen and Fagre 1993; Ambrose and Norr 1993; Ayliffe et al. 2004). Secondly, tooth enamel mineralization takes many months to complete, thus isotopic overprinting further attenuates the dietary signal (Balasse 2002; Passey and Cerling 2002). For instance, field observations indicate that the eland consumes a small portion of grass (Skinner and Chimimba 2005). Isotopically this would be masked by the predominance of browsing behaviour. Secondly, researchers may misinterpret dietary behaviour base solely on the isotopic signal. The $\delta^{13}C$ signature shows lechwe is a mixed feeder (Sponheimer et al. 2003), but field observations indicate this species is commonly a grazer (Skinner and Chimimba 2005). The mixed signature in this case may be related to the lechwe preference for grazing both C_4 grasses and C_3 sedges, which the dental microwear analysis may clarify.

As with stable carbon isotopes, dental microwear provides direct evidence of the diet of the consumer (Solounias et al. 1988; Teaford 1988a, b; Solounias and Moelleken 1993; Solounias and Hayek 1993; Rose and Ungar 1998; Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Schubert et al. 2006; Merceron et al. 2004 a, b, 2005 a, b, 2006; Merceron and Ungar 2005; Ungar et al. 2007). As the animal masticates, food particles leave distinctive microwear patterns (such as scratches and/or pits) on the dental occlusal surfaces. Dental microwear captures the last few days of dietary intake before death. This method is useful for capturing dietary information that would otherwise be masked by other techniques. For example, eland will graze to a small extent, and although the graze may not be picked up using stable carbon isotope analysis, microwear patterns may pick up the grazing aspect of their diet. The majority of specimens provide browsing signatures, but a few specimens may manifest a grazing signature.

Although discrepancies are revealed among the methods, this should not be taken to minimize one method over another. The best understanding of feeding ecology will be obtained if we consider the results provided by all methods and try to recognize possible causes that provoke contrasting results (Kingston and Harrison 2007). Researchers have noted that combined techniques with multiple proxies provide more detailed palaeodietary inferences, and robust palaeoenvironmental reconstructions (Solounias and Moelleken 1993; Sponheimer and Lee-Thorp 1999a).

The following two points should be considered when determining the appropriate combination of methods to determine diet. Firstly, the relationship of the different time scales involved should be established. It should utilize both long-term and short-term contexts of the dietary behaviour of a species. Long-term effects provide a general picture of the diet, whereas short-term effects may capture the diet versatility of the species or population (i.e. herd). Secondly, the methods should limit subjectivity and possible interobserver errors, these methods being based on quantitative analysis that provides repeatability, and hence results in a more robust interpretation of palaeoenvironments. Two such approaches involve using stable light isotopes (the long-term effect), and examining dental microwear texture analysis (the short-term effect). Reconstructing bovid dietary behaviour utilizing a dual proxy approach provides empirical data on dietary behaviour (Schubert et al. 2006). These empirical approaches are independent of inferences that are a major drawback of other techniques. Few studies have combined these approaches, especially for the South African bovid community.

While there has been proliferation of research on the feeding strategies of bovids, dietary behaviour of fossil taxa from *P. robustus* sites have hitherto not been examined. Furthermore, studies regarding diet variability across space and time are seldom documented (Codron 2006). Refining concepts about the relationship between diet and ecology requires study that rigorously addresses intraspecific variation (op. cit.) My research examines diet variability within bovid species and through the *P. robustus* sequence.

The palaeodiets of various bovid taxa from Cooper's Cave and Swartkrans is investigated. Bovids from five discrete deposits from these sites were analyzed (Cooper's D, and Swartkrans Member 1 Hanging Remnant and Lower Bank, Swartkrans Member 2 and Swartkrans Member 3). Both sites have *P. robustus* remains, and an abundant and diverse faunal assemblage with many bovid species represented. The fauna from these deposits represent the complete time range for *P. robustus* (ca. 1.8 to 1.0 Ma).

Much research has focused on reconstructing the palaeoecology of Swartkrans hominins using various fauna from Members 1 (Hanging Remnant and Lower Bank), 2 and 3. The dominant palaeoecological interpretation has been that of a mosaic landscape, with a major part of the area comprising of open and grassy ecosystems, as well as elements of woodland and riverine components accompanied these deposits a drier climate (Vrba 1975; 1980, 1985; Brain 1995; McKee 1991; Watson 1993; Avery 2001; Reed 1997; Reed and Rector 2007; Lee-Thorp et al. 2007; de Ruiter et al. 2008). Recent palaeoecological interpretations of Cooper's D, based only on taxonomic uniformitarianism, indicates a similar ecosystem as Swartkrans (de Ruiter et al. 2009).

This research is the first to combine dental microwear texture analysis with stable carbon isotope analysis in order to examine the dietary behaviour and diet versatility of several bovid taxa from five discrete *P. robustus* deposits.

1.2 Objectives

This research seeks to interpret the foraging strategies of fossil bovids and by inference, the vegetation structure in which *P. robustus* lived. The assumption is that food preferences of bovids are linked to ecological characteristics of the habitat. The specific aims of the research are:

1. To detail the foraging strategies of fossil bovids using stable carbon isotope analysis. This method is based on an extant baseline series of bovids collected from southern Africa. I have added two bovid species, *Oreotragus oreotragus* (klipspringer) and *Pelea capreolus* (grey rhebok) to the existing modern baseline given that they are common in the early Pleistocene South African assemblages. The resulting isotopic data will reflect the average and range of dietary behaviour. It is hypothesised that the dietary behaviour of fossil bovids from Cooper's D and Swartkrans is similar to that of their modern counterparts.
2. To use dental microwear texture analysis in order to determine the foraging behaviour of modern bovids and compare it to Cooper's D and Swartkrans fossil bovids. The unique combinations of microscopic

features on the occlusal surface of teeth should distinguish between diet categories and reveal unique diet differences between species. Because of the rapid turnover of microwear, it is expected that there should be more dietary variation in comparison to stable carbon isotope analysis and that microwear patterns for fossil bovids should be similar to those of modern counterparts.

3. To determine the vegetation structure of the environment that *P. robustus* occupied and if any changes to the ecosystem may have led to the extinction of *P. robustus*. It is expected that analysis of the dietary behaviour of bovids derived from these two techniques would show a grass-dominated ecosystem throughout the *P. robustus* sequence.

1.3 Thesis outline

In the following Chapter 2, I present a description of the geology, associated dates and, where possible, previously proposed palaeoecological reconstruction of Cooper's D and Swartkrans Members 1, 2 and 3. In Chapter 3, known foraging behaviours of extant bovids based on field observations and rumen content in the available literature is provided. Bovid species is discussed in terms of where they are found in southern Africa, the habitat(s) they prefer, habitat requirements and dietary behaviour. This information is used as a baseline for further comparisons with stable carbon isotopes and dental microwear texture analysis of modern bovids in the ensuing chapters. Components of the data are presented in a series of chapters, each addressing specific question(s). Chapters' 4 and 5 present results of stable carbon isotope analysis and dental microwear texture analysis respectively, each outline the principles behind the technique and my interpretations of the data. In Chapter 4, the isotope results are presented in two parts: (1) palaeodiet profile for modern and fossil bovids examined in the present study, and (2) palaeoecological profile using all available bovid taxa from each deposit. The palaeodiet profile examines the dietary behaviour of each fossil species in comparison to its modern counterpart or closely related taxa, and than by deposit. This helps to identify any temporal changes in dietary behaviour. The palaeoecological profile is identified for deposit using the dietary behaviour of bovids. The palaeoecological profiles are then used to examine potential ecological differences between deposits. Chapter 5 details the dental microwear texture analysis of both modern and fossil bovid taxa. Microwear data are then compared to the isotope data to examine similarities and differences. Due to the limited number of taxa represented in each deposit, palaeoecological profiles using just dental microwear texture analysis was not feasible. Chapter 6 presents the conclusion of the thesis in which the dietary reconstructions of bovids from Cooper's D and Swartkrans are compared by integrating the results from the stable carbon isotopes and dental texture microwear analysis. Finally, the implications of these results for palaeoecological reconstructions are discussed. Interpretation of the vegetation structure which *P. robustus* occupied is addressed as well as whether changes to the vegetation structure could have led to the extinction of *P. robustus*.

Chapter 2. Cooper’s Cave and Swartkrans

2.1 Introduction

This research involves two early Pleistocene hominin fossil sites from South Africa, Cooper’s Cave and Swartkrans (Figure 2.1). Together these sites include five deposits that span the known temporal range for *P. robustus*. A large faunal assemblage has been described from both sites. For each site, I here review briefly the geological structure and stratigraphy, the spatio-temporal context, previous ecological interpretations and taphonomy.

Cooper’s Cave and Swartkrans are located in dolomites of the Monte Cristo Formation (Malmani Subgroup, Transvaal Supergroup) that forms a karstic landscape with numerous infilled caves. Like most of the caves in the area, the two sites occur on the intersection of two fault lines that trend roughly East-West and North-South (Brain 1993a; Partridge 2000). Only two kilometres separate Cooper’s Cave from Swartkrans (Figure 2.1).

2.2 Cooper’s Cave

This is the first comprehensive site history review of Cooper’s Cave. The early history of Cooper’s Cave contains many unanswered questions regarding the provenance of the fossils collected prior to 1995. There are reports of fossil mammals being collected by Julius Staz and J.C. Middleton Shaw around Mr. Cooper’s farm in the early 1930s (Middleton Shaw 1937, 1939, 1940). On an annual tour of the Sterkfontein Caves in December 1938, dental students from the

University of the Witwatersrand, Johannesburg, took a leisurely walk across the landscape towards the newly found hominin site of Kromdraai (Phillip V. Tobias, personal communication). Along the way Julius Staz, Middleton Shaw's senior assistant, found an entrance to a cave with hundreds of blocks of stone excavated by miners. He proceeded to break open some blocks and in one, he found an upper third molar of a hominin (Middleton Shaw 1939, 1940). Middleton Shaw suggested that the tooth be provisionally unidentified, but later in the same article stated that the tooth presents 'an early African human type' (Middleton Shaw 1940). Subsequently, Broom and Schepers (1946) suggested that the features on the tooth aligned it closely with *Plesianthropus* (*Australopithecus*). Robinson's (1956, p. 97) reanalysis of the tooth came to the same conclusion. Unfortunately, the tooth is missing today. Robert Broom assigned the tooth a specimen number 'TM 1514'at the Transvaal Museum[2]. In the museum logbook, in a handwritten message next to the specimen number (in a different hand from Broom's and likely to be that of John Robinson) it is indicated that the specimen was moved to the Dental Museum at the University of the Witwatersrand, Johannesburg. Phillip V. Tobias last saw it in Julius Staz's office in the 1950's (personal communication).

After the tooth was found, Robert Broom and John Robinson periodically made trips to the farm to look for fossils in the miner's dump (C.K. Brain, personal communication).

For his doctoral thesis, C.K. Brain initiated a geological investigation of fossil-bearing caves in the Sterkfontein Valley. One of these sites was Cooper's

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[2] Recently changed to the Ditsong Museum in Pretoria.

Cave. With Robinson as a guide, the location of where the tooth was found was shown to Brain (C.K. Brain, personal communication). Brain assigned the location as ‘Cooper’s B’. He states that ‘a large volume of breccia was excavated and numerous loose mining blocks were broken up’ from this location, but that the cave was sterile of fossils (Brain 1958, p. 100). His field notes, however, indicates otherwise: ‘Daniel and Lobelo have not got any bone from the loose blocks of breccias on the surface above the Cooper’s ape-man site, so I started them breaking blocks underneath the overhang and we got several bones almost immediately, including the incisor of a porcupine’ (Brain field notes, 31 March 1955).

Brain’s investigations at Cooper’s Cave lasted for a few months between 1954 and 1955. On 31 March 1955, Brain indicates in his field notes that ‘another small site quite close to Cooper’s faunal site (Cooper’s B) yielded a number of isolated teeth in the decaying breccias on the surface; ‘two of these appear to be of *Simopithecus* (*Theropithecus*).’ It is most likely that these specimens came from Cooper’s A. A large sample of breccia from this locality and a limited sample from Cooper’s B were taken back to the Transvaal Museum for preparation (C.K. Brain, personal communication). At least prior to 1957, all specimens were labelled as ‘CO’ followed by a number and then a letter (e.g., CO 106B, CO 106C, CO 134D). Sometime after 1957, the specimens in the museum were relabelled as ‘COA’ through to ‘COE’ and even ‘KA2’. Peculiar was the ‘KA2’, some of which still had ‘CO’ labeled on them. The letter that precedes the number is probably unrelated to the provenance of the specimen. There is no record of where these specimens came from, or why the specimens were relabeled.

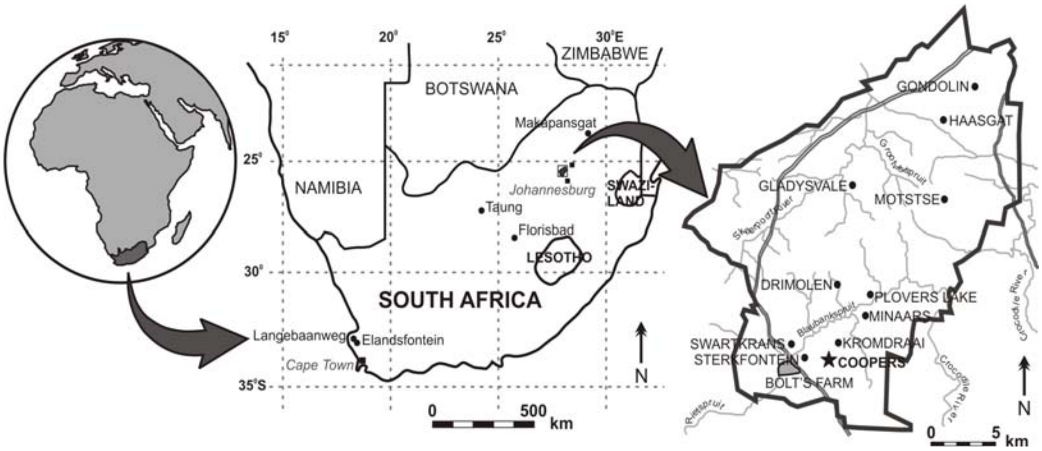

Figure 2.1. Map of early Pleistocene sites in South Africa (from de Ruiter et al. 2009).

Renewed interest in the site began in the early 1990s. During this time, Lee Berger and graduate students from the University of the Witwatersrand, Johannesburg, selected several fossiliferous mining blocks from the outer rim of Cooper's A and took them back to the university for preparation. In 1994 Martin Pickford found a central incisor of a hominin in the collections housed at the Transvaal Museum (Berger et al. 1995; de Ruiter et al. 2009).

In 1998, I was appointed by Lee Berger (then the site permit holder) to manage the excavations of Cooper's Cave. In order to understand the assemblage profile prior to excavation, I sorted through the collection, where I found a crushed partial face of *P. robustus* that had been misidentified as a pelvis (Steininger et al. 2008). Excavations at Cooper's A were carried out periodically between 1999 and 2001. Several faunal specimens were collected and accessioned at the Ditsong National Museum of Natural History labeled 'COA 1000' and up (removing any confusion between older and newer collections). Roughly 200 specimens have been collected from Cooper's A (Steininger in preparation). During an investigation of another deposit at Cooper's, I found an isolated *Metridiochoerus andrewsi*[3] tooth *in situ*. The tooth provided a last recorded appearance date of ca 1.6 Ma for this species and the area, which is now known as Cooper's D, was identified as a potentially new locality for future excavations.

In 2001, excavation work on the Cooper's D deposits began with the help of Duke University students. Within the first week, we were rewarded with a deciduous hominin tooth and several other faunal remains. Between 2003 and 2009, the permit for Cooper's Cave was held jointly by Lee Berger and the author. During this period, excavations concentrated on Cooper's D. The faunal assemblage proved to be species rich and abundant with hominin remains and early stone tools (Berger et al. 2003; de Ruiter et al. 2009). Thus far, *P. robustus* has been the only hominin species recovered from this deposit (Berger et. al 2003; de Ruiter et al. 2009). As of 2010, the sole permit holder of Cooper's Cave has been the author, Christine Steininger.

2.2.1 Geological context

An EDM laser theodolite was utilized to plot the north, east and height coordinates of all specimens excavated from 1999 onwards. The datum reference points follow the Gauss Conform System Lo27°. The Global Positioning System (GPS) location of Cooper's Cave is 26°00'46"S, 27°44'45"E. The excavations

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[3] Extinct species of pig, similar to modern warthog.

have focused on three spatially distinct localities (Cooper’s A, B, D), all of which preserve fossil-bearing calcified sediments (de Ruiter et al. 2009). Recently, Cooper’s D has been the focus of excavations, as this locality is abundant in fossils and species-rich. Another two localities near Cooper’s D with fossiliferous calcified clastic sediments have been identified, but to date these deposits have not been excavated.

Like other caves in the Witwatersrand area, Cooper's speleothems[4] (mainly flowstones and stalagmites) were mined for lime, which was used as a flux in the gold-mining industry, as well as an ingredient in fertilizer and toothpaste (Pickering, 2004). Piles of waste rock is still present on many sites. Recently published work on Cooper’s Cave has focused on Cooper's D, and has considered the palaeontology, chronology of chemical sediments and cave geology (sedimentology in particular) at macro-scale (Berger et al. 2003; de Ruiter et al. 2009).

The fauna of Cooper's D provided a biostratigraphic age of 1.6 to 1.9 Ma for Cooper's D (Berger et al. 2003). This was determined by correlating the faunal assemblage with the known assemblages at nearby deposits of Swartkrans and Kromdraai A and East African fossil sites.

Cooper’s Cave comprises two distinct episodes of fill that has been termed ‘Cooper's D east’ and ‘Cooper's D west’ (Figure 2.2), with Cooper's D west having smaller, finer grained and more fossiliferous deposits of the two (Berger et al. 2003; de Ruiter et al. 2009). Based on the faunal assemblage from the two deposits, Cooper’s D east and Cooper’s D west are contemporaneous (Berger et

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[4] Secondary mineral deposits formed in a cave. They are mainly composed of calcium carbonate ($CaCO_3$).

al. 2003; de Ruiter et al. 2009). The deposits in the east are characterized by a fining upward sequence of well-calcified massive sediments with abundant fossil bone, dolomite blocks up to 50cm diameter, as well as quartz (op. cit.) The clasts are dominantly stained with manganese oxides. The deposits in the west show some weak laminations and finer grain size, but are generally large and well-calcified (op. cit.)

There are three distinct facies, the classification based on abundance, degree of sorting and type of clasts and fossils (Figure 2.2). Facies A consists of a coarse-grained, relatively fossil-poor deposit. Facies B consists of finer grain sizes and is abundant in fossil bone, teeth and other clasts. A finely laminated, very fine-grained and fossil-rich deposit was defined as Facies C, this being particularly rich in microfossils and entirely devoid of large collapse dolomite blocks. The facies formed because of hydrodynamic sorting, where coarser grained material has accumulated near the two entrances, and the finer grained material (sediment and microfauna) has washed further into the cave. Detailed sedimentary analysis (at macro and micro-scale), the geochemistry and petrography of Cooper's Cave are currently in preparation for publication.

Uranium series yielded an age range of 1.413 Ma for the top of Cooper's D deposit and 1.526 ± 0.088 for the bottom (de Ruiter et al. 2009). Presently, the U-Pb dates for Cooper's D are the best-constrained dates of any *P. robustus* deposit.

2.2.2 Palaeoecological profile

The faunal assemblage composition of Cooper's D is species rich and abundant. Aside from the recovered hominin material, Cooper's is rich in carnivores, suids, bovids, cercopithecids and other mammals (Berger et al. 2003). Many species recovered at Cooper's Cave are uncommon for the early Pleistocene fossil assemblages in the Witwatersrand area (Berger et al. 2003). Recent faunal analysis based on taxonomic uniformitarianism suggests a mosaic environment (de Ruiter et al. 2009). The Alcelaphini, Antilopini, Reduncini, *Equus*, *Metridiochoerus* and *Theropithecus* indicate the presence of grass, while the *Sivatherium* and *Tragelaphus strepsiceros* suggest the presence of a woodland component. Comparable to other *P. robustus* sites, Cooper's D fauna suggest a drier mosaic palaeoenvironment with both grassland and woodland components present.

2.3 Swartkrans Members 1, 2 and 3

A comprehensive discussion of Swartkrans has been published in several articles and books (for an in-depth site history, see Brain 1993a). A brief discussion of the content is given here. Early work at Swartkrans was conducted by Robert Broom and John Robinson between 1948 and 1949 (Broom 1949; Broom and Robinson 1952). After Broom's death in 1951, Robinson continued excavations until 1953 (Brain 1993a). Some of the Swartkrans Hanging Remnant fossils were derived from a large block that was removed and processed (SKR specimens) and from *ex situ* specimens that were taken from the mining dumps (Brain 1981). It was during this time that most of the *P. robustus* and early *Homo* specimens

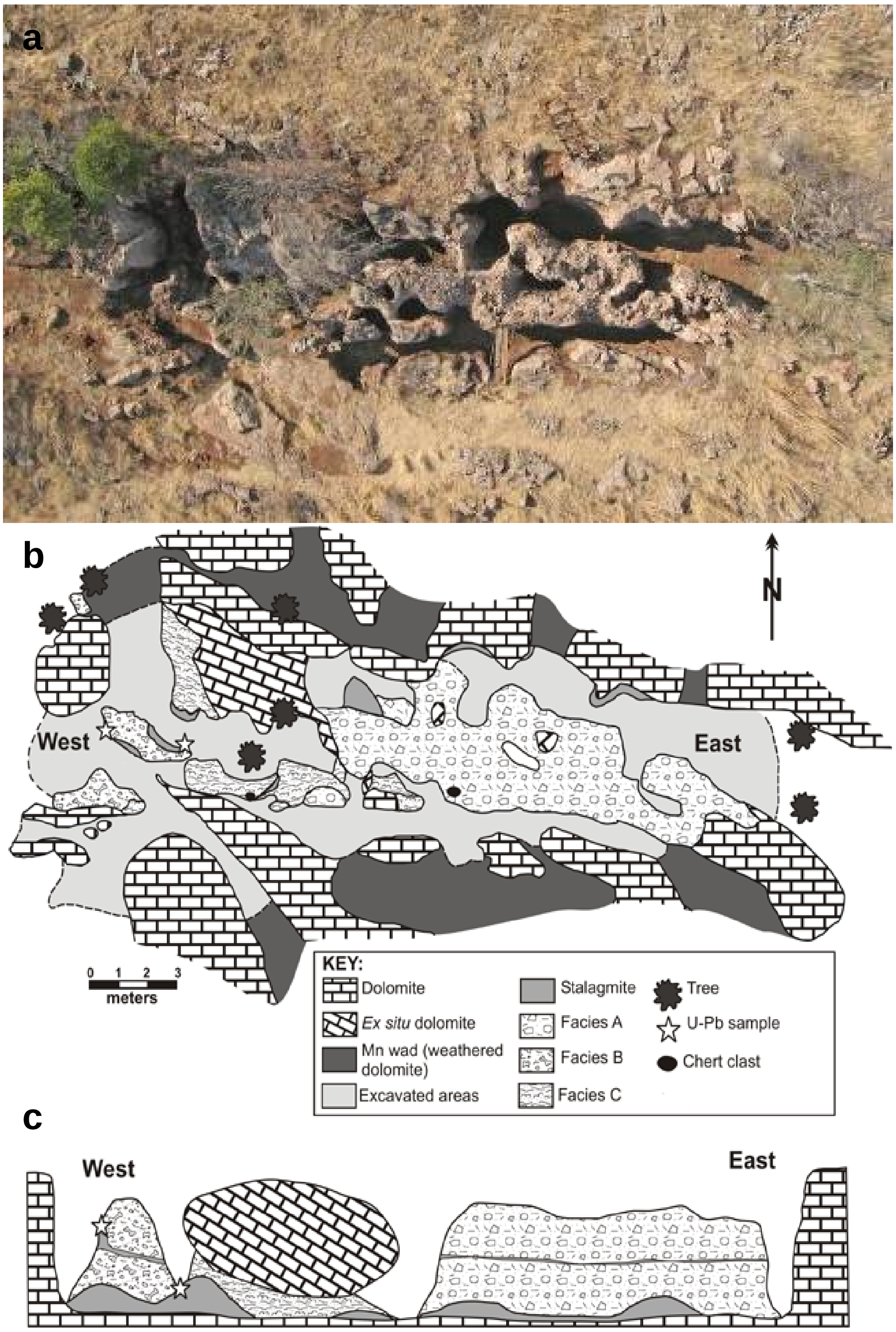

Figure 2.2. Cooper's D locality (a) aerial photograph, (b) Plane-table geological map and (c) simplified cross-section.

were recovered (Broom and Robinson 1952; Clarke et al. 1970; Clarke and Howell 1972; Clarke 1977). The site remained in a state of hiatus until C.K. Brain resumed excavations in 1965 (Brain 1993a). Subsequently, Brain's work at Swartkrans (1965 to 1986) has resulted in the recovery of numerous faunal and archeological samples from Swartkrans Member 1 Lower Bank, Member 2 and Member 3 (Brain 1981, 1993a). *Paranthropus robustus* was found at Swartkrans Members 1–3, while early *Homo* was found in Members 1 and 2. Stone tools have been found in all members, except the Hanging Remnant (Clark 1993; Field 1999). Bone tools have been found in Swartkrans Member 1 Lower Bank, Members 2 and 3, with small samples coming from the Hanging Remnant (Brain and Shipman 1993; Backwell and d'Errico 2001, 2003, 2008; d'Errico and Backwell 2009). It has been hypothesized that the bone and stone tools in the Hanging Remnant may have been reworked into the Lower Bank (Backwell and d'Errico 2003). Most of the Hanging Remnant material comes from the mining dumps that were collected and processed by Broom and Robinson. At the original cave entrance of Swartkrans Member 3, burnt bone was found, suggestive of the controlled use of fire (Brain and Sillen 1988; Brain 1993d).

In 2005 the Swartkrans Palaeoanthropological Research Project was initiated by C.K. Brain and Travis Pickering and excavations managed by Morris Sutton (Sutton et al. 2009). The focus of the project was to excavate Member 4 and the extension of Swartkrans Lower Bank (op. cit.) Several middle Stone Age tools have been recovered from Swartkrans Member 4. From the Lower Bank, several new hominin specimens were recovered along with an array of other faunal remains (op. cit.) Swartkrans Member 4 is not discussed here as it consists predominantly of Middle Stone Age artefacts (Brain 1993a; Sutton et al. 2009), or Swartkrans Member 5, which has been dated to 11,000 years BP (Brain 1993).

2.3.1 Geology

The current subdivisions of the Swartkrans formation into five members comes from the work done by Brain (1958, 1993b). This literature forms the basis of the following summary of Swartkrans Members 1–3. Members 4 and 5 are not discussed here, as they are much younger in age (ca. 110 and 11 Ka respectively) and are not included in this research.

Swartkrans Member 1

Member 1 Unit A has an approximately two-metre thick flowstone band, formed when the cave had a competent roof. In the southeast corner, the cave roof opened to the surface allowing surface sediments to deposit into a thirty-metre vertical shaft. The accumulation formed a steep talus cone consisting of a well-calcified clast-rich reddish-brown sandy matrix. This forms Member 1 Unit B, commonly known as the Lower Bank. According to Brain (1993a), this unit formed rapidly, within 20 thousand years. Member 1 Unit C or the Hanging Remnant accumulated in a new shaft opening near the north wall of the cave comprising a series of 20–40° dips of infill influxes separated by pale reddish brown, well-calcified sand silt with flowstone lenses.

Based on biostratigraphy, the Lower Bank was considered older than the Hanging Remnant, at approximately 1.7 Ma (Vrba 1985; Churcher and Watson 1993; de Ruiter 2003b), although some have suggested an even older date of 1.8

Ma (Brain 1995; Vrba 2000). Based on various faunal remains, Hanging Remnant has been biostratigraphically dated to 1.6 Ma (Vrba 1982, 1985; Delson 1984; Brain 1995; Berger et al. 2002; de Ruiter 2003b). Taken together, the fauna from Swartkrans Hanging Remnant and Lower Bank were estimated between 2.1 to 1.65 Ma. This is broadly supported by Electron Spin Resonance supplying an age of 2.0 Ma from hominin enamel and 1.4 Ma from bovid enamel (Curnoe et al. 2001), although one bovid tooth provided a date of 0.6 Ma. The author notes that the precise provenience of the bovid enamel is unknown and may have been eroded out of younger deposits (Curnoe et al. 2001; Herries et al. 2009). The first attempts of U-Pb dating of bovid enamel for Swartkrans Member 1 suggest a date of 2.0 ± 0.02 Ma (Albarède et al. 2006), which concurs with faunal dates.

According to Partridge (1973), cave openings occurred through an incision and widening of valleys during the erosional cycles. The possible date of the cavern opening can be determined using rates of cyclic nickpoint migration (op. cit.) Nickpoint migration suggests that the cave opened at 2.6 Ma (op. cit.) Speleothem samples from the bottom of Lower Bank to the top of Hanging Remnant were dated using uranium-lead, and are currently in preparation for publication (Robyn Pickering, personal communication).

Swartkrans Member 2

At the centre of the cave, an erosional period created a gap between the Hanging Remnant and Lower Bank. The gap was filled with a heavily calcified reddish-brown sand-silt matrix with the flowstone bands dividing subunits of calcified sediments into Member 2 (Partridge 2000). At roughly the same time, at the north end of the cave behind the Hanging Remnant, another small shaft opened to the surface and accumulated well-stratified subunits (op. cit.) The estimated ages based on the fauna are between 1.7 and 1.1 Ma (Brain 1995; Vrba 1995; Herries et al. 2009). Uranium series suggest an age between 1.65 and 1.07 Ma (Balter et al. 2008; see Herries et al. 2009).

Swartkrans Member 3

Swartkrans Member 3 consists of a six-metre-deep gully along the west wall of the cave that eroded into parts of Members 1 and 2. Based on faunal evidence, the age of this site has been reported as being anywhere from 1.5 to 0.7 Ma (Brain 1993b, 1995; Vrba 1995; Herries et al. 2009). Uranium series suggest an age of 1.04 and 0.61 Ma (Balter et al. 2008; see Herries et al. 2009).

2.3.2 Palaeoecological profile

Swartkrans Member 1

The majority of reconstructions for Swartkrans Member 1 combine Hanging Remnant and Lower Bank fauna to interpret two discrete members. Several reconstructions point to an open habitat with woodlands on the banks of a natural watercourse (Vrba 1975; Watson 1993; Lee-Thorp et al. 2007; Reed and Rector 2007; de Ruiter et al. 2008) and edaphic grasses[5] present (Reed 1997; Avery 2001). Based on taxonomic abundance, de Ruiter et al. (2008) suggest some 'underrepresentation of grassland taxa at Swartkrans Hanging Remnant', but concludes that the palaeoenvironments of all older members of Swartkrans are

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[5] These include grasses from seasonally flooded valley grasslands (Spencer 1997).

‘predominantly open grasslands’. Conversely, Benefit and McCrossin (1990) identified the palaeoecology as mesic, closed woodland.

Swartkrans Member 2

The reconstructed environment for Swartkrans Member 2 was considered similar to Member 1. According to several authors, however, there is an increase in grazing animals for this member (Vrba 1975; Reed 1997; Lee-Thorp et al. 2007).

Swartkrans Member 3

Only Reed (1997) considered a palaeohabitat for Swartkrans M3 separately. Based on the ecological diversity, she observed an increase in fresh-grass grazing animals and reconstructed Member 3 as open grassland with a river nearby supporting edaphic grasslands (Reed 1997).

2.4 Taphonomy

Most of the faunal assemblages that occur in cave deposits in South Africa were collected by multiple taphonomic agents (Brain 1981, 1993c; de Ruiter and Berger 2000; Pickering 2001; Newman 1993). Based on correspondence analysis, de Ruiter et al. (2009) have shown that carnivore-produced bone accumulations are broadly representative of animal communities and are reliable indicators of the surrounding environment (Behrensmeyer et al. 1979; Reed 1997; de Ruiter et al. 2008: Kuhn et al. 2010).

2.5 Bovids from Cooper's D and Swartkrans Members 1 – 3

Representative taxa of alcelaphini, antilopini, bovini, hippotragini, neotragini, ovibovini, peleini, reduncini and tragelaphini are found in all deposits (Table 2.1). In this study, ovibovini is represented by *Makapania* sp. and has been recovered from only Swartkrans Hanging Remnant.

2.6 Discussion

Though similar in composition, each cave deposit has its own unique complexity. The deposits are consistently homogeneous in terms of their bovid assemblage. The uranium series dates for Swartkrans Member 2 and Swartkrans Member 3 are similar to fauna dates. The infills represent temporally distinct units that were deposited later than Swartkrans Member 1. Swartkrans Member 1 is more problematic and may represent a series of depositional events. The younger ESR dates for Member 1 suggests intermixing from younger deposits, however, the provenience of the bovid enamel used to extract the ESR dates are questionable. *Paranthropus robustus* seems consistently associated with a mosaic landscape. Many reconstructions follow similar scenarios: open grassland, with a nearby riparian wooded area adjacent to the extensive water source that also supports edaphic grasses (Vrba 1975, 1985; McKee 1991; Watson 1993; Avery 2001; Reed 1997; de Ruiter et al. 2009; Reed and Rector 2007).

Table 2.1. Minimum number of individuals (MNI) of bovids recovered from Cooper's D and Swartkrans Members 1 (including Hanging Remnant and Lower Bank), 2 and 3.

Tribe	Taxa	CD	SK HR	SK LB	SK M2	SK M3
Alcelaphini	*Connochaetes* sp.	15	48	23	19	33
	Damaliscus sp.	7	18	7	29	17
	***Megalotragus* sp.**	5	7	3	4	4
	Rabaticeras porrocornutus	0	2	0	0	0
Antilopini	***Antidorcas bondi***	0	33	3	0	0
	Antidorcas marsupialis	18	0	13	19	28
	Antidorcas recki	12	12	0	3	5
	Gazella sp.	0	7	5	5	14
Bovini	*Syncerus* sp.	2	2	2	2	3
	***Pelorovis* sp.**	0	0	0	1	0
Hippotragini	*Hippotragus* sp.	5	2	0	9	3
	Hippotragus gigas	0	1	0	0	1
Neotragini	*Oreotragus oreotragus*	1	1	1	3	1
	Ourebia ourebi	0	0	0	3	0
	Raphicerus campestris	2	1	1	7	4
Ovibovini	***Makapania* sp.**	0	3	0	0	0
Reduncini	*Kobus leche*	0	0	0	1	1
	Redunca arundinum	0	1	0	0	0
	Redunca fulvorufula	2	0	0	0	0
Peleini	*Pelea* sp.	3	3	1	10	2
Tragelaphini	*Tragelaphus* sp. aff. *angasii*	0	0	0	1	0
	Tragelaphus oryx	0	0	0	1	2
	Tragelaphus scriptus	0	0	0	4	0
	Tragelaphus strepsiceros	7	7	0	6	2
	Tragelaphus sp.	2	0	0	1	0

For the majority of bovids, estimates of minimum number individuals (MNI) were from de Ruiter (2003a) and de Ruiter et al. (2008). Taxa in bold indicate extinct species.

Chapter 3. Profile of Modern Bovid Diets and Ecology

3.1 Introduction

Bovidae family is species rich and prominent on the African landscape. They are dietarily diverse across taxa, occupy a range of ecological niches and form an integral component of the animal community, making them suitable for reconstructing palaeoecology (Kappelman 1984; Vrba 1980, 1982, 1985; Shipman and Harris 1988; Harris 1991; Plummer and Bishop 1994; Reed 1997; Spencer 1997; Sponheimer et al. 1999). Modern bovid diets are often studied along a browser-grazer continuum. (Hofmann and Stewart 1972; Jarman 1974; Demment and Van Soest 1985; Janis 1988; Owen-Smith 1997; Reed 1996; Fortelius and Solounias 2000; Mendoza et al. 2002; Perez-Barberia et al. 2004; Merceron et al. 2004 a, b, 2005a, b). 'Browse' refers to the consumption of leaves, shoots and fruits, while 'graze' is primarily the consumption of various grasses. The browser-grazer continuum forms the basis for most distinctions of bovid dietary preferences.

3.2 History of bovid diets

Temporal changes in diet preferences have been observed in the fossil bovid record. Generally, browsing has been regarded as an ancestral condition, with transitions to grazing occurring in the Late Miocene (Janis et al. 1994, 2000; Perez-Barberia et al. 2001). The origins of Bovidae with brachydont dentition is dated back to the Middle Miocene, ca. 17 Ma, with the appearance of *Eotragus* sp. (Tribe: Boselaphini) found in Gebel Zelten, Lybia (Vrba 1995; Solounias 2007).

The emergence of grazing ungulates coincided with the expansion of the Grassland Biome (e.g., Coupland 1993; O'Connor and Bredenkamp 1997; see Mucina and Rutherford 2006), which became globally prominent in the Late Miocene (Cerling 1992; Cerling et al. 1997 a, b; Retallack 2001; Ségalen et al. 2007). During the grassland expansion in the Late Miocene in East Africa C_4 plants were an important part of the local ecosystem though they make up less than half of the total biomass (Cerling 1992). This theory is supported by the work of Ségalen et al. (2007) on pedogenic and biomineral carbonates, in which the authors suggest that C_4 plants were present at low-latitudes at ca. 7 to 8 Ma, later expanding to mid-latitudes. Interestingly, the appearance of Alcelaphini (5 Ma), a bovid tribe adapted to open habitats coincided with this expansion (Vrba 1995). By ca. 1.7 Ma, the cooling temperatures of the sea and land resulted in further xericification[6] (Marlow et al. 2000), allowing C_4 plants to become a dominant feature in the biomass (Cerling, 1992; Quinn et al. 2007; Hopley et al. 2007). At the same time, isotopic analyses for South African and East Africa suggest a greater C_4 component (Luyt 2001; Luyt and Lee-Thorp 2003; Lee-Thorp et al. 2007; Sponheimer and Lee-Thorp 2009; Plummer et al. 2009). Thus, temporal changes in the dietary behaviour of bovid taxa may provide evidence of local ecological changes (van der Merwe and Thackeray 1997; Kingston and Harrison 2007; Lee-Thorp et al. 2007; Plummer et al. 2009).

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[6] Extremely dry habitat

3.3 Profile of modern bovid diets and ecology

The review provided here is used as a baseline with which to compare in later chapters modern dietary behaviour with fossil forms. The bovid species selected represent eight tribes and 18 species, all found in southern Africa with the exception of the gerenuk. I have included the gerenuk to increase the number of browsers examined and because other researchers have included them for isotopic and microwear analysis. The bovids used in this research were chosen because of their varied dietary behaviours and habitat ranges, and because most have fossil counterparts that are found in the early Pleistocene fossil record.

The modern taxa examined consist of *Aepyceros melampus* (impala), *Antidorcas marsupialis* (springbok), *Connochaetes taurinus* (blue wildebeest), *Damaliscus lunatus* (tsessebe), *Damaliscus pygargus* (blesbok), *Hippotragus niger* (sable), *Kobus leche* (lechwe), *Litocranius walleri* (gerenuk), *Oreotragus oreotragus* (klipspringer), *Oryx gazella* (gemsbok), *Ourebia ourebi* (oribi), *Pelea capreolus* (grey rhebok), *Raphicerus campestris* (steenbok), *Redunca arundinum* (southern reedbuck), *Redunca fulvorufula* (mountain reedbuck), *Syncerus caffer* (African buffalo), *Tragelaphus oryx* (eland), and *Tragelaphus strepsiceros* (kudu). These bovids live in a wide range of biomes in South Africa: Fynbos, succulent Karoo, desert, Nama-Karoo, grassland, savanna, Albany thicket forest, Indian Ocean coastal belt, forests and azonal (Figure 3.1).

I present a synthesis of the dietary behaviour and ecology of modern bovids. The synopsis derives from a variety of literature based on field observations and stomach contents. Bovid species are presented in alphabetical order by tribe.

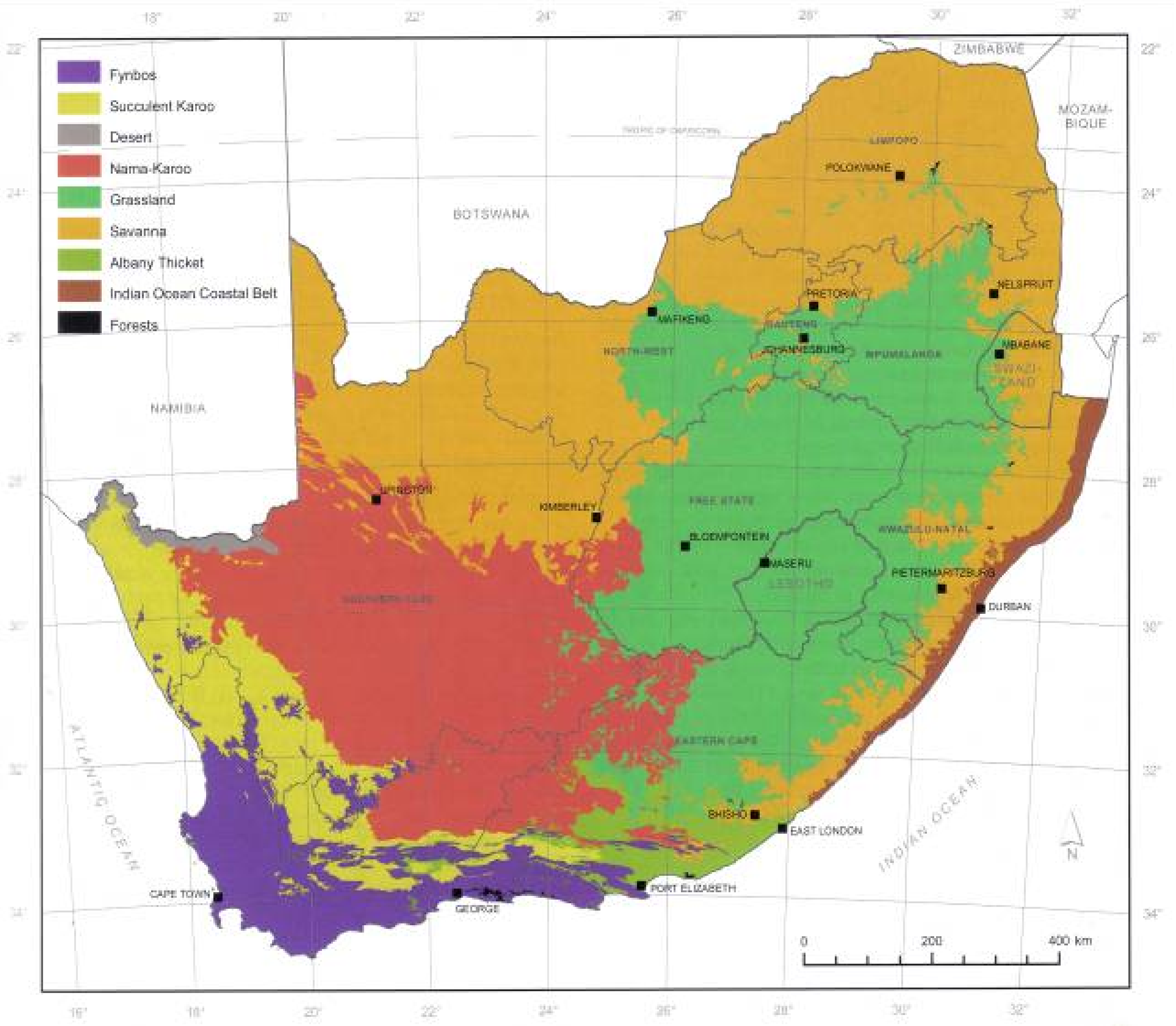

Figure 3.1. Biomes of South Africa (Mucina and Rutherford 2006).

3.3.1 Aepycerotini

Aepyceros melampus (impala)

This is the only modern species within the tribe Aepycerotini. The impala is distributed throughout the eastern woodland ecosystems of northeastern part of southern Africa. The species occurs on the ecotone of woodland and open grassland or on the floodplain (Skinner and Smithers 1990). In woodland habitats, impalas prefer light, open areas and low to medium grasses (Rowe-Rowe 1994). Cover and availability of surface water are essential habitat requirements (op. cit.) Impalas never venture a few kilometres from a water source they depend on daily (Young 1972). Their home range may increase depending on the region and seasonality (Murray 1982). Impalas are classified as mixed feeders (Hofmann 1973). During the wet season, they inhabit open grasslands and floodplains to feed on fresh grasses (Dunham 1980). During the dry season, they move to near riverines where grass is available, but their grass consumption decreases and the selection of eudicots[7] increases (op. cit.) If they are not close to a water source, they may obtain their moisture requirements from succulents (Skinner and Smithers 1990). Impalas have a catholic diet, which includes a variety of grasses and C_3 vegetation: forbs, twigs of shrubs or trees, fresh leaf buds, wild fruits and seedpods (Dunham 1980). Van Rooyen and Skinner (1989) found differences in diet between sexes, noting that females tend to select a greater amount of eudicots during pregnancy and lactation (op. cit.) Based on carbon isotope composition of faeces, impala individuals varied widely in the amount of grass they consumed on a monthly, seasonal, annual and regional scale (Codron 2006; Codron et al. 2006;

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[7] Flowering plants following Doyle and Hotton (1991).

Codron et al. 2007a, b). Impalas select foods – whether browse or graze – based on the quality of food available (Codron 2006; Codron et al. 2006). An increase in grass intake is related to the high crude protein and high energy levels found in the available grass (Codron 2006; Codron et al. 2006). The selective nature and variability of consumed plant species for this species illustrates complexity of dietary behaviour.

3.3.2 Alcelaphini

***Connochaetes taurinus* (blue wildebeest)**

This species was widely distributed throughout southern Africa in the past. Currently, this species is restricted to the savannas of the Limpopo and Mpumalanga provinces of South Africa (Skinner and Smithers 1990). Shade and water are habitat requirements with a preference for short grasses (no more than 100 to 150 mm high). The blue wildebeest are known to consume small portions of eudicots and fruit (Skinner and Smithers 1990). They are migratory and will travel large distances during the rainy season in search of patches of fresh, short grass. Skinner and Smithers (1990) have noted their sensitivity to localized rainstorms and that they will move several kilometres towards an oncoming storm in search of fresh grazing. Blue wildebeest select different species of grass depending on the season and locality. Hypsodont dentition, wide blunt snout morphology and physiology of the digestive system of the blue wildebeest are well adapted for consuming short grasses in bulk quantities (Estes 1991; Skinner and Smithers 1990).

***Damaliscus lunatus* (tsessebe)**

This species was once widespread throughout Africa. In South Africa, it is today found in the Limpopo, North-West, Mpumalanga and Northern Cape provinces. Tsessebe require grass, water and shade. During the dry season, they prefer the floodplains where palatable grass is plentiful, but during the wet season, they tend to move out into open woodland habitats. Their highest densities are found in hydromorphic[8] grasslands (Garstang 1982). The tsessebe are exclusive grazers (Skinner and Smithers 1990).

***Damaliscus pygargus* (blesbok)**

Blesbok and bontebok are endemic to southern Africa. Once considered two separate species, genetic evidence now groups them into one species, *Damaliscus pygargus* (Kumamoto et al. 1996). Many zoologists still recognize two subspecies based on their colour pattern, *D. p. pygargus* (bontebok) and *D. p. phillipsi* (blesbok) (Fabricius et al. 1989). I treat them as one species here and use the common name of 'blesbok'. Once numbered in the thousands, blesbok are now restricted to game reserves in the highveld plateau grasslands, near water sources (Skinner and Chimimba 2005). They are water dependent, requiring it daily in the morning and afternoon (op. cit.) Their habitat tolerances are wide ranging from grassland, savanna and Nama-Karoo biomes. They are associated with short to medium length grasses (Van Zyl 1965; David, 1973; Rowe-Rowe 1983). Blesbok are variable grazers preferring fresh grass. On rare occasions, they have been seen

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[8] The presence of excess water all or part of the time.

to browse (Van Zyl 1965). Although they prefer sweetveld grasses, they are known to select sourveld grasses during the dry season (Estes 1991).

3.3.3 Antilopini

***Antidorcas marsupialis* (springbok)**

The southern Africa endemic springbok is found in the Free State, Northern Cape, Eastern Cape and Western Cape provinces (Skinner and Chimimba 2005). Recently, this species was introduced into KwaZulu-Natal and the Limpopo provinces (op. cit.) Springbok are mainly found in arid regions of the desert, succulent Karoo, Nama-Karoo and in the savanna and grassland biomes. Springbok are mixed feeders with an inclination to select leaves and fruit when available (Hofmann and Stewart 1972). In areas where summer is hot and raining, they consume sprouting fresh grass, herbs and melons (Hofmann and Stewart 1972). In areas where the winters are cool and dry, they consume karroid and other shrubs, leaves of select trees, roots, tubers and succulents (op. cit.) They are also known to consume pods and fruit (Skinner and Smithers 1990). There are dietary differences between the sexes: rams utilize less nutrient plants than females or their young (Davies et al. 1986). Dreyer's (1987) thesis notes that the springbok is not dependent on water, but will drink up to three litres every day when available (as cited by Skinner and Chimimba 2005). In dry areas, they dig up roots and tubers to obtain their moisture quota (Williamson 1987). They have wide habitat tolerances in arid regions and may vary their diet depending on wet and dry seasons (Liversidge 1970).

