Revisiting the palaeoenvironments of the South African hominid-bearing Plio-Pleistocene sites: New isotopic evidence from Sterkfontein

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Declaration

I declare that this is my own unaided work unless otherwise acknowledged. It has not been submitted before for any other degree at any other university.

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Abstract

This thesis offers a revised palaeoenvironmental reconstruction of South African Plio-Pleistocene sites based on $\delta^{13}C$ and $\delta^{18}O$ isotopes extracted from enamel of fossil fauna. New isotopic results from Sterkfontein Members 4 and 5 are reported to supplement existing data from Makapansgat and Swartkrans in order to examine the changing environment from approximately 3 to 1.4 million years ago (Ma). This provides both evidence for the dietary requirements of extinct fauna and also enables a C_3/C_4 index to be calculated, which provides a means to quantify the open or closed nature of past environments. Previous research of certain key bovid species suggest that earlier reconstructions of the environments at Sterkfontein and other sites, based on faunal abundances and assumptions about habitat preferences of fossil animals based on their modern relatives, underestimated the woodland elements.

Detection of different dietary preferences from the isotopic composition of faunal tooth enamel is possible because plants following the C_3 photosynthetic pathway (trees, shrubs, herbs and temperate grasses) discriminate more markedly against the heavier ^{13}C isotope during photosynthesis than do C_4 plants (tropical grasses). These distinctions are passed along to the consumers of these plants and deposited in their tissues, including their bones and teeth. $\delta^{18}O$ isotope analysis provides pointers to different aspects of faunal palaeoecology, especially those related to drinking behaviour and thermophysiology.

The C_3/C_4 index as calculated in this study gave percentages of 37% for Sterkfontein Member 4, indicating a rather closed environment not that different from Makapansgat Member 3. Sterkfontein Member 5 as a whole had a C_3/C_4 index of 65%, but when this was broken down into the two infills (the older Oldowan infill or East infill and the West infill), the index was found to be 40% for the Oldowan infill and 77% for the West infill. This gives an even higher resolution of the changes that were occurring in the environment. Although the $\delta^{18}O$ values in this study were difficult to interpret, some differences were noted. The carnivores were found to be slightly more depleted in comparison to the herbivores, a pattern noted elsewhere.

The isotopic evidence from this study indicates that the change from a wooded to a more open environment was gradual between 3.0 Ma - 1.8 Ma, but showed a marked difference at 1.8 Ma. This pinpoints the major change to after 2.0 Ma, rather than before.

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CHAPTER 1: INTRODUCTION

The ancient environment in which our ancestors lived has always been of great interest to students of human evolution. It is understood that environmental change has had a significant effect on hominid evolution, but the timing and nature of environmental shifts is still under debate. Their environments provided the ecological framework for their existence, and constrained their behavioural adaptations. Researchers have used numerous approaches to enhance our understanding of the ancient environments inhabited by hominids. This study contributes to our understanding by applying newly developed isotope-based techniques to enhance environmental information from faunal assemblages at Sterkfontein.

The site

Sterkfontein is a rich fossiliferous Plio-Pleistocene site situated south west of Pretoria in a karstic landscape. Sterkfontein's cave infills have yielded many hominid fossils, including *Australopithecus* and some early *Homo* sp. specimens, a large faunal assemblage and Oldowan stone artefacts (Tobias 1992; Kuman 1994; Clarke and Tobias 1995). The deposits at Sterkfontein were laid down during a key time period that is of great relevance to questions about the relationship between environmental change and the evolutionary pathways of hominids and various other faunal lineages.

The chronology of Sterkfontein is, and has been for some time, still under investigation, but progress has been made recently. The stratigraphic units, or members, on which I will focus in this study are Members 4 and 5, which were deposited at approximately 2.6 and 1.7 million years ago (Ma) respectively. Chronology is based almost entirely on faunal comparisons (biostratigraphy) with well-dated sites in East Africa (Clarke 1988) although other methods have been attempted (Schwarcz *et al* 1994). The Sterkfontein chronology is still not settled and will likely only be resolved when other independent methods such as palaeomagnetism are applied.

Sterkfontein effectively forms a chronological link between Makapansgat Limeworks and Swartkrans, both having undergone thorough isotopic studies (Lee-Thorp *et al* 1994; Lee-Thorp *et al* 2000; Sponheimer *et al* 1999; Sponheimer and Lee-Thorp 1999a). The members of those sites to be discussed can be placed in approximate chronological order, as seen in Table 1.1.

Makapansgat Limeworks Member 3	~3.0 Ma
Sterkfontein Member 4	~2.6 Ma
Swartkrans Member 1	~1.8 Ma
Sterkfontein Member 5	~1.7 Ma
Swartkrans Member 2	~1.4 Ma

Table 1.1

Approximate chronological sequence of South African Plio-Pleistocene hominid sites discussed in this thesis (given in Million of years).

(Sources: Brain and Watson 1992; Brain 1993; Vrba 1982; Sponheimer *et al* 1999; Clarke 1994; Kuman and Clarke 2000)

Palaeoenvironmental background

The periods represented by these sites span a period of change in the earth's climatic history that is believed by some to have had an important bearing on pathways of evolution of humans and other savanna dwelling fauna. A major global climatic shift took place at approximately 2.5 Ma, when orbital parameters (Milankovitch cycles) changed from a precessional (23 - 19 thousand year) mode to an obliquity (41 thousand year) pattern (deMenocal 1995; Feibel 1997). This patterning of global climate change is known from marine sediment cores, in which oxygen isotope ratios of marine forams show changes in ice volume and temperature (Shackleton and Opdyke 1973).

It has proved more difficult to establish the climatic shifts on different continents. One clue for the African climate is the Saharan dust found in marine sediments that show cyclic episodes of aridity occurred with increasing frequency and amplitude after 2.6 Ma (deMenocal 1995). Key clues to the effects on land have come from pollen evidence (Bonnefille 1983) and faunal assemblages (Vrba 1974, 1975, 1985a; Behrensmeyer *et al* 1997). Elizabeth Vrba has been a strong proponent of the idea that a major faunal turnover occurred at this time (Vrba 1985b). Although this idea has been contested on the grounds that no unusual or exceptional levels of extinctions and radiations occurred at this time in East Africa (Behrensmeyer *et al* 1997), it seems certain that a radiation of bovid lineages occurred at about this time in Southern Africa.

Elizabeth Vrba was also responsible for a great deal of the research on the fossil ungulates from the dolomite cave deposits at Sterkfontein and other sites (Vrba 1974, 1975, 1982, 1985a, 1985b). One key approach to assessing these ancient environments is based on the abundances and habitat preferences of the bovids found in the assemblages. Vrba (1975) showed that the percentage of alcelaphines plus antilopines within the total bovid assemblage in modern environments was a good indication of their grassy, open, and often relatively arid nature. The converse was also true, and that low percentages of alcelaphines plus antilopines indicated relatively wooded, closed habitats.

Vrba applied this principle to the South African Plio-Pleistocene hominid deposits. Her results suggested that the environments from the members in Table 1.1 followed a time-transgressive trend from a more wooded environment at the earliest, Makapansgat Limeworks (3 Ma), to a more grassy, open one at Swartkrans Member 2 at about 1.4 Ma (Vrba 1975, 1982). One key assumption of this approach is that the fossil fauna had the same dietary, and therefore habitat, requirements as their modern relatives. This is a justifiable assumption, but there are some problems. One is that some extinct species have no modern relatives or descendents, and another is that extinct species may not have had similar dietary and habitat requirements to their modern conjoiners. Recent carbon isotope research has in fact suggested some notable exceptions (Sponheimer *et al* 1999; Sponheimer and Lee-Thorp 1999b).

Stable isotopic analyses and laboratory work

The primary aim of this study is to enrich existing palaeoenvironmental data on the South African hominid-bearing cave sites by means of isotope data from enamel samples of fossil fauna found in Members 4 and 5 of Sterkfontein.

Briefly, the rationale behind an isotopic approach is as follows: there are three different photosynthetic pathways (C_3, C_4 and CAM), each using a different physiochemical pathway to fix carbon. In regions with warm temperatures in the growing season, almost all the grasses follow the C_4 pathway, while trees, shrubs and herbs follow the C_3 photosynthetic pathway. This is the case in the African savanna regions including South Africa where the rainy season is in summer. In temperate regions where the growing season is cool, all plants including the grasses follow the C_3 pathway. The CAM pathway is restricted mostly to succulent-type plants that have restricted distributions mostly towards the south and west coasts; this pathway is not discussed further.

The different pathways for fixing carbon during photosynthesis leads to distinct carbon isotopic signatures in plant tissues due to differences in fractionation against the heavier ^{13}C in these processes. The isotopic distinctions in plants are passed on to their consumers, and are registered in the tissues of herbivores. Since enamel usually survives the longest, and has been shown frequently to be resistant to diagenesis, it is the tissue of preference for isotopic analysis of ancient specimens (Lee-Thorp 1989; Lee-Thorp *et al 1997*; Sponheimer and Lee-Thorp 1999c). It is preferred much more than bone in which isotopic signals may only survive at best for a hundred thousand years (Lee-Thorp 2000).

Carbon isotope data has shown that the environment was much more "closed" during Makapansgat Limeworks 3 times than originally thought (Sponheimer *et al* 1999). Isotopic data showed that in several cases the extinct fauna assumed to have been grazers or mixed feeders were in fact browsers. The high percentage of fauna requiring trees and/or shrubs for survival were indicative of fairly dense woodland conditions.

In this study, isotopic analyses were performed on herbivores, primates and carnivores from Sterkfontein Members 4 and 5. Samples were prepared using methods developed and recently refined by Lee-Thorp and Sponheimer (see Sponheimer and Lee-Thorp 1999c) in order to minimise damage to fossil material, and maximise removal of contaminants without too much loss of small samples.

Isotopic data of Sterkfontein fossil fauna enables us to obtain two key pieces of information:

1) clarification of assumptions regarding the dietary preferences of individual fauna, so that we can test the original conclusions and model of the opening of environments
2) Establishing a ratio of browsers (C_3 feeders) to grazers (C_4 feeders).

This method makes no assumptions about the dietary and hence habitat preferences of fossil taxa. It is essentially a development of the environmental reconstruction tool used by Vrba (1975), with the aim of refining our understanding of the Plio-Pleistocene environment.

Chapter summaries

After this introductory chapter, the background to palaeoenvironmental research at Plio-Pleistocene hominid sites in South Africa is reviewed in Chapter 2. This section outlines the history and importance of palaeoenvironmental research at these sites, and the important steps in development of this field.

The rationale for use of the stable light isotopes of carbon and oxygen in fossil tooth enamel is given in Chapter 3. The theory and application of palaeoenvironmental reconstruction by means of stable light isotopes is described. A method for using the ratios of fauna to produce a 'C_3/C_4 index' in order to quantify changes in ancient environments is detailed.

The results of earlier isotopic studies at the sites of Makapansgat, Sterkfontein and Swartkrans are summarised in Chapter 4. The discussion is largely restricted to application of these data to palaeoenvironmental reconstruction.

Chapter 5 describes the sampling and methods used in this study. It includes a description of the site, Sterkfontein. Preparation methods are outlined as well as details of isotope measurements, calibration, and checks for reliability of the results. A problem with low yields was noted early on, and overcome once the limits of reliable measurement of small gas samples were established by running tests on an internal standard.

The results are given in Chapter 6. In addition to observations about general trends between the two Members, the carbon and oxygen isotope values are discussed for individual species and for a series of associated breccia samples. The data are applied to produce an index of the proportions of C_3 and C_4 feeders within the herbivore assemblage.

The results are discussed in Chapter 7. The $\delta^{13}C$ and $\delta^{18}O$ results for all fauna, including herbivores, primates and carnivores are discussed with reference to their relevance to palaeo-environmental reconstruction. Chronological trends as inferred from the C_3/C_4 index are discussed.

Finally in Chapter 8 the conclusion summarises the main findings of this study.

CHAPTER 2: BACKGROUND

The locations of the three hominid-bearing sites discussed in this project, Makapansgat Limeworks, Sterkfontein and Swartkrans are shown in figure 2.1. The sites were discovered towards the beginning of the twentieth century by miners looking for lime used to extract gold from gold-bearing rocks in the Witwatersrand mines. They are all solution caverns within a dolomitic landscape, formed in Pre-Cambrian dolomite of the Transvaal Supergroup (Brain 1993). These cavities acted as traps leading to the accumulation of large amounts of faunal bones and sediments. Carbonates that precipitated from the groundwater caused the sediments to harden into a cement-like consistency called cave earth or breccia, an Italian word meaning "broken things".

In the absence of appropriate chronometric methods, the antiquity of the South African sites has been estimated mainly by faunal composition. Fossils in the Southern African sites have been compared to those in securely dated East African sites (Vrba 1975; Kuman 1994; Kuman and Clarke 2000), by Potassium-Argon, Argon-Argon, and palaeomagnetic methods. Recently, palaeomagnetic studies have been initiated at the South African sites (Herries *et al* 2001).

Sterkfontein forms an important chronological link between Makapansgat Limeworks and Swartkrans, and together the three sites form a chronological sequence. This chapter will discuss parts of the history of palaeoenvironmental research in South Africa focussing on Sterkfontein, Makapansgat Limeworks and Swartkrans.

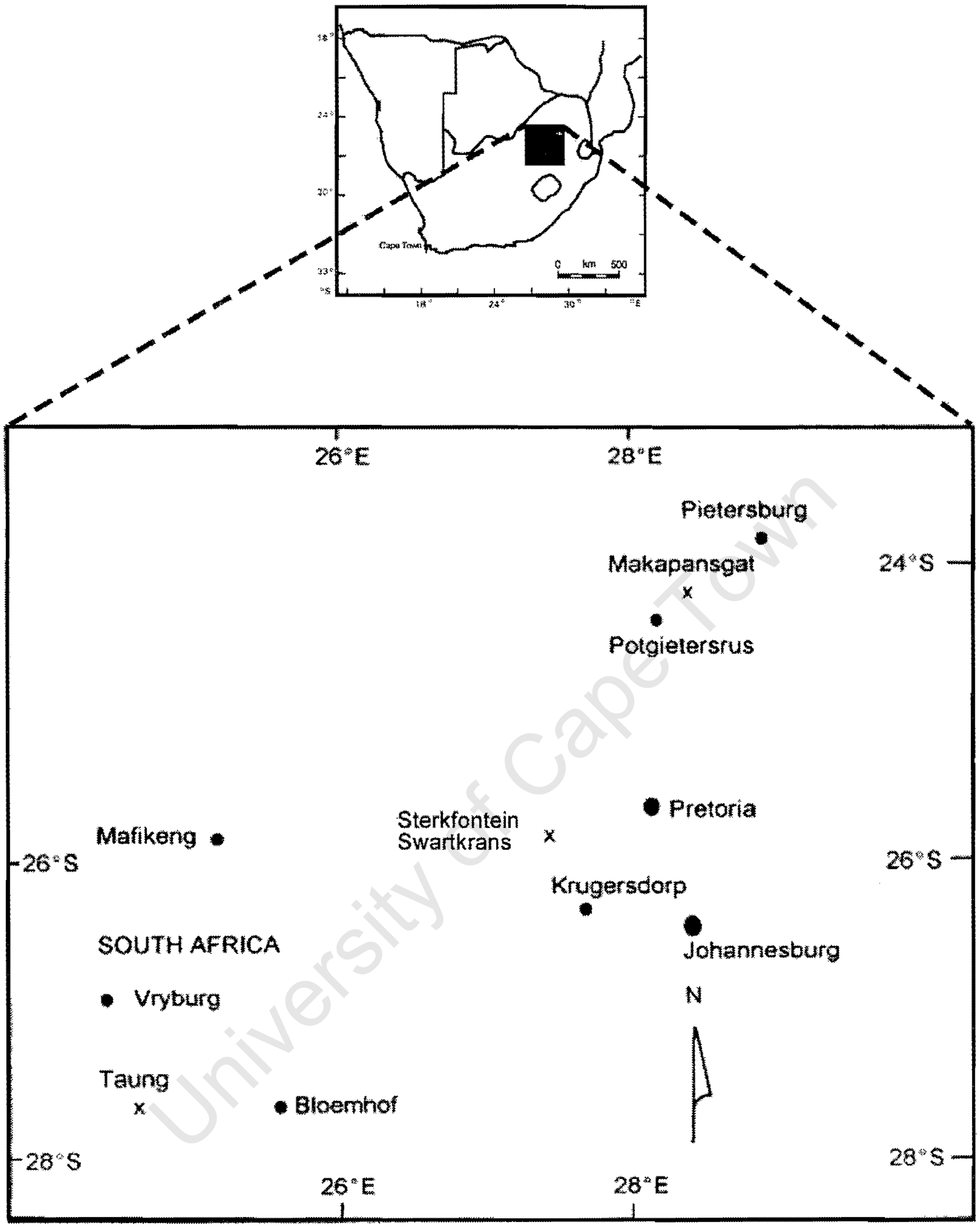


Figure 2.1

Map of South Africa indicating the location of Sterkfontein, Makapansgat and Swartkrans.

(Adapted from Bamford 1999a)

Palaeoenvironmental research of the South African hominid sites

Palaeoanthropological research at the South African hominid sites has a history stretching far back into the last century. Dart (1925), assuming that the dry landscape in which the Taung child was found had been similar in the past, needed to explain how an ape-like creature lived in a dry open landscape so unlike that of the forest-dwelling great apes. Understanding of past environment has improved vastly since the 1920's, as will be described in this chapter.

For the larger part of the first half of the twentieth century it was thought that environments were largely unchanged over the last several million years. Gradually it was realised that this could not have been the case. Some of the first key research undertaken to understand environmental change was done at Swartkrans. Swartkrans is located 10 km NNW of Krugersdorp, 1 km NW of Sterkfontein. It was first excavated by Robert Broom and JT Robinson in 1948 and 1949. Thereafter for a year it was commercially used for lime-quarrying after which studies were resumed by Robinson in 1951 following Broom's death. Various hominid specimens were found including the famous SK 48, *Australopithecus robustus* cranium. Bob Brain worked on the infills extensively from 1953 - 1957 and again from 1965 for 21 continuous years (Brain 1981, 1993).

The faunal assemblages from Sterkfontein, situated south west of Pretoria in the Bloubank River Valley, 9.6 km NNW of Krugersdorp, were laid down during a time period that is of great interest to students of palaeoenvironmental research. A very important step in the history of the development of palaeontology in Southern Africa was the discovery in 1948 of an adult *Australopithecus africanus*, 'Mrs. Ples', at Sterkfontein in what is now called Member 4. It was after this discovery that funding was made available to Broom and he was asked to commence work at both Sterkfontein and Swartkrans, situated across the valley.

Much research into resolving the palaeoenvironmental changes that took place has also been done on assemblages from Makapansgat Limeworks, as will be described. The Makapansgat valley is located in the Northern Province, 325 km north of Johannesburg (figure 2.1). The valley is 1.5 km long with the major fossil-bearing site, Makapansgat Limeworks, lying at its mouth. As with the Taung child, fossils were sent to Raymond Dart at the University of Witwatersrand School of Anatomical Sciences for examination. Collections at the site began in 1925, while systematic investigations were begun in 1947 by Dart. Dart and his team focussed mainly on clearing the dumps of cave breccia left by the limeworkers.

Stratigraphic sequences in karstic landscapes

All three sites under discussion are erosional remnants of karstic caves that have been filled by sediments and then eroded as the cave opens up to the surface. The stratigraphic sequences are therefore not as simple as many other archaeological sites. Although each of these caves is unique, the formation processes are as follows:

Limestone is formed by chemical precipitation formed in shallow, tropical to warm marine environments. The original limestone is aragonite or calcite precipitated by marine animals for shell and skeleton building or expelled as faeces (Ford and Williams 1989).

When the sea level falls, meteoric water invades the marine sediment and there is dissolution as the ratio of fresh: salt moves toward 40:1. The formation of dolomite ($Ca(Mg)(CO_3)_2$) is poorly understood, but it is generally thought that dolomite forms with the replacement of this earlier calcium by magnesium (Ford and Williams 1989).

When the water table is still near the surface and a cavern is dissolved under the water table. This is caused by a subsurface stream, or by solution below the water table. Once the water table drops, the cavern moves to a position above the water table. Then a combination of rainwater and weak organic acids fills fissures (bedding planes, joints or faults) and moves by the force of gravity and dissolves rocks. The chemicals that were dissolved are deposited in other places, forming speleothems such as flowstones, stalagmites and stalactites due to a change in partial pressure (Doerr 1990).

Later, the cave is opened up to the surface by further dissolution and material from the surface including bones and sediments entering the cave by simply falling in or by occupation of the cave (Brain 1981). As dissolution continues, larger caverns develop and pieces of the roof fall into the cave, while deposition continues in other areas of the cave. The recognition of this sequence of events was a major breakthrough for understanding the site history and stratigraphy of these sites.

The stratigraphy of Swartkrans is now relatively well understood (Brain 1981) due to the key realisation that the deposit is the result of many cycles of deposition and erosion (Brain and Watson 1992). Five depositional members are recognized, each separated by an erosional discontinuity. Member 1 consists of: a Lower Bank, with fossiliferous stony breccia that is poorly calcified; an erosional area with a connection between the southern and northern walls; a Hanging Remnant, with pink breccia, which is rich in fossils and probably older than the rest of Member 1 (Brain 1981). Member 2 consists of an Outer brown breccia and stratified inner brown breccia yielding many Developed Oldowan artefacts (Brain and Watson 1992) as well as fossil fauna and hominids. Member 2 is very similar in faunal composition to Member 3 and Brain has subsequently suggested that Members 1-3 might be of a similar age (Brain 1993).

Swartkrans has yielded the largest single sample of the hominid *Paranthropus* sp. that currently numbers in excess of 90 individuals. *Paranthropus robustus* has been found mainly in Member 1, but continues into Member 2, while *Homo ergaster* has been found in both Members 1 and 2 (Howell 1993) (see figure 2.2). A hominid presence is assumed during Member 3 times from the material remains (Brain and Watson 1993). Although the exact timing is unknown, co-occurrence of the two species in these Members strongly suggests a co-habitation of two hominid species in the same landscape. The idea of how this might have been overcome by competitive exclusion has been the subject of many debates.

Obtaining absolute dates for this site has proven to be difficult. Vrba made a complete study of the fossil bovids from Swartkrans as well as Sterkfontein and other australopithecine sites during the 1970s (Vrba 1974; Vrba 1975; Vrba 1976; Vrba 1980; Vrba 1982). She suggested that the Hanging Remnant was between 1.8 and 1.5 Ma. Member 2 was estimated to be of an age between 1.4 and 1.0 Ma (Brain and Watson 1992).

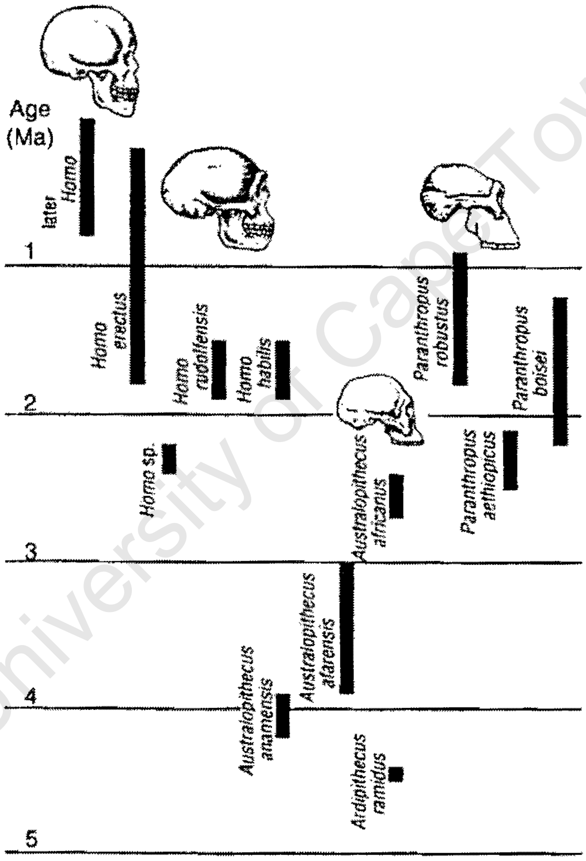


Figure 2.2

Species of hominids found in African sites, shown in approximate chronology. (From Feibel 1997*).*

Makapansgat was also divided into 5 members (Partridge 1979). Makapansgat Limeworks Member 3 has been dated by biostratigraphic and palaeomagnetic means to around 3 million years old (Brock *et al* 1977; Vrba 1982; Maguire 1985).

Geologic studies of speleothems have recently refined this sequence (Herries 1998), stating that: Member 1 consists mainly of speleothem deposits and very small areas of bone; Member 2, the oldest fossil-bearing deposit at the site consists of waterlain deposits and unexplored mammalian remains (currently being excavated by Kevin Kuykendall from the University of Witwatersrand); Member 3 consists of a rich bone breccia in a calcite matrix; Members 4 and 5 consists of breccia that accumulated after 3 million years ago to the present day, and deposited in an entirely different area to that of the first 3 members. The latter two members consist of aeolian deposits, suggesting that a substantial entrance to the cave had developed shortly after 3 Ma. (Herries 1998); Member 5 has yielded no hominids or other primates.

A number of *Australopithecus africanus* remains were found mainly in Member 3 (see figure 2.2), as well as many other mammals such as baboons, antelopes, giraffes, rhinos, elephants, carnivores, and rodents.

Palaeoenvironmental reconstruction based on geological studies

Some of the earlier work on environmental reconstruction of Makapansgat was based on the assumption that the valley looked the same as it does today. However, it has been shown (Partridge 1985) that due to the rejuvenation of the northeastern Transvaal rivers, the incision by these rivers has modified the valley. Around 3 Ma the valley would have been less pronounced and at a lower elevation, whereas now there are steep valley sides at a much higher altitude. This kind of change over time has implications for a number of features such as soil types and groundwater levels, all of which influence the vegetation found in the region (Rayner *et al* 1993).

Rayner *et al* (1993) summarised past environmental reconstructions, including information from sedimentary and fossil sources. These authors found many reconstructions to be unsatisfactory because they compare different sites rather than make comparisons to modern, known conditions.

Their own reconstruction is based mainly on the geomorphology of the valley. They concluded that the area was more forested in Member 3 times than it is today. Based on Partridge's geomorphologic reconstructions, the topography was more moderate and together with higher rainfall and deeper soils was able to support small patches of sub-tropical forest (Partridge 1985).

Palaeoenvironmental reconstruction based on faunal assemblages

Vrba has been responsible for much of the palaeoenvironmental research at many South African sites until very recently having performed comprehensive studies of all the fossil bovids at these sites. These studies were used to provide estimates of relative chronology. Vrba's ideas on faunal turnover near 2.5 Ma were informed by those studies (Vrba 1974; Vrba 1975; Vrba 1976). She proposed a turnover-pulse hypothesis that implied a climatic event caused the drying out of the African continent at 2.5 Ma.

Vrba also examined the distribution of modern bovids in 16 game parks or reserves with differing environments. She showed that the percentage antilopines plus alcelaphines (hereafter the AA index) in modern environments is a good indication of the "openness" (i.e. grassy and with few trees) of the landscape. This index was applied to the reconstruction of past environments (Vrba 1974). It was suggested that an assemblage dominated by "arid-adapted" species indicates an open environment (and by analogy with the modern grassy areas, relatively arid), whereas assemblages with few of these species would indicate a relatively closed and moist, wooded environment. The model and index is shown in figure 2.3.

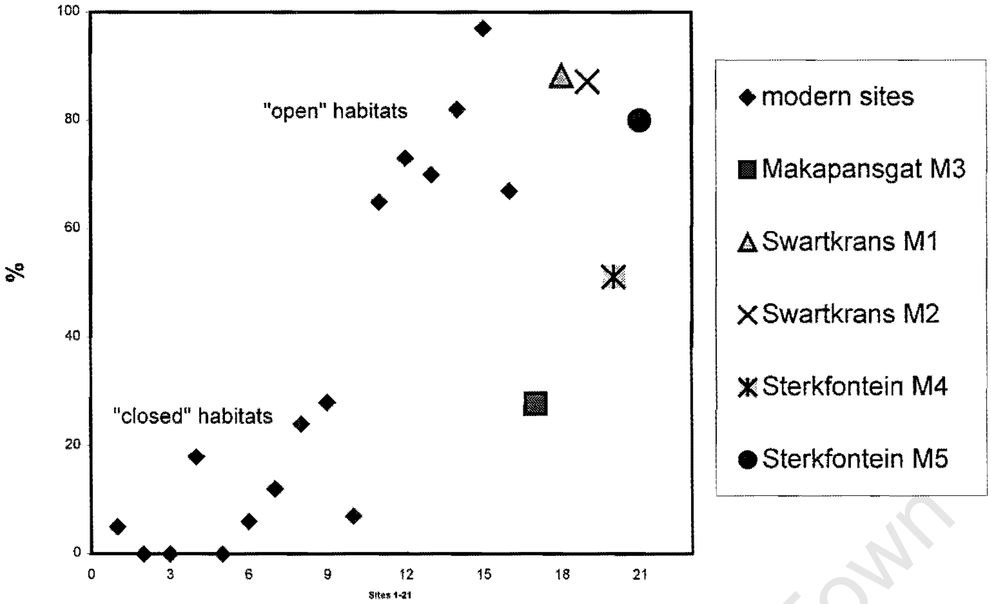


Figure 2.3

Antilopini plus alcelaphini as a percentage of the total bovid assemblage (AA index) in 16 modern sites ranging from relatively forested (sites 1-10) to progressively more open (sites 11-16) habitats. The results for various Members in the three fossil sites are shown (Vrba 1980). (M=Member).

This model provided an environmental framework as the basis for palaeoenvironmental reconstructions. Of all the sites and members, the index showed the highest percentages for Swartkrans Members 1 and 2, at 87% and 88% respectively, indicating the most open environments.

Sterkfontein Member 5 had the next highest percentage of 'open-indicator' species at 80%, while the considerably older Member 4 had 51% "open" indicating fauna. Vrba interpreted the bovid assemblages from Sterkfontein Member 4 as indicating medium density woodland with grassland elements (Vrba 1975). The occurrence of both *Makapania broomi* and the hippotragines in the faunal assemblage suggests that there was a significant woodland element, while the number of alcelaphines and antilopines show that there must have been grasslands as well.

Makapansgat was shown to fall just within the "closed" habitat constituency with approximately 30% "open" indicating fauna.

The final result of this series of reconstructions was a marked trend from a woodier habitat at Makapansgat Member 3 and Sterkfontein Member 4, to more "open" habitats in Swartkrans Member 1, Sterkfontein Member 5 and Swartkrans member 2.

Ecological diversity and cranial morphology studies

Using a combination of functional morphology and ecological structure analysis of the fauna Reed (1997, 1998) tested Vrba's reconstructions. Reed's (1997) palaeoenvironmental research assessed the percentages of animal occurrences in the deposits. She based her research on ecological diversity studies that demonstrated modern habitats could be predicted by knowing what kinds of animals occur in them e.g. arboreal, terrestrial or aquatic. Using the same principle, she then assessed the Plio-Pleistocene environments by looking at what kinds of fauna were represented in the assemblages.

