Taxon-free ecomorphological analysis of fossil bovids from the Sterkfontein and Swartkrans deposits, South Africa

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science

FACULTY OF SCIENCE

UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

2020

Declaration

I, Recognise Sambo, hereby declare that this dissertation "Taxon-free ecomorphological analysis of fossil bovids from the Sterkfontein and Swartkrans deposits, South Africa" is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

Recognise Sambo

Date: October 2020

Abstract

Sterkfontein and Swartkrans caves (1 km apart) are situated in the Cradle of Humankind World Heritage Site, Gauteng, South Africa. The two sites hold records of the two Earlier Stone Age tool technologies (Oldowan and Acheulean), and have yielded significant fossil hominins in southern Africa that span the late Pliocene and early Pleistocene period. This is the first study in the Cradle which applies a 'taxon-free' ecomorphological approach to investigates palaeoenvironmental changes at Sterkfontein and Swartkrans caves between 2.8 and 1.5 Ma through the functional morphology of well-preserved bovid astragali. Seven measurements were taken on 55 bovid astragali following methods employed by previous studies. A Discriminant Function Analysis (DFA) was conducted to compare morphologies of unknown fossil bovids astragali from these two sites to published modern bovid astragali of known ecological adaptations (e.g., open cover, light cover, heavy cover, forest). Results show that morphologically, bovids from the two sites are adapted to a mosaic of habitats. Bovids from Sterkfontein Member 4 (STK-M4) ~2.8-2.4 Ma manoeuvered in less complex environmental settings such as open plains, grasslands, tall grasses, light bushes, as well as medium density heavy cover environments (e.g., bushlands, woodlands), and a riparian forest. Similar environmental conditions persisted to the time of Sterkfontein Member 5 East, Oldowan infill (STK-M5E) ~2.18 Ma although with more tree cover. In contrast, the environment at Swartkrans during the deposition of Member 1 Lower Bank, Oldowan (SKX-M1 LB) ~ 2.2 Ma was favourable to bovids adapted to light cover, moderate open cover and forest habitats with no heavy cover. The same conditions are evident during Swartkrans Member 2, Acheulean (SKX-M2) times ~1.5 Ma but it seems the environment was opening up more. These results suggest a time transgressive trend from medium density heavy cover and forest environments to more light cover and open environments associated with the expansion of grasslands between ca. 2.8 Ma to 1.5 Ma at the two sites. This fits well with the broader reconstructions of palaeoclimatic change in Africa and in the Cradle, which suggest drying trends resulting in more varied and open environments during the Plio-Pleistocene onwards.

Acknowledegments

Funding for this research was provided by the National Research Foundation (NRF) and the DSI-NRF Centre of Excellence in Palaeosciences (CoE Palaeo). I will forever be indebted to these organizations for providing funding for the two years of my research.

This study would not have been possible without the assistance of the following people:

My supervisor, Prof Dominic Stratford:

Thank you for accepting to be my primary supervisor when I needed one and for treating me as a mature student and allowing me to explore all options in my studies in archaeology. Your willingness to always help is priceless and I really appreciate it.

Dr Maria Carmen Arriaza, my co-supervisor:

You were more than just a supervisor; you were a sister and a friend that I needed the most in this journey. I really appreciate you for allowing me to inconvenience you when I needed you, you would leave everything just to attend to my cases and you gave the best academic and personal advices. Thank you, my psychologist.

Professor Kathleen Kuman, my co-supervisor:

Describing you is very difficult because to me you have always been a mother I never had. Throughout the years, you have taken it upon yourself to be concerned about my academics and wellbeing. You have imparted in me a skill of academic writing which I will forever use and pass it on as I continue with my academics. Your recommendations, and support letters are mind blowing and only you can describe me better in this field. You always look out for opportunities for me to fill and I will forever be indebted to you. You are my role model in this field, and I cannot trade your love and kindness for anything.

Dr Matthew Caruana, my statistics advisor:

I learnt a lesson from you that “It is never too late to learn something new”. I never had any statistics background before I began this project, but you walked me through it, although it was not easy you made sure that I do not panic because it was all a learning process. You always took time off your hectic schedule to accommodate me and I am truly grateful.

Professor Travis Pickering, my advisor:

Although you were not in the country most of the time, you helped me develop this project with all the knowledge you have. I knew nothing about taxon-free, but you broke it down for me to easily understand it and believed in me to take up such a huge project. Thank you.

I would also like to thank the following persons who were part of my committee:

Drs Christine Steininger, Jerome Reynard, Matthew Caruana, and Stephanie Baker as well as Prof Amanda Esterhuysen for their valuable comments in the early days of my research, your input gave my research a sense of direction and made a huge difference. I regard myself to be extremely privileged for having knowledgeable people like you as part of committee members, and I appreciate all of you.

Dr Irene Esteban:

Thank you for your valuable input on the issue of palaeoenvironmental reconstruction. Your contributions have bettered my understanding and interpretations when engaging with the literature.

In addition, I thank:

My colleagues, family and friends for all their support and encouragement, and most importantly, I would like to appreciate my Fiancé Kobby for his love and support throughout this journey, your patience is indescribable. Thanks for sharing in my interests even when what I study does not always make sense to you.

Without all of you, this dissertation would still be a dream. Many thanks!

Dedication

First, I dedicate this thesis to myself for having the courage to take up such a huge task and for allowing myself to learn through the process.

I appreciate myself for the time and effort I invested in this study. I believe that self-appreciation is all about being kind to yourself.

Secondly, I dedicate this thesis to Professor Kathleen Kuman, about six years ago you said to me the very first time I spoke to you, it is possible to survive in this field if only you are driven by love and passion for it. It is not really a field for those who want to lead a luxurious life, but if you are focused then you will thrive. You have always been my greatest motivation, and I will forever be indebted to you for taking me under your wing and believing in me from the early days of my university life.

Today, I believe I can do anything I put my mind to because of your constant reminder that where there is will there is a way.

Lastly, I would like to dedicate this thesis to Dr Maria Carmen Arriaza. You are the most selfless supervisor I have ever encountered throughout my university days and really, I am putting a proposal down for you to come back and be my PhD supervisor. You are just the best.

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Chapter 1: Introduction

The Sterkfontein and Swartkrans caves are two of the richest and most informative fossil hominin localities of the late Pliocene and early Pleistocene period (Balter *et al.* 2008; Kuman *et al.* 2018). The two sites are located just over one km apart, across the Sterkfontein Valley from each other (Avery 2001; Kuman & Field 2009; Kuman *et al.* 2018) in the Cradle of Humankind World Heritage Site, approximately 50 km north-west of Johannesburg in Gauteng Province, South Africa (Stratford e*t al.* 2011) (see Figures 1.1 and 1.2). The two sites yielded abundant and diverse faunal assemblages (Brain 1981; Pickering 1999; Pickering *et al.* 2004, 2007, 2008; Kibii 2004; Ogola 2009; Reynolds & Kibii 2011) in association with hominins (Broom *et al.* 1950; Leakey 1970; Clarke 1988, 2008, 2013; Grine 1993; Kuman & Clarke 2000; Reynolds *et al.* 2003, 2007; Pickering *et al.* 2012, 2016; Wood & Boyle 2016), and other archaeological traces, i.e., stone tools (Kuman 1994, 1998; Kuman & Clarke 2000; Kuman & Field 2009), butchered animal bones, and bone tools (Brain 1993; Backwell & d'Errico 2001, 2003; d'Errico & Backwell 2009; Pickering & Brain 2010). These assemblages represent a broad period from the Late Pliocene and Early Pleistocene to the Middle Pleistocene (~3.0-1.0 Ma) which coincided with critical events of hominin evolution.

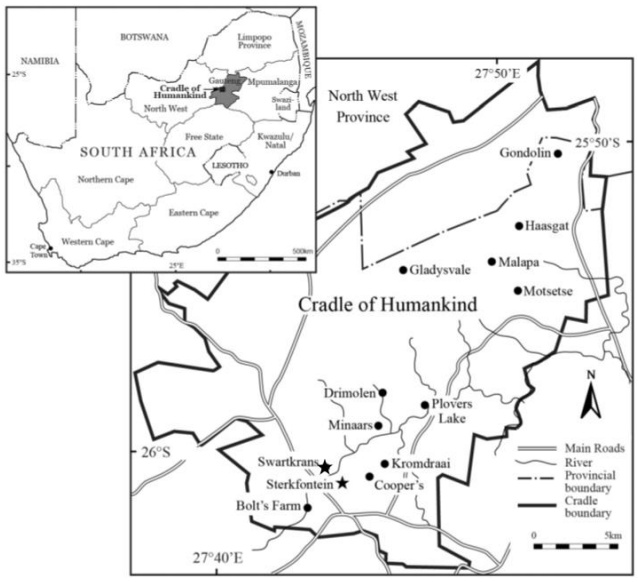


Figure 1.1: Map of southern African showing Sterkfontein and Swartkrans caves in the Cradle of Humankind to the other key fossil sites (from Stratford et al. 2014).

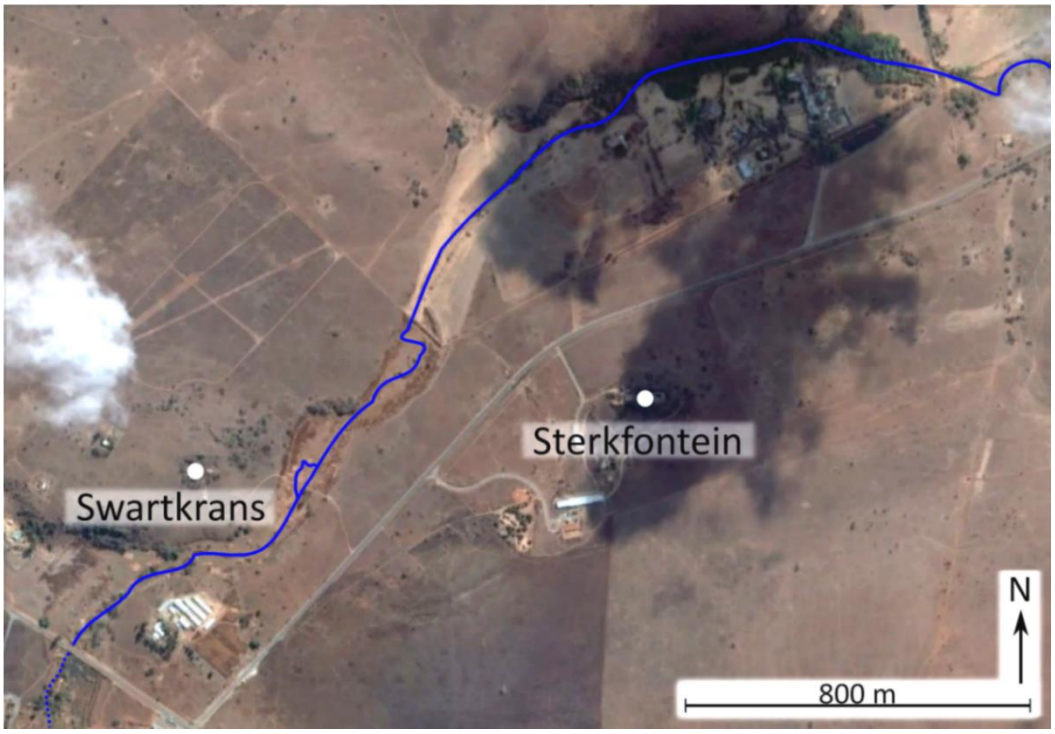


Figure 1.2: Map showing the position of Sterkfontein and Swartkrans sites to the Bloubank River in the Cradle of Humankind World Heritage Site (from Kuman et al. 2018).

For this reason, the two Cradle sites are relevant to investigating major events underlying hominin evolution during the Plio-Pleistocene. The majority of these investigations are based on the hypothesis that at approximately ca. 3 to 1.0 million years ago (Ma), large scale climatic shifts and increased aridity changed the Cradle landscape from closed wooded environments to more open savanna environments (Vrba 1985, 1988, 1995; de Menocal 1995, 2004, 2011; Reed 1997; Maslin & Christen 2007; Potts 2013; Maslin *et al.* 2014). In trying to understand these links, an increasing amount of research has been dedicated to studying the palaeoenvironmental records. As Potts (2013:10) notes, "palaeoclimate, vegetation, and faunal and landscape change are likely to reflect, and potentially predict, the selective forces that shaped the survival and extinction of early hominin populations over time and space". In these contexts, selective pressures forced extinction, speciation, changes in morphological and behavioural adaptations that gave hominins selective advantage to traits (Antón *et al.* 2014), such as toolmaking (Leakey 1970, 1971; Clark 1993; Kuman 1994; Plummer 2004; Roche *et al.* 2009; Potts 2013), increased dietary flexibility (Vrba 1988a; de Menocal 1995, 2004,

2011), and carnivory (Blumenschine 1988, 1995; Dominguez-Rodrigo 1997; Pobiner & Blumenschine 2003; Pickering & Domínguez-Rodrigo 2006; Pickering & Brain 2010), increased foraging (Pickering 2001; Domínguez-Rodrigo *et al.* 2007; Braun *et al.* 2010; Ungar 2012; Ferraro *et al.* 2013; Lemorini *et al.* 2014), increased cognitive function with larger brain size and body size (Vrba 1994; Stout *et al.* 2008), improved locomotion and long-distance mobility (Shipman & Walker 1989; Ruff & Walker 1993; Aiello & Wheeler 1995; Bramble & Lieberman 2004), and other adaptive traits.

Because "important selective pressures that have shaped hominin evolution are environmentally driven, reliable reconstructions of past environmental conditions are essential for building and testing hypotheses about human evolution" (Forrest 2012:3). Most palaeoenvironmental reconstructions are based on mammalian fossils, particularly that of bovids, because they provide the most informative ecological insights or clues of the environments they inhabit, and ultimately, the environments they shared with hominins.