***Litocranius walleri* (gerenuk)**

This species range is bounded by the western wall of the Rift Valley in Ethiopia, Somalia and Kenya (Estes 1991) and typically inhabits semiarid bush (op. cit.) The gerenuk avoids open savanna, preferring habitats with woody vegetation (op. cit.) They feed only on C_3 vegetation: leaves, shoots, flowers, lianas and fruits (Leuthold 1978). During the wet season, they prefer new leaves of deciduous trees. In the dry season they feed on evergreen scrub and trees (Estes 1991).

3.3.4 Bovini

***Syncerus caffer* (African buffalo)**

This is the only African species belonging to the Bovini tribe (Gentry 1992). It is found in the Limpopo, Mpumalanga and KwaZulu-Natal provinces and in a small coastal area in the Eastern Cape, South Africa. Currently, they occupy the savanna and Indian Ocean coastal biomes. Their habitat requirements include plenty of grass, cover for shade and water (Skinner and Chimimba 2005). Buffaloes require water twice a day and will graze near it (Skinner and Smithers 1990), generally favouring mixed tree savannas in the summer and riverine habitats in the winter (Funston 1992). Open grasslands and floodplains are only utilized for transit (Skinner and Chimimba 2005). In Central and East Africa, they occupy swamps and floodplains. They are found in the montane grasslands and forests of major mountains (Estes 1991). Classified as a grazer, they feed on old tall grass and are less partial to fresh grass than other grazers (Hofmann 1973; Skinner and Smithers 1990). Buffaloes can digest fibrous food more efficiently than other bovids (op. cit.) Their grazing on older coarse grasses thereby reduces grasslands to heights preferred by other grazers (Estes 1991). They have been observed browsing, but this is rare and usually only when grass is scarce or of poor quality (Skinner and Smithers 1990).

3.3.5 Hippotragini

***Hippotragus niger* (sable)**

Historically the sable range included the North-West and Mpumalanga provinces. They are now restricted to the savanna biome of the Limpopo province. Sable prefers open woodland for shade and nearby grassland for food and lives in close proximity to a water source (Skinner and Chimimba 2005). They are predominately grazers, preferring fresh grass, but will also feed on dry grasses. Their preferred grazing height is between 40 to 140 mm, but they have been observed (rarely) consuming grasses up to 300 mm high (Grobler 1981). In winter, sable will browse to a small extent on forbs, leaves and fruits (Wilson and Hirst 1977; Grobler 1981). Estes (1991) notes that browse make-up 20% of their diet, and they should be classified as a variable grazer (Gagnon and Chew 2000). Field observations have shown that some individuals chew bones to supplement their calcium and phosphorus requirements (Sekulic and Estes 1977).

***Oryx gazella* (gemsbok)**

The species is distributed in the arid regions of the Nama-Karoo and desert biomes of the Northern Cape, Western Cape, Eastern Cape and the Free State provinces and distributed in the savanna biome of the Northern Cape, North-West and Limpopo provinces. The habitat requirements for this species include arid open areas: open grassland, open bush and open woodland. The gemsbok consume a large variety of food, preferring green grass, but are capable of browsing when grass is minimal (Dieckmann 1980) and require a minimum of 2.5 litres of water per day (Taylor 1968; Knight 1995). In arid areas, roots, bulbs, tubers, wild melons and cucumbers are favoured fulfilling their moisture requirements (Dieckmann 1980; Williamson 1987). Reissig's (1995) study showed that gemsbok have adapted mechanisms to retain most of their body water (as cited in Skinner and Chimimba 2005), and are well suited to hot, dry habitats (Skinner and Chimimba 2005).

3.3.6 Neotragini

***Oreotragus oreotragus* (klipspringer)**

Klipspringer occurs throughout most of the South African provinces, except for Gauteng. They are also found in every type of biome, except for forests. They favour rocky habitats and have been known to travel up to 10 km on open flat terrain between rocky outcrops (Wilson and Child 1965). Klipspringers are adapted to extreme elevations and temperatures, and are predominately browsers (Norton 1984). On rare occasions, some individuals may consume grass, but this represents only a small departure from their normal diet since they have little capacity for digesting cellulose (Dunbar and Dunbar 1974; Norton 1984). Among the browse items consumed are leaves, berries, fruits, seedpods, flowers, herbs and young shoots (Wilson and Child 1965; Norton 1984). They are capable of standing on their hind limbs to browse at heights of 1.2 metres (Kok and van Wyk 1982). They have also been observed to climb trees up to 5.4 m to browse (op.

cit.) They can live relatively independently of water, but when seasonally available they will drink (Skinner and Chimimba 2005).

Ourebia ourebi **(oribi)**

Oribi are associated with open habitats (Skinner and Chimimba 2005). In South Africa, they are found in small patches of open savanna in KwaZulu-Natal and in the grassland biome of the Limpopo, Mpumalanga, Free State and Eastern Cape provinces (op. cit.) They have specific habitat requirements that include short grass for food and tall grass for shade (Perrin and Everett 1992). They also have specific topography requirements; preferring ridge terraces inclined less than 10° on the northern and eastern sides of terraces (Rowe-Rowe 1983). The oribi is predominately a grass feeder preferring fresh shoots in burnt areas (Shackleton and Walker 1985; Everett et al 1991, 1992). Reilly et al. (1990) noted that oribi select certain forbs during the South African summer months. They are not dependent on water and obtain most of their moisture requirements through food (Skinner and Chimimba 2005).

Raphicerus campestris **(steenbok)**

Steenbok are found in the various biomes of the nine provinces of South Africa and have few habitat requirements, among them open areas with some shade in the form of tall grasses, bush or scrub (Skinner and Chimimba 2005). This species favours ecologically unstable low rainfall conditions, and benefit from the destruction of woodland by other animals, (Estes 1991). Based on gut morphology and stomach contents, steenbok are mixed feeders (Hofmann 1973), consuming a wide variety of resources: forbs, leaves, shoots of low scrubs and trees, creepers, lianas, seeds, seedpods, berries, fruits and fresh grass (Smithers 1971; du Toit 1993), with forbs making up the bulk of their dietary intake (du Toit 1993). Depending on the location, they will consume grass in varying degrees, up to 66% particularly after rains (Smithers 1971; Hofmann 1973). Because of their gut morphology, they are unlikely to subsist on grass alone (Hofmann 1973). They are also known to select succulents and dig for roots and tubers in extremely dry environments (Skinner and Chimimba 2005). Steenbok will drink when water is available, but are not dependent on it (op. cit.)

3.3.7 Peleini

Pelea capreolus (grey rhebok)

Pocock (1910) originally classified this species as Reduncini (as cited in Skinner and Chimimba 2005) and then reclassified by Gentry (1978) as Caprini. Currently, the grey rhebok falls into a distinct subfamily, Peleinea (Spinage 1986) and tribe Peleini (Vrba 1985). It is the only South African species represented in this tribe. Grey rhebok are endemic to South Africa and are widely distributed throughout the region (Skinner and Chimimba 2005). They frequent rocky terrain in open areas and prefer good grass coverage in these areas. They are not water dependent (Skinner and Chimimba 2005). According to field observations, grey rhebok are mostly browsers that feed on leaves, forbs and green shoots (Ferreira and Bigalke 1987; Beukes 1988).

3.3.8 Reduncini

***Kobus leche* (lechwe)**

In the southern African subregion, lechwe occur in northern Namibia and Botswana near floodplains. They are water adapted with specialized habitat requirements of permanent water nearby, usually on shallow floodplains that border swamps, rivers or lakes adjacent to terrestrial plant communities (Williamson 1979). They feed on grasses, sedges and eudicots, preferring new plant growth. They are known to feed on grasses and sedges in water up to their bellies or shoulders (op. cit.) During cool dry weather, they are not dependent on water, but during dry hot weather, they will drink up to three times per day (Williamson 1979; see Skinner and Smithers 1990).

***Redunca arundinum* (southern reedbuck)**

They are found in Limpopo, Kwa-Zulu Natal, Mpumalanga, Free State and Eastern Cape provinces of the eastern parts of South Africa, and in Swaziland. The biomes where they are found consist of the savanna, grassland and Indian Ocean coastal belt. Essentially this species requires cover and a nearby water supply – water is a daily requirement. The greatest numbers are observed in floodplains, but in drier areas, grasslands near permanent water are also a known habitat (Skinner and Chimimba 2005; Estes 1991). Observations on the feeding behaviour of reedbuck indicate that they are predominately grazers that feed on various types of grasses, but also reeds. In limited quantities, they will feed on forbs or browse when the nutritional value of grass is low during the dry months.

***Redunca fulvorufula* (mountain reedbuck)**

Once found throughout southern Africa the species is currently restricted to the eastern parts of the region. Mountain reedbuck is found in the Limpopo, North-West, Gauteng, Mpumalanga, Free State, KwaZulu-Natal, Eastern Cape and Western Cape provinces. They occur in the grassland and savanna biomes. As a testament to their colloquial name, mountain reedbuck are found on grass covered hills and mountains, preferring lower altitude areas of southern-facing slopes that are moister and cooler (Rowe-Rowe 1983). They will venture into flatter terrain only to feed and drink. Mountain reedbucks are able to digest coarse low-quality grass efficiently, but prefer fresh grass (Hofmann and Stewart, 1972). They are exclusive grazers that select different species of grass depending on the season (op. cit.)

3.3.9 Tragelaphini

***Tragelaphus oryx* (eland)**

Commonly known as *Taurotragus oryx*, new mtDNA evidence places the eland in the genus *Tragelaphus* (Gatesy et al. 1997; Matthee and Robinson 1999). Eland are widely distributed in a variety of habitats, which include the Nama-Karoo, succulent Karoo, fynbos, grassland and savanna biomes of the North-West, Northern Cape, Limpopo, KwaZulu-Natal and Western Cape provinces (Skinner and Chimimba 2005). They are found in low and high altitudes (Estes 1991), avoiding deserts and dense forests (op. cit.) Eland are well adapted to arid habitats, versatile in their ability to select different types of foods and independent of water (Posselt 1963). They are mixed feeders (Hofmann 1989), but in some areas, they may browse extensively (Hillman 1979). Although some observers have noted they are primarily browsers (Estes 1991). During the wet season, they may consume from 50% to 80% grass of their total dietary intake (Hillman 1979). They consume a variety of plants: leaves, seedpods, seeds, forbs, tubers, fruits and fresh grass (Hofmeyr 1970; Estes 1991).

***Tragelaphus strepsiceros* (kudu)**

In South Africa, the kudu have a patchy distribution in the savanna, Nama-Karoo and grassland biomes of the North-West, Gauteng, Mpumalanga, Limpopo, KwaZulu-Natal, Free State and Northern Cape provinces. Their habitat requirements include the presence of woodland or scrub and they prefer broken rocky terrain (Skinner and Chimimba 2005). The species is considered a browser (Hofmann 1989), consuming a wide variety of resources: leaves, shoots, seedpods, forbs, herbs, fallen fruits, succulents, vines, tubers, flowers and some fresh grass. Grass consumption increases after rains (Du Plessis and Skinner 1987).

3.4 Discussion

Bovids show a remarkably high diversity and abundance in the modern ecosystems. They are found in varied habitats, ranging from forest to desert environments, and show a remarkable versatility in diet behaviour. Based on modern observations, stomach contents and faeces, some bovids may alternate their diet depending on their sex, food seasonality and spatial distribution of resources. Some are specialized feeders selecting only one type of food source such as grass. Other may have preferences, for example browse, but may also select grass when seasonally available. Yet others will select a wide range of vegetation. There tends to be a pattern in choice of diet reflecting availability and by inference vegetation structure.

The relatively high abundance of bovids compared to other faunal remains in fossil assemblages, and their association with early hominins make them an essential component for inferring the ecological context in which early hominins lived.

Chapter 4. Stable Carbon Isotopes

4.1 Introduction

The stable carbon isotope composition of modern and fossil herbivore tooth enamel is directly related to the isotopic composition of terrestrial plants in the food web (DeNiro and Epstein 1978; Tiezsen et al. 1983; Ambrose and DeNiro 1986; Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999; Cerling et al. 2003; Sponheimer et al. 2003). Plants using different photosynthetic pathways under varying climatic and environmental conditions are differentiated by the ratios of two naturally occurring stable isotopes of carbon, ^{12}C and ^{13}C. These isotopic differences in plants are passed on to the consumer and can be analyzed to reveal dominant dietary sources. Atmospheric CO_2 contains roughly 1.1% of the nonradioactive isotope ^{13}C and 98.9% of ^{12}C. In the last 200 years of industrialization, the $\delta^{13}C$ value of atmospheric CO_2 has become 1.5‰ lighter, depleted from -6.5‰ to -8.0‰ (Friedli et al.1986; Marino and McElroy 1991; Marino et al. 1992).

In plants, the stable carbon isotopes are fractionated by photosynthesis. The $^{13}C/^{12}C$ isotopic ratios of plants decrease relative to atmospheric isotopic ratios (Bender 1971). The lighter isotope is preferentially used because of the physical and chemical properties associated with its mass (O'Leary 1988). Plants utilize three different types of metabolic pathways to process carbon. These pathways are: (1) the C_4 pathway (the Hatch-Slack cycle) where the dicarboxylic acid utilizes CO_2 through carboxylation of phosphoenolpyruvate and forms a four-molecule carbon (O'Leary 1988). (2) In the C_3 pathway (the Calvin-Benson cycle), the first phase of photosynthesis, the phosphoglyceric acid utilizes CO_2 through the enzyme ribulose biphosphate carboxylase to fix CO_2, forming a three-molecule carbon (O'Leary 1988). (3) The Crassulacean Acid Metabolism (CAM) pathway also uses ribulose biphosphate carboxylase to take in CO_2, but in the last phase, the process is similar to the C_4 pathway (Bender 1971; O'Leary 1988).

4.2 Stable carbon isotope variation in the African ecosystems

4.2.1 C_3 pathway

In the African ecosystem, the C_3 pathway is characteristic of trees, forbs, shrubs, flowers, and some species of sedges, as well as, high altitude grasses that grow in cool wet seasons. Various researchers report different C_3 plants values. In one study, C_3 plants ranged from -35 to -22‰ with a mean $\delta^{13}C$ of -26.5‰ (Smith and Epstein 1971). In other studies, C_3 plants ranged from -32 to -20‰ with a mean value of -27.1‰ (Deines 1980; O'Leary 1981, 1988; Farquhar et al. 1982, 1989).

Variability in $\delta^{13}C$ values reflect the dynamics of a particular environment. The $\delta^{13}C$ value of C_3 plants in closed canopy habitats with low light and high humidity and where the exchange of atmospheric CO_2 is limited, tend to be more negative (Medina and Minchin 1980; Sternberg et al. 1989; van der Merwe and Medina 1989, 1991). The C_3 plants in open, arid and hot environments are less negative; this is also the case for C_3 plants at higher elevations (Tieszen et al. 1979; Körner et al. 1991; Sparks and Ehleringer 1997).

4.2.2 CAM pathway

The CAM plants consist primarily of desert succulents (O'Leary 1988) and are common in the Fynbos biome (Jones et al. 2003). CAM plants have a range of -10 to -20‰, which distinguishes them from C_3 plants, but not C_4 plants (O' Leary 1988).

4.2.3 C_4 pathway

C_4 plants are characteristically found in warm, arid environments. C_4 plants include tropical grasses, some sedge species, and some fruits and vegetables (O'Leary 1988). C_4 plants have $\delta^{13}C$ values ranging from -17 to -9‰ with a mean of -13.1 ± 1.2 (O'Leary 1988). There are two main C_4 subpathways based on plant anatomy and the biochemical pathways of the plant. The arid-adapted C_4 species utilize the NAD-me and PEP-ck subpathway (Hattersley 1982; Chapman 1996), with an average $\delta^{13}C$ value of −13.0 ± 0.7‰ (Cerling et al. 2003). The third, the NADP subpathway, is found in mesic environments, such as riparian or lake margin setting, and has an average $\delta^{13}C$ of −11.8 ± 0.2‰ (Cerling et al. 2003).

When herbivores consume plants, the carbon isotopes are fractionated once again. By determining the fractionation factor of the consumer, the carbon isotopic signature can be used to determine the dietary pattern, in terms of C_3 and C_4 consumption (DeNiro and Epstein 1978; van der Merwe 1982).

Stable carbon isotope analyses of bone collagen were first used in archaeology to determine the diets of Holocene humans and animals (van der Merwe and Vogel, 1978; DeNiro and Epstein 1978; van der Merwe 1982; Ambrose and DeNiro 1986). Bone collagen is composed of carbonated hydroxyapatite (akin to, but not identical) $Ca_{10}(PO_4)_6(OH)_2$ with structural carbonate that is susceptible to alteration (Lee-Thorp 2000). Because of isotopic exchange during diagenesis, the bones may increase in precipitation and absorb ions from their surrounding deposits that tend to increase reactivity and solubility (Driessen et al. 1978; LeGeros 1991; Lee-Thorp 2000).

Enamel is roughly 96% inorganic by weight, is comprised of greater than 95% hydroxyapatite, and has low porosity compared to bone. Because of these factors, the recrystallization and crystal growth is low during diagenesis. Because enamel remains relatively stable, it is less susceptible to diagenesis and can maintain its isotopic signature for millions of years (Lee-Thorp and van der Merwe 1987; Quade et al. 1992; Wang and Cerling, 1994; Koch et al. 1997; Sponheimer and Lee-Thorp 1999b). Thus, enamel retains the original biogenic signal reflecting the diet of the consumer. This has implications for not only interpreting modern and ancient diets of bovids (Vogel 1978, van der Merwe and Thackeray 1997; Lee-Thorp and van der Merwe 1993; Lee-Thorp et al. 1994; Cerling and Harris 1999; Cerling et al. 2003; Lee-Thorp et al. 2000; Sponheimer and Lee-Thorp 1999a; Sponheimer et al. 1999; Sponheimer et al. 2003; Sponheimer and Lee-Thorp 2003), but also using diets to measure shifts in C_3 and C_4 biomass of modern and ancient environments (Cerling and Harris 1999; Sponheimer et al. 1999; Luyt 2001; Franz-Odendaal et al. 2002; van der Merwe et al. 2003; Lee-Thorp and Sponheimer 2005; Kingston and Harrison 2007; Lee-Thorp et al. 2007).

Several values have been reported for the ^{13}C enrichment factors for dietary carbon and bioapatite carbonate for bovids, ranging from 14.6‰ (Passey et al. 2005), 14.1‰ (Bocherens and Mariotti 1992; Cerling and Harris 1999), and 13.7‰ (Balasse 2002) to 12-13‰ (Krueger and Sullivan 1984; Lee-Thorp and van der Merwe 1987). These various reported enrichment factors make little difference in the $\delta^{13}C$ distinction between C_3 and C_4 consumers since the bioapatite-diet spacing can be between 12‰ and 14‰ (Figure 4.1; Lee-Thorp and van der Merwe 1987; Passey et al. 2005; Lee-Thorp and Sponheimer 2007).

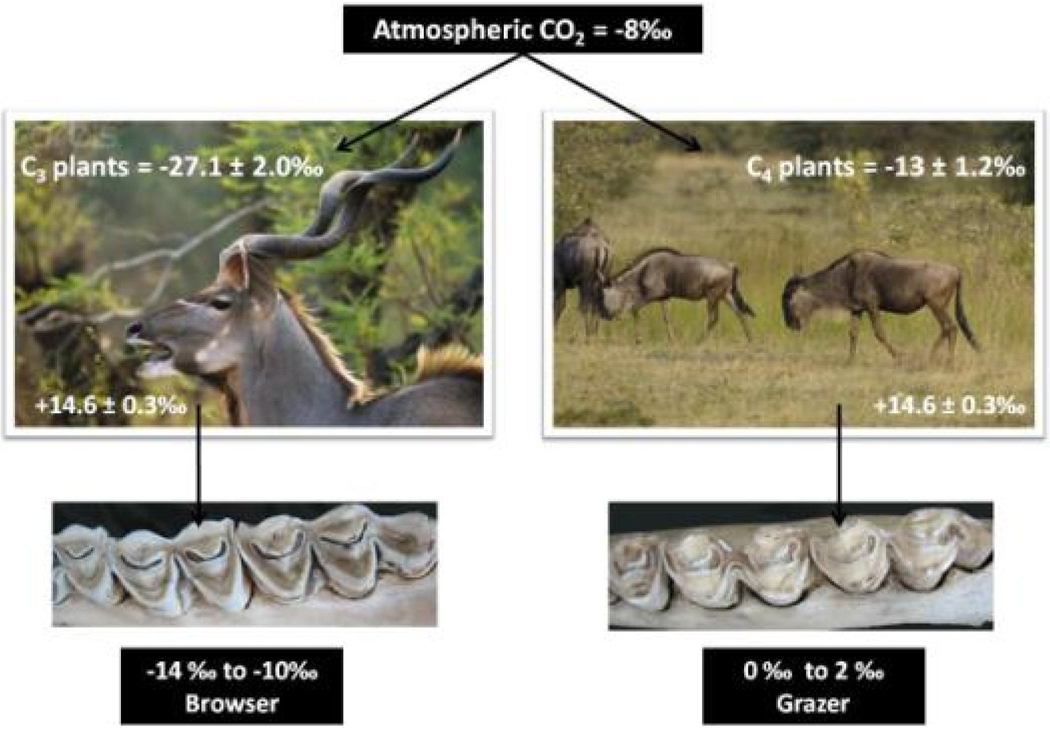

Figure 4.1. Isotope fractionation between atmospheric CO_2 and C_3 and C_4 plants (O'Leary 1988), as well as fractionation between plants and bovid bioapatite (Passey et al. 2005).

4.3 Materials

4.3.1 Modern Bovids

As museums and institutions have become increasingly hesitant in allowing continuous sampling of their modern and fossil material, it was necessary to request reliable $\delta^{13}C$ data (i.e., those that followed similar sampling and cleaning procedures) from other researchers. The majority of the modern $\delta^{13}C$ data come from specimens collected from various southern African localities. Matt Sponheimer, Daryl Codron, Julia Lee-Thorp and Nikolaas van der Merwe generously provided $\delta^{13}C$ data. Thure Cerling kindly provided the mean, standard deviation and ranges for some of the modern taxa from East Africa. Modern comparisons were limited to bovids that included the same species, or bovid forms closely related to those found in Cooper's Cave and Swartkrans.

A number of these studies have reconstructed the dietary behaviour of modern bovids using calculated means (Cerling et al. 2003; Sponheimer et al. 2003; Codron 2006). While the calculated mean is useful for interpreting the typical diet, it limits our understanding of diet versatility within a species (Kingston and Harrison 2007). Some species have a broad dietary range, while others have a narrow range. To examine intraspecific dietary variability, each species from southern Africa was separated into localities. Cerling et al. (2003) noticed intraspecific discrepancies in $\delta^{13}C$ values for some East African taxa. These dietary differences may be related to the composition of the local vegetation (Cerling et al. 2003, 2004). Detailed isotopic work on South African bovids incorporating locality with associated vegetation structure was first done by Codron (2006), but the study was conducted only in or around the Kruger

National Park. All modern bovids from southern Africa were examined by locality to look for intraspecific dietary differences in their $\delta^{13}C$ signatures. In addition, these differences help to identify species that might represent 'isotopic ecological indicators' (Kingston and Harrison 2007). The data from East Africa did not indicate specific localities where the individual bovid samples were collected; therefore, the data was used only to compare the two regions. Modern taxa were used as a baseline for interpreting fossil bovid dietary behaviour.

Modern bovid taxa from southern Africa (Sponheimer et al. 2003; Codron 2006) were compiled for analysis (Table 4.1). Species that were analyzed comprise *Antidorcas marsupialis* (springbok), *Connochaetes taurinus* (blue wildebeest), *Damaliscus lunatus* (tsessebe), *Damaliscus pygargus* (blesbok), *Hippotragus niger* (sable), *Oryx gazella* (gemsbok), *Ourebia ourebi* (oribi), *Raphicerus campestris* (steenbok), *Redunca fulvorufula* (mountain reedbuck), *Syncerus caffer* (African buffalo), *Tragelaphus oryx* (eland), and *Tragelaphus strepsiceros* (kudu).

Oreotragus oreotragus (klipspringer) and *Pelea capreolus* (grey rhebok) were sampled by this author because these species are usually associated with *P. robustus* sites (Table 4.2).

Table 4.1. Modern bovid taxa used for comparison with fossil bovids.

Tribe	Taxa	Common Name	Abbreviation
Alcelaphini	*Connochaetes taurinus*	blue wildebeest	Ct
	Damaliscus lunatus	tsessebe	Dl
	Damaliscus pygargus	blesbok	Dp
Antilopini	*Antidorcas marsupialis*	springbok	Ama
Bovini	*Syncerus caffer*	African buffalo	Sc
Hippotragini	*Hippotragus niger*	sable	Hn
	Oryx gazella	oryx	Og
Neotragini	*Oreotragus oreotragus*	klipspringer	Oor
	Ourebia ourebi	oribi	Oou
	Raphicerus campestris	steenbok	Rc
Peleini	*Pelea capreolus*	grey rhebok	Pc
Reduncini	*Redunca fulvorufula*	mountain reedbuck	Rf
Tragelaphini	*Tragelaphus oryx*	eland	To
	Tragelaphus strepsiceros	kudu	Tst

Table 4.2. Specimens of *P. capreolus* and *O. oreotragus* sampled by this author. Pre-industrial ‰ values are more positive than δ^{13}C enamel ‰ by 1.5‰.

Tribe	Taxa	Specimen	δ^{13}C enamel ‰	Pre-industrial ‰
Peleini	*Pelea capreolus*	BPI/C/71	-16.0	-14.5
		BP/C/72	-14.0	-12.5
		BPI/C/608	-12.9	-11.4
		BP/4/897	-12.8	-11.3
		BP/4/605	-12.7	-11.2
		BPI/C/673	-11.7	-10.2
Neotragini	*Oreotragus oreotragus*	TM13376	-16.6	-15.1
		BP/4/1156	-13.5	-12.0
		BPI/C/675	-12.4	-10.9
		BPI/C/681	-12.2	-10.7
		TM10908	-10.8	-9.3

4.3.2 Fossil bovids

Isotopic research was conducted on various mammalian groups at Swartkrans, but only a limited sample of bovids was used (Lee-Thorp and van der Merwe 1993; Lee-Thorp et al. 1994; Lee-Thorp et al. 2000; Lee-Thorp et al. 2007). The bovid taxa selected for these studies were often used to identify endmembers for browsing (C_3) and grazing (C_4) guilds that were then used to establish the dietary behaviour of hominins (Lee-Thorp and van der Merwe 1993; Lee-Thorp et al. 1994; Lee-Thorp et al. 2000). These isotopic contributions have in part been constrained by the difficulty of taxonomic identification beyond the tribe level (Kingston and Harrison 2007). Various species within a tribe may have different dietary behaviours. For example, species within the Neotragini and Antilopini tribes have variable diets from browsers to grazers. Here all specimens collected were identified at least to generic level.

As per museum regulations, previously sampled fossil specimens were not resampled. The published $\delta^{13}C$ data of fossil bovid taxa (Lee-Thorp and van der Merwe 1993; Lee-Thorp et al. 1989, 1994, 2000, 2007) supplements the data presented in this study. Of 140 bovid specimens examined here, 105 were collected by the author. Several new species were added along with new specimens for each deposit. All specimens used in other studies were re-examined to determine their accuracy of taxonomic identification. There were no discrepancies in individual identifications.

The fossil bovid taxa analyzed in this study include (Table 4.3): *Antidorcas bondi, A. marsupialis, A. recki, Connochaetes* sp., *Damaliscus* sp., *Gazella* sp., *Hippotragus* sp., *Makapania* sp., *Megalotragus* sp., *Ourebia ourebi,* *Pelea capreolus, Rabaticeras porrocornutus, Raphicerus campestris, Redunca fulvorufula, Syncerus* sp., *Tragelaphus oryx*, *Tragelaphus strepsiceros* and *Tragelaphus* sp.

Since enamel removal is an invasive procedure, curation policies of the Ditsong National Museum of Natural History, Pretoria, and the University of the Witwatersrand, Johannesburg, where fossil samples were taken, have strict guidelines as to the number of damaged teeth that may be used per species and the amount of enamel that may be removed. Only selected samples of damaged upper and lower molars were used, with a preference for second and third molars. Enamel removed by other researchers was not duplicated. The total allowable number of six specimens per species per deposit was adhered to as outlined by these institutions.

Another key aspect of interpreting the dietary behaviour of fossil bovid taxa from South Africa was to evaluate changes in $\delta^{13}C$ values through time. Published $\delta^{13}C$ enamel datasets of bovid taxa from Makapansgat Member 3 (Sponheimer et al. 1999; Lee-Thorp et al. 2007; Sponheimer and Lee-Thorp 2009) and Sterkfontein Members 4 and 5 (Luyt 2001; van der Merwe et al. 2003; Sponheimer and Lee-Thorp 2009) were utilized for comparison (Table 4.4). Makapansgat Member 3 was assigned an age using palaeomagnetic reversals. According to Herries (2003), Makapansgat Member 3 had normal polarity and was dated between 2.9 to 2.6 Ma. The new uranium series dates from Sterkfontein set Member 4 between 2.6 to 2.0 Ma (Pickering and Krammers 2010). Sterkfontein Member 5 was suggested to be no older than 2.0 Ma (op. cit.) Based on ESR (Electron Spin Resonance) dates, Sterkfontein Member 4 was estimated at

2.37 Ma and Sterkfontein Member 5 at 1.72 Ma (Schwartz et al. 1994). Makapansgat Member 3 and Sterkfontein Member 4 were older than the *P. robustus* deposits, but Sterkfontein Member 5 was of similar age.

Table 4.3. Cooper's D and Swartkrans Members 1- 3 fossil bovid specimens.

Specimen	Taxa	Deposit
Tribe Alcelaphini		
CD 7452	*Connochaetes* sp.	Cooper's D
CD 7414	*Connochaetes* sp.	Cooper's D
CD 1896	*Connochaetes* sp.	Cooper's D
CD 7402	*Connochaetes* sp.	Cooper's D
CD 6181	*Connochaetes* sp.	Cooper's D
CD 244	*Connochaetes* sp.	Cooper's D
CD 3702	*Connochaetes* sp.	Cooper's D
SK 2703	*Connochaetes* sp.	Swartkrans M1 HR
SK 2482	*Connochaetes* sp.	Swartkrans M1 HR
SK 2284	*Connochaetes* sp.	Swartkrans M1 HR
SK 2422	*Connochaetes* sp.	Swartkrans M1 HR
SK 2586	*Connochaetes* sp.	Swartkrans M1 HR
SKX 8530	*Connochaetes* sp.	Swartkrans M1 LB
SKX 13821	*Connochaetes* sp.	Swartkrans M1 LB
SKX 5843	*Connochaetes* sp.	Swartkrans M1 LB
SKX 9353a	*Connochaetes* sp.	Swartkrans M1 LB
SKX 2829	*Connochaetes* sp.	Swartkrans M2
SKX 29279	*Connochaetes* sp.	Swartkrans M3
SKX 20050	*Connochaetes* sp.	Swartkrans M3
SKX 37639	*Connochaetes* sp.	Swartkrans M3
SKX 29325	*Connochaetes* sp.	Swartkrans M3
SKX 37187a	*Connochaetes* sp.	Swartkrans M3
CD 297	*Damaliscus* sp.	Cooper's D
CD 8153	*Damaliscus* sp.	Cooper's D
CD 5405	*Damaliscus* sp.	Cooper's D
CD 1928	*Damaliscus* sp.	Cooper's D
CD 6202	*Damaliscus* sp.	Cooper's D
CD 219	*Damaliscus* sp.	Cooper's D
CD 1926	*Damaliscus* sp.	Cooper's D
CD 8182	*Damaliscus* sp.	Cooper's D
SK 3832	*Damaliscus* sp.	Swartkrans M1 HR
SK 3135	*Damaliscus* sp.	Swartkrans M1 HR
SK 11777	*Damaliscus* sp.	Swartkrans M2
SK 3123	*Damaliscus* sp.	Swartkrans M2

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Table 4. 3. continued

Specimen	Taxa	Deposit
Tribe Alcelaphini		
SK 1520	*Damaliscus* sp.	Swartkrans M2
SK 5123	*Damaliscus* sp.	Swartkrans M2
SK 11390	*Damaliscus* sp.	Swartkrans M2
SK 7335	*Damaliscus* sp.	Swartkrans M2
SKX 32639	*Damaliscus* sp.	Swartkrans M3
CD 6190	*Megalotragus* sp.	Cooper's D
CD 1247	*Megalotragus* sp.	Cooper's D
CD 5411	*Megalotragus* sp.	Cooper's D
SK 3031	*Megalotragus* sp.	Swartkrans M1 HR
SK 2245	*Megalotragus* sp.	Swartkrans M1 HR
SKX 9582	*Megalotragus* sp.	Swartkrans M1 LB
SKX 1349	*Megalotragus* sp.	Swartkrans M2
SK 1953	*Megalotragus* sp.	Swartkrans M2
SK 3249	*Megalotragus* sp.	Swartkrans M2
SKX 1243	*Megalotragus* sp.	Swartkrans M2
SKX 29602	*Megalotragus* sp.	Swartkrans M3
SKX 27800	*Megalotragus* sp.	Swartkrans M3
SK 1961	*Rabaticeras porrocornutus*	Swartkrans M1 HR
SK 3002	*Rabaticeras porrocornutus*	Swartkrans M1 HR
SK 2985	*Rabaticeras porrocornutus*	Swartkrans M1 HR
SK 3043	*Rabaticeras porrocornutus*	Swartkrans M1 HR
Tribe Antilopini		
SK 2404	*Antidorcas bondi*	Swartkrans M2
SK 9385	*Antidorcas bondi*	Swartkrans M2
CD 1273	*Antidorcas marsupialis*	Cooper's D
CD 6209	*Antidorcas marsupialis*	Cooper's D
CD 7449	*Antidorcas marsupialis*	Cooper's D
CD 8171	*Antidorcas marsupialis*	Cooper's D
CD 8161	*Antidorcas marsupialis*	Cooper's D
CD 3160	*Antidorcas marsupialis*	Cooper's D
CD 3701	*Antidorcas marsupialis*	Cooper's D
CD 7485	*Antidorcas marsupialis*	Cooper's D
CD 5853	*Antidorcas marsupialis*	Cooper's D
SK 3037	*Antidorcas marsupialis*	Swartkrans M2
SKX 33839	*Antidorcas marsupialis*	Swartkrans M3
CD 8179	*Antidorcas recki*	Cooper's D
CD 7448	*Antidorcas recki*	Cooper's D
CD 6165	*Antidorcas recki*	Cooper's D
CD 1886	*Antidorcas recki*	Cooper's D
CD 8166	*Antidorcas recki*	Cooper's D
SKX 811[3]	*Antidorcas recki*	Swartkrans M2
SK 2972	*Gazella* sp.	Swartkrans M1 HR

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Table 4. 3. continued

Specimen	**Taxa**	**Deposit**
Tribe Bovini		
CD 11062	*Syncerus* sp.	Cooper's D
SK 3130	*Syncerus* sp.	Swartkrans M1 HR
SK 3074	*Syncerus* sp.	Swartkrans M1 HR
Tribe Hippotragini		
CD 6179	*Hippotragus* sp.	Cooper's D
CD 3119	*Hippotragus* sp.	Cooper's D
CD 7456	*Hippotragus* sp.	Cooper's D
SKX 34892	*Hippotragus* sp.	Swartkrans M3
SKX 37042	*Hippotragus* sp.	Swartkrans M3
Tribe Neotragini		
SK 14168	*Ourebia ourebi*	Swartkrans M2
CD 1214	*Raphicerus campestris*	Cooper's D
SK 2108	*Raphicerus campestris*	Swartkrans M2
SK 2719	*Raphicerus campestris*	Swartkrans M2
SK 5930	*Raphicerus campestris*	Swartkrans M2
SK 4287	*Raphicerus campestris*	Swartkrans M2
SKX 38091	*Raphicerus campestris*	Swartkrans M3
Tribe Ovibovini		
SK 3113	*Makapania* sp.	Swartkrans M1 HR
SK 2373	*Makapania* sp.	Swartkrans M1 HR
SK 3150	*Makapania* sp.	Swartkrans M1 HR
SK 2759	*Makapania* sp.	Swartkrans M1 HR
Tribe Peleini		
CD 5430	*Pelea capreolous*	Cooper's D
CD 15604	*Pelea capreolous*	Cooper's D
SK 2273	*Pelea capreolous*	Swartkrans M1 HR
SK 2682	*Pelea capreolous*	Swartkrans M1 HR
SK 2990	*Pelea capreolous*	Swartkrans M2
SK 6047	*Pelea capreolous*	Swartkrans M2
SK 2981	*Pelea capreolous*	Swartkrans M2
SK 2246	*Pelea capreolous*	Swartkrans M2
Tribe Reduncini		
CD 1220	*Redunca fulvorufula*	*Cooper's D*
Tribe Tragelaphini		
SK 114171	*Tragelaphus oryx*	Swartkrans M2
SKX 4026	*Tragelaphus oryx*	Swartkrans M2
CD 255	*Tragelaphus* sp.	Cooper's D
CD 7473	*Tragelaphus* sp.	Cooper's D
CD 7474	*Tragelaphus strepsiceros*	Cooper's D
CD 309	*Tragelaphus strepsiceros*	Cooper's D
CD 5399	*Tragelaphus strepsiceros*	Cooper's D
SK 3000	*Tragelaphus strepsiceros*	Swartkrans M1 HR

Table 4.4. δ^{13}C values for fossil bovid taxa from other studies.

Specimen	Taxa	Deposit	Source
Tribe Alcelaphini			
SK 2061	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2110	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2261	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2354	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 5946	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2483	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 2007
SK 3097	*Connochaetes* sp.	Swartkrans M1 HR	Lee-Thorp et al. 2007
SF91	Connochaetes sp.	Sterkfontein M5	Luyt 2001
SF334	Connochaetes sp.	Sterkfontein M5	Luyt 2001
SF92	Connochaetes sp.	Sterkfontein M5	Luyt 2001
SF95	Connochaetes sp.	Sterkfontein M5	Luyt 2001
Sts2200	Connochaetes sp.	Sterkfontein M4	Luyt 2001
SF114	Connochaetes sp.	Sterkfontein M4	van der Merwe et al. 2003
SF112	Connochaetes sp.	Sterkfontein M4	van der Merwe et al. 2003
SK 10653	*Damaliscus* sp.	Swartkrans M2	Lee-Thorp et al. 2007
SK 4241	*Damaliscus* sp.	Swartkrans M2	Lee-Thorp et al. 2007
SK 9897	*Damaliscus* sp.	Swartkrans M2	Lee-Thorp et al. 2007
SE1185	Damaliscus sp.	Sterkfontein M5	Luyt 2001
SE1828	Damaliscus sp.	Sterkfontein M5	Lee-Thorp et al. 2007
SE1728.1	Damaliscus sp.	Sterkfontein M5	Lee-Thorp et al. 2007
SK 2063	*Megalotragus* sp.	Swartkrans M1 HR	Lee-Thorp et al. 1994
Tribe Antilopini			
SK 12273	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 2574	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 3841	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 5907	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 5922	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 5962	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
SK 6123	*Antidorcas bondi*	Swartkrans M2	Lee-Thorp et al. 2000
Sts1577	*Antidorcas bondi*	Sterkfontein M4	Luyt 2001
Sts1125	*Antidorcas bondi*	Sterkfontein M4	van der Merwe et al. 2003
SKX 1896	*Antidorcas marsupialis*	Swartkrans M2	Lee-Thorp et al. 2007
SKX 2736	*Antidorcas marsupialis*	Swartkrans M2	Lee-Thorp et al. 2007
SKX 811	*Antidorcas recki*	Swartkrans M2	Lee-Thorp et al. 1994
SE 1855.1	*Antidorcas recki*	Sterkfontein M5	Luyt 2001
SE 1258	*Antidorcas recki*	Sterkfontein M5	Luyt 2001
Sts 1944	*Antidorcas recki*	Sterkfontein M4	van der Merwe et al. 2003
Sts 1435	*Antidorcas recki*	Sterkfontein M4	van der Merwe et al. 2003
Sts 1325a	*Antidorcas recki*	Sterkfontein M4	van der Merwe et al. 2003

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Table 4.4. continued

Specimen	**Taxa**	**Deposit**	**Source**
Tribe Antilopini			
Sts 1400	*Antidorcas recki*	Sterkfontein M4	Luyt 2001
Sts 2076	*Antidorcas recki*	Sterkfontein M4	Luyt 2001
Sts 2369	*Antidorcas recki*	Sterkfontein M4	van der Merwe et al. 2003
Sts 1596	*Antidorcas recki*	Sterkfontein M4	Luyt 2001
Tribe Ovibovini			
Sts 952	*Makapania broomi*	Sterkfontein M4	Luyt 2001
Sts 1925	*Makapania broomi*	Sterkfontein M4	Luyt 2001
Sts 2059b	*Makapania broomi*	Sterkfontein M4	Luyt 2001
Sts 1721	*Makapania broomi*	Sterkfontein M4	Luyt 2001
Sts 2565	*Makapania broomi*	Sterkfontein M4	Luyt 2001
M 978	*Makapania broomi*	Makapansgat M3	Sponheimer 1999
M 1398	*Makapania broomi*	Makapansgat M3	Sponheimer 1999
M 6528	*Makapania broomi*	Makapansgat M3	Sponheimer 1999
M 6274	*Makapania broomi*	Makapansgat M3	Sponheimer 1999
Tribe Neotragini			
SK 1631	*Oreotragus oreotragus*	Swartkrans M2	Lee-Thorp and van der Merwe 1993
M 6293	*Oreotragus oreotragus*	Makapansgat M3	Sponheimer 1999
M 997	*Oreotragus oreotragus*	Makapansgat M3	Sponheimer 1999
Tribe Tragelaphini			
SK 2329	*Tragelaphus* sp.	Swartkrans M2	Lee-Thorp and van der Merwe 1993
SK 2304	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2576	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2681	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 3023	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 1989
SK 2541	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 1994
SK 14112	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 2007
SK 2095	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 2007
SK 2281	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 2007
SK 3110	*Tragelaphus strepsiceros*	Swartkrans M1 HR	Lee-Thorp et al. 2007
Sts 1573	*Tragelaphus strepsiceros*	Sterkfontein M4	Luyt 2001
Sts 46	*Tragelaphus strepsiceros*	Sterkfontein M4	Luyt 2001
Sts 2121	*Tragelaphus strepsiceros*	Sterkfontein M4	Luyt 2001
Sts 1300	*Tragelaphus strepsiceros*	Sterkfontein M4	Luyt 2001

4.4 Methods

4.4.1 Cleaning and treatment of samples

Enamel samples were removed under a low-power microscope (10x to 40x) where available.When a microscope was not available, a head visor with 10-x magnification was used to ensure removal of impurities and adherent dentine. Enamel samples were first cleaned, and then 4 mg of the sample was removed. Both processes used a rotary drill with an attached diamond grit 1.0 mm diameter dental burr (Proxxon D-54518 Niersbach, Germany), set to approximately 10% to 20% of maximum speed to avoid thermal decomposition of carbonate. Larger pieces of enamel that flaked off from broken samples were first cleaned with the diamond drill bit and then ground manually with an agate mortar and pestle. All tools were cleaned with 1.0 molarity[9] (M) of hydrochloric acid and distilled water between samples to prevent contamination. The resultant powdered enamel was measured into individual 5ml microcentrifuge tubes. The powered enamel was pretreated to remove diagenetic carbonates using the protocol developed by Lee-Thorp et al. (1997). 1.0 ml of 1.75%v/v of sodium hypochlorite (50% NaOCl: distilled water) was placed into centrifuge tubes for 45 minutes and then centrifuged for three minutes. The diluted NaOCl was vacuum-suctioned out and rinsed with distilled water. This procedure was repeated three times. Samples were treated with 0.1 M acetic acid (CH_3COOH), 0.1 ml per mg for 15 minutes. Koch et al. (1997) has shown 0.1 M of CH_3COOH causes minimal bioapatite alteration, while an increase of CH_3COOH to 1.0 M treatment would cause

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[9] The concentration of a solution, expressed as the number of moles of solute per liter of solution.

recrystallization of bioapatites leading to incomplete removal of impurities (Lee-Thorp and van der Merwe 1991).

After treatment, the samples were centrifuged. Then the treatment solution vacuum-suctioned out and the sample was rinsed with distilled water. This process was repeated three times, after which samples were freeze-dried. Purified enamel bioapatite samples (2 mg) and standards (0.1 mg) were reacted with 100% phosphoric acid (H_3PO_4) at 70°C in individually sealed reaction tubes, cryogenically cleaned and combusted using an automated Elemental Analyzer (Carlo Erba Instruments, Milan, Italy). The resultant CO_2 gas was introduced into the Finnigan MAT 252 mass spectrometer (Finnigan, Bremen, Germany). The raw data were calibrated using Cavendish marble and Carrara Z marble (carbonate internal lab standards) and the National Bureau of Standards, NBS18 (carbonate external lab standard). The standard deviation of 10 replicates of three standard was less than 0.1 in all cases: Cavendish Marble, 0.49 ± 0.08‰, Carrara Z marble, 2.28 ± 0.04‰ and NBS 18 -4.81 ± 0.07‰. The precision for $\delta^{13}C$ values of the standards was a standard deviation of 0.1‰. Only data between 1000 and 7000 amplitude were used. Anything below or above these numbers was considered unreliable.

Stable carbon isotopes results are reported in standard notation and in parts per mil[10] (‰). $^{13}C/^{12}C$ ratios are expressed in delta notation (δ). The differences of the $^{13}C/^{12}C$ ratio are measured with reference to Vienna Pee Dee Belemnite, derived from the equation: $\delta^{13}C$ (‰) = $(R_{sample} / R_{standard} - 1) \times 1000$, where R = the $^{13}C/^{12}C$ ratio of the sample and standard.

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[10] parts per thousand

4.4.2 Trophic categories

Traditional trophic classifications used in isotope analysis are generally broad and are based on three categories: browser, mixed feeder and grazer. Though these categories are useful, Gagnon and Chew (2000) attempted to provide a more detailed dietary classification scheme based on a synthesis of available literature on African bovids, they include: frugivores (>70% fruits, little monocots), browsers (>70% dicots), generalist (>20 of all food types), browser-grazer intermediates (30 – 70% of dicots and monocots, <20% fruits), variable grazers (60 – 90% monocots) and obligate grazers (>90% monocots consumption). In an effort to provide a more detailed classification for isotopic analysis, Cerling (et al. 2003) applied similar parameters and classified dietary behaviour in five categories: hyperbrowsers or frugivores, browsers, mixed feeders, grazers and hypergrazers. Because of the varied diets, and the multiple and sometimes contradicting techniques used to determine diet, there is no consensus as to how one classifies the dietary behaviour of bovids. In order to express the dietary behaviour of Lateoli herbivores along the browser-grazer continuum using isotopic analysis, Kingston and Harrison (2007) identified five categories: obligate browser (>95% dicots), variable browser (75 – 95% dicots), browser-grazer intermediate, variable grazer (75 – 95% monocots), and obligate grazer (>95% monocots). These categories were based on the combination of methods by Tiszen et al. (1979), Gagnon and Chew (2000), and Cerling et al. (2003).

I have based my classification on a number of factors. (1) Unlike other studies that have a category for frugivores, I have chosen not to use it since frugivores are difficult to separate from browsers by isotopic analysis. (2) Trophic categories follow Kingston and Harrison (2007). The bovid taxa are divided into five trophic categories based on modern bovid $\delta^{13}C$ data sampled from southern Africa (Sponheimer et al. 2003; Codron 2006) (Figure 4.2). The five trophic categories used are obligate C_3 consumer (OC_3, < -12.8‰), variable C_3 consumer (VC_3, -10.0‰ to -12.8‰), mixed C_3–C_4 (-3.3 to -10.0‰), variable C_4 consumers (VC_4, 0.5‰ to -3.3‰) and obligate C_4 consumer (> 0.5‰) (see Table 4.5 and Figure 4.2). (3) Using terms such as 'browser' or 'grazer' is incorrect, as the type of vegetation an individual bovid may select varies. For example, a browser may select a wide variety of foods that include leaves, fruits, forbs, seeds and grass, where a grazer may select C_3 or C_4 grasses and include other types of vegetation. In order to bypass these terms, I use the categories stated above in (2) to isotopically designate the vegetation the bovid selects (Lee-Thorp et al. 2007). (4) In order to compare modern bovids to fossil forms, it was necessary to add 1.5‰ to the modern enamel values to correct for the depletion of atmospheric $\delta^{13}C$ instigated by industrialization (Table 4.5).