Reed's (1997) study of the percentages of animal occurrences in the deposits of Makapansgat Member 3 showed a high percentage frugivorous mammals (fruit leaf eaters and fruit insect eaters) compared with the arboreal fauna (a mammal that moves or feeds in trees at least 90% of the time). She therefore positioned the Makapansgat Member 3 habitat with bushland and medium density woodland (Reed 1997), very similar to Vrba's assessment. Amongst the fauna in the assemblage a small percentage of grass grazers and aquatic animals were found indicating a water source and edaphic grasslands (those grasslands where grasses grow in waterlogged soils, such as wetlands) (Reed 1997).

Reed's (1997) work indicates an open woodland with bushland similar to Vrba's medium density woodland for Sterkfontein Member 4 (Vrba 1975). Since she found a high percentage of frugivorous mammals, she suggested that the environment was fairly similar to the Makapansgat Member 3 environment.

Assessments of the faunal assemblage of Swartkrans Member 1 by Brain (1981) indicated an open habitat at this time (1.8 Ma). Reed (1997) indicated that riverine elements were also present due to the lack of arboreal animals (those mammals that spend more than 90% of their time in trees), relatively few (<14%) fruit and leaf eaters (frugivorous animals) (<14%) and few (<6%) aquatic animals. She suggests that it was probably the river that supported the trees needed for the fruit eaters to survive and edaphic grasslands to support some of the specilaised grass eaters.

Reed (1997) placed Sterkfontein Member 5 in the open or wooded grassland region because of a high percentage (>43%) of grazing animals. This agrees with the reconstruction given by Vrba, as an open savanna (Vrba 1975).

Kuman and Clarke (2000) suggest that after 2.0 Ma the fauna imply a drier climate, in Sterkfontein Member 5. *Theropithecus oswaldi*, the giant Gelada baboon, is represented by one molar fragment found in the Member 5 Oldowan infill. This species has a known habitat preference for open grasslands. In general, the open-habitat faunas are dominant, including *Equus* sp. (zebra) and *Panthera leo* (lion). Water must have been available locally since frogs form part of the microfaunal assemblage. Member 5 yielded *Paranthropus* specimens consistently found near well-watered areas (Reed 1997).

Swartkrans Member 2 shows a decline of fruit and leaf eaters (<9%), an increase to approximately 33% grazing animals, 100% terrestriality with aquatic animals, indicating a drier, more wooded area with some wetlands (Reed 1997), agreeing with Vrba's (1975) reconstruction.

Lillian Spencer adopted another strategy for inferring behaviour and habitat preferences of fossil animals (Spencer 1997). Using a sample of 31 species of modern bovids to relate morphological specialisations to dietary behaviours, she determined preferred diets and hence preferred habitats from cranial morphology.

She found that species that ate different kinds of grasses or had varying habitat preferences showed differences in cranial morphology (Spencer 1997). Her study also found that savanna grasslands became widespread in Plio-Pleistocene Africa around 2.0 Ma, because of the appearance of species such as *Connochaetes gentryi* in the fossil record which specialise on short grasses in secondary grasslands (Spencer 1997).

One important feature of this study is that it does not assume the behaviour of fossil taxa, but is based on the functional relationships between the morphology of the cranium (the feeding apparatus) and known feeding habits observed today. Thus, it can be used as a reference point. In theory, one can compare the morphology measurements of a bovid fossil with that of Spencer's study and find out the type of feeder.

Environmental information from fossil flora

Botanical remains from dolomitic caves of an age similar to that of Sterkfontein are extremely rare. Of the australopithecine bearing sites, pollen has only been found at Makapansgat Limeworks (Cadman and Rayner 1989), Kromdraai and Sterkfontein (Scott 1995). Experts believe that the data from Makapansgat should be treated with caution; mixing is a concern because non-indigenous *Pinus* pollen was observed in some deeper levels (Scott 1995). Due to a low percentage *Pinus* pollen in the Sterkfontein Member 5 and Kromdraai sample it is believed to have been subject to minimal contamination. The Proteaceae pollen found in Sterkfontein Member 5 was assigned to *Protea*, a species that occurs in the region today. Although the paucity of the pollen data puts a limitation on the interpretation that can be made, Scott (1995) indicated that from this data the area must have been rather similar during Member 5 times to what it is today.

Fossil seeds of a palm, *Phoenix reclinata,* have been found in the 'stony breccia' at Gladysvale, a mid-Pleistocene site near to Sterkfontein (Bamford 1999a). Rare fossil wood was found by Alun Hughes, in Member 4 sediments, and has subsequently been studied by Marion Bamford (Bamford 1999a; 1999b).

Eighteen pieces of wood from Member 4 were described, identifying two main species; *Dichapetalum mombuttense*, a liana that today occurs in dense forest; and *Anastrabe integeriima*, a shrubby plant that occurs today only on rocky hillsides on the fringes of forests and along streams (Bamford 1999a).

These two species do not occur near Sterkfontein today. The area presently receives summer rainfall and winter frost and has nothing that can be described as dense forest or thicket, probably due at least partly to the influence of winter frost. Bamford argues that since lianas require support from large trees in forests, their presence in the deposit clearly implies that mature forest occurred in the vicinity. The extent of the forest cannot, however, be ascertained from only one cave deposit. She concluded that there must have been at least a refugium of the present day tropical forests such as those found in Cameroon and the Democratic Republic of the Congo, where lianas are common. *Anastrabe integeriima* is not as restricted in habitat as the lianas, and is therefore less useful in determining the past environment. It does however, imply a higher rainfall at Sterkfontein during the Pliocene, because its present distribution is confined to the humid areas of eastern South Africa.

Bamford (1999b) later identified a shrub as a third indicator species, *Tricalysia,* which occurs in large tropical forests and on the margins of the forests or in woody ravines, further supporting her reconstruction.

The palaeobotanical evidence therefore points to a moist, warm climate and an environment with mature gallery forest containing large trees housing lianas, and surrounded by grasslands at the time of Member 4 at approximately 2.6 Ma.

Palaeoenvironmental reconstructions based on isotopic analysis

Isotopic analysis of faunal tissues was a further advance in the palaeoenvironmental reconstruction research. Inferences about past environments from fossil faunal abundances have relied on the known habitat preferences of extant fauna. This assumption is called 'taxonomic uniformitarianism'. Although it is a reasonable starting point, there are a number of problems with this approach including occurrence of completely extinct genera or lack of allowance for evolutionary change in evolving genera (Sponheimer *et al* 1999) therefore a means of testing these assumptions is highly desirable.

The isotopic signatures left in enamel from fossil fauna provide an appropriate test. The principles are discussed in more detail in the next chapter (Chapter 3).

A stable isotope approach applied to fauna from Makapansgat Limeworks found that some of the fauna were incorrectly classified with respect to their dietary preferences (Sponheimer *et al* 1999) and therefore two of the bovid species' dietary reconstructions were incorrect. The problem is that the further one moves back in time, the less likely it is that ancestral forms showed the dietary and habitat preferences of the modern relatives. The two species *Aepyceros* sp. and *Gazella vanhoepeni*, were shown to be almost exclusively browsers and not the mixed feeders their modern relatives are (Sponheimer *et al* 1999). Another non-bovid example is given in the case of a recent carbon isotope study of elephant lineages that found almost all African elephants older than approximately 1 million years were grazers in sharp distinction to the modern African elephant (Cerling *et al* 1999). It is clear, therefore, that assumptions regarding the behaviour of extinct fauna should to be tested. The question arises as to whether incorrect dietary assignments of species and their inferred preferred habitats might affect the weight given to the percentage of "open" indicating fauna at any of the sites.

Summary

The well-known AA index was the basis for information on the dietary preferences inferred directly from their modern counterparts. It is now understood from a number of isotopic and morphological studies that extinct species did not always share the same dietary and habitat preferences as the modern counterparts. For example, antilopines such as *Antidorcas recki* may not have been habitual mixed feeders and open-country indicators as originally believed.

In general, the reconstructions first proposed by Vrba (1980) indicate a long-term shift from an earlier wooded environment at Makapansgat Member 3 through to a more "open" savanna environment by the period represented by Swartkrans Member 2. The pattern or trajectory of environmental changes through time are of interest to us here. The general picture is understood from various sources including cranial and postcranial morphology and percentages arboreal, aquatic or other forms adapted to specific habitats. What is less well known is the confidence placed on environmental inferences based on taxonomic uniformitarianism. This problem has been addressed in this study using isotopic analyses. No prior assumption about the habits of fossil taxa is required. It is a development of the environmental reconstruction tool used by Vrba. A refined or revised index (as described in the next chapter) allows more secure deductions about how closed or open past environments had to be to support the observed numbers of C_3 - or C_4 - dependent fauna. The rationale behind this method will be discussed in the next chapter.

CHAPTER 3: STABLE LIGHT ISOTOPES AND THEIR APPLICATION TO FOSSIL DIETS AND PALAEOENVIRONMENTS

This chapter outlines the rationale of using isotopic analyses for palaeoenvironmental research. First it outlines the traditional methods for performing carbon and oxygen isotopic analyses. Carbon isotopes are used to determine the isotopic signatures of the fauna in order to make inferences regarding the vegetation that was available for consumption. Oxygen isotope ratios provide information about water-related behaviors and possibly thermo-physiology of fauna.

A key limitation for both carbon and oxygen isotope analysis is that diagenesis might have influenced the isotopic signature. This chapter also outlines how one establishes that this was not the case.

Finally the refined C_3/C_4 index is discussed in the palaeo-environmental context.

Stable Carbon Isotopes

Many elements occur naturally as a number of isotopes which isotopes have the same number of protons and electrons, but differ in the number of neutrons. Hence, the chemical properties of these isotopes are the same, but they have different masses (Hoefs 1987). Due to the difference in the mass of these isotopes, they take part in biological or chemical reactions at different rates. As carbon moves along the food chain, the different isotopes are discriminated against to varying degrees. This is called fractionation (Hoefs 1987).

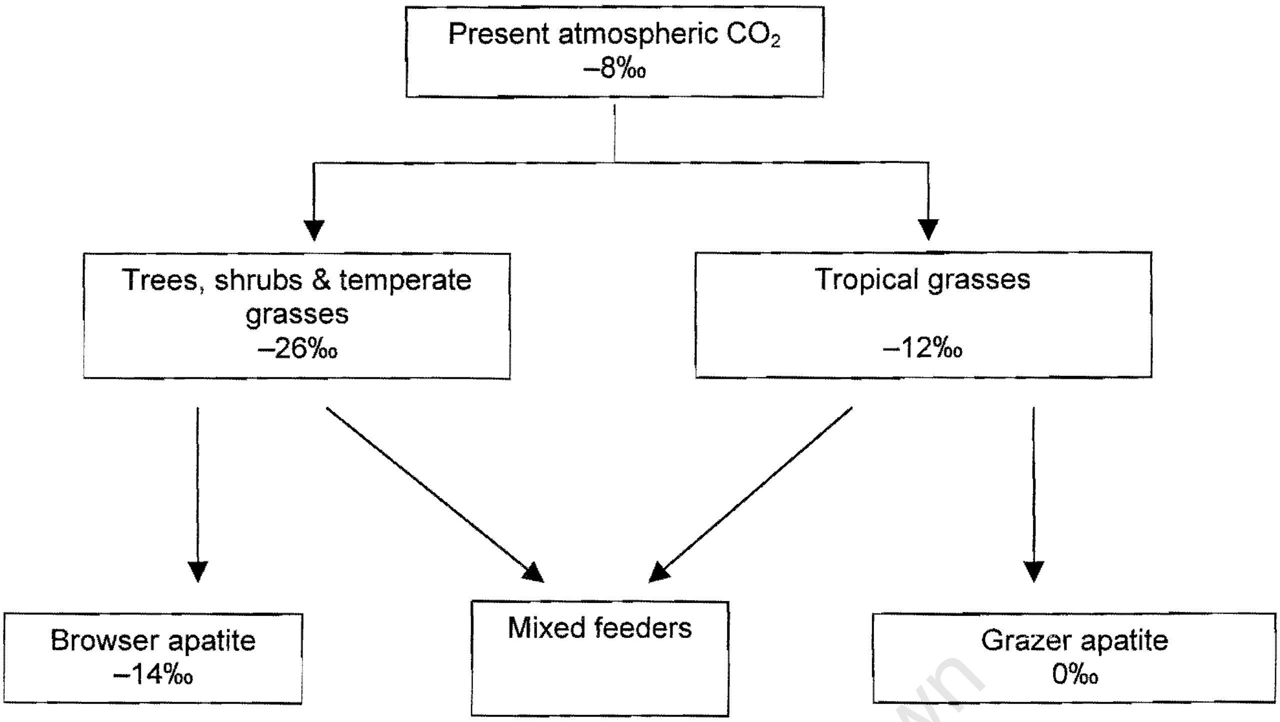
Terrestrial plants are depleted in ^{13}C in comparison to atmospheric CO_2. The degree of depletion in ^{13}C is constrained depending on which photosynthetic pathway the plant follows. There are three main groups of plants that have differential fractionation of carbon isotopes during photosynthesis: C_3, C_4 or CAM (Smith and Epstein 1971).

When the plant fixes the CO_2, C_3 plants form a 3-molecule carbon (phosphoglyceric acid). This is called the Calvin-Benson photosynthetic pathway. C_3 plants are most common and include trees, shrubs and temperate grasses (Calvin and Benson 1948).

Other plants (C_4 plants) initially form 4-molecule carbons (malic acid and aspartic acid) as a first step during photosynthesis. The malic acid and aspartic acid is then broken down by enzymes again and released into the Calvin-Benson pathway. This is called the Hatch-Slack pathway. C_4 plants are the tropical grasses (Hatch and Slack 1966)

Both of these types of plants discriminate against ^{13}C, but C_3 plants do so more than C_4 plants and are therefore more depleted in it. When fractionation occurs (see figure 3.1) during photosynthesis C_4 plants are depleted by about $-5^{0}/_{00}$ and C_3 plants by about $-19^{0}/_{00}$, relative to the atmospheric $^{13}CO_2$ (expressed in terms of parts per thousand, or per mil ($^{0}/_{00}$)). Therefore C_3 and C_4 plants have distinct $^{13}C/^{12}C$ ratios that do not overlap (Vogel 1978).

CAM plant isotopic values can have similar values to C_3 plants, C_4 plants, or in-between. Plants that follow the C_4 pathway have a range between $-10^{0}/_{00}$ to $-14^{0}/_{00}$ while those plants following the C_3 pathway have a range between $-22^{0}/_{00}$ to $30^{0}/_{00}$. It is because of this distinction that they have been used so widely and are so useful when trying to establish past environments (Vogel *et al* 1978; Lee-Thorp *et al* 1994).



$\delta^{13}C_{PDB} = (R_{sample}/R_{ref} - 1) \times 1000$ relative to the PDB standard

Figure 3.1

Diagram showing changes in $^{13}C/^{12}C$ in a modern savanna food web.

(Adapted from Lee-Thorp 1989)

These distinct carbon isotope ratios are passed along the food chain to the herbivores that eat the plants and grass and are deposited in body tissues. Herbivores are tied to their particular type of food source. The isotopic values of the herbivores are about 12 $^{0}/_{00}$ more enriched than the plant source (see figure 3.1) (Lee-Thorp 1989).

The distribution of C_3 and C_4 grasses is constrained by the temperature during their growing season. C_3 grasses grow in cool growing seasons while C_4 grasses prefer warm growing seasons. Most of South Africa has C_4 grasses because of the predominant summer rainfall found in those areas (see figure 3.2 for distribution).

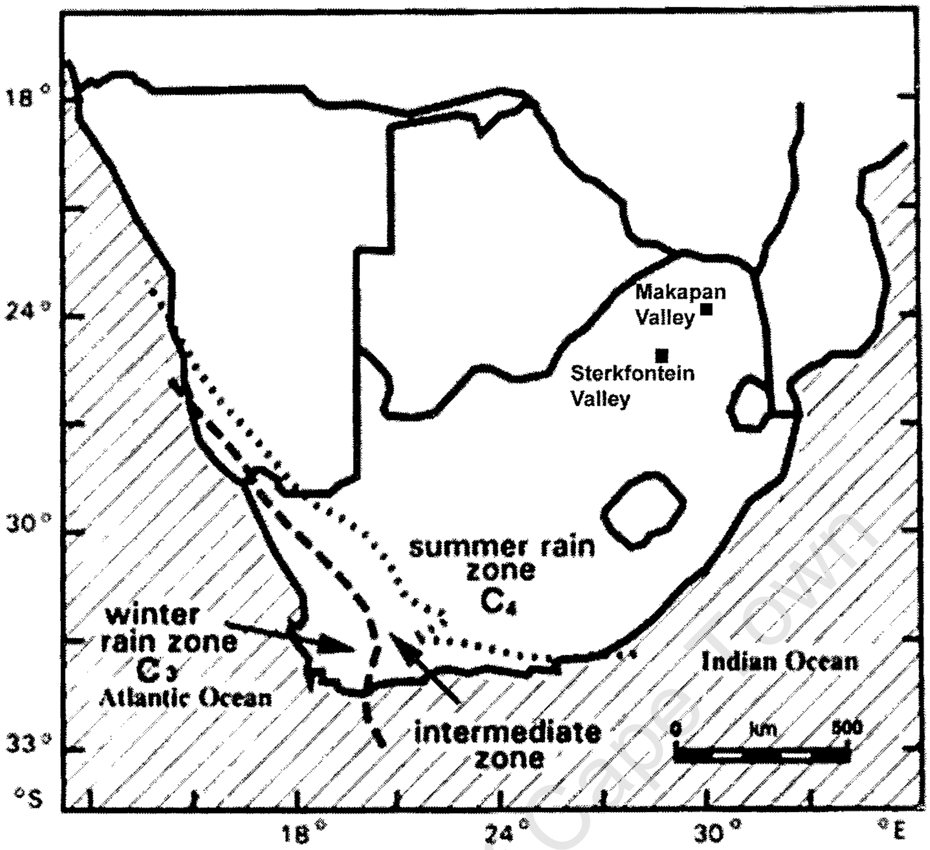


Figure 3.2

A map of Southern Africa showing the distribution of summer and winter rainfall zones that control the distribution of C_3 and C_4 grasses, indicating the location of the sites under investigation well within the summer rainfall area

(Adapted from Lee-Thorp and Beaumont 1995, but originally from Vogel, Fulls and Ellis 1978)

The body tissues that survive longest archaeologically are teeth and bones. Tooth enamel and bone contain both inorganic and organic components. The inorganic (mineral) component is called a biological apatite and is made up of Calcium and PO_4, with a small amount of CO_3 (Lee-Thorp 1989; Lee-Thorp submitted). The density of the mineral phase varies from tissue to tissue, but enamel has a very small organic component and is mostly mineral (~99%).

The porosity of bone is much higher than enamel as it contains only about 65-70% apatite (Wang and Cerling 1994). Diagenesis (alteration of carbonate or phosphate after deposition) is a serious consideration when dealing with bone samples (Lee-Thorp and van der Merwe 1987). The addition of new non-apatitic material in pores or other spaces (diagenesis) is more likely in bone as it is porous. The 20-30% collagen is lost by consumption by bacteria and filled by new minerals (Lee-Thorp 2000). Enamel has a much lower porosity and fewer substitutions occur, and there is little organic material to lose. It is hence less susceptible to diagenesis (Sponheimer and Lee-Thorp 1999c) and therefore used in many more palaeoenvironmental reconstruction studies, as in this study. Lee-Thorp (1989) has shown that by performing a pre-treatment to remove diagenetic $CaCO_3$, its use is reliable in palaeoenvironmental reconstruction. Studies have also shown that fossil tooth enamel from sites with ages as those under discussion in this study still retain the original isotopic signal (Lee-Thorp and van der Merwe 1987).

Stable Oxygen Isotopes

In general, the oxygen isotope composition of different fauna found in an ecosystem is likely to be explained by the differences in isotopic composition of the oxygen in food and liquid water.

Oxygen isotopes that occur naturally (^{18}O and ^{16}O) have been widely used in fields such as palaeotemperature reconstruction from shells, corals, and speleothems, as well as in hydrology and the oxygen isotopic deep-sea marine record. These studies have mainly been based on the oxygen found in PO_4 as this bond is thought to be very strong. The systematics of the oxygen isotopes in fossil fauna is a little more complex and somewhat less well understood. A number of studies (Bocherens *et al* 1996; Kohn 1996) observed intra-species variations in the ratio of oxygen isotopes and proposed that their diet was influencing this to some degree. Inferences can be made about the local hydrology and water use of animals by investigating oxygen isotopes. One can, as is researched in this study, research water-related behaviour and thermo-physiology in fossil fauna.

Oxygen is found in both the phosphate (PO_4^{3-}) and the carbonate (CO_3^{2-}) of the enamel. The oxygen in these two ions has been shown to be highly correlated (Iacumin *et al* 1996). Because the P-O bond is exceptionally strong, most researchers have considered this to be the ion of choice for investigating $\delta^{18}O$ in fossils. But although the P-O chemical bond is stronger, it has been shown that the enamel carbonate also exhibits satisfactory biogenetic isotopic signals (Bocherens *et al* 1996; Cerling *et al* 1997a). Since the carbonate of the enamel has been used for the carbon, oxygen values are also extracted from the carbonate in the enamel for the purposes of this study.

The oxygen isotopes that are found in the carbonate and phosphate of fossil enamel are directly related to the oxygen that enters and leaves the body (Kohn 1996; Sponheimer and Lee-Thorp 2001). The main sources are water ingested by drinking, atmospheric oxygen and oxygen found in food. Since the atmospheric oxygen is relatively stable, it is only liquid water and the oxygen bound in food that cause differences in the oxygen isotope makeup of fauna. Variability in $\delta^{18}O$ in plant and drinking water is fairly well understood. The ^{18}O bound in foods available to mammals is less well understood. The reason liquid water and water bound in food causes an alteration in the oxygen isotope mass balance is because oxygen exchanges readily with water (H_2O) and other forms (e.g. CO_2 and PO_4^{3-})(Sponheimer and Lee-Thorp 2001, in press a).

Liquid water enters the body through drinking water and free water in food. Water found in plant roots is very similar to that of the drinking water of the local region. However leaf water is usually isotopically more enriched in ^{18}O, due to the fact that the lighter ^{16}O is evaporated first, leaving the heavier ^{18}O molecules behind (Epstein *et al* 1977). It is because of this discrimination that researchers have searched for a difference in oxygen isotopes for browsers and grazers.

Oxygen leaves the body in three main ways: CO_2, liquid water and water vapour. Urine, faeces and perspiration are ways in which liquid water leaves the body, and have similar isotopic ratios to that of the body water (Sponheimer and Lee-Thorp 2001, Sponheimer and Lee-Thorp in press a). Water vapour is depleted in ^{18}O and is lost through the mouth, nose and skin (Wong *et al* 1988; Lee-Thorp and Sponheimer 2000). This will affect $\delta^{18}O$ values differently in various animals with different physiological adaptations to heat stress (Sponheimer and Lee-Thorp 2001; Sponheimer and Lee-Thorp in press a).

For instance if two animals with the same oxygen input respectively pant or sweat to loose heat, the former will have a higher $\delta^{18}O$ value as it is losing isotopically depleted oxygen in the process of panting (Sponheimer and Lee-Thorp 2001). Also, an animal that is semi-aquatic, like the Hippopotamidae, will have a depleted $\delta^{18}O$ value, as it keeps the isotopically lighter oxygen molecule.

The C_3/C_4 index

In the past carbon isotope analyses (as applied to palaeoenvironmental reconstructions) has been used primarily to establish whether or not C_3 or C_4 plants existed in a certain area (Lee-Thorp *et al* 1994; Sponheimer and Lee-Thorp 1999a; Luyt *et al* 2000) or to ascertain the diets of certain fauna. This is useful in some instances, as described above. However, it does not tell us much about the entire landscape and whole ecology of the ancient environment. So even though we know, for instance, that C_4 grasses existed at some sites, it does not tell us if they occurred in an open or closed environment. It is for this reason that another method has been developed and successfully applied, as is described below (Sponheimer and Lee-Thorp 1999b).

Bovids are normally plentiful in fossil assemblages. Herbivorous animals, such as bovids, are very important as palaeoenvironmental indicators since they are dependent on the vegetation available (Kappelman *et al* 1997). They also tend to specialise in different types of vegetation (Spencer 1997), as can be seen in modern bovids (Vrba 1980). The large Bovidae family has a high number of species. Because of the speciose nature of this family, its members are sensitive indicators of the environment.

As discussed in Chapter 2, Vrba developed an index based on the percentage alcelaphines plus antilopines that was used as a proxy for the "openness" of a habitat. The total percentage of alcelaphines plus antilopines (AA index) never exceeded 30% of the total bovid population in areas considered to be "closed" environments i.e. those areas with considerable tree or bush cover. This AA index always exceeded 60% in areas considered to be "open" environments, i.e. those areas where there were few trees or bushes (Vrba 1980). Hence, she suggested that if these arid-adapted alcelaphines and antilopines dominated in a fossil site it would indicate a relatively open (and possibly arid) environment. Whereas those sites with few arid adapted fauna would indicate a relatively closed environment (Vrba 1980, 1985a).

This method however, relied on the assumption that these alcelaphines and antilopines were arid-adapted animals as their modern counterparts are (Sponheimer *et al* 1999). In other research it has been shown that while fossil alcelaphines do have the same habitat preferences to their modern counterparts (Spencer 1997; Reed 1998), this is not necessarily the case for antilopines (Sponheimer *et al* 1999). It would thus be useful to derive a method of using bovids for environmental signals that does not make any assumptions about the behaviour of fossil taxa.

Carbon isotopic analysis has proven a useful tool to check on the diets of fossil taxa. It is possible to go further and develop a C_3/C_4 dietary index that is independent of assumptions about diet, as will be shown in this study. This method was applied to the Makapansgat Member 3 fauna (Sponheimer and Lee-Thorp in press b). It relies on the simple ecological principle that in an area with open grasslands, there will be relatively little C_3 vegetation and therefore little ecospace for C_3 consumers. As the percentage of woody vegetation increases there will be an increase in the C_3 vegetation, and so an increased number of C_3 consuming animals (see Table 3.1). In C_4 dominant biomes (i.e. grassy) the percentages of C_3 and C_4 consuming animals provides information about the local environment (see Table 3.1 for environment type indicated by certain percentages). When applying this method to the fossil record there is a distinct advantage in that assumptions do not need to be made about the diet or habitat, but are derived empirically. Although this approach makes no prior assumptions about the fossil taxa based on their phylogeny, it does require that species be correctly identified in genera and species wherever possible. In essence, it is a development of the environmental reconstruction tool used by Vrba. Using this index, one can deduce how "closed" or "open" the environment had to be to support the number of fauna that were C_3 or C_4 dependent.

C_3	C_4	**Environment type**
>60 %	<40 %	➢ Closed woodland
~50 %	~50%	➢ Bushland/Shrubland
< 30 %	>70 %	➢ Open woodland
<10 %	>90 %	➢ Grassland

Table 3.1

Table showing the approximate (as mixed feeders have not been separated) percentages C_3 and C_4 feeders that indicate certain habitats

(Sources: K. Reed pers. comm.; Sponheimer and Lee-Thorp in press b)

The first step of the new method used in this study requires one to measure the isotopic composition of each specimen to determine the percentages of C_3 and C_4 consumers.

Summary

This study is based on the fact that plants using different photosynthetic pathways have different isotopic signatures that are passed onto their consumers. Plants that use the C_3 or C_4 photosynthetic pathways have different abundances in different climatic conditions. Therefore it is possible to make inferences regarding the vegetation available in ancient environments from the isotopic signatures of the fauna found in each assemblage. Furthermore, this tool is developed as a C_3/C_4 index to quantify how the environment changes from predominantly wooded to a more open one.

The next chapter outlines how researchers in previous studies have applied isotopic results to environments of Plio-Pleistocene hominid sites.

CHAPTER 4: EXISTING ISOTOPIC RESULTS OF PREVIOUS APPLICATIONS IN SOUTH AFRICAN PLIO-PLEISTOCENE ENVIRONMENTS

The isotope study of Sterkfontein fauna described in this thesis builds on earlier research at sites of Makapansgat, Sterkfontein and Swartkrans. There were a number of difficulties, particularly for Swartkrans, where the existing study did not include many herbivore faunas.

The results from these sites are reported in the approximate chronological sequence: Makapansgat, Sterkfontein and finally Swartkrans.

Makapansgat

An extensive isotopic survey was performed on Makapansgat Member 3 fauna; the results are represented in figure 4.1 (Sponheimer *et al* 1999; Sponheimer *et al* in press). These isotopic results clearly show the differentiation between browsers and grazers that underscored earlier preliminary data that showed diagenesis did not obscure this distinction (Lee-Thorp and van der Merwe 1987).

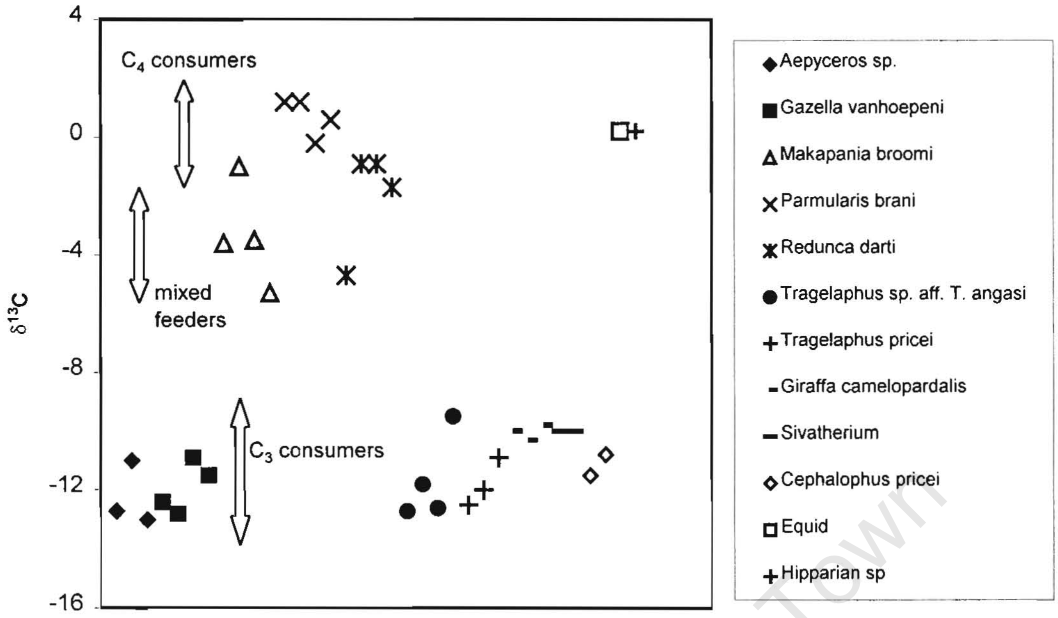


Figure 4.1

Distribution of $\delta^{13}C$ values for fauna from Makapansgat Member 3, indicating where C_4, C_3 and mixed feeders fall within the spectrum.

(From Sponheimer et al 1999; Lee-Thorp and Sponheimer 2000)

The results in figure 4.1 suggest an abundance of woody vegetation, where seven out of the twelve taxa represented are browsers, i.e. C_3 consumers. The isotopic results therefore agree with past reconstructions that suggest the area had edaphic grassland, riverine forest and bushland (Reed 1997; Sponheimer *et al* 1999). Sponheimer *et al* (1999) show that the assumption of taxonomic uniformitarianism was incorrect for the two species, *Gazella vanhoepeni* and *Aepyceros* sp. As a member of the Antilopine subfamily, *Gazella vanhoepeni* is of particular interest as it formed part of the percentage AA index calculations as to the "openness" and hence the aridity of an area. By measuring the $\delta^{13}C$ value of this species, it was found that *G. vanhoepeni* is, in fact, a browser.