Traditionally, attempts at reconstructing past environments using bovids often relied on taxon-based methods which assumes that past ecological frameworks of fossil species are the same as the ecological preference of their extant relatives (Vrba 1977; Gentry 1978; Reed 1998). This method is useful but requires some level of certainty in taxonomic identifications to species level and phylogenetic information (Vrba 1980, 1984, 1985a, 1995, 2000; Bobe & Eck 2001; Bobe *et al.* 2002; Bobe & Behrensmeyer 2004; de Ruiter *et al.* 2008). Similarly, isotope studies (Lee-Thorp & van der Merwe 1993; Lee-Thorp 2000; Lee-Thorp *et al.* 2007; Sponheimer & Lee-Thorp 1999; van der Merwe *et al.* 2003; Sponheimer & Lee-Thorp 2003; Sponheimer *et al.* 2003; Cerling *et al.* 1997; Cerling & Harris 1999; Luyt 2001; Luyt & Lee-Thorp 2003; Codron 2006; Kingston & Harrison 2007; Plummer *et al.* 2009; White *et al.* 2009; Steininger 2011) using bovid dietary behaviour to yield past ecological insights rely on the assumption of taxon uniformitarianism. Although taxon uniformitarianism has proven to be useful, researchers also highlighted some problems associated with this method that can

limit clear reconstructions: 1) extinct species may not necessarily have modern counterparts; 2) bovids, in particular, may access a wide range of ecosystems because of their flexible behaviour; and 3) due to their flexible behaviour in various ecosystems, a species can change its diet preference through time (Sponheimer & Lee-Thorp 2003; Codron 2006; Steininger 2011).

The current study uses a taxon-free ecomorphological analysis approach for inferring palaeoenvironments from the functional morphology ('ecomorphology') of astragalus bones (ankle bones) from members of the Family Bovidae, recovered from the Sterkfontein and Swartkrans deposits that span from 2.8 to 1.5 Ma. This approach is labelled 'taxon-free' because this approach is independent of taxonomic identifications of taxa or species. The underlying assumption of 'ecomorphology' is that the locomotor anatomy of an animal has adaptations to the substrate in which it navigates (Degusta & Vrba 2003). This study builds upon and expands on previous ecomorphological studies done on bovid postcranial bones. A qualitative assessment following Gentry (1970); Kappelman (1988); Plummer & Bishop (1994); Kappelman *et al.* (1997); Kovarovic *et al.* (2002); Degusta & Vrba (2003, 2005); and Bishop *et al.* (2011) is performed by taking linear caliper measurements from samples of astragali and analysed using a Discriminant Function Analysis (DFA). This study presents the first attempt to predict habitats, based on the functional morphology of bovids postcranial bones, from these two significant hominin localities in the Cradle, South Africa.

The application of taxon-free ecomorphological analysis in this study provides a means of adding another perspective to the results obtained with traditional taxonomic methods. The method has the potential to search for detailed similarities and differences in the morphological and locomotor adaptations of bovids within two micro-habitats (small specialized habitats within large habitats). The taxon-free analysis thus provides another means of investigating the palaeoecology of hominins associated with the bovid assemblages during the time of deposition. If the taxon-free analysis shows differences between the two sites, explanations may be explored. Variation may be the result of (1) geographic differences between the

two sites; (2) time-averaging due to the long depositional time of these deposits. Alternatively, taphonomic bias may be responsible due to the different accumulating agents at the two sites. (1) The Sterkfontein Member 4 (STK-M4) bovid assemblage was a result of a death-trap, slope wash, carnivore accumulation with little porcupine action (Kibii 2004); (2) Sterkfontein Member 5 East, Oldowan infill (STK-M5E) also accumulated via natural death trap and slope wash, (Pickering 1999) with porcupine, hominin, and little carnivore contribution; (3) the Swartkrans Member 1 Lower Bank, Oldowan (SKX-M1 LB), and Member 2, Acheulean (SKX-M2) bovid assemblages were largely a carnivore accumulation (leopards feeding on primates and bovids), and birds, with some hominin influence (Brain 1981, 1993; Pickering *et al*. 2004, 2005, 2007, 2008; Pickering & Brain 2010); (4) there is an extreme skewness in bovid size-types between the two site assemblages. For example, the Sterkfontein bovid assemblages have bovids ranging from size classes I to III, whereas Swartkrans bovids range from size classes II to III. This could suggest prey selection at Swartkrans based on animal size. Alternatively, the differentiation in the environmental settings for both sites could be due to ecomorphology in general without taphonomic biases.

1.1 Research Questions

The goal of this project was to address the following research questions:

1. What can a taxon-free ecomorphological analysis of postcranial bone assemblages from Sterkfontein and Swartkrans caves tell us about the morphological and locomotor adaptations of bovids ca 2.8 Ma to 1.5 Ma?
2. What are the palaeoenvironmental implications of the ecomorphological evidence from the fossil bovid astragali for the following deposits: Sterkfontein Member 4 (STK-M4) and Member 5 East, Oldowan infill (STK-M5E) ca. 2.8-2.18 Ma, Swartkrans Member 1 Lower Bank, Oldowan (SKX-M1 LB), as well as Member 2, Acheulean (SKX-M2) deposits ca. 2.2-1.5 Ma?

1.2 Aims and Objectives

The aim of this research was to place these assemblages within their ecological contexts to search for similarities or differences between the two sites, but specifically to provide another analysis for that period's environment and potentially understand variability in the hominin habitats across a (geologically brief) chronology and over (a minimal) geographic span.

The objective was to use taxon-free analysis of abundant bovid astragali to provide a new perspective that may help to clarify localized palaeoenvironments between ca. 2.8 to 1.5 Ma.

1.3 Null Hypothesis

As Sterkfontein and Swartkrans are only one kilometre apart and lie at the same elevation, no difference in locomotor adaptations of bovids is expected because they inhabited similar palaeoenvironmental settings.

1.4 Alternative Hypothesis

Locomotor differences in bovid postcranial bones can be expected because of one or more of the following differences: a) as mentioned earlier, the taphonomy of the two sites differs, (for Sterkfontein see Pickering 1999; Kibii 2004, and for Swartkrans see Brain 1981, 1993; Pickering *et al*. 2004, 2005, 2007, 2008; Pickering & Brain 2010); b) the wetter geographic context at Swartkrans, which is directly influenced by flooded grasslands and reed beds (Watson 1993; Reed 1997; Kuman & Clarke 2000), may be seen in differences in the bovid fauna using the two sites; c) the Bloubank river is known to be much larger and wider in the past (Martin *et al.* 2003; Kuman 1996; Kuman & Clarke 2000; Kuman *et al.* 2018), and could have created a boundary between the two sites, so regardless of bovid home ranges and sizes, bovids from the two sites accessed different microhabitats; d) there could be tens of thousands of years between the accumulations of STK-M4, STK-M5E Oldowan as well as Swartkrans SKX-M1 LB, Oldowan and SKX-M2, Acheulean which create adaptive differences; or e) we may be studying climatic

and environmental change (including millennial-scale change) across the two sites over time.

1.5 Organisation of the Thesis

This project is part of a wider discussion on Plio-Pleistocene environments based on faunal remains in the Earlier Stone Age. Each chapter has a brief introduction which describes the layout and the structure of the chapter.

Chapter 1- General Introduction: introduces the study, research questions, the aims, objectives, hypotheses, and highlights the significance of the project.

Chapter 2- Site Background and Literature Review: in this chapter I present a background to the sites in question which includes site descriptions, site formations and site age determinations. I provide the background and review of traditional palaeoenvironmental studies and ecomorphological studies done in Africa and other parts of the world.

Chapter 3- Materials and Methods: in this chapter I present detailed descriptions of the materials and taxon-free ecomorphological methods referred to and used for this project.

Chapter 4- Results: data for this project is presented in three sections: 1) statistics summary for the raw measurements obtained for comparison; 2) Discriminant Function Analysis (DFA) results for all raw measurements for the extant bovid specimen sample for a four-habitat model is presented; 3) Lastly, habitat prediction results for a four-habitat model for all raw measurements of the fossil samples for each Member and each site (e.g., STK-M4, STK-M5E, SKX-M1 LB, SKX-M2) are presented.

Chapter 5- Discussion and Conclusion: the final chapter of the dissertation presents the discussion and analysis of the data obtained in the results section and subsequent outcomes. The conclusion is a summary of the research presented in this dissertation, as well as future avenues for continued research.

Chapter 2: Site Background & Literature Review

This chapter is divided into two sections. The first section provides a detailed overview of the early discovery of the two hominin-bearing sites, Sterkfontein and Swartkrans caves. The stratigraphy of each site is described with a brief emphasise on the site's geological contexts, and cave formations processes describing each deposit that make up the two sites, as well as their age determinations. The second section presents a review of previous palaeoenvironmental reconstructions using faunas from the Sterkfontein and Swartkrans deposits that are the subject of study in this research, a review of previous ecomorphological studies using various cranial and postcranial bovid bones, and the application of a Discriminant Function Analysis (DFA).

2.1 Sterkfontein Caves

The Sterkfontein caves lie within the dolomitic limestone hills approximately 50 km northwest of Johannesburg, in Gauteng Province, South Africa (Stratford *et al*. 2011). It was first recognised in 1936 as a significant palaeoanthropological site and placed in the international limelight when Dr Robert Broom discovered the first adult *Australopithecus* fossil--then the type specimen of *Australopithecus transvaalensis* but now placed in *A. africanus* (Broom 1936). At this time, Sterkfontein breccia deposits were exposed due to the lime quarrying operations at the site. These exposed deposits became known as the 'Type Site', where Broom and John Robinson conducted systematic excavations from 1947-1949 and discovered many *Australopithecus* fossils (i.e., the Sts 5 cranium of *A. africanus* known as 'Mrs Ples' and the Sts 14 partial skeleton), as well as associated fauna and archaeological specimens (Broom 1947; Broom *et al.* 1950; Robinson 1997).

These and subsequent discoveries urged numerous researchers to analyse and interpret the complex depositional context of the Sterkfontein artefacts and fossil-bearing breccia with the first stratigraphic interpretations by Cooke (1938). Following Cooke, other stratigraphic analyses were done by researchers: Robinson (1957, 1962); Brain (1958); Wilkinson (1973, 1983, 1985); Partridge (1978); Partridge & Watt (1991); Clarke (1994, 2006); Kuman & Clarke (2000). More

recent investigations by several researchers have recently provided refined interpretations of the complex depositional and post-depositional process that makes up the underground Sterkfontein deposits (Stratford *et al.* 2012, 2014; Bruxelles *et al.* 2014, 2019).

2.2 Stratigraphy

2.2.1 Geological Context and Sterkfontein Formation

The Sterkfontein karst system probably formed at approximately 20 to 30 million years ago within the Oaktree and Monte Christo Formations of the Malmani subgroup of the Chuniespoort Group (Eriksson *et al.* 1993) "of late Archaean age ~2.5-2.6 billion years" (Martini *et al.* 2003:48). It is formed within a heavily faulted dolomitic-limestone rock at levels some 50 or 60 metres below the original surface (Martini *et al.* 2003). The faulted dolomitic limestone and formation of passages were a result of "the gradual chemical dissolution of the soluble elements of the host rock by weakly acidic waters, and the simultaneous removal of the dissolved minerals, and the chemical erosion of the insoluble particles" in the phreatic zone (Dubois *et al*. 2014:118; and see Martini *et al.* 2003). As we see today, the morphology of the developing karst network at Sterkfontein is a result of this gradual dissolution of the dolomite forming numerous caverns underground prior to the collapse of cave roof that led to the various openings of the caves to the surface (Wilkinson 1983; Martini *et al.* 2003; Dubois *et al*. 2014). It is within this underground karst system that a wealth of the Sterkfontein fossiliferous deposits and artefact assemblages were deposited through geogenic and biogenic processes (Pickering 1999; Pickering *et al.* 2004; Kibii 2004; Stratford 2011).

It was through the study of various exposed sections that Partridge (1978) first defined the 'Sterkfontein Formation' with older deposits at the lower levels and younger ones at higher levels (see Figure 2.1). As known today, the Sterkfontein deposits are grouped into six principal stratigraphic members (Member 1 to Member 6, or M1-M6), the oldest being Member 1 and the youngest Member 6 (Partridge 1978; Partridge & Watt 1991; Clarke 1994, 2006; Kuman & Clarke 2000; Stratford 2008, 2011; Pickering & Kramers 2010; Reynolds & Kibii 2011).

Geological Members 1, 2, and 3 are found within the oldest underground chamber known as the Silberberg Grotto, whereas the younger Members 4, 5 and 6, as well as the Post-Member 6 Infill is what we see today exposed on the landscape surface (Partridge 1978; Partridge & Watt 1991).

Member 1

M1 which is not yet dated, developed in the cave network before the opening of the cave to the surface through the initial collapse and break-down of the roof of the cave. It is a basal deposit resting on the dolomitic floor of the Silberberg Grotto (Partridge 1978; Martini *et al.* 2003; Reynolds & Kibii 2011). The sterile deposit is a 12m-thick layer made up angular dolomitic blocks and chert (Martini *et al.* 2003; Stratford 2008; Reynolds & Kibii 2011).

Member 2

M2 is the first deposit to contain externally derived material (Partridge & Watt 1991) and hence is the "earliest fossiliferous infilling at Sterkfontein which is partially contained within the Silberberg Grotto" (Stratford *et al.* 2014:156). It is the resting place of StW 573 famously known as the 'Little Foot' (*Australopithecus*) skeleton (Clarke 1998, 2019). Recent stratigraphic work suggests that M2 originally spreads into the lower chambers, like Milner Hall (Stratford *et al.* 2014). Based on cosmogenic burial dating, recent dates provided by Granger (*et al.* 2015) for this member are 3.67 ± 0.16 Ma.