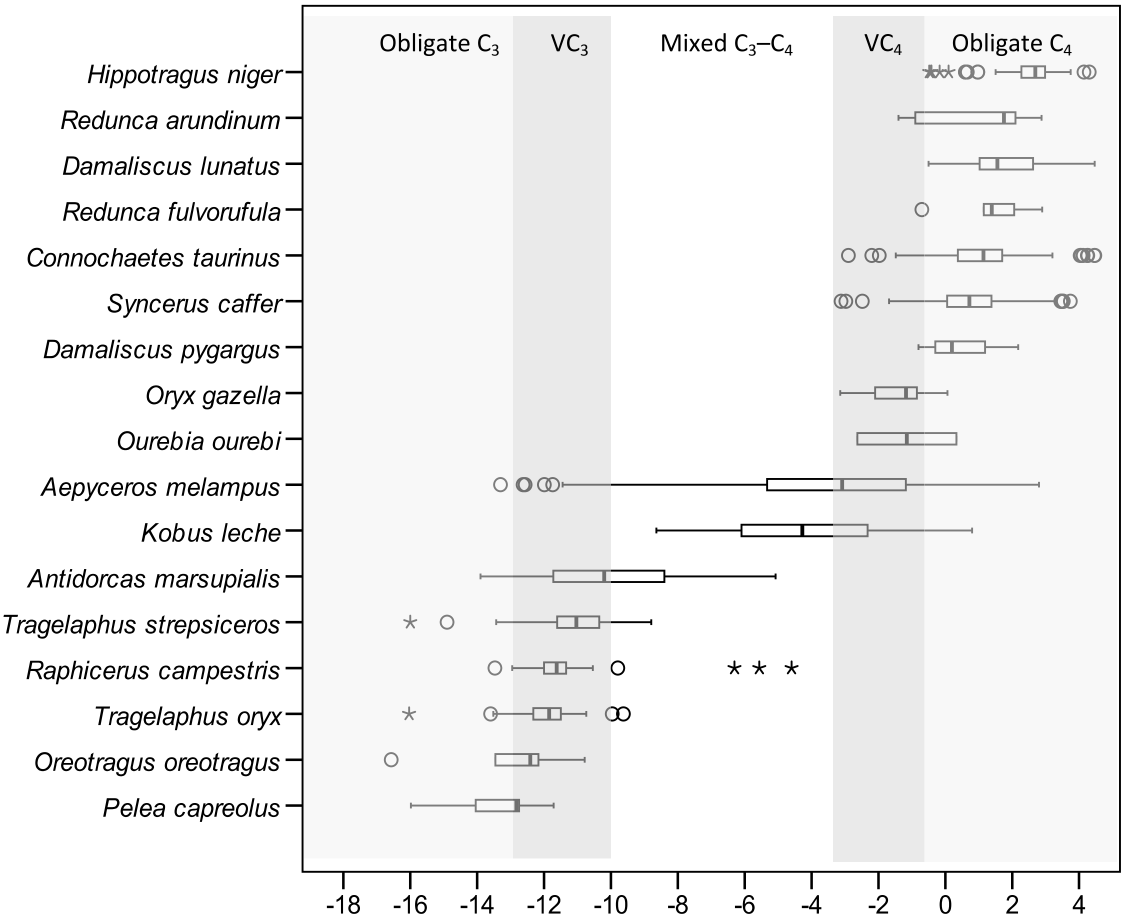

Figure 4.2. Box and whiskers plot of $\delta^{13}C$ enamel of relevant modern samples. Taxa placed in order of $\delta^{13}C$ values (preindustrial effect of 1.5‰ was not added to these values). Each box encloses 50% of the data with the median value of the variable indicated by a vertical line in the box. The sides of the box mark the limits of ± 25% of the variable population. The lines extending from the sides mark the minimum and maximum values within the data set. Outliers (circles) and extreme outliers (stars) are displayed as individual points.

Table 4.5. Dietary classification with $\delta^{13}C$ ranges.

Diet classification	Abbrev.	Foraging strategy	Approximate modern $\delta^{13}C$ range	Pre-industrial (+1.5‰) $\delta^{13}C$ range
Obligate C_3	OC_3	Almost exclusively eudicot	< −12.8‰	<-11.3‰
Variable C_3	VC_3	Predominantly eudicot	−12.8 to −10.0‰	−11.3 to -8.5‰
Mixed C_3–C_4	mixed	Intermediate eudicot and monocot	−10.0 to −3.3 ‰	−8.5 to -1.8‰
Variable C_4	VC_4	Predominantly monocot	−3.3 to 0.5 ‰	-1.8 to 2.0‰
Obligate C_4	OC_4	Almost exclusively monocot	> 0.5‰	> 2.0‰

Categories based on modern bovid foraging strategies from field observations and rumen content (Skinner and Chimimba 2005), and stable carbon isotopes (Sponheimer et al. 2003; Codron 2006). For pre-industrial $\delta^{13}C$ range, 1.5‰ was added to the modern enamel values to offset the 'fossil fuel effect' to facilitate comparisons with fossil taxa.

4.4.3 Incorporating faecal data

A large number of modern bovid data used in this thesis are from Codron (2006). He examined various plants and modern herbivore faeces from various localities near or in the Kruger National Park. In order to incorporate faecal data into this study it was important to note the differences in scale between faeces and enamel $\delta^{13}C$. This is due to the different isotope discriminations between the two materials. Relative to diet (i.e., plant), faeces were –0.9‰ depleted in $\delta^{13}C$ (Sponheimer et al. 2003; Codron et al. 2005). To obtain the original $\delta^{13}C$ value before the offset, 0.9‰ was added. While enamel bioapatite can range between 12‰ to 14.6‰ enriched, the Passey et al. (2005) enrichment factor of 14.6‰ was selected, which provided a $\delta^{13}C$ enamel value. This enrichment factor seems to be consistent with other studies that examine the fractionation between diet and enamel of ruminants (Cerling and Harris 1999; Balasse 2002). Temporal scale is an important issue that must be addressed when using faecal data. Fecal data records what the bovid ate in the last few days and should show more diet variability then observed for enamel, which shows long-term dietary intake. The carbon signature is laid down as the tooth is developing which gives a dietary profile only from the first few years of an animal's life. Whereas the carbon signature obtained from faecal remains may provide the overall diet of the animal at any stage of life. Here difference and similarities were examined between the two datasets, and vetted on a case-by-case basis.

4.4.4 Statistics

Comparisons between faecal and enamel $\delta^{13}C$ calues were compared using an independent t-test. Since faecal samples were large compared to enamel samples, this disparity may produce large sample bias. In a large sample, very small differences can be detected as significant. In order to test this, 1000 recombination using bootstrapping was performed.

A one-way ANOVA or Independent t-test depending on sample size was applied to assess if significant variation exists between localities for each species. The multiple comparison (pairwise) tests were used to determine the sources of significant variation. Because even small sample sizes for bovid species were expected to indicate dietary differences, Fisher's LSD a priori test was used to compare species. Fisher's LSD does not adjust the ear rate and as the least conservative of the *post hoc* tests has been criticized for false positives (Proschan 1997). It does nonetheless indicate the presence of variation. A Tukey's HSD *post hoc* test was also performed to balance risks of Type I and Type II errors (Cook and Farewell 1996). If the variance were unequal between the taxa then the Tamhane's T2 *post hoc* test was applied.

4.5 Dietary profiles for modern bovids

Descriptive statistics using preindustrial $\delta^{13}C$ values for southern African modern bovids by locality are given in Table 4.8. Where possible, the southern African bovids where compared to East African bovids (Table 4.9). For some of the descriptive tables, abbreviations (see pages xv – xvi) were used instead of full taxa designation. Statistical analyses for stable carbon isotopes are shown in Table 4.10. The distributions of $\delta^{13}C$ values for bovid taxa are shown in Figures 4.3 to 4.11.

4.5.1 Alcelaphini

***Connochaetes taurinus* (Ct)**

There were significant differences between faecal and enamel (Independent t-test, t = -2.8, P < 0.05; Table 4.6). The faecal sample showed more positive $\delta\ ^{13}C$ values compared to the enamel sample (Table 4.7). However, both enamel and faecal $\delta^{13}C$ means (1.3 ± 1.7‰ and 2.7 ± 1.0‰ respectively) show modern wildebeest to be a dedicated C_4 feeder (Table 4.7). A compilation of ^{13}C values from southern Africa indicates that the blue wildebeest have a C_4 diet ($\bar{x}$ = 2.6 ± 1.1‰, range 1.4‰ to 6.0‰). When the sample was split into eleven localities in southern Africa (Table 4.8), the blue wildebeest consistently had a predominately C_4 diet (Figure 4.3). Of 274 specimens, only two specimens had negative values. Isotopic profiles for the East African forms have similar ranges (1.0‰ to 5.4‰). Compared to other localities, three specimens from the Central Kalahari Game Reserve had values that were slightly more negative (-1.4 to 0.2‰). The Central Kalahari Game Reserve is mostly a flat landscape covered with open grassland, grass-covered dunes and bushveld vegetation (Van Rooyen 2001). A small percentage of C_3 foods may have supplemented wildebeest diets in an arid environment that has low rainfall and high temperatures.

Codron (2006) noted there were differences in dietary intake between the Hans Merensky Nature Reserve outside the Kruger National Park (n = 110) and

Northern basalts in the Kruger National Park (n = 115). The significant differences between the two localities may not be behaviourally relevant since the difference in mean was only 0.4‰. This disparity may perhaps be a reflection of large sample size bias. In large sample sizes, very small differences can be detected as significant. In order to test this, recombination using bootstrapping was performed. After 1000 recombination, there were no significant differences between the two localities (Independent t-test, $t = 1.3$, $P > 0.05$; Table 4.10).

Damaliscus lunatus (Dl)

There were significant differences between faecal and enamel (Independent t-test, $t = 2.2$, $P < 0.05$; Table 4.6). The faecal sample was variable, however, the means for enamel (3.9 ± 0.7‰) and faecal (3.2 ± 1.0‰) indicated obligate C_4 feeders (Table 4.7). The combined South Africa mean ($\bar{x}$ = 3.3 ± 1.0‰, n = 62; Table 4.8) was similar to East African specimens ($\bar{x}$ = 3.4 ± 1.0‰, n = 11; Table 4.9).

Damaliscus pygargus (Dp)

The modern blesbok was examined only from South Africa. Similar to the tsessebe, blesbok are OC_4 consumers, $\bar{x}$ = 2.0 ± 1.5‰ (Table 4.8 and Figure 4.4).

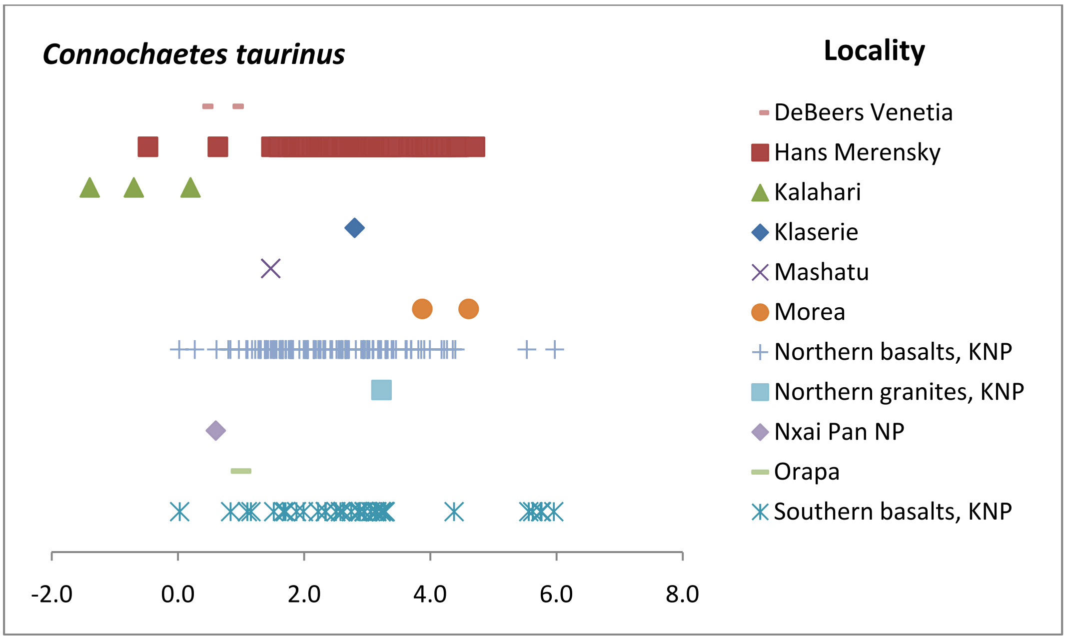

Figure 4.3. δ^{13}C values of modern wildebeest by locality.

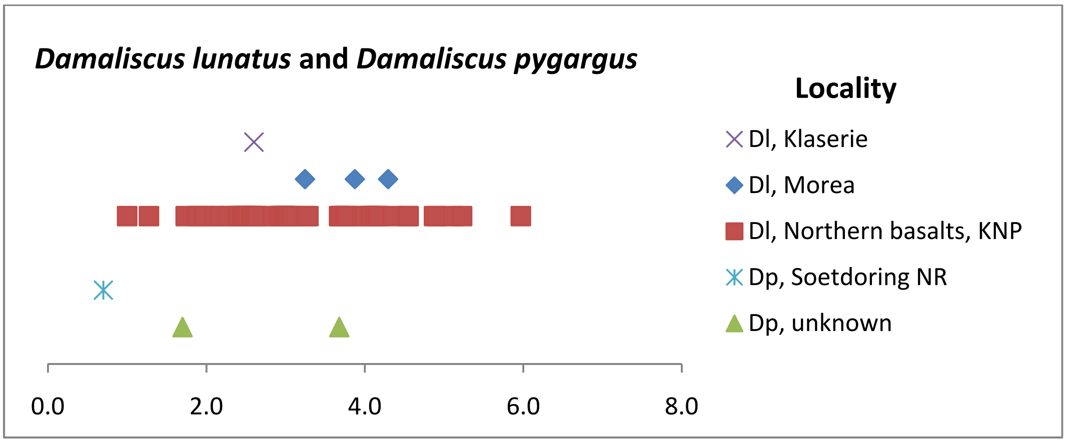

Figure 4.4. δ^{13}C values of modern tsessebe and blesbok by locality.

4.5.2 Antilopini

***Antidorcas marsupialis* (Ama)**

Modern springboks were selected from five localities from southern Africa (Table 4.8). The dietary intake for this species ranged from OC_3 (-12.4‰) to mixed C_3–C_4 (-3.6‰) with an average of -8.6 ± 2.1‰ (n = 21) (Table 4.8 and Figure 4.5). Field observations have shown the springboks consume a mixture of C_3 and C_4 vegetation (Hofmann and Stewart 1972). The δ^{13}C range supports the fact that they select a variety of vegetation, although on average, they tend to concentrate on C_3 vegetation.

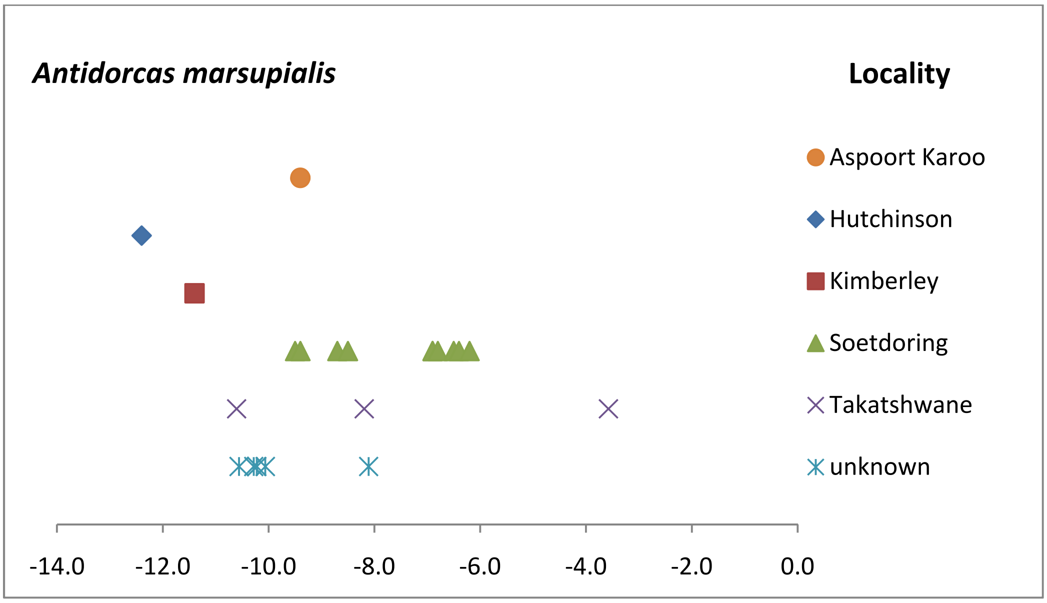

Figure 4.5. δ^{13}C values of modern springbok by locality.

4.5.3 Bovini

Syncerus caffer (Sc)

There were significant differences between faecal and enamel (Independent t-test, t = -4.1, $P < 0.05$; Table 4.6). The faecal sample was more variable than the enamel sample (Table 4.7). The minimum $\delta^{13}C$ values for enamel (-1.6‰) and for faecal (-1.5‰) were similar. However, the maximum values for faecal (5.2‰) were higher than enamel (1.7‰). Nonetheless, both samples show that this species is predominately a C_4 feeder (Figure 4.6). Isotopic signals from 325 specimens from seven localities within southern Africa had a mean of 2.3 ± 1.1‰ (Table 4.8). Specimens from three areas within the Kruger National Park were selected for statistical analysis: Northern basalts (n = 146), Punda Maria (n = 131) and Southern basalts (n = 37). There were no dietary differences between the various localities (ANOVA, F = 1.4, $P > 0.05$).

The 'savanna' dwelling African buffalo from East Africa had similar $\delta^{13}C$ values to those of southern Africa specimens (Table 4.8 and 4.9). The dietary behaviour of African buffaloes is complex. Cerling et al. (2004) analyzed the carbon isotope signature of buffaloes from the Ituri Forest in the Democratic Republic of Congo; they had an extremely negative $\delta^{13}C$ value of -16.2‰ and it was noted that they selected fruits, seeds and leaves. To highlight habitat and diet versatility, buffaloes in the succulent thickets of the Eastern Cape browse up to 28% in the wet season and 35% in the dry season (Tshabalala et al. 2010). Modern African buffaloes are capable of adjusting their diet to include large amounts of C_3 plants, the selection of which may depend on the availability of prevalent resources within their habitat. This species may be an isotopic ecological indicator, but further research is required.

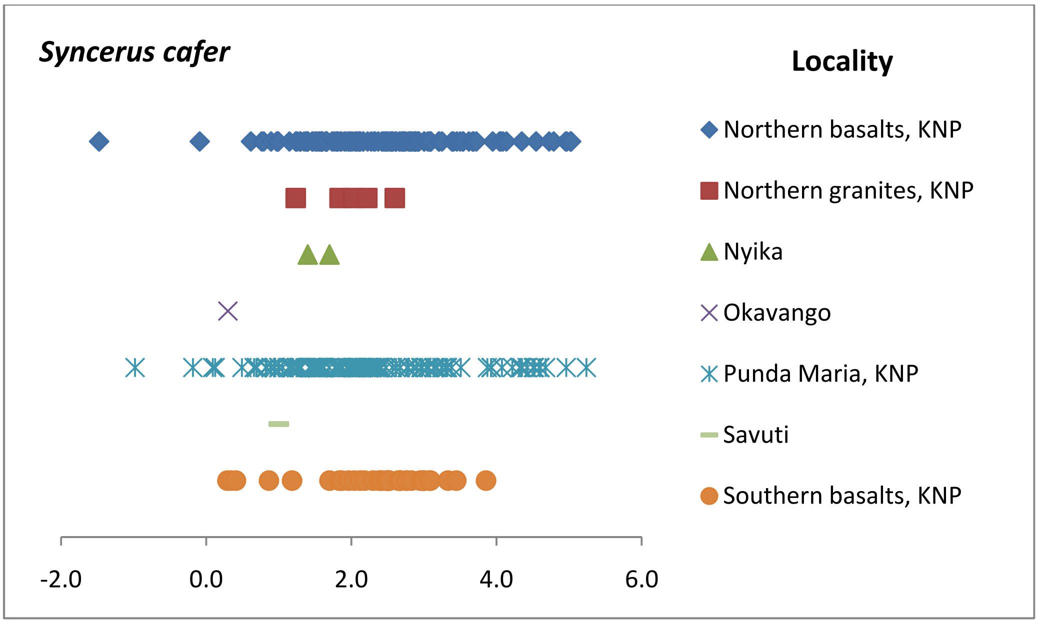

Figure 4.6. δ^{13}C values of modern African buffaloes by locality.

4.5.4 Hippotragini

***Hippotragus niger* (Hn)**

There were no significant differences between faecal and enamel values (Independent t-test, $t = -1.7$, $P < 0.05$; Table 4.6). The modern sable was examined from southern Africa (Table 4.8). The δ^{13}C means for southern Africa 4.0 ± 0.8‰ (n = 128, range 1.0‰ to 5.8‰; Figure 4.7) and for East Africa was 2.5 ± 2.5‰ (n = 4, range -0.8‰ to 4.6‰; Table 4.9). Both regions reflect an obligate C_4 diet.

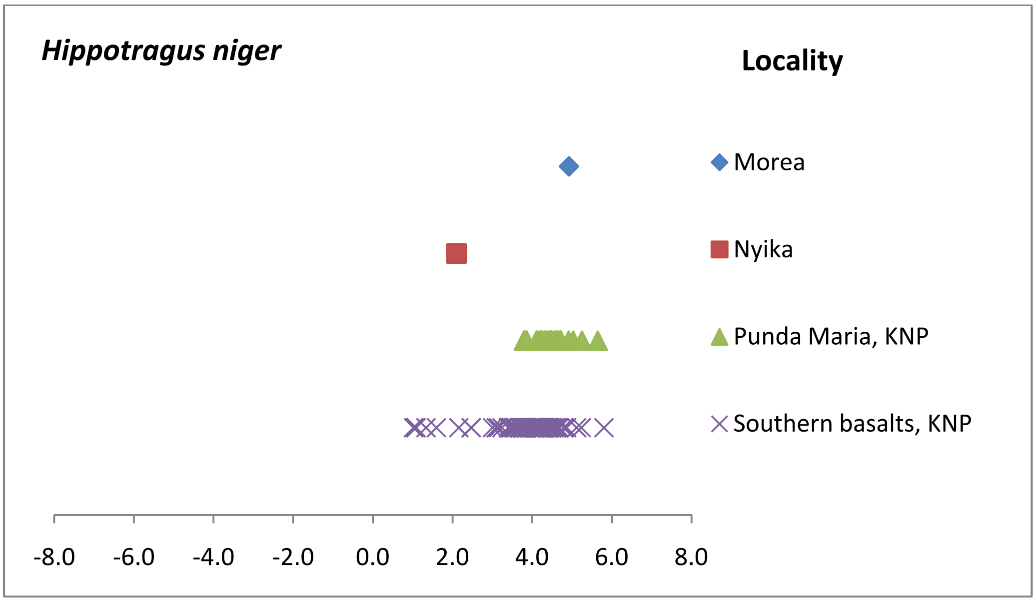

Figure 4.7. δ^{13}C values of modern sables by locality.

4.5.5 Neotragini

***Oreotragus oreotragus* (Oor)**

For the present study, five specimens of modern klipspringers from South Africa were sampled. This species ranged from -15.1‰ to -9.3‰, $\bar{x}$ = -11.6 ± 2.2‰.

***Ourebia ourebi* (Oou)**

Two oribis were examined from South Africa (Table 4.8). They had a VC_4 diet (n = 2, $\bar{x}$ = 0.3 ± 2.1‰). One specimen from East Africa had a mixed C_3–C_4 diet (-3.8‰; Table 4.9). In different habitats and seasons, oribis will range from obligate C_4 to mixed C_3–C_4 feeders especially during the dry season (Hofmann 1973; Estes 1991).

***Raphicerus campestris* (Rc)**

There were no significant differences between faecal and enamel (Independent t-test, t = -1.6, P > 0.05; Table 4.6). The steenbok sampled from five localities in South Africa suggest a variable diet from OC_3 (-12‰) to mixed C_3–C_4 (-3.1‰) with a mean of -9.7‰ (Table 4.8 and Figure 4.8). Two localities were statistically compared: Northern granites (n = 13) and Punda Maria (n = 7) in the Kruger National Park. There were no significant differences between the localities (Independent t-test, t = 1.5, P > 0.05). In comparison to other localities, Northern granites and Southern basalts in the Kruger National Park had a few outliers that were more ^{13}C-enriched, ranging into mixed C_3–C_4. These outliers come from faecal samples that highlight the occasional selection C_4 vegetation.

Based on gut morphology and stomach contents, the steenbok were considered mixed feeders (Hofmann 1973). However, the carbon signatures for the steenbok suggest a preference for C_3 foods.

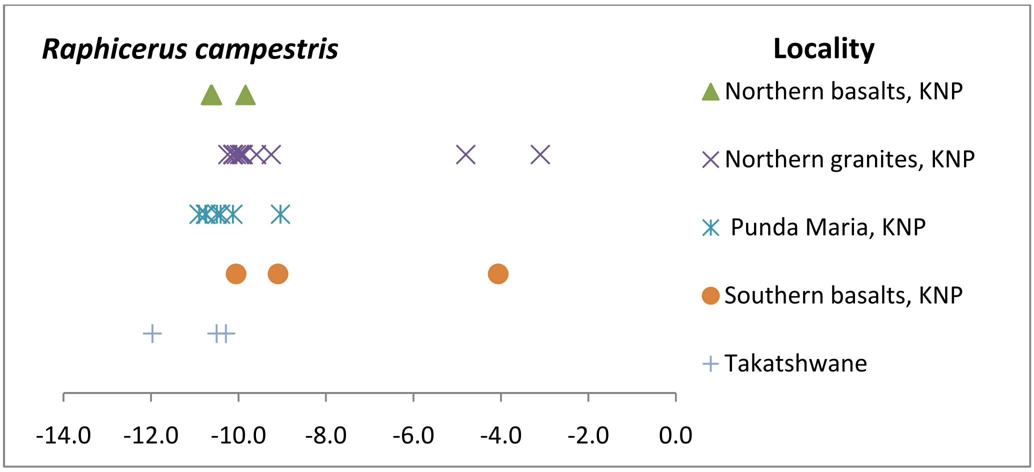

Figure 4.8. δ^{13}C values of modern steenbok by locality.

4.5.6 Peleini

***Pelea capreolus* (Pc)**

Six South African grey rhebok had an OC_3 diet ($\bar{x}$ = -11.9 ± 1.5‰). Their $\delta^{13}C$ values ranged between -14.5‰ to -10.2‰.

4.5.7 Reduncini

***Redunca fulvorufula* (Rf)**

Mountain reedbucks were examined from southern Africa (Table 4.8). The values ranged from VC_4 (0.8‰) to OC_4 (4.4‰) (Figure 4.9). The one specimen from East Africa was within the range of southern African reedbucks (Table 4.9).

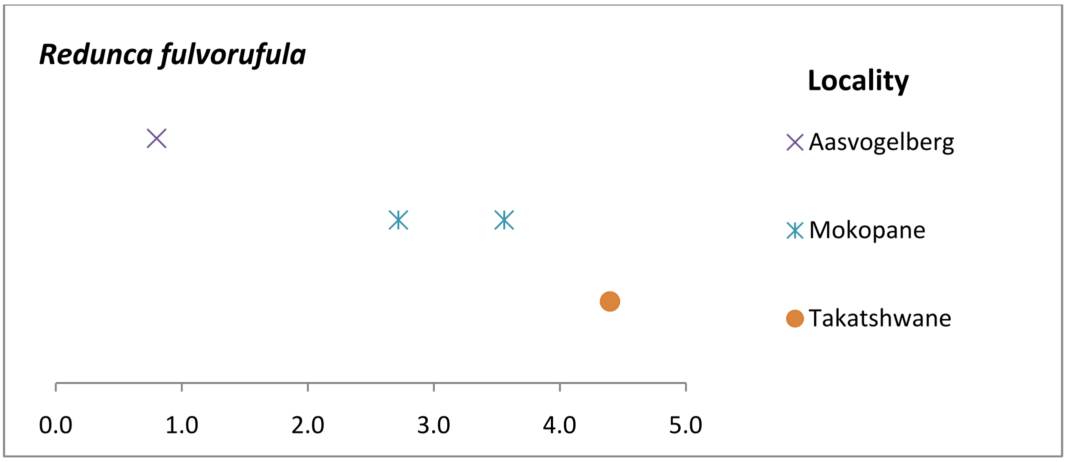

Figure 4.9. $\delta^{13}C$ values of modern mountain reedbucks by locality.

4.5.8 Tragelaphini

***Tragelaphus oryx* (To)**

There were no significant differences between faecal and enamel (Independent t-test, t = -1.7, P > 0.05; Table 4.6). Modern eland were sampled from southern Africa (Table 4.8). Field observations have noted that eland are mixed feeders that consume over 50% grass during the wet season (Hofmann 1989), but in some areas they may browse exclusively (Hillman 1979; Estes 1991). Taken together, the eland from southern Africa ranged from OC_3 (-14.5‰) to mixed C_3–C_4 (-7.3‰) (Figure 4.10). The eland from East Africa had slightly more positive values (-11.7‰ to -6.0‰; Table 4.9) than from southern Africa. On average in all five localities examined, the eland were variable C_3 feeders. Only two localities had sample sizes sufficient for statistical analysis: Mountain Zebra National Park (n = 4) and Northern basalts (n = 5). Eland showed no dietary difference between the two localities (Independent t-test, t = -2.2, P > 0.05).

***Tragelaphus strepsiceros* (Tst)**

There were significant differences between faecal and enamel (Independent t-test, t = -5.9, P < 0.05; Table 4.6). The mean $\delta^{13}C$ values for both faecal (-9.4‰) and enamel (-10.8‰) samples are predominately C_3 feeders (Table 4.7 and Figure 4.11). However, some of the faecal samples showed a mixed C_3–C_4 diet. This highlights the capable range of food selection by the Kudu. The mean values for southern Africa kudu (-9.5 ± 0.9‰) where similar to East African specimens (-10.3 ± 1.0) (Table 4.9).

Of the nine southern African localities, four were suitable for statistical analysis: Central Etosha, Namibia (n = 6), Northern granites (n = 21), Punda Maria (n = 107) and Southern basalts (n = 14). There are significant dietary differences between localities (ANOVA, F = 5.6, P < 0.05; Table 4.10). Specifically pairwise comparisons demonstrated that kudu from Central Etosha were different from those from Punda Maria. Kudu from Punda Maria in the Kruger National Park had a more variable diet (range from -10.5‰ to -7.6‰), whereas specimens from Central Etosha had a predominately C_3 diet (range -11.0‰ to -9.7‰). However, this does not appear to be a true reflection of differences between localities as the range for Etosha was within the Punda Maria range, and most likely a factor of sample size difference between the two localities. When bootstrapping was performed, after 1000 recombination there were no significant differences between the two localities (Independent t-test, t = 1.3, P > 0.05).

Kudu from Nyika, Malawi and the Okavango Delta, Botswana were more ^{13}C-depleted compared to other localities. Nyika Plateau is situated roughly 2,607 metres above sea level and miombo woodland covers 60% of the plateau (Burrows and Willis 2005). The depleted values from Nyika may be related to the plateau's higher altitude (Tieszen et al. 1979). Okavango Delta which has an altitude of 1000 metres comprises many habitats, but unique to this area are the variety of sedges and semi-aquatic grasses that grow there (Roodt 1998), however this would not account for the ^{13}C- depletion observed. Caution must be applied here since in each area only one specimen was sampled.

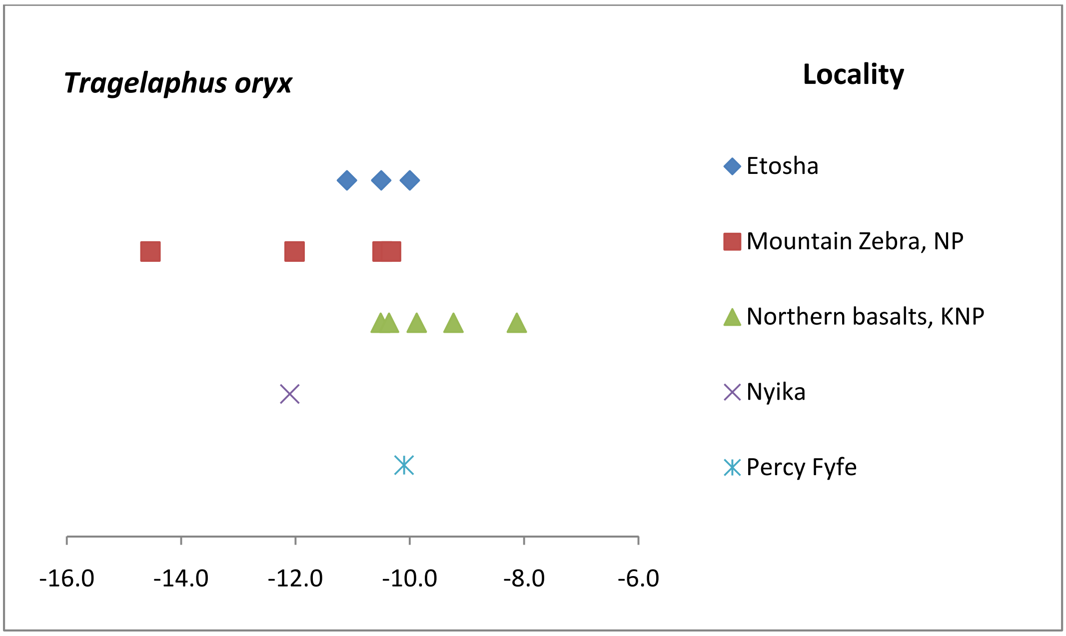

Figure 4.10. δ^{13}C values of modern eland by locality.

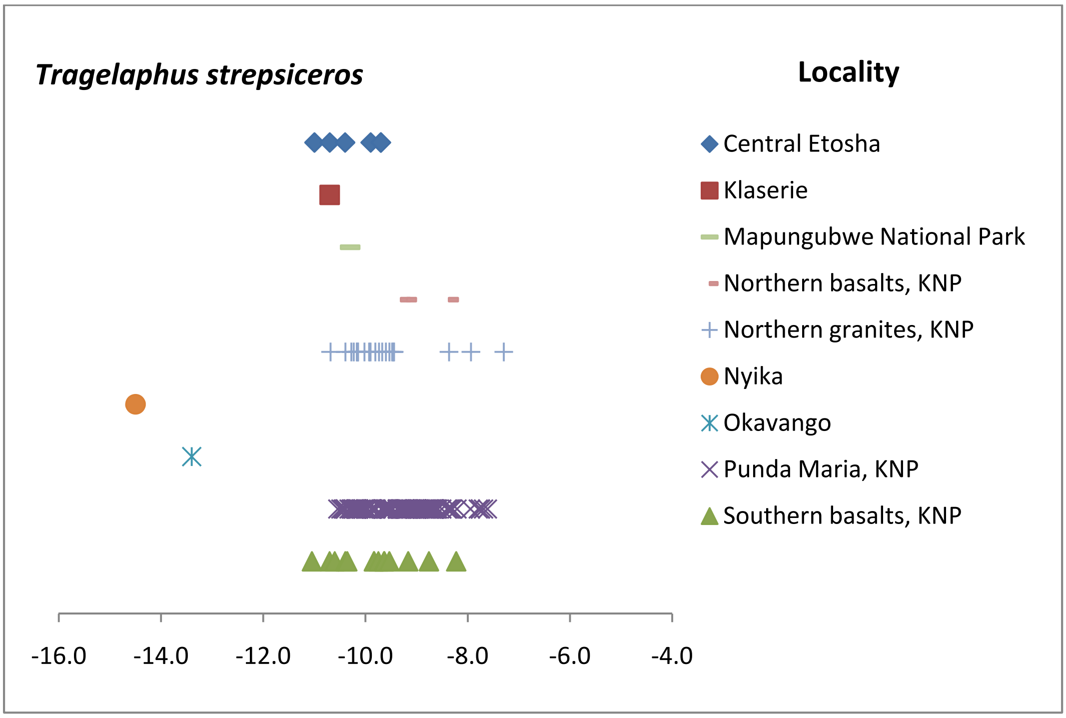

Figure 4.11. δ^{13}C values of modern kudu by locality.

Table 4.6. Independent t-test comparison between faecal and enamel $\delta^{13}C$ values.

Taxa	t	df	P value
Connochaetes taurinus	-4.3	272	**.02**
Damaliscus lunatus	1.7	60	**.05**
Hippotragus niger	-1.7	126	.18
Raphicerus campestris	-1.6	32	.09
Syncerus caffer	-4.1	323	**.01**
Tragelaphus oryx	-1.7	16	.09
Tragelaphus strepsiceros	-5.9	157	**.01**

Table 4.7. Faecal and enamel $\delta^{13}C$ values compared.

Tribe	Taxa		N	Min	Max	Range	Mean	SD
Alcelaphini	*Connochaetes taurinus*	Enamel	13	-1.4	4.6	6.0	1.3	1.7
		Faecal	261	-.5	6.0	6.4	2.7	1.0
	Damaliscus lunatus	Enamel	7	2.6	4.6	2.0	3.9	.7
		Faecal	55	1.0	6.0	5.0	3.2	1.0
Bovini	*Syncerus caffer*	Enamel	6	-1.6	1.7	3.3	.5	1.2
		Faecal	319	-1.5	5.2	6.7	2.3	1.1
Hippotragini	*Hippotragus niger*	Enamel	6	2.1	4.9	2.8	3.5	1.1
		Faecal	122	1.0	5.8	4.8	4.0	.8
Neotragini	*Raphicerus campestris*	Enamel	8	-12.0	-8.3	3.7	-10.6	1.1
		Faecal	26	-10.9	-3.1	7.8	-9.4	2.1
Tragelaphini	*Tragelaphus oryx*	Enamel	13	-14.5	-8.5	6.1	-10.8	1.4
		Faecal	5	-10.5	-8.1	2.4	-9.6	1.0
	Tragelaphus strepsiceros	Enamel	14	-14.5	-9.1	5.4	-10.8	1.5
		Faecal	145	-11.0	-7.3	3.8	-9.4	.8

Table 4.8. Descriptive statistics using preindustrial $\delta^{13}C$ values for modern bovid taxa by southern African locality.

Tribe	Taxa	Locality	N	Min	Max	Mean	SD
Alcelaphini	Ct	De Beers Venetia NR	2	0.4	0.9	0.6	0.3
		Hans Merensky NR	110	-0.5	4.7	2.8	0.8
		Central Kalahari Game Reserve	3	-1.4	0.2	-0.6	0.8
		Klaserie NR	1	.	.	2.8	.
		Mashatu Game Reserve	2	1.5	1.5	1.5	0.0
		Morea (Mpumalanga) Estates	2	3.9	4.6	4.2	0.5
		Northern basalts, KNP	115	0.0	6.0	2.4	1.0
		Northern granites, KNP	1	.	.	3.2	.
		Nxai Pan NP	1	.	.	0.6	.
		Orapa NR	1	.	.	1.0	.
		Southern basalts, KNP	35	0.0	6.0	2.9	1.4
		unknown	1	.	.	2.3	.
		Total	**274**	**-1.4**	**6.0**	**2.6**	**1.1**
	Dl	Klaserie NR	1	.	.	2.6	.
		Morea (Mpumalanga) Estates	3	3.2	4.3	3.8	0.5
		Northern basalts, KNP	55	1.0	6.0	3.2	1.0
		unknown	3	4.3	4.6	4.4	0.2
		Total	**62**	**1.0**	**6.0**	**3.3**	**1.0**
	Dp	Soetdoring NR	1	.	.	0.7	.
		unknown	2	1.7	3.7	2.7	1.4
		Total	**3**	**0.7**	**3.7**	**2.0**	**1.5**
Antilopini	Am	Aspoort Karoo	1	.	.	-9.4	.
		Hutchinson	1	.	.	-12.4	.
		Kimberley	1	.	.	-11.4	.
		Soetdoring NR	10	-9.5	-6.2	-7.6	1.3
		Takatshwane	3	-10.6	-3.6	-7.5	3.6
		unknown	5	-10.6	-8.1	-9.8	1.0
		Total	**21**	**-12.4**	**-3.6**	**-8.6**	**2.1**
Bovini	Sc	Northern basalts, KNP	146	-1.5	5.0	2.4	1.0
		Northern granites, KNP	5	1.2	2.6	2.0	0.5
		Nyika NP	2	1.4	1.7	1.6	0.2
		Okavango	1	.	.	0.3	.
		Punda Maria, KNP	131	-1.0	5.2	2.2	1.1
		Savuti	1	.	.	1.0	.
		Southern basalts, KNP	37	0.3	3.9	2.3	0.8
		unknown	2	-1.6	0.4	-0.6	1.4
		Total	**325**	**-1.6**	**5.2**	**2.3**	**1.1**
Hippotragini	Hn	Morea (Mpumalanga) Estates	1	.	.	4.9	.
		Nyika NP	2	2.1	2.1	2.1	0.0
		Punda Maria, KNP	32	3.8	5.6	4.4	0.4
		Southern basalts, KNP	90	1.0	5.8	3.9	0.9
		unknown	3	3.8	4.2	3.9	0.2
		Total	**128**	**1.0**	**5.8**	**4.0**	**0.8**

continued on next page

Table 4.8. continued

Tribe	Taxa	Locality	N	Min	Max	Mean	SD
Neotragini	Oor	unknown	**5**	**-15.1**	**-9.3**	**-11.6**	**2.2**
	Oou	unknown	**2**	**-1.1**	**1.8**	**0.3**	**2.1**
	Rc	Northern basalts, KNP	3	-10.6	-9.8	-10.4	0.5
		Northern granites, KNP	13	-10.2	-3.1	-9.0	2.3
		Punda Maria, KNP	7	-10.9	-9.0	-10.4	0.6
		Southern basalts, KNP	3	-10.1	-4.1	-7.7	3.2
		Takatshwane	3	-12.0	-10.3	-10.9	0.9
		unknown	5	-11.5	-8.3	-10.4	1.3
		Total	**34**	**-12.0**	**-3.1**	**-9.7**	**1.9**
Peleini	Pc	unknown	**6**	**-14.5**	**-10.2**	**-11.9**	**1.5**
Reduncini	Rf	Aasvogelberg	1	.	.	0.8	.
		Mokopane	2	2.7	3.6	3.1	0.6
		Takatshwane	1	.	.	4.4	.
		unknown	2	2.7	3.1	2.9	0.3
		Total	**6**	**.8**	**4.4**	**2.9**	**1.2**
Tragelaphini	To	Etosha (Western)	3	-11.1	-10.0	-10.5	0.6
		Mountain Zebra NP	4	-14.5	-10.3	-11.8	2.0
		Northern basalts, KNP	5	-10.5	-8.1	-9.6	1.0
		Nyika NP	1	.	.	-12.1	.
		Percy Fyfe NR	1	.	.	-10.1	.
		unknown	4	-10.8	-8.5	-9.9	1.0
		Total	**18**	**-14.5**	**-8.1**	**-10.5**	**1.4**
	Ts	Etosha (Central)	6	-11.0	-9.7	-10.2	0.6
		Klaserie	1	.	.	-10.7	.
		Mapungubwe NP	1	.	.	-10.3	.
		Northern basalts, KNP	3	-9.3	-8.4	-9.0	0.5
		Northern granites, KNP	21	-10.7	-7.3	-9.6	0.8
		Nyika NP	1	.	.	-14.5	.
		Okavango	1	.	.	-13.4	.
		Punda Maria, KNP	107	-10.5	-7.6	-9.3	0.7
		Southern basalts, KNP	14	-11.0	-8.2	-9.8	0.8
		unknown	4	-11.9	-9.1	-10.1	1.2
		Total	**159**	**-14.5**	**-7.3**	**-9.5**	**0.9**

1. δ^{13}C data for modern bovids, with the exception of *Oreotragus oreotragus* and *Pelea capreolus* were compiled from Sponheimer et al. (2003) and Codron (2006).
2. Park or Reserve classifications: Kruger National Park (KNP), National Park (NP), and Nature Reserve (NR).

Table 4.9. Descriptive statistics using preindustrial $\delta^{13}C$ values for modern bovid taxa from East Africa (Cerling et al. 2003).

Tribe	**Taxa**	**N**	**Min**	**Max**	**Mean**	**SD**
Alcelaphini	*Connochaetes taurinus*	38	1.0	5.4	3.4	1.3
	Damaliscus lunatus	11	1.7	5.0	3.4	1.0
Bovini	*Syncerus caffer* (forest)	12	-14.7	2.2	-5.0	5.4
	Syncerus caffer (savanna)	61	-1.0	4.3	2.6	1.0
Hippotragini	*Hippotragus niger*	4	-0.8	4.6	2.5	2.5
Neotragini	*Ourebia ourebi*	1	.	.	-3.8	.
Reduncini	*Redunca fulvorufula*	1	.	.	1.0	.
Tragelephini	*Tragelaphus oryx*	13	-11.7	-6.0	-9.4	1.4
	Tragelaphus strepsiceros	4	-11.4	-9.0	-10.3	1.0

Table 4.10. Statistical analysis of $\delta^{13}C$ data of modern southern African bovids.

A. ANOVA

Taxa	**Sum of Squares**	**Df**	**Mean Square**	**F**	**P value**
Connochaetes taurinus	11.8	2	5.9	5.7	**.004**
Syncerus caffer	4.8	3	1.6	1.4	.231
Tragelaphus strepsiceros	9.3	3	3.1	5.6	**.001**

Significant differences in bold (P= < 0.05)

B. Pairwise comparisons

1. *Connochaetes taurinus*

Tamhane T2	Hans Merensky	Northern basalts
Northern basalts	**.005**	
Southern basalts	.958	.161

Significant differences in bold (P= < 0.05)

2. *Tragelaphus strepsiceros*

Tukey HSD	Central Etosha	Northern granites	Punda Maria
Northern granites	.297		
Punda Maria	**.014**	.200	
Southern basalts	.664	.878	*.054*

Significant differences in bold (P= < 0.05)

C. Independent t-test

Taxa	**t**	**df**	**P value**
Connochaetes taurinus	1.3	79	.214
Raphicerus campestris	1.5	18	.149
Tragelaphus oryx	-2.2	7	.060

Significant differences in bold (P= < 0.05)

4.6 Dietary profiles for fossil bovids

A list of $\delta^{13}C$ values for fossil bovids is found in Table 4.11 and 4.12. Descriptive statistics for Cooper's D and Swartkrans Members 1–3 bovids examined in this study are summarized in Table 4.13. Descriptive statistics from other studies are summarized in Table 4.14 and 4.15. Statistical analyses for stable carbon isotopes are shown in Table 4.16. The distribution of $\delta^{13}C$ values for fossil bovid taxa is shown in Figures 4.12 to 4.23.

4.6.1 Alcelaphini

***Connochaetes* sp. (Csp)**

This species was sampled from all four deposits utilized in this study (Table 4.11, Figure 4.12). The average for *Connochaetes* sp. from Cooper's D ($\bar{x}$ = -2.1 ± 1.7‰), Swartkrans Member 2 ($\bar{x}$ = -2.1‰), and Swartkrans Member 3 ($\bar{x}$ = -1.9 ± 0.9‰) indicate mixed C_3–C_4 diets (Table 4.13). Swartkrans Hanging Remnant specimens ranged from mixed C_3–C_4 (-2.7‰) to VC_4 (0.4‰) (Table 4.13). Seven other specimens from the Swartkrans Hanging Remnant examined by Lee-Thorp et al. (1989, 2007) had similar ranges (-3.7‰ to 1.0‰) (Table 4.14). Specimens from Swartkrans Lower Bank were VC_4 consumers (range -1.1‰ to 0.2‰). The values from these deposits were more negative compared to those of modern wildebeest.

From other deposits, three specimens from Sterkfontein Member 4 and three of the four specimens from Sterkfontein Member 5 (Table 4.15) had similar mean values (-2.5‰ and 0.2‰, respectively) compared to Cooper's D and

Swartkrans Members 1–3 specimens. One specimen from Sterkfontein Member 5 had an OC_4 diet (2.7‰). This was inconsistent with the data from other deposits.

ANOVA was performed to compare specimens from Cooper's D, Swartkrans Hanging Remnant, Swartkrans Lower Bank, Swartkrans Member 3, Sterkfontein Member 5 and modern bovids. There were significant differences (ANOVA, $F = 70.1$, $P = 0.000$). Pairwise comparisons indicate dietary differences between fossil and modern *Connochaetes* (Table 4.16). There were also significant differences between Cooper's D and Sterkfontein Member 5 (Table 4.16). This is due to the one outlier for Sterkfontein.

From 2.6 Ma (Sterkfontein M4) to 1.0 Ma (Swartkrans Member 3), *Connochaetes* sp. consumed a significant amount of C_3 plants, indicating at least in South Africa that fossil *Connochaetes* were not dedicated C_4 specialists.