Using carbon isotopes as an indicator of C_3 or C_4 diets, Sponheimer and Lee-Thorp (in press b) showed 51% of the bovids found in Member 3 were C_3 consumers. This is essentially an inverse of Vrba's "open" faunas index (AA index). This percentage of C_3 consumers is higher than all areas used in Vrba's original study except Cuelei, Angola, which has 52% C_3 consumers and contains woodland, thicket and riverine forest. Accordingly the study suggested that the Makapansgat Member 3 environment looked rather similar in density of tree/bush cover (Sponheimer and Lee-Thorp in press b).

Since the percentage AA index suggests an environment that already fell into the woodland category (Vrba 1980), it implies a denser woodland than previously thought. This is of utmost significance, as many past palaeoenvironmental reconstructions relied on comparisons of sites. A misinterpretation of the starting point, substantially affects further reconstructions.

Sterkfontein

Less isotopic work has been done on the complex stratigraphic site of Sterkfontein. The only published isotopic results from Sterkfontein come from a small study done on ungulate species (mammals with hooves) shown in Figure 4.2 (van der Merwe and Thackeray 1997). This study was done in order to establish an isotopic ecology framework for existing hominid diets. There are further results being prepared for publication (van der Merwe *et al* in prep.).

To establish this ecological framework for mixed feeders, such as the hominids, it was necessary to determine the end points for browsing (C_3) and grazing (C_4) animals at each end of the $\delta^{13}C$ spectrum. They used *Tragelaphus* cf. *strepsiceros* (the greater kudu) as the browsing ('C_3') end member and *Damaliscus* sp. and *Connochaetes* sp. as the grazing ('C_4') end point. The original paper by van der Merwe and Thackeray (1997) base some of their findings on the end members for C_3 and C_4 feeders being $-9.5^0/_{00} \pm 1.1\ ^0/_{00}$ and $2.0^0/_{00} \pm 0.3\ ^0/_{00}$. In light of the new results given in this thesis and in the paper in preparation (van der Merwe *et al* in prep.) these original end points were shown to be a little confined on the browsing end.

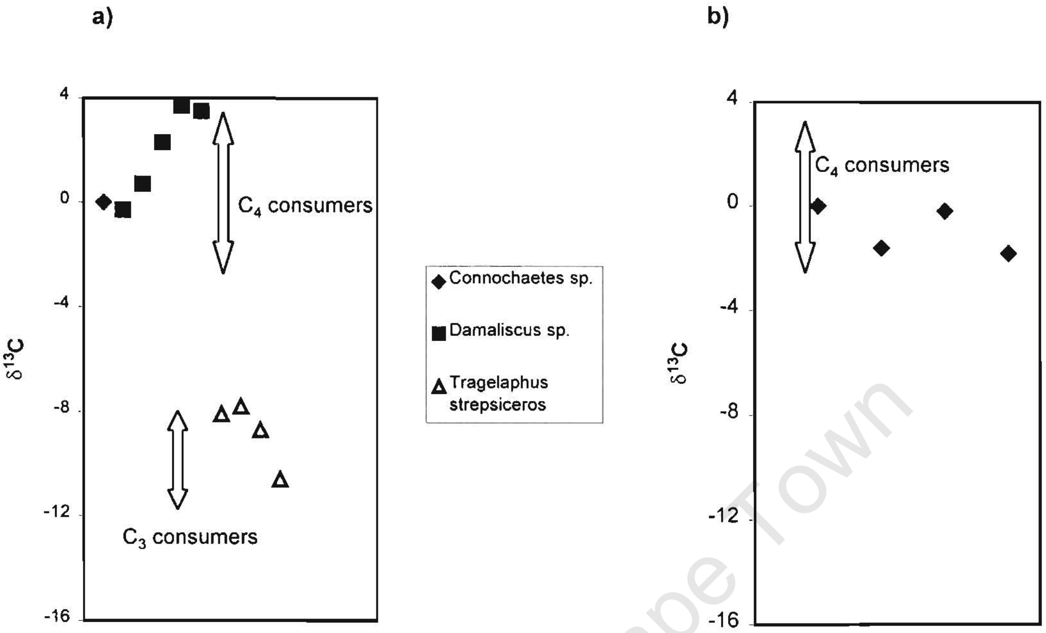


Figure 4.2

Distribution of $\delta^{13}C$ values for fauna from Sterkfontein, indicating where C_4, and C_3 feeders fall within the spectrum.

a) Member 4

b) Member 5

(from van der Merwe and Thackeray (1997))

The study was performed during a time when the pre-treatment for enamel specimens was not yet as refined as it is today (current pre-treatment fully outlined in following chapter).

In the current study these specimens were re-analysed with the newer pretreatment for two reasons;

1. The first reason was that the pre-treatment (to eliminate certain contaminants) had been refined recently by Matt Sponheimer.
2. The second reason was the unusual and somewhat puzzling feature of the rather positive $\delta^{13}C$ value for a browser, *Tragelaphus strepsiceros* (mean $\delta^{13}C$ of $-8.8^0/_{00}$ n=4). This $\delta^{13}C$ value is more positive than usual for a browser end point member found at Swartkrans or Makapansgat. The method of pre-treatment might have affected this value (this seemed unlikely but needed to be tested), or this browser was not typical.

Unpublished data on Sterkfontein from van der Merwe and colleagues (van der Merwe *et al* in prep.) in the University of Cape Town laboratory includes isotopic values for a few more animals, including mostly hominids (van der Merwe *et al* in prep.). This data, although important for individual dietary preferences of hominids, is not very useful for establishing a C_3/C_4 index for the site.

Swartkrans

Extensive isotopic research has been done on various families of fauna at Swartkrans (Lee-Thorp and van der Merwe 1993; Lee-Thorp *et al* 1994; Lee-Thorp *et al* 2000), as outlined below.

This work was performed primarily to obtain an 'isotopic ecology' in order to fit hominids into the ecosystem and determine their diets, but also to establish what the environment consisted of in terms of woodland and grassland composition. In one such study animals with known diets, *Tragelaphus strepsiceros* (the kudu and C_3 browser) and *Connochaetes* sp. (the wildebeest and C_4 grazer) were used as the two end points for the browser and grazer ends of the spectrum (Lee-Thorp *et al* 1994). These browsers and grazers provide a framework for $\delta^{13}C$ values that are considered typical for C_3 and C_4 consumers in this ecosystem. This framework is important because, the spectrum of C_3 and C_4 diets may shift slightly due to differences in climatic conditions which would affect the fractionation in plants and therefore the signals left in the fauna consuming these (Lee-Thorp *et al* 2000). It is also it is important to understand the role that diagenesis played, as little is known about diagenesis at the time the deposits were lain down.

Lee-Thorp *et al* (1994; Lee-Thorp 1987) found that most of the results conformed to the expectation based on modern isotopic ecology (see figure 4.3 for results). The grazers fell near 0 $^0/_{00}$ confirming that the area had C_4 grass at that time, as it does today. The browsers' $\delta^{13}C$ value fell between -11 and -12 $^0/_{00}$, maintaining the distinction between grazers and browsers. A few exceptions did not conform and are discussed below.

a)

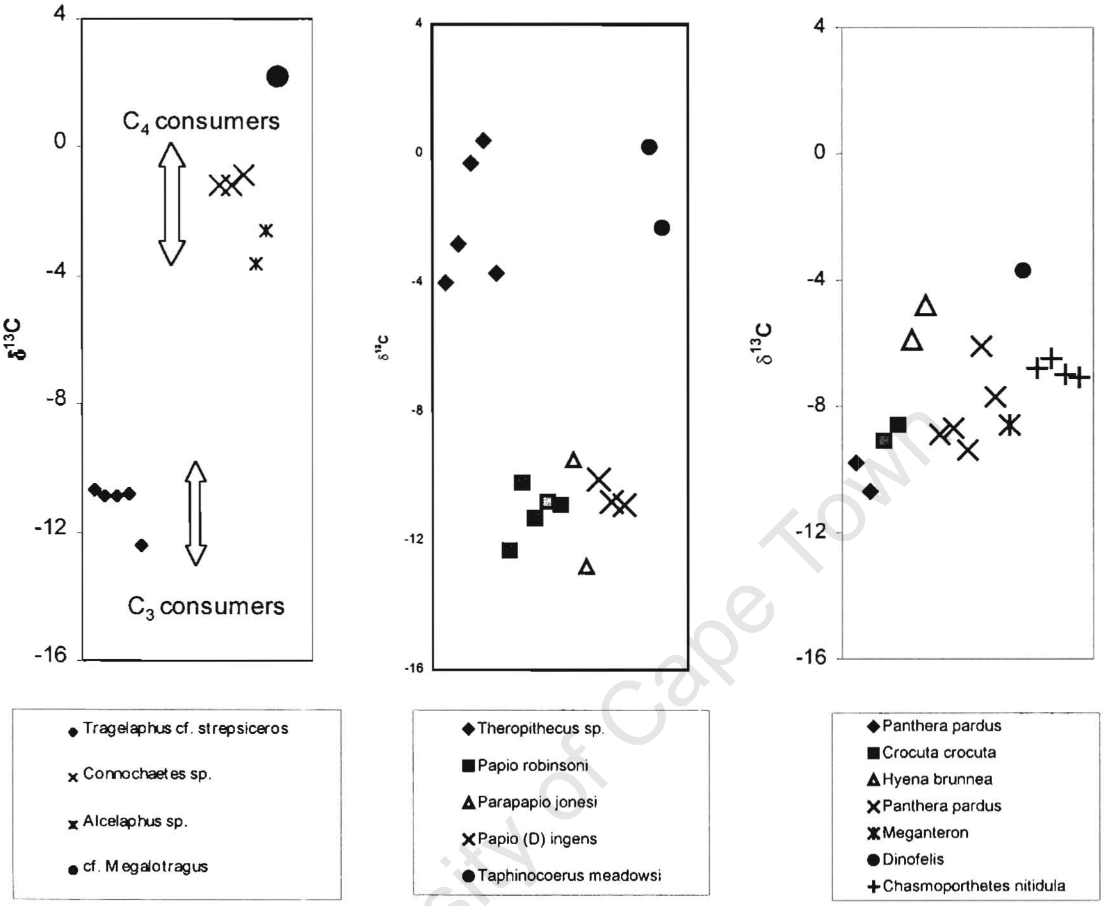


Figure 4.3 a

Distribution of $\delta^{13}C$ values for fauna from Swartkrans Member 1. Data are separated into 3 diagrams: herbivores, primates & suids and carnivores, respectively.

(Data from Lee-Thorp *et al* (1994) and Lee-Thorp *et al* (2000)) b)

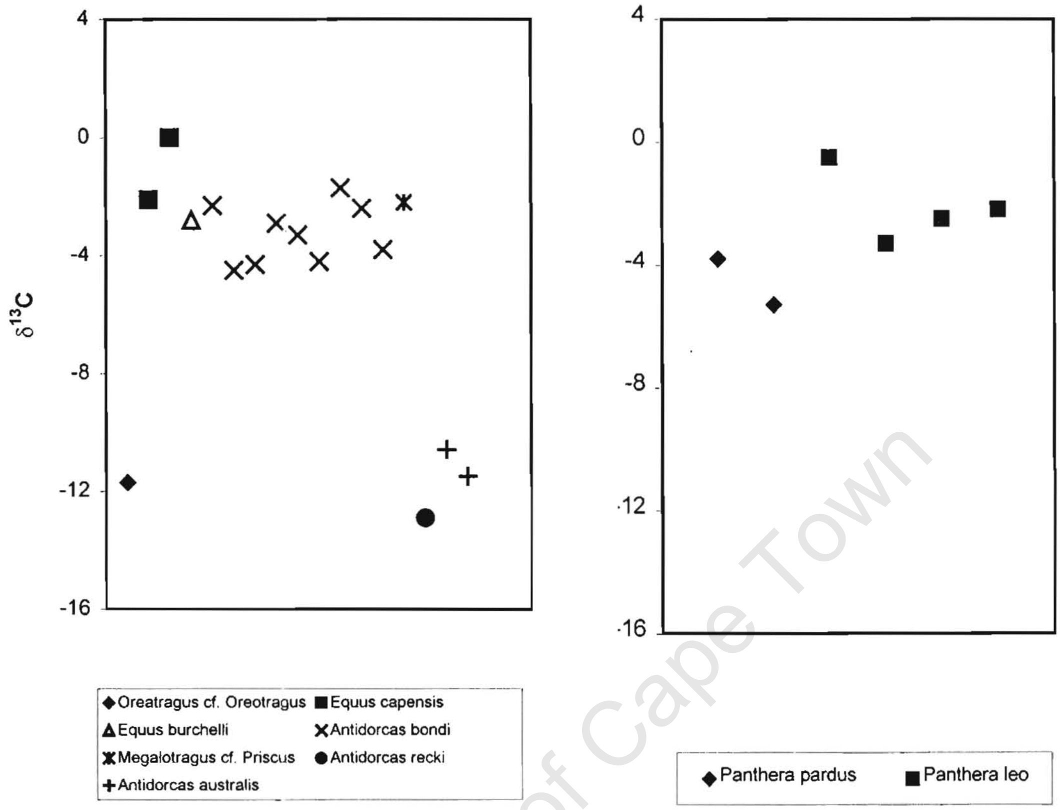


Figure 4.3 b

Distribution of $\delta^{13}C$ values for fauna from Swartkrans Member 2. Data are separated into 2 diagrams: herbivores and carnivores, respectively.

(Data from Lee-Thorp *et al* (1994) and Lee-Thorp *et al* (2000))

Antidorcas recki did not conform to predictions based on the modern descendants' ecology and habitat preferences. Their $\delta^{13}C$ value was negative in the C_3 spectrum, indicating a browser, unlike its modern counterpart, *Antidorcas marsupialis*, a mixed feeder. The finding that the species *A. recki* were C_3 consumers and not mixed feeders impacts the calculations determining the "openness" of an area based on the percentage antilopini and alcelaphini (AA index).

Furthermore, the isotopic research for carnivores showed that although the C_4 consuming fauna component was relatively large, more C_3 elements were present than originally thought in Member 1 (Lee-Thorp *et al* 2000). Some of these large predators include *Chasmoporthetes nitidula*, *Megantereon* sp. and *Dinofelis* sp. Predators, specifically leopards, show a marked shift from C_3 fauna in Member 1 to C_4 fauna in Member 2, perhaps indicating a necessary move to prey on what was available in the environment. Lions (*Panthera leo)* also show that they fed on C_4 fauna during member 2 times. Although the degree of individual choice is uncertain, it tends to support suggestions that more C_4 prey in Member 2, and that the environment was an open, arid one.

The isotopic work at Swartkrans has showed, not only that little diagenesis has taken place and hinted at the diets of hominids, but has also provided information on an aspect of the environment that includes habitat preferences and diets of individual species. The C_3/C_4 index has not yet been applied to these isotopic data. However, a bias might occur using this data, since species were chosen for sampling specifically for their being known grazers or browsers.

Summary

Extensive isotopic data for fauna at Swartkrans Members 1 and 2 and Makapansgat Member 3 exists. Using a C_3/C_4 index developed for Makapansgat, it was found that Makapansgat Member 3 indicated a more closed wooded environment than originally thought, although there were clear C_4 patches present. Swartkrans was placed in the fairly open environment with some woodland elements. The isotopic data, especially those for *Gazella vanhoepeni, Antidorcas recki* and the predators, showed that more C_3 consumers (i.e. woodland/shrub feeders) were present than suggested by the AA index (Vrba 1975). Furthermore, it was shown that by assuming taxonomic uniformitarianism we might be incorrectly classifying certain faunal species. Sponheimer *et al* (1999) showed that two species thought to be grazers or mixed feeders were in fact browsers at Makapansgat and one species at Swartkrans. These changes assume significance when the species forms an important element/concentration of the AA index.

This goes to show that the assumption of taxonomic uniformitarianism needs to be tested and this gap in our knowledge needs to be filled. This observation suggested that the AA index overemphasises the open nature of the environment. Isotopic research at Sterkfontein proposes to contribute towards closing this gap. The next chapter outlines the Sterkfontein site, and details the stratigraphy and which samples were taken.

CHAPTER 5: SITE, SAMPLING AND ANALYSIS

In earlier chapters existing information about palaeoenvironments of the area under discussion was outlined. Some gaps have been pointed out and it is proposed that this study on isotopic research will contribute to our knowledge of the environments represented by the deposits laid down during that time. This chapter describes the site under investigation bearing in mind that Sterkfontein has a complex stratigraphy consisting of depositions, infill collapses and erosions, still under investigation. Recently Kuman and Clarke (2000) suggested that some specimens previously assigned to Member 4 should be reassigned to Member 5. Problems with context of specimens to members obviously greatly affect any interpretations that can be confidently produced based on faunal assemblage composition, and isotopic analysis.

The site: Sterkfontein

The dolomitic solution cavities at Sterkfontein have been formed in what is called Malamani Subgroup and it consists of chert and dolomite horizons in succession (Partridge 1978). Sterkfontein's cave infills yielded the first adult cranium of a fossil hominid, which was classified as *Australopithecus africanus* (Tobias 1992). The excavations took place on and off from 1936 to 1958 by Dr Robert Broom and Dr John Robinson. Subsequently, Dr Philip Tobias started a new excavation at the site in the 1960s. Of the six members that have been recognised (Partridge 1978), two (Member 4 and 5) have yielded hominids. The hominids found in Member 4 (dated to around 2.6 Ma) have been attributed to *Australopithecus africanus.* The hominids in Member 5 (dated to around 1.7 Ma) have been assigned to *Homo habilis* (Tobias 1992).

The fossils and artefacts uncovered at this site have been accumulated via various pathways i.e. large cats dropping bones from the trees above into the cave, while other bones and artefacts were simply washed into the deep vertical shafts (Clarke 1994). The bones of the cats themselves have also been found along with the bones of the baboons on which they might have preyed.

Partridge (1978) classified the Sterkfontein lithostratigraphy in terms of 6 members. The lithostratigraphy was refined by Partridge and Watt (1991). It is now known that as with Swartkrans, the Sterkfontein deposits were subject to many depositional, erosional, and collapsing cycles (see figure 5.1). Although Partridge recognised 6 members, the stratigraphy is now understood to be very complex and is continually being refined.

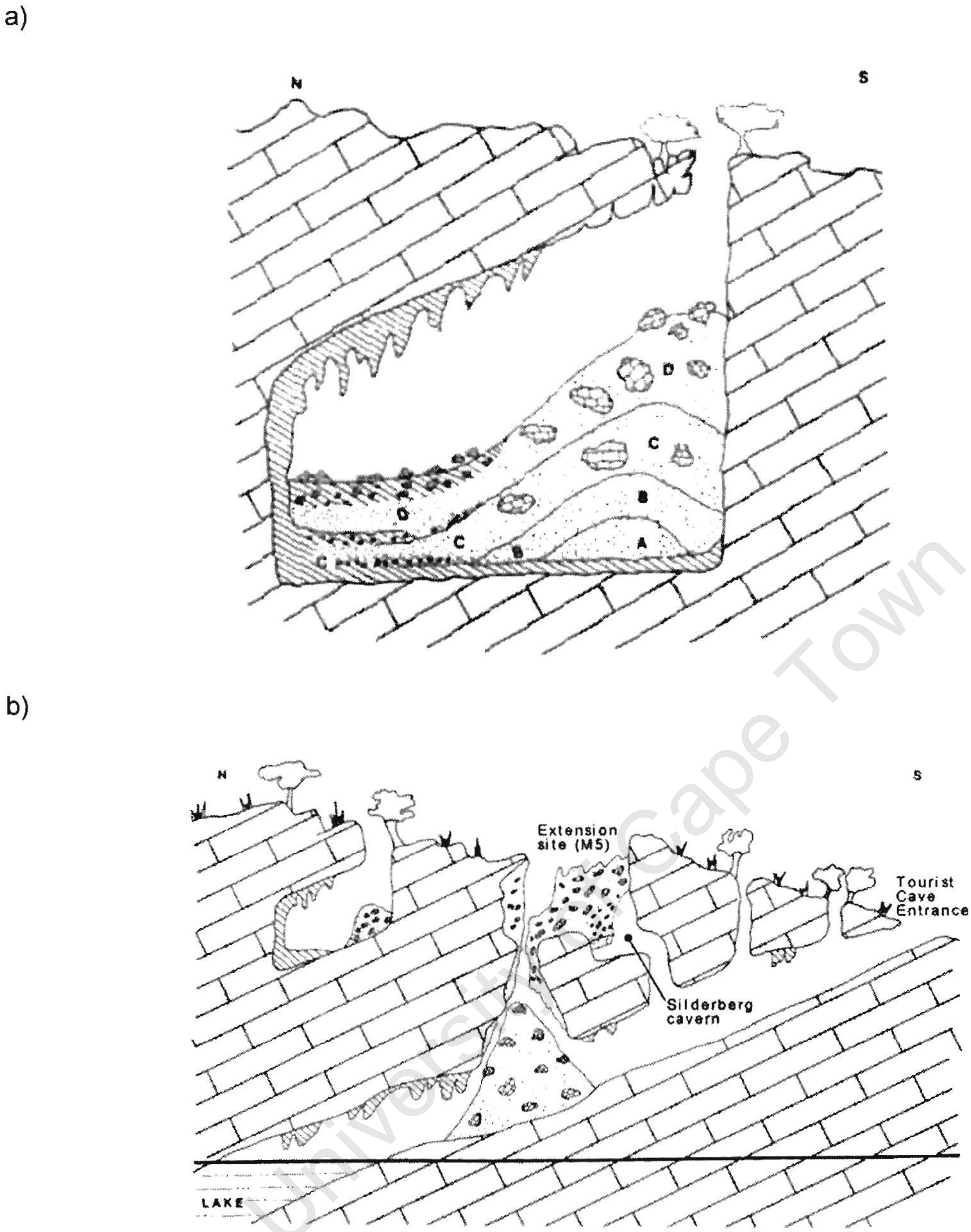


Figure 5.1

Cross-sectional N-S diagrams of the Sterkfontein caves showing

a) Member 4 breccia

b) Member 5, Tourist Cave and the Silderberg Grotto

(From Clarke (1994))

Members 1, 2 and 3 are found in the Silderberg cavern, named after Dr Kurt Silderberg (see figure 5.1 for location relative to Members 4 and 5) who found a maxilla of a hunting hyaena in 1942, which has now been named *Chasmoporthetes silderbergi*. Alun Hughes was responsible for much of the clearing of the deposits from dumps of rubble left by the limeworkers.

Member 1, the oldest member, yielded little bone and so has not been studied in detail. Fossils assigned to Member 2 have been found *in situ* in the breccia within Silderberg Grotto (Clarke 1994), including many cercopithecoid fossils. Large cats and other carnivore remains have also been found. New palaeomagnetic dates suggest an age of about 3.3 million years (Clarke 1999). A partial skeleton of an Australopithecine is currently being excavated by Clarke from this Member. Member 3 has not been excavated, for safety reasons.

Member 4 (STS in many older publications) consists of two areas on the eastern side of the site: the calcified quarry where Broom found his fossils and the decalcified area excavated by Alun Hughes. Over 50 hominid fossils have been found in this Member. It has been suggested that due to the fact that many pieces of fossil wood have recently been found in this decalcified breccia (discussed in Chapter 2), that it might have been a talus cone (Clarke 1994), as had also been suggested by Robinson (1962). The hypothesis is that large cats dropped bones into an opening from above and formed this talus (material that has been deposited on a slope and causes the deposit to form a cone shape, also called "skree" slope). A cross-section of this member is shown in figure 5.1a. The way in which the deposit formed affects the interpretation of what is found in the deposit. According to current interpretation at this site, it seems that the lowest deposit is not simply the oldest.

Big rocks were found nearer to the entrance (called clast supported breccia), while smaller rocks and fossils rolled further back where they cemented into the lime that was deposited there from water dripping from the roof (called matrix supported breccia)(Clarke 1994). It has now been suggested that Member 4 extends much further than previously thought (Kuman and Clarke 2000) (see figure 5.2). The new interpretations are based partly on the absence of stone tools as well as the absence or presence of certain faunal and floral elements (Kuman and Clarke 2000).

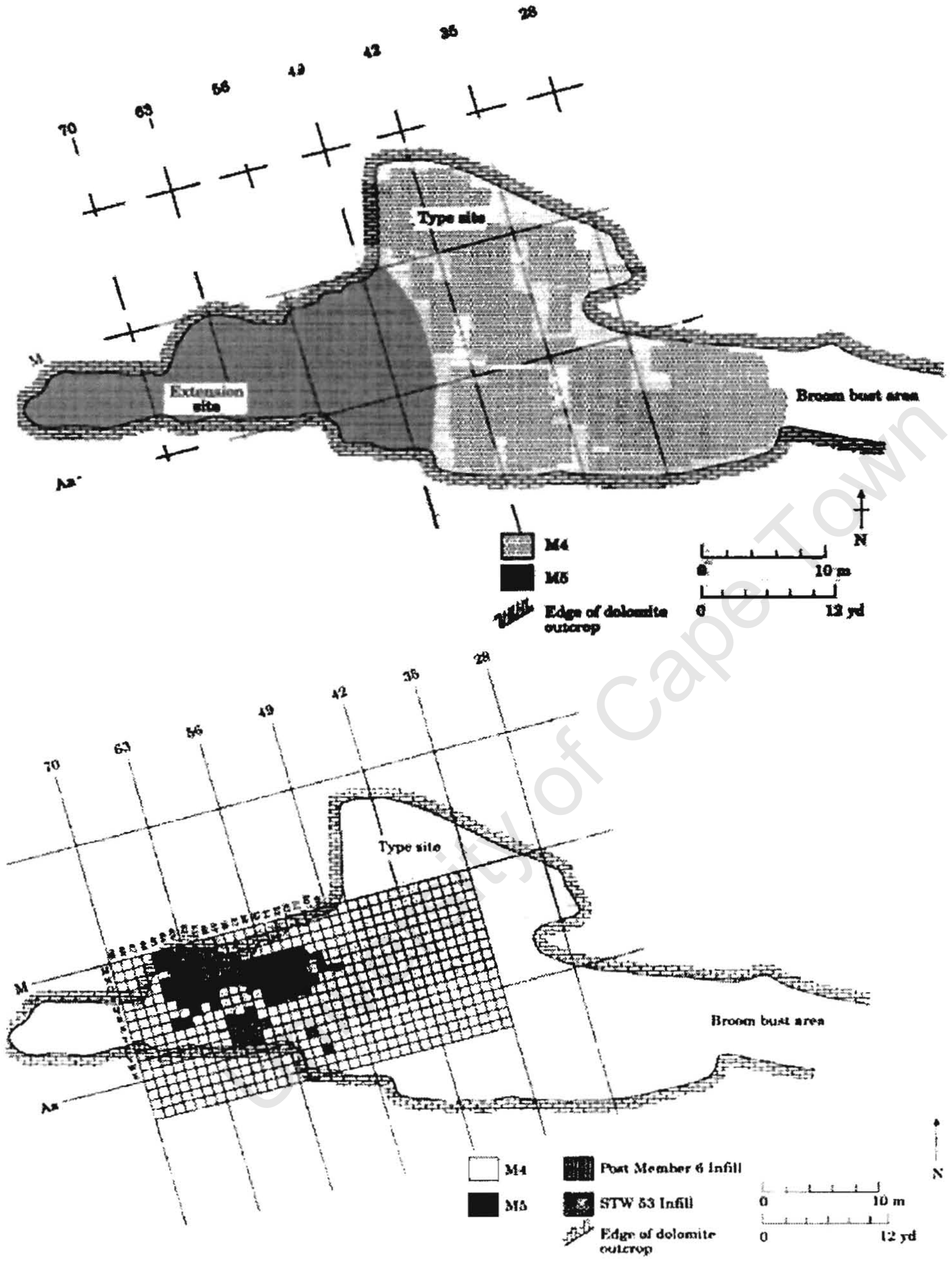


Figure 5.2

Plans of the surface distributions of Member 4 (Type site: STS) and Member 5 (Extension site: SE) at Sterkfontein

a) Traditional view

b) More recent proposal after Kuman and Clarke (2000)

(from Kuman and Clarke (2000)

Member 5 (previously SE), the artefact-bearing unit, can be found in the Extension site west of member 4. Originally it was thought that this, too, was a large underground cave into which carcasses fell from the trees above (Robinson 1962). It now seems, however, that deposition was far more complicated. In absence of a horizontal sequence, it is very easy to become confused between 2 layers if their source is similar, unless one looks carefully at the archaeology or faunal composition to distinguish them (Kuman and Clarke 2000). One must stay very objective with this method as it can become circular if the researcher has already decided in their mind what will be found in certain deposits.

Member 5 shows much evidence of erosional and depositional cycles. Originally Member 4 covered much of the area of the site, until a large pre-historic collapse occurred which meant that later, Member 5 sediments could fill these spaces (Clarke 1994). At least two infills occurred. The first infill that took place is called the Oldowan infill (around 2.0 - 1.7 Ma). A further infill occurred and is called the Acheulean, since stone artefacts such as bifaces have been found in its deposits. This infill occurred at a time when the cave's opening was very much larger than before, and so it could fill more of the area (Kuman and Clarke 2000). Both of these can be found in Member 5 East. The member 5 West includes the area formerly called the "extension site" by Robinson (Robinson 1962) (see figure 5.2). The deposits are very calcified in this region unlike that of member 5 East which is likely to have mixing of sediments through solution pockets (Kuman and Clarke 2000).

Finally, Member 6 has been exposed at the northern end of Member 5 west. Since very little faunal material was preserved it will not be considered further here.

Notwithstanding the difficulties implied by the complex stratigraphy of Members 4 and 5, it was decided to sample specimens from these Members, because they lie within important time periods of the earth's history.

Sampling

The fauna sampled from member 4 and 5 were mostly large herbivores (including bovids and equids) and to a lesser extent primates and carnivores. Where possible, a sample of 5 specimens was taken in order to obtain a representative sample of each species. A set of grazers and browsers was chosen from the ungulates in order to test whether the distinction between grazers and browsers has been maintained.

In some cases identification of certain specimens were uncertain, for example it remains undecided as to whether or not *Parapapio broomi* and *P. jonesi* are male and female of the same species or separate species (F. Thackeray pers. comm.). Because of this problem, bucco-lingual (length) and mesio-distal (width) measurements were taken to supplement the isotopic data and to quantify the difference.

In the case of *Damaliscus* sp., samples removed along the tooth growth axis of the tooth were taken in order to examine any change in isotopic signature as the tooth grew (examining intra-individual variation).

Where possible, breccia samples were taken from areas adjacent to where enamel samples were taken. This was done for two reasons:

1. To compare adjacent enamel and breccia in order to establish whether any diagenesis occurred.
2. To examine differences in isotopic value of the breccia from Member 4 to 5.

Species sampled are given in Table 5.1.

Analysis

Laboratory procedures

Pre-treatment procedures described below were developed for very small, finely powdered samples in our laboratory (Lee-Thorp *et al* 1997), and subsequently refined and vigorously tested (Sponheimer 1999). The difficulty is to eliminate contaminants without altering the enamel structurally, or the isotopic values to any significant degree.