Member 3

M3 is a fossil-bearing breccia which is preserved in the Silberberg Grotto. This breccia built up against the stalagmite boss (flowstone) covering M2 (Clarke 2006:61). According to Partridge & Watt (1991), M3 breccia (not yet excavated) is calculated to be at least 10m thick and consists of recalcified reddish-brown sediments (and see Partridge 1978; Martini *et al.* 2003). Pickering & Kramers (2010) suggested that M3 should be regarded as M4 because they claim it represent the distal portion of M4. However, Reynolds & Kibii (2011) suggested that it is

only with the excavation and analysis of M3 that this hypothesis can be confirmed. If correct, M4 is far greater in extent than previously known. Most recently, Bruxelles *et al.* (2019) disproved this argument with their detailed stratigraphic work on underground deposits.

Member 4

As mentioned earlier, Members 4, 5 and 6 and Post-Member 6 are exposed on the landscape surface and had accumulated into one or two larger upper chambers. M4 (~2.8-2.4 Ma) is the most well-known deposit of the Sterkfontein Formation. There have been different dates proposed for M4 over the years, but in this section, I only present more recent dates. Based on Uranium-Lead and Uranium-Thorium dating by Pickering & Kramers (2010) M4 is dated around 2.65-2.01 Ma, while Electron spin resonance (ESR) dating and palaeomagnetism by

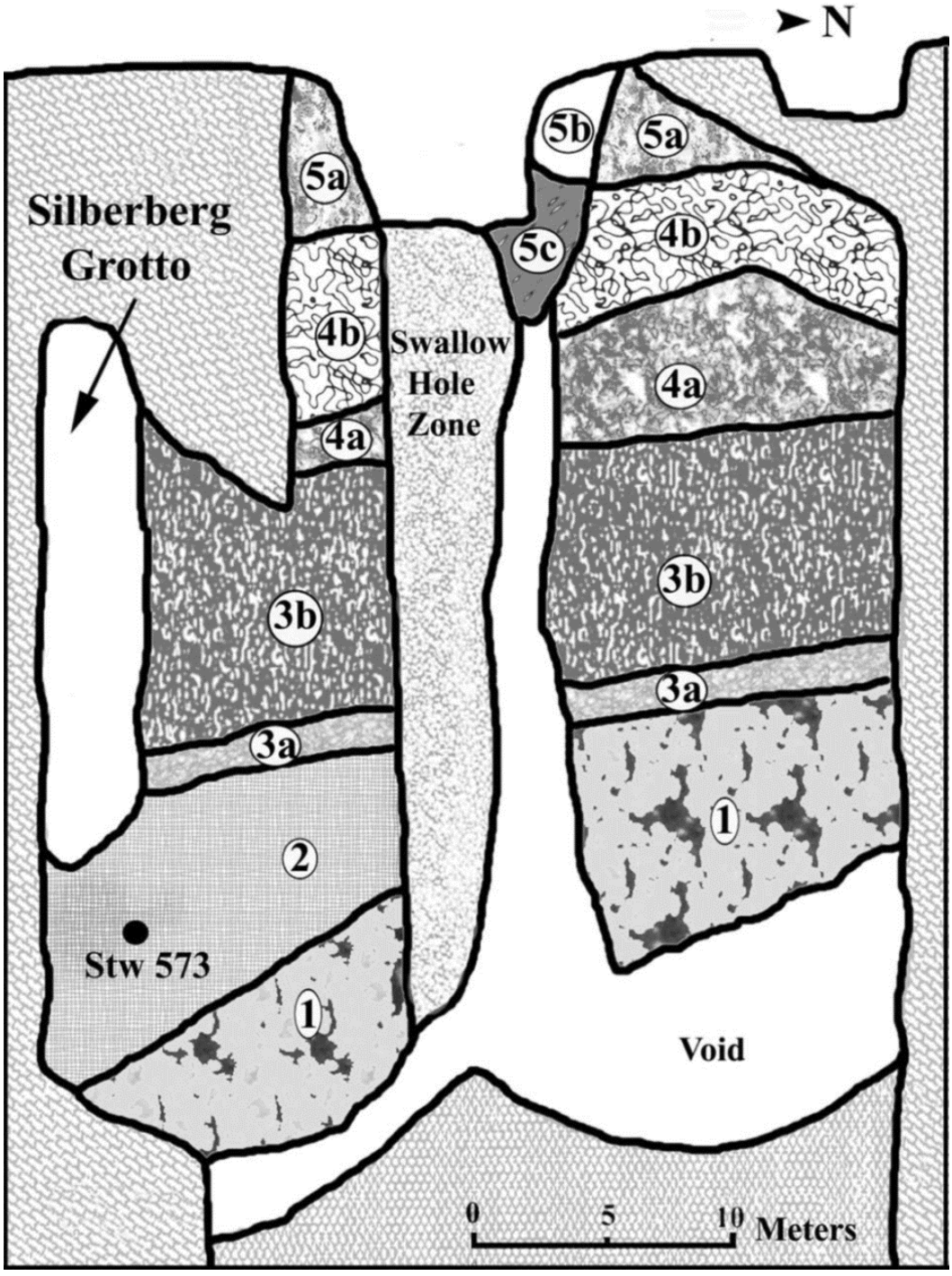


Figure 2.1: South-north section through the Sterkfontein Formation showing the relative position of the oldest Members (1,2, and 3) within the Silberberg Grotto and the younger Members 4 and 5 (from Partridge and Watt 1991; Partridge 2000). Members 6 and Post Member 6 Infill are not included in this figure as they were regarded to be part of Member 5.

Herries & Shaw (2011) propose dates around 2.8-2.0 Ma. This member yielded a large number of *Australopithecus* specimens (Clarke 1988, 2008, 2013). It is from this deposit that over 300 fossil wood fragments were found, most of which belongs a to species of liana (*Dichapetalum mombuttense*) (Bamford 1999). Large samples of antelope, primates and carnivore remains are found consistent with "open woodland with bushland and thicket areas or a medium density woodland and moderate savanna" Reed (1997:306); also see (Vrba 1975, 1985a; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Reynolds & Kibii 2011). There is no representation of stone artefacts, or *Homo* remains in this member (Kuman & Clarke 2000; Clarke 2006).

Member 5

The M5 deposit is made up of three major infills, namely: the StW 53 infill, Member 5 East, and Member 5 West (Clarke 1998; 2006; Kuman & Clarke 2000; Reynolds & Kibii 2011). The StW 53 infill postdate is undated. Originally considered to postdate 2.6-2.0 Ma (Kuman & Clarke 2000; and see Herries & Shaw 2011 who proposed dates between 1.8-1.5 Ma), the StW 53 infill is considered as a hanging remnant of M4 (Clarke 2008). It was named for the discovery of the StW 53 cranium (assigned to *Homo habilis*--Hughes & Tobias 1977) made in 1976, but the cranium was later assigned to *Australopithecus africanus* based on its morphology, and the infill breccia was shown not to be part of M5 (Clarke 1994; Kuman & Clarke 2000). No stone tools are present in this breccia, and stratigraphic revision by L. Bruxelles (in prep.) place it earlier than the original suggestions. The infill contains some fossil macromammalian species that have been taxonomically identified by Pickering (1999), e.g., cercopithecine monkey (*Cercopithecoides williamsi* cf.), *Theropithecus oswaldi*; Carnivora species: Canidae (*Canis* cf. *mesomelas*), Hyaenidae (*Chasmaporthetes* sp.), Viverridae (*Suricata* sp.); as well as Bovidae species: Bovinae (*Boselaphini* cf.), Antilopinae (*Gazella* cf. *gracilior*); Alcelaphinae (*Damaliscus* sp.) and (*Connochaetes* sp.) to mention a few. Member 5 East and Member 5 West deposits hold evidence of the earliest stone tool use in southern African sites. For example, M5 East contains the 'Oldowan infill' below 22 feet depth. This is a breccia that yielded over 3000 Oldowan artefacts known to

be the oldest stone tool industry in southern Africa This deposit was previously estimated to 2.0-1.7 Ma (Kuman & Clarke 2000), but it is now dated to "2.18 ± 0.21 Ma" by (Granger *et al.* 2015:85). *Paranthropus* fossils were found in association with these artefacts (Kuman & Clarke 2000), but *Homo habilis* is also present (Reddy 2015). The M5 Acheulean-bearing breccias are present across the eastern and western parts of M5 and contain early Acheulean lithics, but only the M5 West deposit is well preserved. It has been estimated to date around ca. 1.7-1.4 Ma, and *Homo ergaster* is also present (Kuman & Clarke 2000).

Member 6 and Post-Member 6 Infill

M6 is a hanging remnant of Upper Breccia (Robinson 1962) that overlies Member 5. It was named Member 6 by Partridge (1978) and dates to the Middle Pleistocene (Kuman & Clarke 2000; Ogola 2009). Most of this member has eroded. Based on Brain's (1981) analysis and a recent study by Ogola (2009), porcupine, carnivore, rodents and hominin remains make up the faunal assemblage of Member 6. The Post-Member 6 Infill occupies an erosional channel that separates M5 West and East. This infill contains younger sediments mixed with material eroded from M5 West (Clarke 1994; Kuman & Clarke 2000), as Acheulean artefacts and early *Homo* teeth were found in the Post-Member 6 Infill (Ogola 2009).

2.3 Swartkrans Caves

Swartkrans is located within the Sterkfontein Valley, approximately one km from Sterkfontein caves, Johannesburg, in Gauteng Province, South Africa (Sutton *et al.* 2009). In 1948, Drs Robert Broom and John Robinson began palaeontological work at Swartkrans caves. They recognised it as a significant palaeoanthropological site which contained fossil-bearing sediments similar to those found within the Sterkfontein caves. Excavations at Swartkrans continued throughout 1949 with the support of the Transvaal Museum, which provided financial aid for this work. When no further funds were available from the South African government, the excavations ended in late 1949 (Robinson 1952; Watson 1993). By this time, excavations at Swartkrans had exposed a substantial seam of pure travertine or a

dripstone “which is a general term applied to the variety of calcium and magnesium carbonate that develops in caves” (Brain 1958:15). This attracted the attention of lime-miners who blasted the exposed travertine from late 1949 throughout 1951 for commercial purposes to the dismay of palaeoanthropologists who had carried out excavations there. Several damaged and incomplete but valuable specimens (e.g., *Paranthropus robustus* cranium SK 48 and mandible SK 23) were recovered from the miners’ dumps during the periodic visits to the site (Robinson 1952; Watson 1993). However, this was the second extensive mining; the first mining had taken place during the 1930s. Palaeontological work at Swartkrans recommenced in 1951 and continued into 1953 under the supervision of Dr Robison funded by the Nuffield Foundation, yielding many significant specimens. Thereafter the site was abandoned for 12 years. After this hiatus, Dr C.K. Brain who was appointed as a palaeontologist at the Transvaal Museum in 1965 started a project at Swartkrans that ran smoothly for 21 years. His work yielded numerous fossils including hominin specimens (Brain 1970), some belonging to *Homo* (Clarke *et al.* 1970).

In 2005, a new research program was begun by Travis Pickering called the Swartkrans Palaeoanthropogical Research Project (SPRP) following the work of Drs Robert Broom and John Robinson (1948-1949) and C.K. Brain (1965-1986) (Sutton *et al.* 2009; Gibbon *et al.* 2014; Pickering *et al.* 2016; Kuman *et al.* 2018). This project is aimed at clarifying issues related to stratigraphy, behaviour, and the evolution of the hominins, i.e., *P. robustus* and early *Homo* (Sutton *et al.* 2009; Gibbon *et al.* 2014; Pickering *et al.* 2016). Current work is being done to improve the chronological framework and to provide new interpretations “for the various fossil-bearing Pleistocene deposits preserved within the Swartkrans caves” (Gibbon *et al.* 2014:11). This includes the analysis of large fossils and archaeological samples and the use of different dating techniques (Sutton *et al.* 2009; Gibbon *et al.* 2014; Pickering *et al.* 2016).

2.4 Stratigraphy

2.4.1 Geological context and cave formation

Swartkrans is a site with multiple fossiliferous members referred to the 'Swartkrans Formation' (see Fig 2.2 and 2.3). According to Gibbon *et al*. (2014:11) the Swartkrans Formation "evolved as a phreatic maze cave within the impure dolomitic limestone of the Chuniespoort Group" (and see Palmer 1991; Brain 1993). The first opening of the cave to the surface probably goes back sometime in the early Pleistocene (Butzer 1976; Brain 1976, 1993; Gibbon *et al.* 2014; Pickering *et al.* 2016). The Swartkrans cave contains five depositional members (M1 to M5) which are separated by erosional discontinuities (Gibbon *et al.* 2014; Pickering *et al.* 2016).

Member 1

M1 is the oldest at >1.7 Ma Gibbon *et al.* (2014) and is divided into three subunits namely: the Lower Bank (LB), the Lower Bank East Extension (LBEE), and the Hanging Remnant (HR) (Brain 1993; Sutton *et al.* 2009; Pickering *et al*. 2016). According to Pickering *et al.* (2016:2), the LB and LBEE are "indistinguishable depositionally and sedimentologically, they form a single infill". However, after Sutton *et al*. (2009) identified the eastern portion of this depositional body, the LB and LBEE were classified as two separate units/infills. The soils deposited into the LB/LBEE are known to have been admitted into these chambers via an open shaft(s) to the ground surface above. These surface-derived soils are described by Gibbon *et al.* (2014:12) and Pickering *et al.* (2016:2) as "sandy silt, with occasional clasts of subangular dolomite, chert and quartz (4-120mm in size)". Stone and bone artefacts and fossils were banking against the north wall of the carven filled most of the underground opening (Pickering *et al.* 2016). Most of the deposits in the LB/LBBE have been either lightly calcified or decalcified, with the most heavily calcified breccia in the HR (Sutton *et al.* 2009; Pickering *et al.* 2016). Sediments filled and choked the entryway(s) of the LB/LBBE, and new channels opened from the surface above, admitting slightly younger deposits. These are the deposits known initially as the 'pink breccia' (Robinson 1952; Brain 1958) but now referred to as the Hanging Remnant (HR) of M1. The two flowstones that bound the Lower

Bank (LB) and the Hanging Remnant (HR) sequence of M1 were dated with Uranium-Lead (U-Pb) and provided the age estimates of 2.249 ± 0.077 Ma at the base and 1.706 ± 0.069 Ma at the top (Pickering *et al.* 2011). Most recently, Gibbon *et al.* (2014:14) provided cosmogenic burial dates that place the LB at ca. 2.19 ± 0.08 and 1.80 ± 0.09 Ma, i.e., "average age=1.99 ± 0.19 Ma or 2.19-1.8 Ma". These dates agree with previous age estimates provided by Uranium-Lead dating (U-Pb dating) (e.g., Pickering *et al.* 2011) and fauna data (Vrba 1985a; Churcher & Watson 1993; Brain 1993). They also confirm a minimum age of >1.71 Ma for the youngest part of the member.