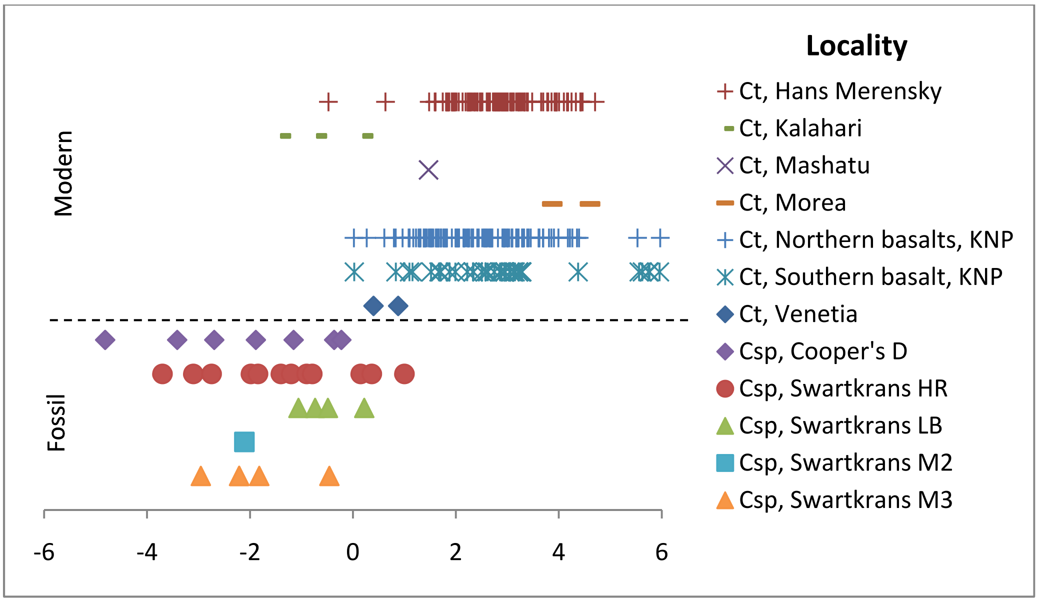

Figure 4.12. $\delta^{13}C$ values of modern and fossil *Connochaetes* by locality.

***Damaliscus* sp. (Dsp)**

This species was sampled from Cooper's D, and Swartkrans Hanging Remnant and Member 2 (Table 4.11, Figure 4.13). *Damaliscus* sp. from Cooper's D, -1.4 ± 1.2‰ (range -3.6‰ to -0.2‰) and Swartkrans Hanging Remnant, -1.5 ± 1.3‰ (range -2.5‰ to -0.6‰) are more ^{13}C-depleted compared to modern forms. Six specimens from Swartkrans Member 2 yield more positive values compared to other deposits, 0.3 ± 1.5‰ and (range -1.6‰ to 2.0‰). Five specimens sampled from Swartkrans Member 2 were analyzed by Lee-Thorp et al. (2007). The isotopic values ranged from -0.7‰ to 2.2‰ (Table 4.14). These values are consistent with the values from Swartkrans Member 2 presented here. When specimens from Cooper's D, Swartkrans Member 2 and modern specimens were statistically analyzed, there were significant dietary differences (ANOVA, F = 75.3, P = 0.000). Pairwise comparisons indicated that fossil specimens exhibited differences in dietary behaviour from modern specimens (Table 4.16). They also showed significant differences between Cooper's D and Swartkrans Member 2 (Table 4.16). The dietary differences observed between the two deposits may be a reflection of the two different species (e.g., *D. niro* and possibly *D. pygargus*) selecting slightly different proportions of C_3. The only other fossil site with *Damaliscus* sp. present is Sterkfontein Member 5 (Luyt 2001; Lee-Thorp et al. 2007). Three specimens from this deposit had a mixed C_3–C_4 diet (-2.7‰) (Table 4.15).

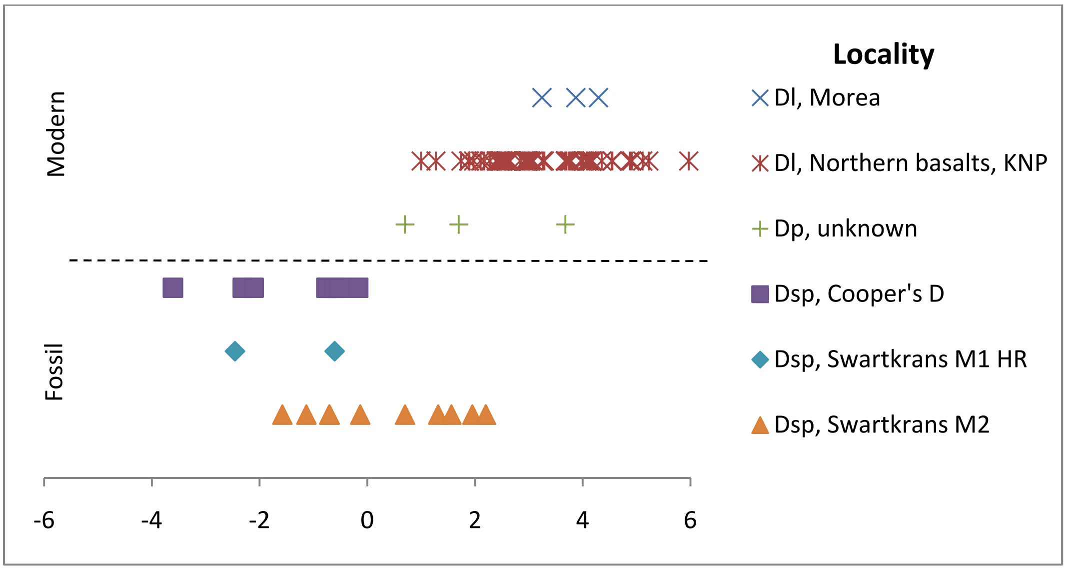

Figure 4.13. $\delta^{13}C$ values of *Damaliscus* by locality.

Megalotragus sp. (Mesp)

This species was sampled from Cooper's D and Swartkrans Members 1 – 3 (Table 4.11, Figure 4.14). Diets ranged from mixed C_3–C_4 (-4.2‰) to OC_4 (0.4‰). Similar to other fossil alcelaphines, *Megalotragus* sp. values from Cooper's D (range -1.9‰ to -0.1‰), Swartkrans Hanging Remnant (range -0.2‰ to 0.4‰), Swartkrans Member 2 (range -4.2‰ to -1.5‰), and Member 3 (range -1.6‰ to -0.8‰) were ^{13}C-depleted compared to modern alcelaphines. Swartkrans Member 2 specimens had consistently more negative values compared to specimens from other deposits. One *Megalotragus* sp. sampled from Swartkrans Hanging Remnant by Lee-Thorp et al. (1994) had a positive $\delta^{13}C$ value of 2.2‰ (Table 4.12). This value was higher than the rest of the samples obtained in the present study. *Megalotragus* sp. were flexible feeders.

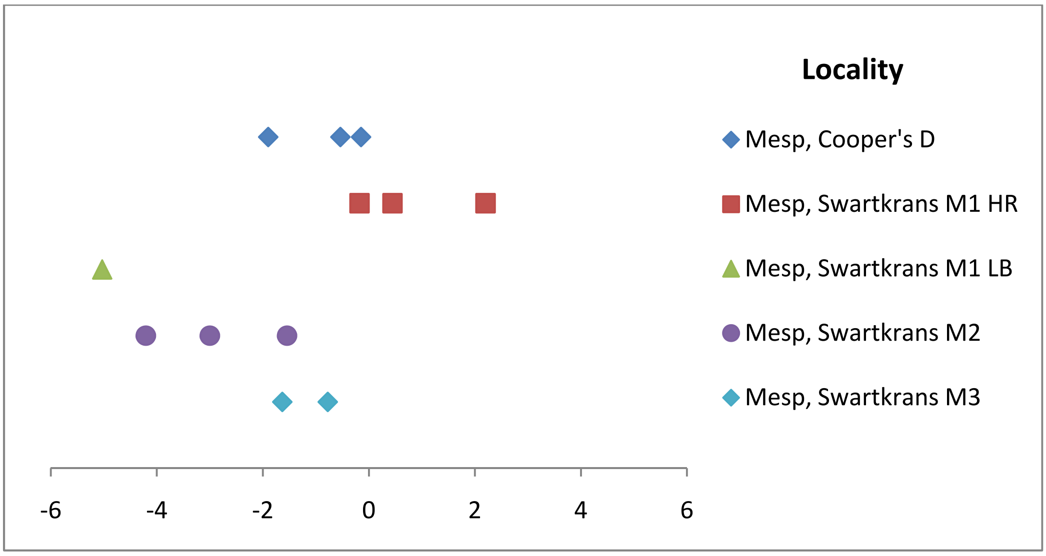

Figure 4.14. δ^{13}C values of *Megalotragus* sp. by locality.

***Rabaticeras porrocornutus* (Rp)**

This species has only been recorded in Swartkrans Hanging Remnant (Watson 1993). Four specimens were analysed with an average of -1.9 ± 2.2‰, ranging from mixed feeder (-3.9‰) to variable grazer (0.2‰).

4.6.2 Antilopini

***Antidorcas marsupialis* (Am)**

Fossil springbok were sampled from Cooper's D, Swartkrans Members 2 and 3 (Table 4.11, Figure 4.15). As with modern springbok, the δ^{13}C values for fossil specimens indicate a flexible diet, specimens ranged from OC_3 (-11.6‰) to mixed C_3–C_4 (-5.6‰). In the current study, one specimen was sampled from Swartkrans Members 2 and one specimen from Member 3. Both had the same δ^{13}C value of -11.6‰. Two specimens from Swartkrans Member 2 in the Lee-Thorp et al. (2007)

study ranged from -11.5‰ to -10.6‰ (Table 4.14). Specimens from Cooper's D ranged from OC$_3$ (-11.5‰) to mixed C$_3$–C$_4$ (-5.6‰) diets. Compared to Swartkrans, on average, the specimens from Cooper's D were more ^{13}C-enriched.

Antidorcas recki (Ar)

Four out of five specimens of *A. recki* from Cooper's D had mixed C$_3$–C$_4$ diets, ranging from -10.5‰ to -4.7‰, with a mean of -7.4 ± 2.2‰ (Table 4.11, Figure 4.15). One specimen was sampled from Swartkrans Member 2 by Lee-Thorp et al. (1994) was an OC$_3$ consumer (-12.9‰) (Table 4.12). Most specimens from Sterkfontein Member 4 (-11.3 ± 3.3‰) and Member 5 (-11.7 ± 1.4‰) had similar means to Swartkrans Member 2, except for one specimen from Sterkfontein Member 4 that had a mixed C$_3$–C$_4$ diet (-4.5‰)(Table 4.12).

Antidorcas recki from Cooper's D and Sterkfontein Member 4 were statistically compared with *A. marsupialis* from Cooper's D and modern specimens. There were significant dietary differences (ANOVA, F = 4, P = 0.000). Pairwise comparisons indicate significant dietary differences between *A. recki* from Cooper's D and Sterkfontein Member 4 (Table 4.16). The range for *A. recki* and *A. marsupialis* from Cooper's D was within the modern *A. marsupialis* range.

Antidorcas bondi (Ab)

One specimen of *A. bondi* from Swartkrans Member 2 was a mixed C$_3$–C$_4$ feeder (-2.8‰) (Table 4.11). This is within the range for the eight specimens sampled (-4.5‰ to -1.7‰) from the same deposit by Lee-Thorp et al. (2000) (Table 4.14).

Antidorcas bondi were more ^{13}C-enriched compared to *A. marsupialis* and *A. recki* (Figure 4.15).

Gazella sp. (Gsp)

One specimen from Swartkrans Member 2 was available for isotopic analysis and had a mixed C_3–C_4 diet (-7.6‰) (Table 4.11, Figure 4.15).

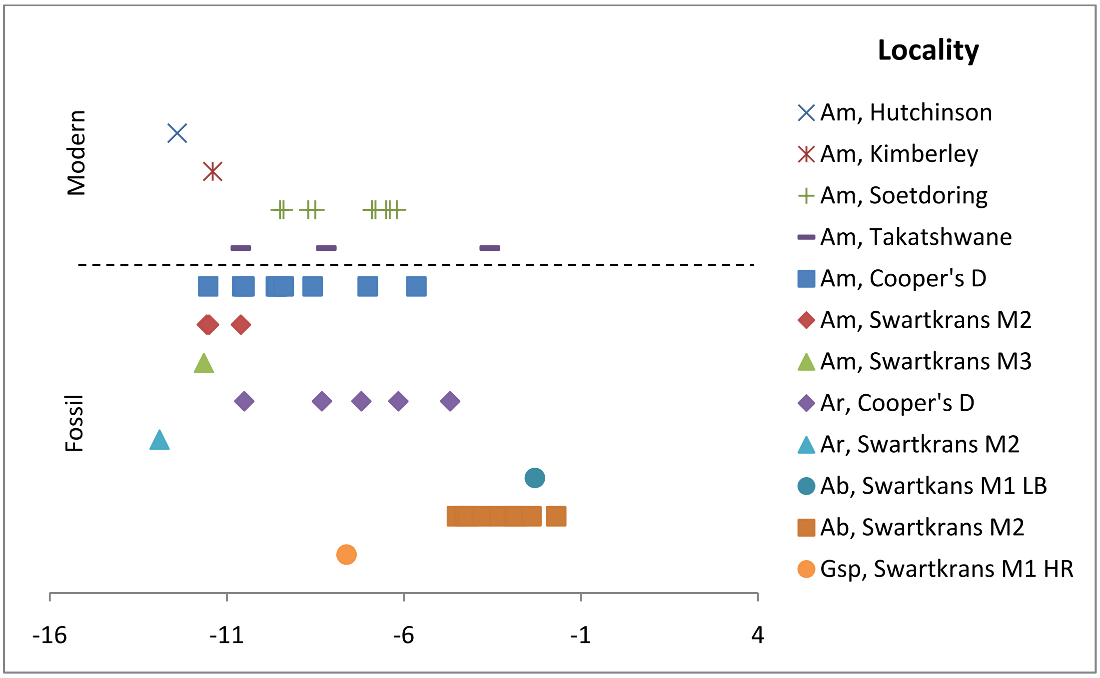

Figure 4.15. δ^{13}C values of modern and fossil Antilopini by locality.

4.6.3 Bovini

***Syncerus* sp. (Ssp)**

This species was sampled from Cooper's D and Swartkrans Member 1 (Table 4.11, Figure 4.16). One specimen from Cooper's D had a VC_3 diet (-10.7‰), and the two specimens from Swartkrans Hanging Remnant had a mixed C_3–C_4 diet (range, -7.6‰ and -6.4‰). Though only three individuals were sampled, all had negative $\delta^{13}C$ values compared to their modern 'savanna' counterparts. The $\delta^{13}C$ values for fossil buffaloes appear similar to their modern counterparts from the forested or highland areas of eastern Africa (see Section 4.5.3).

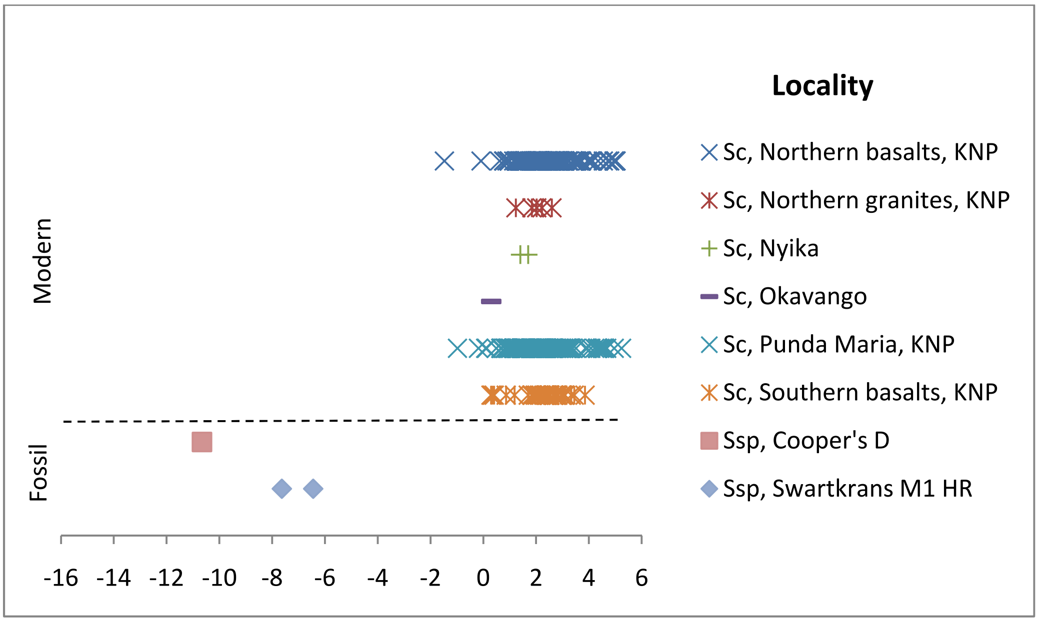

Figure 4.16. $\delta^{13}C$ values of *Syncerus* by locality.

4.6.4 Hippotragini

***Hippotragus* sp. (Hsp)**

This species was sampled from Cooper's D and Swartkrans Member 3 (Table 4.11, Figure 4.17). Data from Cooper's D yielded a mean of -3.4 ± 2.4‰ (range -5.4‰ to -0.7‰) and from Swartkrans Member 3, a mean of -3.4 ± 1.9‰ (range -4.7‰ to -2.1‰). Specimens from these two fossil deposits indicate some C_3 plant selection. In contrast to the modern forms that have an OC_4 diet, fossil *Hippotragus* sp. had a flexible diet.

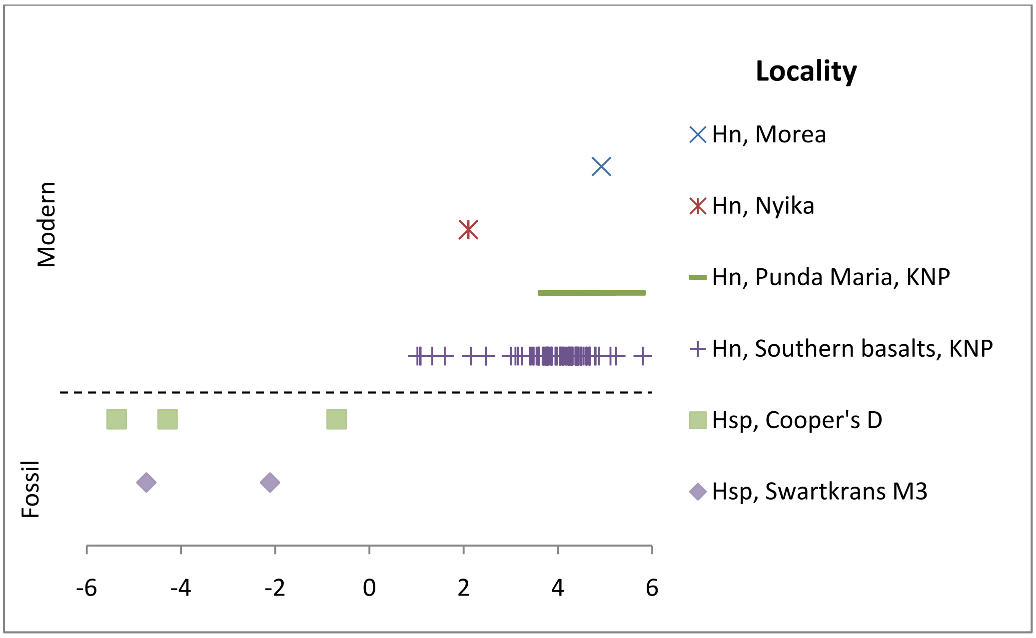

Figure 4.17. $\delta^{13}C$ values of modern and fossil *Hippotragus* by locality.

4.6.5 Neotragini

***Oreotragus oreotragus* (Oor)**

The fossil klipspringer from Swartkrans Member 2 had a δ^{13}C value of -11.7‰ (Table 4.11, Figure 4.18). Two specimens from Makapansgat Member 3 had a value of -11.6‰ (Table 4.12). The fossil klipspringer had similar values to modern forms.

***Ourebia ourebi* (Oou)**

One specimen sampled from Swartkrans Member 2 indicates a mixed C_3–C_4 diet (-4.2‰) and was more negative than modern oribi (Table 4.11, Figure 4.18).

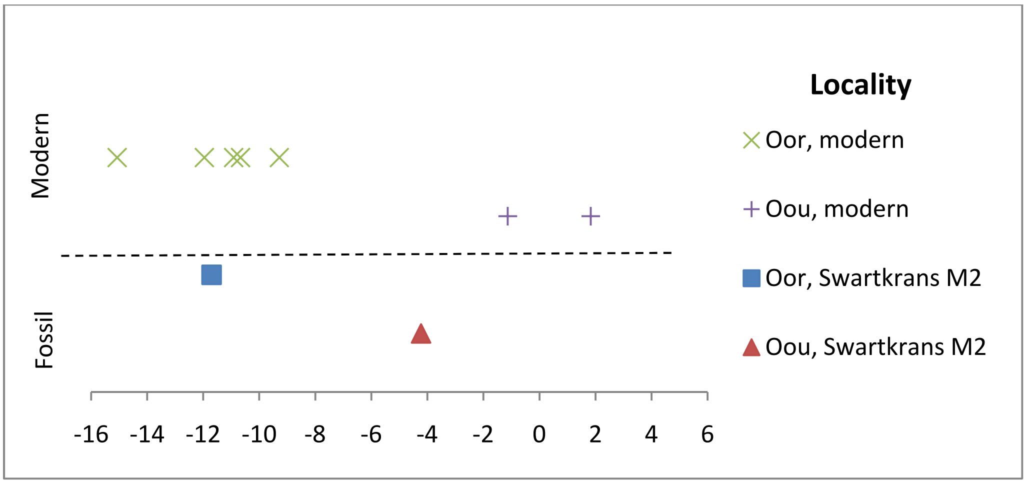

Figure 4.18. δ^{13}C values of modern and fossil *O. oreotragus* and *O. ourebi* by locality.

***Raphicerus campestris* (Rc)**

One specimen from Cooper's D and Swartkrans Member 3 had a mixed C_3–C_4 diet (5.9‰ and -8.0‰, respectively; Table 4.11 and Figure 4.19). Four specimens from Swartkrans Member 2 ranged from OC_3 (-11.4‰) to mixed C_3–C_4 (-7.1‰). There were no significant dietary differences between modern and fossil specimens from Swartkrans Member 2 (ANOVA, $F = 1.2$, $P>0.05$; Table 4.16). On average, the modern springbok is a C_3 feeder. The fossil steenbok from Cooper's D had more positive $\delta^{13}C$ values compared to the modern form suggesting a more sustained and important reliance on C_4 vegetation.

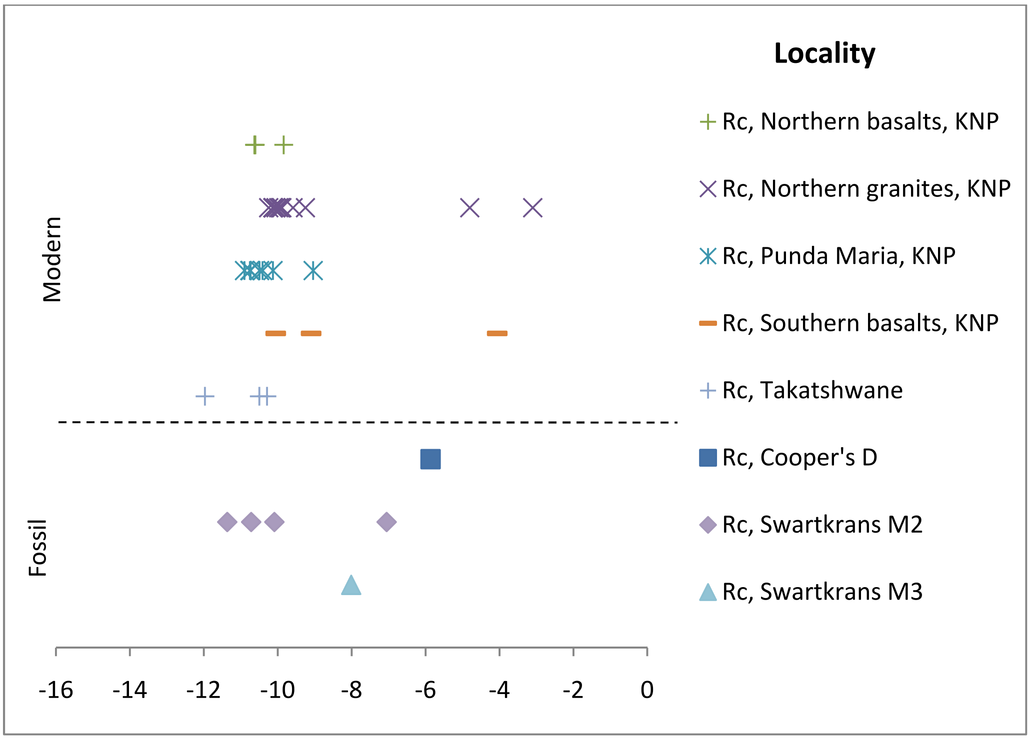

Figure 4.19. $\delta^{13}C$ values of modern and fossil *R. campestris* by locality.

4.6.6 Ovibovini

***Makapania* sp. (Masp)**

Four specimens were sampled only from Swartkrans Hanging Remnant (Table 4.11). These specimens had flexible diets, ranging from -5.1‰ to -2.0‰. Several specimens of *Makapania broomi* from Makapansgat Member 3 and Sterkfontein Member 4 were examined (Table 4.12). The specimens from Sterkfontein Member 4 had values that ranged from VC_3 (-10.3‰) to mixed (-3.2‰). Four specimens from Makapansgat Member 3 had similar values to Swartkrans Hanging Remnant, ranging from -5.3‰ to -1.0‰. ANOVA was used to determine if there were significant differences between fossil deposits. There were dietary differences ($F = 5.5$, $P = 0.024$; Table 4.16). Pairwise comparisons indicate differences between Sterkfontein Member 4 and Makapansgat Member 3 and Swartkrans Hanging Remnant (Table 4.16).

4.6.7 Peleini

***Pelea capreolus* (Pc)**

The mean $\delta^{13}C$ value for Cooper's D, (-9.3 ± 1.7‰), Swartkrans Member 1, (-10.0 ± 2.9) and Swartkrans Member 2, (-10.1 ±.8) indicate an average VC_3 diet (Table 4.11, Figure 4.20). The fossil rhebok diet ranged from OC_3 (-12.0‰) to mixed C_3–C_4 (-7.9‰). Modern specimens had more positive $\delta^{13}C$ values than fossil forms. To examine if there were any significant dietary difference between modern and fossil *P. capreolus*, an Independent t-test was performed with no significant dietary differences observed ($t = -2.2$, $P > 0.05$; Table 4.16).

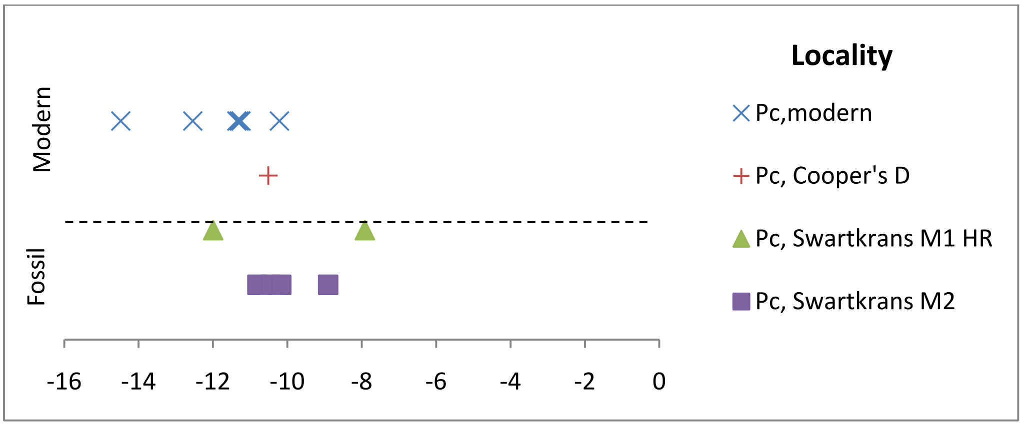

Figure 4.20. δ^{13}C values of *P. capreolus* by locality.

4.6.8 Reduncini

Redunca fulvorufula (Rf)

Only one specimen was sampled from Cooper's D and had an OC$_4$ diet (2.5‰) similar to its modern counterpart (Table 4.11, Figure 4.21).

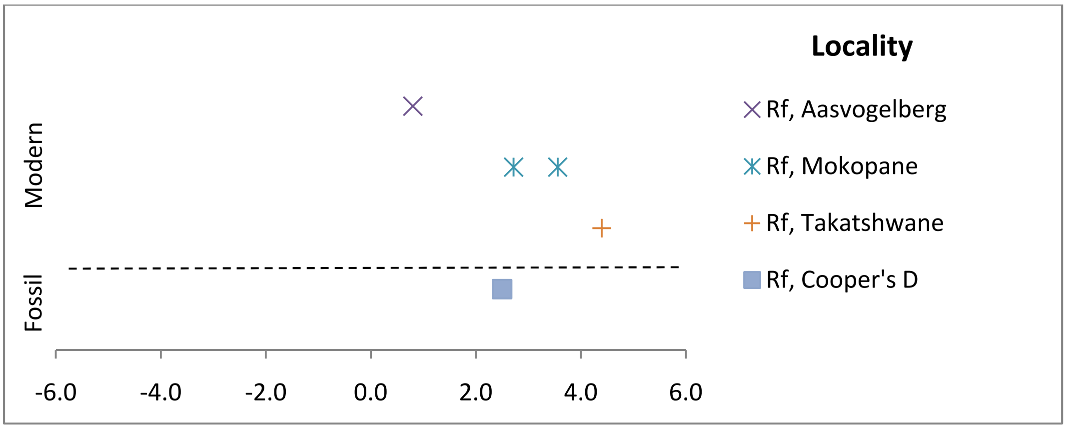

Figure 4.21. δ^{13}C values of modern and fossil *R. fulvorufula* by locality.

4.6.9 Tragelaphini

Tragelaphus oryx **(To)**

Two specimens were sampled from Swartkrans Member 2 and had values of -10‰ and -9‰ with an average -9.5 ± 0.7‰ (Table 4.11, Figure 4.22).

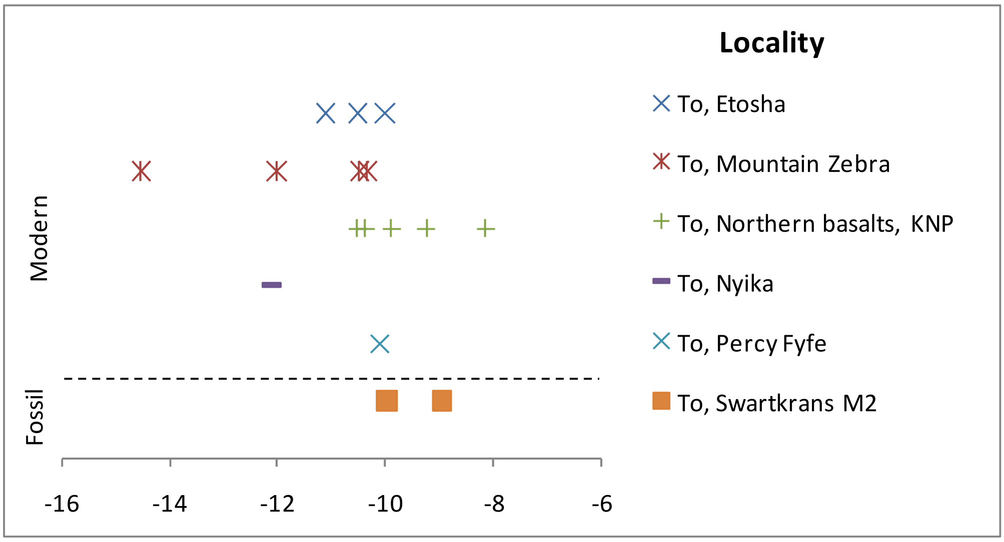

Figure 4.22. $\delta^{13}C$ values of modern and fossil *T. oryx* by locality.

Tragelaphus strepsiceros **(Tst)**

Fossil kudu were sampled from Cooper's D and Swartkrans Hanging Remnant (Table 4.11, Figure 4.23). Specimens from Cooper's D had $\delta^{13}C$ values of -9.2 ± 2.5‰ (range -10.9‰ to -6.3‰). The Swartkrans Hanging Remnant specimen was within the range for Cooper's D (-10.1‰). Nine specimens from Swartkrans Hanging Remnant were sampled by previous studies (Table 4.12). The $\delta^{13}C$ values for these specimens ($\bar{x}$ = -10.4 ± 1.2‰, range -12.4 to -8.2) were slightly more negative than Cooper's D (Table 4.13). Four kudu specimens from

Sterkfontein Member 4 were variable and ranged from -10.0‰ to -8.1‰ with a mean of -8.8 ± 0.8‰ (Table 4.15). Fossil kudu from Sterkfontein Member 4 and Swartkrans Hanging Remnant were statistically compared to moderns and significant differences were found (ANOVA, $F = 5.3$, $P = 0.006$; Table 4.16). Pairwise comparisons support dietary differences between Swartkrans Hanging Remnant and Sterkfontein Member 4 (Table 4.16).

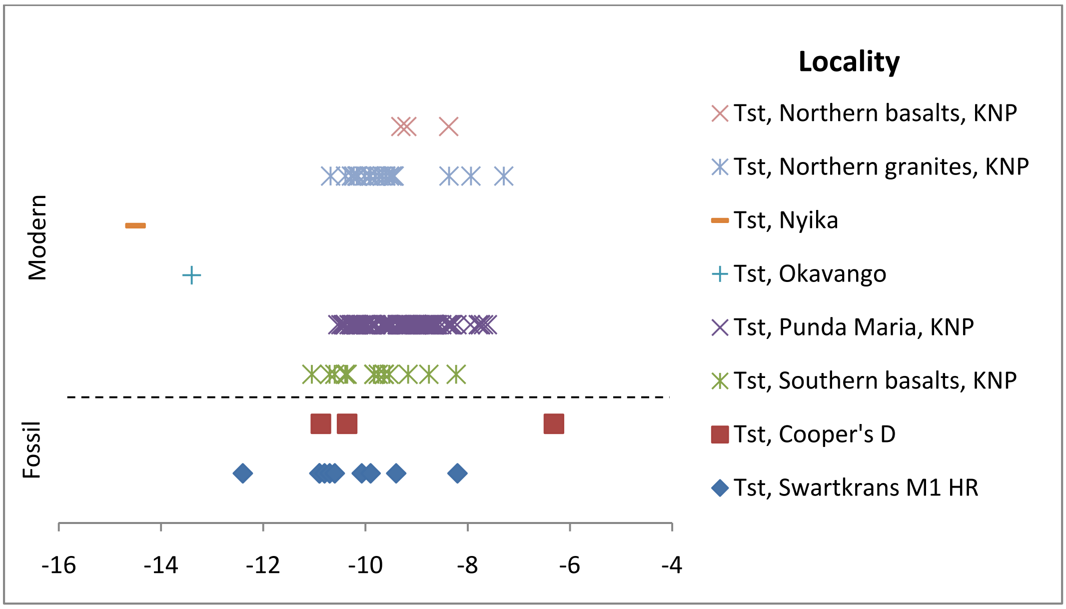

Figure 4.23. δ^{13}C values of modern and fossil *T. strepsiceros* by locality.

***Tragelaphus* sp. (Tsp)**

The two specimens from Cooper's D had a mixed C_3–C_4 diet (-3.1‰) and a specimen from Swartkrans Member 2 had a δ^{13}C value of -1.4‰ (Lee-Thorp and van der Merwe 1993). These specimens are more reliant on C_4 resources compared to fossil specimens of *T. oryx* and *T. strepsiceros*. Both, sitatunga (*T. spekei*) and nyala (*T. angasii*) specimens range from C_3 to C_4 feeders (Sponheimer et al. 2003; Codron 2003) and the specimens from Cooper's D and Swartkrans Member 2 may represent either of these species. However, classification to species level is not permissible at this point and requires more material for appropriate identification.

Table 4.11. δ^{13}C values for fossil bovid taxa from Cooper's D and Swartkrans Members 1–3.

Specimen	Taxa	Deposit	δ^{13}C	Diet
Tribe Alcelaphini				
CD 7452	*Connochaetes* sp.	Cooper's D	-4.8	Mixed C_3-C_4
CD 7414	*Connochaetes* sp.	Cooper's D	-3.4	Mixed C_3-C_4
CD 1896	*Connochaetes* sp.	Cooper's D	-2.7	Mixed C_3-C_4
CD 7402	*Connochaetes* sp.	Cooper's D	-1.9	Mixed C_3-C_4
CD 6181	*Connochaetes* sp.	Cooper's D	-1.2	VC_4
CD 244	*Connochaetes* sp.	Cooper's D	-0.4	VC_4
CD 3702	*Connochaetes* sp.	Cooper's D	-0.2	VC_4
SK 2703	*Connochaetes* sp.	Swartkrans M1 HR	-2.7	Mixed C_3-C_4
SK 2482	*Connochaetes* sp.	Swartkrans M1 HR	-2.0	Mixed C_3-C_4
SK 2284	*Connochaetes* sp.	Swartkrans M1 HR	-1.8	VC_4
SK 2422	*Connochaetes* sp.	Swartkrans M1 HR	-0.8	VC_4
SK 2586	*Connochaetes* sp.	Swartkrans M1 HR	0.4	VC_4
SKX 8530	*Connochaetes* sp.	Swartkrans M1 LB	-1.1	VC_4
SKX 13821	*Connochaetes* sp.	Swartkrans M1 LB	-0.7	VC_4
SKX 5843	*Connochaetes* sp.	Swartkrans M1 LB	-0.5	VC_4
SKX 9353a	*Connochaetes* sp.	Swartkrans M1 LB	0.2	VC_4
SKX 2829	*Connochaetes* sp.	Swartkrans M2	-2.1	Mixed C_3-C_4
SKX 29279	*Connochaetes* sp.	Swartkrans M3	-3.0	Mixed C_3-C_4
SKX 20050	*Connochaetes* sp.	Swartkrans M3	-2.2	Mixed C_3-C_4
SKX 37639	*Connochaetes* sp.	Swartkrans M3	-2.2	Mixed C_3-C_4
SKX 29325	*Connochaetes* sp.	Swartkrans M3	-1.8	VC_4
SKX 37187a	*Connochaetes* sp.	Swartkrans M3	-0.5	VC_4
CD 297	*Damaliscus* sp.	Cooper's D	-3.6	Mixed C_3-C_4
CD 8153	*Damaliscus* sp.	Cooper's D	-2.3	Mixed C_3-C_4
CD 5405	*Damaliscus* sp.	Cooper's D	-2.1	Mixed C_3-C_4
CD 1928	*Damaliscus* sp.	Cooper's D	-0.8	VC_4
CD 6202	*Damaliscus* sp.	Cooper's D	-0.8	VC_4
CD 219	*Damaliscus* sp.	Cooper's D	-0.6	VC_4
CD 1926	*Damaliscus* sp.	Cooper's D	-0.5	VC_4
CD 8182	*Damaliscus* sp.	Cooper's D	-0.2	VC_4
SK 3832	*Damaliscus* sp.	Swartkrans M1 HR	-2.5	Mixed C_3-C_4
SK 3135	*Damaliscus* sp.	Swartkrans M1 HR	-0.6	VC_4
SK 11777	*Damaliscus* sp.	Swartkrans M2	-1.6	VC_4
SK 3123	*Damaliscus* sp.	Swartkrans M2	-1.1	VC_4
SK 1520	*Damaliscus* sp.	Swartkrans M2	-0.1	VC_4
SK 5123	*Damaliscus* sp.	Swartkrans M2	1.3	VC_4
SK 11390	*Damaliscus* sp.	Swartkrans M2	1.6	VC_4
SK 7335	*Damaliscus* sp.	Swartkrans M2	2.0	VC_4
SKX 32639	*Damaliscus* sp.	Swartkrans M3	-7.2	Mixed C_3-C_4
CD 6190	*Megalotragus* sp.	Cooper's D	-1.9	Mixed C_3-C_4
CD 1247	*Megalotragus* sp.	Cooper's D	-0.5	VC_4
CD 5411	*Megalotragus* sp.	Cooper's D	-0.1	VC_4
SK 3031	*Megalotragus* sp.	Swartkrans M1 HR	-0.2	VC_4
SK 2245	*Megalotragus* sp.	Swartkrans M1 HR	0.4	VC_4
SKX 9582	*Megalotragus* sp.	Swartkrans M1 LB	-5.0	Mixed C_3-C_4

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Table 4.11. continued

Specimen	Taxa	Deposit	$\delta^{13}C$	Diet
Tribe Alcelaphini				
SKX 1349	*Megalotragus* sp.	Swartkrans M2	-9.1	VC_3
SK 1953	*Megalotragus* sp.	Swartkrans M2	-4.2	Mixed C_3-C_4
SK 3249	*Megalotragus* sp.	Swartkrans M2	-3.0	Mixed C_3-C_4
SKX 1243	*Megalotragus* sp.	Swartkrans M2	-1.5	VC_4
SKX 29602	*Megalotragus* sp.	Swartkrans M3	-1.6	VC_4
SKX 27800	*Megalotragus* sp.	Swartkrans M3	-0.8	VC_4
SK 1961	*Rabaticeras porrocornutus*	Swartkrans M1 HR	-3.9	Mixed C_3-C_4
SK 3002	*Rabaticeras porrocornutus*	Swartkrans M1 HR	-3.7	Mixed C_3-C_4
SK 2985	*Rabaticeras porrocornutus*	Swartkrans M1 HR	-0.1	VC_4
SK 3043	*Rabaticeras porrocornutus*	Swartkrans M1 HR	0.2	VC_4
Tribe Antilopini				
SK 2404	*Antidorcas bondi*	Swartkrans M2	-2.8	Mixed C_3-C_4
SK 9385	*Antidorcas bondi*	Swartkrans M2	-3.3	Mixed C_3-C_4
CD 1273	*Antidorcas marsupialis*	Cooper's D	-11.5	OC_3
CD 6209	*Antidorcas marsupialis*	Cooper's D	-10.6	VC_3
CD 7449	*Antidorcas marsupialis*	Cooper's D	-10.5	VC_3
CD 8171	*Antidorcas marsupialis*	Cooper's D	-9.6	VC_3
CD 8161	*Antidorcas marsupialis*	Cooper's D	-9.6	VC_3
CD 3160	*Antidorcas marsupialis*	Cooper's D	-9.4	VC_3
CD 3701	*Antidorcas marsupialis*	Cooper's D	-8.6	VC_3
CD 7485	*Antidorcas marsupialis*	Cooper's D	-7.0	Mixed C_3-C_4
CD 5853	*Antidorcas marsupialis*	Cooper's D	-5.6	Mixed C_3-C_4
SK 3037	*Antidorcas marsupialis*	Swartkrans M2	-11.6	OC_3
SKX 33839	*Antidorcas marsupialis*	Swartkrans M3	-11.6	OC_3
CD 8179	*Antidorcas recki*	Cooper's D	-10.5	VC_3
CD 7448	*Antidorcas recki*	Cooper's D	-8.3	Mixed C_3-C_4
CD 6165	*Antidorcas recki*	Cooper's D	-7.2	Mixed C_3-C_4
CD 1886	*Antidorcas recki*	Cooper's D	-6.2	Mixed C_3-C_4
CD 8166	*Antidorcas recki*	Cooper's D	-4.7	Mixed C_3-C_4
SKX 811[3]	*Antidorcas recki*	Swartkrans M2	-12.9	OC_3
SK 2972	*Gazella* sp.	Swartkrans M1 HR	-7.6	Mixed C_3-C_4
Tribe Bovini				
CD 11062	*Syncerus* sp.	Cooper's D	-10.7	VC_3
SK 3130	*Syncerus* sp.	Swartkrans M1 HR	-7.6	Mixed C_3-C_4
SK 3074	*Syncerus* sp.	Swartkrans M1 HR	-6.4	Mixed C_3-C_4
Tribe Hippotragini				
CD 6179	*Hippotragus* sp.	Cooper's D	-5.4	Mixed C_3-C_4
CD 3119	*Hippotragus* sp.	Cooper's D	-4.3	Mixed C_3-C_4
CD 7456	*Hippotragus* sp.	Cooper's D	-0.7	VC_4
SKX 34892	*Hippotragus* sp.	Swartkrans M3	-4.7	Mixed C_3-C_4
SKX 37042	*Hippotragus* sp.	Swartkrans M3	-2.1	Mixed C_3-C_4
Tribe Neotragini				
SK 14168	*Ourebia ourebi*	Swartkrans M2	-4.2	Mixed C_3-C_4
CD 1214	*Raphicerus campestris*	Cooper's D	-5.9	Mixed C_3-C_4
SK 2108	*Raphicerus campestris*	Swartkrans M2	-11.4	OC_3

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Table 4.11. continued

Specimen	Taxa	Deposit	$\delta^{13}C$	Diet
SK 2719	*Raphicerus campestris*	Swartkrans M2	-10.7	VC$_3$
SK 5930	*Raphicerus campestris*	Swartkrans M2	-10.1	VC$_3$
SK 4287	*Raphicerus campestris*	Swartkrans M2	-7.1	Mixed C$_3$-C$_4$
SKX 38091	*Raphicerus campestris*	Swartkrans M3	-8.0	Mixed C$_3$-C$_4$
Tribe Ovibovini				
SK 3113	*Makapania* sp.	Swartkrans M1 HR	-5.1	Mixed C$_3$-C$_4$
SK 2373	*Makapania* sp.	Swartkrans M1 HR	-3.8	Mixed C$_3$-C$_4$
SK 3150	*Makapania* sp.	Swartkrans M1 HR	-2.7	Mixed C$_3$-C$_4$
SK 2759	*Makapania* sp.	Swartkrans M1 HR	-2.0	Mixed C$_3$-C$_4$
Tribe Peleini				
CD 5430	*Pelea capreolous*	Cooper's D	-10.5	VC$_3$
CD 15604	*Pelea capreolous*	Cooper's D	-8.1	Mixed C$_3$-C$_4$
SK 2273	*Pelea capreolous*	Swartkrans M1 HR	-12.0	OC$_3$
SK 2682	*Pelea capreolous*	Swartkrans M1 HR	-7.9	Mixed C$_3$-C$_4$
SK 2990	*Pelea capreolous*	Swartkrans M2	-10.8	VC$_3$
SK 6047	*Pelea capreolous*	Swartkrans M2	-10.4	VC$_3$
SK 2981	*Pelea capreolous*	Swartkrans M2	-10.2	VC$_3$
SK 2246	*Pelea capreolous*	Swartkrans M2	-8.9	VC$_3$
Tribe Reduncini				
CD 1220	*Redunca fulvorufula*	*Cooper's D*	2.5	OC$_4$
Tribe Tragelaphini				
SK 114171	*Tragelaphus oryx*	Swartkrans M2	-10.0	VC$_3$
SKX 4026	*Tragelaphus oryx*	Swartkrans M2	-9.0	C$_3$
CD 255	*Tragelaphus* sp.	Cooper's D	-4.0	Mixed C$_3$-C$_4$
CD 7473	*Tragelaphus* sp.	Cooper's D	-2.2	Mixed C$_3$-C$_4$
CD 7474	*Tragelaphus strepsiceros*	Cooper's D	-10.9	VC$_3$
CD 309	*Tragelaphus strepsiceros*	Cooper's D	-10.4	VC$_3$
CD 5399	*Tragelaphus strepsiceros*	Cooper's D	-6.3	Mixed C$_3$-C$_4$
SK 3000	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.1	VC$_3$

Table 4.12. δ^{13}C values for fossil bovid taxa from Swartkrans Members 1–3 from other studies.