A small sample of between 2 and 3 milligrams of enamel powder was obtained from each tooth using a rotary drill fitted with a 1.2-mm diamond-tipped drill bit. Any visible glue on the teeth was first removed using an abrasive drill bit. The powder samples were treated with 1 ml of 1.75 % v/v sodium hypochlorite for 45 minutes, to remove the organic materials including humic acids from the sample. They were rinsed 3 times with distilled water and centrifuged for three minutes in a high-speed microcentrifuge. The samples were then pretreated with 0.5 ml 0.1M acetic acid for 15 minutes to remove the highly soluble mineral component. Again, the samples were rinsed several times in distilled water and centrifuged. The powder was then freeze-dried (Lee-Thorp *et al* 1997; Sponheimer 1999).

Between 0.8 – 1.0 mg of the sample enamel was weighed into individual reaction vessels for the first series of enamel samples. No apatite standards are available, but $CaCO_3$ (Calcium carbonate) standards were used. Approximately, 0.06 mg was weighed out for each standard sample. The following standards were used: NBS 18, NBS 19, Carrara Z (external standard) and Cavendish marble (internal standard).

Release of CO_2 by 100 % H_3PO_4 acid hydrolysis at 70°C took place in an automated single acid bath system with a micro-inlet, "Kiel" device, interfaced with a Finnigan Matt 252 mass spectrometer. The CO_2 was purified using cryogenic separation and introduced to the mass spectrometer for analysis. The dual-inlet design allows a reference gas (with a known isotopic ratio) and the sample gas to be admitted into the device alternately. The gases are ionized and accelerated through a magnetic field that disperses the ions according to their isotopic weight and the isotope beams are measured as voltages [V] at the analyser. This voltage is reported along with the isotopic result. Previous experience with experiments with the FM252+ interfaced with the Kiel device indicated that voltages of gas in the source needed to be >2[V] to provide consistent and reliable results.

The results are reported in standard notation relative to the *Peedee Belemnite* (PBD) marine carbonate standard, which has a $\delta^{13}C$ value of $0^0/_{00}$. By convention the $^{13}C/^{12}C$ and $^{18}O/^{16}C$ ratios are expressed as per mil (1000) in the delta (δ) notation using the following equation:

$$\delta^{13}C = (R_{sample}/R_{ref} - 1) \times 1000$$

$$\delta^{18}O = (R_{sample}/R_{ref} - 1) \times 1000$$

Where R = $^{13}C/^{12}C$ or $^{18}O/^{16}C$

The reference gas was calibrated against known NBS standards, and precision was found to be better than $0.1^0/_{00}$.

Calibration and yields

The calculations incorporated into the FM252 software for the conversion to PDB are not quite precise. Once the raw results have been obtained, they are therefore calibrated against set standards. In this study, the following standards were used: NBS 18, NBS 19, Carrara Z and Cavendish marble. A regression curve was obtained by plotting the observed against internationally accepted (or previously determined) isotopic ratios. The curve changes slightly with time, as the calculations change slightly in the Mass spectrometer and therefore the set of calibrations used change every month. The fossil samples that are currently under investigation were adjusted using the regression calculation for the month in which they were analysed.

	OBSERVED		'EXPECTED'	
	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$
NBS 18	-5.1	-25.1	-5.1	-23.0
NBS 19	1.6	-5.5	1.9	-2.2
CM	0.2	-11.4	0.4	-8.5
CZ	2.0	-4.1	2.3	-1.3

Table 5.2

Observed vs. 'Expected' values for standards used to calibrate samples for the month of November 2000 (see full table of values at the back of manuscript).

Table 5.2 expresses the data obtained in November 2000 for all four standards as an example. The calibration curves can be seen in figure 5.3 for carbon and oxygen, respectively.

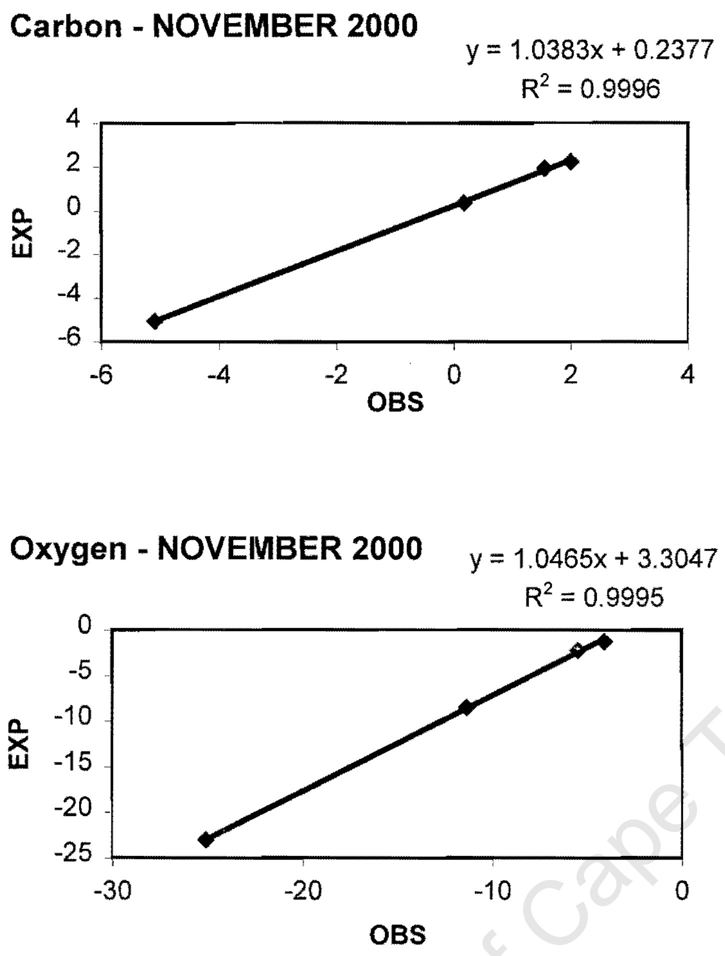


Figure 5.3

Plots of observed vs. known values for isotope standards, showing best-fit regression and r^2 for

a) $\delta^{13}C$

b) $\delta^{18}O$

The raw data ($\delta^{13}C$ and $\delta^{18}O$) was calibrated according to the method described in Chapter 5. Some samples gave very low voltages (as explained in previously: low voltages equate with reduced carbonate). These samples and were re-analysed using more material, where possible and in many cases this produced a satisfactory result. Samples that produced an adequately high gas yield (Voltage) were duplicated for comparison. In some cases, however, there was no more enamel to reproduce the result in which case the result had to be discarded. Because of the small sample size problem, a series of experiments were run to determine the exact effect of sample size i.e. Voltage on data.

This experiment was done to find out what the lowest voltage reading was that could yield a satisfactory result within $0.1^{0}/_{00}$ of the expected result. The isotopic composition of Cavendish Marble is well known. A series of Cavendish Marble samples were analysed at weights ranging from very small (0.008 mg) to much larger (1.0mg). The results (Table 5.3 and Figure 5.4) show that significant shifts in both $\delta^{13}C$ and $\delta^{18}O$ occur below voltages of approximately 1-1.5[V]. A voltage as small as 1[V] seem to yield reliable results for $\delta^{13}C$ but for $\delta^{18}O$ the shift occurs at about 1.5[V].

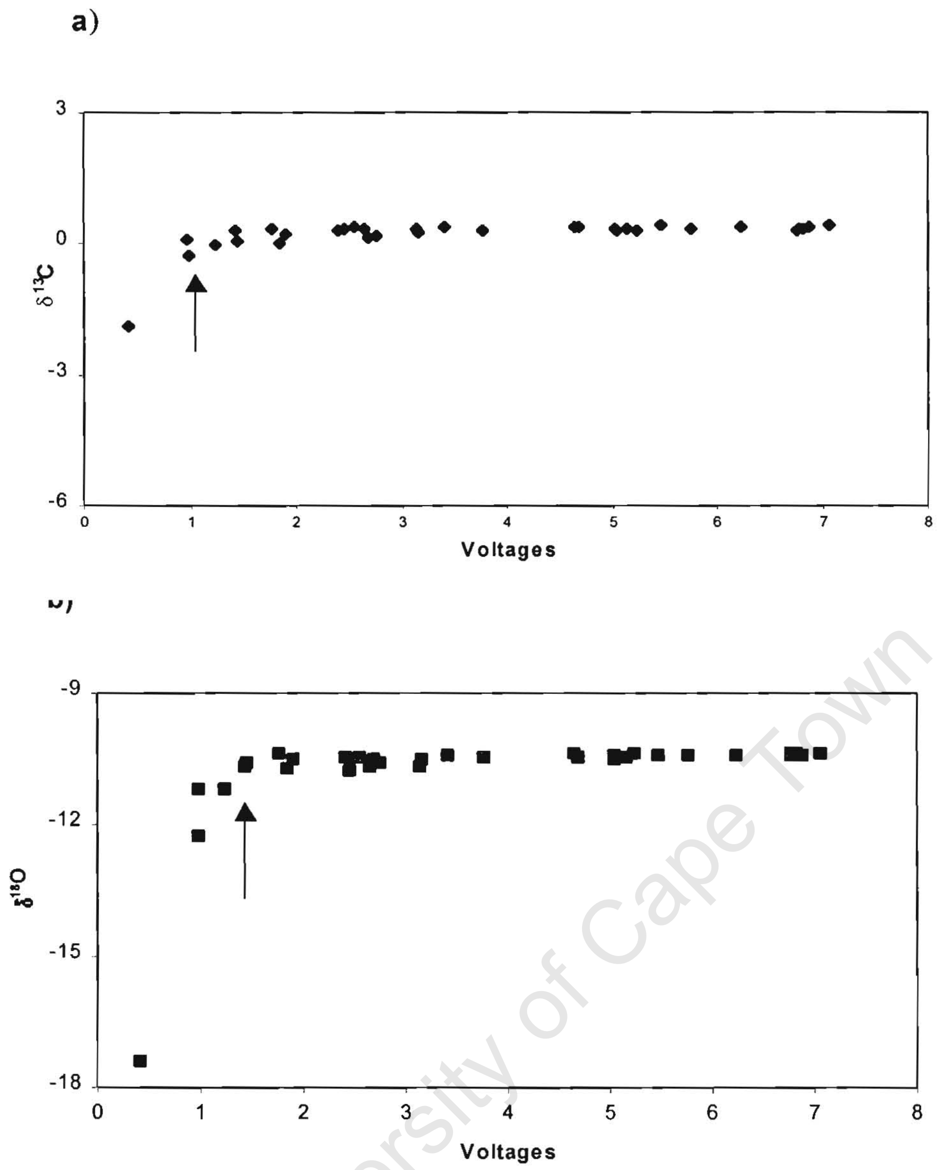


Figure 5.4

Distribution of δ values for Cavendish Marble plotted against Voltage

a) $\delta^{13}C$

b) $\delta^{18}O$

The results allowed a reconsideration of values with low voltages. Those results with voltages below this value for carbon and oxygen were not used in calculations and are not discussed in the results chapter.

Summary

It has been acknowledged that difficulties in interpreting the complex stratigraphy of Sterkfontein and the ages of the deposits will affect or constrain levels of interpretation about environments from isotopic analysis. Difficulties encountered in isotopic measurements, as described, can provide another kind of problem, which was taken into account. Nevertheless the next chapter outlines the results obtained in this study.

CHAPTER 6: RESULTS

This chapter describes all the isotope results. At an early stage a problem of low gas yield following acid hydrolysis of samples emerged. This prompted tests to determine the limits of reliability for small gas samples, as described in the previous chapter. The $\delta^{13}C$ and $\delta^{18}O$ values for all species analysed for Members 4 and 5 are reported. Since there was a question as to whether or not two *Parapapio* primate species were one or two species, the tooth sizes of these primate species teeth are reported. The isotopic values of some associated breccia samples from the two members are reported. Certain specimens of *Damaliscus* sp. were sampled serially along teeth. Finally the C_3/C_4 index is applied to the data.

Isotopic results for Sterkfontein fauna

General observations

The calibrated isotopic results for faunal enamel specimens from Sterkfontein Members 4 and 5 are listed in Tables 6.1-6.3. The results were calibrated against standards using equations in appendix 1.

The expected distinction between the grazing and browsing ungulates for $\delta^{13}C$ is observed for both Members 4 and 5 (see figure 6.1). For Member 4, the mean for grazers is -0.48 $^{0}/_{00}$ ± 1.62, while the mean for browsers is -11.26 $^{0}/_{00}$ ± 2.05. For Member 5 the mean for grazers is -0.89 $^{0}/_{00}$ ± 1.94, while the mean for browsers is -9.78 $^{0}/_{00}$ ± 1.63. This shows although there is a significant shift in the browsers, the grazer values remain similar from Member 4 to 5. In general, the results show a trend towards more C_4 dominant diets (i.e. grazing fauna) in Member 5 from Member 4, where there is a greater distinction between the grazers and browsers. Overall the mean for all Member 4 herbivores is -5.69$^{0}/_{00}$ ± 4.71 $^{0}/_{00}$ and the overall mean for all Member 5 herbivores is -3.11$^{0}/_{00}$ ±

3.73$^{0}/_{00}$, showing an overall trend toward more positive values. The same shift can be observed in the primates, where δ^{13}C mean for Member 4 is -9.00 $^{0}/_{00}$ ± 2.82 $^{0}/_{00}$ and for Member 5 is -3.40 $^{0}/_{00}$ ± 3.17 $^{0}/_{00}$ (figure 6.2). The carnivores show only a slight overall shift (Member 4 δ^{13}C mean -6.68$^{0}/_{00}$ ± 1.85 $^{0}/_{00}$ Member 5 δ^{13}C mean -5.44$^{0}/_{00}$ ± 2.79 $^{0}/_{00}$)(figure 6.3).

δ^{18}O means for all ungulates from Members 4 and 5 is -2.28$^{0}/_{00}$ ± 2.22 and -2.32$^{0}/_{00}$ ± 2.41 $^{0}/_{00}$, respectively. The Member 4 grazers show a very slight enrichment (-1.71$^{0}/_{00}$ ± 1.62 $^{0}/_{00}$) compared to that of the browsers (-2.11$^{0}/_{00}$ ± 2.84 $^{0}/_{00}$). The grazer and browser values of Member 5 are very similar (browsers: -2.23$^{0}/_{00}$ ± 2.83 $^{0}/_{00}$; grazers: -2.47$^{0}/_{00}$ ± 2.37 $^{0}/_{00}$). These differences are not statistically significant. The primates, on the other hand, show a shift toward more negative values from Member 4 to Member 5 (Member 4 mean: -0.66$^{0}/_{00}$ ± 1.81; Member 5 mean: -3.19$^{0}/_{00}$ ± 1.34). A shift toward more negative values is also observed in the carnivores (Member 4 mean: -2.28$^{0}/_{00}$ ± 1.88 $^{0}/_{00}$; Member 5 mean: -4.08$^{0}/_{00}$ ± 0.81$^{0}/_{00}$).

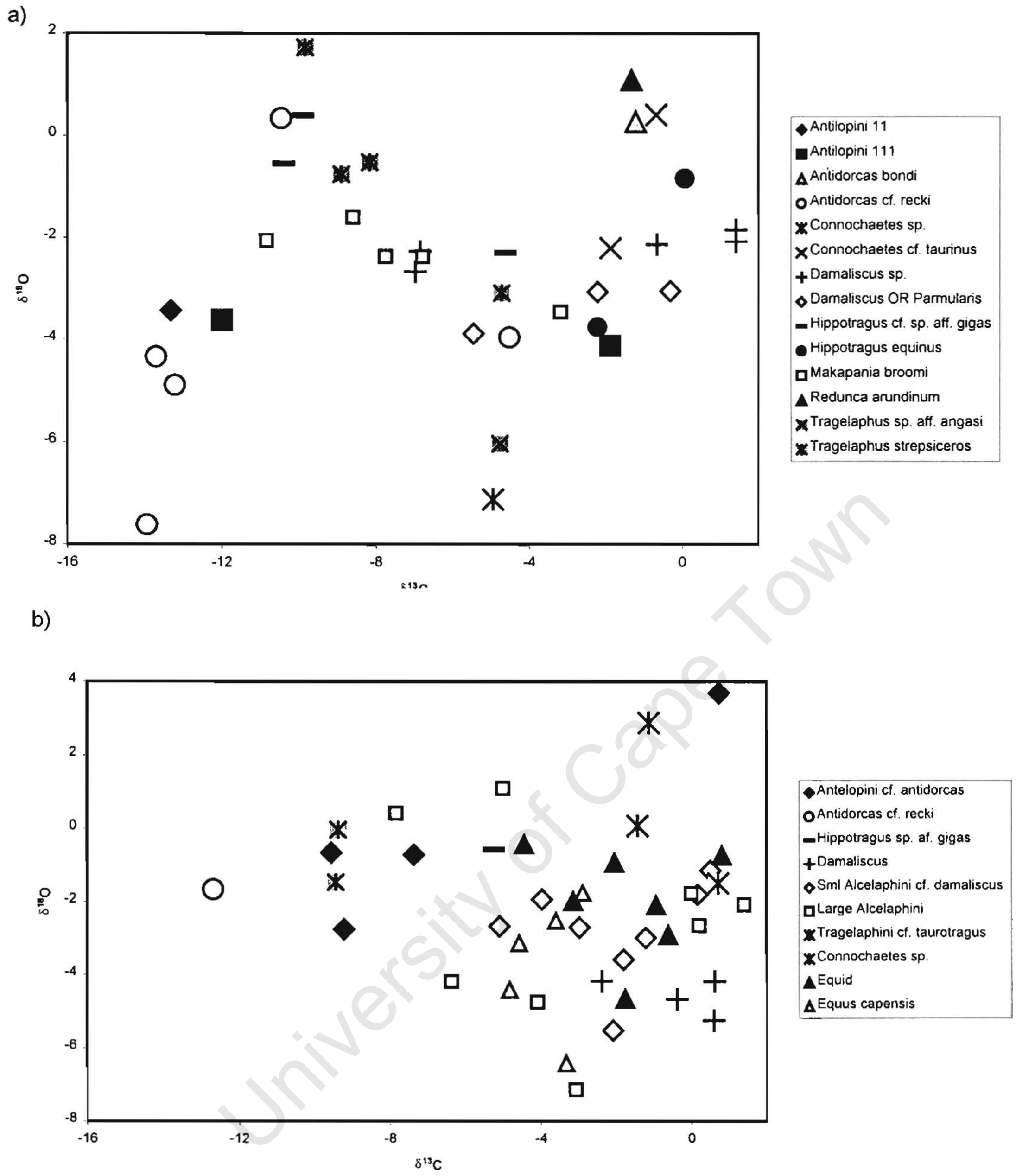


Figure 6.1

Sterkfontein Ungulates δ^{13}C and δ^{18}O results (duplicates averaged)

a) Member 4

b) Member 5 (split into Oldowan (East) infill and West Infill in the Member 5 results section)

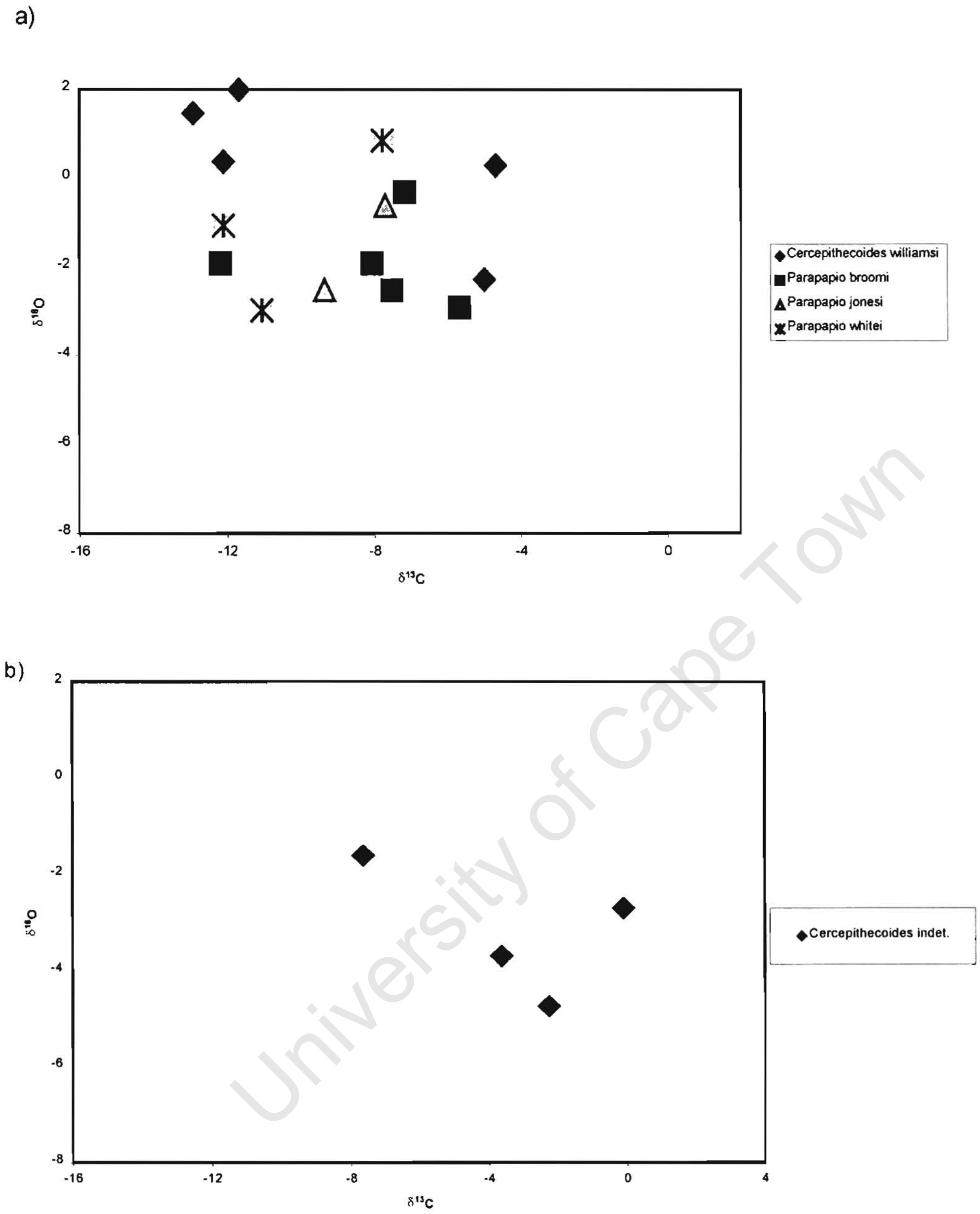


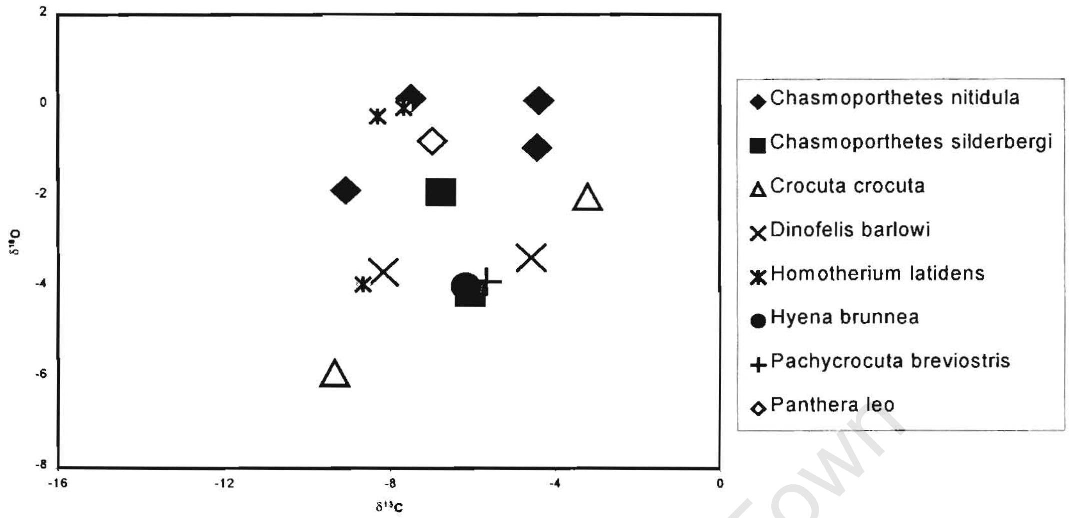
Figure 6.2

Sterkfontein Primates δ^{13}C and δ^{18}O results (duplicates averaged)

a) Member 4

b) Member 5

a)



b)

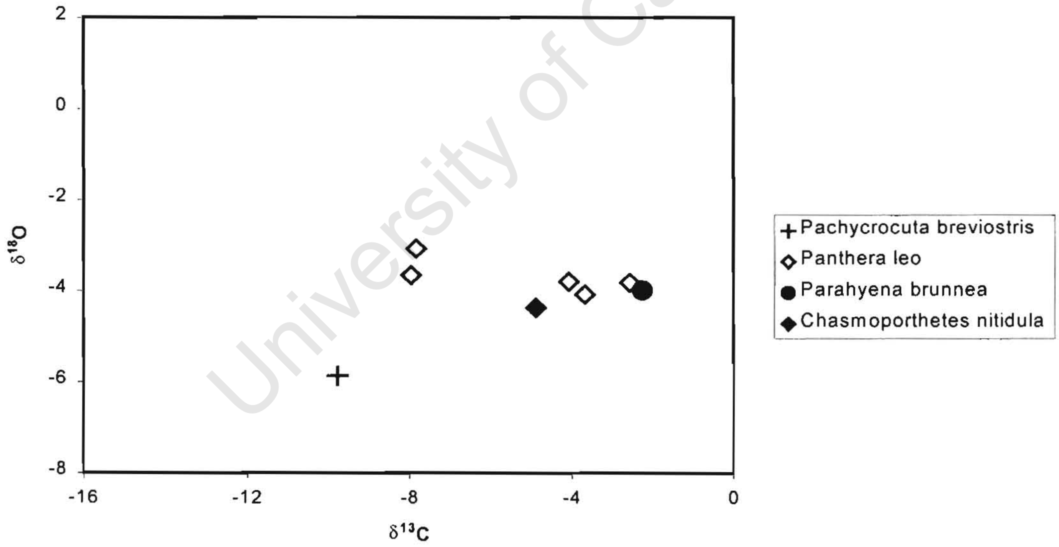


Figure 6.3

Sterkfontein Carnivores δ^{13}C and δ^{18}O results

a) Member 4

b) Member 5

Comparison of earlier results with this study

Van der Merwe and Thackeray (1997) analysed a small set of grazers and browsers from Sterkfontein. These samples were re-analysed for this study for reasons stated in chapter 4: the species used to establish the C_3/browser end of the spectrum gave rather positive results and was in fact a reliable browser, and the pre-treatment method had since been greatly refined. The values obtained by the two techniques are reported for comparison in Table 6.4.

The differences in pre-treatment are briefly as follows. The earlier methods required 1 -2 grams of enamel that was ground using a Spex Mill, and therefore particle size was relatively large. Treatment with 2% solution of sodium hypochlorite and 1M acetic acid was more prolonged. The newer method, as described in Chapter 5, is more gentle. It is based on smaller particle sizes and shorter chemical treatment. Another physical difference was that the samples were analysed in the VG 602 Mass spectrometer and different methods of calibration were used. This might also contribute to differences in results.

No significant differences can be observed in the carbon isotope values, which are highly correlated, with the mean difference being 0.2$^{0}/_{00}$ for Member 4 and 0.03$^{0}/_{00}$ for Member 5, respectively. The oxygen isotope values are on average 2.91$^{0}/_{00}$ more positive for Member 4 and 1.83$^{0}/_{00}$ more positive for Member 5, respectively, indicating that the old pre-treatment affected the oxygen values, but not that of the carbon values.

δ^{13}C and δ^{18}O results for Member 4 faunal specimens:

C_3 consumers

Hippotragus gigas, the giant Hippotragine, fell into two δ^{13}C groups; one with values of -10.15$^{0}/_{00}$ (n=2) and -5.37$^{0}/_{00}$ (n=2), respectively. This data shows that the latter group included more grass into their diet, and although the data are few, the results suggest the presence of two distinct groups/taxa. The δ^{18}O mean for *H. gigas* is -0.06$^{0}/_{00}$ ± 1.89 (n=4). The 2 groups noted in the carbon have very similar $\delta^{18}O$ values the first being -0.08$^{0}/_{00}$ (n=2) and the latter -0.04$^{0}/_{00}$ (n=2).

Antidorcas recki, the extinct springbok, has values at the browsing end of the spectrum ($\delta^{13}C$ value of -12.83$^{0}/_{00}$ ± 1.61 n=4) with one outlier at -4.5$^{0}/_{00}$. These values confirm results obtained earlier for a single *A. recki* and two *A. australis* specimens from Swartkrans (Lee-Thorp *et al* 1994). The isotopic results show them to have been browsers, a result which conflicts with a view that Antilopines were mixed feeders (or grazers in the case of *A. bondi*) and inhabited open, grassy environments. These animals would have needed significant tree and shrub cover in order to obtain enough browse to show such consistently negative carbon isotope values.

A. recki, with a $\delta^{18}O$ mean of -4.09 $^{0}/_{00}$ ± 2.86, has a relatively low, depleted value in comparison to other herbivores from this member. The reason is not entirely clear since elsewhere browsers have usually been identified with more positive $\delta^{18}O$, but one explanation could be related to a dependence on foliage (browse) in shaded habitats.

Specimen UCT # 7900 has an anomalously negative $\delta^{13}C$ value (-16.5 $^{0}/_{00}$) and equally negative $\delta^{18}O$ value (-10.7 $^{0}/_{00}$). From experience in the UCT Archaeometry laboratory, this low value has been attributed to likely inclusion of glue into the sample. We have previously noted that traces of glue may cause anomalously low $\delta^{13}C$ and $\delta^{18}O$ values. Although every attempt was made to remove glue from samples physically, it seems that some remained in some cases. Hence the results from this sample and all the other samples marked (‡) on Tables 6.1, 6.2 and 6.3 were therefore discarded, due to suspected glue contamination.

Of the 3 other specimens attributed to the family Antilopini, but not to species level, 2 have negative values at the browsing end of the spectrum ($\delta^{13}C$ -13.3$^{0}/_{00}$ and -12.0$^{0}/_{00}$), while the third, attributed to a large Antilopini (possibly the large *Gazella granti*, as is currently found in Eastern Africa), has a $\delta^{13}C$ of -1.9$^{0}/_{00}$, on the grazing end. The δ^{18}O value for the first group is slightly more enriched (-$3.5^{0}/_{00}$) than the second Large Antilopini (-$4.1^{0}/_{00}$).

Tragelaphus strepsiceros, the kudu, had δ^{13}C values of -$8.97^{0}/_{00}$ ± 0.84 (n=3) with one outlier at -$4.7^{0}/_{00}$, values are similar to those found by van der Merwe and Thackeray (1997). Although this species has been shown to be predominantly a browser, it is known to be opportunistic at times; this might account for the rather more positive values than obtained for other browsers in the assemblage. Another possibility for the very positive specimen is that it was misidentified. Tragelaphines at Olduvai Gorge (dated to around 1.8 million years ago) have also been found to have mixed feeder values (N. van der Merwe pers. comm.). The results presented here strongly suggest that these values cannot be regarded as "typical" for browsers.