New samples for cosmogenic isochron dating have refined the dates of the LB to ca. 2.2 Ma and are currently being submitted for publication (Kuman *et al.* in prep.). The HR contains surface-derived soils as well as sandy sediments with stony allogenic and authogenic inclusions of dolomite and cherts (Brain 1958; Sutton *et al.* 2009; Gibbon *et al.* 2014; Pickering *et al.* 2016). The breccia yielded abundant fossils and a few purported bone tools (Pickering *et al.* 2008) but no stone tools. When sediments filled the HR, a subsequent period of erosion created a void (several metres in width) between it and the Lower Bank, into which Member 2 sediments were later admitted.

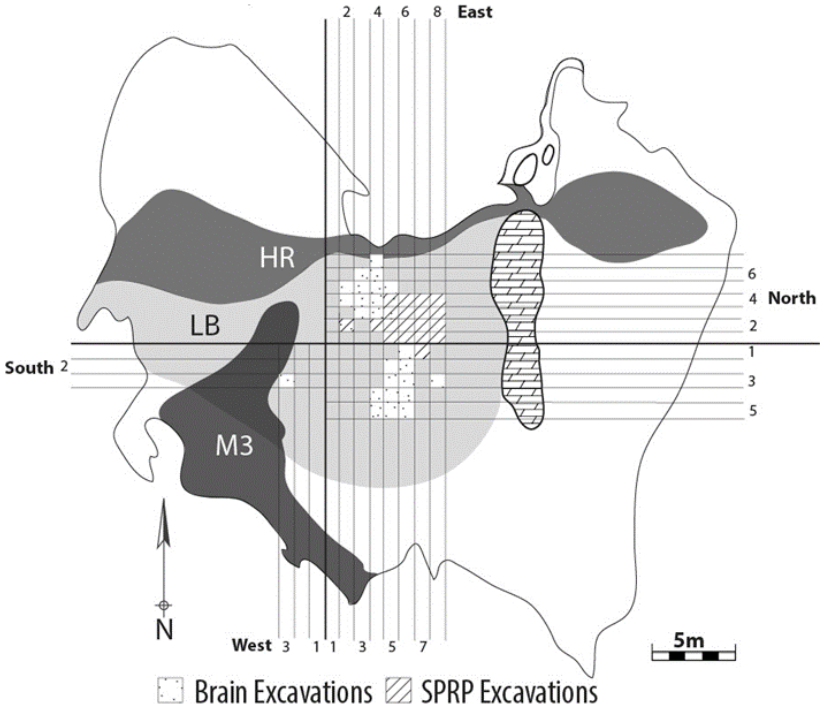


Figure 2.2: Excavation grid showing the Member 1 Lower Bank areas (dotted) dug by Brain through 1986 and the SPRP from 2005 (from Kuman et al. 2018)

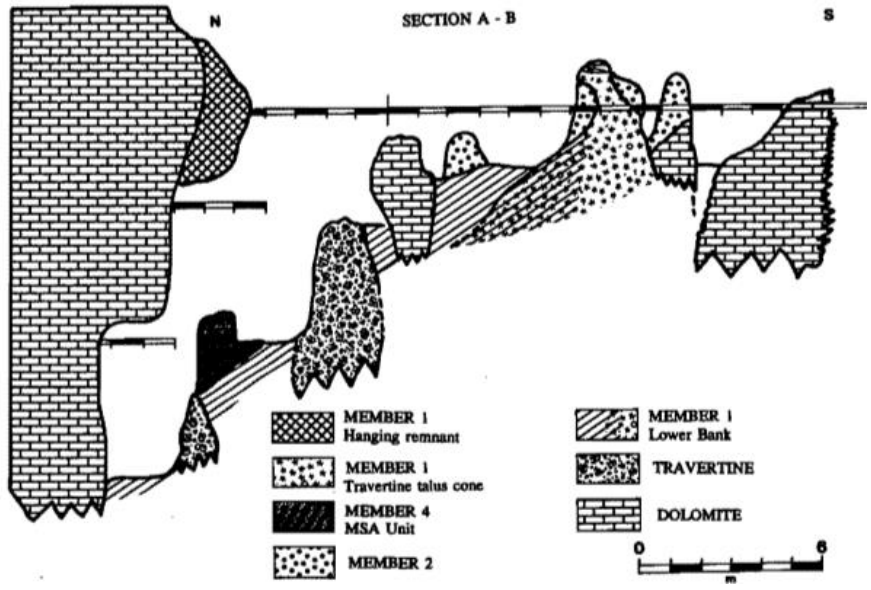


Figure 2.3: Schematic section, designated on the plan in (A), running north-south through the filling of the outer portion of Swartkrans cave showing deposits From oldest to youngest respectively: the Lower Bank (LB) Oldowan and Hanging Remnant (HR) of Member 1; Member 2 Acheulean, and Member 4 (from Brain 1993).

Member 2

The first sediments deposited as M2 (ca. 1.5 Ma) are beds of water-lain, coarser-grained sands. These sediments were admitted into the eroded void that separates the LB and HR (Gibbon *et al.* 2014). The second ingress of sediments attributed to Member 2 is represented by thin layers of water-lain, stratified sediments forming against the northwest wall of the cave (Brain 1993; Gibbon *et al.* 2014; Pickering *et al.* 2016). M2 consists of 'brown breccia' which is distinguished by its lack of large stones, but it includes "fallen blocks of calcified pink breccia from the HR" (Pickering *et al.* 2016:2). Numerous fossils and stone tools are also found in M2 (Gibbon *et al.* 2014; Pickering *et al.* 2016).

Member 3

Member 3 is dated to ca. 1.0 Ma based on early fauna-derived estimates by Vrba (1985), Churcher & Watson (1993), and Brain (1993), and new cosmogenic nuclide dates by Gibbon *et al.* (2014) refined this date to 0.96 ± 0.09 Ma. The M3 sediments are located in a north to south oriented "gully that was eroded into Members 1 and 2 along the west wall of the cave" (Pickering *et al.* 2016:3), and cosmogenic burial dating refined the age of this unit to "0.96 ± 0.09 Ma" (Gibbon *et al.* 2014:3). M3 deposit consists of lightly to heavily calcified sediments in the uppermost exposed levels. Angular to sub-angular clasts (between 4-120 mm), are present. There are large cobbles, and boulder-sized dolomite clasts, which may be broken pieces of stones or chips from the roof of the cave are also found but in the deeper portions of the gully (Gibbon *et al.* 2014; Pickering *et al.* 2016). M3 has also yielded a wealth of fossils, artefacts, bone tools and burned bones (Pickering *et al.* 2016).

Member 4

Member 4 dates between 110,000 ± 1980 or <110 ka based on uranium-thorium (U-Th) of speleothem (Sutton *et al.* 2009). It is a colluvial deposit that covers an area of ~62 m^2 artefacts (Brain 1993; Sutton *et al.* 2009; Pickering *et al.* 2016). This extensive deposit contains dark reddish-brown, loose, non-calcified silty sand sediments and more than 1500 Middle Stone Age (MSA) lithic artefacts. No fossils

were found in M4 because the deposit was surface colluvium that did not enter the cave system and it was not suitable for bone preservation. In other words, “there was no cave roof overhanging the area now occupied by Member 4 during the period when MSA sediments and artifacts were deposited” (Sutton *et al.* 2009:689).

Member 5

Member 5 is a four-metre-thick lightly calcified deposit that partially fills larger erosional spaces surrounding a huge stalagmitic boss within the Swartkrans Formation (Brain 1993; Watson 1993; Sutton *et al.* 2009). Most of this deposit has presumably lost through weathering and mining (Brain 1993). Many fossils were recovered from this deposit, including the remains of the extinct springbok (*Antidorcas bondi*), dating to 11,000 years (Watson 1993).

Table 2.1: Summary table for Sterkfontein (STK) and Swartkrans (SKX) based on previous palaeoenvironmental methods.

Site	Members	Published dates for deposits & References	Palaeoenvironment	Previous Method for reconstruction	Lithics & Hominins	References
STK	Member 1	Not yet dated	-	-	-	-
STK	Member 2	**2.6-2.8 Ma,** Uranium-Lead and Uranium-Thorium isotopes (Pickering & Kramers 2010) **2.6-1.8 Ma,** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) **3.67 ± 0.16 Ma**, Cosmogenic Nuclides (Granger *et al.* 2015)	Open grassland with rocky outcrops and wetter habitats	Bovid taxonomy	StW 573/ *Australopithecus* sp.	Pickering *et al.* (2004); Reynolds & Kibii (2011)
STK	Member 3	-	-	-	-	-
STK	Member 4	**2.8-2.4 Ma**, Bovid biochronology (Vrba 1974b, 1980)	Mosaic habitat: forest, open woodland/ bushland and grassland	Bovid taxonomy, palaeobotany, bovid carbon isotope analysis of micromammals	*Australopithecus africanus*	Vrba (1975,1980), Reed (1997); Bamford (1999); Kuman & Clarke (2000);

Table 2.1: Continued. Summary table for Sterkfontein (STK) and Swartkrans (SKX) based on previous palaeoenvironmental methods.

		2.8-2.01 Ma, ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)				Avery (2001); Luyt & Lee-Thorp (2003); Leichliter *et al.* (2017)
STK	StW 53 Infill south of Member 5	**2.6-2.0 Ma,** Biochronology and archaeology (Kuman & Clarke 2000) **1.8-1.5 Ma,** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	Open, drier, grassland conditions	Bovid taxonomy	*Homo habilis* or *Australopithecus africanus*	Vrba (1975, 1980); Reed (1997); Kuman & Clarke (2000); Reynolds & Kibii (2011)
STK	Member 5 East, Oldowan infill	**2.0-1.7 Ma,** Biochronology and archaeology (Kuman & Clarke 2000) **1.4-1.1 Ma**, ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) **2.18 ± 0.21 Ma,** Cosmogenic Nuclides (Granger *et al.* 2015)	Drier and more open habitat with tree cover	Bovid taxonomy, taxon-free analysis of bovids, carbon isotopes	Oldowan, *Paranthropus* and *Homo habilis*	Bishop *et al.* (1999); Kuman & Clarke (2000); Avery (2001); Luyt & Lee-Thorp (2003); Reynolds & Kibii (2011); Reddy (2015)

Table 2.1: Continued. Summary table for Sterkfontein (STK) and Swartkrans (SKX) based on previous palaeoenvironmental methods.

STK	Member 5 West Acheulean	**1.7-1.4 Ma**, Biochronology and archaeology (Kuman & Clarke 2000) **1.3-1.1 Ma**, ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	Open or wooded grassland or open savanna	Bovid taxonomy & isotopes analysis of bovids	*Homo ergaster* Acheulean	Vrba (1975); Reed (1997); Kuman & Clarke (2000); Luyt & Lee-Thorp (2003)
STK	Member 6 and Post-Member 6 Infill	**Mid-Late Pleistocene age**, faunal correlations and Archaeology (Reynolds *et al.* 2007) **0.5-0.3 Ma**, ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	Open savanna	Bovid taxonomy	Middle Stone Age in Post M6 debitage, *Homo* sp.	Kuman & Clarke (2000); Ogola (2009)
SKX	Member 1, HR and LB	**Member 1 as a whole:** **1.8-1.6 Ma /1.7 Ma,** bovid and equid data (Vrba 1985b; Churcher & Watson 1993; Brain 1993) **1.83** ± **1.38 Ma,** Uranium-Lead (U-Pb) (Balter *et al.* 2008)	Moderately open savanna, grassland with tree cover, savanna woodland near a river with reed beds	Alcelaphini-Antilopini Index (ACC), bovid taxonomy, functional morphology & carbon isotopes of micromammals	*Paranthropus robustus*, *Homo ergaster*, *Homo* sp.	Vrba 1975,1980); Brain (1981); Watson (1993); Reed (1997); Avery (1998); Kuman & Clarke (2000); Lee-Thorp *et al.* (2007); Reed &

Table 2.1: Continued. Summary table for Sterkfontein (STK) and Swartkrans (SKX) based on previous palaeoenvironmental methods.

SKX	Member 1, HR and LB	**2.0 Ma,** electron spin resonance (ESR) (Herries *et al.* 2009) **HR- 2.249** ± 0.077 Ma, Uranium-Lead (U-Pb) (Pickering *et al.* 2011) **LB-1.706** ± 0069 Ma, Uranium-Lead (U-Pb) (Pickering *et al.* 2011) **LB-2.19-1.8 Ma,** Cosmogenic Nuclides (Gibbon *et al.* 2014) **LB unpublished date~2.2 Ma,** (Kuman *et al.* in prep.)				Rector (2007); de Ruiter *et al.* (2008); Leichliter *et al.* (2017)
SKX	Member 2	**1.5 Ma,** bovid and equid data (Vrba 1985b; Churcher & Watson 1993; Brain 1993) **1.36** ± **0.29 Ma**, Uranium-Lead (U-Pb) dating (Balter *et al.* 2008)	Wooded grassland with wetlands, open savanna	Bovid functional morphology & taxonomy	*Paranthropus robustus*, *Homo* sp. Acheulean	Vrba (1975); Watson (1993); Reed (1997); Lee-Thorp *et al.* (2007)

Table 2.1: Continued. Summary table for Sterkfontein (STK) and Swartkrans (SKX) based on previous palaeoenvironmental methods.