Specimen	**Taxa**	**Deposit**	**δ^{13}C**	**Diet**
Tribe Alcelaphini				
SK 2061	*Connochaetes* sp.	Swartkrans M1 HR	1.0	VC$_4$
SK 2110	*Connochaetes* sp.	Swartkrans M1 HR	-3.1	Mixed C$_3$-C$_4$
SK 2261	*Connochaetes* sp.	Swartkrans M1 HR	-1.2	VC$_4$
SK 2354	*Connochaetes* sp.	Swartkrans M1 HR	-1.4	VC$_4$
SK 5946	*Connochaetes* sp.	Swartkrans M1 HR	-0.9	VC$_4$
SK 2483	*Connochaetes* sp.	Swartkrans M1 HR	-3.7	Mixed C$_3$-C$_4$
SK 3097	*Connochaetes* sp.	Swartkrans M1 HR	0.1	VC$_4$
SF91	Connochaetes sp.	Sterkfontein M5	-1.4	VC$_4$
SF334	Connochaetes sp.	Sterkfontein M5	-1.1	VC$_4$
SF92	Connochaetes sp.	Sterkfontein M5	0.7	VC$_4$
SF95	Connochaetes sp.	Sterkfontein M5	2.7	OC$_4$
Sts2200	Connochaetes sp.	Sterkfontein M4	-4.9	Mixed C$_3$-C$_4$
SF114	Connochaetes sp.	Sterkfontein M4	-1.9	Mixed C$_3$-C$_4$
SF112	Connochaetes sp.	Sterkfontein M4	-0.7	VC$_4$
SK 10653	*Damaliscus* sp.	Swartkrans M2	-0.7	VC$_4$
SK 4241	*Damaliscus* sp.	Swartkrans M2	0.7	VC$_4$
SK 9897	*Damaliscus* sp.	Swartkrans M2	2.2	OC$_4$
SE1185	*Damaliscus* sp.	Sterkfontein M5	-4.9	Mixed C$_3$-C$_4$
SE1828	*Damaliscus* sp.	Sterkfontein M5	-1.6	VC$_4$
SE1728.1	*Damaliscus* sp.	Sterkfontein M5	-1.5	VC$_4$
SK 2063	*Megalotragus* sp.	Swartkrans M1 HR	2.2	OC$_4$
Tribe Antilopini				
SK 12273	*Antidorcas bondi*	Swartkrans M2	-3.8	Mixed C$_3$-C$_4$
SK 2574	*Antidorcas bondi*	Swartkrans M2	-4.5	Mixed C$_3$-C$_4$
SK 3841	*Antidorcas bondi*	Swartkrans M2	-1.7	VC$_4$
SK 5907	*Antidorcas bondi*	Swartkrans M2	-2.9	Mixed C$_3$-C$_4$
SK 5922	*Antidorcas bondi*	Swartkrans M2	-2.4	Mixed C$_3$-C$_4$
SK 5962	*Antidorcas bondi*	Swartkrans M2	-4.2	Mixed C$_3$-C$_4$
SK 6123	*Antidorcas bondi*	Swartkrans M2	-4.3	Mixed C$_3$-C$_4$
Sts1577	*Antidorcas bondi*	Sterkfontein M4	-1.9	Mixed C$_3$-C$_4$
Sts1125	*Antidorcas bondi*	Sterkfontein M4	-1.2	VC$_4$
SKX 1896	*Antidorcas marsupialis*	Swartkrans M2	-10.6	VC$_3$
SKX 2736	*Antidorcas marsupialis*	Swartkrans M2	-11.5	OC$_3$
SKX 811	*Antidorcas recki*	Swartkrans M2	-12.9	OC$_3$
SE 1855.1	*Antidorcas recki*	Sterkfontein M5	-12.7	OC$_3$
SE 1258	*Antidorcas recki*	Sterkfontein M5	-10.8	VC$_3$
Sts 1944	*Antidorcas recki*	Sterkfontein M4	-13.9	OC$_3$
Sts 1435	*Antidorcas recki*	Sterkfontein M4	-13.7	OC$_3$
Sts 1325a	*Antidorcas recki*	Sterkfontein M4	-13.3	OC$_3$
Sts 1400	*Antidorcas recki*	Sterkfontein M4	-13.3	OC$_3$
Sts 2076	*Antidorcas recki*	Sterkfontein M4	-12.0	OC$_3$
Sts 2369	*Antidorcas recki*	Sterkfontein M4	-10.5	VC$_3$
Sts 1596	*Antidorcas recki*	Sterkfontein M4	-4.5	Mixed C$_3$-C$_4$

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Table 4.12. continued

Specimen	**Taxa**	**Deposit**	**$\delta^{13}C$**	**Diet**
Tribe Ovibovini				
Sts 952	*Makapania broomi*	Sterkfontein M4	-10.8	VC_3
Sts 1925	*Makapania broomi*	Sterkfontein M4	-8.6	VC_3
Sts 2059b	*Makapania broomi*	Sterkfontein M4	-7.7	Mixed C_3-C_4
Sts 1721	*Makapania broomi*	Sterkfontein M4	-6.8	Mixed C_3-C_4
Sts 2565	*Makapania broomi*	Sterkfontein M4	-3.2	Mixed C_3-C_4
M 978	*Makapania broomi*	Makapansgat M3	-5.3	Mixed C_3-C_4
M 1398	*Makapania broomi*	Makapansgat M3	-3.6	Mixed C_3-C_4
M 6528	*Makapania broomi*	Makapansgat M3	-3.5	Mixed C_3-C_4
M 6274	*Makapania broomi*	Makapansgat M3	-1.0	VC_4
Tribe Neotragini				
SK 1631	*Oreotragus oreotragus*	Swartkrans M2	-11.7	OC_3
M 6293	*Oreotragus oreotragus*	Makapansgat M3	-11.7	OC_3
M 997	*Oreotragus oreotragus*	Makapansgat M3	-11.4	OC_3
Tribe Tragelaphini				
SK 2329	*Tragelaphus* sp.	Swartkrans M2	-1.4	VC_4
SK 2304	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.9	VC_3
SK 2576	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.8	VC_3
SK 2681	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.9	VC_3
SK 3023	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.7	VC_3
SK 2541	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-12.4	OC_3
SK 14112	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-10.6	VC_3
SK 2095	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-8.2	Mixed C_3-C_4
SK 2281	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-9.4	VC_3
SK 3110	*Tragelaphus strepsiceros*	Swartkrans M1 HR	-9.9	VC_3
Sts 1573	*Tragelaphus strepsiceros*	Sterkfontein M4	-10.0	VC_3
Sts 46	*Tragelaphus strepsiceros*	Sterkfontein M4	-9.0	VC_3
Sts 2121	*Tragelaphus strepsiceros*	Sterkfontein M4	-8.2	Mixed C_3-C_4
Sts 1300	*Tragelaphus strepsiceros*	Sterkfontein M4	-8.1	Mixed C_3-C_4

Table 4.13. Descriptive statistics for fossil bovid enamel from Cooper's D and Swartkrans Members 1–3.

Tribe	Taxa	Locality	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.	CD	7	-4.8	-0.2	-2.1	1.7
		SK HR	5	-2.7	0.4	-1.4	1.2
		SK LB	4	-1.1	0.2	-0.5	0.5
		SK M2	1	.	.	-2.1	.
		SK M3	5	-3.0	-0.5	-1.9	0.9
	Damaliscus sp.	CD	8	-3.6	-0.2	-1.4	1.2
		SK HR	2	-2.5	-0.6	-1.5	1.3
		SK M2	6	-1.6	2.0	0.3	1.5
	Megalotragus sp.	CD	3	-1.9	-0.1	-0.9	0.9
		SK HR	2	-0.2	0.4	0.1	0.4
		SK LB	1	.	.	-5.0	.
		SK M2	4	-4.2	-1.5	-2.9	1.3
		SK M3	2	-1.6	-0.8	-1.2	0.6
	Rabaticeras porrocornutus	SK HR	4	-3.9	0.2	-1.9	2.2
Antilopini	*Antidorcas bondi*	SK M2	1	.	.	-2.8	.
	Antidorcas marsupialis	CD	9	-11.5	-5.6	-9.2	1.8
		SK M2	1	.	.	-11.6	.
		SK M3	1	.	.	-11.6	.
	Antidorcas recki	CD	5	-10.5	-4.7	-7.4	2.2
	Gazella sp.	SK HR	1	.	.	-7.6	.
Bovini	*Syncerus* sp.	CD	1	.	.	-10.7	.
		SK HR	2	-7.6	-6.4	-7.0	0.8
Hippotragini	*Hippotragus* sp.	CD	3	-5.4	-.7	-3.4	2.4
		SK M3	2	-4.7	-2.1	-3.4	1.9
Neotragini	*Ourebia ourebi*	SK M2	1	.	.	-4.2	.
	Raphicerus campestris	CD	1	.	.	-5.9	.
		SK M2	4	-11.4	-7.1	-9.8	1.9
		SK M3	1	.	.	-8.0	.
Ovibovini	*Makapania* sp.	SK HR	4	-5.1	-2.0	-3.4	1.4
Peleini	*Pelea capreolus*	CD	2	-10.5	-8.1	-9.3	1.7
		SK HR	2	-12.0	-7.9	-10.0	2.9
		SK M2	4	-10.8	-8.9	-10.1	.8
Reduncini	*Redunca fulvorufula*	CD	1	2.5	2.5	2.5	.
Tragelaphini	*Tragelaphus oryx*	SK M2	2	-10.0	-9.0	-9.5	0.7
	Tragelaphus strepsiceros	CD	3	-10.9	-6.3	-9.2	2.5
		SK HR	1	.	.	-10.1	.
	Tragelaphus sp.	CD	2	-4.0	-2.2	-3.1	1.2

Table 4.14. Descriptive statistics for fossil bovid taxa from other studies.

Tribe	Taxa	Locality	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.[1, 5]	SKHR	7	-3.7	1.0	-1.3	1.7
	Damaliscus sp.[5]	SK2	5	-0.7	2.2	0.7	1.5
	Megalotragus sp.[3]	SKHR	1	.	.	2.2	.
Antilopini	*Antidorcas bondi*[4]	SK2	8	-4.5	-1.7	-3.4	1.0
	Antidorcas marsupialis[5]	SK2	2	-11.5	-10.6	-11.1	0.6
	Antidorcas recki[3]	SK2	1	.	.	-12.9	.
Neotragini	*Oreotragus oreotragus*[2]	SK2	1	.	.	-11.7	.
Tragelaphini	*Tragelaphus* sp.[2]	SK2	1	.	.	-1.4	.
	Tragelaphus strepsiceros[1, 3, 5]	SKHR	9	-12.4	-8.2	-10.4	1.2

Data from: [1]Lee-Thorp et al. (1989), [2]Lee-Thorp and van der Merwe (1993), [3]Lee-Thorp et al. (1994), [4]Lee-Thorp et al. (2000), and [5]Lee-Thorp et al. (2007).

Table 4.15. Descriptive statistics for fossil bovid taxa from other South African deposits.

Tribe	Taxa	Deposit	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.[2,3]	Sterkfontein M5	4	-1.4	2.7	0.2	1.9
		Sterkfontein M4	3	-4.9	-0.7	-2.5	2.2
	Damaliscus sp.[2,4]	Sterkfontein M5	3	-4.9	-1.5	-2.7	1.9
Antilopini	*Antidorcas bondi* [2,3]	Sterkfontein M4	2	-1.9	-1.2	-1.6	0.5
	Antidorcas recki [2,3]	Sterkfontein M5	2	-12.7	-10.8	-11.7	1.4
		Sterkfontein M4	7	-13.9	-4.5	-11.6	3.3
	Gazella sp.[1]	Makapansgat M3	2	-12.4	-10.7	-11.5	1.2
Neotragini	*Oreotragus oreotragus* [1]	Makapansgat M3	2	-11.7	-11.4	-11.6	0.2
Ovibovini	*Makapania broomi* [1,2]	Sterkfontein M4	5	-10.8	-3.2	-7.4	2.8
		Makapansgat M3	4	-5.3	-1.0	-3.3	1.7
Tragelaphini	*Tragelaphus strepsiceros* [2]	Sterkfontein M4	4	-10.0	-8.1	-8.8	0.9

Data from: [1]Sponheimer (1999), [2]Luyt (2001), [3]van der Merwe et al. (2003), and [4]Lee-Thorp et al. (2007).

Table 4.16. Statistical analysis of $\delta^{13}C$ data comparing fossil bovid taxa.

A. ANOVA

Taxa	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P value**
Connochaetes	454.0	5	90.8	70.1	**.000**
Damaliscus	188.9	2	94.5	75.3	**.000**
Antidorcas	63.9	3	21.3	4.0	**.015**
Raphicerus campestris	8.6	2	4.3	1.2	.326
Makapania sp.	50.6	2	25.3	5.5	**.024**
Tragelaphus strepsiceros	9.5	2	4.7	5.3	**.006**

Significant differences in bold (P= < 0.05)

B. Pairwise comparisons

1. *Connochaetes* fossils compared to moderns

Tukey HSD	Cooper's D	Modern	Sterkfontein M5	Swartkrans HR	Swartkrans LB
Modern	**.000**				
Sterkfontein M5	**.017**	**.001**			
Swartkrans HR	.754	**.000**	.163		
Swartkrans LB	.245	**.000**	.941	.805	
Swartkrans M3	1	**.000**	*.056*	.928	.434

Significant differences in bold (P= < 0.05)

2. *Damaliscus* fossils compared to moderns

Tukey HSD	Cooper's D	Northern Basalts
Northern basalts	**.000**	
Swartkrans M2	**.002**	**.000**

Significant differences in bold (P= < 0.05)

3. *Antidorcas* fossils compared to moderns

Tukey HSD	*A. marsupialis,* CD	*A. marsupialis,* modern	*A. recki,* CD
A. marsupialis, modern	.930		
A. recki, CD	.518	.713	
A. recki, Sts M4	.173	**.025**	**.017**

Significant differences in bold (P= < 0.05)

4. *Makapania*

Tukey HSD	Makapansgat M3	Sterkfontein M4
Sterkfontein M4	**.042**	
Swartkrans HR	1	**.044**

Significant differences in bold (P= < 0.05)

4. *Tragelaphus* fossils compared to moderns

Tukey HSD	Modern	Sterkfontein M4
Sterkfontein M4	.341	
Swartkrans HR	**.013**	**.016**

Significant differences in bold (P= < 0.05)

C. Independent t-test

Taxa	**t**	**df**	**P value**
P. capreolus	-2.2	8	.063

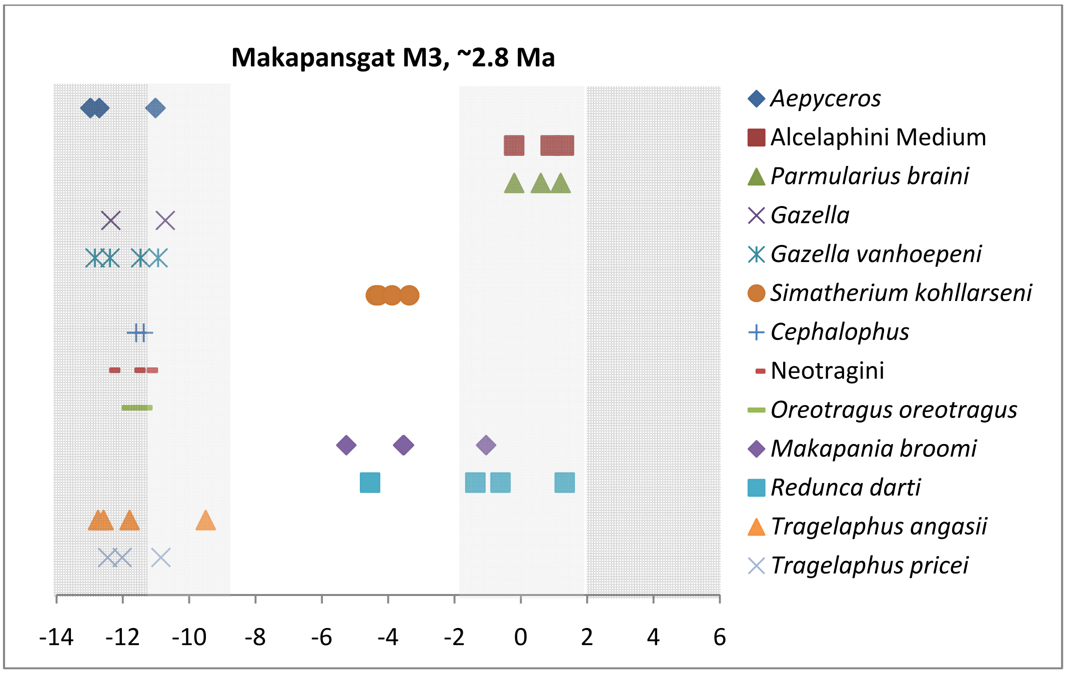
Significant differences in bold (P= < 0.05)

4.7 Palaeoecological profile

The relatively low number of taxa for Swartkrans Lower Bank (n = 2) and Swartkrans Member 3 (n = 6) were excluded from interpretations of vegetation structure for these deposits. Though not all bovid species from Swartkrans Hanging Remnant and Swartkrans Member 2 were sampled numerous bovid species are represented from each deposit.The sampled carbon isotopic data from these two deposits indicate a wide range of dietary strategies, and were used to develop an ecological profile. All known bovid species from Cooper's Cave were sampled. In this study, Cooper's Cave provides the most comprehensive ecological profile based on the dietary behaviour of bovids.

The first appearance of the modern "grazing" guild (*Connochaetes* sp., *Damaliscus* sp., *A. bondi, H. equinus*, and *R. arundinum*) and extinct forms (*Parmularius* sp., *Hippotragus cookei* and *Redunca* cf. *darti*) coexist at Sterkfontein M4 (Kibii 2004). The $\delta^{13}C$ values for alcelaphines tend to be more versatile from Sterkfontein Member 4 compared to Makapansgat Member 3 (Figure 4.24). The bovids from Sterkfontein Member 4 may have required adaptability in their diet along with niche jostling as several new 'graze' species move into the area all within the context of a changing environment (Kingston and Harrison 2007). At this time, southern Africa was moving into a cooler and drier climate (deMenocal 2004; Maslin and Christensen 2007) (Figure 4.27). A significant component of mixed C_3–C_4 first observed at Sterkfontein Member 4 remained dominant in the *P. robustus* sequence (Figures 4.25 and 4.26). The relatively few C_4 specialists and the increase of mixed feeders do not support the interpretations that these deposits were dominated by extensive open grassland habitats (e.g. Reed and Rector 2007; Lee-Thorp et al. 2007; de Ruiter et al. 2009). Although grasses were present, proportions and distribution of grass with respect to other types of vegetation is unknown. Here, grass presence does not equate to grassland-dominated ecosystem. During the early Pleistocene, and even today to a lesser extent, these deposits were adjacent to a river, and were topographically locally diverse suggesting that the fauna had access to variable habitats (Reed 1997). Uniquely, Swartkrans Member 2 (ca. 1.6 Ma) contains substantially more C_3 feeders. A few researchers have hinted that Swartkrans Member 2 was more 'closed and wet' compared to other Swartkrans Members, yet interpret 'predominantly open grassland' for all *P. robustus* deposits at Swartkrans (Lee-Thorp et al. 2007; de Ruiter et al. 2008). A shift to a drier period was observed at Sterkfontein Member 4 and continues throughout the *P. robustus* sequence with a possible wet pulse within this trend at Swartkrans Member 2.

Differential timing of grass expansion between East Africa and southern Africa is proposed. A C_4-dominated ecosystem occurred in East Africa prior to its occurrence in southern Africa. This is supported by $\delta^{13}C$ studies of Olduvai and Kanjera bovids. Kanjera is dominated by C_4 consumers (Plummer et al. 2009), and at Olduvai Tuff 1B and 1F, the 'graze' bovids are more ^{13}C-enriched compared to similar species found in *P. robustus* deposits (van der Merwe *in press*). The dietary behaviours of bovid taxa from the East Africa deposits suggest the presence of a C_4-dominated ecosystem between 2.3 Ma and 1.75 Ma (Figures 4.28 and 4.29; Plummer et al. 2009; van der Merwe *in press*). Whereas Sterkfontein Member 4 and *P. robustus* assemblages suggest a mosaic landscape that had more C_3 vegetation compared to East African deposits around the same time. I hypothesize that a C_4-dominated ecosystem in the Witwatersrand area of South Africa probably only occurred with the onset of pronounced 100 Kyr glacial cycles after 1.2 – 0.8 Ma (deMenocal 2004; Maslin and Christensen 2007) (Figure 4.28).



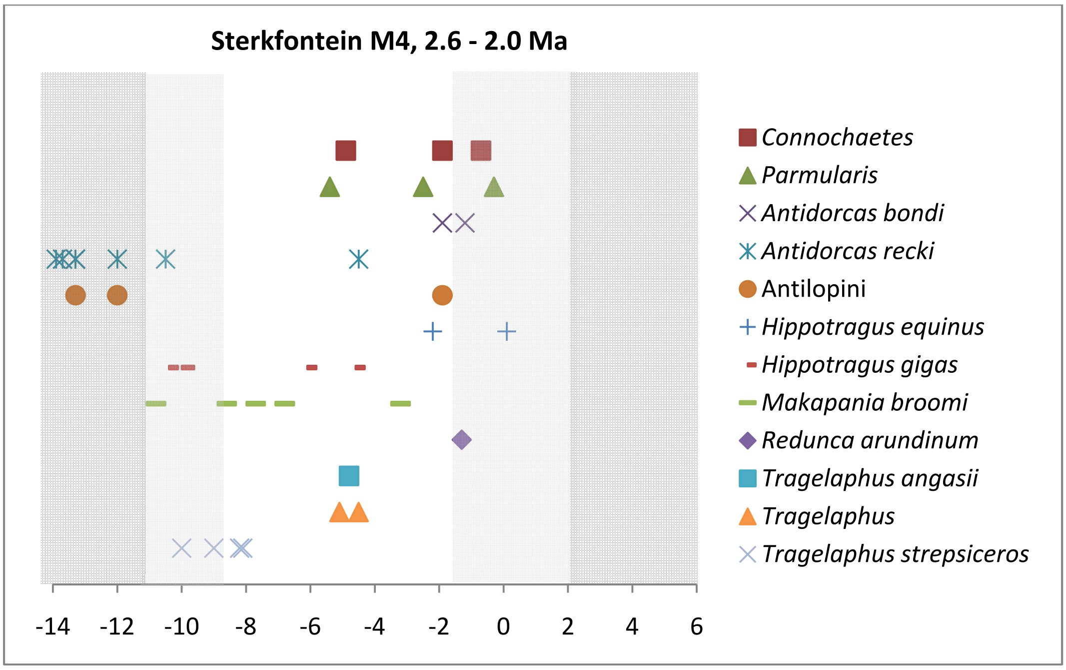
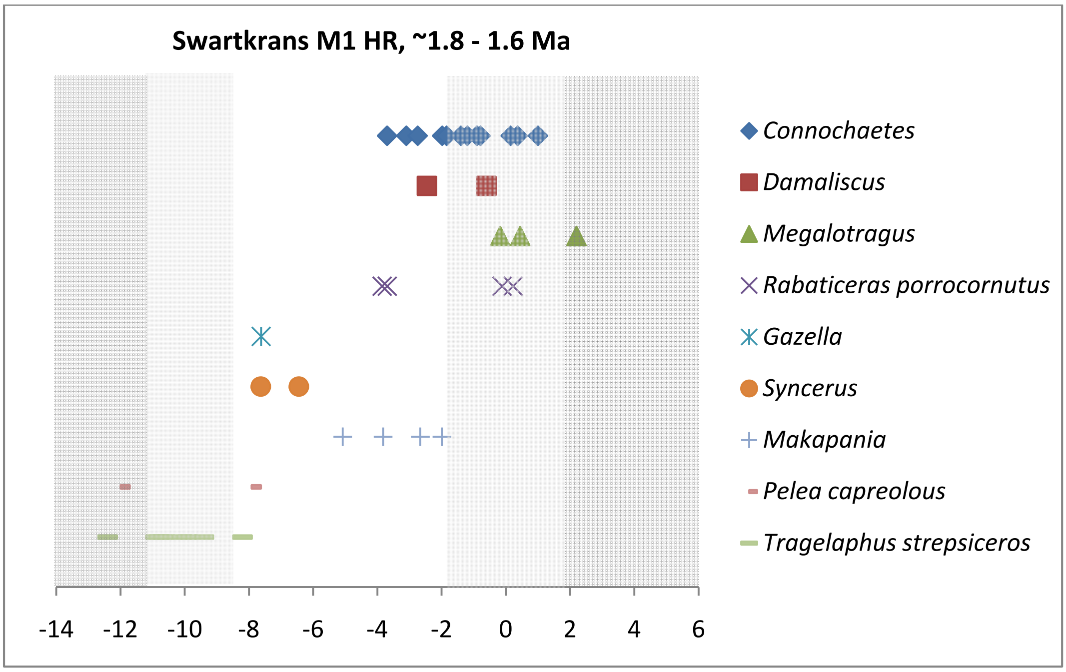


Figure 4.24. δ^{13}C results of bovids from Makapansgat Member 3 and Sterkfontein Member 4. The shading reflects the relative importance of C_3 versus C_4 in the diets of bovids. Values less than -8.5‰ reflect a diet of C_3 vegetation and greater than -1.8‰ a diet of C_4 vegetation.



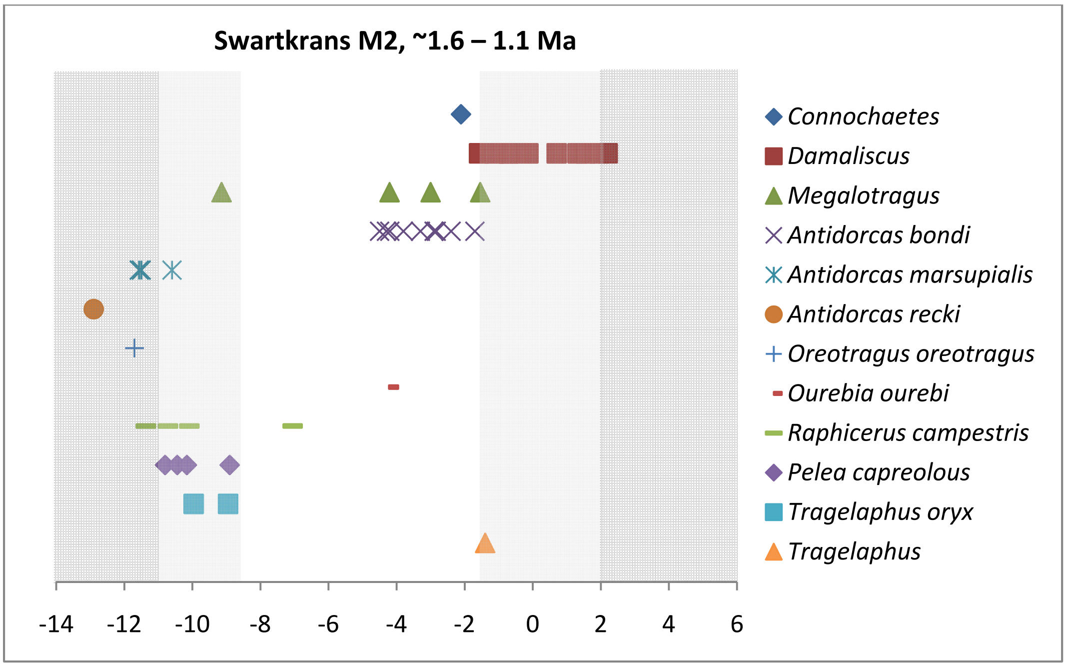


Figure 4.25. $\delta^{13}C$ results of bovids from Swartkrans Member 1 Hanging Remnant and Swartkrans Member 2. The $\delta^{13}C$ values from the present study were combined with Lee-Thorp et al. (1989; 1994, 2000, 2007) and Lee-Thorp and van der Merwe (1993) data from both deposits. The shading reflects the relative

importance of C_3 versus C_4 in the diets of bovids. Values less than -8.5‰ reflect a diet of C_3 vegetation and greater than -1.8‰ a diet of C_4 vegetation.

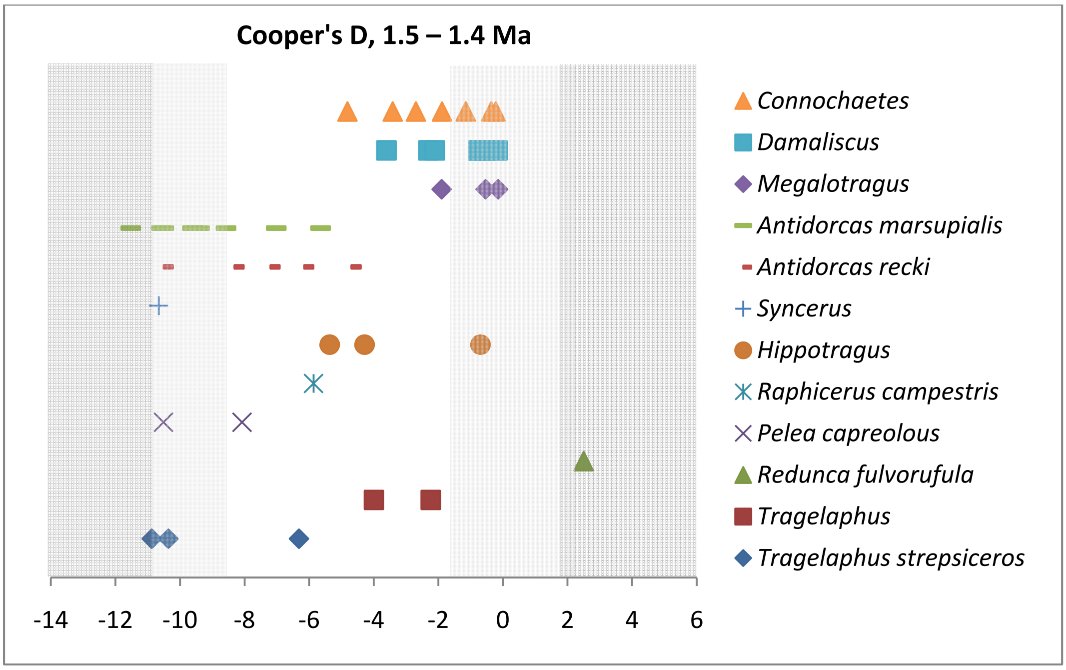


Figure 4.26. $\delta^{13}C$ results of bovids from Cooper's D. The shading reflects the relative importance of C_3 versus C_4 in the diets of bovids. Values less than -8.5‰ reflect a diet of C_3 vegetation and greater than -1.8‰ a diet of C_4 vegetation.

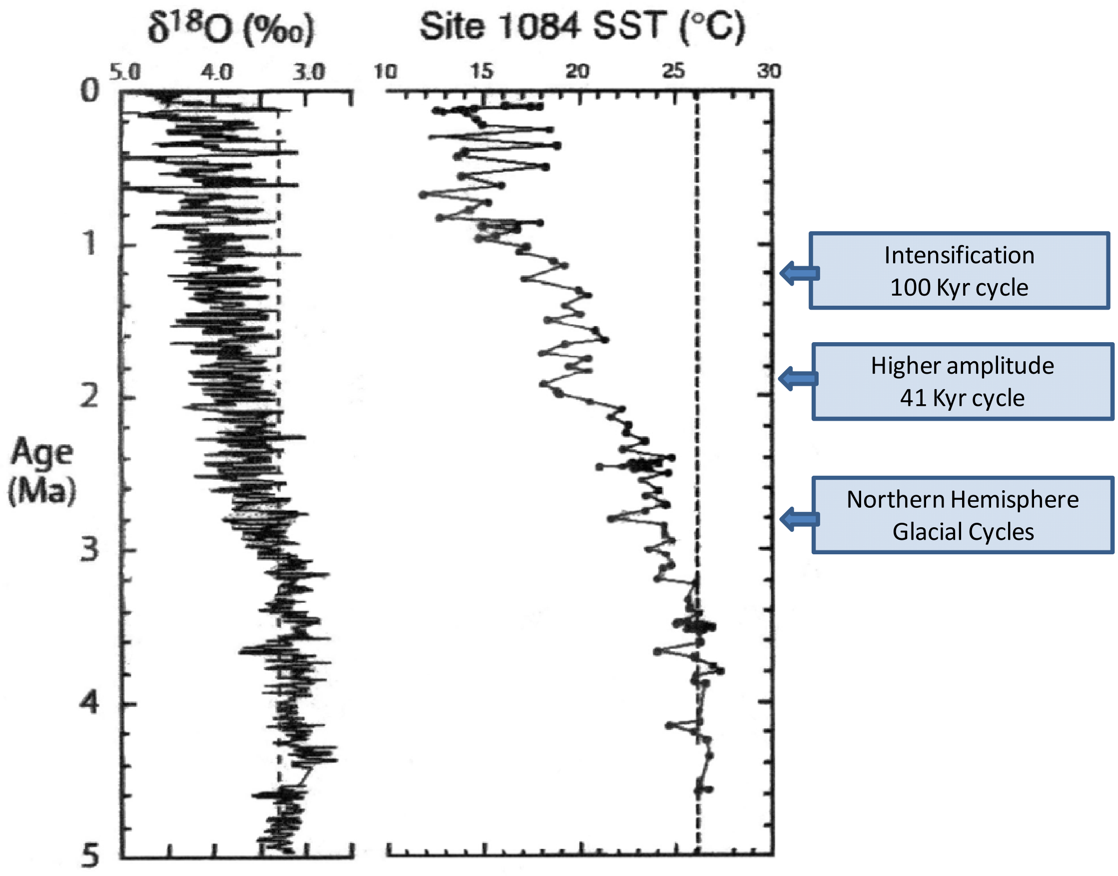


Figure 4.27. Sea surface temperatures from marine sediments. Cores taken from South Atlantic ODP Site 1084 document changes over the last 5 million years (graph from deMenocal 2004). After 3 Ma, the palaeoclimatic indices that demonstrate a drier cooler trend with intermittent wet pulses.

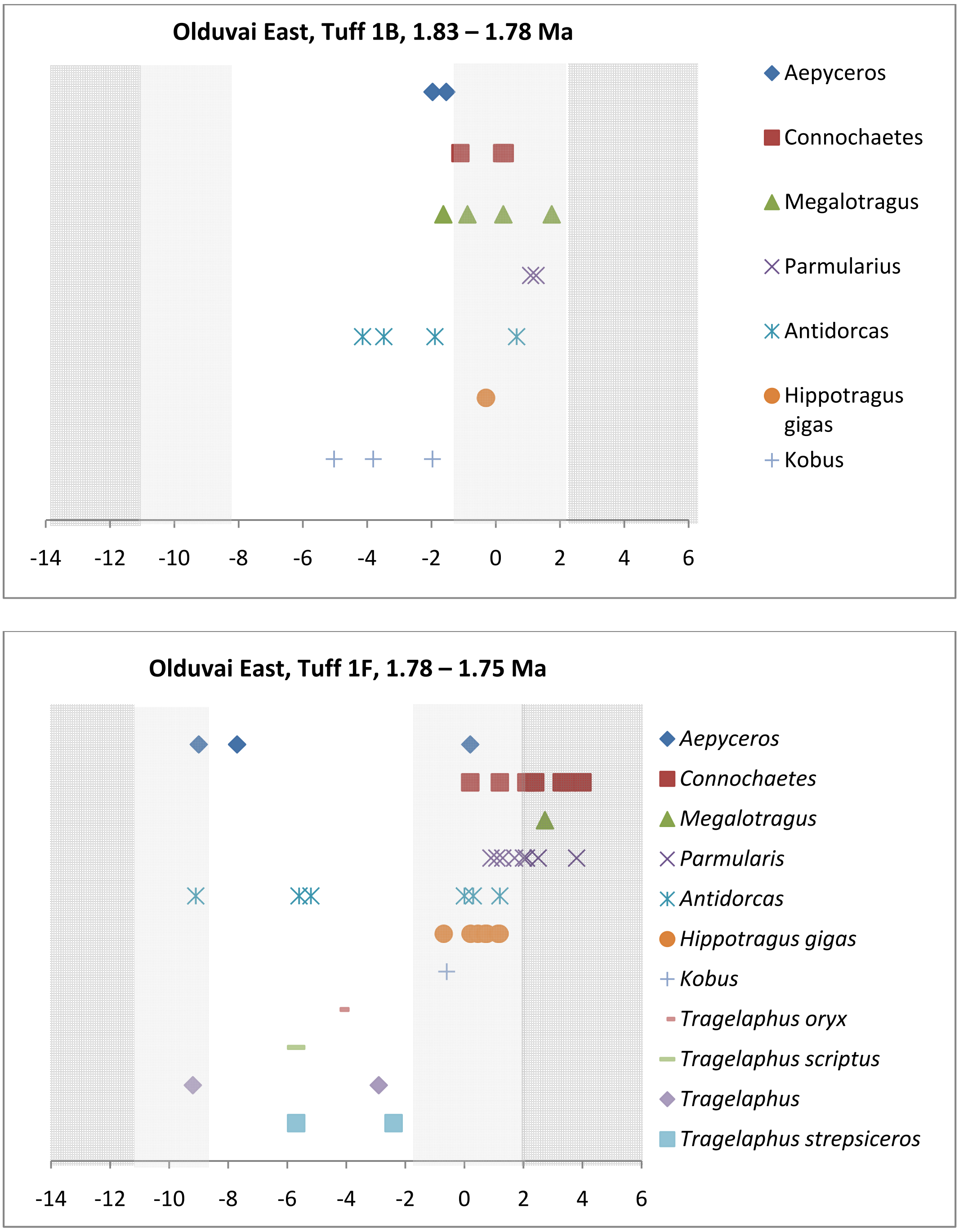


Figure 4.28. $\delta^{13}C$ results of bovids from Olduvai East Tuff 1B and 1F ($\delta^{13}C$ values from van der Merwe *in press*). The shading reflects the relative importance of C_3 versus C_4 in the diets. Values less than -8.5‰ reflect a diet of C_3 vegetation and greater than -1.8‰ a diet of C_4 vegetation.

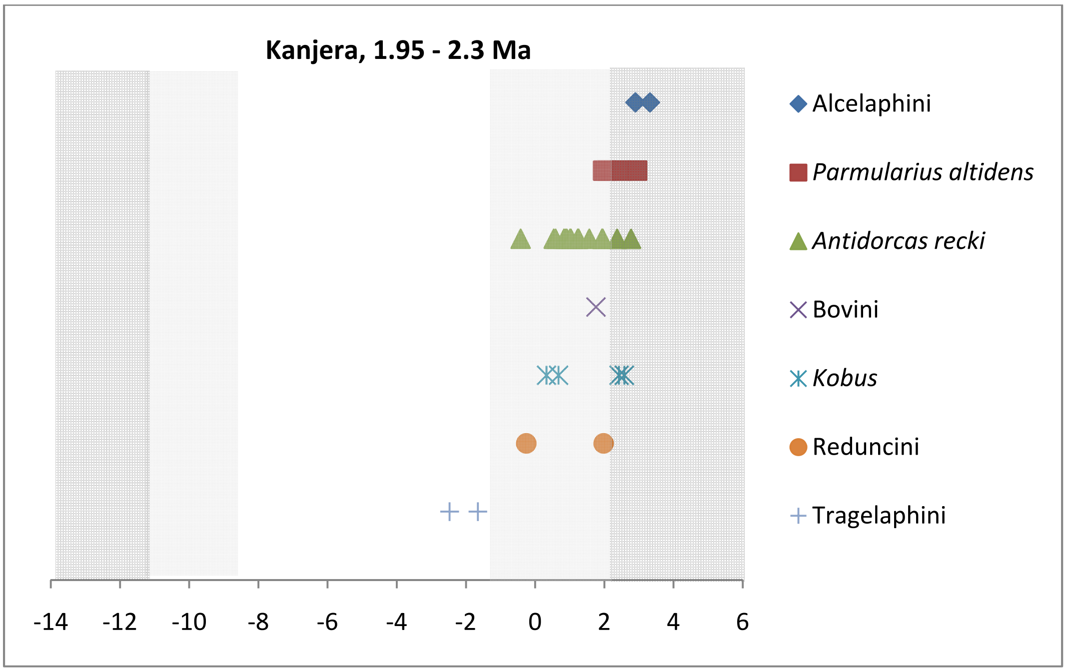


Figure 4.29. $\delta^{13}C$ results of bovids from Kanjera ($\delta^{13}C$ values from Plummer et al. 2009). The shading reflects the relative importance of C_3 versus C_4 in the diets. Values less than -8.5‰ reflect a diet of C_3 vegetation and greater than -1.8‰ a diet of C4 vegetation.

4.8 Discussion

In general, $\delta^{13}C$ values for modern bovids follow the predicted diets based on field observations and rumen content. A few discrepancies are noted. From field observations, springbok, steenbok and eland are considered to have a mixed diet. Although a few individuals were mixed feeders, most specimens from southern Africa selected C_3 vegetation.

For the majority of fossil bovids, dietary variations are poorly documented. Only a few studies have yielded invaluable insights into dietary changes on a temporal and local scale (e.g., Kingston and Harrison 2007). The present study included a considerable number of bovid taxa analysed for five *P. robustus* deposits, providing the first detailed diet profiles for some of these bovid taxa. In addition, studies from South Africa which tracked environmental changes for *P. robustus* use a variety of herbivores and carnivores, but with a negligible sample of bovids. The dietary data gleaned from the present study of several fossil bovid taxa provides the full range of dietary strategies. This study offers new information that can be used to decipher changes in vegetation structure.

The overall dietary patterns in fossil bovids are more diverse than modern forms. The isotope signals suggest that many of the fossil taxa were more generalist relative to modern taxa. The isotopic profiles for modern alcelaphines from southern Africa reflect C_4 diets (Sponheimer et al. 2003; Codron 2006). This is a similar pattern to that of East African alcelaphines (Cerling et al. 2003). Fossil Alcelaphines from Cooper's D and Swartkrans Members 1–3 were ^{13}C-depleted suggesting a flexible diet with some selection of C_3 vegetation. From other South African early hominin sites, alcelaphines from Sterkfontein Members 4 and 5 had more negative $\delta^{13}C$ values than those of Makapansgat Member 3 (Lee-Thorp et al. 2007). With the exception of Makapansgat Member 3, fossil alcelaphines are less specialized in grazing niches compared to their modern counterparts. The low percentage of alcelaphines in the assemblage and the positive values from Makapansgat Member 3, may suggest less competition for resources in a limited grazing niche, thereby allowing the alcelaphines to select their preferred resource.

Although grass was available, the more negative $\delta^{13}C$ values associated with *P. robustus* assemblages indicate a stronger reliance on C_3 vegetation compared to their modern counterparts. A higher proportion and selection of forbs and/or C_3 grasses in the past may account for the ^{13}C-depleted values.

Based on modern $\delta^{13}C$ values, springbok are predominately C_3 feeders (Sponheimer et al. 2003). Fossil Antilopini had variable diets, ranging from obligate C_3 to mixed C_3–C_4 diets. *Antidorcas bondi* had the most positive $\delta^{13}C$ values from mixed C_3–C_4 leaning towards a more C_4 diet. Specimens from Sterkfontein M4 were more ^{13}C-enriched compared to specimens from Swartkrans Lower Bank and Member 2. Fossil *A. marsupialis* and *A. recki* were similar in their dietary behaviours. Both had variable diets ranging between OC_3 to mixed feeders. This range is similar to that of their modern counterpart. Previous studies indicate that *A. recki* from Sterkfontein Members 4 and 5, and Swartkrans Hanging Remnant had a predominately C_3 diet (Lee-Thorp et al. 1994; Luyt 2001). However, one specimen from Sterkfontein Member 4 had a mixed C_3–C_4 diet (Luyt 2001). *Antidorcas marsupialis* and *A. recki* from Cooper's D were on average more $\delta^{13}C$-enriched than specimens from other deposits. Interestingly, where *A. bondi* was absent from deposits, *A. marsupialis* and *A. recki* tend to have values that were more positive (Cooper's D). The one *Gazella* from Swartkrans Hanging Remnant was a mixed feeder. This was in contrast to Makapansgat Member 3 were *Gazella* had an OC_3 diet (Sponheimer 1999) showing a temporal change in dietary behaviour for this genus.

Syncerus sp. from Swartkrans Hanging Remnant and Cooper's D selected a significant portion of C_3 vegetation. These values were more negative compared to those of modern savanna buffalo (Cerling et al. 2003; Sponheimer et al. 2003) and for middle Pleistocene buffalo (Bedaso et al. 2010), but not atypical for the forest buffalo with values as low as -16.2‰ (Cerling et al. 2004). This result was not surprising when dental morphology was considered. *Syncerus* has mesodont dentition, and the hypsodonty index align this species with mixed feeders (Janis 1988). The mesodont dentition and C_3 selection suggest that although the *Syncerus* may prefer fresh grass, they are capable of consuming a variety of vegetation. The $\delta^{13}C$ values for fossil and modern buffalo highlight the fact that not only is *Syncerus* capable of selecting a wide range of resources, but it was adapted to a wide range of environments.

Modern hippotragines had a similar C_4 range to that of alcelaphines (Cerling et al. 2003; Sponheimer et al. 2003; Codron 2006). For Swartkrans and Cooper's D assemblages, fossil hippotragines and alcelaphine also have similar ranges, although dietarily they are more versatile than their modern counterparts, ranging from mixed to VC_3. Hippotragines from Sterkfontein Members 4 and 5 are also ^{13}C-depleted compared to modern forms.

Overall, neotragines were similar to their modern counterparts. The mixed feeding $\delta^{13}C$ signature of the fossil ourebi was similar to the modern ourebi from East Africa, being mixed C_3-C_4, where in South Africa they had a more ^{13}C-enriched diet. Unfortunately, the locality of the East African sample was unknown and only one tooth was sampled (Cerling et al. 2003). The average OC_3 diet of *O. oreotragus* has remained constant in specimens from Makapansgat Member 3, Swartkrans Member 2 and modern forms. The majority of fossil steenbok specimens from Swartkrans Member 2 and Member 3 were within modern range.

This is consistent behaviour of South African steenboks where they tend to be predominately C_3 feeders (Du Toit 1993). However, a specimen from Swartkrans Member 2 and Member 3 and a specimen from Cooper's D were more ^{13}C-enriched, suggesting that a few individuals had incorporated a significant proportion of C_4 vegetation into their diet.

The mixed diet for *Makapania* was observed from Swartkrans Hanging Remnant and Makapansgat Member 3, however from Sterkfontein Member 4, *Makapania* had a wider dietary repertoire, ranging from VC_3 to mixed feeder. The arrive of new 'modern' species at Sterkfontein Member 4 may have temporarily forced some individuals of Makapania into increasing their C_3 intake.

Fossil grey rhebok were predominately C_3 consumers, but some ranged into mixed C_3-C_4. A mixed C_3-C_4 diet was not observed for their modern counterparts.

Redunca fulvorufula from Cooper's D had an OC_4 diet similar to that of modern specimens.

Modern tragelaphines have variable diets (Cerling et al. 2003; Sponheimer et al. 2003; Codron 2006). Eland and kudu are predominately browsers, but kudu have a versatile diet ranging from OC_3 to mixed C_3-C_4. The dietary behaviour of fossil tragelaphines was variable, ranging from OC_3 to VC_4 diets. On average, fossil kudu and eland had similar $\delta^{13}C$ values to their modern counterparts. Some species of *Tragelaphus* consume variable portions of C_4 foods. *Tragelaphus* sp. from Cooper's D and Swartkrans Member 2 had unusually more positive values compared to other *Tragelaphus* species, indicating a reliance on more C_4 resources.

The stable isotopic data from the *P. robustus* sequence indicate a wide range of foraging strategies. Many species have highly variable diets. Lee-Thorp et al. (2007) noted an increase in C_4 diets and decrease in C_3 diets throughout the southern African early Pleistocene sequence. The results of dietary behaviour of bovids presented in this study show an apparent shift in the increased selection mixed C_3–C_4 vegetation throughout the *P. robustus* sequences. Many specimens that are typical 'grazing' species such as alcelaphines and hippotragines had flexiable diets with many individuals having mixed C_3–C_4 diets. *Connochaetes*, *Damaliscus* and *Hippotragus* were not C_4 specialists like their modern counterparts. Although C_4 grasses were a component of the available vegetation, only *R. fulvorufula* from Cooper's D had a pure C_4 diet. A significant C_3 signature was present at Swartkrans Member 2 and Cooper's D. The relatively few C_4 specialists and an increase of mixed feeders with a significant component of C_3 selectors suggests that although C_4 grass was available, it was not an open C_4 dominated grassland as suggested by other researchers. Swartkrans Member 2 (ca. 1.6 Ma) contains substantially more C_3 feeders than other *P. robustus* deposits, signifying a vegetation structure that was more C_3-dominated than other deposits.

Chapter 5. Dental Microwear Texture Analysis

5.1 Introduction

This chapter discusses the application of Dental Microwear Texture Analysis (DMTA) on modern and fossil bovid tooth surfaces. Fossil specimens come from Cooper's D and Swartkrans Members, 1, 2, and 3. These fossil specimens provide the first dental microwear texture analysis of early Pleistocene bovids from both sites.

There is an association between diet and resource availability. Bovids that consume C_4[11] vegetation indicate the availability of monocots, whereas bovids that select C_3 foods represent eudicot accessibility (Sponheimer et al. 1999; Skinner and Chimimba 2005). The relationship between diet and microwear patterns has allowed researchers to infer feeding behaviours of both fossil and modern taxa (Rose and Ungar 1998; Schubert et al. 2006). The data from dental microwear analysis is important not only for reconstructing palaeodiets, but it also has the potential for reconstructing past ecologies.

Dental wear occurs when foods are masticated between upper and lower dentition. During mastication, different foods leave unique microwear patterns on the occlusal surface of the tooth. Wear can be produced by attrition (tooth-to-tooth contact) or abrasion (tooth-food-tooth) contact (Baker et al. 1959; Walker et al. 1978; Grine 1981; Kay and Covert 1983; Walker 1984; Teaford and Runestad

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[11] As stated in Chapter 4, the terms 'browser' and 'grazer' are misnomers. Both groups consume a variety of vegetation. 'Grazers' are able to select C_3 and C_4 grasses, and forbs, and will at times browse. 'Browsers'consume a wide range of foods: leaves, fruits, seeds, forbs and a small amount of grass. Here I use modal diet categories as outlined in Chapter 4.

1992; Fortelius and Solounias 2000). Abrasion may be caused by other factors such as sand or other hard objects entering the mouth (Teaford and Runestad 1992).

Bovids chew their food using a translatory masticatory cycle. This type of chewing requires a one-phase upward and inward jaw movement. There is differential width of upper and lower dentition so that one row moves across the other while maintaining occlusal contact (Rensberger 1973; Fortelius 1985; Franz-Odendaal and Kaiser 2003).