The δ^{18}O values for all herbivorous fauna range from $0.27^{0}/_{00}$ to -$7.12^{0}/_{00}$, a difference of almost $7^{0}/_{00}$. This result tends to confirm earlier findings (Sponheimer and Lee-Thorp 2001) that animals in the same assemblage may have different δ^{18}O values.

C_4 consumers

Antidorcas bondi, another extinct springbok, is one of the grazing fauna at -1.2 $^{0}/_{00}$ (n=1) for δ^{13}C. This animal is found in abundance at Swartkrans Member 2, where similar grazing values were found for this species (Lee-Thorp *et al* 2000). The δ^{18}O value for this specimen is $0.3^{0}/_{00}$. This value is more enriched than the values for the browsing springbok, which has a mean of -$4.1^{0}/_{00}$, however it is not possible to attach too much significance to a result from one individual.

Connochaetes cf. taurinus, the blue wildebeest, has a mean δ^{13}C value of -1.27 $^{0}/_{00}$ (n=2), indicating a C_4 grass dominated diet, and a mean δ^{18}O value of -$0.9^{0}/_{00}$. The third *Connochaetes* specimen, which has not been identified down to species level, has a δ^{13}C value of -$4.9^{0}/_{00}$, which suggest a mixed feeder such as

Connochaetes gnou, the black wildebeest and a $\delta^{18}O$ value of -7.1$^{0}/_{00}$. This value is significantly more depleted than the other two.

$\delta^{13}C$ values for the *Damaliscus* sp. or "*Damaliscus* or *Parmularis*" specimens also divided into two distinct groups, at 0.46$^{0}/_{00}$ ± 1.88 (n=6), and -6.41$^{0}/_{00}$ ± 0.84 (n=3) respectively. The former group were grazers while the latter were mixed feeders. The differences might be attributed to species differences. It is possible that what is observed is a grouping of these specimens into *Damaliscus* and *Parmularis*. The same bimodal distribution is seen at Kromdraai (Catherine Smith, unpublished Ph.D. results). The $\delta^{18}O$ mean of the two groups is very similar at -2.19 $^{0}/_{00}$ ± 0.78 for the former, and -2.94$^{0}/_{00}$ ± 0.84 for the latter.

Hippotragus equinus, the roan antelope, also falls at the grazing end of the spectrum, (mean $\delta^{13}C$ value of -1.06 $^{0}/_{00}$ (n=2)). Analyses of modern bone apatite from Ethosa of *H. equinus* in the UCT Archaeometry laboratory have also found this species to be grazers, with $\delta^{13}C$ values of between 0.0 and -2.0 (Lee-Thorp pers. comm.). The $\delta^{18}O$ mean for the two Sterkfontein fossil specimens is -2.29 $^{0}/_{00}$.

The single *Redunca arundinum* (common reedbuck) specimen has a $\delta^{13}C$ value of -1.3$^{0}/_{00}$, consistent with observations of modern specimens. Today, the main ecological constraint for this species is proximity to water, and as with other Reduncini today, it has a preference for the grasses of edaphic grasslands or wetlands (Sponheimer *et al* 1999). The $\delta^{18}O$ value is 1.1$^{0}/_{00}$, a higher value than would be expected for an animal that spends much time near water.

Mixed feeders

Some $\delta^{13}C$ values of *Damaliscus* sp. and *Hippotragus gigas* specimens that grouped with some values indicating mixed feeding have already been mentioned. *Makapania broomi* has a mean $\delta^{13}C$ value of -6.57$^{0}/_{00}$ ± 2.39 (n=4)). These show that it was a mixed feeder, although this species has been used as an indication of a wooded environment in the past (Kuman and Clarke 2000). An outlier at $-10.8^{0}/_{00}$ indicates that this particular specimen included much more C_3 plants than any of the others. The $\delta^{18}O$ mean for *M. broomi* is $-2.37^{0}/_{00} \pm 0.69^{0}/_{00}$.

Tragelaphus sp. aff. angasi (n=1) $\delta^{13}C = -4.8^{0}/_{00}$, was a mixed feeder, but lent towards the more positive C_4 end of the spectrum, indicating a higher C_4 percentage into its diet. This species has one of the lowest $\delta^{18}O$ values ($-4.8^{0}/_{00}$). If this value can be considered representative as it is difficult to interpret only one result, it could be suggestive of behaviour of an animal which remains close to a water source and/or shade, possibly like the behaviour of waterbuck today (Sponheimer and Lee-Thorp 2000).

Primates

The $\delta^{13}C$ values for the Member 4 primates all lie between $-5.0^{0}/_{00}$ and $-12.9^{0}/_{00}$ with an overall mean of $-9.00^{0}/_{00}$. Overall, a combination of C_3 and C_4 food was being consumed, but the proportion varies.

Cercopithecoides williamsi, an extinct colobus monkey, has two groupings of $\delta^{13}C$ values. One of these averages ($-12\ 23^{0}/_{00} \pm 0.63$ (n=3)) while the other has a mean of $-4.85\ ^{0}/_{00}$ (n=2). This indicates that the latter group included a significant amount of C_4 food into the diet (~60%) while the former did not. This bimodal distribution of the *C. williamsi* values could be again indicative of misidentification, as according to isotopic results, this species has been believed to have eaten a C_3 diet up. Whether or not any of these specimens have been mis-identified, the isotope results underscore the danger of assuming dietary preferences and habitat requirements for extinct taxa. The $\delta^{18}O$ mean for *C. williamsi* is $0.37^{0}/_{00} \pm 1.90^{0}/_{00}$.

Mean $\delta^{13}C$ values for *Parapapio broomi* are $-7.11^{0}/_{00} \pm 1.20$ (n=4) with one outlier at $-12.2\ ^{0}/_{00}$ (a similar region as the first group of *C. williamsi). Parapapio jonesi* has a mean of $-8.54^{0}/_{00}$ (n=2). These means show a difference of $1.43^{0}/_{00}$. It has been considered that these species might be part of the same species, with size differences being attributed to sex differentiation (F. Thackeray pers. comm.). Bearing this problem in mind, the teeth were measured. These results (Table 6.5 and Figure 6.4) show clearly that *P. jonesi* is smaller in both length and width to *P. broomi*. As male and female animals of the same species are not likely to eat different things, this 1.4 $^0/_{00}$ difference in $\delta^{13}C$ shows that it is not likely these are male and female specimens of the same species. However, it is not enough evidence to discount one species, as these groups might relate to small (young) and larger (older) specimens of the same species.

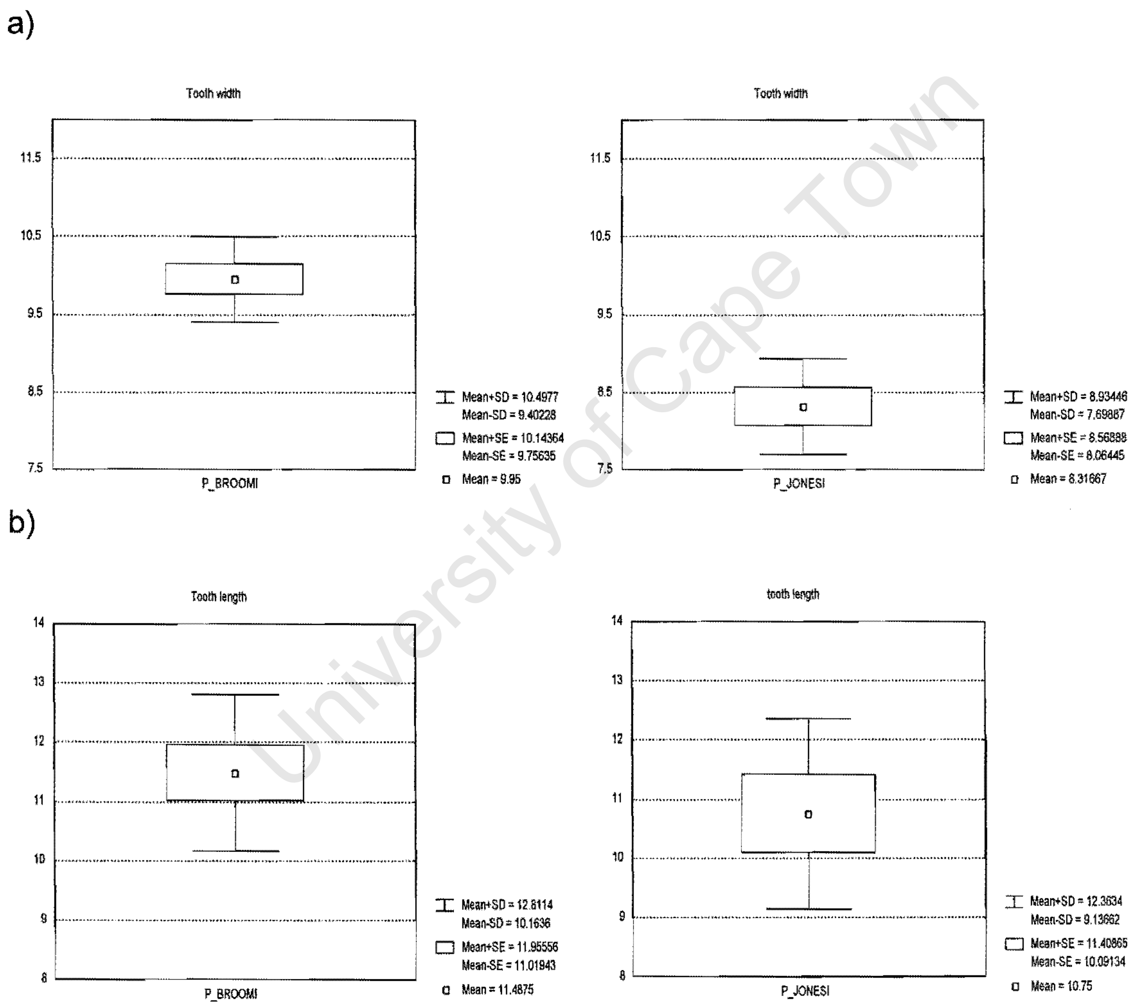


Figure 6.4

Comparison of for Parapapio broomi and Parapapio jonesi from Sterkfontein Member 4

a) meso-distal dimension (width in millimeters)

b) bucco-lingual dimension (length in millimeters)

The δ^{18}O means for these two species are very similar. δ^{18}O mean for *P. jonesi* is -1.57 $^{0}/_{00}$ (n=2) and the mean for *P. broomi* is -1.92 $^{0}/_{00}$ ± 1.40$^{0}/_{00}$ (n=4).

Parapapio whitei has a δ^{13}C mean of -11.58 $^{0}/_{00}$ (n=2) with a third value at -7.8$^{0}/_{00}$. As the specimens with the depleted δ^{13}C values have unreliable oxygen values for the reasons stated above, it is only the third, more positive value that can be reported here, +0.8$^{0}/_{00}$.

Many of the oxygen values for the primates gave very depleted (lower than -9$^{0}/_{00}$), perhaps indicating the contamination of glue. The satisfactory oxygen results all lie between 0.32 $^{0}/_{00}$ and -2.91 $^{0}/_{00}$. The overall mean δ^{18}O value for all the Member 4 primates is -0.66$^{0}/_{00}$. This relatively positive value is somewhat surprising given that elsewhere primates have been shown to be depleted compared with most of the fauna (Sponheimer and Lee-Thorp 2000). This observation has been ascribed to one or a number of factors including inclusion of fruit and fruitwater, frequent drinking, and/or shady habitats. *P. broomi* has the lowest δ^{18}O value of the primates (-1.92 $^{0}/_{00}$ ± 1.40 (n=3)),.

Carnivores

Chasmoporthetes nitidula, a hunting hyaenid, is an intermediate feeder with a δ^{13}C mean of -6.35 $^{0}/_{00}$ ± 2.33 (n=4). *Chasmoporthetes silderbergi* has a mean close to that of *C. nitidula* (δ^{13}C value of -6.41 $^{0}/_{00}$ (n=2)). UCT # 7984 is another sample that is thought to have been contaminated by glue, and the result has been discarded.

Two *Crocuta crocuta* (spotted hyaena) values, are almost 6$^{0}/_{00}$ apart (-9.3$^{0}/_{00}$ and -3.2$^{0}/_{00}$). These two individuals must have been eating very different food sources.

Dinofelis barlowi, the false sabre-toothed cat, has a δ^{13}C mean of -6.37 $^{0}/_{00}$ (n=2), while *Homotherium latidens*, the sabre-toothed cat, has a mean of -8.20 $^{0}/_{00}$ ± 0.51 (n=3), almost 2$^{0}/_{00}$ more negative. This would perhaps indicate that it included more C_3 feeding fauna in its diet. The mean δ^{18}O value of *D. barlowi* is

-3.52$^0/_{00}$ ± 0.23, while that for *H. latidens* has a wider range with a mean of -1.41$^0/_{00}$ ± 2.2.

Unfortunately there is only one δ^{13}C result for each of the following: *Hyaena brunnea* (-6.2$^0/_{00}$); *Pachycrocuta breviostris* (-5.7$^0/_{00}$); *Panthera leo* (-7.0$^0/_{00}$). These indicate that these carnivores were also obtaining a mixture of isotopic signatures from both C_3 and C_4 consuming fauna. The δ^{18}O values of *H. brunnea* and *P. breviostris* are -4.0$^0/_{00}$ and -3.9$^0/_{00}$, respectively, while that for *P. leo* is more enriched with a value of -0.8$^0/_{00}$.

The means of δ^{18}O values of all carnivores are -2.28$^0/_{00}$ ± 1.88. *Chasporthetes nitidula* has the most enriched δ^{18}O mean of all (-0.63 $^0/_{00}$ ± 0.97). *H. latidens* has a mean of -1.41$^0/_{00}$ ± 2.20 (n=3).

The now familiar δ^{18}O distinctions between herbivores, primates and carnivores do not seem to hold except in a few cases. This may be an indication that parts of the assemblage were deposited under different climatic conditions.

δ^{13}C and δ^{18}O results for Member 5 faunal specimens:

C_3 consumers

The δ^{13}C value for *Antidorcas recki* are low and fall towards the browsing end of the spectrum (mean δ^{13}C -11.74 $^0/_{00}$ (n=2)). In common with a general small shift to positive values, these values are slightly more positive than those are for *A. recki* in Member 4. *Antilopini cf. antidorcas* has a mean δ^{13}C value of -8.72$^0/_{00}$ ± 1.18 (n=3)) excluding the outlier of 0.7$^0/_{00}$, again, more positive than the *A. recki* in Member 4. Since these specimens are not identified to species, however, the likely cause is not clear.

Mean δ^{13}C for *Tragelaphus cf. taurotragus* is -9.41 $^0/_{00}$ (n=2). This result is in keeping with modern observations about eland, which are thought to opportunistic browsers, occupying a wide range of habitats from forests to open woodland (Sponheimer *et al* 1999). The δ^{18}O mean for this species is -0.75 $^{0}/_{00}$ ±1.02$^{0}/_{00}$.

C_4 consumers and Mixed feeders

Hippotragus sp. aff. gigas divided into two groups in Member 4, one exclusively grazing, the other as a mixed feeder. The single specimen of *H. sp. aff. gigas* in Member 5 has a δ^{13}C value of -5.25$^{0}/_{00}$, clearly a mixed feeder.

Damaliscus and what has been identified as Small Alcelaphini cf. *Damaliscus* again group into two as seen in Member 4. One group with a mean δ^{13}C of -0.66 $^{0}/_{00}$ ± 1.22 (n=9), while the other has a δ^{13}C mean of -4.01$^{0}/_{00}$ ± 1.07(n=3). This latter value for the group of mixed feeders is again more enriched than the mixed feeding group in Member 4.

The δ^{18}O values for fauna in Member 5 is in general more depleted than that of Member 4. The second lowest mean is for all the *Damaliscus* sp. with -3.39$^{0}/_{00}$. Groups that separate on the basis of δ^{13}C are not separated by the δ^{18}O values, so the oxygen isotope values do not help to produce any further distinguishing features.

'Large Alcelaphini' (identified by T. Pickering) also group bimodally; one group (δ^{13}C value of 1.14 $^{0}/_{00}$ ±1.36 (n=4)) were clearly grazers, while the other were mixed feeders (δ^{13}C value of -5.27 $^{0}/_{00}$ ± 1.88 (n=5)). The Large Alcelaphini identified here as grazers have very similar δ^{13}C values to those identified as *Connochaetes* sp. (δ^{13}C value of 0.22 $^{0}/_{00}$ ± 1.92 (n=4)). The grazing grouping may belong to *Connochaetes taurinus*, which is known as a predictable grazer, while the more negative group of Large Alcelephini might possible be assigned to *Connochates gnou*, which browses occasionally.

Finally, the Equids results fall towards the grazing spectrum as expected. Those that have been identified to species level have a δ^{13}C mean of -3.82 $^{0}/_{00}$ ± 0.83 (n=5). Those have only been identified as Equidae have a δ^{13}C mean of -1.73 $^{0}/_{00}$ ± 1.72 (n=7), almost 2$^{0}/_{00}$ more positive. The specimens that have been identified to species level (i.e. those with the more depleted values) were originally labeled as Member 4. However, since the refining of the stratigraphy at Sterkfontein, Kuman and Clarke (2000) have argued that there should be no Equids in Member 4. Equids are only known in Southern Africa from 2 million years ago (K. Reed pers. comm.).

Elsewhere, others have observed slightly more negative $\delta^{13}C$ values for equids, compared to other grazers (Thackeray and Lee-Thorp 1992; Cerling *et al* 1997b). It's not certain whether this is related to dietary preferences or metabolism. In new feeding experiments, Sponheimer (pers. comm.) observed up to 2 $^{0}/_{00}$ lower values for equids compared to bovids on the same diet. This however, does not account for the almost 4 per mil differences observed for the identified equids with disputed provenience from Sterkfontein. There is clearly a significant difference *Equus capensis* and those specimens identified merely as 'Equid'. The Equid species seem to have been fairly reliable grazers as shown by values of -1.73$^{0}/_{00}$. Elsewhere, in Equus Cave, *E. capensis* and *E. burchelli* have very similar carbon isotope values (Lee-Thorp and Beaumont, 1995), therefore an explanation that proposes more opportunistic behaviour for *E. capensis* seems unlikely. Another, more likely, explanation is that the depleted *Equus capensis* values, originally assigned to Member 4, *are* in fact from Member 4 after all. That would conform to the shift that has been noted in most of the other fauna i.e. from more negative in Member 4 (-3.82$^{0}/_{00}$) to more positive in Member 5 (1.73$^{0}/_{00}$). An important implication is that Equids occur in Southern Africa a little earlier than currently thought, or alternatively, that Member 4 includes deposits that are not as old as they are currently thought. Deposits associated with Member 4 may span a considerable period of time and may not be confined to a time *circa* 2.6 Ma.

The $\delta^{18}O$ mean for the *E. capensis* specimens is -3.65 $^{0}/_{00}$ ± 1.82 (n=5). This low, depleted $\delta^{18}O$ value for these specimens shifts to a more enriched value for those marked Equidae (-1.97$^{0}/_{00}$ ± 1.48$^{0}/_{00}$ n=7) definitely assigned to Member 5.

Member 5 Oldowan infill (East) compared to Member 5 West:

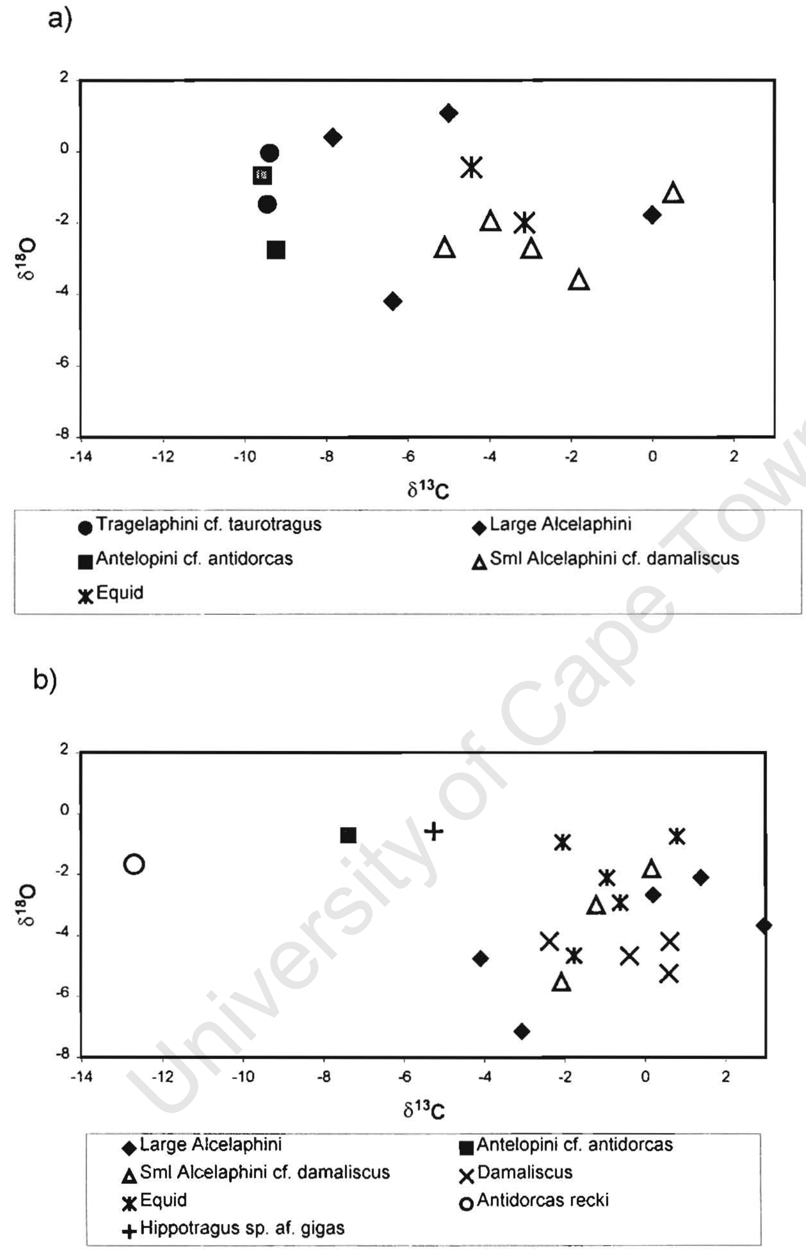


Figure 6.5

Sterkfontein Member 5 Ungulates $\delta^{13}C$ and $\delta^{18}O$ results

a) Member 5 East (Oldowan infill)

b) Member 5 West

One further important observation arises from the isotope data for Member 5, that is, there is a difference in overall $\delta^{13}C$ mean between the 'Oldowan', or East infill, and the West infill (figure 6.5). (These observations are based on those specimens that could be placed into either infill with certainty). The older Oldowan infill shows a mean $\delta^{13}C$ of -5.18$^{0}/_{00}$, while for Member 5 West it is -2.14$^{0}/_{00}$. Although the Member 5 West browser average is lower (-11.74$^{0}/_{00}$) than the Member 5 East browser mean (-9.40$^{0}/_{00}$), there are only two browsers in the West assemblage contributing to this (apparently) low mean. The grazer mean for Member 5 West is -0.41$^{0}/_{00}$, while the Member 5 East grazer mean is -1.90$^{0}/_{00}$, slightly more depleted.

This could explain some of the bimodal distributions in certain fauna. One is *Damaliscus* sp. It has been shown here that the two groupings of isotopic results for this species could be a result of deposits of different ages and therefore different environmental conditions. The implications of the different results for these infills will be discussed in Chapter 7.

Primates

The primates of member 5 have unfortunately only been identified to family level, Cercepithecoides indet. In addition, due to problems with the contamination by glue, low voltages and small sample sizes, only 4 samples of the 10 originally analysed can be reported here and included in the discussion. Judging from the Member 4 groupings of primates, it is possible that UCT # 8043 (with a $\delta^{13}C$ value of -7.6$^{0}/_{00}$) could be assigned with the *Cercopithecoides* genus, while the other 3 values with a mean of -1.99 $^{0}/_{00}$ ± 1.02 belong to the *Parapapio* genus.

The Member 5 primate $\delta^{18}O$ mean is -3.19 $^{0}/_{00}$ ± 1.34, almost 2$^{0}/_{00}$ more depleted than the mean primate value of Member 4. This result is more depleted than that found for the Member 5 ungulates (-1.09$^{0}/_{00}$). This is an expected pattern, as similar distinctions between ungulates and primates have been noted elsewhere (Kohn 1996; Sponheimer and Lee-Thorp 1999) but why the pattern should hold for Member 5 and not for Member 4 is not clear.

Carnivores

The *Chasmoporthetes nitidula* specimen (UCT # 7963) was marked Member 5, but according to Turner (Turner 1997) there are no more listings for *C. nitidula* in Member 5. This sample is reported here in Member 5, but could be re-assigned to Member 4 in line with Turner (1997). It has $\delta^{13}C$ value of $-4.9^{0}/_{00}$ and a $\delta^{18}O$ of $-4.4^{0}/_{00}$.

Panthera leo, the lion, has an overall $\delta^{13}C$ mean value of $-5.22^{0}/_{00} \pm 2.5$ (n=5), more positive than in member 4, in keeping with the general trend for the other fauna. The results do seem to be bimodal as also seen in other faunas. One mean is $-3.43^{0}/_{00} \pm 0.78^{0}/_{00}$ and the other is $-7.90^{0}/_{00} \pm 0.09^{0}/_{00}$. This would indicate that at least some of the lions were eating more C_4 prey, and others less, during Member 5 times. *P. leo* (n=4) has a $\delta^{18}O$ value of $-3.69^{0}/_{00}$, a value in keeping with lower values for carnivores (Sponheimer and Lee-Thorp 2000).

The $\delta^{13}C$ value of *Parahyaeyna brunnea* ($-2.3^{0}/_{00}$) is somewhat enriched in comparison to that of *Hyaena brunnea* of member 4. *Pachycrocuta breviostris* is the most depleted in $\delta^{13}C$ of all the Member 5 carnivores at $-9.8^{0}/_{00}$, indicating the inclusion of mostly C_3 consumers into its diet. The single *P. breviostris* $\delta^{18}O$ value is $-5.9^{0}/_{00}$.

Breccia results

These results are shown in Table 6.6 and displayed graphically in figure 6.6. In many cases the enamel samples taken along with breccia samples had to be discarded due to low Voltages. Those enamel samples with asterixes (*) are not discussed further. The remaining results can be used show no correlation between breccia and enamel. Although diagenesis is not completely discounted, these results make it less likely because there has been no significant exchange, enough to alter predicted $\delta^{13}C$ values, between enamel and breccia.

There is, however, a significant shift ($p=0.00015$; t-test) in the isotopic value of the breccia from Member 4 to Member 5 with no values overlapping. The $\delta^{13}C$ mean for member 4 is $-3.40^0/_{00} \pm 1.30$ (n=8) and that of Member 5 is $-0.29^0/_{00} \pm 1.35$ (n=10). The $\delta^{18}O$ mean for Members 4 and 5 are not significantly different (Member 4 mean $=-3.58^0/_{00}$; Member 5 mean $= -3.58^0/_{00}$). This is potentially a useful finding for assigning specimens with disputed proveniences into different Members, as will be discussed in the following chapter.

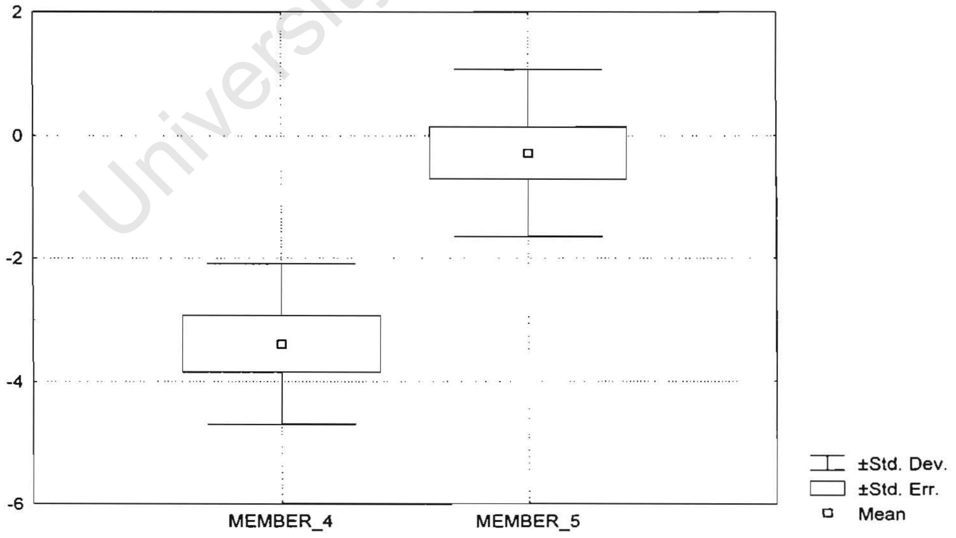


Figure 6.6

Sterkfontein breccia $\delta^{13}C$ results, indicating Member 4 and Member 5 results

Serial sampling of teeth

Three *Damaliscus* sp. teeth were sampled from root to tip to determine intra-individual variation of $\delta^{13}C$. These results can be seen in table 6.7 and displayed graphically in figure 6.7. One (1) is always closest to the root (i.e. later development) and the highest number is the highest sample on the tooth toward the crown (i.e. early in the lifetime of the animal).