SKX	Member 2	**1.65-1.07 Ma,** Uranium-Lead (U- Pb) (Herries *et al.* 2009)				
SKX	Member 3	**1.0 Ma**, bovid and equid data (Vrba 1985b; Churcher & Watson 1993; Brain 1993) **0.83 ± 0.21 Ma**, Uranium-Lead (U-Pb) dating (Balter *et al.* 2008) **1.04-.0.61 M**a, Uranium-Lead (U-Pb) (Herries *et al.* 2009) **0.96 ± 0.09 Ma**, Cosmogenic Nuclide date (Gibbon *et al.* 2014)	Open grassland with river or stream nearby	Bovid functional morphology & taxonomy	*Paranthropus robustus* Acheulean	Watson (1993); Reed (1997); Gibbon *et al.* (2014)
SKX	Member 4	**110. 00 ± 1980 Ma or <110 ka**, Uranium-Thorium (U-Th) (Sutton *et al.* 2009)	-	-	MSA lithic artefacts	Brain (1993)
SKX	Member 5	**~11,000 years,** Fauna Brain (1993) and Watson (1993)	-	-	-	Watson (1993)

2.5 Palaeoenvironmental studies

This section presents a review of different palaeoenvironmental studies done at fossil-bearing sites in the Cradle of Humankind, a brief discussion of ecomorphology and Discriminant Function Analysis (DFA), a short explanation of the reasons why bovids are most often used for palaeoenvironmental studies, and a more detailed discussion on taxon-free-ecomorphological analysis.

2.5.1 Taxon-based or uniformitarianism methods

Vrba (1974a, 1975, 1980) used an Alcelaphini-Antelopini Index (AAC) to study species of the family Bovidae, to reconstruct the amount of open versus closed or mixed habitat-adapted taxa at certain South African key Pleistocene sites. She and other researchers concluded Swartkrans Member 1, ca. 1.8-1.6 Ma, to be a moderately open savannah (Vrba 1985b; Churcher & Watson 1993; Brain 1993). At this time, the two separate components of Member 1 had not been distinguished. Now the first ingress of Member 1 is called the Lower Bank, and a somewhat younger component the Hanging Remnant (Brain 1993). Nevertheless, Vrba's results showed that a high proportion of these bovid tribes indicated more open environments, while relatively low proportions suggest more closed habitats. Most palaeoenvironmental reconstructions of East African sites continued to apply and expand on Vrba's AAC method (e.g., Kappelman 1984; Potts 1988; Shipman & Harris 1988; Plummer & Bishop 1994; Kovarovic *et al.* 2002; Kovarovic & Andrews 2007; Plummer *et al.* 2008, 2015; Bishop *et al.* 2011). Based on Vrba's (1975, 1980) observations, Brain (1981) applied traditional taxonomic analysis to three Cradle of Humankind sites. For Swartkrans Member 1, Brain (1981) argued that the environment at ca. 1.7 Ma was an open highveld dominated by grassland with some tree cover, particularly around cave openings, where leopards fed on prey, such as bovids and primates. Watson (1993) also used traditional taxon-based method for Brain's excavated sample from Swartkrans M1 LB but proposed a diversity of the following Bovidae tribes: Alcelaphini (*Connochaetes* sp., *Beatragus* sp., *Damaliscus* sp.), Antilopini (*Antidorcas* sp., *Gazella* sp., *Raphicerus* sp., *Oreotragus oreotragus*), Bovini (*Syncerus* sp.), Tragelaphini (*Tragelaphus oryx, Tragelaphus strepsiceros*), Hippotragini (*Hippotragus* cf. *niger*), and *Pelea*

sp. The presence of these tribes suggested that the overall habitat spectrum of the Lower Bank was an open savanna woodland which accommodated springbok (*Artiodorcas* sp.), *Gazella* sp. and alcelaphines (primary grazers); rocky hills, which favoured klipspringer (*Oreotragus* sp.) adjacent to the Bloubank River which supported buffalo (*Syncerus* sp.), kudu (*Tragelaphus strepsiceros*), and sable (*Hippotragus niger*) as well as reedbeds that would have been required by reedbuck (*Redunca* sp.).

Although she studied the Lower Bank and Hanging Remnant as a single unit and did not specify the sub-units, Reed (1997) provides the most comprehensive study of Early Pleistocene Cradle of Humankind sites environments since Vrba and Watson's work. She studied entire communities of animals and reconstructed their ecological adaptations. Her findings for Swartkrans Member 1 showed high percentages (13.9%) of frugivorous and of aquatic mammalian animals (5.6%), while only 2.8% of grazers are present. This suggests an open environment with the presence of a river or stream that probably supported "a woodland or forest as suggested by the percentage of frugivorous mammals that fall in the range of medium density woodland and bushland" (Reed 1997:306). This assumption also agrees with previous habitat reconstructions of this member (Watson 1993).

Acheulean-bearing Member 2, at Swartkrans (ca. 1.5 Ma) is another deposit of study here, for which previous habitat reconstructions were also based on traditional taxon-based methods. According to Watson (1993:51), Member 2 bovids are represented by a variety of species which were the primary source of prey for carnivores. These species range from "a high percentage 32.35% of grazers and 100% total terrestrially" (Reed 1997:307). This is indicative of a drier habitat with a wooded savanna grassland with wetlands, as suggested by Vrba (1975) and Reed (1997), and thus similar to the habitat reconstruction of Member 1.

Although Sterkfontein and Swartkrans caves are one km apart, the Bloubank River was not as close to Sterkfontein; hence no water-dependent species are found there, however, hippopotamus may be found from MSA-aged deposits, e.g., Lincoln cave

North (Watson 1993; Kuman & Clarke 2000; Reynolds *et al.* 2007; Kuman *et al.* 2018). There are no river cobbles in these deposits except for manuports brought into the site by hominids. The closest gravels are about 300 m away from Sterkfontein, and although the river is near to Swartkrans, the gravels in the river terrace lie below the site and these members did not experience flooding (Kuman & Field 2009; Kuman *et al.* 2018). Based on bovid taxonomy, habitat construction for Member 4 at Sterkfontein is known to be a mosaic of thicket and bushland, a medium-density woodland which supported *Makapania broomi* and hippotragines, with open grasslands indicated by species such as alcelaphines and antilopines (Vrba 1975, 1980; Reed 1997; Kuman & Clarke 2000).

Bishop *et al.* (1999) conducted a preliminary study of the Sterkfontein Oldowan fauna (eight bovid metapodials) from Member 5 East (Oldowan infill) and indicated that although an open habitat was dominant, the morphologies of some bovid specimens reflected tree cover in the area. This study has remained unpublished but was cited by Kuman & Clarke (2000), which discussed only the open-country species in the Oldowan fauna in order to contrast this deposit with the older Member 4 fauna.

2.5.2 Isotope studies

An early attempt to combine different approaches was applied by Sponheimer *et al.* (1999), who used isotopic, ecomorphological, and taxonomic uniformitarianism data to propose a refined palaeodietary reconstruction for Pliocene bovids from Makapansgat, which according to (Delson 1984; Brain 1993; Kuman & Clarke 2000; Partridge 2000; Clarke & Partridge 2002; Sponheimer & Lee-Thorp 2009) dates to ca. 3 Ma. This study followed the work of MacFadden & Shockey (1997), who used isotope data in conjunction with morphological data for dietary reconstruction of Pliocene bovids, and Reed (1997) who focused on cranio-dental ecomorphology of the Member 3 deposit fauna at Makapansgat. For ecomorphology, 215 bovid cranial specimens (mandibles and dentition) from Member 3 were measured and used to create morphological indices (Reed 1997; Sponheimer *et al.* 1999). Sponheimer *et al.* (1999:707) also used DFA to classify

"individual bovid specimens into five feeding categories (e.g., grazing, fresh grass grazing, mixed-feeding preferring leaves, mixed-feeding preferring grass, and browsing groups)" and produced 91.7% to 100% accuracy. Stable carbon isotope analysis of bovid enamel from permanent molars was performed using mass spectrometry to determine the proportion of C_3 and C_4 vegetation in bovid diets (Sponheimer *et al.* 1999). Results for these analyses suggested that bovids feeding on C_3 have relatively high $\delta^{13}C$ values compared to those that feed on C_4 vegetation, whereas mixed-feeders fall in between these two extremes (Sponheimer *et al.* 1999). Overall, this analysis diagnosed a densely wooded environment for Member 3. This study provided different results to the analysis conducted only using taxon-based methods.

A similar but slightly altered approach was followed by Luyt and Lee-Thorp (2003) to assess bovid and equid dietary preferences for reconstructing the environmental settings of Sterkfontein Member 4 and Member 5 deposits (Oldowan Member 5 East and Early Acheulean in Member 5 West). Like Sponheimer *et al.* (1999), Luyt & Lee-Thorp (2003) criticised the use of the taxonomic uniformitarianism approaches to infer diet because of its potential limitation, and they applied a carbon isotope analysis to Sterkfontein faunal dental material. Specimens from Sterkfontein were not taxonomically identified, thus making it impossible to calculate proportions of C_3 and C_4 to species or tribe level as was applied for Makapansgat. However, available dental material (enamel) from both Members 4 and 5 were used for carbon isotope analyses (Luyt & Lee-Thorp 2003). The isotope ratio for each individual specimen was measured on a Finnigan Mat 252 mass spectrometer interfaced with a Kiel auto carbonate device (Luyt & Lee-Thorp 2003). Ratios obtained were then calibrated and reported by "convention in the δ notation relative to the Pee Dee Belemnite (PDB) standard" (Luyt & Lee-Thorp 2003:272). Dietary frequencies, e.g., (grazers, browsers, and mixed feeders) were determined by calculating the number of specimens showing enriched values. Percentages of individual specimens were calculated based on these groupings (grazers, browsers, and mixed feeders). The percentage results for the dietary frequencies of bovids from Member 4 indicate a wooded to moderately wooded

environment. Most importantly, carbon isotope analysis of the Oldowan and Early Acheulean faunal assemblages in Member 5 showed that there was a transgressive trend or shift from medium density woodland continuing into the Oldowan period to more open environments around 1.7 Ma (Luyt & Lee-Thorp 2003). Thus, it was only after 1.7 Ma that a marked transition to an open environment occurred in the Member 5 West (Acheulean deposit), indicated by the increase in the proportion of grazers (Luyt & Lee-Thorp 2003).

Most studies, including the current study, use large-to medium sized mammals to understand past habitats; however, a recent study by Leichliter *et al.* (2017:57) showed that carbon isotope analysis of "small mammals has potential as proxies for reconstructing past habitats" for sites in the Cradle of Humankind World Heritage Site, South Africa. Small mammals are relatively abundant in the archaeological and palaeontological record and have diverse habitat preferences and dietary habits (Leichliter *et al.* 2017). Leichliter *et al.* (2017) performed an isotopic analysis using tooth enamel of small mammals, i.e., rodents and shrews. Modern specimens used for comparative analysis came from the Kimberly roost site (KRS), Malapa roost site (MRS), and Gladysvale roost site (GRS), and the fossil component from fossil sites in the Sterkfontein Valley, namely: Sterkfontein Member 4 (Sts), Swartkrans Member 1 (SW), and Gladysvale (GV). This was done to assess the degree to which carbon isotope compositions of small mammal enamel from different habitats, "varying from open grassland to mixed woodlands record spatial changes in habitat in a South African savanna environment" (Leichliter *et al.* 2017:57). Results for the KRS, MRS, and GRS show that this assessment is complex and suggest that carbon isotope composition of small mammals can only reveal information about past habitat structures with appropriate taxonomic control (Leichliter *et al.* 2017). Given this proviso, carbon isotope compositions of micromammals from the Sterkfontein, Swartkrans, and Gladysvale fossil sites were analysed. Results from this analysis suggest a significant difference between the carbon isotope values of small mammal teeth enamel from these sites. Swartkrans Member 1 has significantly lower mean δ13C value (−8.8‰) relative to the Sterkfontein (−6.0‰) and Gladysvale fossil site (−6.1‰) (Leichliter *et al.* 2017). This result is somewhat different from that

obtained with taxonomic and ecomorphological analyses of larger mammals (e.g., Vrba 1975a, 1985a; Reed 1997). As recorded in these studies, Swartkrans M1 is associated with open and C4-dominated environments relatively to Sterkfontein M4. However, according to Leichliter *et al.* (2017), the low mean δ13C value for micromammals at Swartkrans possibly suggests a closed environment with high C3 vegetation. When taxonomy was taken into consideration to investigate the patterning with isotopic datasets, and the results show that the lower mean δ13C value at Swartkrans was influenced by the presence of *Otomys* sp. found in and around C3 vegetation near water (Leichliter *et al.* 2017).