Many of the foods bovids consume contain hard silica bodies called 'phytoliths' which are found in the cell walls of eudicot and monocot plants. Because phytoliths can be harder than enamel, they can leave wear patterns on the occlusal surfaces of teeth (Baker et al. 1959). Older grasses and leaves have a higher concentration of phytoliths on their cell walls, whereas fresh grass, shoots and young leaves have a lower concentration (Marion Bamford, personal communication).

Different foods have different properties and shapes, requiring a variety of different strategies for mastication. Bovids that consume tough and fibrous grasses move their lower teeth in an extreme lateral motion across their upper teeth in a cyclical pattern (Figure 5.1). This grinding action causes the phytoliths and grit adherent to food items to move across the occlusal surfaces of teeth, resulting in heavy abrasion. This abrasion at the microscopic level appears as linear scratches and is usually oriented bucco-lingually. Bovids that select C_4 vegetation have more linear scratches on the occlusal surfaces of teeth than C_3 selectors. Alternatively, consuming hard, brittle foods of various sizes and shapes such as twigs, fruit and seeds causes the jaw to apply vertical pressure for breaking (Figure 5.1). Vertical pressure is concentrated in a small focal area, causing less abrasion than grinding and higher attrition (tooth–on–tooth contact). Microscopically, browsers have more pitting on occlusal surfaces of teeth. Different size pits may suggest different aetiologies. Larger pits may indicate concentrated pressure on hard food items between the teeth. Smaller pits may be due to more tooth-on-tooth contact resulting in microscopic fracturing of prisms at pit boundaries (Walker 1984; Teaford and Oyen 1989 a, b; Teaford and Runestad 1992). Fracturing of prisms at the boundaries would be seen in animals like primates with larger enamel occlusal surfaces. However, since bovids have smaller tooth–on–tooth enamel contacting surfaces, smaller pits may not be the result of prism fracturing. Other factors such as differential size and depth in pitting and striations may be due to the varying shapes and sizes of phytoliths occurring within different plants and plant elements.

Most dental microwear studies conducted on fossil ungulates were based on photomicrographs produced by scanning electronic microscopy (Solounias et al. 1988; Hayek et al. 1992). Because of the expensive nature of SEM work, the use of a light stereomicroscope using 35x magnification resurfaced (Solounias and Semprebon 2002; Kaiser 2003; Godfrey et al. 2004; Semprebon et al. 2004; Green et al. 2005). Microwear features were identified and classified by the eye of the observer. A variant of this approach involves compromise techniques that combine imaging by light stereomicroscopy with a camera attachment and measurement of features on a computer screen using a semi-automated software programme (Merceron et al. 2004 a, b; Merceron et al. 2005 a, b). Specimens were then examined using a Sensofar Plμ white-light scanning confocal microscope (Merceron and Ungar 2005; Schubert et al. 2006). Once again, the microwear was analyzed using a semi-automated software programme (Microwear 4.02). These programmes allow the user to identify and demarcate features, although they are hampered by measurement errors that often lead to subjective classifications and interobserver errors (Grine et al. 2002). Further, the various techniques provide noncomparable results (Schubert et al. 2006; Ungar et al. 2008).

Dental Microwear Texture Analysis conducted on fossil dentition is a new technique that has been applied to several species including bovids (Ungar et al. 2007). This technique uses a white-light confocal microscope to scan a section of the tooth surface providing cloud points on the X, Y and Z axis and combines it with scale-sensitive fractal analysis (SSFA). The Sensofar Plμ confocal imaging profiler then uses the cloud points to reconstruct a 3D image of the tooth surface. The results provide a quantitative description of the microwear surface.

5.2 Materials

All available adult teeth from Cooper's D and Swartkrans Member 1, 2 and 3 consisting of M^2, M_2 and M_1 were examined. Most previous microwear research has focused on primates where the amount of wear depends on the position of the tooth (Gordon 1982). Upper and lower M3 yield more observable microwear than upper and lower M1 (op. cit.) with the upper and lower M2 having intermediate wear. It has been shown recently that artiodactyls followed the same differential wear as primates (Merceron et al. 2005b). Recently, Schubert (2004) incorporated lower M1s of modern and fossils bovid species in his studies. His results demonstrated that there was ‘no relationship between the percentages of pitting in M1s versus M2s (Schubert 2004). All teeth were assessed for obvious taphonomic damage on occlusal surfaces, such as chipping, breakage or obscurity due to heavy manganese coating. Heavy manganese staining has been observed on fossil dentition from Swartkrans and Cooper’s Cave. Criteria for assessing taphonomic damage followed Teaford (1988b) and King et al. (1999). Also excluded from the sample are heavily worn or unworn teeth. Only those that preserved unobstructed antemortem microwear were included in this analysis. For more obscure microscopic wear or damage, an Olympus SZ51 light microscope with an 8 to 40 objective was used.

High-resolution casts of the occlusal surfaces were produced following Ungar (1996), Grine (1986) and Rose (1983). The samples were first cleaned with cotton swabs soaked in acetone. The cotton swabs were gently rolled across the surface of the tooth to clean away debris, and then discarded. This process was repeated until the occlusal surface under observation was clear of all noticeable debris. Polyvinylsiloxane dental impressions were made using Affinis™ Perfect Impressions Regular Body, no. 6510 (Coltene/Whaledent Inc.) and buttressed with Affinis™ Perfect Impressions Soft Putty, no. 6530 (Coltene/Whaledent Inc.). Positive replicas were made using 1:5 ratios of hardener and Epotek 501 epoxy resin (Epoxy Technologies Inc.).

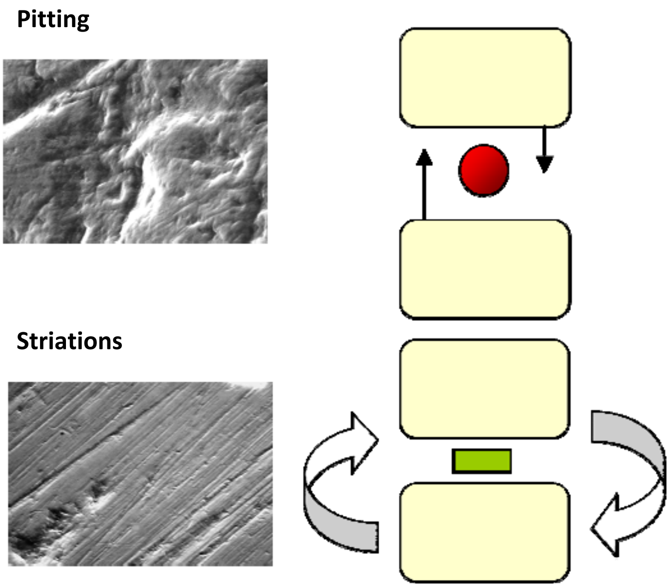

Figure 5.1. Differential food particles result in pitting or striated features on the enamel occlusal surface.

5.2.1 Modern Bovids

Modern African bovids were analyzed to serve as a core sample for interpretation of the Swartkrans and Cooper's Cave fossil bovids. Specimens included wild shot museum specimens from the Iziko South African Museum in Cape Town (SAM), the Northern Flagship Institute, Ditsong National Museum of Natural History (TM) in Pretoria, the Museum of Natural History (AMNH) in New York, and The Harvard Museum of Comparative Zoology (MCZ) in Massachusetts. Some of the moulds were made available through Blaine Schubert and Peter Ungar (see Schubert et al. 2006); the rest were collected by this author (Table 5.2). Of the 193 modern specimens examined, 61 specimens were usable. These included 13 taxa representing a wide range of diets and habitat preferences (Table 5.1 and 5.2 and Figure 5.2), among them the following: *Aepyceros melampus* (impala), *Antidorcas marsupialis* (springbok), *Connochaetes taurinus* (blue wildebeest), *Damaliscus pygargus* (blesbok), *Hippotragus niger* (sable), *Kobus leche* (lechwe), *Litocranius walleri* (gerenuk), *Oreotragus oreotragus* (klipspringer), *Oryx gazella* (gemsbok), *Raphicerus campestris* (steenbok), *Syncerus caffer* (African buffalo) and *Tragelaphus strepsiceros* (kudu).

Table 5.1. Bovid taxa used for DMTA.

Tribe	**Species**	**Common Name**	**Abbrev.**
Aepycerotini	Aepyceros melampus	impala	Ame
Alcelaphini	*Connochaetes taurinus*	blue wildebeest	Ct
	Damaliscus pygargus	blesbok	Dp
Antilopini	*Antidorcas marsupialis*	springbok	Ama
	Litocranius walleri	gerenuk	Lw
Bovini	*Syncerus caffer*	African buffalo	Sc
Hippotragini	*Hippotragus niger*	sable	Hn
	Oryx gazella	oryx	Og
Neotragini	*Oreotragus oreotragus*	klipspringer	Oor
	Raphicerus campestris	steenbok	Rc
Reduncini	*Kobus leche*	lechwe	Kl
Tragelaphini	*Tragelaphus strepsiceros*	kudu	Tst

5.2.2 Fossil Bovids

Fossil bovids from Cooper's Cave and Swartkrans Members 1, 2 and 3 have been identified to species or genus level. The Cooper's D sample comes from The Palaeosciences Centre, University of the Witwatersrand, Johannesburg. The Swartkrans sample is housed at the Ditsong National Museum of Natural History in Pretoria. Of the large number of bovid teeth in the deposits of Swartkrans and Cooper's D, a high proportion of specimens are unsuitable for microwear analysis. Taphonomic damage is common for fossil bovid molars as their thin enamel bands are frequently chipped or broken. An added factor particularly relevant to the Witwatersrand early Pleistocene fossil sites is the presence of manganese that precipitates out of dolomite (Cukrowska et al. 2005). Many of Cooper's Cave and Swartkrans fossils are heavily coated with manganese that obscures microwear on the already thin enamel bands. The combination of taphonomic damage and manganese staining proved problematic and samples for some species were limited. Of the 226 specimens from 21 taxa selected for possible surface microwear, only 39 specimens representing 12 fossil taxa were useable (Table 5.3 and Figure 5.3). The available sample is represented by *Antidorcas bondi*, *A. recki*, *A. marsupialis*, *Connochaetes* sp., *Damaliscus* sp., *Gazella* sp., *Makapania* sp., *Megalotragus* sp., *Oreotragus oreotragus, Pelea capreolus*, *Rabaticeras porrocornutus* and *Tragelaphus strepsiceros*.

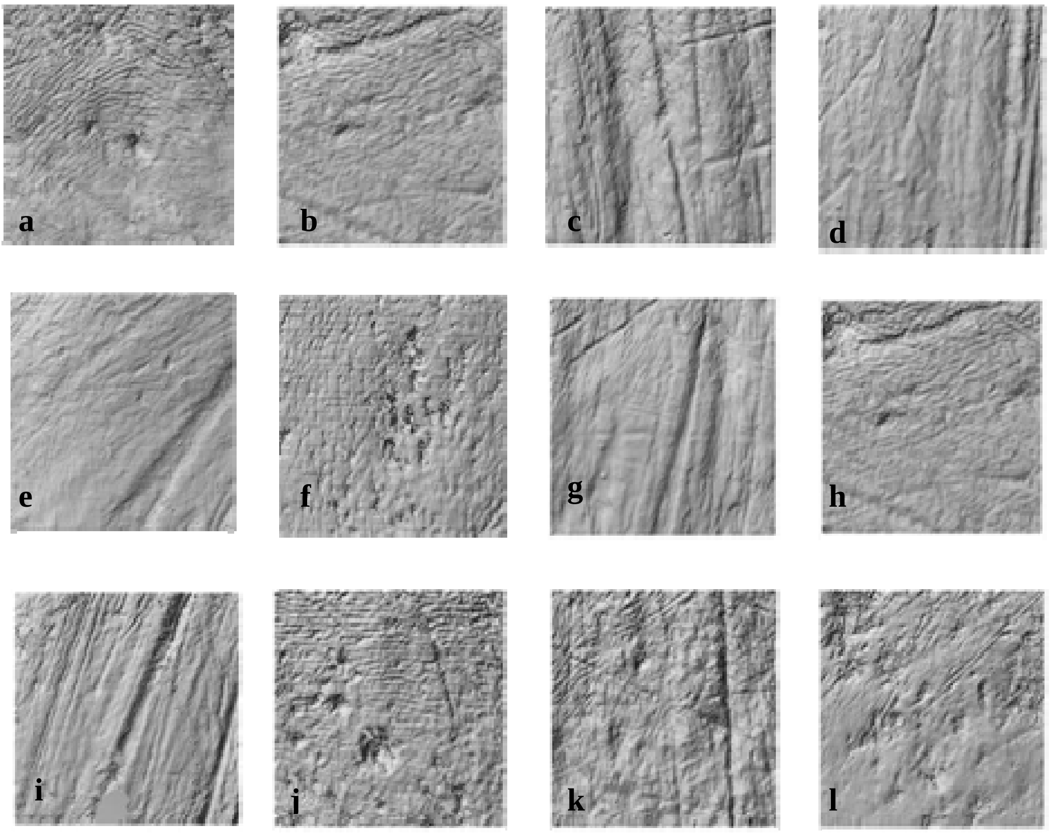

Figure 5.2. Photosimulations of surfaces used for DMTA (Field of view 138 x 102 µm) of modern bovids (a-l): (a) *Aepyceros melam*pus, MCZ 25542; (b) *Antidorcas marsupialis*, ZM 36916; (c) *Connochaetes taurinus*, AMNH 81850; (d) *Damaliscus pygargus*, ZM 38681; (e) *Hippotragus niger*, TM 13136; (f) *Kobus leche*, TM 35485; (g) *Litocranius walleri*, (h) *Oreotragus oreotragus*, ZM 33992; (i) *Oryx gazella*, AMNH 81155; (j) *Raphicerus campestris*, ZM 36032; (k) *Syncerus caffer*, ZM 36855; (l) *Tragelaphus strepsiceros*, TM 16601.

Table 5.2. DMTA values for modern taxa.

Specimen	**Taxa**	***epLsar***	***Asfc***	***Smc***	$HAsfc_{9\ \text{cells}}$	***Tfv***	***FTfv***
Tribe Aepycerotini							
MCZ 25542	*Aepyceros melampus*	0.0049	1.11	0.27	0.70	2364.9	8897.0
TM 17657	*Aepyceros melampus*	0.0061	2.10	0.15	0.65	7232.0	13671.7
TM 17686	*Aepyceros melampus*	0.0065	1.15	0.27	0.57	19961.6	26623.7
Tribe Alcelaphini							
AMNH 81789	*Connochaetes taurinus*	0.0079	2.02	0.27	0.31	15687.6	20255.3
AMNH 81790	*Connochaetes taurinus*	0.0041	2.92	0.15	0.35	12340.0	20454.6
AMNH 81794	*Connochaetes taurinus*	0.0060	1.38	0.21	0.35	18757.7	26452.1
AMNH 81799	*Connochaetes taurinus*	0.0070	3.16	0.15	0.57	23578.0	32341.0
AMNH 81850	*Connochaetes taurinus*	0.0081	1.16	0.42	0.27	17151.3	22957.0
TM 13161	*Connochaetes taurinus*	0.0058	1.94	0.15	0.42	13547.8	19840.5
TM 13165	*Connochaetes taurinus*	0.0035	1.23	0.21	0.40	15913.7	24895.4
TM 3095	*Connochaetes taurinus*	0.0058	0.71	0.15	0.28	7763.2	15015.7
ZM 36085	*Connochaetes taurinus*	0.0040	0.87	0.27	0.43	18465.8	25377.8
ZM 36147	*Connochaetes taurinus*	0.0073	1.84	0.42	0.54	13251.2	20776.3
AMNH 118481	*Damaliscus pygargus*	0.0033	1.94	0.27	0.32	18109.7	26451.1
AMNH 81729	*Damaliscus pygargus*	0.0034	2.08	0.27	0.36	18109.7	26451.1
AMNH 81731	*Damaliscus pygargus*	0.0039	2.01	0.15	0.53	14881.2	21263.1
AMNH 81733	*Damaliscus pygargus*	0.0037	0.77	0.15	0.35	23635.5	29671.8
TM 12601	*Damaliscus pygargus*	0.0032	0.57	.	0.54	24658.0	31270.4
ZM 36949	*Damaliscus pygargus*	0.0063	1.35	0.15	0.44	14836.2	22735.3
ZM 38681	*Damaliscus pygargus*	0.0060	0.98	.	0.40	18986.8	24791.3
ZM 9772	*Damaliscus pygargus*	0.0056	1.63	0.15	0.48	18109.0	25303.1
Tribe Antilopini							
ZM 35718	*Antidorcas marsupialis*	0.0064	3.00	0.21	0.58	4957.1	11781.9
ZM 36916	*Antidorcas marsupialis*	0.0040	1.76	0.34	0.66	1880.7	7837.9
ZM 36923	*Antidorcas marsupialis*	0.0079	2.93	0.15	0.36	15623.0	23026.8
AMNH 179216	*Litocranius walleri*	0.0012	2.30	0.21	0.48	447.2	4087.2
AMNH 161172	*Litocranius walleri*	0.0028	2.61	0.15	0.43	11235.6	15785.5
AMNH 179218	*Litocranius walleri*	0.0030	2.53	0.27	0.61	784.3	8272.3
AMNH 179221	*Litocranius walleri*	0.0018	1.21	0.15	0.58	.	1354.4
AMNH 187829	*Litocranius walleri*	0.0013	3.59	0.15	0.40	5515.9	12028.3
AMNH 54204	*Litocranius walleri*	0.0012	2.45	0.21	0.42	6155.0	10511.4
ANMH 98140	*Litocranius walleri*	0.0025	1.90	0.34	0.52	2915.0	7611.2
MC Z13231	*Litocranius walleri*	0.0029	2.46	0.21	0.49	3584.9	10445.9
MC Z8734	*Litocranius walleri*	0.0036	0.66	0.15	0.51	5632.2	10316.2

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Table 5.2. continued

Specimen	**Taxa**	***epLsar***	***Asfc***	***Smc***	$HAsfc_{9\ \text{cells}}$	***Tfv***	***FTfv***
Tribe Bovini							
ZM 36248	*Syncerus caffer*	0.0087	1.22	0.84	0.36	9774.6	16164.2
ZM 36855	*Syncerus caffer*	0.0033	1.10	0.71	0.58	10283.7	16810.8
ZM 37780	*Syncerus caffer*	0.0067	1.11	0.89	0.36	7133.6	14398.6
Tribe Hippotragini							
AMNH 216381	*Hippotragus niger*	0.0085	2.68	0.15	0.32	10468.9	14580.4
AMNH 83606	*Hippotragus niger*	0.0065	1.12	0.60	0.49	14519.8	21996.0
TM 13136	*Hippotragus niger*	0.0066	0.62	0.74	0.34	9909.8	17710.5
AMNH 161701	*Hippotragus niger*	0.0081	1.29	0.15	0.46	11659.7	18329.5
AMNH 184662	*Hippotragus niger*	0.0079	1.36	0.21	0.47	15517.5	23178.6
AMNH 184663	*Hippotragus niger*	0.0041	0.84	0.15	0.37	16110.9	24112.6
AMNH 81154	*Oryx gazella*	0.0047	0.82	0.51	0.36	17233.2	23850.5
AMNH 81155	*Oryx gazella*	0.0076	1.12	0.15	0.54	10545.6	16741.6
AMNH 165102	*Oryx gazella*	0.0035	0.41	.	0.39	17083.0	23389.6
ZM 15806	*Oryx gazella*	0.0045	1.56	0.27	0.69	9116.4	15095.7
ZM 38707	*Oryx gazella*	0.0064	1.05	0.51	0.58	13246.0	20459.8
AMNH 81153	*Oryx gazella*	0.0074	0.82	0.15	0.43	7726.3	16133.5
Tribe Neotragini							
ZM 33992	*Oreotragus oreotragus*	0.0025	1.48	0.51	0.49	4384.0	11495.8
ZM 36032	*Raphicerus campestris*	0.0014	3.98	0.15	0.62	6281.4	14063.4
ZM 36286	*Raphicerus campestris*	0.0045	2.44	0.27	0.38	788.6	3720.4
ZM 37136	*Raphicerus campestris*	0.0015	2.85	0.15	0.37	4806.0	9837.7
ZM 37426	*Raphicerus campestris*	0.0015	1.75	0.21	0.52	7072.6	13413.8
ZM 38440	*Raphicerus campestris*	0.0017	2.88	0.21	0.44	4941.3	12903.2
Tribe Reduncini							
TM 35481	*Kobus leche*	0.0018	1.01	0.51	0.43	10283.3	17612.0
TM 35485	*Kobus leche*	0.0061	1.23	0.34	0.50	10955.0	17441.3
TM 35507	*Kobus leche*	0.0028	1.05	0.27	0.95	9241.6	16531.4
Tribe Tragelaphini							
TM 1030	*Tragelaphus strepsiceros*	0.0050	2.34	0.21	0.37	10063.7	15601.0
TM 13170	*Tragelaphus strepsiceros*	0.0042	1.61	0.15	0.55	16461.0	23082.3
TM 16601	*Tragelaphus strepsiceros*	0.0014	3.71	0.15	0.83	9205.5	15428.5

Cast of modern teeth were made by Blaine Schubert and Peter Ungar. These teeth were sampled from the American Museum of Natural History, New York (AMNH); the Museum of Comparative Zoology, Cambridge, MA (MCZ); Iziko Museum, Cape Town (ZM); and the Ditsong National Museum of Natural History, Pretoria (TM). This author made casts of modern teeth that were sampled from the Ditsong National Museum of Natural History.

A blank space indicates corrupt data for more than two scans. In this case, the value was not used for analysis.

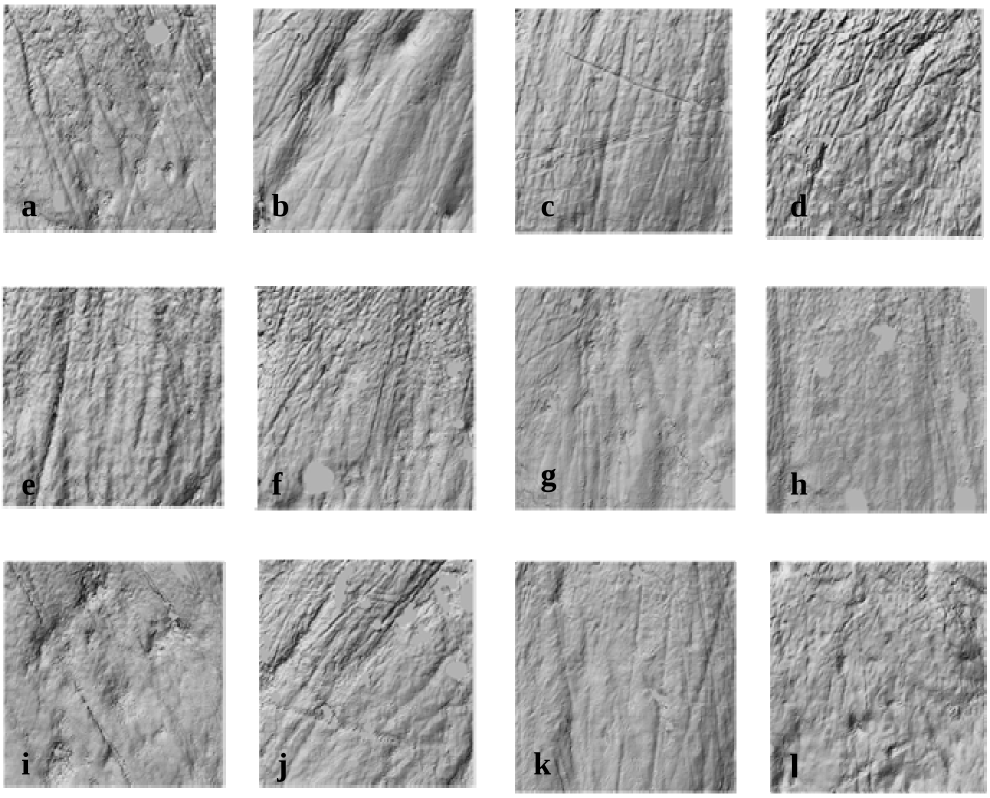

Figure 5.3. Photosimulations of surfaces used for DMTA (Field of view 138 x 102 µm) of fossil bovids (a-l): (a) *Antidorcas bondi*, SK 3092: (b) *Antidorcas marsupialis*, SKX 35038; (c) *Antidorcas recki*, SK 3009; (d*) Connochaetes* sp., SKX 1491; (e) *Damaliscus* sp., SK 14122; (f) *Gazella* sp., SK 10440; (g) *Makapania* sp., SK 3150; (h) *Megalotragus* sp., CD 3194; (i) *Oreotragus oreotragus*, SKX 14059; (j) *Pelea capreolus*, SK 10694; (k) *Rabaticeras porrocornutus*, SK 3213; (l) *Tragelaphus strepsiceros*, CD 5410.

Table 5.3. DMTA values for fossil bovid taxa.

Specimen	**Taxa**	**Deposit**	***epLsar***	***Asfc***	***Smc***	***HAsfc*$_{9cell}$**	***Tfv***	***FTfv***
Tribe Alcelaphini								
CD6180	*Connochaetes* sp.	CD	0.0030	2.00	0.27	0.35	16000.05	23086.64
SK2482	*Connochaetes* sp.	SK1HR	0.0064	1.73	0.21	0.42	16410.26	23016.78
SKX6195	*Connochaetes* sp.	SK3	0.0028	0.54	0.34	0.43	16182.37	23099.63
SKX2829	*Connochaetes* sp.	SK2	0.0022	2.54	0.27	0.47	14148.98	21503.74
SKX1266	*Connochaetes* sp.	SK2	0.0028	1.29	0.34	0.54	16304.83	22570.64
SKX1491	*Connochaetes* sp.	SK2	0.0048	1.09	0.34	0.40	14203.58	19730.24
SKX2856	*Connochaetes* sp.	SK2	0.0068	1.89	0.21	0.30	13849.41	21737.44
SKX4034	*Connochaetes* sp.	SK2	0.0069	0.95	.	0.39	13034.55	20005.61
SKX19832	*Connochaetes* sp.	SK3	0.0052	1.93	0.34	0.58	10007.73	16487.85
SKX28027	*Connochaetes* sp.	SK3	0.0037	3.37	0.15	.	17967.17	26388.00
SKX29279	*Connochaetes* sp.	SK3	0.0037	1.59	0.21	0.31	18386.10	27776.55
SKX35041	*Connochaetes* sp.	SK3	0.0069	1.86	0.15	0.78	14054.40	18312.54
SKX35753	*Connochaetes* sp.	SK3	0.0061	2.52	0.21	0.62	15705.83	22296.86
SKX39541	*Connochaetes* sp.	SK3	0.0028	1.58	0.21	0.38	15678.10	23528.67
SKX39601	*Connochaetes* sp.	SK3	0.0026	1.74	0.21	0.74	9678.95	15650.17
SKX39872	*Connochaetes* sp.	SK3	0.0069	1.57	0.28	0.46	12008.28	20586.19
SK2957	*Damaliscus* sp.	SK1HR	0.0051	1.81	0.74	0.44	13444.33	19925.11
SK14122	*Damaliscus* sp.	SK2	0.0050	2.34	0.21	0.37	10063.66	15600.97
CD1247	*Megalotragus* sp.	CD	0.0090	5.78	0.15	0.48	16103.91	22846.81
CD3194	*Megalotragus* sp.	CD	0.0030	1.51	0.27	0.35	11819.18	16628.08
SK3081	*Rabaticeras porrocornutus*	SK1HR	0.0039	1.53	0.43	0.35	20634.72	26398.06
SK3213	*Rabaticeras porrocornutus*	SK1HR	0.0061	1.48	0.42	0.38	8578.44	15165.29
Tribe Antilopini								
CD10891	*Antidorcas marsupialis*	CD	0.0059	1.19	.	0.38	11616.91	18479.02
CD7453	*Antidorcas marsupialis*	CD	0.0035	1.31	0.27	0.34	9195.66	15612.48
SKX35038	*Antidorcas marsupialis*	SK3	0.0071	1.22	0.42	0.37	10598.09	16839.99
SKX35320	*Antidorcas marsupialis*	SK3	0.0025	1.12	0.27	0.49	9604.13	15302.82
SKX39908	*Antidorcas marsupialis*	SK3	0.0042	1.91	0.21	0.65	10555.94	17934.70

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Table 5.3. continued

Specimen	Taxa	Deposit	*epLsar*	*Asfc*	*Smc*	$HAsfc_{9cell}$	*Tfv*	*FTfv*
Tribe Antilopini								
SK3092	*Antidorcas bondi*	SKM2	0.0057	0.89	0.25	0.28	12495.8	19550.1
SK3095	*Antidorcas recki*	SK1HR	0.0028	3.66	0.15	0.45	2029.39	7690.32
SKX14147	*Antidorcas recki*	SK1LB	0.0069	1.96	0.27	0.55	12948.22	18708.96
SK2256	*Antidorcas recki*	SK2	0.0057	1.39		0.49	12375.35	19666.02
SK3009	*Antidorcas recki*	SK2	0.0083	1.01		0.58	9554.73	15728.58
SK3054	*Antidorcas recki*	SK2	0.0019	1.19	0.15	0.66	5634.79	14498.98
SK3092	*Antidorcas recki*	SK2	0.0057	0.89	0.28	0.36	12495.84	19550.10
SK 10440	*Gazella* sp.	SK1HR	0.0043	1.88	0.21	0.67	1124.05	7560.05
Tribe Ovibovini								
SK3150	*Makapania* sp.	SK1HR	0.0042	1.23	0.27	0.36	9846.07	16345.88
Tribe Neotragini								
SK14059	*Oreotragus oreotragus*	SK1HR	0.0063	2.18	0.21	0.57	7879.34	14773.08
Tribe Peleini								
SK10694	*Pelea capreolus*	SK2	0.0040	1.64	0.27	0.47	6509.95	14320.94
Tribe Tragelaphini								
CD5410	*Tragelaphus strepsiceros*	CD	0.0044	1.18		0.25	9221.88	16528.19

Collections were sampled from the Ditsong National Museum of Natural History, Pretoria and the University of the Witwatersrand, Johannesburg. All specimens were collected by the author.

Blank spaces indicate corrupt data for more than two scans. In this case, the value was not used for analysis.

5.3 Methods

Sensofar Plμ confocal imaging profiler (Solarius Developments Inc., Sunnyvale, California) using a 100x objective, was used to scan surface data on Facet 1 of each replicated tooth. During chewing, Facet 1 on the upper and lower dentition is in contact (Teaford and Walker 1984; Merceron et al. 2004b, 2005b; Schubert et al. 2006; Ungar et al. 2007). Facet 1 is located on the distobuccal enamel band of the mesial cuspid of M_1 or M_2, or the mesiobuccal enamel band of the mesial cusp of M^2 (Figure 5.4).

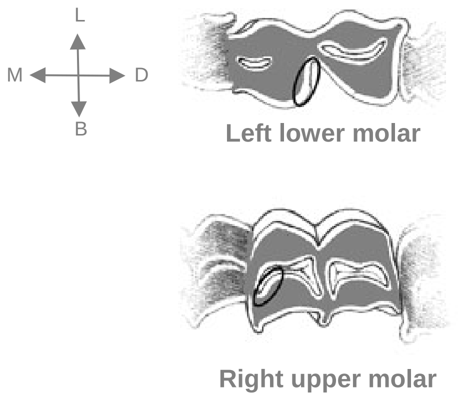

Figure 5.4. Shearing facet 1 on bovid permanent molars. The area of observation is circled. Drawing courtesy of Merceron et al. (2004b).

The white-light confocal microscope collects 3D cloud points representing the surface, with a lateral (x, y) sampling interval of 0.18 μm, a vertical (z) resolution of 0.005 μm and with a field of view of 138 x 102 μm. Four adjoining fields were collected totalling an area of 276 x 204 μm. The raw data from the scans were prepared and edited using Solarmap Universal Software (Solarius

Inc.). In Solarmap, the surface of each scan was leveled. Irregular artifacts due to fossilization, recovery and curation were erased in Solarmap.

The resulting scans were analyzed in ToothFrax and Sfrax programmes (Surfract Corporation, www.surfract.com) using scale-sensitive fractal analysis (SSFA). The latter is based on the principle of fractal geometry whereby the length of a rough profile, the area of a rough surface and the volume within it change with the scale of observation (Scott et al. 2006). At course scales, the surface appears smooth and at fine scales, the surface appears rough (op. cit.). The SSFA principle was used for length-scale, area-scale and volume-scale analysis. Length-scale, area-scale and volume-scale algorithms were used to generate measurements that characterize surface texture (op. cit.). In the present study, five parameters were used to characterize dental microwear surface texture: anisotropy, complexity, scale of maximum complexity, heterogeneity and textural fill volume. Length-scale algorithm (one-dimensional) was used to calculate anisotropy (op. cit.). Area-scale algorithm (three-dimensional) was used to calculate complexity, scale of maximum complexity and heterogeneity (op. cit.). Volume-scale algorithm (three-dimensional) was used to calculate textural fill volume (op. cit.). For a more detailed discussion on the technical considerations of dental microwear texture analysis using the SSFA principle, see Scott et al. (2006). A brief description of the five parameters follows.

5.3.1 Length-scale analysis

Length-scale rotational algorithm calculates relative lengths (RelL). Relative lengths are the sum of segments of a curved line of a given scale fit to a profile[12] divided by the projected length of the profile. Not only can different scales of measurement be used, but also profiles can be taken from different orientations from any given profile orientation, as the scale of measurement decreases the relative lengths of a curved line increases providing a more accurate digital representation of the surface (Figure 5.5).

Anisotropy (*epLsar*)

Relative lengths of profiles differ with orientation when the roughness of the surface has directionality (Bergstrom and Brown 1999). As described by Scott et al. (2006) and Ungar et al. (2007), relative lengths at given orientations are defined as vectors. Here the vectors were calculated at intervals of 5^o at 1.8 µm scale of observation and then normalized using the exact proportion method. Normalized relative length vectors can be graphically displayed as a rosette diagram for a visual interpretation of directionality (Figure 5.6). The length of the mean vector is a measure of surface anisotropy called exact proportion Length-scale anisotropy of relief (*epLsar*). The median *epLsar* was calculated for all four adjoining scans for each specimen in ToothFrax (Surfract Corporation, www.surfract.com).

Anisotropy can distinguish a diet of hard foods from tough foods. Tough foods are often associated with scratches and produce a directional pattern,

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[12] A cross section through a surface.

particularly when occlusal morphology dictates constrained chewing motions (Figure 5.7). A surface dominated by parallel striations will have greater anisotropy (*epLsar*) values (Scott et al. 2006; Ungar et al. 2007). For example, the sable consuming grass will have a higher *epLsar* value compared to the gerenuk that consumes leaves (Ungar et al. 2007).

5.3.2 Area-scale analysis

Using the same SSFA principle, area-scaling tiling algorithm calculates relative areas (RelA) using replicated triangular tiles to represent the surface. The area-scaling algorithm calculates relative area across a range of scales up to the sampling interval of the selected microwear surface. The relative area is calculated by dividing the surface area (calculated by the sum of the triangles of a selected scale) by area of that surface. As the scale becomes finer on a rough surface, the more triangles are needed to recreate the surface, and thus the relative area of the surface becomes greater (Figure 5.8).

Complexity (*Asfc*)

Complexity depends on the change in roughness at decreasing scales of observation and uses area-scale tiling algorithm to calculate relative area. The differences between the scales can be used to describe the overall surface complexity using the calculation of relative area over a range of scales. The relative areas for each scan used ranged from 7200 μm^2 to 0.20 μm^2 with one order magnitude in ToothFrax (Scott et al. 2006). Surface complexity is measured by Area-scale fractal complexity (*Asfc*). Complexity is calculated by the slope of "the steepest part of the curve, fit to a log-log plot of relative area over the range of scales multiplied by -1000" (Scott et al. 2006, p. 341) (Figure 5.9). Median *Asfc* for the four adjoining scans was used to calculate a single value for each specimen.

Microwear, dominated by pits of various sizes or deep pits and scratches, will have higher complexity values (Figure 5.10). Ungar et al. (2007) have noted that among ruminants, *Tragelaphus strepsiceros* (a browser) consumes harder plant elements, and has higher *Asfc* values than *Redunca arundinum* (a grazer).

Scale of maximum complexity (*Smc*)

This is the fine scale limit of the steepest part of the curve described for the complexity (*Asfc)* measure. Surfaces with lower values for scale of maximum complexity (*Smc*) tend to have more wear at very fine scales. A surface dominated by fine scratches and the absence of large pits will have a low *Smc*. For example, two cercopithecoids, *Cebus apella* and *Lophocebus albigena*, are both hard object feeders, but the *Smc* variable for each is very different. While *C. apella* has fine microwear features, *L. albigena* has very coarse features (Scott et al. 2006) suggesting two varied diets. The *Smc* variable is able to separate between two similar diets.

Heterogeneity (*HAsfc*)

This parameter is a measure of variation of complexity across a surface. Four adjoining scans per specimen may each give varying values. This indicates that the amount of variation in complexity across subsections of a facet may be important in characterizing microwear (Figure 5.11). To quantify this variation, the heterogeneity of area-scale fractal complexity algorithm, or *HAsfc*, is calculated. Heterogeneity is calculated by splitting each individual scan into smaller sections with equal numbers of rows and columns beginning first with 2 x 2 then into smaller subsections up to 13 x 13. The resulting distributions are typically skewed, so the relative variation in complexity for each set of subregions are calculated as the median absolute deviation of *Asfc* divided by the median of *Asfc*. The median *HAsfc* is then calculated for each specimen. Scott et al. (2006) have noted that this variable has been successful in distinguishing between hard object feeders, and may be related to factors such as varying sizes of wear-causing particles.

5.3.3 Volume-scale analysis

Volume-scaling algorithm fills a surface with square cuboids of different volumes. This is calculated using the Sfrax program (Surfract Corporation, www.surfract.com).

Textural fill volume (*Tfv*)

This examines the summed volume of squared cuboids of a given scale that fill a surface. This is computed as the difference in summed volume for larger 10 µm cuboids (the shape of the surface) and at very fine 2 µm cuboids (texture of the surface) (Figure 5.12). The summed differences between the two scales remove the overall shape of the surface and limit characterization to the microwear features. The fill volume can be calculated at either fine (*FTfv*) or course scale

(*Tfv*). Deeply excavated wear means more rectangular prisms are packed in and greater *Tfv*. High *Tfv* values indicate features that are 'larger, deeper and more symmetrical' (Scott et al. 2006). The *Tfv* value may have the potential to distinguish between individuals that consume foods with different fracture properties (op. cit.)

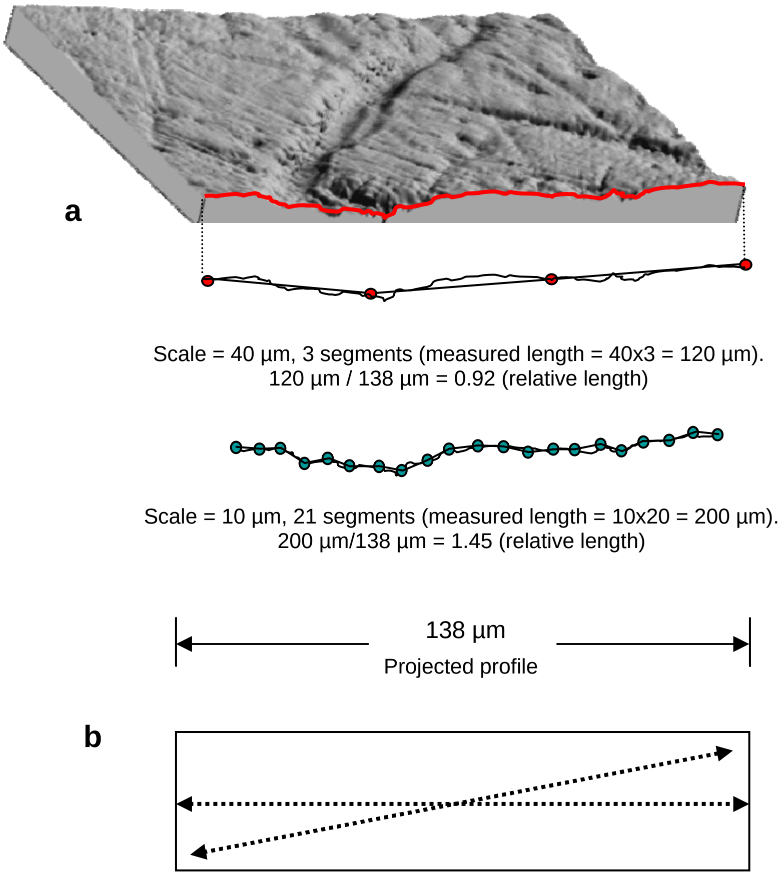

Figure 5.5. Length-scale analysis. (a) As the scale of measurement decreases the relative length of a curved line increases. (b) Profiles can be taken in different orientations. Drawing modified from Scott et al. (2006).

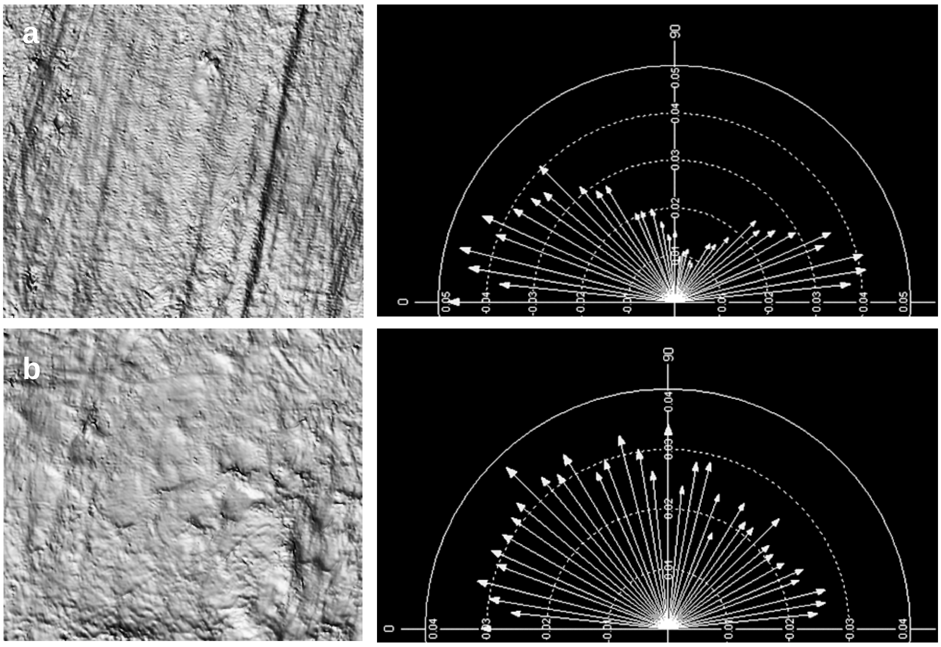

Figure 5.6. Rosette plots of relative lengths. Photosimulations represent (a) striated surface and (b) pitted surface. Illustrations courtesy of Peter Ungar.

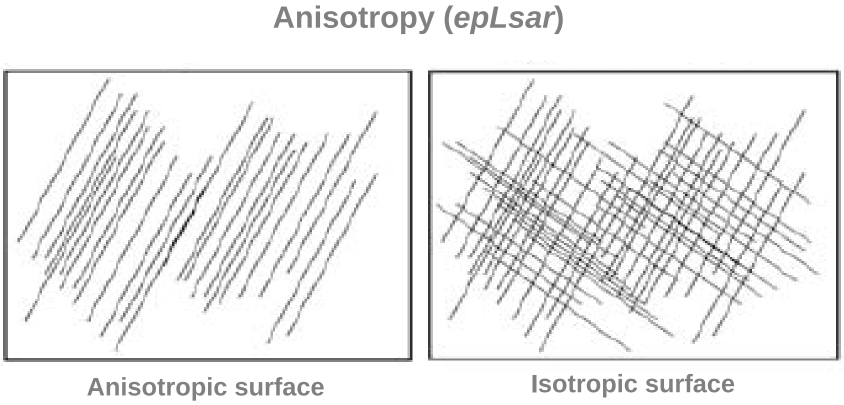

Figure 5.7. *epLsar* variable. Anisotrophic and isotropic striations. Figure from Ungar et al. (2007).

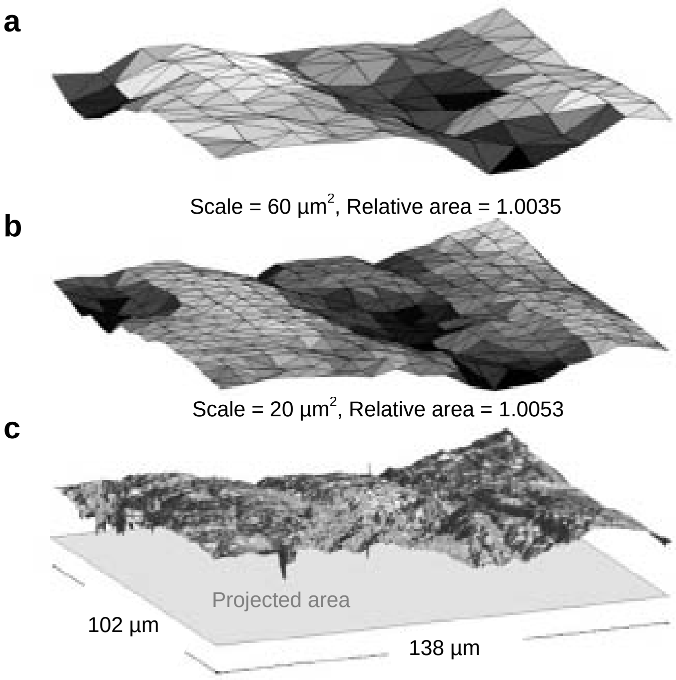

Figure 5.8. Area-scale analysis. An area-scale algorithm using triangles of different sizes used to measure surface roughness (a-c). Note that roughness of surface increases with a finer scale of measurement. Figure from Scott et al. (2005).

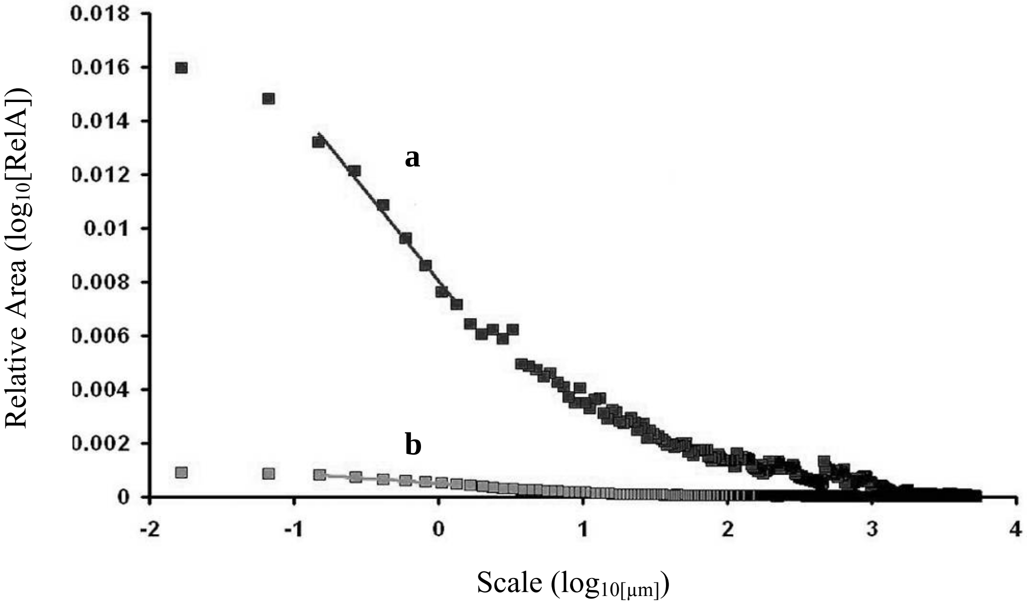

Figure 5.9. Plot of relative area over scale. Here complexity has been calculated for pitted surface (a) and a striated surface (b). Figure courtesy of Peter Ungar.

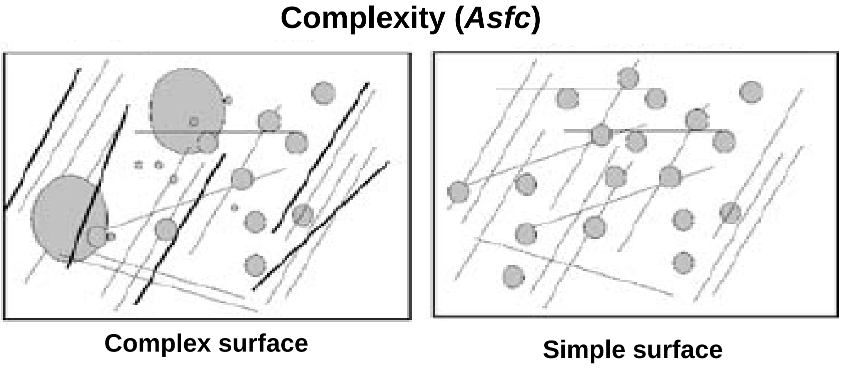

Figure 5.10. *Asfc*, complex and simple microwear surfaces. Figure from Ungar et al. (2007).