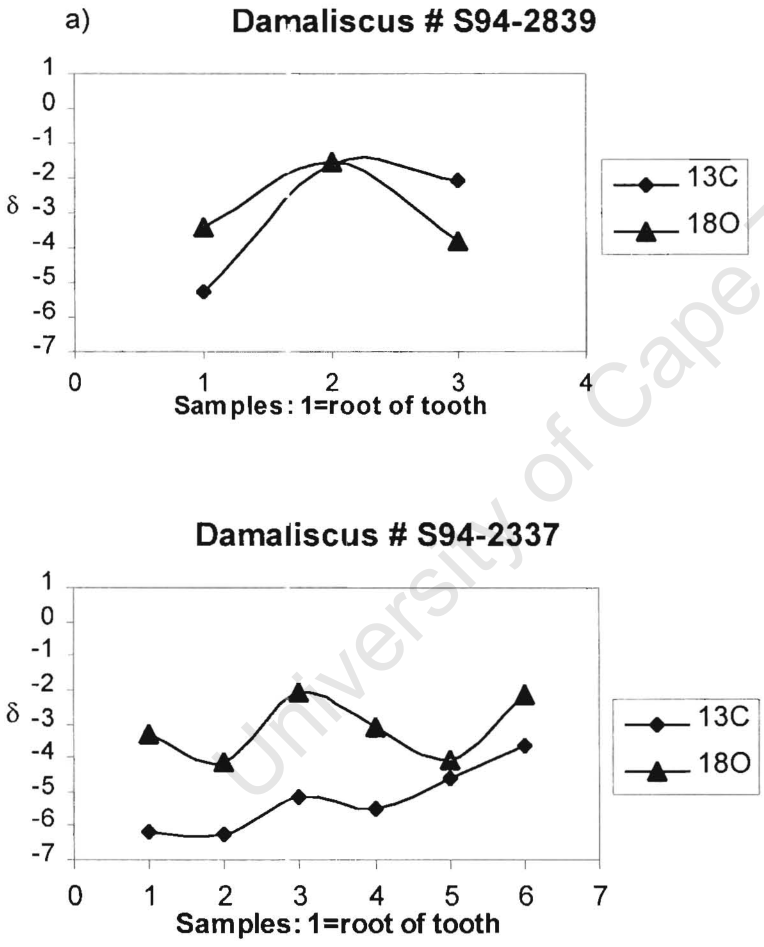


Figure 6.7

Sampling along tooth rows of Damaliscus with sample #1 being closest to the root

a) S94-2839

b) S94-2337

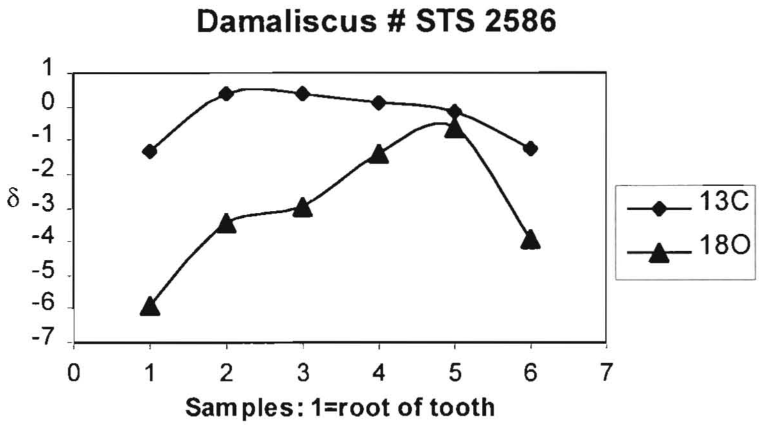


Figure 6.7

Sampling along tooth rows of Damaliscus with sample #1 being closest to the root

c) STS 2586

For specimen number S94-2839 the intra-individual variation is quite high for $\delta^{13}C$, ranging from $-5.2^{0}/_{00}$ to $-1.6^{0}/_{00}$, the range is lower for specimen number S94-2337. The values decrease towards the crown of the root, showing that during the early stages of this animal's life it had a more enriched $\delta^{13}C$ value ($-3.6^{0}/_{00}$). The last sample (specimen number STS 2586) shows an enrichment of $\delta^{13}C$ during the middle stages of the tooth development.

This means that at least in 2 out of 3 cases, intra-individual variation as observed from the period of growth represented by 1 tooth (perhaps one year), is not very high for carbon. The sampling technique used in this study extracted enamel from a small area of the tooth, but these results suggest that this approach is not likely to bias isotopic results too far, if one also takes into account that teeth were chosen virtually at random (therefore representing different developmental stages).

C_3/C_4 index

Now that we have a clearer idea of which species were browsers, grazers or mixed feeders, based on their $\delta^{13}C$ values, we can develop this information further to establish the percentages of these faunas in the assemblage.

As outlined earlier, Sponheimer and Lee-Thorp (in press b) developed a C_3/C_4 'index' for the Makapansgat Member 3 fauna, by assigning bovid species to the C_3, or C_4 diets based on the mean $\delta^{13}C$ for each taxon, whereupon a percentage was calculated for the C_3 and C_4 categories.

Unfortunately, due to the nature of the identification of the faunal assemblage, it was not possible to calculate a C_3/C_4 index in the same manner for Sterkfontein. There were two problems.

1) In both the Sterkfontein Member 4 and 5, fauna that had been identified as one species showed distinct bimodality in isotope values, showing that the two groups had different dietary preferences and suggesting that two species were likely involved.

2) Another problem was that some taxa were identified only to family or sub-family, and again distinct isotopic clusters indicated groups with different dietary preferences.

The C_3/C_4 'index' was therefore calculated using individual specimen $\delta^{13}C$ values, and not on the basis of species means as was done earlier by Sponheimer (Sponheimer and Lee-Thorp in press b). This percentage of "open habitat" forms was calculated by counting the number of specimens that showed enriched values at the grazing (C_4) end of the spectrum (all values more positive than -3.99/$_{00}$ were included[1]), and as a percentage of the total number of herbivores analysed. The procedure was repeated for Member 4 and 5. The calculations and all Sterkfontein fauna included in this calculation are given in Table 6.8.

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[1] The author understands this value is rather generous for grazers, but was chosen and applied to all assemblages and therefore does not affect the comparisons

In order to produce an environmental comparison across the entire chronological sequence represented by deposits in all the sites, similar calculations were made for Swartkrans, and the existing C_3/C_4 index for Makapansgat was adapted to the method used in this study (although very similar results were obtained using the two different methods). The Swartkrans data presented another problem; as mentioned earlier existing isotopic data for herbivores were collected for the purposes of obtaining the C_3 and C_4 'endpoints', and not to assess the spread of herbivore diets. Therefore there will have been some bias in the numbers of grazers vs. browsers. The "openness" of the Swartkrans landscape may therefore be seriously underestimated due to the under-sampling of grazers. Nevertheless an index calculated from existing Swartkrans data has been included in Table 6.9 which shows the final percentages as they appear on Figure 6.8.

This method allows one to count the animals that were feeding on browse those feeding on grass, and those with mixed diets, without making prior assumptions about diets of fossil fauna based on their taxonomy. Since the C_4 signatures are of necessity associated with open grassy habitats, this enabled the calculation of percentages of "open" landscape indicators against the total. For Sterkfontein Member 4 the percentage is 37%, and for Member 5 the percentage is 65%.

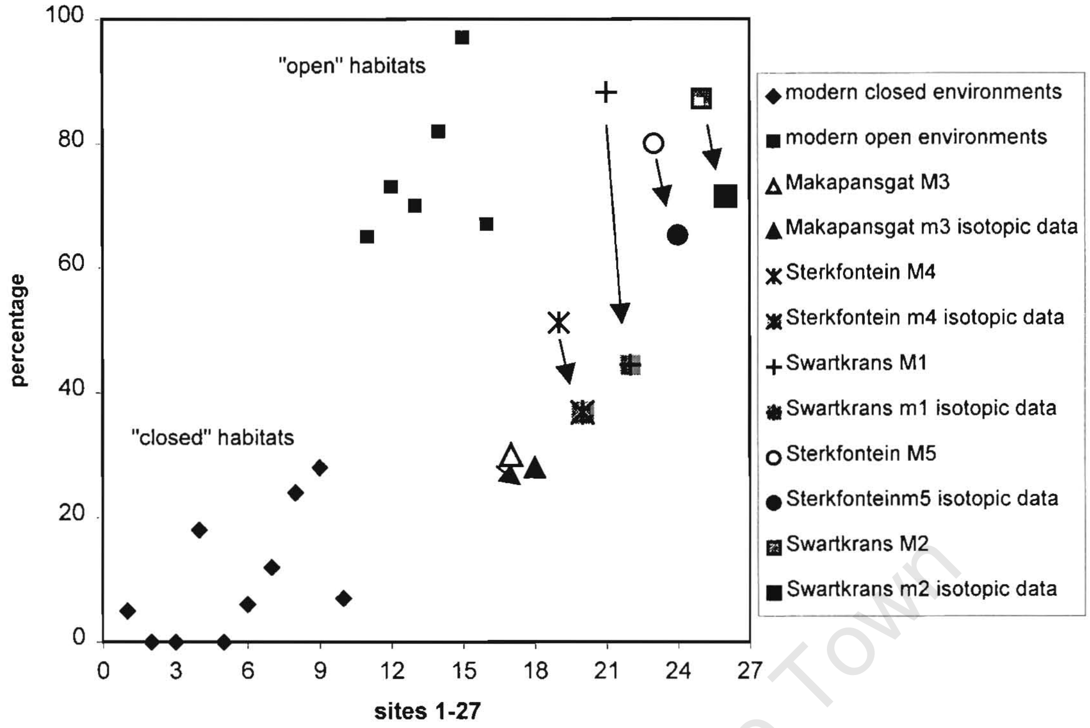

Figure 6.8

A combination plot where the C_4 open habitat index calculated from $\delta^{13}C$ results in this study for Sterkfontein Members 4 and 5, and from earlier studies of Makapansgat and Swartkrans are superimposed on the original 'open habitat' indicator diagram established by Vrba (1975; 1980). (M=Member)

Two observations can be made from Fig 6.8. Firstly, $\delta^{13}C$-based indices suggest a time-transgressive progression from earlier, more closed environments, to later, more open environments similar to the trend noted originally by Vrba (1975, 1980). The isotope-based results, however, indicate that almost all of these environments were rather more wooded, and less open, than previously estimated. For Sterkfontein Member 4 the isotopic results indicate that 37% of the fauna in the assemblage are indicative of an open environment, while the original estimate based on proportions of fauna was 51% (Vrba 1980). For Member 5 isotopic results show that 65% of the fauna indicate an open environment, while the earlier estimate (of proportions of fauna) was 80% (Vrba 1975). If one revises this estimate to include the separation between the Oldowan and West infills, the index gives 40% and 77%, respectively. This will be discussed further in the next chapter.

The results for both Swartkrans Member 1 and 2 indicate a much more wooded environment than expected. These results, however, are likely to be biased due to the unrepresentative lack of grazing fauna in the results given by Lee-Thorp *et al* (1994; 2000).

The differences observed in this study compared to the earlier study by Vrba (1975; 1980) can be largely ascribed to reassignment of the diets of certain key taxa. Diets of some fossil antilopines have been shown to be almost entirely C_3 dependent, rather than mixed feeders, suggesting preference for wooded, more closed habitats. Since these were key elements used as 'open' indicator taxa in the original calculations (Vrba 1975, 1980), it is not surprising that reassignment has shifted the entire environmental spectrum away from very open towards more wooded habitats.

Summary

$\delta^{13}C$ analyses of fossil taxa provide the means for dietary assignments independent of assumptions about behaviour based on that of their modern relatives. The results show that in the case of most herbivore species, diets of extinct species have been correctly assigned. In certain cases, however they were not. Reassignment of these species as browsers, and not mixed feeders, has important implications for the indication of <u>how</u> wooded or open an area was. The isotope data can be used to calculate new indices of the percentages of 'open' versus 'closed' taxa. The revised index suggests that the degree and trend towards 'open, arid' habitats in the South African Plio-Pleistocene may have been over-estimated. The implications of these observations are discussed in the following chapter.

CHAPTER 7: DISCUSSION

The results of this study have resolved several problems. We now know more about the dietary ecology of extinct species from their $\delta^{13}C$ values. Some extinct bovid species formerly considered to be mixed feeders, such as *Antidorcas recki*, have been shown to be consistent browsers. The results affect the proportions of the assemblage assigned as C_3 or C_4 feeders, and hence affect interpretations of the open or closed nature of the environments. In general the extent of wooded elements has been underestimated. $\delta^{13}C$ trends for carnivores and primates lend support to this revised environmental reconstruction. $\delta^{18}O$ values for the Sterkfontein assemblages are more difficult to interpret and their complexity may reflect multiple deposition episodes.

Diet and ecology of Sterkfontein Member 4 and 5 fauna

$\delta^{13}C$ values of faunal tooth enamel provide data about food types ingested by different fauna due to the retention of these dietary signals in their body tissues. Herbivore and carnivore $\delta^{13}C$ values reflect different aspects of the environment. The mean $\delta^{13}C$ for browsers in Member 4 is -11.26 $^0/_{00}$ and -9.78$^0/_{00}$ in Member 5, almost 1.5$^0/_{00}$ more depleted in Member 4 than in Member 5. This may indicate that browsers were forced to become more opportunistic, or more likely, that conditions became drier and/or warmer by Member 5 times. C_3 plants have been known to respond by a + 1.5-3$^0/_{00}$ shift in $\delta^{13}C$ values in response to aridity (Ehleringer and Cooper 1988), which might have been what happened in this case.

The Antilopini fauna that show low $\delta^{13}C$, indicating browsing diets, are more depleted during Member 4 times, consistent with the scenario for a wetter environment at around 2.6 Ma. The browsing Antilopini fauna in Member 5 have slightly more enriched values, consistent with a drying out and opening up of landscapes at that time (1.7 Ma).

Several species or groupings had two distinct groups of isotope signals. These include *Hippotragus gigas* which has two groups showing slightly different isotopic signals in Member 4; one group mainly browsing and one being mixed feeders. This bimodal distribution may reflect the conflation of two species, i.e. that one group has been mis-identified as *H. gigas*.

Both those species identified as Small and Large Alcelaphines show a bimodal distribution with one more negative set of values (indicating mixed feeding) and one more enriched in ^{13}C, indicating more inclusion of C_4 plants. This observation might also be related to misidentifications, as such a high percentage of browse in the diet has not been noted elsewhere in other isotopic studies for Alcelaphines (Lee-Thorp *et al* 1994; Sponheimer and Lee-Thorp 1999a; Lee-Thorp 2000; van der Merwe *et al* in prep.).

One other possible explanation is that C_3 grass was present in the environment for habitual grazers such as Alcelaphines to subsist on. This could have occurred for the following reasons:

1. The temperature during the growing season i.e. the summer rainfall season would have been lower at that time.
2. Or some rain fell during the colder winter months.

The latter reason is unlikely as the summer rainfall season scheme is known to have been in place for some time and not likely to have shifted during this period of deposition. Also, if C_3 grass did exist, one would then expect fauna such a *Connochaetes* sp. also to show a similar depletion in $\delta^{13}C$ values, if this much C_3 grass was available. This is however not the case. The values for *Connochaetes* are enriched with mean of $-1.3/_{00}$ in Member 4 and $0.22^{0}/_{00}$ in Member 5.

It is thought that the Equidae family is only found in Member 5, and not in Member 4 (Kuman and Clarke 2000). This occurrence has been used as an indication of a more arid environment during this time.

The samples of *Equus capensis* analysed in this study were identified as coming from Member 4 in the original excavations. If the provenience is correct, and these specimens are in fact from Member 4, the average $\delta^{13}C$ values *for E. capensis* also show a shift from slightly more negative (mean $\delta^{13}C = -3.85^0/_{00}$) in Member 4 to slightly more enriched (mean $-1.73^0/_{00}$) for the Equidae in Member 5. This indicates the same shift as observed by the isotopic values of other fauna. If both the Equus capensis specimens and those identified as Equidae do in fact come from Member 5, it would imply two sets of Equids having slightly different dietary requirements.

Two different sets of conditions are clearly represented by the division of the results for Member 5 fauna into the older Oldowan (East) infill dated to between 2.0 - 1.7 and the West infill. The Oldowan infill results as a whole are more negative (mean $\delta^{13}C$ $-5.18^0/_{00} \pm 3.39^0/_{00}$ for all herbivores), while the fauna in the West infill have more enriched values (mean $-2.14^0/_{00}$ $\pm 3.88^0/_{00}$ for all herbivores). This significant distinction implies a far more open, grassy environment for the period represented by the West infill, that of the Oldowan infill, as well as a difference in timing. There are more browsers during the Oldowan infill, indicating that more C_3 vegetation was available for consumption.

The differing conditions represented by these two infills might also help to explain some of the bimodal distributions that are seen in the isotopic values of a few Member 5 species. Those specimens identified as Large Alcelaphini in the Oldowan infill have a mean $\delta^{13}C$ of $-4.40^0/_{00}$, while the West infill set has a mean of $-0.52^0/_{00}$. These more depleted Oldowan infill values could indicate that one group of Large Alcelaphines is eating more C_3, and are mixed feeders, while the other group indicates a time later when they are grazers. However, a difference of close to $4^0/_{00}$ is rather a large isotopic difference for the same species even at different times. This might therefore be further evidence that mis-identifications might be the cause of these bimodal distributions.

A similar pattern, although less clear-cut, is seen for the *Damaliscus* sp. and Small Alcelaphini cf. *damaliscus* specimens. The West infill consists of all those specimens that indicate mainly C_4 foods, while the Oldowan has the more depleted values (indicating an inclusion of C_3 plants).

The primate $\delta^{13}C$ values also show a similar overall shift to more C_4 foods in Member 5. The mean for all Member 4 primates is $-9.0^{0}/_{00} \pm 2.28^{0}/_{00}$ while the member 5 primates have a mean $\delta^{13}C$ value of $-3.4^{0}/_{00} \pm 3.17^{0}/_{00}$. Although the identification of the Member 5 primates is not to genus level and it is not clear what individual species were eating, it is possible to infer that these values would imply that C_4 grass formed a greater proportion of dietary carbon and hence was more widely available during Member 5. The results confirm observations based on the herbivore values. The observation that these primates show such enriched $\delta^{13}C$ values, is very noteworthy, as primates have always been used in the past as closed environment indicators. Here, however, it is observed that they do include C_4 elements into their diet, indicative of at least some open grassland elements.

The primate $\delta^{18}O$ mean for Member 5 is $-3.19^{0}/_{00} \pm 1.34^{0}/_{00}$. The relatively low $\delta^{18}O$ values observed for the primates might also be explained by their diets and linked drinking behaviour. Water in fruit, the primary dietary source for frugivorous primates, is depleted in ^{18}O relative to leaf water, although probably more enriched than surface water. These values will therefore be relatively depleted in comparison to the herbivores that are mainly eating leaves. Also underground storage organs are depleted in $\delta^{18}O$, which might further deplete their $\delta^{18}O$ value.

A similar shift in $\delta^{13}C$ also exists for he carnivores, but less marked. The overall mean $\delta^{13}C$ for Member 4 carnivores is $-6.57^{0}/_{00} \pm 1.85^{0}/_{00}$ while that for Member 5 is $-5.44^{0}/_{00} \pm 2.79^{0}/_{00}$. Since carnivores take on the average $\delta^{13}C$ value of their prey the shift in $\delta^{13}C$ for carnivores suggests that on the whole more C_4-dependent animals were available as prey. This result lends strong support to observations for an ecosystem-level shift towards a grassier, more open environment.

The $\delta^{18}O$ values of enamel carbonate are most valuable when used for comparisons between fauna in an assemblage, but some general trends may be observed. $\delta^{18}O$ has been used for inter-specific variation within an assemblage where the aim is to detect the ecological differences of these ancient faunas (Bocherens *et al* 1996, Sponheimer and Lee-Thorp and Sponheimer 2000).

In this study the $\delta^{18}O$ values are not as clearly grouped into different values at different trophic levels as has been noted in other studies. It is therefore difficult to interpret them in relation to observations from existing studies. In general, however, carnivores are more depleted in ^{18}O than the ungulates in both Members 4 and 5: Member 4 $\delta^{13}C$ ungulate mean = -5.06$^{0}/_{00}$, Member 5 $\delta^{13}C$ ungulate mean = -3.11$^{0}/_{00}$; Member 4 $\delta^{13}C$ carnivore mean = -6.68$^{0}/_{00}$, Member 5 $\delta^{13}C$ carnivore mean -5.37$^{0}/_{00}$. This relationship (expanded to include all faunivores) has been consistently observed elsewhere in fossil and modern sites (Sponheimer and Lee-Thorp 1999c, 2001)

The relative depletion in ^{18}O of carnivores compared to herbivores may be ascribed to one or a combination of the following reasons:

1. Carnivores eat larger amounts of proteins, which are relatively depleted in ^{18}O compared to carbohydrates (Sponheimer and Lee-Thorp 2001).
2. The carnivores could simply be drinking more meteoric water than the ungulates, thus depleting the $\delta^{18}O$ signal.

The $\delta^{18}O$ values in general are rather more complex, possibly the result of multiple depositional episodes as was already recognised in the $\delta^{13}C$ as an explanation for bimodal results. The other possibility that should not be discounted is that of diagenesis. Although the $\delta^{13}C$ results do not show signs of alteration (see breccia results), oxygen isotopes are more prone to being affected as has been described. Also, it is not certain how the changes in the environment from warmer to cooler or wetter to drier reflect in $\delta^{18}O$ values. However, $\delta^{18}O$ values for certain specific animals are sufficiently distinctive to allow some inferences to be drawn about drinking behaviour and/or thermophysiology. *C. cf. taurinus* , the wildebeest, for example, had relatively depleted $\delta^{18}O$ values (mean = -2.97$^{0}/_{00}$ ± 3.8 $^{0}/_{00}$) in Member 4 compared to the grazing fauna in the Member 4 assemblage, (mean = -1.71$^{0}/_{00}$ ± 1.62$^{0}/_{00}$). Relatively depleted values have elsewhere been used to argue that this species obtains most of its water from surface water rather than from plant water. This lower $\delta^{18}O$ is only observed during Member 4. The $\delta^{18}O$ mean value for *Connochaetes* in Member 5 is 0.77$^{0}/_{00}$. This shift to more positive values during Member 5 times provides further proof of an overall more open environment in which species lose much more water due to sweating when they do not have tree cover to prevent this from happening.

Makapania broomi also has a depleted $\delta^{18}O$ value during Member 4 times (mean = -2.37$^{0}/_{00}$ ± 0.68$^{0}/_{00}$). This species is not found in Member 5.

Breccia analyses were originally undertaken to determine any exchange between tooth enamel and the matrix. This was found not to be the case. However, the results from the two Member showed up as significantly different ($p=0.00015$; t-test). These breccia results could be a method for resolving proveniences that are in question. If a breccia associated with a fossil result has a $\delta^{13}C$ range between -2$^{0}/_{00}$ and -6.6 $^{0}/_{00}$ it would belong to Member 4, or a range between 1.5$^{0}/_{00}$ and +3$^{0}/_{00}$ it would belong to Member 5. This could resolve issues where it is not certain to which Member specimens belong, as in the *E. capensis* specimens brought to light in this study. This is potentially a very useful tool that could be used in future studies.

Environmental inferences and chronological trends

These isotopic results for individual species can collectively be used to infer environmental change. This study outlines how an index of open indicating fauna can be calculated to quantify this change.

The isotopic results suggest that the original palaeoenvironmental reconstructions for these sites including Sterkfontein provided a reasonable idea of the *general direction* of climate and environmental change trend through time.

The results suggest a time transgressive trend from moister, more closed environments at 3 Ma to drier, more open environments by about 1.7 Ma. The isotopic data confirm this trend, but suggests, however, that the extent of woodland elements at each site has been consistently underestimated. As seen in figure 6.7, both Makapansgat Member 3 and Sterkfontein Members 4 and 5 fall below the AA index originally assessed by faunal abundances alone. The isotope-based environmental reconstructions for Makapansgat Member 3 (shown by Sponheimer and Lee-Thorp in press b) and for Sterkfontein Members 4 and 5 in this thesis indicate more wooded environments in both cases.

The differences can be partly ascribed to wider 'coverage' of the faunal assemblage which demonstrated greater numbers of C_3-consumers in general, and also to reassignment of certain key species as C_3 rather than mixed-feeders.

The results for Members 1 and 2 at Swartkrans, similar in age to Sterkfontein Member 5, also suggest fewer "open" environment-indicating fauna than proposed by Vrba (1975) or Reed (1997). This result must be considered with extreme caution as pointed out elsewhere in this thesis. The faunal samples chosen in the original studies, from which this data was extracted, are very likely biased towards the C_3 consumers. Therefore, an 'unbiased' larger sample of herbivores should be analysed to provide a more accurate C_3/C_4 index. Although this is the case for the C_3/C_4 index given here, the leopard $\delta^{13}C$ values as described in Chapter 4 (Lee-Thorp *et al* 1994) show a shift of eating C_3-consuming prey during Member 1 times to preying on C_4-consuming fauna in Member 2 as will be discussed below.

At around 3.0 Ma, the period represented by Makapansgat Member 3, the C_3/C_4 index as provided by the isotopic data, indicates a faunal composition similar to that of Culei, Angola today. The Culei environment is relatively closed with riparian woodland and edaphic grasslands. It is likely that the Makapansgat Member 3 environment was similar since the isotopic data showed that 7 out of 12 taxa were browsers (Sponheimer *et al* 1999). Reed's analysis showing 15% frugivorous species and 5.5% arboreal species was taken as an indication of a bushland with medium density woodland, perhaps indicating slightly less woodland (Reed, 1997).

The isotopic results from this study strongly suggest that the Sterkfontein Member 4 environment at about 2.5 Ma, was one of a medium density woodland, but with a significant open savanna landscape with areas of thicket. This result shows a more closed environment than originally proposed by Vrba, but one which agrees well with the fossil wood evidence which include lianas, commonly found today in lightly forested areas (Bamford 1999a). Other fossil wood found in Member 4 included species that occur on the fringes of woodlands indicating a forest mosaic. Other support for this environmental reconstruction includes the occurrence in Member 4 of *Cercopithecoides williamsi*, the extinct colobus monkey, a species believed to have preferred wooded areas (Kuman and Clarke 2000). Although monkeys such as the colobus monkey do require forested areas, they are not only indicative of wooded elements, as can be noted by the isotopic results provided in this study. Some fairly enriched values in ^{13}C were observed. Two of the five *C. williamsi* specimens had isotopic signals that indicate a large proportion of the diet included C_4 grasses (STS394B = $-5^0/_{00}$ and STS282 = $-4.7^0/_{00}$). The C_3/C_4 index for this Member is 37%, not very much higher than that for Makapansgat Member 3, indicating that the environment was similar to that at Makapansgat Member 3.

It is at approximately this time that Vrba (1988) describes a major faunal turnover event, including a series of extinctions and radiation of bovids in Southern and East Africa in response to a global climatic shift at about this time. The global shift is known from marine sediment records but does not appear to have been a single 'event' (Shackleton and Opdyke 1973). Periodicity of Saharan dust in the marine records shows that amplitude and periodicity of arid events increased about this time, with a change from 23 thousand years (ka) to 41 ka dominated cycles (deMenocal 1995). Other evidence comes from pollen (*Ericaceae* and Myrica) from Ethiopia, indicating a cooler and drier climate at this time (Bonnefille 1983). The Sterkfontein data, including the new isotopic data, cannot address questions about long-term periodicity, or whether shifts were pulsed or gradual.

In combination the Sterkfontein Member 4 data seems to suggest that a large-amplitude event did not take place, rather that relatively small shifts took place by 2.6 Million years. Reed (1997), too, believed that there was a gradual change, as indicated by the gradual decline of abundance in arboreal species in Southern African sites. An assessment based on faunal abundances in the Turkana Basin also proposed gradual change (Behrensmeyer *et al* 1997). Furthermore, it has been suggested that the large-scale shift in African climates and environments took place later at about 1.7 Ma (Cerling 1992; Wynn and Feibel 1995; Feibel 1997).

The isotopic evidence seems to support this proposal of a later change occurring (subject of course, to the uncertainty in the chronologies of the SA sites). The C_3/C_4 index calculated for the Oldowan Member 5 infill is significant here as the infill has been dated to 2.0 - 1.7 Ma, and would therefore fit into our chronological sequence after Sterkfontein Member 4 but possibly before Swartkrans Member 1. With a percentage of 40%, it indicates an environment only slightly more open than Sterkfontein Member 4.

By 1.8 Ma, the period represented by Swartkrans Member 1, the environment had changed. Many of the woodland elements were much reduced. Various lines of evidence support this. As outlined earlier, the isotopic evidence showed that carnivores, such as leopards, moved from eating mostly C_3 prey during Member 1 times to eating far more C_4 prey during Member 2 times (Lee-Thorp *et al* 1994). A shift to C_4 prey most likely reflects a greater abundance of C_4 prey of suitable size in the landscape during member 2. The precise C_3/C_4 index, however, is not certain for Swartkrans, as explained above, because of the lack of grazers in the sample.

No arboreal species were found in Swartkrans Member 1; about 14% species were fruit and leaf eaters and 6% were aquatic species, indicating an open environment with the proximity of a river (Reed 1997). The river might have been able to support micro-environments in which trees were found in order to support the frugivorous fauna (Reed 1997). Avery also suggested the presence of a band of riparian woodland from micro-faunal abundances (Avery 1995).

Sterkfontein Member 5, at about 1.7Ma or slightly later than Swartkrans Member 1, shows from the new isotopic evidence that it was possibly more of an "open" environment than the latter. Reed (1997) placed Member 5 in an open or wooded grassland environment as there were *no* arboreal or frugivorous fauna and almost 44% grazing fauna. The C_3/C_4 index as indicated by this study is 65%, indicating that the proportion of "open" habitat indicators out-weighs the C_3 or woodland indicators. This is the time at which a major African climate and environment shift occurred (Cerling 1992; Wynn and Feibel 1995). A significant expansion of C_4 (secondary grasslands) occurred. Spencer (1997) noted the appearance of a number of grazing taxa such as *Connochaetes gentryi* at around 2 Ma in East Africa.

The Member 5 West C_3/C_4 index at 77% indicates also a very open environment by this time. This is slightly higher than the Member 5 index as a whole. The high number of browsers in the Oldowan infill assemblage would have lowered the overall Member 5 percentage. This percentage for the West infill is therefore more accurate for representing the environment at this time after 1.7Ma.

Finally, at Swartkrans Member 2 at approximately 1.4 Ma, Reed (1997) observed a decline in fruit and leaf eaters compared with Swartkrans Member 1. Reed found that almost 33% of the Member 2 fauna were grazing fauna, and the faunal assemblage showed 100% terrestriality. The C_3/C_4 index presented in this study is 71%, indicating a grassy, open habitat. The existing isotopic data (Lee-Thorp *et al* 1994) also indicated an opening up of the environment as more C_4 consuming herbivores were being selected as their prey by carnivores.

A new isotope-based reconstruction of the proportions of open-indicating fauna in the landscape during each of the different depositional periods represented by each site can be seen in figure 7.1.

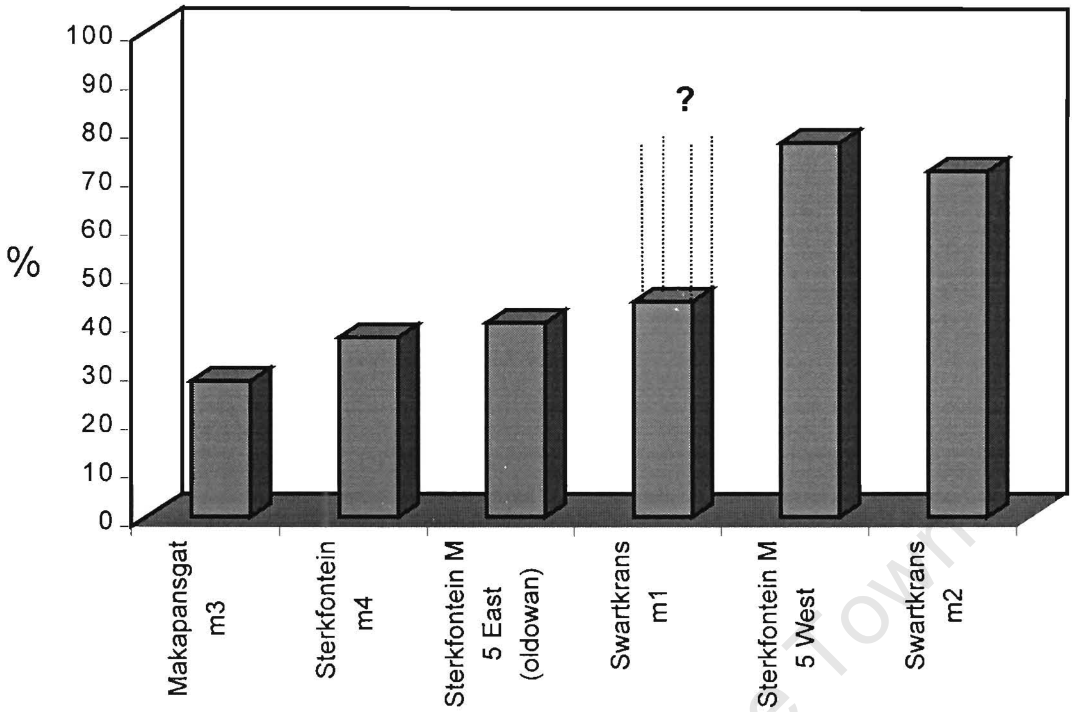

Figure 7.1

Percentage "open" indicating fauna calculated from the carbon isotopic evidence, for the three sites of Makapansgat, Sterkfontein and Swartkrans. As explained in the text (Chapter 6) the number of herbivores with $\delta^{13}C$ values more positive than $-3.99^{0}/_{00}$, were calculated against the herbivore total. A possible unbiased value for Swartkrans is indicated.