Another recent study specific to the archaeological members in this current research was conducted by (Sewell *et al.* 2018). Their study focusses on the changes in the diets of springbok (*Antidorcas*) for inferring palaeovegetational changes spanning over ca. 2 Ma for hominin bearing sites in the Cradle of Humankind, South Africa. Sewell *et al.* (2018:1) used four dietary methods, namely: "dental linear measurements, mesowear, microwear, and stable carbon isotope analysis". Their results for the analysis of *Antidorcas* sp. teeth, e.g., *A. marsupialis*, *A. bondi*, *A.australis* and *A. recki* from Sterkfontein Members 4 and 5 (StW 53 Infill, M5E, and M5W) and Swartkrans Member 1 (Lower Bank, and Hanging Remnant) agree with the theoretical framework proposed in early studies which states that African Plio-Pleistocene environments experienced dramatic climatic aridification and an increased spread of grassland post ca 1.7 Ma, impacting human evolution as well as fauna (Cerling 1992; Vrba 1995). The results further suggest more mosaic habitats for Swartkrans Member 2 with reduced grassland presence indicated by *A. bondi* (assumed-to-be a grazer) "yielding a slightly mixed feeding dietary signal from carbon isotope values" (Sewell *et al.* 2018:10). This reconstruction for Member 2 at Swartkrans agrees with Steininger's (2011) conclusions based on isotopic analysis that suggested that a few bovids from M2 incorporated a significant amount of C_4 vegetation into their diet, while there were more C_3 feeders, signifying the presence of a C_3-dominated vegetation structure, possibly accompanied by a wet pulse.

2.6 Ecomorphology

Previous research on taxon-free ecomorphological analysis has been conducted for East African sites, e.g., Olduvai Gorge and Koobi Fora by Plummer & Bishop (1994) and Kappelman *et al.* (1997), but this approach has not yet been applied to the Cradle of Humankind sites in South Africa. Many researchers in palaeoanthropology and palaeoecology have investigated the association between fossil bovids and their habitats for understanding human evolution (e.g., Gentry 1970; Vrba 1980, 1985a,b, 1988; Kappelman 1988, 1991; Plummer & Bishop 1994; Kappelmen *et al.* 1997; Kovarovic & Andrews 2007; Plummer *et al.* 2008; Klein & Steele 2010; Bishop *et al.* 2011; Barr 2014, 2015). This is known as 'ecomorphology' or ecological morphology. In zooarchaeological literature, ecomorphology is the study of the functional locomotor/ morphological adaptations of fossil bovids in relation to their ecology or habitats (Plummer *et al.* 2008; Curran 2012; Meloro & Louys 2014), while examining the "interface between organism's phenotype and its environment" (Bishop *et al. 2*011:356). Ecomorphological studies are useful because they are implicitly about fitness and adaptation, "which helps to investigate the organismal structure/design of fossil bovids to understand their performance ecologically" (Plummer *et al.* 2008:3017; Meachen-Samuels & Van Valkenburgh 2009). In essence, ecomorphology studies define the relationship between species bone metrics and phenotypic characteristics and habitat preferences in extant taxa (Forrest 2017) and in turn apply that relationship to fossils with unknown ecological context to determine their habitat preferences. It is important to note that ecomorphology is not entirely 'taxon-free', as it is required that fossil specimens be identified taxonomically to the family level, e.g., Bovidae, as this could demonstrate some functionally informative traits that signal a strong phylogenetic history (Degusta & Vrba 2003; Barr 2014; Forrest 2017). A Discriminant Function Analysis (DFA) is a statistical tool that has been used in ecomorphology. It is a form of classification algorithm that classifies cases into previously determined naturally occurring groups (James 1985; Kappelman 1986, 1988, 1991; Plummer *et al.* 2008, 2015; Bishop *et al.* 2011). This is done by using the linear metrics and indices from an animal's anatomical element "in question that best discriminates among habitat preference groups, hence the name

discriminant function" Plummer *et al.* (2008:3018); also see (Kovarovic & Andrews 2007; Klein & Steele 2010; Bishop *et al.* 2011). Most ecomorphological studies use bovid load-bearing postcranial elements such as the astragali, femora, metapodials, tali, radii, and phalanges just to mention a few, this is simply because the morphology of these elements are adapted to locomotion and interact closely with the substrate, and considered to best extract accurate palaeoenvironmental information.

2.7 Why bovids?

Bovidae Gray 1821 is a biological family of cloven-hoofed mammals of Class *Mammalia* Linnaeus 1758, order Artiodactyla Owen 1848. Bovids are mainly known as a group of diverse terrestrial mammals found in different environmental settings (see Figure 2.5). Fossil bovids have been used in palaeoanthropological and zooarchaeological research as proxies for palaeoenvironmental reconstruction (Kappelman 1986, 1988, 1991; Plummer & Bishop 1994; Kappelman *et al.* 1997; Spencer 1997; Degusta & Vrba 2003, 2005; Weinand 2007; Klein & Steele 2010; Bishop *et al.* 2011; Barr 2014; Forrest 2017). In ecomorphological studies, fossil bovids are used because of the following reasons: (1) bovids are abundant in both extant African communities of large mammals and in the African Pio-Pleistocene fossil record (Gentry & Gentry 1978; Weinand 2007; Klein & Steele 2010; Bishop *et al.* 2011), and particularly in the Sterkfontein, and Swartkrans fossil record; and (2) bovids are found within a variety of African habitat types (e.g., from the extremes of tropical forest to desert), thus reflecting different morphological and locomotor adaptations, body size, diets, behavioural, and other ecological characteristics (Kappelman 1988, 1991; Degusta & Vrba 2003, 2005; Plummer *et al.* 2008). As a group of cursorial mammals (fast running), bovid postcranial remains provide excellent information for finer-scale associations between morphology and function with a limited locomotor category and across a variety of habitats (Kappelman 1988). Predation is a major selective force for bovids, meaning that they use their locomotion to escape predators by outrunning them and as they acquire food daily "they are theoretically likely to have postcranial characters which are good habitat predictors" (Degusta & Vrba 2003:1011; and see Degusta & Vrba

2005; Plummer *et al.* 2008). For example, if a species morphological function is adapted for running fast (i.e., for highly cursorial locomotion) and straight over flat terrain, it is more likely to live in open habitat, whereas a species adapted for lateral dodging to escape predators and for moving over uneven terrain reflects a closed habitat (Kappelman 1988; Degusta & Vrba 2003, 2005; Barr 2014, 2015).

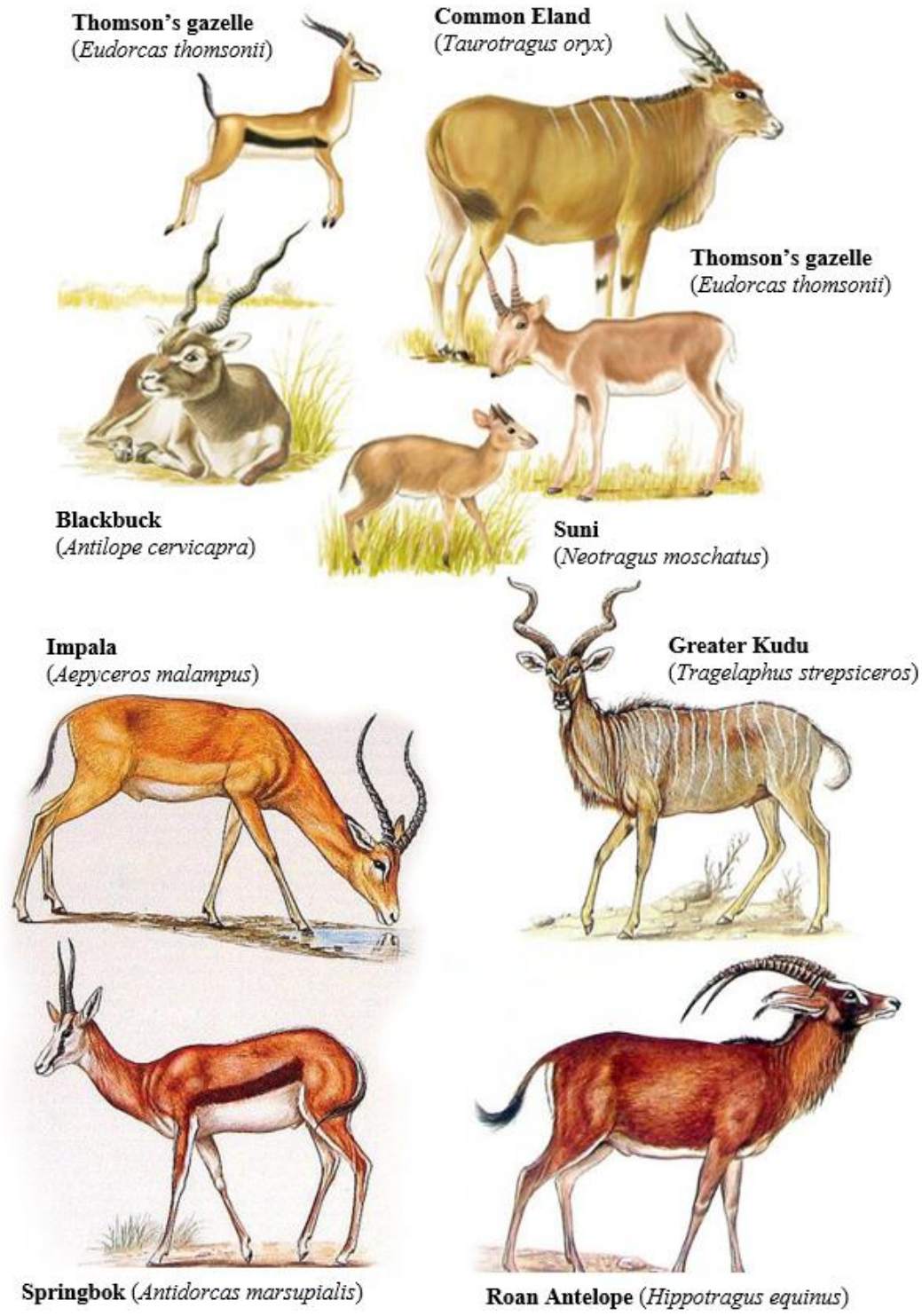


Figure 2.4: Mammals of Africa showing species of the Bovidae family in their respective habitats (from Kingdon et al. 2013:120).

2.8 Three types of weight-bearing bones for taxon-free analyses:

Femora

The first ecomorphological study was conducted by Kappelman (1988, 1991) on femora. Kappelman built his study upon and expanded the work of Gentry (1970), who pioneered the study of limb bone specializations of cursorial antelopes. Gentry (1970) noted that specific skeletal specializations or morphologies of bovids represent different functional complexes that can be used to link locomotor patterns and habitat preferences. In his work, Kappelman (1988, 1991) analysed the morphological and locomotor differences of extinct bovid femora in relation to habitat preferences. Four potential characters of the femur were studied based on femoral head shape, shaft dimensions, and knee structure (patella lip and patella groove), on a total of 195 specimens from eight bovid tribes and 41 species. Measurements were taken using digital calipers, flexible tapes, and osteometric boards. These characters were statistically analysed, and the results used to support "statistically significant separation of the different morphological complexes present in bovids related to locomotor patterns from three habitats categories, e.g., forest, broken cover, and savanna" (Kappelman 1988:119). These results appeared to have been determined by habitat complexities and predator avoidance strategies (Kappelman 1988, 1991; Kappelman *et al.* 1997).

In expanding these observations, Kappelman (1991) later demonstrated the utility of this method by using fossil bovid femora to predict palaeohabitats at the Fort Ternan site in Kenya. The measurements of five complete and proximal femora of extinct bovids from this site predicted the three-habitat category scheme with an accuracy of 73% (Kappelman 1991). An improved method was then conducted by Kappelman *et al.* (1997) to reconstruct the Early Pleistocene environment of two East African sites, namely Koobi Fora and Olduvai Gorge. In their study, Kappelman *et al.* (1997) used a linear discriminant functional analysis and taxon-free data set (bovid femur metrics) to reconstruct the palaeohabitat preferences of bovids from the sampled localities of both the sites. Although their sample was relatively small compared to that used by Kappelman (1988, 1991), the bovid femur

characters used in this study were the same. A DFA was employed on 22 femora to test whether different features of the femur can be used to classify extant species within four broad habitats (e.g., plains, light cover, heavy cover, and forest), and the results showed that these features had high discriminating power (Kappelman *et al.* 1997). For example, "the analysis of the complete femur improved results to 85% (3.4 better than chance), and the proximal femur improved to 81% (3.2 better than chance)" (Kappelman *et al.* 1997:249). The femur was used because it is one of the bovid postcranial elements with a wide range of functional complexes that indicates links between bovid locomotor patterns and modern habitat preferences (Kappelman *et al.* 1997). Results of the measurements of the femora also suggested that bovids from more closed habitats often have a more rounded spherical femoral head that allows for flexible mobility of the hip joint for easy manoeuvrability (Kappelman 1988, 1991; Kappelman *et al.* 1997). Those from more open habitats locomote in a more two-dimensional substrate and have a more expanded and cylindrical femoral head that limits movements laterally to the sagittal plane, with a distal femur acting as an extensor (Kappelman 1988, 1991; Kappelman *et al.* 1997). Nonetheless, bovids living in mixed habitats (for example, forests and plains) have intermediate femoral morphologies (Kappelman 1988, 1991; Kappelman *et al.* 1997). This approach suggested that during the Early Pleistocene bovids from both Koobi Fora and Olduvai Gorge inhabited a wide range of habitats. Koobi Fora had more closed habitats compared to Olduvai Gorge, where habitats were relatively open (Kappelman *et al.* 1997).