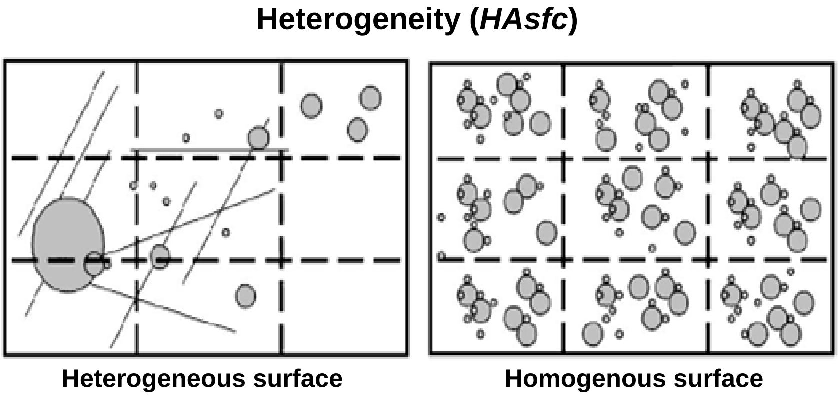

Figure 5.11. *HAsfc*, heterogeneous and homogenous microwear surfaces. Illustration from Scott et al. (2006).

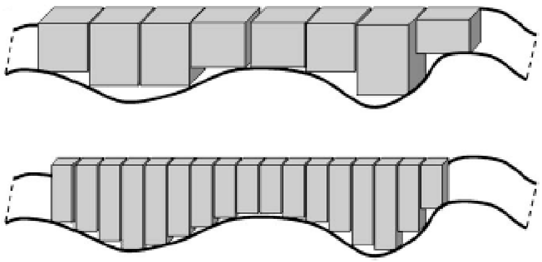

Figure 5.12. *Tfv* and *FTfv*, square cuboids at coarse (a) and fine (b) scale filling a surface relief. Illustration from Scott et al. (2006).

5.3.4 Statistics

Descriptive statistics for each species were calculated, including the mean, median and standard deviation (SD). All statistical analyses were performed in SPSS 11.0 (SPSS Corp.) or PAST (Palaeontological Statistics, version 1.81: Hammer et al. 2001). Statistical analyses were performed to determine the extent of variation in microwear texture between species following Ungar et al. (2007). All data were rank-transformed before analysis because unranked microwear data typically violate assumptions associated with parametric statistical tests (Conover and Iman 1981).

Spearman's rho correlations were used to measure linear relationships between paired variables. A score of +1 indicates the paired variables have an identical relationship, whereas a score of -1 indicates the variables are an inverse relationship. There is no relation between the paired variables if the score is zero.

For multivariate analysis of variance, model data for the variables were compared among species, with species as the factor, and dental microwear variables (*epLsar*, *Asfc*, *Smc*, *HAsfc*, and *Tfv*) as the dependent variables, and values for each individual as the replicates. This test assesses the significance of variation among the taxa in overall microwear surface texture.

A one-way ANOVA was used to determine the sources of significant variation. Multiple comparison tests were used to determine the source of significant variation. Because even small sample sizes were expected to reflect dietary differences, Fisher's LSD a priori tests were used to compare species. This is the least conservative of the *post hoc* tests and has been criticized for false positives (Proschan 1997). It does nonetheless indicate the presence of variation. A Tukey's HSD *post hoc* test was also performed to balance risks of Type I and Type II errors (Cook and Farewell, 1996). For unequal variances, the conservative Tamhane's T2 will balance the risk of Type I error.

To identify dietary patterns in the data, Principal Components Analysis (PCA) was used. PCA seeks to describe in a few dimensions the patterns of dietary variation present in a larger multidimensional data set. The PCA is used to form unrelated linear combinations of the observed variables (Dytham 1999). The first component has the greatest variance and successive components explain progressively lesser portions of the variance. These are all uncorrelated with each other. The correlation matrix is used as the basis for determining the principal components of different variables with different variances. Correlated variables are given equal loadings in the determination of maximum variance. These loading indicate how strongly a variable affects the distribution of the sample. It is important to determine how many axes are necessary to depict adequately a range of variation. In the present analysis, the sample sizes are small and it is noted that small sample sizes have little impact on axes determination (Falsetti et al. 1993). Biplots were also examined within the Principal Component Analysis. The biplot shows inter-unit distances and indicates clustering of units as well as display correlations of the variables (Gabriel 1971).

The main purpose of a Discriminant Function Analysis (DFA) is to predict group membership based on a linear combination of the interval variables. The predictors do not have to be normal distribution, equal variance or linearly related (Tabachnick and Fidell 1996). The procedure begins with a set of observations where both group membership and the values of the interval variables are known. This results in a model that allows prediction of group membership. DFA is applied to predict whether diet classifications were correct using DMTA variables. The analysis will determine how often an individual of known diet (based on $\delta^{13}C$ averages for modern bovids) would be attributed to the correct group using DMTA variables (*epLsar*, *Asfc*, *Smc*, *HAsfc*, and *Tfv*). The grouping variable was the diet, and the independents were the DMTA variables. The DFA could then be used to determine which variables were the best predictors of diet classifications. Second, DFA is used to understand of the data set, as a careful examination the prediction model can give insight into the relationship between group membership and the variables used to predict group membership.

5.4 Results of modern bovid diets

Lists of DMTA values for modern bovid taxa are found in Tables 5.2. Examples of microwear surfaces are illustrated in Figures 5.2. Statistical analyses for DTMA are shown in Tables 5.4 – 5.8 and Figures 5.13– 5.17. Descriptive statistics for modern bovid taxa are in Table 5.9.

5.4.1 Statistics

Ungar et al. (2007) have noted that C_3 feeders exhibit more complex microwear surfaces and as a result, they tend to have higher *Asfc* and lower *epLsar* values. The microwear surface of bovids that select C_4 vegetation will have more striations, hence higher *epLar* and lower *Asfc* values. These differences in diet categories were confirmed by ANOVA results ($P = 0.000$). They also observed variations between species within diet categories (browsers, $P = 0.046$; grazers, $P= 0.0017$).

The importance of these variables for analysing different feeding guilds is tested on a larger sample of modern bovids. A bivariate plot of *epLsar* and *Asfc* for the various bovid species shows that the C_3 and C_4 consumers tend to fall into two clusters with some overlap between them (Figure 5.13). Here C_3 feeders tend to have lower *epLsar* values and higher *Asfc* values compared to C_4 feeders. *Asfc* and *epLsar* values are quite variable for each feeding category. Notable taxa were lechwe, springbok and impala. Each group had unique microwear features. Lechwe had variable *epLsar* values similar to C_3 feeders, but low *Asfc* values similar to C_4 feeders. Impala had moderate *epLsar* values with lower to moderate *Asfc* values. Springbok had highly variable *epLsar* values and the *Asfc* values were in the range of C_3 feeders. The $\delta^{13}C$ values show both lechwe and impala as mixed feeders, and springbok as a variable C_3 feeder. In addition to *Asfc* and *epLsar*, other variables, such as *Smc*, *HAsfc*, *Tfv* and *FTfv*, may offer finer resolution in explaining the dietary behaviours of bovids. Nonetheless, these results highlight the efficiency of the DMTA technique for differentiating diet categories.

Spearman's rho correlations show linear relationships between paired variables (Table 5.4), including *epLsar*, *Asfc*, *Smc*, *HAsfc*, *Tfv* and *FTfv*. Most correlations were low between variables, suggesting that variables can be differentiated and treated independently. A significant association exists between *Tfv* and *FTfv* (0.98). Both variables examine textural fill volume, *FTfv* being at a finer resolution than *Tfv*. Since both variables provide similar information, only the *Tfv* variable will be considered in the remaining analyses.

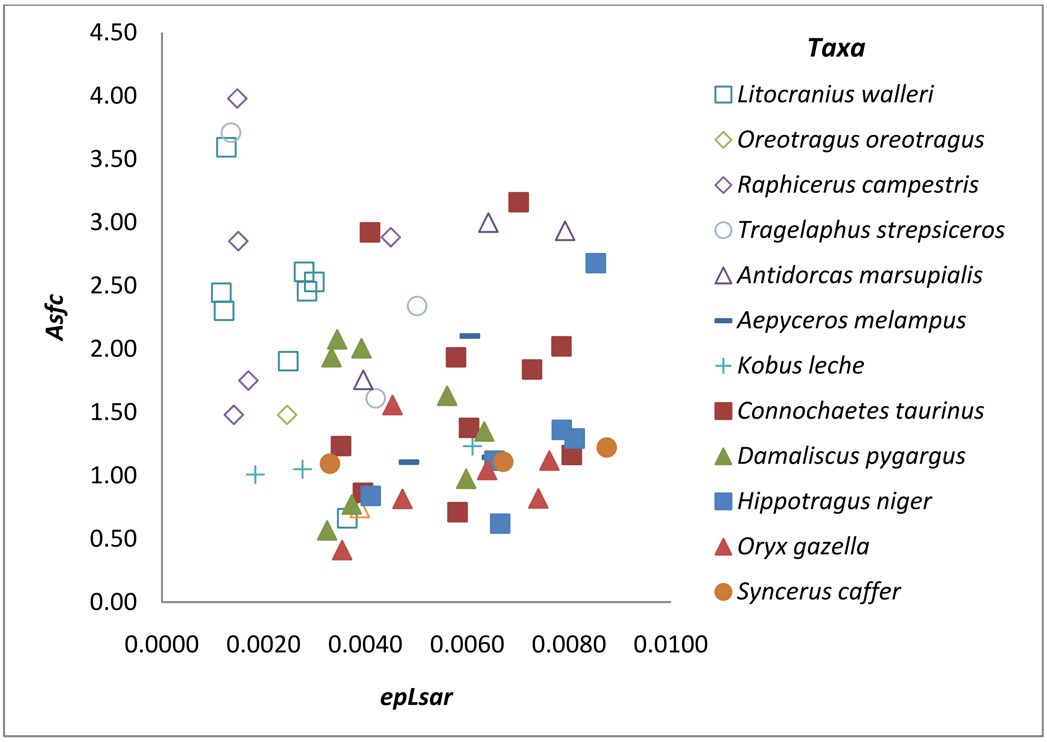

Figure 5.13. Bivariate plot of *epLsar* and *Asfc* for modern bovid taxa. Individual point values for each specimen have been plotted. Open symbols represent C_3 feeders, closed symbols indicate C_4 feeders, and hash and cross markers are mixed C_3–C_4 feeders.

Table 5.4. Spearman's rho correlations between variables for modern bovid taxa.

Variables	*epLsar*	*Asfc*	*Smc*	*HAsfc*	*Tfv*
Asfc	-.275				
Smc	.117	-.418			
HAsfc	-.216	.109	.031		
Tfv	.385	-.259	.033	-.338	
FTfv	.370	-.299	.074	-.299	.980

Multivariate test results indicated significant variation among modern bovid taxa in overall microwear texture (Table 5.5a). In ANOVA, the individual variables for variables *epLsar*, *Asfc* and *Tfv* showed significant variation among the taxa (Table 5.5b). The results for *Smc* were insignificant (*P* = .143), and *HAsfc* was borderline insignificant (*P* = .052). Most species had additional wear at very fine scales (*Smc*) and a low degree of within-facet variation in microwear across different scales (H*Asfc*). Pairwise comparisons indicated unique texture patterns for several of the modern taxa. At least one or more species exhibited differences from one or more other species for *epLsar*, *Asfc* and *Tfv* (Table 5.5c). The Tukey's test results indicated significant variation between species for the variable *epLsar*. For this variable, gerenuk and steenbok (obligate C_3 consumers) varied from wildebeest, buffalo, sable (obligate C_4 consumers), gemsbok (variable C_4 consumers) and impala (mixed C_3–C_4 consumer). Gerenuk varied from springbok (variable C_3 consumer). The Fishers LSD tests indicated significant variation between species for the variable *Asfc*. For the most part C_3 and mixed C_3–C_4 feeders varied from C_4 feeders. The steenbok varied from C_4 consumers and springbok. Gerenuk and springbok varied from lechwe, sable and gemsbok. Springbok also varied from buffalo. Gemsbok varied from kudu and another C_4 feeder, wildebeest. The Tamhane's T2 test showed significant variation for *Tfv* variable. Gerenuk and steenbok (obligate C_3 feeders) varied from wildebeest; blesbok and sable (obligate C_4 feeders).

Table 5.5. Statistical analysis of DMTA data of modern bovids.

A. Multivariate tests

Effect	**Value**	**F**	**df**	**P**
Pillai's Trace	1.96	2.13	60.0	**.000**
Wilks' Lambda	.05	2.60	60.0	**.000**
Hotelling's Trace	5.09	3.17	60.0	**.000**

Significant differences in bold (P= < 0.05)

B. ANOVA between modern bovid taxa

Variables	Sum of Squares	df	Mean Squares	F	P
epLsar	9162.93	10	916.29	6.90	**.000**
Asfc	6491.11	10	649.11	3.44	**.002**
Smc	3952.08	10	395.21	1.58	.143
H*Asfc*	4864.14	10	486.41	2.04	.052
Tfv	8929.29	10	892.93	7.16	**.000**

Significant differences in bold (P= < 0.05)

C. Pairwise comparisons results for modern bovid taxa

1. Anisotropy (*epLsar*)

Taxa	Ame	Ama	Ct	Dp	Hn	Kl	Lw	Og	Rc	Sc
Ama	1									
Ct	1	1								
Dp	.785	.914	.617							
Hn	.999	.990	.919	.089						
Kl	.566	.728	.431	1	.071					
Lw	**.014**	**.032**	**.000**	.326	**.000**	.964				
Og	1	1	1	.579	.998	.390	**.002**			
Rc	**.044**	.086	**.005**	.598	**.000**	.991	1	**.010**		
Sc	1	1	1	.808	.999	.590	**.016**	1	**.048**	
Tst	.683	.827	.574	1	.114	1	.908	.515	.970	.706

Significant differences in bold (P > .05) with Tukey's HSD Multiple Comparisons Test.

2. Complexity (*Asfc*)

Taxa	Ame	Ama	Ct	Dp	Hn	Kl	Lw	Og	Rc	Sc
Ama	.060									
Ct	.072	.583								
Dp	.084	.645	.944							
Hn	**.012**	.695	.219	.299						
Kl	**.008**	.393	.112	.152	.551					
Lw	.494	.108	.123	.154	**.014**	**.010**				
Og	**.003**	.315	**.049**	.084	.448	.958	**.002**			
Rc	.974	**.034**	**.029**	**.041**	**.003**	**.003**	.393	**.001**		
Sc	**.011**	.479	.157	.205	.670	.882	.016	.827	**.005**	
Tst	.768	.109	.147	.161	.027	.016	.742	**.007**	.716	**.023**

Significant differences in bold (P > .05) with Fisher's Least Significance Test.

3. Textural fill volume (*Tfv*)

Taxa	Ame	Ama	Ct	Dp	Hn	Kl	Lw	Og	Rc	Sc
Ama	1									
Ct	1	1								
Dp	1	1	1							
Hn	1	1	1	.526						
Kl	1	1	.213	.051	.984					
Lw	1	1	**.001**	**.000**	**.012**	.204				
Og	1	1	.998	.793	1	1	.551			
Rc	1	1	**.000**	**.000**	**.009**	.169	1	.544		
Sc	1	1	.226	.119	.876	1	.874	1	.838	
Tst	1	1	1	1	1	1	.993	1	.995	1

Significant differences in bold (P > .05) with Tamhane’s T2 for unequal variances

Principal Component Analysis (PCA) seeks to describe the patterns of diet variation present in the dataset. Each bovid species were assigned to a diet category based on the stable carbon isotope averages (see Table 4.4). Three dietary categories (C_3, mixed and C_4) were used instead of the five categories discussed in Chapter 4 (Table 4.5) because the sample sizes for each of the five categories were too small. Component 1 represents a sample variability of 39.4% for data comparing DMTA variables. This component separates C_3 feeders from C_4 feeders. Generally, C_4 and C_3 feeders are widely separated from each other by *epLsar, Smc* and *Tfv* values indicating a surface pattern dominated by course scale microwear with deep striations (Table 5.6). This pattern is consistent with a diet of tough fibrous foods, such as grass. Conversely, C_3 feeders were explained by *Asfc* and *HAsfc* variables (Figure 5.15) showing a complex microwear surface. Mixed feeders (lechwe and impala) were allocated between C_3 and C_4 feeders. Component 2 was less variable at 23.1%. Component II was explained by *HAsfc* and *Smc* variables (Figure 5.14). Lechwe, buffalo and gemsbok loaded almost exclusively for *HAsfc* and *Smc*, while wildebeest and blesbok loaded for *Asfc*, *epLsar* and *Tfv* (Figure 5.15). Component 2 tends to distinguish between C_4 feeders and lechwe, a mixed feeder. PCA highlighted not only interspecific dietary variability, but also intraspecific variability. The PCA showed the variables that contributed most to differences between taxa. The technique emphasizes interspecific and intraspecific dietary differences. Based on these results, it appears evident that these same variables will differentiate feeding guilds between fossil bovid species.

For DFA, each species was assigned a diet category based on known $\delta^{13}C$ averages for modern bovids. First, species were assigned broad dietary categories: C_3, mixed and C_4. Function 1 discriminated C_4 from C_3 consumers by variables *epLsar*, *Smc* and *Tfv* representing 86.3% of variance (Figure 5.16, Table 5.7). Mixed feeders overlap between the two groups (Figure 5.6). Function 2 shows 13.7% of variance and discriminates groups by H*Asfc* (Table 5.7). This function only separated mixed feeders from the other two groups. Using these broad diet categories, 84.2% of the original grouped cases were correctly classified (Table 5.7).

In the next analysis, diet categories were expanded to include five diet categories (OC_3, VC_3, mixed, VC_4 and OC_4). Function 1 accounted for 77.5% of variance, while Function 2 only had 19% of variance (Figure 5.17, Table 5.8). Similar to the first analysis, Function 1 discriminated the groups by *epLsar*, *Smc* and *Tfv*, and Function 2 by *HAsfc*. For this test, 77.2% of the original grouped cases were classified correctly (Table 5.8).

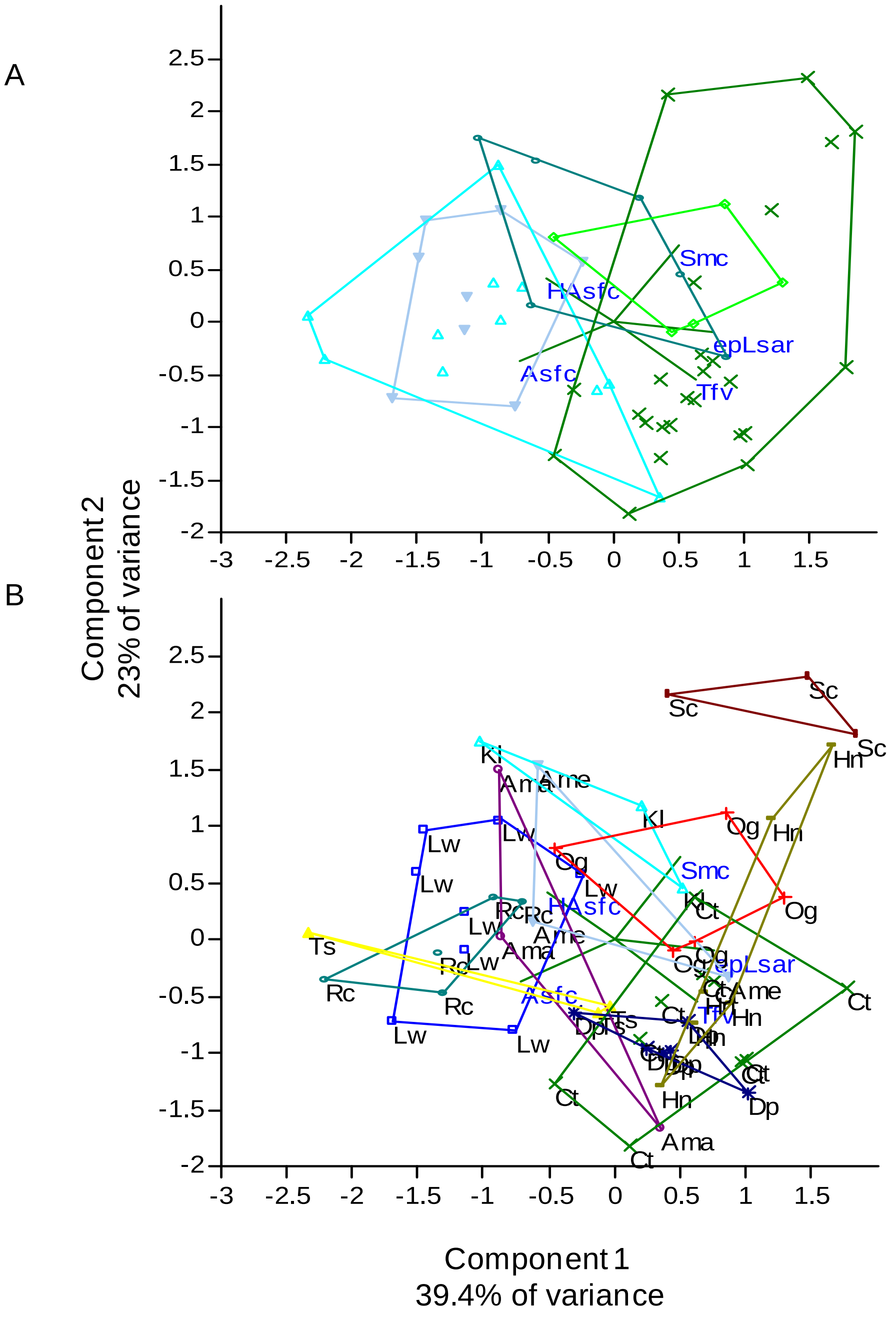
A
B
Component 2
23% of variance
Component 1
39.4% of variance
Smc
HAsfc
epLsar
Asfc
Tfv
Sc
Hn
Ki
Ama
Ame
Lw
Og
Rc
Ct
Ts
Dp
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Figure 5.14. PCA results for modern bovid taxa demonstrating unique dietary patterns and variation with each diet category. Diagram (A) shows clusters based on diet. Each species was placed into a diet category based on the δ^{13}C averages for modern bovids. This diagram represents where diets cluster. Each feeding category was grouped by convex hulls representing ranges that connect. Symbols represent different feeding guilds: ▼ = Obligate C$_3$, △ = Variable C$_3$, ○ = Mixed C$_3$-C$_4$, ◇ = Variable C$_4$ and × = Obligate C$_4$. Diagram (B) shows the same cluster as diagram A, but based on taxon. Each taxon was grouped by convex hulls. A specimen is associated with individual values. Abbreviations represent different species: *Aepyceros melampus* = Ame, *Antidorcas marsupialis* = Ama, *Connochaetes taurinus* = Ct, *Damaliscus pygargus* = Dp, *Hippotragus niger* = Hn, *Oryx gazella* = Og, *Kobus leche* = Kl, *Litocranius walleri* = Lw, *Pelea capreolus* = Pc, *Syncerus caffer* = Sc and *Tragelaphus strepsiceros* = Ts.

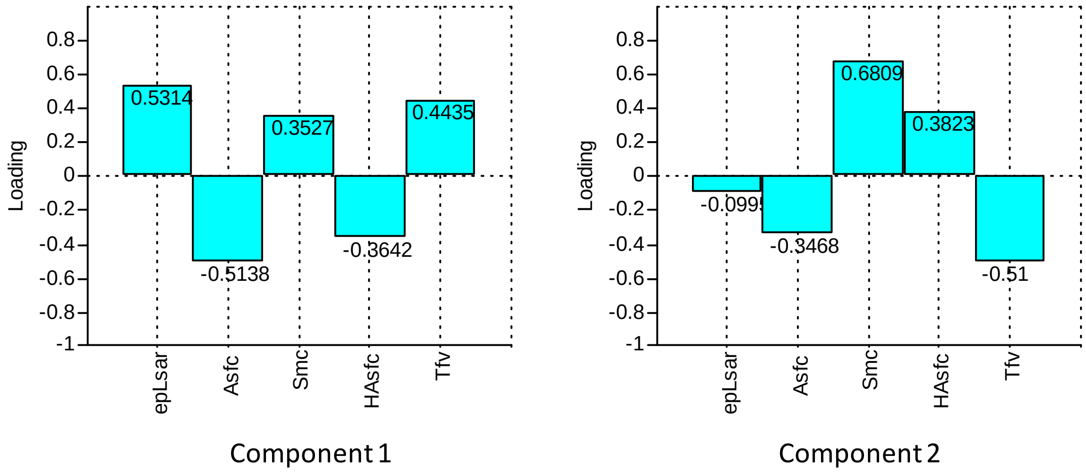

Figure 5.15. Loadings for Components 1 and 2.

Table 5.6. PCA for modern bovid taxa.

A. Eigenvalue

PC	Eigenvalue	% of Variance	Cumulative %
1	1.97	39.4	39.4
2	1.15	23.1	62.5
3	0.81	16.2	78.7
4	0.60	12.1	90.8
5	0.46	9.2	100

B. Principal Component Loadings

PC 1	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
epLsar	0.53	-0.10	0.20	0.80	-0.17
Asfc	-0.51	-0.35	-0.26	0.49	0.56
Smc	0.35	0.68	-0.29	0.05	0.57
H*Asfc*	-0.36	0.38	0.82	0.12	0.18
Tfv	0.44	-0.51	0.36	-0.33	0.55

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Table 5.6. continued

C. Scores

Taxa	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Lw	-1.14	-0.08	-1.17	-0.90	-0.05
Lw	-1.50	0.60	-1.10	-0.52	-0.87
Lw	-1.69	-0.72	-1.61	-0.01	0.63
Lw	-0.87	1.05	-0.63	-0.31	-0.39
Lw	-0.76	-0.80	-0.53	-0.43	0.37
Lw	-1.13	0.24	-0.70	0.16	-0.46
Lw	-1.44	0.96	-0.20	0.62	-0.28
Lw	-0.24	0.57	0.36	-0.99	-2.23
Ama	-0.88	1.50	0.45	0.51	-0.57
Ama	-0.86	0.02	0.18	2.16	0.03
Ama	0.34	-1.67	-0.29	1.75	0.56
Rc	-2.22	-0.36	-0.19	0.51	1.53
Rc	-1.32	-0.47	-1.60	-0.44	-0.26
Rc	-0.93	0.36	-0.16	-1.23	-0.44
Rc	-1.34	-0.11	-1.21	-0.24	0.18
Rc	-0.70	0.33	-1.57	0.98	-0.99
Ts	-2.35	0.06	1.52	0.34	2.09
Ts	-0.04	-0.59	1.12	-0.77	0.20
Ts	-0.14	-0.64	-0.81	0.42	-0.15
Ame	-0.59	1.53	1.19	0.43	-1.47
Ame	-0.62	0.16	1.19	1.26	-0.63
Ame	0.86	-0.33	1.67	-0.24	0.56
Kl	0.20	1.17	-0.80	-1.87	0.45
Kl	-1.03	1.74	3.16	-0.80	0.15
Kl	0.50	0.45	0.39	0.24	-0.38
Og	-0.47	0.80	1.39	0.07	-0.08
Og	1.28	0.37	-0.43	-1.26	0.76
Og	0.83	1.12	0.88	0.23	0.67
Og	0.60	-0.03	0.30	0.63	-2.37
Og	0.44	-0.09	1.15	0.86	-1.50

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Table 5.6. continued

C. Scores

Taxa	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Ct	0.34	-0.56	0.02	-1.47	-0.18
Ct	0.75	-0.36	0.46	-1.64	0.10
Ct	-0.46	-1.27	-0.97	0.23	0.51
Ct	0.18	-0.88	0.09	0.28	-0.32
Ct	0.66	-0.32	-0.84	-0.36	-2.58
Ct	0.95	-1.08	0.08	-0.48	-0.03
Ct	0.11	-1.82	1.51	1.16	2.40
Ct	0.60	0.36	0.59	1.14	0.84
Ct	0.99	-1.05	-0.53	1.06	0.15
Ct	1.76	-0.44	-0.66	0.42	0.10
Dp	0.36	-1.00	-0.74	-1.28	0.95
Dp	0.24	-0.95	-0.50	-1.08	1.15
Dp	1.01	-1.36	0.49	-2.36	0.05
Dp	-0.31	-0.65	0.71	-0.52	0.36
Dp	0.41	-0.97	0.89	-0.31	0.15
Dp	0.55	-0.73	0.56	0.00	-0.73
Hn	0.60	-0.74	0.12	-1.55	-0.93
Hn	1.19	1.06	0.18	0.16	1.14
Hn	1.65	1.71	-1.22	0.06	0.35
Hn	0.88	-0.57	0.87	0.75	-0.48
Hn	0.67	-0.48	0.68	1.04	-1.40
Hn	0.35	-1.29	-0.77	2.18	-0.54
Sc	0.40	2.16	-0.01	-0.88	1.58
Sc	1.47	2.31	-1.69	0.74	1.16
Sc	1.84	1.80	-1.26	1.53	1.17

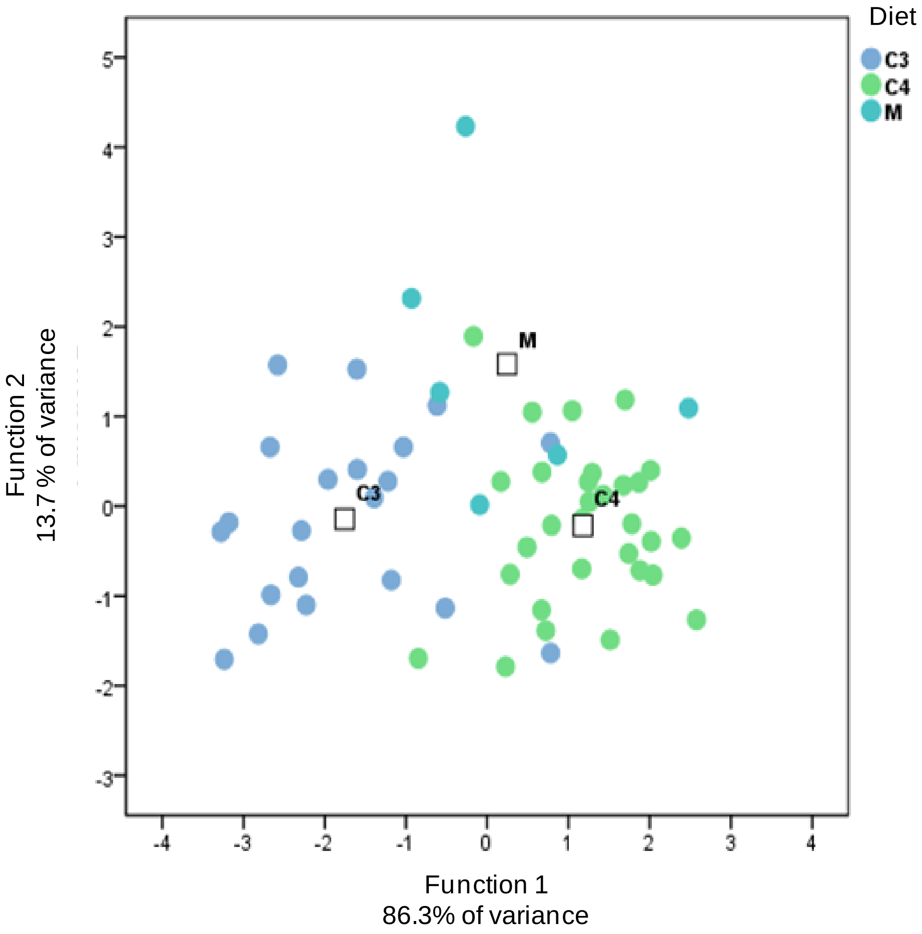


Figure 5.16. DFA results for modern bovid taxa based on broad diet categories.

Table 5.7. DFA results using three diet categories.

A. Classification

Diet	Predicted Group Membership			Total
	C_3	Mixed	C_4	
C_3	18	1	2	21
M	0	3	3	6
C_4	1	2	27	30

84.2% of original grouped cases correctly classified

B. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.972	86.3	86.3	.815
2	.312	13.7	100	.488

C. Standardized Canonical Discriminant Function Coefficients

DMTA variables	Function	
	1	2
epLsar	.505	.003
Asfc	-.473	-.490
Smc	.239	-.089
H*Asfc*	.021	.925
Tfv	.773	-.031

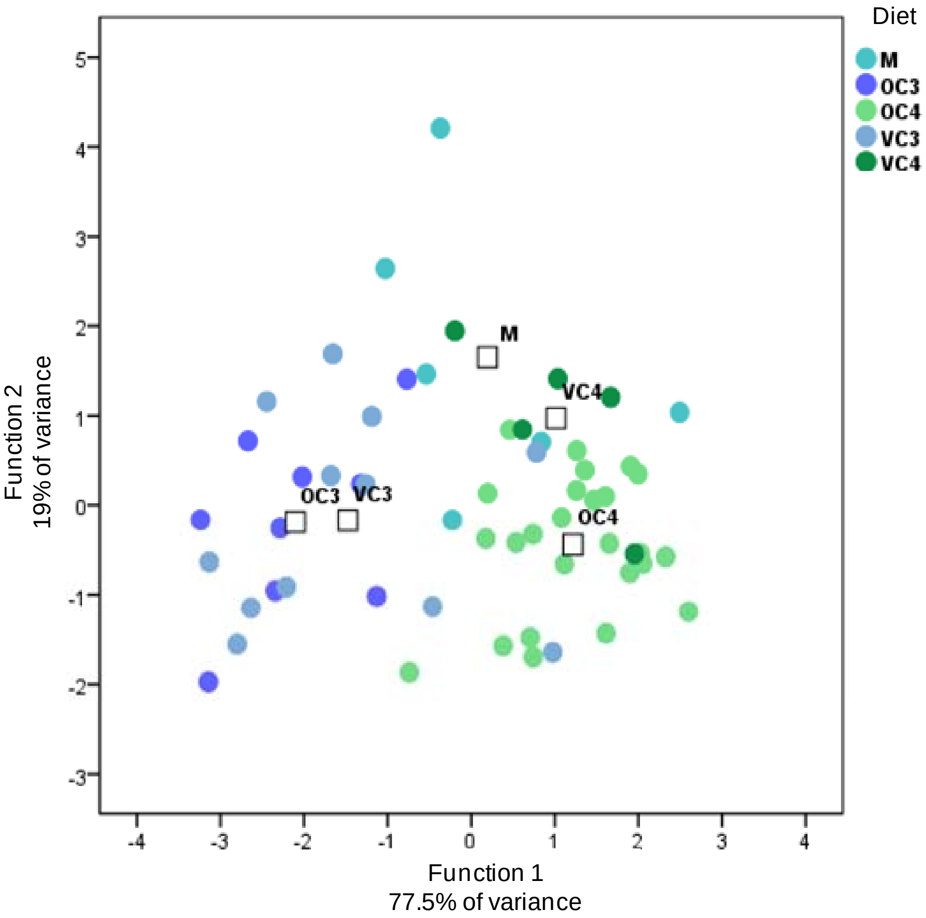


Figure 5.17. DFA results for modern bovid taxa based on five diet categories.

Table 5.8. DFA results using five diet categories.

A. Classification

Diet	Predicted Group Membership					Total
	OC_3	VC_3	Mixed	VC_4	OC_4	
OC_3	9	0	0	0	0	9
VC_3	3	6	1	0	2	12
M	0	0	6	0	0	6
VC_4	0	0	0	5	0	5
OC_4	0	2	1	4	18	25

77.2% of original grouped cases correctly classified

B. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2.083	77.5	77.5	.822
2	.510	19.0	96.5	.581
3	.074	2.8	99.3	.263
4	.020	.7	100	.140

C. Standardized Canonical Discriminant Function Coefficients

DMTA variables	Function			
	1	2	3	4
epLsar	.535	.125	.527	-.646
Asfc	-.398	-.587	.694	.207
Smc	.243	-.179	-.106	.450
H*Asfc*	.023	.895	.406	.298
Tfv	.781	-.156	.161	.661

5.4.2 DMTA dietary profiles for modern bovids

Descriptive statistics are summarized in Tables 5.9 and 5.10. For some of the descriptive tables, abbreviations are used (page xv – xiv). These abbreviations are listed next to the species in the results section. Distribution of DMTA values for bovid taxa are shown in Figures 5.18 – 5.20.

5.4.2.1 Aepycerotini

***Aepyceros melampus* (Ame)**

Impalas have a catholic diet that includes a variety of vegetation: forbs, twigs of shrubs or trees, fresh leaf buds, wild fruits, seedpods, and during the wet season they feed on fresh grass (Skinner and Chimimba 2005). The mean for impala were .0058 *epLsar*, 1.45 *Asfc*, 0.23 *Smc*, 0.64 *HAsfc* and 9852.9 *Tfv*. The microwear surface was varied with parallel scratches and some pitting. These features were moderately deep. The DMTA values indicate a variable diet that includes grass and other types of vegetation.

5.4.2.2 Alcelaphini

***Connochaetes taurinus* (Ct)**

Blue wildebeest will select fresh short grasses and feed on eudicots and fruit in small quantities (Skinner and Smithers 1990). The DMTA mean for the wildebeest were .0059 *epLsar*, 1.72 *Asfc*, 0.24 *Smc*, 0.39 *HAsfc* and 15645.6 *Tfv*. The microwear surface was complex with deep scratches and pits. The DMTA variables showed that this species is a grazer, but the high *Asfc* values may indicate that they may select other types of vegetation or short grasses that could have contained grit from the adjacent soil.

Damaliscus pygargus (Dp)

Blesbok feed on short to medium length grasses (Van Zyl 1965). On the rare occasion, they have been observed selecting tree leaves (Van Zyl 1965). They had mean of .0044 *epLsar*, 1.41 *Asfc*, 0.19 *Smc*, 0.43 *HAsfc* and 18915.8 *Tfv*. This species had moderately complex microwear surface. The features were deep and symmetrical. The blesbok has a very similar diet to the wildebeest.

Antilopini

Antidorcas marsupialis (Ama)

Springbok select a variety of vegetation: fresh grass, leaves, roots, tubers, succulents, forbs, melons, seedpods and fruit (Hofmann and Stewart 1972). They had mean of .0061 *epLsar*, 2.56 *Asfc*, 0.23 *Smc*, 0.54 *HAsfc* and 7487.0 *Tfv*. Of the modern bovids observed in this study, springbok were distinct in having high *epLsar*, *Asfc* and *HAsfc* values. The microwear surface was complex, dominated by fine striations and pits of varying sizes and shapes. The high *HAsfc* values indicate variations in complexity for each set of subregions. This species consumed a higher portion of tough fibrous food then other browsers.

Litocranius walleri (Lw)

Gerenuks are concentrated C_3 feeders. They will select tree leaves, shoots, flowers, lianas and fruits (Leuthold 1978). The mean for gerenuk were .0023 *epLsar*, 2.19 *Asfc*, 0.20 *Smc*, 0.50 *HAsfc* and 4533.8 *Tfv*. The microwear was a combination of pits and striations of varying sizes overlaying one another. This species had a conservative diet, consuming mostly hard foods. The *epLsar* and *Asfc* values presented here are similar to Ungar et al. (2007) (Table 5.10).

5.4.2.3 Bovini

***Syncerus caffer* (Sc)**

African buffaloes feed on old tall grass that other bovids would avoid (Skinner and Smithers 1990). The species had mean of .0062 *epLsar*, 1.14 *Asfc*, 0.81 *Smc*, 0.43 *HAsfc* and 9064.0 *Tfv*. The overall surface was dominated by parallel striations with some pitting. The features were coarse. African buffalo had the highest *Smc* value, suggesting it selected a different type of C_4 resource to that of other grazing bovids.

5.4.2.4 Hippotragini

***Hippotragus niger* (Hn)**

Sables prefer fresh grass, but will to a small extent select forbs, tree leaves and fruits (Grobler 1981). The mean for the sable were .0070 *epLsar*, 1.32 *Asfc*, 0.33 *Smc*, 0.41 *HAsfc* and 13031.1 *Tfv*. This species had the highest *epLsar* value among the bovids. The tooth surface was dominated by deep scratches and some pitting. The DMTA results here suggest a diet comprised mainly of grass. The *epLsar* and *Asfc* results presented here are similar to Ungar et al. (2007) (Table 5.10).

***Oryx gazella* (Og)**

Gemsbok consume a variety of food, preferring green grass, but also select roots, tubers, melons and wild cucumbers (Dieckmann 1980). The mean for the gemsbok were .0057 *epLsar*, 0.96 *Asfc*, 0.32 *Smc*, 0.50 *HAsfc* and 12491.8 *Tfv*. The overall microwear surface was dominated by deep symmetrical striations. Ungar et al. (2007) results for *epLsar* (.0070) and *Asfc* (1.39) were dissimilar to the present study (Table 5.10). The difference in values between the two studies may be due to the different part of the facet that was selected for scanning. Nonetheless, the five DMTA values used in the PCA grouped gemsbok with other C_4 feeders.

5.4.2.5 Neotragini

***Oreotragus oreotragus* (Oor)**

Klipspringers consume leaves, berries, fruits, seedpods, flowers, herbs, young shoots and on rare occasions fresh grass (Wilson and Child 1965; Norton 1984). The species had a mean of .0025 *epLsar*, 1.48 *Asfc*, 0.49 *HAsfc* and 4384.0 *Tfv* (Table 5.9). The tooth surface was moderately complex with fine features. The DMTA values presented here show a diet of soft C_3 vegetation.

***Raphicerus campestris* (Rc)**

Steenbok feed on mainly forbs, but also eat tree leaves, shoots, creepers, lianas, seeds, seedpods, berries, fruits and fresh grass (Smithers 1971; du Toit 1993). Five specimens had a mean of .0021 *epLsar*, 2.75 *Asfc*, 0.20 *Smc*, 0.47 *HAsfc* and

4778.0 *Tfv*. The microwear surface was complex, dominated by fine pits. Steenbok selected mostly hard, brittle foods.

5.4.2.6 Reduncini

***Kobus leche* (Kl)**

Lechwes feed mainly on grasses that include sedges. They rarely consume eudicots, but when they do, they prefer new growth (Williamson 1979). Three specimens had mean of .0036 *epLsar*, 1.10 *Asfc*, .37 *Smc*, .63 *HAsfc* and 10160.0 *Tfv*. The overall description that best describes the microwear features was moderate. The *epLsar*, *Asfc*, *Smc* and *Tfv* values all fell within the mid-range. The high *HAsfc* values indicated variations in complexity for each set of subregions. The results suggest they consume a variety of foods. In comparison to Ungar et al. (2007) study, the *Asfc* values were similar, but the *epLsar* values were different. The higher *epLsar* value in the Ungar et al. (2007) study was similar to field observations (Table 5.10), which showed that this taxon consumes mostly monocots (Williamson 1990).

5.4.2.7 Tragelaphini

***Tragelaphus strepsiceros* (Tst)**

Kudu consume a wide variety of resources: leaves, shoots, seedpods, forbs, herbs, fallen fruits, succulents, vines, tubers, flowers and some fresh grass (Du Plessis and Skinner 1987; Owen-Smith and Cooper 1989). The mean for kudu were .0035 *epLsar*, 2.55 *Asfc*, 0.17 *Smc*, 0.58 *HAsfc* and 11910.1 *Tfv*. The tooth surface was complex with some striations, but mostly dominated by varying size and shaped pits. There were variations in complexity across the surface. One individual (.0014 *epLsar*, 3.71 *Asfc*) was similar to the results of Ungar et al. (2007) in which it was found that it consumed mostly hard, brittle eudicots. In Ungar et al. (2007) study, the *epLsar* value was lower (.0018) and the *Asfc* value was higher (4.45). Although kudu are browsers, they select a large variety of vegetation. The results in this study reflect field observations made by Du Plessis and Skinner (1987), Hofmann (1989), and Owen-Smith and Cooper (1989).

Table 5.9. Summary of DMTA descriptive statistics for modern bovid taxa.

A. Anisotropy (*epLsar*)

Tribe	**Taxa**	**N**	**Min**	**Max**	**Mean**	**SD**
Aepycerotini	*Aepyceros melampus*	3	.0049	.0065	.0058	.0008
Alcelaphini	*Connochaetes taurinus*	10	.0035	.0081	.0059	.0016
	Damaliscus pygargus	8	.0032	.0063	.0044	.0013
Antilopini	*Antidorcas marsupialis*	3	.0040	.0079	.0061	.0020
	Litocranius walleri	9	.0012	.0036	.0023	.0009
Bovini	*Syncerus caffer*	3	.0033	.0087	.0062	.0027
Hippotragini	*Hippotragus niger*	6	.0041	.0085	.0070	.0016
	Oryx gazella	6	.0035	.0076	.0057	.0017
Neotragini	*Oreotragus oreotragus*	1	.	.	.0025	.
	Raphicerus campestris	5	.0014	.0045	.0021	.0013
Reduncini	*Kobus leche*	3	.0018	.0061	.0036	.0022
Tragelaphini	*Tragelaphus strepsiceros*	3	.0014	.0050	.0035	.0019

B. Complexity (*Asfc*)

Tribe	**Taxa**	**N**	**Min**	**Max**	**Mean**	**SD**
Aepycerotini	*Aepyceros melampus*	3	1.11	2.10	1.45	.56
Alcelaphini	*Connochaetes taurinus*	10	.71	3.16	1.72	.82
	Damaliscus pygargus	8	.57	2.08	1.41	.59
Antilopini	*Antidorcas marsupialis*	3	1.76	3.00	2.56	.70
	Litocranius walleri	9	.66	3.59	2.19	.85
Bovini	*Syncerus caffer*	3	1.10	1.22	1.14	.07
Hippotragini	*Hippotragus niger*	6	.62	2.68	1.32	.72
	Oryx gazella	6	.41	1.56	.96	.38
Neotragini	*Oreotragus oreotragus*	1	.	.	1.48	.
	Raphicerus campestris	5	1.75	3.98	2.78	.81
Reduncini	*Kobus leche*	3	1.01	1.23	1.10	.12
Tragelaphini	*Tragelaphus strepsiceros*	3	1.61	3.71	2.55	1.07

continued on next page

Table 5.9. continued

C. Scale of maximum complexity (*Smc*)

Tribe	Taxa	N	Min	Max	Mean	SD
Aepycerotini	*Aepyceros melampus*	3	.15	.27	.23	.07
Alcelaphini	*Connochaetes taurinus*	10	.15	.42	.24	.10
	Damaliscus pygargus	6	.15	.27	.19	.06
Antilopini	*Antidorcas marsupialis*	3	.15	.34	.23	.10
	Litocranius walleri	9	.15	.34	.20	.07
Bovini	*Syncerus caffer*	3	.71	.89	.81	.09
Hippotragini	*Hippotragus niger*	6	.15	.74	.33	.27
	Oryx gazella	5	.15	.51	.32	.18
Neotragini	*Raphicerus campestris*	5	.15	.27	.20	.05
Reduncini	*Kobus leche*	3	.27	.51	.37	.12
Tragelaphini	*Tragelaphus strepsiceros*	3	.15	.21	.17	.03

D. Heterogeneity ($HAsfc_{9\text{ cells}}$)

Tribe	Taxa	N	Min	Max	Mean	SD
Aepycerotini	*Aepyceros melampus*	3	.57	.70	.64	.07
Alcelaphini	*Connochaetes taurinus*	10	.27	.57	.39	.10
	Damaliscus pygargus	8	.32	.54	.43	.08
Antilopini	*Antidorcas marsupialis*	3	.36	.66	.54	.16
	Litocranius walleri	9	.40	.61	.50	.07
Bovini	*Syncerus caffer*	3	.36	.58	.43	.12
Hippotragini	*Hippotragus niger*	6	.32	.49	.41	.08
	Oryx gazella	6	.36	.69	.50	.13
Neotragini	*Oreotragus oreotragus*	1	.	.	.49	.
	Raphicerus campestris	5	.37	.62	.47	.10
Reduncini	*Kobus leche*	3	.43	.95	.63	.28
Tragelaphini	*Tragelaphus strepsiceros*	3	.37	.83	.58	.23

continued on next page

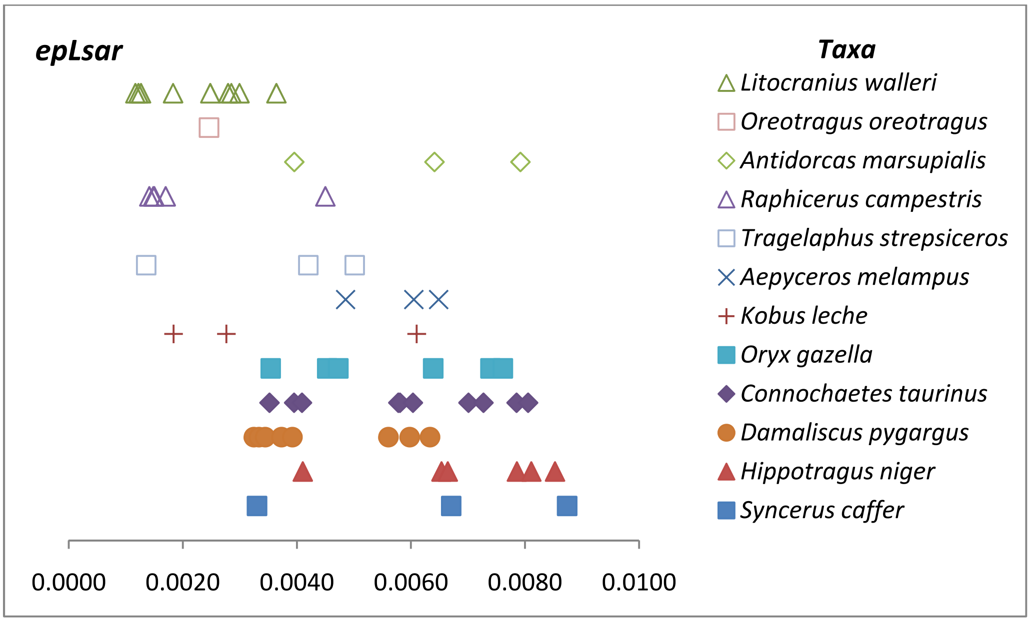
Table 5.9. continued

E. Textural fill volume (*Tfv*)

Tribe	Taxa	N	Min	Max	Mean	SD
Aepycerotini	*Aepyceros melampus*	3	2364.9	19961.6	9852.9	9086.4
Alcelaphini	*Connochaetes taurinus*	10	7763.2	23578.0	15645.6	4295.9
	Damaliscus pygargus	8	14836.2	24658.0	18915.8	3588.2
Antilopini	*Antidorcas marsupialis*	3	1880.7	15623.0	7487.0	7212.0
	Litocranius walleri	8	447.2	11235.6	4533.8	3464.0
Bovini	*Syncerus caffer*	3	7133.6	10283.7	9064.0	1691.0
Hippotragini	*Hippotragus niger*	6	9909.8	16110.9	13031.1	2686.0
	Oryx gazella	6	7726.3	17233.2	12491.8	4050.2
Neotragini	*Oreotragus oreotragus*	1	.	.	4384.0	.
	Raphicerus campestris	5	788.6	7072.6	4778.0	2422.2
Reduncini	*Kobus leche*	3	9241.6	10955.0	10160.0	863.4
Tragelaphini	*Tragelaphus strepsiceros*	3	9205.5	16461.0	11910.1	3964.5

Table 5.10. Descriptive statistics for DMTA of modern bovid taxa from Ungar et al. (2007).