Summary

Both existing, and the new isotopic evidence shows that assuming diets and hence habitat preferences of fossil taxa from modern relatives can be hazardous. Isotopic analysis allows one to circumvent a number of assumptions about diets inherent to that method, thus allowing us to ascertain what a fossil animal was eating and how it was behaving with greater certainty. The diets of certain key species have been revised and assigned to C_3 consumers on the $\delta^{13}C$ evidence.

Here an isotopic approach has not only allowed clarification about individual animal dietary preferences, but has also proven useful in obtaining a more precise general picture of changing environments around the time these stratigraphic members were laid down.

We know now that although the general shift followed the established pattern from a more wooded in Makapansgat member 3 to a more open savanna environment at Swartkrans Member 2, some revisions can be made. Firstly, woody elements were underestimated during most of these periods. Secondly, the landscape seems to have remained closed until after 2.5 Ma, and the most significant shift occurs after 2 Ma.

CHAPTER 8: CONCLUSION

Herbivores, primates and carnivores retain distinct isotopic signals indicating their diets, and hence habitat preferences. The isotope data from the hominid sites were used to investigate environmental trends through the Plio-Pleistocene as represented by the South African hominid sites.

Results and problems

Enamel samples were obtained from Sterkfontein Members 4 and 5 in order to perform isotopic analyses on these calcified tissues. This data supplements data already obtained in other studies of sites such as Makapansgat and Swartkrans as well as Sterkfontein. In this study samples were taken from a wide variety of faunal species, including ungulates, primates and carnivores. This was done to enable a broad reconstruction of the ecology.

The results show that fossil fauna did not always behave similarly to their modern counterparts, therefore existing palaeoenvironmental research using faunal taxonomic uniformitarianism was not always supported. Isotopic analysis, which can be applied without making assumptions regarding the behaviour fossil taxa, offers new opportunities for testing these methods.

Samples were taken from various institutions and analysed for stable carbon and oxygen isotope ratios in the Archaeometry laboratory. Early on in the project a problem of low yields and voltage readings was noted. This was investigated by repeated analyses of a known internal standard at varying weights, in order to find the lowest voltage reading at which results were still reliable. The samples with a voltage reading below this value were discarded and not discussed.

The $\delta^{13}C$ results showed that the distinction between grazers, browsers and mixed feeders was maintained. Diagenesis is unlikely to have played a role in shaping of the isotopic results; this may however not have been entirely true for the $\delta^{18}O$ results as they are more prone to chemical alteration.

Several of the fauna identified as one species showed bimodal distributions in $\delta^{13}C$ values, indicating that taxonomic assignments might have played a role. Future work should be directed towards a careful re-examination of these specimens in order to eliminate incorrect identifications, or perhaps, over-enthusiastic "lumping" of species.

The overall $\delta^{13}C$ for Member 4 browsers was $1.5^{0}/_{00}$ more depleted than the browsers found in Member 5. This difference is best ascribed to variations in C_3 plant $\delta^{13}C$ and might be related to climate stresses in Member 5 such as greater warmth or aridity.

Palaeoenvironmental reconstruction from Plio-Pleistocene sites

Isotopic analyses show that the woodland elements were under-emphasized at Sterkfontein Member 4 and 5 and possibly also at Swartkrans Members 1 and 2. This was due to animals that were originally used as "open" indicators, such as *Antidorcas recki*, being incorrectly classified as mixed feeders. Isotopic analyses clearly show that this animal required trees and shrubs because it was a predictable browser. This finding has implications for palaeoenvironmental reconstructions that used fauna such as *A. recki* as an indicator of an "open" environment.

I was able to quantify this environmental change by establishing a C_3/C_4 index for each site. The isotopic data showed that the environment during Sterkfontein Member 4 times was more wooded than the environment at Swartkrans Member 1, which was again more wooded than Sterkfontein Member 5. Once the isotopic results for Member 5 were divided according to the two infills - the Oldowan (east) and West infill - a higher resolution of environmental change was obtained. The isotopic evidence from this and other studies combined, indicate that a gradual change from more wooded to more open occurred from 2.6 Ma to 1.8Ma.

At about this time there seems to be a marked change to more open, arid environments indicated by a major jump in the C_3/C_4 index from 44% to 77%.

Future research

Significant advances in our knowledge of the environment between 3.0 Ma and 1.4 Ma have been made. The trend in environmental change over this long time period is far better understood. It has also been shown that change was relatively gradual until after 2.0 Ma when a major change to more open savanna environment occurred. This result is in good agreement with research in East Africa. Future studies should focus on using techniques such as the one outlined in this thesis, which has the benefit of making fewer assumptions about the habits of fossil taxa, to improve our understanding of the environment in which our hominid ancestors were evolving.

Future work at the Sterkfontein should include the examination of species that showed bimodal distributions in this study, as this might be a clue that two species are represented. These specimens need to be positively identified.

New sites are continuously being found and excavated. By doing similar analyses at sites of different ages, the palaeoenvironmental sequence of environmental change during this important period for human evolution can be made more comprehensive. Changes during these crucial time periods need to be fleshed out to place our own species evolution in better context.

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TABLES

Table 5.1

Species list of samples taken from Sterkfontein

a) Member 4

n= number is specimens sampled

Order Artiodactyla	**n**
Family Bovidae	
Subfamily Tragelaphinae	
Tragelaphus strepsiceros	**4**
Taurotragus oryx	**1**
Tragelaphus angasi	**1**
Tragelaphus scriptus	**1**
Subfamily Hippotragine	
Hippotragus gigas	**5**
Hippotragus equinus	**2**
Subfamily Reduncinae	
Redunca arundinum	**1**
Subfamily Alcelaphinae	
Damaliscus sp.	**7**
Damaliscus or *Parmularis*	**3**
Connochaetes taurinus	**2**
Connochaetes sp	**1**
Makapania broomi	**5**
Subfamily Antilopine	
Antidorcas recki	**6**
Antidorcas bondi	**1**
Antilopini II	**1**
Antilopini III	**2**
Order Carnivora	
Family Canidae	
Canis mesomelas	**4**
Family Hyaenidae	

Crocuta crocuta	**3**
Hyaena brunnea	**1**
Chasmaporthetes nitidula	**5**
Chasmaporthetes silderbergi	**4**
Pachycrocuta breviostris	**1**
Family Felidae	
Homotherium latidens	**4**
Subfamily Machairodontinae	
Dinofelis barlowi	**5**
Subfamily Felinae	
Panthera leo	**2**
Order Primates	
Family Cercopithecidae	
Subfamily Cercopithecinae	
Parapapio broomi	**8**
Parapapio jonesi	**6**
Parapapio whitei	**5**
Cercopithecoides williamsi	**6**

b) Member 5

Order Perissodactyla	
Equus capensis	**5**
Equid	**8**
Order Artiodactyla	
Family Bovidae	
Subfamily Tragelaphinae	
Tragelaphini cf. *Taurotragus*	**2**
Subfamily Hippotragine	
Hippotragus gigas	**1**
Subfamily Alcelaphinae	
Damaliscus dorcas	**1**
Damaliscus sp	**4**
Sml Alcelaphini cf.Damaliscus	**8**
Connochaetes taurinus	**4**
Large Alcelaphini	**9**
Subfamily Antilopine	
Antidorcas recki	**2**
Antelopini cf. *Antidorcas*	**4**
Order Carnivora	
Family Hyaenidae	
Crocuta crocuta	**1**
Parahyaena brunnea	**2**
Chasmaporthetes nitidula	**1**
Pachycrocuta breviostris	**1**
Subfamily Felinae	
Panthera leo	**7**
Order Primates	
Family Cercopithecidae	
Cercopithecidae indet.	**10**

Table 5.2 cont. from pp.51
Standards

	$\delta^{13}C$	$\delta^{18}O$
NBS 18	-5.233	-25.688
	-4.932	-24.909
	-5.046	-24.964
	-4.992	-24.773
	-5.104	-25.077
	-4.946	-24.862
	-5.399	-26.18
	-5.121	-24.482
average	**-5.097**	**-25.117**
NBS 19	1.332	-6.102
	1.781	-4.753
	1.762	-4.883
	1.339	-6.217
average	**1.5535**	**-5.4888**
Cavendish Marble	0.282	-11.151
	0.237	-11.001
	0.127	-10.973
	0.258	-11.142
	-0.012	-12.331
	0.135	-11.592
average	**0.1712**	**-11.3650**
Cararra Z	2.007	-3.828
	1.958	-4.05
	2.004	-4.379
	2.02	-4.212
	2.043	-3.864
	2.012	-4.061
	2.077	-3.888
	1.87	-4.481
average	**1.9989**	**-4.0954**

Table 5.3
δ^{13}C and δ^{18}O results for Cavendish Marble at different Voltages

Sample 44

Voltage	δ^{13}C	δ^{18}O
0.420	-1.907	-17.394
0.978	0.081	-11.164
0.987	-0.260	-12.235
1.233	-0.018	-11.180
1.424	0.295	-10.684
1.453	0.046	-10.56
1.772	0.329	-10.383
1.846	0.004	-10.706
1.902	0.203	-10.496
2.404	0.322	-10.452
2.452	0.349	-10.766
2.556	0.405	-10.464
2.646	0.334	-10.647
2.687	0.151	-10.489
2.755	0.186	-10.566
3.146	0.354	-10.643
3.153	0.243	-10.479
3.412	0.371	-10.392
3.774	0.321	-10.460
4.653	0.375	-10.364
4.684	0.373	-10.433
5.031	0.356	-10.504
5.047	0.308	-10.405
5.150	0.338	-10.445
5.233	0.304	-10.383
5.464	0.413	-10.397
5.755	0.356	-10.411
6.233	0.391	-10.412
6.768	0.313	-10.428
6.774	0.346	-10.379
6.818	0.364	-10.380
6.878	0.396	-10.405
7.067	0.426	-10.344

Table 6.1a
Member 4 Sterkfontein Ungulate results

UCT #	**Catelogue #**	**Species**		δ^{13}**C**	δ^{18}**O**
7883	STS 1400	Antilopini 11		-13.3	-3.4
7888	STS 2076	Antilopini 111		-11.3	-4.0
			duplicate	-12.5	-4.8
			duplicate	-12.2	-2.1
7892	STS 1577	Antilopini 111		-2.1	-4.8
			duplicate	-1.7	-3.5
7909	STS 1125	*Antidorcas bondi*		-1.2	0.2
			duplicate	-1.3	0.4
7897	STS 1435	*Antidorcas cf. recki*		-13.7	-4.3
7900	STS 1996	*Antidorcas cf. recki*		*-16.5‡*	-10.7*
7886	STS 2369	*Antidorcas recki*		-9.7	-0.1
			duplicate	-11.2	-0.6
7907	STS 1944	*Antidorcas recki*		-13.9	-9.0
			duplicate	-14.0	-6.2
7911	STS 1325A	*Antidorcas recki*		-11.5	-3.6
			duplicate	-15.0	-6.2
7912	STS 1596	*Antidorcas recki*		-5.1	-4.6
			duplicate	-4.0	-3.3
7903	STS 2200	*Connochaetes*		-4.9	-7.1
1830	SF 114	*Connochaetes cf. taurinus*		-2.0	-1.9
			duplicate	-1.7	-2.5
2753	SF 112	*Connochaetes cf. taurinus*		-0.7	0.4
7959	STS 1980	*Damaliscus*		-6.8	-2.3
7960	STS 2027	*Damaliscus*		-7.1	-1.8
			duplicate	-6.8	-3.6
2754	SF 327	*Damaliscus sp.*		-0.9	-1.9
			duplicate	-0.4	-2.4
2755	SF 328	*Damaliscus sp.*		1.4	-2.1
2756	SF 329	*Damaliscus sp.*		1.4	-1.8
2758	SF 332	*Damaliscus sp.*		3.1	-1.0

7893	STS 1319	*Damaliscus OR Parmularis*	-2.5	-3.4
		duplicate	-2.0	-2.8
7895	STS 2046	*Damaliscus OR Parmularis*	-5.4	-3.9
		duplicate	-5.5	-3.9
7901	STS 2586(2)	*Damaliscus OR Parmularis*	0.4	-3.4
7901	STS 2586(4)	*Damaliscus OR Parmularis*	0.1	-1.4
7901	STS 2586(5)	*Damaliscus OR Parmularis*	-0.2	-0.7
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	-4.5	-11.2*
	STS 2586(1)		-1.3	-5.9
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	-0.9	-2.3
	STS 2586(3)		0.4	-3.0
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	0.3	-1.9
	STS 2586(6)		-1.2	-3.9
7890	STS 2336A	*Hippotragus cf. sp. aff. gigas*	-10.4	-0.6
7906	STS 1438	*Hippotragus cf. sp. aff. gigas*	-9.4	0.6
		duplicate	-10.4	0.2
7885	STS 2145A	*Hippotragus gigas*	-4.6	-2.3
7881	STS 789	*Hippotragus sp. aff. gigas*	-12.2	-14.6*
		duplicate	-8.3	-9.0
		duplicate	-11.4	-12.5*
2784	SF 314, D13	*Hippotragus sp aff gigas*	-6.1	2.2
7887	STS 2599	*Hippotragus equinus*	0.1	-0.8
7913	STS 1630	*Hippotragus equinus*	-2.3	-4.6*
		duplicate	-2.1	-3.0*
7884	STS 2059B	*Makapania broomi*	-9.0	-11.2*
		duplicate	-6.5	-8.5
7889	STS 1925	*Makapania broomi*	-8.6	-1.6
7896	STS 952	*Makapania broomi*	-10.8	-2.1
7902	STS 2565	*Makapania broomi*	-3.2	-3.5
7914	STS 1721	*Makapania broomi*	-6.0	-9.3*
		duplicate	-7.5	-9.6*
7904	STS 2075	*Redunca arundinum*	-1.3	1.1
7882	STS 2092	*Tragelaphus sp. aff. angasi*	-4.8	-6.0
2759	046	*Tragelaphus strepsiceros*	-8.9	-0.8
2761	STS 1573	*Tragelaphus strepsiceros*	-10.0	1.8
		duplicate	-9.7	1.7

2762	STS 2121	*Tragelaphus strepsiceros*	-8.2	-0.4
		duplicate	-8.1	-0.6
2781	SF 1300	*Tragelaphus strepsiceros*	-4.7	-3.1
1829	SF 336, D13	*Taurotragus cf. oryx*	-5.3	-2.6
		duplicate	-4.8	-2.0
1828	SF 130, D8	*Tragelaphus cf scriptus*	-4.5	-1.5

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue. Those samples are marked (‡) .

Table 6.1 b
Member 5 Sterkfontein Ungulate results

UCT #	**Catalogue #**	**Species**		δ^{13}**C**	δ^{18}**O**
7925	S94-6124	*Antelopini cf. antidorcas*		-9.3	*-0.7**
			duplicate	-9.8	-0.7
7928	S94-7314	*Antelopini cf. antidorcas*		0.5	3.7
			duplicate	1.0	*4.2**
7932	BP/3/16974	*Antelopini cf. antidorcas*		-9.2	-2.8
7943	S94-7958	*Antelopini cf. antidorcas*		-6.7	-0.2
			duplicate	-8.0	-1.2
7944	SE 1258	*Antidorcas cf. recki*		-10.5	*-8.3**
			duplicate	-11.1	*-0.5**
7947	SE 1855.1	*Antidorcas recki*		-12.7	-1.7
7948	SE 1125.1	*Hip. sp. af. gigas*		-5.1	-0.7
			duplicate	-5.4	-0.5
7945	SE 1334	*Damaliscus*		-0.3	-4.7
			duplicate	-0.5	-4.7
7949	SE 1233.1	*Damaliscus*		-3.8	*-11.1**
			duplicate	-1.0	-4.2
7950	SE 1770	*Damaliscus*		1.5	*-3.2**
			duplicate	-0.3	-5.3
7946	SE 1614.1	*Damaliscus cf. sp2*		0.6	-4.2
7951	SE 1185	*Damaliscus dorcas*		-4.9	*-10.3**
7930	S94-3459	Sml Alcelaphini cf. damaliscus		-4.0	-1.9
7934	BP/3/19870	Sml Alcelaphini cf. damaliscus		0.7	-0.8
			duplicate	0.3	-1.6
7938	BP/3/17143	Sml Alcelaphini cf. damaliscus		-1.8	-3.6
7939	S94-2839(1)	Sml Alcelaphini cf. damaliscus		-5.2	-3.4
			duplicate	-5.4	-3.9
7939	S94-2839(2)	Sml Alcelaphini cf. damaliscus		-1.6	-1.5
			duplicate	-1.1	-0.1
7939	S94-2839(3)	Sml Alcelaphini cf. damaliscus		-2.0	-3.8
			duplicate	-2.4	-3.5
7918	S94-2837(1)	Sml Alcelaphini cf. damaliscus		-6.2	-3.3
7920	S94-2837(3)	Sml Alcelaphini cf. damaliscus		-5.1	-2.1

7921	S94-2837(4)	Sml Alcelaphini cf. damaliscus	-5.5	-3.2
		duplicate	-5.5	-3.1
7923	S94-2837(6)	Sml Alcelaphini cf. damaliscus	-3.6	-2.2
7931	S94-9669	Sml Alcelaphini cf. damaliscus	0.4	-1.7
		duplicate	-0.02	-1.9
7935	S94-7927	Sml Alcelaphini cf. damaliscus	-0.8	-2.5
		duplicate	-1.6	-3.5
7937	S94-7251	Sml Alcelaphini cf. damaliscus	-2.1	-5.5
7916	S94-7030	Large Alcelaphini	-4.7	1.6
		duplicate	-4.9	1.1
		duplicate	-5.4	0.6
7924	S94-7923	Large Alcelaphini	3.0	-3.7
7926	S94-9660	Large Alcelaphini	-2.8	-6.9
		duplicate	-3.4	-7.3
7927	S94-9592	Large Alcelaphini	1.4	-2.1
7929	S94-3385	Large Alcelaphini	-6.0	-4.4
		duplicate	-6.6	-4.9
		duplicate	-6.5	-3.3
7941	S94-8228	Large Alcelaphini	-4.1	-4.8
7942	S94-2631	Large Alcelaphini	-7.4	1.2
		duplicate	-8.3	-0.4
7917	S94-7327	Large Alcelaphini	0.8	-2.7
		duplicate	-0.4	-2.6
7940	S94-3898	Large Alcelaphini	0.01	-2.2
		duplicate	0.0	-1.8
		duplicate	-0.01	-1.4
7933	BP/3/16956	*Tragelaphini cf. taurotragus*	-9.4	-0.03
7936	BP/3/16947	*Tragelaphini cf. taurotragus*	-8.8	-1.0
		duplicate	-10.1	-2.0
2749	SF 334	*Connochaetes sp.*	-1.1	-2.9
2750	SF 92	*Connochaetes sp.*	0.7	-1.5
2751	SF 95	*Connochaetes sp.*	2.7	1.6
2752	SF 91	*Connochaetes sp.*	-1.4	-0.1
8038	S94-1787	Equid	-0.6	-2.9
8039	S94-390	Equid	-2.0	-0.9
8040	S94-349	Equid	-0.9	-2.1
8041	S94-1750	Equid	0.8	-0.7
8035	S94-339	Equid	-3.1	*-2.0**

8036	S94-329	Equid	-4.4	*-0.4**
8037	S94-369	Equid	-1.8	*-4.7**
7898	STS 3004	*Equus capensis*	-3.3	*-6.4**
7899	STS 3006	*Equus capensis*	-3.6	-2.5
7905	STS 2102&1717	*Equus capensis*	-2.9	-1.8
7910	STS 1972	*Equus capensis*	-4.6	-3.1
7915	STS 2313	*Equus capensis*	-4.8	-4.4

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue.
Those samples are marked (‡).

Table 6.2 a
Member 4 Sterkfontein Primates

UCT #	Catalogue number	Species	$\delta^{13}C$	$\delta^{18}O$
8005	STS 394B	*Cercepithecoides williamsi*	-5.0	-2.3
8006	STS 300	*Cercepithecoides williamsi*	-11.7	2.0
8007	STS 282	*Cercepithecoides williamsi*	-4.7	0.3
8010	STS 279	*Cercepithecoides williamsi*	-12.9	1.5
8015	STS 260	*Cercepithecoides williamsi*	-12.1	-10.2
8024	STS 337	*Parapapio broomi*	-7.5	-2.5
8026	STS 326	*Parapapio broomi*	-5.7	-2.9
8028	STS298	*Parapapio broomi*	-12.2	-11.8
8030	STS 466	*Parapapio broomi*	-8.1	-9.7*
8031	STS 339	*Parapapio broomi*	-7.2	-0.3
8018	STS 306	*Parapapio jonesi*	-8.1	-1.6
		duplicate	-7.3	0.3
8021	STS 340	*Parapapio jonesi*	-9.4	-2.5
8012	STS 263	*Parapapio whitei*	-7.8	0.8
8014	STS 253	*Parapapio whitei*	-11.1	-3.0*
8015	STS 260	*Parapapio whitei*	-12.1	-10.2
8016	STS 352	*Parapapio whitei*	*-15.4‡*	-13.6

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue. Those samples are marked (‡).

Table 6.2 b
Member 5 Sterkfontein Primates

UCT #	Catelogue #	Species	$\delta^{13}C$	$\delta^{18}O$
8043	SWP 2674	Cercepithecoides indet.	-7.6	-1.6
8044	SWP 2207	Cercepithecoides indet.	-3.8	-5.5*
		duplicate	-3.5	-3.7
8047	SWP 2465	Cercepithecoides indet.	-0.1	-2.7
8054	SWP 2145	Cercepithecoides indet.	-2.3	-4.7

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue. Those samples are marked (‡).

Table 6.3 a
Member 4 Sterkfontein Carnivores

UCT #	Catelogue number	Species	δ^{13}C	δ^{18}O
7964	S94-3	*Chasmoporthetes nitidula*	-4.4	-0.9
7965	S94-7195	*Chasmoporthetes nitidula*	-9.1	-1.9
7981	SF 409	*Chasmoporthetes nitidula*	-4.4	0.1
7982	SF363	*Chasmoporthetes nitidula*	-7.5	0.2
7984	SF 452	*Chasmoporthetes silderbergi*	*-17.2‡*	-18.7*
7985	SF 408	*Chasmoporthetes silderbergi*	-6.1	-4.1*
7986	SF 369+372	*Chasmoporthetes silderbergi*	-6.8	-1.9*
7993	414	*Crocuta crocuta*	-9.3	-5.9*
8003	STS 128	*Crocuta crocuta*	-3.2	-2.0
7970	S94-56A	*Dinofelis barlowi*	*-20.4‡*	-23.3*
7972	S94-9	*Dinofelis barlowi*	-8.2	-3.7*
7997	STS 132	*Dinofelis barlowi*	-4.6	-3.4
7959	SF 420	*Homotherium latidens*	-7.7	-0.1
7960	SF 434	*Homotherium latidens*	-8.3	-0.2
7961	397	*Homotherium latidens*	-7.6	-9.3*
7962	388	*Homotherium latidens*	-8.7	-4.0*
7994	436	*Hyena brunnea*	-6.2	-4.0*
7988	416	*Pachycrocuta breviostris*	-5.7	-3.9*
7967	S94-2	*Panthera leo*	-7.0	-0.8*

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue. Those samples are marked (‡).

Table 6.3 b
Member 5 Sterkfontein Carnivores

UCT #	**Catelogue #**	**Species**	δ^{13}**C**	δ^{18}**O**
7963	S94-8061	*Chasmoporthetes nitidula*	-4.9	-4.4
7990	S94-112	*Crocuta crocuta*	*-28.0‡*	-28.6*
7987	376	*P.breviostris*	-9.8	-5.9
7968	SF 4151	*Panthera leo*	-7.8	-3.1
7969	S94-149+150	*Panthera leo*	-9.0	-3.7
7973	SF 2858	*Panthera leo*	-10.3	-5.5
7974	S94-23	*Panthera leo*	-2.6	-3.8
7975	S94-7228	*Panthera leo*	-3.7	-4.1*
7978	BP/3/19777	*Panthera leo*	-4.1	-3.8*
7995	S94-7238	*Parahyena brunnea*	-2.3	-4.0

As the inclusion value is greater for carbon, there are some oxygen values that are included in this results list, but that will not be discussed. Those samples are marked (*).

Anomolous results i.e. very negative were ascribed to a contamination with glue. Those samples are marked (‡).

Table 6.4
Comparisons between this study and Van der Merwe and Thackeray's results from 1997

	member4		$\delta^{13}C$			$\delta^{18}O$		
UCT #	**specimen #**	**Species**	**New result**	**Previous**	***difference***	**New result**	**Previous**	***difference***
1830	SF 114	Connochaetes cf. taurinus	-1.97	*-1.81*	***0.2***	-1.94	*1.38*	***3.3***
2753	SF 112	Connochaetes cf. taurinus	-0.67	*-0.21*	***0.5***	0.41	*2.13*	***1.7***
2754	SF 327	Damaliscus sp.	-0.92	*-0.28*	***0.6***	-1.91	*-1.3*	***0.6***
2755	SF 328	Damaliscus sp.	1.42	*0.66*	***-0.8***	-2.07	*1.18*	***3.3***
2756	SF 329	Damaliscus sp.	1.42	*2.32*	***0.9***	-1.84	*1.45*	***3.3***
2757	SF 330	Damaliscus sp.	-0.08	*3.66*	***3.7***	-5.42	*-1.86*	***3.6***
2758	SF 332	Damaliscus sp.	3.10	*3.52*	***0.4***	-1.00	*1.9*	***2.9***
2784	SF 314, D13	Hippotragus sp aff gigas	-6.13	*-5.61*	***0.5***	2.22	*5.04*	***2.8***
1829	SF 336, D13	Taurotragus cf. oryx	-5.32	*-5.74*	***-0.4***	-2.62	*-0.08*	***2.5***
1828	SF 130, D8	Tragelaphus cf scriptus	-4.51	*-9.67*	***-5.2***	-1.50	*0.56*	***2.1***
2759	046	Tragelaphus strepsiceros	-8.90	*-7.69*	***1.2***	-0.75	*2.55*	***3.3***
2761	STS 1573	Tragelaphus strepsiceros	-9.97	*-10.59*	***-0.6***	1.76	*4.38*	***2.6***
2762	STS 2121	Tragelaphus strepsiceros	-8.24	*-8.73*	***-0.5***	-0.39	*1.97*	***2.4***
2781	SF 1300	Tragelaphus strepsiceros	-4.70	*-8.12*	***-3.4***	-3.08	*3.37*	***6.4***
		average	**-3.25**	**-3.45**	**-0.20**	**-1.29**	**1.62**	**2.91**
	member 5							
2749	SF 334	Connochaetes sp.	-1.13	*-0.03*	***1.1***	-2.88	*1.24*	***4.1***
2750	SF 92	Connochaetes sp.	0.71	*0.01*	***-0.7***	-1.50	*-0.06*	***1.4***
2751	SF 95	Connochaetes sp.	2.73	*2.65*	***-0.1***	1.61	*2.22*	***0.6***
2752	SF 91	Connochaetes sp.	-1.43	*-1.64*	***-0.2***	-0.07	*1.07*	***1.1***
		average	**0.22**	**0.25**	**0.03**	**-0.71**	**1.12**	**1.83**

Table 6.5
Primate tooth measurements

Those identified as Parapapio jonesi

	WIDTH (mm)	LENGTH (mm)
STS 329	8.5	13.1
STS 340	7.5	9.7
STS 446	9.2	12.0
STS 306	7.8	10.0
STS 406A	8.7	11.0
STS 441	8.2	8.7
AVERAGE	8.3	10.8

Those identified as Parapapio broomi

	WIDTH (mm)	LENGTH (mm)
STS 331	9.9	12.6
STS 466	9.6	10.2
STS 380b	10.0	10.8
STS339	10.1	10.6
STS 337	9.9	11.0
STS 326	10.6	13.2
STS 346	10.6	13.3
STS 298	8.9	10.2
AVERAGE	10.0	11.5

Table 6.6 a
Sterkfontein breccia samples from member 4

UCT #	**Catelogue number**	**Species**	δ^{13}**C**	δ^{18}**O**	**voltages**
7914	STS 1721	Makapania broomi	-6.0*	-9.3*	1.3
7914	STS 1721	Breccia	-3.3	-4.4	6.8
8008	STS 532	Cercepithecus williamsi	-12.9*	-0.9*	0.7
8009	STS 532	Breccia	-2.8	-2.6	6.7
8010	STS 279	Cercepithecus williamsi	-13.3*	-5.8*	0.4
8011	STS 279	Breccia	-3.1	-2.3	6.9
8028	STS298	Parapapio broomi	-12.2	-11.8	2.6
8029	STS 298	Breccia	-2.9	-1.9	6.6
8031	STS 339	Parapapio broomi	-7.2	-0.3	2.4
8032	STS 339	Breccia	-3.1	-2.8	6.8
8023	STS 329	Parapapio jonesi	-110.1*	-156.8*	0.1
8024	STS 329	Breccia	-2.3	-2.7	6.9
8003	STS 128	Crocuta crocuta	-3.2	-2.0	1.6
8004	STS 128	Breccia	-6.5	-7.3	4
7970	S94-56A	Dinofelis barlowi	-20.4*	-23.3*	1.3
7971	S94-56A	Breccia	-3.2	-4.6	6.7
		Average breccia	**-3.40**	**-3.58**	

Table 6.6 b
Sterkfontein breccia samples from member 5

UCT #	**Catelogue number**	**Species**	$\delta^{13}C$	$\delta^{18}O$	**voltages**
member 5					
7937	S94-7251	Sml Alcelaphini cf. damaliscus	-12.0	-19.6	2.9
7937	S94-7251	Breccia	-0.8	-2.2	3.1
7917	S94-7327	Large Alcelaphini	0.8	-2.7	2.1
7917	S94-7327	Breccia	-0.6	-4.5	6.7
7940	S94-3898	Large Alcelaphini	0.0	-2.2	1.9
7940	S94-3898	Breccia	-0.9	-4.2	4.3
8048	SWP 2311	Cercopithecoides indet.	-3.6*	-7.7*	0.5
8049	SWP 2311	Breccia	0.4	-3.2	5.9
8050	SWP 2420	Cercopithecoides indet.	-7.3*	-2.8*	0.9
8051	SWP 2420	Breccia	-1.1	-4.1	2.2
8052	SWP 2446	Cercopithecoides indet.	-5.6*	-11.8*	0.2
8053	SWP 2446	Breccia	3.3	-31.6	0.06
8054	SWP 2145	Cercopithecoides indet.	-2.3	-4.7	5.1
8055	SWP 2145	Breccia	-0.6	-1.9	6.5
8056	SWP 2174	Cercopithecoides indet.	-3.0*	-3.1*	0.9
8057	SWP 2174	Breccia	-0.6	-4.5	4.2
7990	S94-112	Crocuta crocuta	-28.0*	-28.6*	1.4
7991	S94-112	Breccia	-1.5	-4.6	6.6
7978	BP/3/19777	Panthera leo	-4.1*	-3.8*	1.2
7979	BP/3/19777	Breccia	-0.4	-3.3	6.6
		average breccia	**-0.29**	**-3.58**	