Metapodials

Similarly, Plummer & Bishop (1994) applied a taxon-free discriminant function analysis on bovid metapodials recovered from Bed I at Olduvai Gorge, Tanzania. The metapodials were used because their morphologies can be linked easily to locomotor adaptations, and they are also more durable than other long bones, they preserve well and are well represented at Olduvai sites. Plummer & Bishop (1994) argued that the assessment of bovid habitat preferences indirectly informed about the palaeoecology of hominins because, at the time of deposition, hominids were involved in the accumulation of the bovid assemblage. The study focused on three

broad habitats, namely: open (grassland), intermediate (bushland, woodland), and closed (forest) (Plummer & Bishop 1994). For understanding the functional anatomy of the metapodials, they measured 319 specimens and tested 14 metric characters on both the metacarpals and metatarsals. This allowed for the prediction of habitat preferences with an accuracy of 62-89% (1.8-2.7 times better than chance) for the three broad habitat categories mentioned above using quadrant discriminant function analysis (QDA). Their aim was to obtain dimension ratios that would reflect the shape and the most abundant morphological features associated with specific habitat preferences (Plummer & Bishop 1994). Interestingly, the results obtained were similar to other taxon-free and isotopic reconstructions of the Olduvai palaeohabitats and different from the taxon-based analysis of the same sample (e.g., Kappelman 1984; Cerling & Hay 1986; Potts 1988). The results also showed that the proportion of metapodials decreased with closed habitat morphologies but were increased markedly in open habitats in the sampled localities (Plummer & Bishop 1994). They further argued that bovid metapodials from each of the sampled sites were varied morphologically. This suggests that antelopes had a wide range of habitat adaptations (and hence habitats also available to hominids). However, the highest accuracy was obtained by using complete elements of limb bones that are rarely found in palaeoanthropological contexts (Plummer & Bishop 1994). The metapodial method developed by Plummer & Bishop (1994:57) requires using almost all the portions of the metapodial, e.g., "complete, proximal articular ends, and distal articular ends with enough shafts preserved to distinguish between metacarpals and metatarsals", which makes it more applicable. In contrast, the femur method by Kappelman (1988, 1991) and Kappelman *et al.* (1997) has more limited applicability, because it requires the use of a complete femur or a proximal femur, the efficacy of the data is therefore heavily affected by sample size.

Astragali

To overcome the limitations of the above methods, Degusta & Vrba (2003) applied similar techniques to astragali to investigate the habitat preferences of bovids. With the exception of other postcranial elements (e.g., tali, phalanges, carpals, and

tarsals), recent studies have focused on astragali for ecomorphological analyses because of the following reasons: a) they are found as complete fossils in the palaeontological and archaeological record; b) the morphology of this bone is adapted to locomotion; c) it produces high accuracy rate, and it is widely applicable (Degusta & Vrba 2003, 2005; Kovarovic & Andrews 2007; Plummer *et al.* 2008; Bishop *et al.* 2011; Barr 2014, 2015). A series of eight metric characters of 128 bovid astragali were measured using digital calipers (Degusta & Vrba 2003). Unlike Plummer & Bishop (1994), Degusta & Vrba (2003) did not generate ratios, which ignore body size effects, because they believed that size was also related to habitat. Degusta & Vrba (2003:1019) also argued that "the exploration of the relationship between the measurement and body-weight is certainly merited to ensure that body weight is not driving the prediction". Potential morphological metrics were then used for DFA to predict habitat preferences through comparative analysis with modern taxa. DFA "correctly predicted habitat group for 146 of 218 specimens, for an overall accuracy of 67%, which was less than the accuracy values of complete femora and metapodials but nominally 2.7 times greater than expected by chance with four habitat categories (25%)" (Degusta & Vrba 2003:1015). According to Degusta & Vrba (2003), the accuracy of this method is similar to that of the metapodials used by Plummer & Bishop (1994) and thus contributes to the existing array of techniques for palaeoenvironmental reconstruction. This is because both methods use any portion of the elements--proximal and distal articular surfaces, and shafts-- or complete elements. The accuracy levels for the two methods can be correlated with that used for phalanges (proximal, intermediate, and distal) by Degusta &Vrba (2005), which predicted 95% habitat preferences for 332 out of 468 bovid specimens.

Weinand (2005, 2007) re-examined a subset of measurements used by Degusta & Vrba (2003) and extended the comparative dataset by including Southeast Asian bovids. Weinand's (2005, 2007) study was more of a comparative analysis between parametric and non-parametric methods for predicting Southeast Asian habitats using the morphological function of fossil bovids. Measurements for the Southeast Asian bovid astragali were assessed using a Linear Discriminant Analysis (LDA)

and Recursive partitioning (rpart) method or a classification tree, with the addition of two statistical methods (Weinand 2005, 2007). LDA is simply a procedure "designed to analyse the relationship between a set of predictor variables (measurements taken from skeletal elements) and a grouping variable (habitat classification scheme)" (Weinand 2007:1775). Four habitat classifications were used based on modern species observable behaviour and previous classifications, e.g., 'open', 'light cover', 'heavy cover' and 'forest' (Kappelman *et al.* 1997; Degusta & Vrba 2003). Procedures followed for an LDA analysis were the same as that of Degusta & Vrba (2003). The Statistical Package for Social Sciences (SPSS) was used to calculate probabilities of the discriminant function to determine the "likelihood that an individual case belongs to a specific habitat category" (Weinand 2005:26). This was followed by a preliminary assessment of the dataset, which suggested that the data are not normally distributed. In addition, a Box's M test of covariance equality was run and showed that covariance matrices or characters were not equal (e.g. $p<0.0001$) (Weinand 2005, 2007). In solving the problem of the assumptions of normality and equality of covariance matrices, a recursive partitioning (rpart) method was used to test whether the LDA was a contributing factor to the violation of these attributes (Weinand 2005, 2007). If not, a usable classification model for predicting the palaeoenvironments of Southeast Asia was created (Weinand 2005, 2007). As with other DFA analyses employed in previous studies, the seven measurements obtained were used in conjunction with the four habitat schemes to identify the best rpart model for the data (Weinand 2005, 2007). According to Weinand (2007:1778), "because accuracies assigned to the results of both statistical methods are the products of the data set itself, the calculated accuracies represent a maximum value". To ensure accuracy, numerous tests were done to validate each constructed model (e.g., jackknife procedure and the automated cross-validation test). DFA results accurately classified habitats for 63 of 81 sampled specimens, 77.8% (3.1 times better than chance) was the overall accuracy; this was higher than that of (Degusta & Vrba 2003). The cross-validation test correctly assigned 70.4% of the held-out specimens to habitat class, which is better than the jackknife procedure that obtained 62.5% accuracy from holding out one specimen from each species (Weinand 2005, 2007). Lastly, the 24-specimen

generator test produced an accuracy rate of 66.7% for the habitat class (Weinand 2005, 2007).

A similar but more detailed approach based on bovid astragalus morphology for palaeoenvironmental reconstruction was conducted by (Plummer *et al.* 2008). Their approach presented a DFA model used to investigate the relationship between astragalus morphology and four more refined habitat categories (e.g., open, light cover, heavy cover, and closed) using modern known ecology (Kappelman 1988, 1991; Kappelman *et al.* 1997; Plummer & Bishop 1994; Degusta & Vrba 2003, 2005; Plummer *et al.* 2008). Ratios reflecting the shape of each astragalus were generated for DFA by measuring twenty-four metrics for 286 astragali. DFA was applied, using a stepwise procedure in SYSTAT v.9/9.01 (Plummer *et al.* 2008; Bishop *et al.* 2011). Plummer *et al.* (2008) paid careful attention to variable selection and formulated the best statistically robust model for DFA compared to previous methods (e.g., Degusta &Vrba 2003, 2005). They also carried out numerous analyses, e.g., "resubstitution analysis, jackknife analysis, and the classification of several test samples to ensure the accuracy of their method" (Plummer *et al.* 2008:3017). Results for all these analyses and tests predicted results with an accuracy level of 87%, which means that bovid astragalus morphology can confidently be assigned to specific habitat categories. These results were somewhat better compared to those previously presented by (Degusta & Vrba 2003), because Degusta & Vrba (2003) used a relatively small sample size and a limited number of measurements. Nonetheless, as Kappelman *et al.* (1997) and Degusta & Vrba (2003) noted, Plummer *et al.* (2008) also found that there is a good correlation between bovid body mass and habitat structure, but this was not the main driving factor for the results of their discriminant function models.

Subsequently, Bishop *et al.* (2011) used the ecomorphology of fossil antelopes (bovids) from sites at Laetoli, Tanzania, to investigate the availability of habitats preferred in the region and their variation through time. Three elements (astragali, phalanges, and distal radii) of 36 modern African species less than 250 kg were studied (for bovid sizes used, also see Plummer *et al.* 2008). From the modern 36

species, 291 astragali, 469 phalanges (1st,2nd, and 3rd phalanx), and 257 radii were selected. Numerous measurements were taken from each specimen. Ratios for these measurements were subjected to a DFA as describe fully in previous studies (Kappelman 1988, 1991; Kappelman *et al.* 1997; Plummer & Bishop 1994; Degusta & Vrba 2003, 2005; Kovarovic & Andrews 2007; Plummer *et al.* 2008). Only a few measurements and "ratios calculated to reflect shape differences for each element were used for the final analysis" (Bishop *et al.* 2011:359). These were elements with variables that had the best predictive/discriminating power (Bishop *et al.* 2011). Discrimination analyses for "morphological variables allowed for the separation of the selected modern species into different habitat categories with high accuracy level" (Bishop *et al.* 2011:359). Like Plummer *et al.* (2008), their model's accuracy was tested three times using jackknife, resubstitution analyses, and reclassification tests.

A recent study method based on ecomorphology of the bovid astragalus was conducted by Barr (2014, 2015). The study aimed to predict bovid habitat preferences using a discriminant function model, as discussed above (Kappelman *et al.* 1997; Degusta & Vrba 2003; Plummer *et al.* 2008). However, in contrast to previous methods (Degusta & Vrba 2003; Weinand 2007; Plummer *et al.* 2008), Barr (2014, 2015) considered that the functional analysis of the astragalus is controlled by body size and phylogenetic signal, and the methods thus test the link between these variables. This study introduced new advanced techniques for measuring ratios reflecting functional morphology. A total of 181 astragali specimens from 50 extant bovid species Barr (2014) and 234 astragali from the Shungura fossil collections of southwestern Ethiopia Barr (2015) were sampled. Laser scanning through a 'NextEngine Desktop Scanner' was used to record each specimen. A 3D surface model was produced and then exported to PLY models (Barr 2014). Based on previous ecological literature (Kappelman 1988, 1991; Kappelman *et al.* 1997; Plummer & Bishop 1994; Degusta & Vrba 2003, 2005; Kovarovic & Andrews 2007; Plummer *et al.* 2008), all species were assigned to four respective habitat categories, respectively. In addition, several tests and measurements were taken, for example, "a series of linear and joint surface area

measurements were obtained from each astragalus, a geometric mean body size proxy was used to size correct the measurement data, and a Phylogenetic General Least Squares (PGLS) analysis was used to test the hypothesis of a functional relationship between each variable and the habitat category while controlling for body size and phylogenetic signal" (Barr 2015:100). The PGLS results suggested that highly cursorial bovids in open habitats can be distinguished from less cursorial bovids in closed habitats. For example, highly cursorial bovids have relatively short astragali that help to maintain speed throughout the camming or rotation motion, a greater range of angular excursion at the hock, and relatively larger joint surface areas and vice versa with less cursorial bovids (Barr 2014). According to Barr (2014,2015), the combination of these techniques e.g., surface scans and linear measurements were better at predicting habitats.

Another more recent study has been published by Forrest (2017) who used traditional caliper measurements of extant African bovid astragali as well as other elements such as phalanges and radii to investigate the degree of vegetation cover at Elandsfontein site in South Africa during early hominin occupation. Modern species used for comparative purposes were assigned to four habitat classifications as defined by previous ecological studies (Scott 1979, 1985; Kappelman 1988, 1991; Kappelman *et al.* 1997; Degusta & Vrba 2003), which were as follows: open cover, light cover, heavy cover and forest. All measurements were subjected to DFA method for resubstitution and cross-validation test (jackknife), "to generate classification matrixes and test the predictive value of data sets" using a stepwise procedure in MYSTAT (Forrest 2017:82). A DFA resubstitution classification success matrix results show that both the astragali and radii were classified correctly 88% of the time, and 90% of the time for the phalanges. The cross-validation test using a jackknife procedure produced an overall accuracy for the model which dropped to 86% for the astragali, 84% for the radii, and 87% for phalanges, and indicated adaptations of the four habitat types to varying degrees. These results prove that the method used for astragali, phalanges, and radii is most applicable and accurate for predicting and classifying habitats.

Chapter 3: Methodology

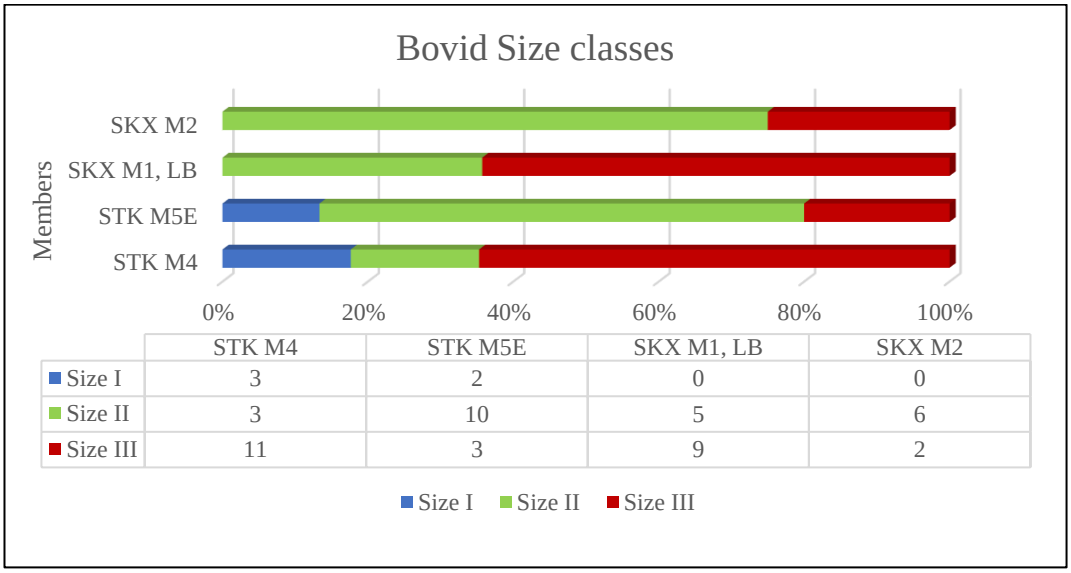
Previous studies have shown that the use of complete postcranial bones such as femora and metapodials achieved the highest prediction accuracies when conducting ecomorphological analyses (e.g., Kappleman 1988, 1991; and Plummer & Bishop 1994). However, these elements are most likely recovered as incomplete bones in the fossil record (Weinand 2005, 2007). This was indeed true for the faunal collections from Sterkfontein and Swartkrans caves analyzed here, hence this study uses the astragalus.