Tribe	Taxon	N	Stats	*epLsar*	*Asfc*
Antilopini	*Litocranius walleri*	9	Mean	0.0020	2.33
			SD	0.0012	0.87
Hippotragini	*Hippotragus niger*	5	Mean	0.0073	1.51
			SD	0.0014	0.70
	Oryx gazella	6	Mean	0.0062	1.99
			SD	0.0024	1.22
Reduncini	*Kobus leche*	5	Mean	0.0056	1.45
			SD	0.0021	1.03
Tragelaphini	*Tragelaphus strepsiceros*	4	Mean	0.0019	4.63
			SD	0.0008	1.82



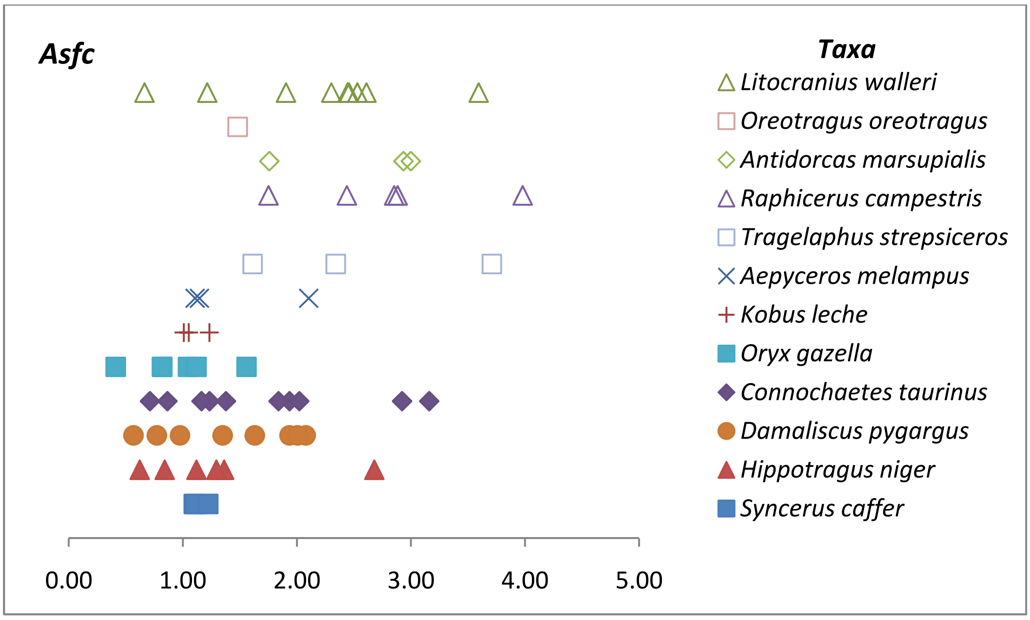
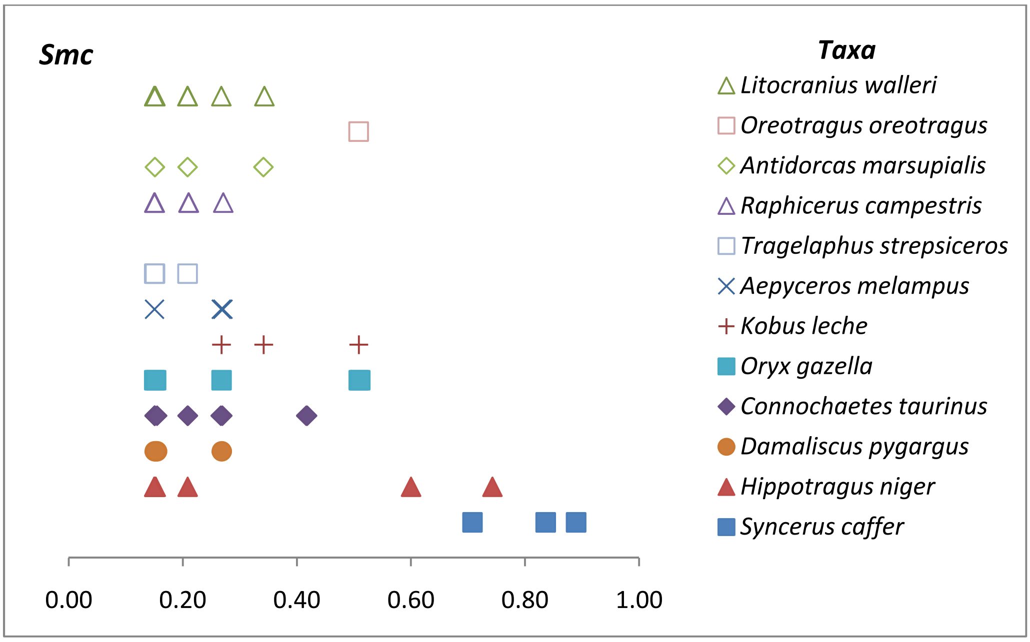


Figure 5.18. *epLsar* and *Asfc* values of modern bovid taxa. Open symbols represent C_3 feeders, closed symbols indicate C_4 feeders and hash and cross markers are mixed C_3–C_4 feeders.



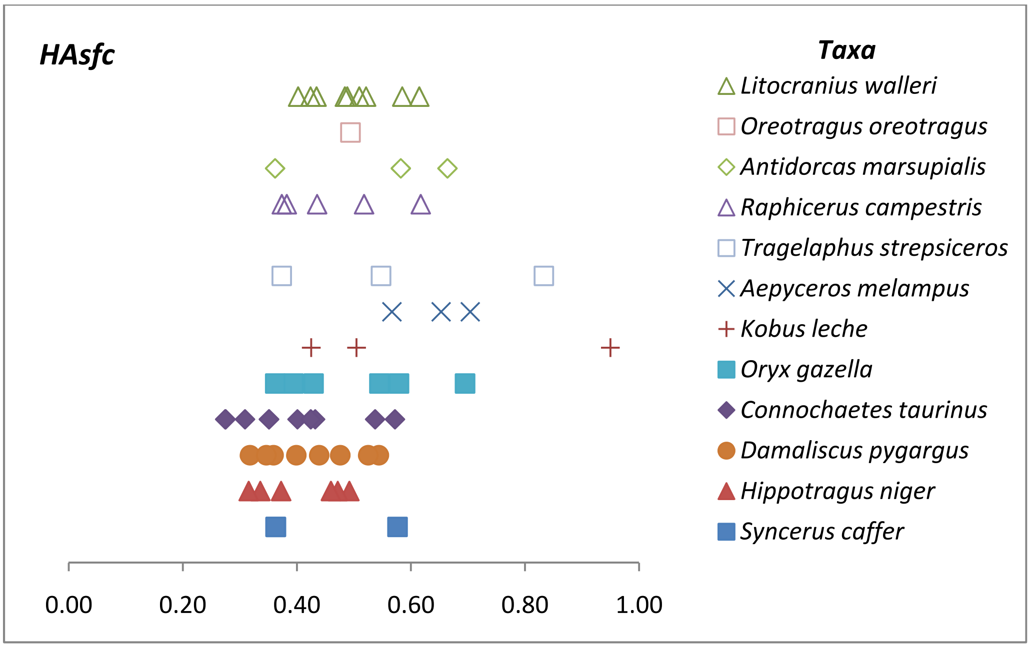


Figure 5.19. *Smc* and *HAsfc* values of modern bovid taxa. Open symbols represent C_3 feeders, closed symbols indicate C_4 feeders and hash and cross markers are mixed C_3–C_4 feeders.

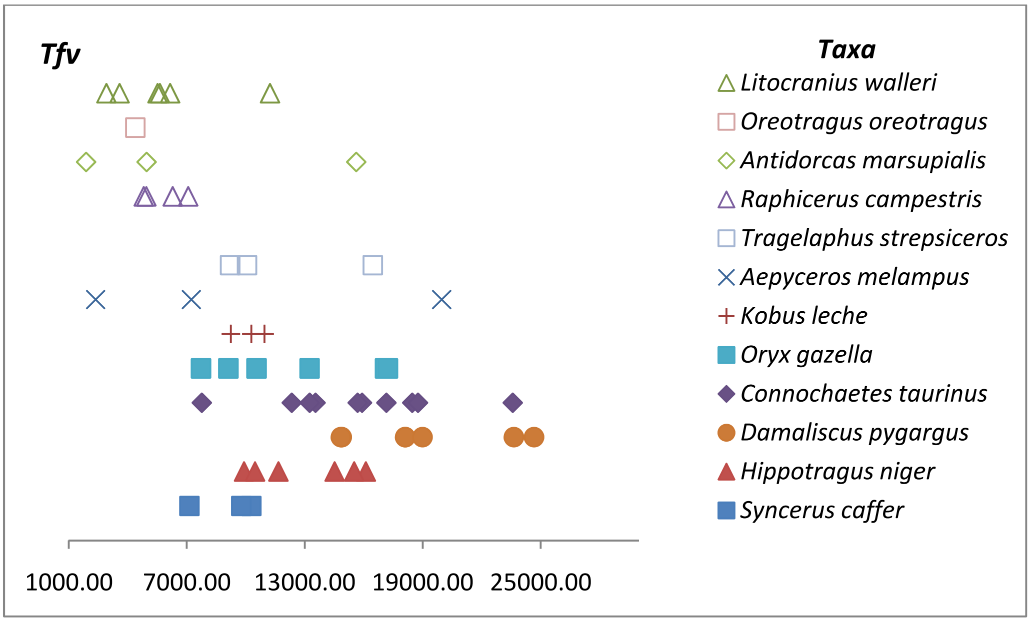


Figure 5.20. *Tfv* values of modern bovid taxa. Open symbols represent C_3 feeders, closed symbols indicate C_4 feeders and hash and cross markers are mixed C_3–C_4 feeders.

5.5 Results of fossil bovid diets

A list of DMTA values are found in Table 5.3. Examples of microwear surfaces for fossil bovid taxa are illustrated in Figure 5.3. Statistical results for DMTA are shown in Figure 5.21.

5.5.1 Statistics

A 3D scatterplot of variables *epLsar*, *Asfc* and *Tfv* was used to demonstrate differences between diet categories (Figure 5.21). Each fossil species was assigned to a diet category based on the stable carbon isotope results (Table 4.11). For each diet category there was great degree of variability for *epLsar* and *Asfc*, while *Tfv* was able for the most part to show C_3 and C_4 feeders tend to fall into two clusters with some degree of overlap. Except for *Tfv*, the same variables used to differentiate modern taxa do not apply here.

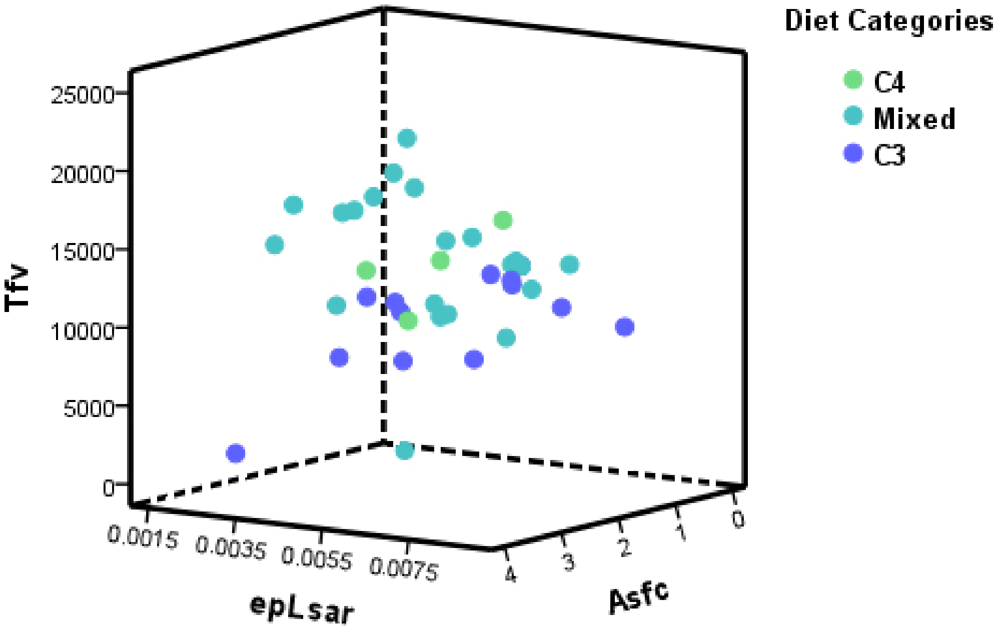


Figure 5.21. 3D scatterplot of *epLsar*, *Asfc* and *Tfv* variables. Each species was assigned a diet category (C_3, mixed or C_3) based on corresponding $\delta^{13}C$ results from the present study.

5.5.2 DMTA dietary profiles for fossil bovids

Descriptive statistics are summarised below, in Table 5.11. Distribution of DMTA values for bovid taxa are shown in Figures 5.22–5.24.

5.5.2.1 Alcelaphini

Connochaetes sp.

The DMTA mean for *Connochaetes* sp. from Cooper's D were .0030 *epLsar*, 2.0 *Asfc*, 0.27 *Smc*, 0.35 *HAsfc* and 16000.1 *Tfv*. The low *epLsar* and high *Asfc* values indicate a surface dominated by deep pits and some striations.

The DMTA mean from Swartkrans Hanging Remnant were .0064 *epLsar*, 1.73 *Asfc*, 0.21 *Smc*, 0.42 *HAsfc* and 16410.3 *Tfv*. The tooth surface was dominated by deep scratches and moderate pitting.

Connochaetes sp. from Swartkrans Member 2 had mean of .0047 *epLsar* 1.55 *Asfc*, 0.29 *Smc*, 0.42 *HAsfc* and 14308.3 *Tfv*. These values indicate deep striations with moderate pitting.

At Swartkrans Member 3, *Connochaetes* sp. mean were .0045 *epLsar*, 1.86 *Asfc*, 0.23 *Smc*, 0.54 *HAsfc* and 14407.7 *Tfv*. The microwear surface was made up of deep scratches with varied sized pits.

***Damaliscus* sp.**

Species from Swartkrans Hanging Remnant had mean of .0051 *epLsar*, 1.81 *Asfc*, 0.74 *Smc*, 0.44 *HAsfc* and 13444.3 *Tfv*. The microwear was dominated by deep scratches and some pitting.

At Swartkrans Member 2, this taxon had mean of .0050 *epLsar*, 2.34 *Asfc*, 0.21 *Smc*, 0.37 *HAsfc* and 10063.7 *Tfv*. The microwear pattern was complex with striations and pits of varied sizes. The surface was uniform throughout.

Megalotragus sp.

Species from Cooper's D had mean of .0030 *epLsar*, 1.51 *Asfc*, 0.27 *Smc*, 0.35 *HAsfc* and 11819.18 *Tfv*. The overall microwear surface had moderately complex features with some striations.

Rabaticeras porrocornutus

Species from Swartkrans Hanging Remnant had mean of .0050 *epLsar*, 1.51 *Asfc*, 0.43 *Smc*, 0.36 *HAsfc* and 14606.6 *Tfv*. The tooth surface was moderately complex with deep features.

5.5.1.2 Antilopini

Antidorcas bondi

Species from Swartkrans Member 2 had mean of .0057 *epLsar*, 0.89 *Asfc*, 0.28 *Smc*, 0.25 *HAsfc* and 12495.8 *Tfv*. The surface was dominated by deep striations.

Antidorcas marsupials

The fossil springbok from Cooper's D had a mean of .0047 *epLsar*, 1.25 *Asfc*, 0.27 *Smc*, 0.36 *HAsfc* and 10406.3 *Tfv*. The microwear surface had striations and some pitting.

The fossil springbok from Swartkrans Member 3 had a mean of .0046 *epLsar*, 1.42 *Asfc*, 0.30 *Smc*, 0.50 *HAsfc* and 10252.7 *Tfv*. The surface comprised of striations and pits. Springbok from Swartkrans Member 3 and Cooper's D had similar values.

Antidorcas recki

From Swartkrans Hanging Remnant, *A. recki* had a mean of .0028 *epLsar*, 3.66 *Asfc*, 0.15 *Smc*, 0.45 *HAsfc* and 2029.4 *Tfv*. The overall surface was dominated by pits of varied size and shape. There was more wear at very fine scales.

Antidorcas recki from Swartkrans Lower Bank had a mean of .0069 *epLsar*, 1.96 *Asfc*, 0.27 *Smc*, 0.55 *HAsfc* and 12948.2 *Tfv*. The microwear surface was complex, with striations and varied sized pits.

This species from Swartkrans Member 2 had a mean of .0054 *epLsar*, 1.12 *Asfc*, 0.22 *Smc*, 0.53 *HAsfc* and 10015.2 *Tfv*. The microwear surface was dominated by striations. These specimens are very similar to those of Swartkrans Lower Bank.

Gazella sp.

This species from Swartkrans Hanging Remnant had mean of .0043 *epLsar*, 1.88 *Asfc*, 0.21 *Smc*, 0.67 *HAsfc* and 1124.05 *Tfv*. The surface was moderately complex with striations and pits.

5.5.1.3 Neotragini

Oreotragus oreotragus

The fossil klipspringer from Swartkrans Hanging Remnant had mean of .0063 *epLsar*, 2.18 *Asfc*, 0.21 *Smc*, 0.57 *HAsfc* and 7879.3 *Tfv*. The species had a complex microwear surface dominated by scratches and pits.

5.5.1.4 Ovibovini

***Makapania* sp.**

This species from Swartkrans Hanging Remnant had mean of .0042 *epLsar*, 1.23 *Asfc*, 0.27 *Smc*, 0.36 *HAsfc* and 9846.07 *Tfv*. Striations and some pitting was found on the microwear surface.

5.5.1.5 Peleini

Pelea capreolus

The fossil grey rhebok from Swartkrans Member 2 had mean of .0040 *epLsar*, 1.64 *Asfc*, 0.27 *Smc*, 0.47 *HAsfc* and 6509.95 *Tfv*. The surface was complex with striations and pitting.

5.5.1.6 Tragelaphini

***Tragelaphus* sp.**

This species from Cooper's D had mean of .0044 *epLsar*, 1.18 *Asfc*, 0.25 *HAsfc* and 9221.88 *Tfv*. The surface had striations and some pitting.

Table 5.11. Descriptive statistics for DMTA of fossil bovids from Cooper's D and Swartkrans Members 1–3.

A. Anisotropy (*epLsar*)

Tribe	**Taxa**	**Deposit**	**N**	**Min**	**Max**	**Mean**	**SD**
Alcelaphini	*Connochaetes* sp.	CD	1	.	.	.0030	.
		SK HR	1	.	.	.0064	.
		SK 2	5	.0022	.0069	.0047	.0022
		SK 3	9	.0026	.0069	.0045	.0018
	Damaliscus sp.	SK HR	1	.	.	.0051	.
		SK 2	1	.	.	.0050	.
	Megalotragus sp.	CD	1	.	.	.0030	.
	Rabaticeras porrocornutus	SK HR	2	.0039	.0061	.0050	.0016
Antilopini	*Antidorcas bondi*	SK 2	1	.	.	.0057	.
	Antidorcas marsupialis	CD	2	.0035	.0059	.0047	.0017
		SK 3	3	.0025	.0071	.0046	.0023
	Antidorcas recki	SK HR	1	.	.	.0028	.
		SK LB	1	.	.	.0069	.
		SK 2	4	.0019	.0083	.0054	.0026
	Gazella sp.	SK HR	1	.	.	.0043	.
Neotragini	*Oreotragus oreotragus*	SK HR	1	.	.	.0063	.
Ovibovini	*Makapania* sp.	SK HR	1	.	.	.0042	.
Peleini	*Pelea capreolus*	SK 2	1	.	.	.0040	.
Tragelaphini	*Tragelaphus strepsiceros*	CD	1	.	.	.0044	.

B. Complexity (*Asfc*)

Tribe	**Taxa**	**Deposit**	**N**	**Min**	**Max**	**Mean**	**SD**
Alcelaphini	*Connochaetes* sp.	CD	1	.	.	2.00	.
		SK HR	1	.	.	1.73	.
		SK 2	5	.95	2.54	1.55	.66
		SK 3	9	.54	3.37	1.86	.77
	Damaliscus sp.	SK HR	1	.	.	1.81	.
		SK 2	1	.	.	2.34	.
	Megalotragus sp.	CD	1	.	.	1.51	.
	Rabaticeras porrocornutus	SK HR	2	1.48	1.53	1.51	.04
Antilopini	*Antidorcas bondi*	SK 2	1	.	.	.89	.
	Antidorcas marsupialis	CD	2	1.19	1.31	1.25	.09
		SK 3	3	1.12	1.91	1.42	.43
	Antidorcas recki	SK HR	1	.	.	3.66	.
		SK LB	1	.	.	1.96	.
		SK 2	4	.89	1.39	1.12	.22
	Gazella sp.	SK HR	1	.	.	1.88	.
Neotragini	*Oreotragus oreotragus*	SK HR	1	.	.	2.18	.
Ovibovini	*Makapania* sp.	SK HR	1	.	.	1.23	.
Peleini	*Pelea capreolus*	SK 2	1	.	.	1.64	.
Tragelaphini	*Tragelaphus strepsiceros*	CD	1	.	.	1.18	.

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Table 5.11. continued

C. Scale of maximum complexity (*Smc*)

Tribe	Taxa	Deposit	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.	CD	1	.	.	.27	.
		SK HR	1	.	.	.21	.
		SK 2	4	.21	.34	.29	.07
		SK 3	9	.15	.34	.23	.07
	Damaliscus sp.	SK HR	1	.	.	.74	.
		SK 2	1	.	.	.21	.
	Megalotragus sp.	CD	1	.	.	.27	.
	Rabaticeras porrocornutus	SK HR	2	.42	.43	.43	.01
Antilopini	*Antidorcas bondi*	SK 2	1	.	.	.28	.
	Antidorcas marsupialis	CD	1	.	.	.27	.
		SK 3	3	.21	.42	.30	.11
	Antidorcas recki	SK HR	1	.	.	.15	.
		SK LB	1	.	.	.27	.
		SK 2	2	.15	.28	.22	.09
	Gazella sp.	SK HR	1	.	.	.21	.
Neotragini	*Oreotragus oreotragus*	SK HR	1	.	.	.21	.
Ovibovini	*Makapania* sp.	SK HR	1	.	.	.27	.
Peleini	*Pelea capreolus*	SK 2	1	.	.	.27	.

D. Heterogeneity ($Hasfc_{9\ cells}$)

Tribe	Taxa	Deposit	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.	CD	1	.	.	.35	.
		SK HR	1	.	.	.42	.
		SK 2	5	.30	.54	.42	.09
		SK 3	8	.31	.78	.54	.17
	Damaliscus sp.	SK HR	1	.	.	.44	.
		SK 2	1	.	.	.37	.
	Megalotragus sp.	CD	1	.	.	.35	.
	Rabaticeras porrocornutus	SK HR	2	.35	.38	.36	.03
Antilopini	*Antidorcas bondi*	SK 2	1	.	.	.25	.
	Antidorcas marsupialis	CD	2	.34	.38	.36	.03
		SK 3	3	.37	.65	.50	.14
	Antidorcas recki	SK HR	1	.	.	.45	.
		SK LB	1	.	.	.55	.
		SK 2	4	.36	.66	.53	.13
	Gazella sp.	SK HR	1	.	.	.67	.
Neotragini	*Oreotragus oreotragus*	SK HR	1	.	.	.57	.
Ovibovini	*Makapania* sp.	SK HR	1	.	.	.36	.
Peleini	*Pelea capreolus*	SK 2	1	.	.	.47	.
Tragelaphini	*Tragelaphus strepsiceros*	CD	1	.	.	.25	.

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Table 5.1l. continued

E. Textural fill volume (*Tfv*)

Tribe	Taxa	Deposit	N	Min	Max	Mean	SD
Alcelaphini	*Connochaetes* sp.	CD	1	.	.	16000.05	.
		SK HR	1	.	.	16410.26	.
		SK 2	5	13034.55	16304.83	14308.27	1209.91
		SK 3	9	9678.95	18386.10	14407.66	3212.26
	Damaliscus sp.	SK HR	1	.	.	13444.33	.
		SK 2	1	.	.	10063.66	.
	Megalotragus sp.	CD	1	.	.	11819.18	.
	Rabaticeras porrocornutus	SK HR	2	8578.44	20634.72	14606.58	8525.08
Antilopini	*Antidorcas bondi*	SK 2	1			12495.84	.
	Antidorcas marsupialis	CD	2	9195.66	11616.91	10406.28	1712.08
		SK 3	3	9604.13	10598.09	10252.72	562.09
	Antidorcas recki	SK HR	1	.	.	2029.39	.
		SK LB	1	.	.	12948.22	.
		SK 2	4	5634.79	12495.84	10015.18	3220.97
	Gazella sp.	SK HR	1	.	.	1124.05	.
Neotragini	*Oreotragus oreotragus*	SK HR	1	.	.	7879.34	.
Ovibovini	*Makapania* sp.	SK HR	1	.	.	9846.07	.
Peleini	*Pelea capreolus*	SK 2	1	.	.	6509.95	.
Tragelaphini	*Tragelaphus strepsiceros*	CD	1	.	.	9221.88	.

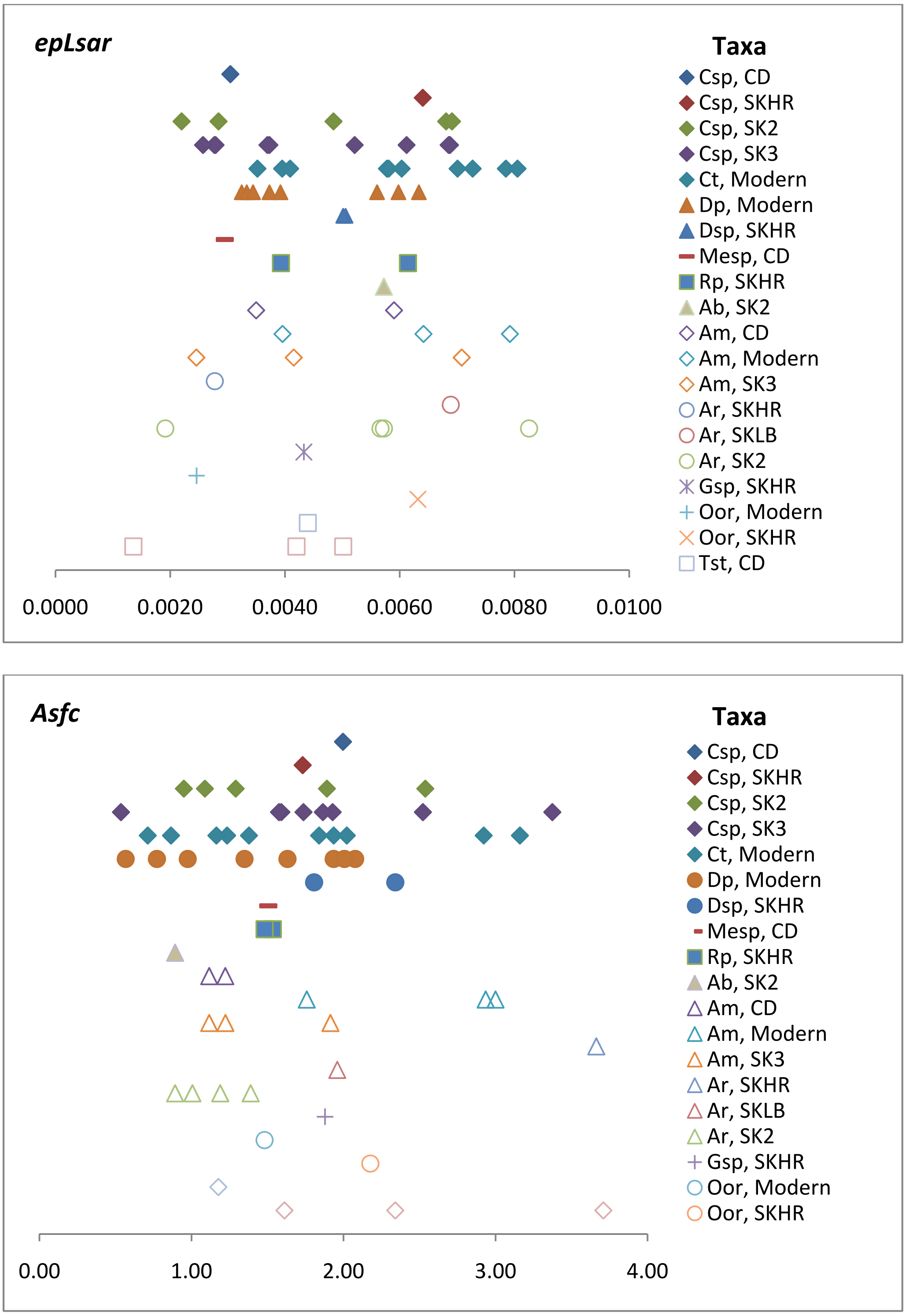
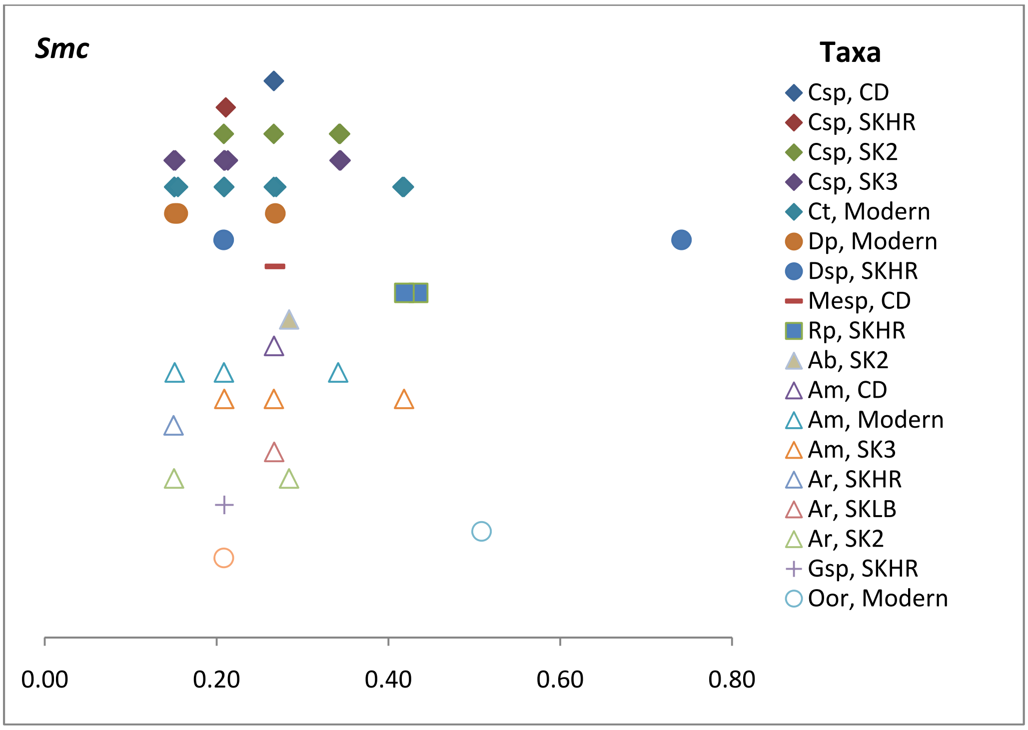


Figure 5.22. *epLsar* and *Asfc* values used to compare fossil bovids to modern taxa. Open symbols represent C_3 feeders, closed symbols indicated C_4 feeders, and hash and cross markers are mixed C_3–C_4 feeders.



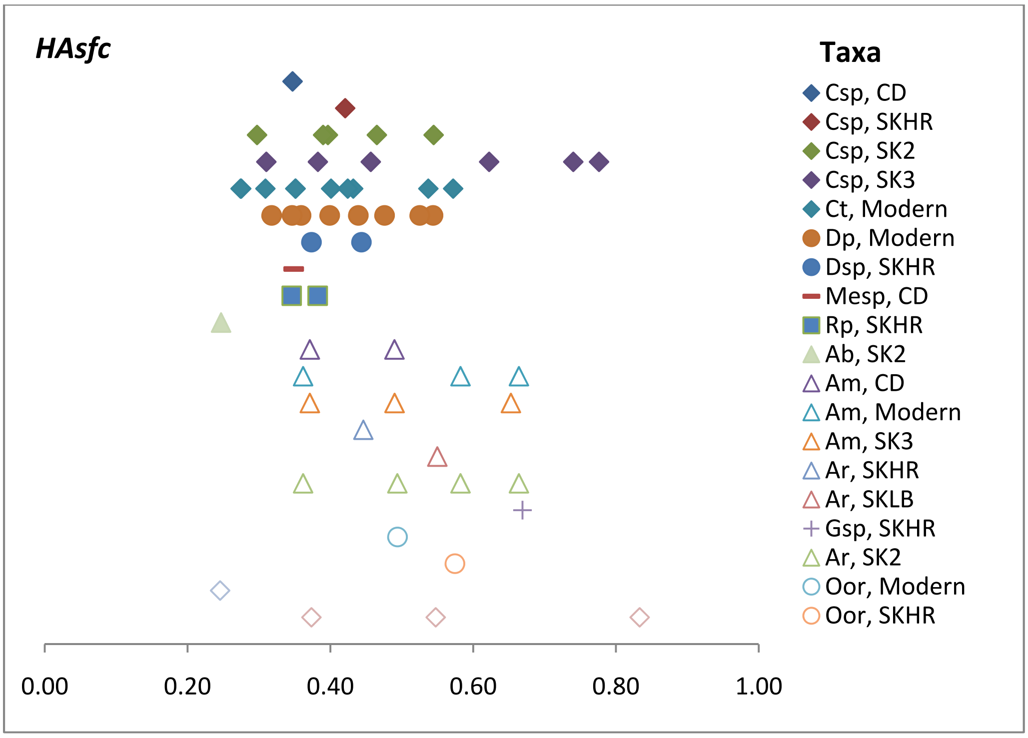


Figure 5.23. *Smc* and *HAsfc* values used to compare fossil bovids to modern taxa. Open symbols represent C_3 feeders, closed symbols indicated C_4 feeders, and hash and cross markers are mixed C_3–C_4 feeders.

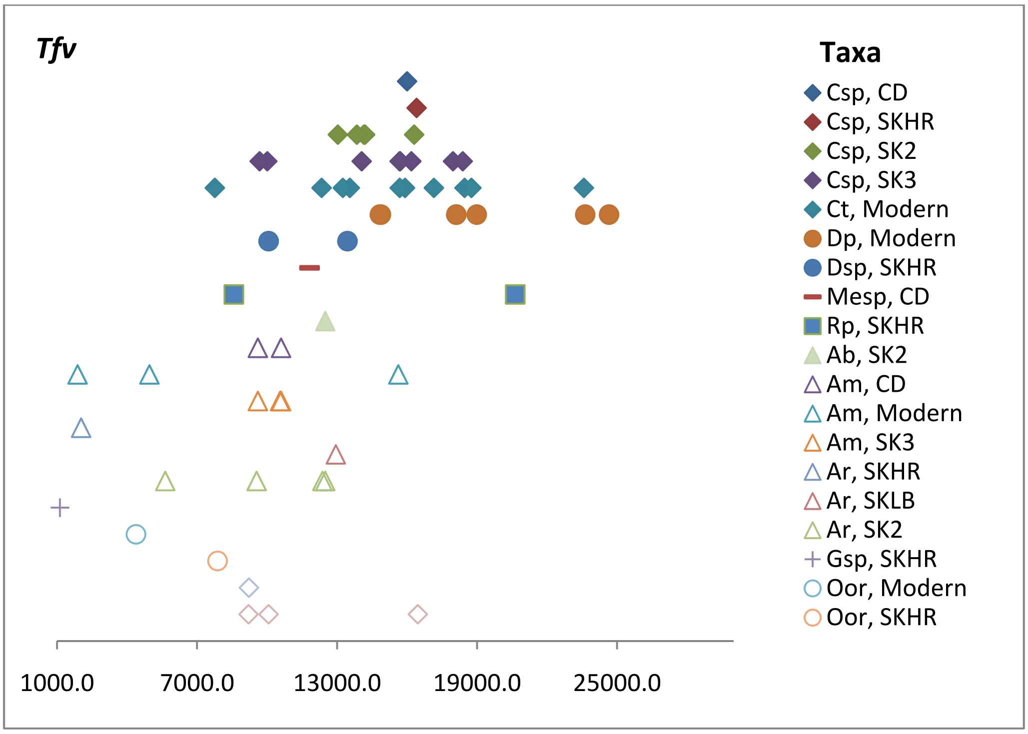


Figure 5.24. *Tfv* values comparing fossil bovids to modern taxa. Open symbols represent C_3 feeders, closed symbols indicated C_4 feeders, and hash and cross markers are mixed C_3–C_4 feeders.

5.6 Discussion

Dental microwear texture analysis accurately reflects the dietary behaviour of modern bovids. The DMTA variables provided details of the unique dietary pattern for each taxon. From the statistical analysis, a few patterns emerged. Among the taxa, interspecific and intraspecific variability existed in diet and some degree of overlap in foraging strategies existed between bovid species. The *epLsar*, *Asfc* and *Tfv* variables showed significant variation between C_3 and C_4 feeders. The modern C_3 consumer tended to have high *Asfc* and low *epLsar* and

Tfv values compared to the modern C_4 consumers that had high *epLsar* and *Tfv* values and moderate to low *Asfc* values.

Ungar et al. (2008) noted that the ability to detect subtle interspecific variation might be the key to realizing the potential of dental microwear texture analyses. Based on the present study, the DMTA variables identified fine-scale diet differences among C_3, mixed and C_4 consumers. Among C_3 feeders, gerenuk, klipspringer and steenbok had low *epLsar*, high to moderate *Asfc* and low *Tfv* values. These variables suggest these species consumed foods that caused fine, shallow pitting on the occlusal surface. All three species consumed leaves, shoots and fruits. The lower *Tfv* values for these bovids suggest that they were mainly feeding on leaves and shoots, as fruits would contain sclereids (stone cells) that would cause large and deeper pitting. Field observations noted the steenbok as a mixed feeder (Hofmann 1973) while others have suggested that they are predominately C_3 feeders in South Africa (Du Toit 1993). The DMTA variables suggested that they were mainly C_3 feeders. Unique among C_3 consumers were the kudu and springbok. Both had more varied diets compared to other bovids. The kudu had low *epLsar*, high *Asfc* and unusually high *Tfv* values. The *Tfv* value indicated deeply excavated features, in this case pits. Though the kudu preferred leaves and shoots, they had a catholic diet and consumed a greater variety of eudicot plants than other bovids (Owen-Smith and Cooper 1989; Skinner and Chimimba 2005). Among the C_3 feeders examined here, kudu consumed a larger portion of fruits (ripe or fallen). In one paper, it was noted that tubers were also found in the rumen of kudu (Wilson 1965). Fruits tend to have stone cells, and although tubers have a low concentration of phytoliths, they have grit on the surface: these two food types were candidates for increased *Tfv* values. Springbok had an unusually high *epLsar*, high *Asfc* and low *Tfv* values. From field observations, springbok (considered intermediate feeders) (Hofmann et al. 1995) incorporated more monocots into their diet in comparison to other C_3 selectors.

Among the mixed feeders, impala had high *epLsar*, moderate *Asfc* and *Tfv*, and unusually high *HAsfc* values. On the other hand, lechwe had low *epLsar* values, with similar values for all other variables. Mixed feeders tended to have a varied diet that included eudicots and monocots and these may account for the high *HAsfc* variable observed for both impala and lechwe. The higher *epLsar* values suggested that the impala from this study consumed a significant proportion of grass. The lower *epLsar* and moderate *Asfc* values for lechwe were perplexing since this species consumed mostly aquatic grasses and sedges. Based on rumen content Williamson (1990) has noted that the lechwe will incorporate 21% of dicots into their diet. This observation is consistent with the moderate values for *Asfc*. As sedges tend to have less robust phytoliths than grass (Albarède et al. 2006), thus this may account for the lower *epLsar* value.

There were a few differences among the predominately monocot feeders. The blue wildebeest, blesbok and sable had similar values for *epLsar*, *Asfc* and *Tfv*. The high *epLsar* and *Tfv* values suggested that they were mainly consuming grass. Grasses, a tough food with coarse phytoliths, are scraped across the tooth surface during mastication, leaving parallel striations that are fairly deep and symmetrical. The isotope data for the forementioned taxa indicated that these bovid species were obligate C_4 consumers (Cerling et al. 2003; Sponheimer et al. 2003; Codron 2006). However, the moderate *Asfc* values indicated that they may be selecting different types of vegetation other than grass or the high *Asfc* values may have reflected grit on the grass blades. Oddly, the stable carbon isotope data for gemsbok suggested a variable C_4 feeder (Sponheimer et al. 2003), but the DMTA values are more consistent with an obligate C_4 feeder. The value for *epLsar* was high, but the *Asfc* value was the lowest among the bovids. Based on rumen contents, almost all grazers consumed varying amounts of eudicots (Skinner and Chimimba 2005). African buffalo were different from other C_4 feeders in that they had moderate *Tfv* and high *Smc* values. Although the *Smc* variables were shown to be insignificant among bovids (ANOVA), the PCA showed that this variable distinguished the taxon from the other C_4 consumers. African buffalo are known to select tall grass compared to other bovids (Skinner and Smithers 1990). The scale of the particles of the grass they were consuming left wide and moderately deep striations.

The DFA correctly classified 84.2% (three diet categories) and 77.2% (five diet categories) of the diets based on $\delta^{13}C$ results and DMTA variables. The results demonstrate that stable carbon isotope and DMTA data reflect similar diet signals. Where slight differences occurred between the two methods, these differences were attributed to the general behaviour of bovids. Whether a bovid preferentially selects C_3 or C_4 vegetation, most will consume various amounts of other food types. For example, as a group, the wildebeest had an average $\delta^{13}C$ value for an obligate C_4 feeder; however, DMTA results reflected a VC_4 feeder. This versatility in vegetation selection was also reflected among some C_3 feeders.

Most of the modern bovids examined in the present study had similar DMTA values compared to other DMTA studies, with the exception of gemsbok and lechwe (Ungar et al. 2007). The difference in values between the two studies may be due to the different part of the facet that was selected for scanning, or vagaries of selection of different specimens given relatively small sample sizes.

The DMTA variables of fossil bovids were dissimilar to modern bovids. Although the sample sizes were small for each species and associated deposit, there was an overall pattern. In particular, the *epLsar* and *Asfc* variables for all fossil bovids regardless of species or deposit were varied. The isotope values provided in this study indicated more variability in dietary behaviour among fossil bovids in comparison to their modern counterparts. Thus, the *epLsar* and *Asfc* values may be a reflection of this versatility. The only DMTA variable to show distinction between dietary groups was *Tfv*. Using a 3D scatterplot, the variable *Tfv* contributed most to the differences between C_3 and C_4 feeders. Bovids that selected C_3 vegetation tended to have lower *Tfv* values and those that selected C_4 foods had higher *Tfv* values. This pattern was supported by the results of modern bovids, where C_3 foods tended to have particles that caused shallow and finer features compared to C_4 grass that caused coarse and deeper features on the microwear surface. This is not to suggest that the higher *Tfv* values indicate a grass dominated landscape. If grass was dominant, the “grazing” guild would preferentially select grass and the microwear surface would be dominated by striations. This is not the case since the occlusal surface of fossil “grazing” bovids show a mixture of pits and striations. However, when grass was consumed it left deep striations. Mixed feeders varied along the C_3–C_4 spectrum for all DMTA variables. The DMTA results were similar to the isotopic results from fossil bovids. In the present study, the DMTA and carbon isotope results indicated that fossil bovids seemed to select from a variety of vegetation.

The DMTA results do warrant caution. The primary concern is related to the small sample sizes for fossil taxa used for this analysis. Sample sizes were related to a combination of factors: manganese staining and curation procedures. Dental remains from both Cooper's Cave and Swartkrans were coated with a layer of manganese. Cooper's D in particular was heavily coated in manganese. Curation procedures of Swartkrans specimens from earlier excavations included preserving material with glue, and extraction of fossils from the calcified clastic sediments left acid etching. Because of the nature of these cave deposits, taphonomic overprinting cannot be excluded. Fossil remains are shifted in sediment through unknown levels of sediment compaction, bioturbation and hydroturbation (de Ruiter et al. 2009).

Chapter 6. Conclusion

The dual proxy approach of stable carbon isotopes and dental microwear analysis has provided a more robust diet reconstruction, and has enhanced the detail of the dietary behaviour of modern bovids. This study has successfully reconstructed the diet of modern species with known dietary preferences. Further, it has shown that the isotopic data and DMTA data were similar to each other.

The stable carbon isotopic analysis and DMTA of several fossil bovid taxa from Cooper's D and Swartkrans Members 1, 2 and 3 were used to reconstruct foraging strategies and by inference vegetation structure. Dietary patterns of the bovids represented in these deposits indicated diverse, mixed C_3–C_4 diets. The variability in both carbon isotopes and DMTA values of the fossil bovids relative to modern bovids, suggested generalized foraging. In particular, the typical 'grazer' guild in the past was more likely to be mixed feeders, unlike their modern counterparts that have specialized diets. Of interest were the $\delta^{13}C$ values of bovid specimens from Cooper's D. Only *R. fulvorufula* from Cooper's D had an obligate C_4 diet. Typical C_3 feeders, *A. marsupialis*, *A. recki*, *R. campestris*, *P. capreolus* and *T. strepsiceros* from Cooper's were more ^{13}C-enriched compared to other deposits. The $\delta^{13}C$ values of *Syncerus* sp. from Cooper's D and Swartkrans Hanging Remnant were ^{13}C-depleted compared to modern *Syncerus* from southern Africa. Two possibilities for these depleted values are: (1) the species had a versatile diet and therefore a wider niche tolerance in the past or (2) a different species of *Syncerus* is represented at these sites.

The foraging strategies of fossil bovids indicate a heterogeneous open woodland ecosystem. A C_4-dominated ecosystem was not present. Evidence of some C_4 selection suggests that grass was present, but to what extent is unknown. Swartkrans Member 2 had substantially more C_3 and mixed feeders than other *P. robustus* deposits, signifying a vegetation community structure that was more C_3-dominated than the other *P. robustus* deposits. There was an apparent indication of shifting vegetation structure between *P. robustus* deposits. Thus, despite its derived craniodental morphology, *P. robustus* seems to have thrived through a range of climatic and ecological shifts. Selection of a variety of available resources may have been advantageous for *P. robustus*. A C_4-dominated ecosystem in the Witwatersrand area of South Africa probably occurred with the onset of pronounced 100 Kyr glacial cycles after 1.2–0.8 Ma. This event might have led to the extinction of *P. robustus*. Future studies of younger deposits from South Africa, within this period, are required.

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