Table 6.7
Damaliscus samples along tooth rows for three teeth

UCT #	Catelogue #	Species	$\delta^{13}C$	$\delta^{18}O$
member 4				
7901	STS 2586(1)	Damaliscus OR Parmularis	-1.3	-5.9
7901	STS 2586(2)	Damaliscus OR Parmularis	0.4	-3.4
7091	STS 2586(3)	Damaliscus OR Parmularis	0.4	-3.0
7901	STS 2586(4)	Damaliscus OR Parmularis	0.1	-1.4
7901	STS 2586(5)	Damaliscus OR Parmularis	-0.2	-0.7
7901	STS 2586(6)	Damaliscus OR Parmularis	-1.2	-3.9
member 5				
7939	S94-2839(1)	Sml Alcelaphini cf. damaliscus	-5.2	-3.4
7939	S94-2839(2)	Sml Alcelaphini cf. damaliscus	-1.6	-1.5
7939	S94-2839(3)	Sml Alcelaphini cf. damaliscus	-2.1	-3.8
7918	S94-2337(1)	Sml Alcelaphini cf. damaliscus	-6.2	-3.3
7919	S94-2337(2)	Sml Alcelaphini cf. damaliscus	-6.23	-4.2
7920	S94-2337(3)	Sml Alcelaphini cf. damaliscus	-5.1	-2.1
7921	S94-2337(4)	Sml Alcelaphini cf. damaliscus	-5.5	-3.1
7922	S94-2337(5)	Sml Alcelaphini cf. damaliscus	-4.6	-4.1
7923	S94-2337(6)	Sml Alcelaphini cf. damaliscus	-3.6	-2.2

Table 6.8a
C_3/C_4 index - Member 4

Catelogue #	**Species**	δ^{13}**C**			
STS 1400	Antilopini 11	-13.32			Browser
STS 2076	Antilopini 111	-11.99			Browser
STS 1577	Antilopini 111	-1.87	Grazer		
STS 1125	*Antidorcas bondi*	-1.21	Grazer		
STS 1435	*Antidorcas cf. recki*	-13.70			Browser
STS 2369	*Antidorcas recki*	-10.46			Browser
STS 1944	*Antidorcas recki*	-13.94			Browser
STS 1325A	*Antidorcas recki*	-13.21			Browser
STS 1596	*Antidorcas recki*	-4.50		Mixed	
STS 2200	*Connochaetes*	-4.94		Mixed	
SF 114	*Connochaetes cf. taurinus*	-1.86	Grazer		
SF 112	*Connochaetes cf. taurinus*	-0.67	Grazer		
STS 1980	*Damaliscus*	-6.83		Mixed	
STS 2027	*Damaliscus*	-6.96		Mixed	
SF 327	*Damaliscus sp.*	-0.65	Grazer		
SF 328	*Damaliscus sp.*	1.42	Grazer		
SF 329	*Damaliscus sp.*	1.42	Grazer		
SF 332	*Damaliscus sp.*	3.10	Grazer		
STS 1319	*Damaliscus OR Parmularis*	-2.20	Grazer		
STS 2046	*Damaliscus OR Parmularis*	-5.44		Mixed	
STS 2586AVE	*Damaliscus OR Parmularis*	-0.30	Grazer		
STS 2336A	*Hippotragus cf. sp. aff. gigas*	-10.40			Browser
STS 1438	*Hippotragus cf. sp. aff. gigas*	-9.90			Browser
STS 2145A	*Hippotragus gigas*	-4.61		Mixed	
SF 314, D13	*Hippotragus sp aff gigas*	-6.13		Mixed	
STS 2599	*Hippotragus equinus*	0.08	Grazer		
STS 1630	*Hippotragus equinus*	-2.20	Grazer		
STS 2059B	*Makapania broomi*	-7.74		Mixed	
STS 1925	*Makapania broomi*	-8.60			Browser
STS 952	*Makapania broomi*	-10.84			Browser
STS 2565	*Makapania broomi*	-3.17	Grazer		
STS 1721	*Makapania broomi*	-6.77		Mixed	
STS 2075	*Redunca arundinum*	-1.32	Grazer		
STS 2092	*Tragelaphus sp. aff. angasi*	-4.76		Mixed	
046	*Tragelaphus strepsiceros*	-8.90			Browser
STS 1573	*Tragelaphus strepsiceros*	-9.84			Browser
STS 2121	*Tragelaphus strepsiceros*	-8.16			Browser
SF 1300	*Tragelaphus strepsiceros*	-4.70		Mixed	
			n=14	n=11	n=13
	total n= 38				
			37%	**29%**	**34%**

Table 6.8b
C_3/C_4 index - Member 5

Catelogue #	**Species**	δ^{13}**C**			
S94-6124	*Antelopini cf. antidorcas*	-9.56			Browser
S94-7314	*Antelopini cf. antidorcas*	0.74	Grazer		
BP/3/16974	*Antelopini cf. antidorcas*	-9.23			Browser
S94-7958	*Antelopini cf. antidorcas*	-7.37		Mixed	
SE 1258	*Antidorcas cf. recki*	-10.79			Browser
SE 1855.1	*Antidorcas recki*	-12.68			Browser
SE 1125.1	*cf. Hippotragus sp. af. gigas*	-5.25	Grazer	Mixed	
SE 1334	*Damaliscus*	-0.38	Grazer		
SE 1233.1	*Damaliscus*	-2.38	Grazer		
SE 1770	*Damaliscus*	0.60	Grazer		
SE 1614.1	*Damaliscus cf. sp2*	0.62	Grazer		
S94-3459	Sml Alcelaphini cf. damaliscus	-3.97	Grazer		
BP/3/19870	Sml Alcelaphini cf. damaliscus	0.51	Grazer		
BP/3/17143	Sml Alcelaphini cf. damaliscus	-1.80	Grazer		
S94-2839Ave	Sml Alcelaphini cf. damaliscus	-2.97	Grazer		
S94-2837Ave	Sml Alcelaphini cf. damaliscus	-5.10	Grazer		
S94-9669	Sml Alcelaphini cf. damaliscus	0.17	Grazer		
S94-7927	Sml Alcelaphini cf. damaliscus	-1.21	Grazer		
S94-7251	Sml Alcelaphini cf. damaliscus	-2.08	Grazer		
S94-7030	Large Alcelaphini	-5.00		Mixed	
S94-7923	Large Alcelaphini	2.96	Grazer		
S94-9660	Large Alcelaphini	-3.07	Grazer		
S94-9592	Large Alcelaphini	1.40	Grazer		
S94-3385	Large Alcelaphini	-6.37		Mixed	
S94-8228	Large Alcelaphini	-4.09		Mixed	
S94-2631	Large Alcelaphini	-7.84		Mixed	
S94-7327	Large Alcelaphini	0.21	Grazer		
S94-3898	Large Alcelaphini	0.00	Grazer		
BP/3/16956	*Tragelaphini cf. taurotragus*	-9.38			Browser
BP/3/16947	*Tragelaphini cf. taurotragus*	-9.44			Browser
SF 334	*Connochaetes sp.*	-1.13	Grazer		
SF 92	*Connochaetes sp.*	0.71	Grazer		
SF 95	*Connochaetes sp.*	2.73	Grazer		
SF 91	*Connochaetes sp.*	-1.43	Grazer		
S94-1787	Equid	-0.61	Grazer		
S94-390	Equid	-2.04	Grazer		
S94-349	Equid	-0.94	Grazer		
S94-1750	Equid	0.81	Grazer		
S94-339	Equid	-3.14	Grazer		
S94-329	Equid	-4.44		Mixed	
S94-369	Equid	-1.76	Grazer		
STS 3004	*Equus capensis*	-3.33	Grazer		
STS 3006	*Equus capensis*	-3.60	Grazer		

STS 2102&1717	*Equus capensis*	-2.89	Grazer		
STS 1972	*Equus capensis*	-4.58		Mixed	
STS 2313	*Equus capensis*	-4.83		Mixed	
	Total n=46		n=30	n=10	n=6
			65%	**22%**	**13%**

Table 6.8c

Member 5 Oldowan

7933	BP/3/16956	*Tragelaphini cf. taurotragus*	-9.38			browser
7936	BP/3/16947	*Tragelaphini cf. taurotragus*	-9.44			browser
7916	S94-7030	Large Alcelaphini	-5.00		mixed	
7929	S94-3385	Large Alcelaphini	-6.37		mixed	
7942	S94-2631	Large Alcelaphini	-7.84		mixed	
7940	S94-3898	Large Alcelaphini	0.00	grazer		
7925	S94-6124	*Antelopini cf. antidorcas*	-9.56			browser
7932	BP/3/16974	*Antelopini cf. antidorcas*	-9.23			browser
7930	S94-3459	Sml Alcelaphini cf. damaliscus	-3.97	grazer		
7934	BP/3/19870	Sml Alcelaphini cf. damaliscus	0.51	grazer		
7938	BP/3/17143	Sml Alcelaphini cf. damaliscus	-1.80	grazer		
7939	S94-2839Ave	Sml Alcelaphini cf. damaliscus	-2.97	grazer		
7918	S94-2837Ave	Sml Alcelaphini cf. damaliscus	-5.10		mixed	
8035	S94-339	Equid	-3.14	grazer		
8036	S94-329	Equid	-4.44		mixed	
		total n=15		n=6	n=5	n=4
				40%	**33%**	**27%**

Member 5 West

7924	S94-7923	Large Alcelaphini	2.96	grazer		
7926	S94-9660	Large Alcelaphini	-3.07	grazer		
7927	S94-9592	Large Alcelaphini	1.40	grazer		
7941	S94-8228	Large Alcelaphini	-4.09		mixed	
7917	S94-7327	Large Alcelaphini	0.21	grazer		
7928	S94-7314	*Antelopini cf. antidorcas*	0.74	grazer		
7943	S94-7958	*Antelopini cf. antidorcas*	-7.37		mixed	
7931	S94-9669	Sml Alcelaphini cf. damaliscus	0.17	grazer		
7935	S94-7927	Sml Alcelaphini cf. damaliscus	-1.21	grazer		
7937	S94-7251	Sml Alcelaphini cf. damaliscus	-2.08	grazer		
8038	S94-1787	*Damaliscus*	-0.38	grazer		
8039	S94-390	*Damaliscus*	-2.38	grazer		
8040	S94-349	*Damaliscus*	0.60	grazer		
8041	S94-1750	*Damaliscus*	0.62	grazer		
8037	S94-369	Equid	-0.61	grazer		
7944	SE 1258	Equid	-2.04	grazer		
7947	SE 1855.1	Equid	-0.94	grazer		
7948	SE 1125.1	Equid	0.81	grazer		
7945	SE 1334	Equid	-1.76	grazer		
7949	SE 1233.1	*Antidorcas cf. recki*	-10.79			browser
7950	SE 1770	*Antidorcas recki*	-12.68			browser
7946	SE 1614.1	*Hiippotragus. sp. af. gigas*	-5.25		mixed	
		total n=22		n=17	n=3	n=2
				77%	**14%**	**9%**

Table 6.9

Percentage of "open" indicating fauna calculated by isotopic results compared with original percentages, where available

	Total n	n Alcelaphini + Antilopini revised	% Alcelaphini + Antilopini revised	original %
ST m4 isotopic data	38	14	37	51
ST M5 Oldowan	15	6	40	n/a
SK m1 isotopic data	9	4	44	88
ST m5 isotopic data (incl. Oldowan and west)	*46*	*30*	*65*	*80*
ST m5 West	22	17	77	n/a
SK m2 isotopic data	14	10	71	87

NOTE: Sterkfontein Member 5 data in italics is included here for information, but should be replaced by Oldowan and West infills.

APPENDICES

Appendix 1a

Raw $\delta^{13}C$ and $\delta^{13}C$ values for Sterkfontein Member 4

UCT #	Catelogue #	Species		Raw Carbon	Raw Oxygen	Voltages
7883	STS 1400	Antilopini 11		-13.9	-5.5	4.3
7888	STS 2076	Antilopini 111		-11.8	-6.1	2
			duplicate	-12.4	-7.1	2.6
			duplicate	-12.1	-4.2	7.1
7892	STS 1577	Antilopini 111		-2.5	-6.8	6.8
			duplicate	-1.7	-5.5	6.5
7909	STS 1125	*Antidorcas bondi*		-1.6	-2.0	2.3
			duplicate	-1.3	-1.8	3.7
7897	STS 1435	*Antidorcas cf. recki*		-14.2	-6.4	4.5
7900	STS 1996	*Antidorcas cf. recki*		-17.1	-12.6	4.5
			duplicate	-50.9	-59.9	1.7
7886	STS 2369	*Antidorcas recki*		-10.2	-2.3	1.5
			duplicate	-11.1	-2.9	2.4
7907	STS 1944	*Antidorcas recki*		-14.4	-10.9	2.5
			duplicate	-13.9	-8.6	3.3
7911	STS 1325A	*Antidorcas recki*		-11.9	-5.7	1.8
			duplicate	-14.9	-8.5	4
7912	STS 1596	*Antidorcas recki*		-5.5	-6.7	3.7
			duplicate	-3.9	-5.4	5.5
7903	STS 2200	*Connochaetes sp.*		-5.4	-9.1	3.5
1830	SF 114	*Connochaetes cf. taurinus*		-1.6	-1.7	6.6
			duplicate	-1.8	-4.5	6.6
2753	SF 112	*Connochaetes cf. taurinus*		-0.3	0.6	3.4
7959	STS 1980	*Damaliscus*		-7.3	-4.4	4.1
7960	STS 2027	*Damaliscus*		-7.6	-3.9	5.8
			duplicate	-6.7	-5.6	6.8
2754	SF 327	*Damaliscus sp.*		-0.5	-1.6	6.6
			duplicate	-0.4	-4.4	6.6
2755	SF 328	*Damaliscus sp.*		1.6	-1.8	3.2
2756	SF 329	*Damaliscus sp.*		1.6	-1.6	4.1
2757	SF 330	*Damaliscus sp.*		0.2	-5.1	0.93

2758	SF 332	*Damaliscus sp.*	3.2	-0.8	5.2
7893	STS 1319	*Damaliscus OR Parmularis*	-2.9	-5.5	5.5
		duplicate	-1.9	-4.8	5.4
7895	STS 2046	*Damaliscus OR Parmularis*	-4.2	-4.4	1.4
		duplicate	-5.4	-6.3	3.6
		duplicate	-5.4	-5.9	4.5
7901	STS 2586(2)	*Damaliscus OR Parmularis*	0.0	-5.5	5
7901	STS 2586(4)	*Damaliscus OR Parmularis*	-0.2	-3.5	6
7901	STS 2586(5)	*Damaliscus OR Parmularis*	-0.5	-2.8	5.4
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	-4.9	-13.0	1.7
	STS 2586(1)		-1.4	-8.2	2.3
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	-1.2	-4.4	4.6
	STS 2586(3)		0.2	-5.3	3
7901	STS 2586(1,3 or 6)	*Damaliscus OR Parmularis*	-0.0	-4.0	3.5
	STS 2586(6)		-1.3	-6.2	2.7
7890	STS 2336A	*Hippotragus cf. sp. aff. gigas*	-10.9	-2.7	5.4
7906	STS 1438	*Hippotragus cf. sp. aff. gigas*	-9.9	-1.6	1.9
		duplicate	-10.3	-2.1	1.8
7885	STS 2145A	*Hippotragus gigas*	-5.1	-4.4	4.8
7881	STS 789	*Hippotragus sp. aff. gigas*	-12.7	-16.3	3.4
		duplicate	-8.2	-11.4	2.1
		duplicate	-11.3	-14.5	5.8
2784	SF 314, D13	*Hippotragus sp aff gigas*	-5.6	2.3	4.9
7887	STS 2599	*Hippotragus equinus*	-0.3	-3.0	4.8
7913	STS 1630	*Hippotragus equinus*	-2.7	-6.6	1.1
		duplicate	-2.2	-5.3	1.2
7884	STS 2059B	*Makapania broomi*	-9.5	-13.1	4.7
		duplicate	-6.5	-10.8	2.1
7889	STS 1925	*Makapania broomi*	-9.1	-3.8	5.3
7896	STS 952	*Makapania broomi*	-11.4	-4.2	3.2
7902	STS 2565	*Makapania broomi*	-3.6	-5.5	5.5
		duplicate	44.1	-102.4	0.02
7914	STS 1721	*Makapania broomi*	-6.5	-11.3	1.3
		duplicate	-14.9	-20.1	3.9
		duplicate	-7.4	-11.6	4.8

7904	STS 2075	*Redunca arundinum*	-1.7	-1.2	5.8
7882	STS 2092	*Tragelaphus sp. aff. angasi*	-5.2	-8.1	6.7
2759	046	*Tragelaphus strepsiceros*	-8.3	-0.6	5.1
2761	STS 1573	*Tragelaphus strepsiceros*	-9.3	1.9	6.5
		duplicate	-9.6	-0.5	6.5
2762	STS 2121	*Tragelaphus strepsiceros*	-7.7	-0.2	5.5
		duplicate	-7.9	-2.8	5.5
2781	SF 1300	*Tragelaphus strepsiceros*	-4.2	-2.8	4.3
1829	SF 336, D13	*Taurotragus cf. oryx*	-4.8	-2.3	5.9
		duplicate	-4.7	-4.1	5.9
1828	SF 130, D8	*Tragelaphus cf scriptus*	-4.1	-1.3	5.4
8005	STS 394B	*Cercepithecus williamsi*	-5.1	-5.3	6.8
8006	STS 300	*Cercepithecus williamsi*	-11.0	-2.1	0.9
		duplicate	-11.5	1.8	3.7
8007	STS 282	*Cercepithecus williamsi*	-5.7	-9.7	0.4
		duplicate	-4.6	-1.8	2
8008	STS 532	*Cercepithecus williamsi*	-12.6	-4.	0.7
8010	STS 279	*Cercepithecus williamsi*	-13.	-8.7	0.4
		duplicate	-12.8	-0.7	4.2
8015	STS 260	*Cercepithecus williamsi*	-11.9	-12.9	1.7
8024	STS 337	*Parapapio broomi*	-7.5	-5.6	1.6
8025	STS 346	*Parapapio broomi*	-9.0	-9.1	0.8
8026	STS 326	*Parapapio broomi*	-5.7	-5.9	3.6
8027	STS 331	*Parapapio broomi*	-9.4	-9.8	0.4
8028	STS298	*Parapapio broomi*	-11.9	-14.4	2.6
8030	STS 466	*Parapapio broomi*	-7.9	-12.4	1.1
8031	STS 339	*Parapapio broomi*	-7.1	-3.5	2.4
8033	STS 380B	*Parapapio broomi*	-18.5	-24.1	0.3
8017	STS 446	*Parapapio jonesi*	-20.9	-35.0	0.2
8018	STS 306	*Parapapio jonesi*	-8.0	-4.7	1.5
		duplicate	-7.3	-1.9	5.7
8019	STS 406A	*Parapapio jonesi*	-15.7	-17.7	0.4
8020	STS 441	*Parapapio jonesi*	-3.5	-7.3	0.6
8021	STS 340	*Parapapio jonesi*	-9.3	-5.6	1.5

8023	STS 329	*Parapapio jonesi*	-106.2	-152.9	0.1
8012	STS 263	*Parapapio whitei*	-7.7	-2.4	3.1
8013	STS 370B	*Parapapio whitei*	-11.4	-18.4	0.2
8014	STS 253	*Parapapio whitei*	-10.9	-5.9	1
8015	STS 260	*Parapapio whitei*	-11.8	-12.9	1.7
8016	STS 352	*Parapapio whitei*	-15.1	-16.2	2.2
7999	STS 139	*Canis mesomelas*	-4.6	-27.7	0.08
8000	STS 136	*Canis mesomelas*	-5.8	-14.6	0.366
8001	STS 2089	*Canis mesomelas*	-3.9	-7.9	0.6
8002	STS 138	*Canis mesomelas*	-5.8	-14.8	0.371
7964	S94-3	*Chasmoporthetes nitidula*	-4.5	-4.1	1.9
7965	S94-7195	*Chasmoporthetes nitidula*	-8.9	-4.9	1.7
7980	SF 435	*Chasmoporthetes nitidula*	-7.6	-10.7	0.6
7981	SF 409	*Chasmoporthetes nitidula*	-4.5	-3.1	3.1
7982	SF363	*Chasmoporthetes nitidula*	-7.4	-3.0	1.8
7983	SF 463	*Chasmoporthetes silderbergi*	-6.5	-5.3	0.576
7984	SF 452	*Chasmoporthetes silderbergi*	-16.8	-21.0	1.1
7985	SF 408	*Chasmoporthetes silderbergi*	-6.1	-7.1	1.1
7986	SF 369+372	*Chasmoporthetes silderbergi*	-6.7	-4.9	1
7992	384	*Crocuta crocuta*	-6.0	-5.2	0.9
7993	414	*Crocuta crocuta*	-9.2	-8.8	1.489
8003	STS 128	*Crocuta crocuta*	-3.3	-5.1	1.6
7970	S94-56A	*Dinofelis barlowi*	-19.8	-25.4	1.3
7972	S94-9	*Dinofelis barlowi*	-8.1	-6.7	1.1
7989	443/444	*Dinofelis barlowi*	-7.4	-7.2	0.8
7997	STS 132	*Dinofelis barlowi*	-4.6	-6.4	2
7998	STS 131	*Dinofelis barlowi*	-6.1	-22.3	0.1
7959	SF 420	*Homotherium latidens*	-7.6	-3.2	3.1
7960	SF 434	*Homotherium latidens*	-8.2	-3.4	2.2
7961	397	*Homotherium latidens*	-7.5	-12.1	0.3
7962	388	*Homotherium latidens*	-8.6	-6.9	0.477
7994	436	*Hyena brunnea*	-6.2	-6.9	1.4
7988	416	*Pachycrocuta breviostris*	-5.7	-6.9	1

7967	S94-2	*Panthera leo*	-6.9	-3.9	1.06
7977	SF 381	*Panthera leo*	-18.4	-21.0	0.8

Appendix 1b

Raw $\delta^{13}C$ and $\delta^{13}C$ values for Sterkfontein Member 5

UCT #	Catelogue #	Species		Raw Carbon	Raw Oxygen	voltages
7925	S94-6124	*Antelopini cf. antidorcas*		-9.8	-2.9	1.3
			duplicate	-9.8	-3.0	1.9
7928	S94-7314	*Antelopini cf. antidorcas*		0.1	1.4	2.5
			duplicate	0.9	1.9	1.3
7932	BP/3/16974	*Antelopini cf. antidorcas*		-9.7	-4.9	2.6
7943	S94-7958	*Antelopini cf. antidorcas*		-7.2	-2.4	5.2
			duplicate	-7.9	-3.3	6.5
7944	SE 1258	*Antidorcas cf. recki*		-11.0	-10.3	3.2
			duplicate	-11.0	-2.8	1.4
7947	SE 1855.1	*Antidorcas recki*		-13.2	-3.8	2.5
7948	SE 1125.1	*Hip. sp. af. gigas*		-5.5	-2.9	1.5
			duplicate	-5.5	-2.8	1.7
7945	SE 1334	*Damaliscus*		-0.7	-6.7	1.9
			duplicate	-0.6	-7.0	1.9
7949	SE 1233.1	*Damaliscus*		-4.2	-12.9	3.1
			duplicate	-1.1	-6.5	2.5
7950	SE 1770	*Damaliscus*		1.1	-5.3	1.2
			duplicate	-0.4	-7.6	2.5
7946	SE 1614.1	*Damaliscus cf. sp2*		0.2	-6.3	2.3
7951	SE 1185	*Damaliscus dorcas*		-1.9	-10.2	0.6
			duplicate	-4.9	-12.7	3
7930	S94-3459	Sml Alcelaphini cf. damaliscus		-4.4	-4.1	3.7
7934	BP/3/19870	Sml Alcelaphini cf. damaliscus		0.3	-2.9	5.5
			duplicate	0.3	-3.7	6.5
7938	BP/3/17143	Sml Alcelaphini cf. damaliscus		-2.2	-5.7	6.9
7939	S94-2839(1)	Sml Alcelaphini cf. damaliscus		-5.7	-5.5	2.2
			duplicate	-5.5	-6.3	1.7
7939	S94-2839(2)	Sml Alcelaphini cf. damaliscus		-1.9	-3.7	2.1
			duplicate	-1.2	-2.4	1.6
7939	S94-2839(3)	Sml Alcelaphini cf. damaliscus		-2.4	-5.9	2.2
			duplicate	-2.5	-5.8	2.4
7918	S94-2837(1)	Sml Alcelaphini cf. damaliscus		-6.6	-5.4	1.8

		duplicate	-5.9	-7.8	0.4
7919	S94-2837(2)	Sml Alcelaphini cf. damaliscus	-6.7	-6.2	0.8
7920	S94-2837(3)	Sml Alcelaphini cf. damaliscus	-5.6	-4.2	3.2
7921	S94-2837(4)	Sml Alcelaphini cf. damaliscus	-5.9	-5.3	2.4
		duplicate	-5.5	-5.4	2.3
7922	S94-2837(5)	Sml Alcelaphini cf. damaliscus	-5.1	-6.2	0.7
7923	S94-2837(6)	Sml Alcelaphini cf. damaliscus	-4.1	-4.3	2.9
7931	S94-9669	Sml Alcelaphini cf. damaliscus	-0.0	-3.8	6.7
		duplicate	-0.1	-4.1	6.7
7935	S94-7927	Sml Alcelaphini cf. damaliscus	-1.2	-4.6	6.6
		duplicate	-1.6	-5.6	5.5
7937	S94-7251	Sml Alcelaphini cf. damaliscus	-12.5	-21.2	2.9
		duplicate	-2.2	-7.9	2.1
7916	S94-7030	Large Alcelaphini	-5.1	-0.7	1.9
		duplicate	-4.9	-1.2	3.6
		duplicate	-5.4	-1.6	3.4
7924	S94-7923	Large Alcelaphini	2.6	-5.8	1.6
		duplicate	2.9	-4.8	1.2
7926	S94-9660	Large Alcelaphini	-3.2	-8.9	6.8
		duplicate	-3.4	-9.4	6.5
7927	S94-9592	Large Alcelaphini	1.0	-4.2	3.3
7929	S94-3385	Large Alcelaphini	-6.5	-6.5	2.2
		duplicate	-6.6	-7.2	2.2
		duplicate	-6.4	-5.4	3.7
7941	S94-8228	Large Alcelaphini	-4.5	-6.8	3.7
7942	S94-2631	Large Alcelaphini	-7.8	-1.0	3.9
		duplicate	-8.2	-2.5	4.9
7917	S94-7327	Large Alcelaphini	0.4	-4.9	2.1
		duplicate	-0.5	-4.9	3.6
7940	S94-3898	Large Alcelaphini	-0.4	-4.3	1.9
		duplicate	-0.2	-4.1	1.8
		duplicate	-0.1	-3.5	4.7
7933	BP/3/16956	*Tragelaphini cf. taurotragus*	-9.9	-2.2	1.9
		duplicate	23.1	-40.6	0.02
7936	BP/3/16947	*Tragelaphini cf. taurotragus*	-9.2	-3.1	1.5
		duplicate	-5.3	-5.6	1.18
		duplicate	-10.0	-4.1	5.5
2749	SF 334	*Connochaetes sp.*	-0.8	-2.6	3.4
2750	SF 92	*Connochaetes sp.*	0.9	-1.3	4.8

2751	SF 95	*Connochaetes sp.*		2.9	1.7	3.7
2752	SF 91	*Connochaetes sp.*		-1.1	0.1	5.2
8038	S94-1787	Equid		-0.8	-5.9	6.6
8039	S94-390	Equid		-2.2	-4.0	3.7
8040	S94-349	Equid		-1.1	-5.2	2.6
8041	S94-1750	Equid		0.6	-3.9	1.9
8034	S94-337	Equid		-1.1	-4.3	0.6
8035	S94-339	Equid		-3.3	-5.1	1.06
8036	S94-329	Equid		-4.5	-3.6	1.08
8037	S94-369	Equid		-1.9	-7.6	1.2
7898	STS 3004	*Equus capensis*		-3.8	-8.4	1.4
7899	STS 3006	*Equus capensis*		-4.0	-4.7	3.5
			duplicate	-4.1	-21.9	0.12
7905	STS 2102&1717	*Equus capensis*		-3.3		5.3
7910	STS 1972	*Equus capensis*		-5.0	-5.3	4.5
7915	STS 2313	*Equus capensis*		-5.3	-6.5	4.3
8042	SWP 2484	*Cercepithecoides* indet.		-6.5	-6.9	0.8
8043	SWP 2674	*Cercepithecoides* indet.		-7.4	-15.9	0.1
			duplicate	-7.5	-3.7	2.8
8044	SWP 2207	*Cercepithecoides* indet.		-3.9	-8.4	1.1
			duplicate	-3.4	-5.8	1.8
8045	SWP 2773	*Cercepithecoides* indet.		-7.7	-9.0	0.5
8047	SWP 2465	*Cercepithecoides* indet.		-0.3	-5.7	6.8
8048	SWP 2311	*Cercepithecoides* indet.		-3.7	-10.5	0.5
8050	SWP 2420	*Cercepithecoides* indet.		-7.2	-5.8	0.9
8052	SWP 2446	*Cercepithecoides* indet.		-5.6	-14.4	0.2
8054	SWP 2145	*Cercepithecoides* indet.		-2.4	-7.7	5.1
8056	SWP 2174	*Cercepithecoides* indet.		-3.1	-6.2	0.9
7963	S94-8061	*Chasmoporthetes nitidula*		-4.9	-7.3	1.8
7990	S94-112	*Crocuta crocuta*		27.1	-30.5	1.4
7987	376	*Pachycrocuta breviostris*		-9.6	-8.8	1.5
7966	S94-132	*Panthera leo*		-2.5	-10.3	0.4
7968	SF 4151	*Panthera leo*		-7.7	-6.1	1.5
7969	S94-149+150	*Panthera leo*		-7.9	-6.7	1.8
7973	SF 2858	*Panthera leo*		-10.2	-8.4	1.6

7974	S94-23	*Panthera leo*	-2.7	-6.8	2.4
7975	S94-7228	*Panthera leo*	-3.8	-7.1	1.09
7978	BP/3/19777	*Panthera leo*	-4.2	-6.8	1.2
7995	S94-7238	*Parahyena brunnea*	-2.4	-6.9	7
7996	S94-25	*Parahyena brunnea*	-4.8	-10.9	0.5

Appendix 2

Monthly Calibration equations

	Carbon calibration	**Oxygen calibration**
August 2000	y = 1.0345x - 0.3016	y = 1.0247x - 0.1798
September 2000	y = 0.9891x + 0.3822	y = 1.0291x + 2.2614
October 2000	y = 1.0177x + 01477	y = 0.9952x + 2.3254
November 2000	y = 1.0383x + 0.2377	y = 1.0465x + 3.3047
April 2001	y = 1.0158x + 0.0476	y = 1.0109x + 2.1478