In this chapter, I present the methodology for analyzing the astragalus. The astragalus is a dense, weight-bearing bone that forms part of the ankle joint, and it is frequently preserved and easily recognizable in the fossil record due to its "double pulley structure" (Plummer *et al.* 2008:3016). It is selected in this study because it is well represented at Sterkfontein and Swartkrans caves and because its anatomic position and function are adapted for locomotion (Degusta & Vrba 2003).

3.1 Materials

The fossil specimens utilized for this study consist of complete astragali elements housed and curated at the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg. The fossil specimens presented here are part of CK Brain's Collection of fossils excavated from Swartkrans Member 1 Lower Bank assemblage associated with the Oldowan (SKX-M1 LB), faunal assemblages from the Hanging Remnant were not included in this study because there were some uncertainties about the stratigraphic position of HR and LB in M1 at the time my sample was selected, but we understand from L.Bruxelles that the HR and LB are part of the same deposit; the Swartkrans Member 2, Acheulean (SKX-M2) assemblage, excavated between 1979-1986; Pickering's PhD sample (Pickering 1999) from the Sterkfontein Member 5 East Oldowan Infill (STK-M5E) assemblage; and Kibii's PhD sample from the Sterkfontein Member 4 (STK-M4) (Kibii 2004). The sample from Swartkrans Member 1 and Member 2 consists of 22 astragali. From Sterkfontein Member 4 and Member 5, the sample comprises 33

astragali. These sample sizes are determined by the availability of complete elements for each member (see Table 3.2). The fossil specimens selected were previously subjected to taphonomic analyses, and for the purpose of this study they are only identified to the family-level Bovidae. Based on the bovid size classes provided in Table 3.1, all specimens included in this study have a body mass ranging from 0 to >250 kg, which are bovid size classes I to III (Brain 1974, 1981; Klein 1976). Specimens exceeding 250 kg are excluded to avoid "scaling differences and behavioural specializations related to large body size that may override any morphological habitat signal" as suggested previously (Bishop *et al.* 2011:356; and see Kappelman 1988). Only complete and adult specimens (determined by the complete fusion of the astragali epiphyses) and without regard to sex were sampled.



	STK M4	STK M5E	SKX M1, LB	SKX M2
Size I	3	2	0	0
Size II	3	10	5	6
Size III	11	3	9	2

Figure 3.1: Bovid size classes ranging from 1-3 for selected astragali by member (from bottom to top): Sterkfontein M4 (STK-M4), Sterkfontein Oldowan Infill (STK-M5E), Swartkrans M1 Lower Bank, Oldowan (SKX-M1 LB), and Swartkrans M2 Acheulean (SKX-M2).

Table 3.1: Bovid size classes (body mass) after Brain (1974, 1981) and Klein (1976).

Class	Category	Mass	Taxa
1	Small bovid (SB)	0-23 kg	*Raphicerus melanotis* (grysbok) *Cephalophus monticola* (blue duiker) *Sylvicapra grimmia* (grey duiker)
2	Small Medium Bovid (SM)	23-84 kg	*Antidorcas* sp.(springbok) *Pelea capreolus* (grey rhebok) *Redunca fulvorufula* (mountain reedbuck) *Tragelaphus scriptus* (bushbuck)
3	Large medium bovid (LM)	84-296 kg	*Alcelaphus buselaphus* (hartebeest) *Connochaetes* sp. (wildebeest) *Damaliscus* sp. (bontebok/blesbok) *Hippotragus leucophaeus* (blue antelope) *Redunca arundinum* (southern reedbuck) *Tragelaphus strepsiceros* (greater kudu)
4	Large bovid (LB)	296-400 kg >900 kg	*Syncerus caffer* (African buffalo) *Tragelaphus oryx* (eland)
5	Very large bovid (VLB)	>900 kg	*Syncerus antiquus* (Long-horn or "giant" buffalo)

3.1.1 Quantification

When dealing with faunal assemblages it is crucial, to quantify the number of specimens presented in each sample. For this study, the Number of Identifiable

Specimens (NISP) and the Minimum Number of Elements (MNE) is the primary and most preferred quantitative units. The NISP is a unit used to estimate taxonomic abundance of a faunal community; it is simply the number of all identified elements per taxon represented in a faunal assemblage (Lyman 1994; Clark 2009). The NISP for each member is shown in Table 3.2. The MNE "estimates the number of complete skeletal parts needed to account for the fragments of each skeletal part" (Rogers 2000:119). The sample from Sterkfontein is more than that from Swartkrans, and I was cognizant of this when comparing the samples. To avoid any biases in sample sizes, the difference between the MNE and the number of complete elements for each member was checked. Table 3.2 shows that the differences are not extreme (e.g., STK M4: 18/22), hence this project is using all complete elements from each member.

Table 3.2: The Number of Identified Specimens (NISP), Minimum Number of Specimens (MNE), and complete elements for Sterkfontein (STK) and Swartkrans (SKX) members.

Site	Member	NISP: MNE	Complete	Reference
Sterkfontein	Member 4	55: 22	18	Kibii (2004)
Sterkfontein	Member 5 East, Oldowan Infill	32: 22	15	Pickering (1999)
Swartkrans	Member 1 Lower Bank, Oldowan	21: 18	14	Brain (1981); Watson (1993)
Swartkrans	Member 2, Acheulean	14: 12	8	Brain (1981); Watson (1993)

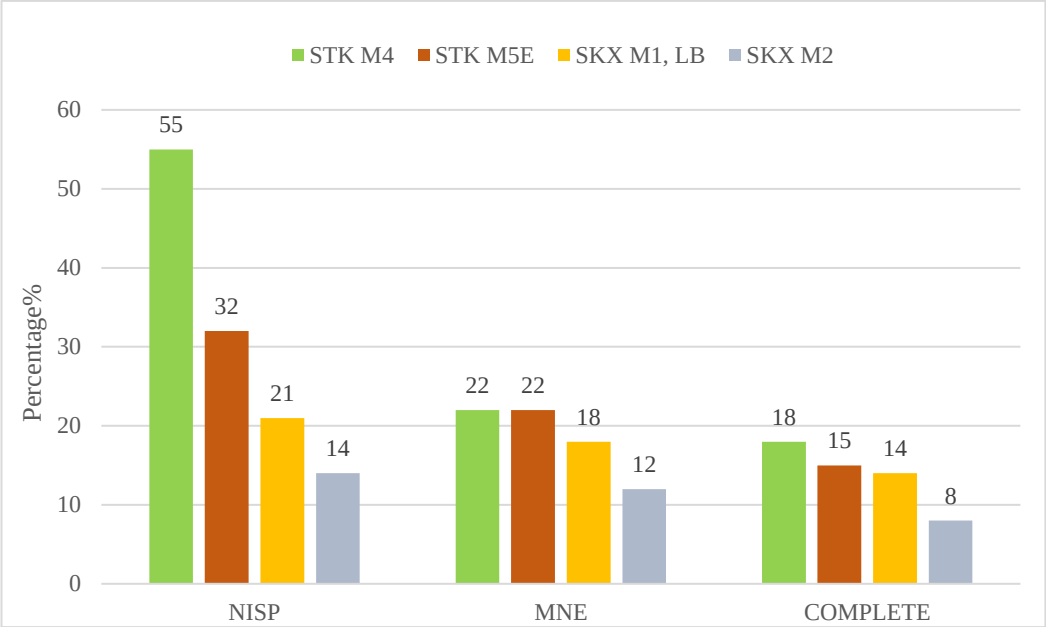


Figure 3.2: The distribution of selected astragali: Number of identified Specimens (NISP), Minimum Number of Elements (MNE), and Complete Elements by member: Sterkfontein M4 (STK-M4), Sterkfontein Oldowan Infill (STK-M5E), Swartkrans M1 Lower Bank, Oldowan (SKX-M1 LB), and Swartkrans M2, Acheulean (SKX-M2).

3.2 Methods

Following measurements outlined by Degusta & Vrba (2003) and Weinand (2005, 2007), seven measurements were taken by the author from each of the 55 fossil astragali specimens from Sterkfontein and Swartkrans (see Appendix A.1. for raw fossil astragali measurements). All measurements were taken with digital calipers to generate ratios for understanding the functional morphology, with specific ultimate relevance to habitat, and recorded to the tenth of a millimetre. Measurements were taken with no preference for element side (right or left) or sex (male/female)**.** In order to maintain accuracy and to avoid intra-observer error, each astragalus was measured twice with a separation of a few days between measurements. An average was calculated for those metrics that were different when measured the second time. In this study, the author considered that the acceptable error margin for those measurements is 0.1 mm (minimum) and 0.5 mm (maximum), and these fall within 0.2% to 1% error. All fragmented fossil specimens were excluded from analysis as such fossils do not have all the features required for measurements. The measurements taken are as follows:

3.2.1 Astragali measurements

These measurements were taken directly from Degusta & Vrba (2003:1011):

1. Medial Length (LM): the maximum proximal-distal dimension of the medial surface taken parallel to the main proximal-distal axis of the astragalus.

2. Lateral length (LL): the maximum proximal-distal dimension of the lateral surface taken parallel to the main proximal-distal axis of the astragalus.

3. Intermediate thickness (TI): the minimum anteroposterior dimension of the lateral surface in the area of the junction between the proximal and distal articular regions.

4. Distal thickness (TD): the anterior-posterior dimensions of the distal regions.

5. Intermediate length (LI): The minimum proximal distal dimension of the astragalus taken parallel to the main proximal distal axis of the element.

6. Intermediate with (WI): the minimum medial-lateral dimension on the anterior surface at the junction of the proximal and distal articular facets.

7. Distal Width (WD): the medial-lateral dimension of the distal end at its distal-most point.

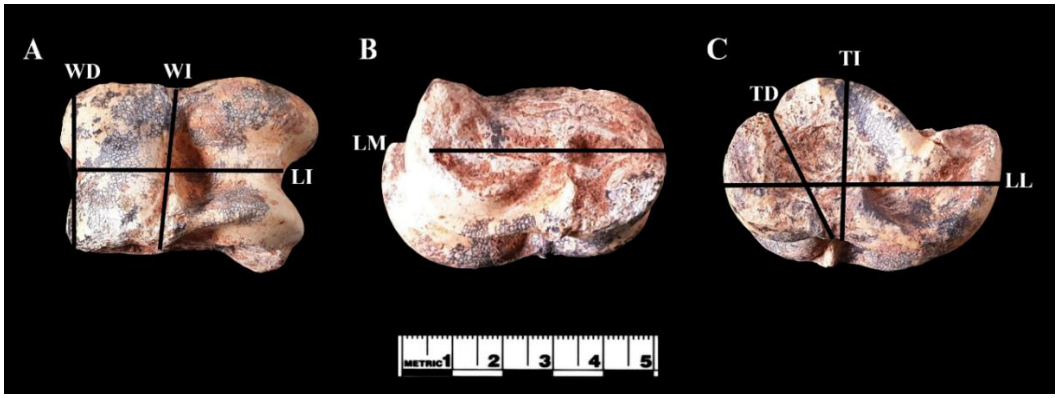


Figure 3.3: Astragalus metrics after (Degusta & Vrba 2003:1011); (A) "anterior view of bovid right astragalus with distal width (WD), intermediate width (WI), and intermediate length (LI) indicated; (B)Medial view of bovid astragalus with medial length (LM); (C) lateral view of bovid right astragalus with distal thickness (TD), intermediate thickness (TI), and lateral length (LL)" indicated (Photographs by R. Sambo).

For comparative purposes, measurements of 61 modern bovids from class sizes ranging from 1-3 were selected from Weinand's (2005) published raw measurements of Southeast Asian modern species and a few African species (see Appendix A.2 for modern measurements). Weinand (2005) obtained measurements of the few African species from Degusta & Vrba (2003) through personal communication (unpublished raw measurements), this includes blue wildebeest (*Connochaetes taurinus*), tsessebe *(Damaliscus lunatus*), blue duiker (*Cephalophus monticola*) and dik-dik (*Madoqua kirkii*). Weinand (2005) found good comparability between Southeast Asian and African specimens in the same habitats.

3.2.2 Body size

Early and recent studies have taken into consideration body size when constructing ecomorphological models (Kappelman 1988, 1991; Plummer & Bishop 1994; Kappelman *et al.* 1997; Weinand 2005, 2007; Kovarovic & Andrews 2007; Plummer *et al.* 2008; Klein & Steele 2010; Bishop *et al.* 2011; Barr 2014, 2015; Forrest 2017). Some have identified it as a complicating factor that must be given attention in analyses to determine whether or not it is a driving factor in the prediction of habitat classifications of species (see Kappelman 1988, 1991; Plummer & Bishop 1994; Weinand 2005, 2007; Plummer *et al*. 2008; Barr 2014, 2015). Previous research shows that the utilization of measurement ratios of the femora length to body size shows a significant correlation between the two (Kappelman 1988). This is a significant result and a merited investigation of the correlation between measurements and body size. The elimination of body size ensures that morphology rather than body size determines habitat classification (Degusta & Vrba 2003). Degusta & Vrba (2003:1019) had argued that the allometric component of size is related to habitat and retains important functional information, and "if habitat prediction is the goal", therefore eliminating body size effects is not an ideal solution, but can be corrected for isometric scaling (Elton *et al.* 2016). However, it is important to understand the effect of eliminating of body mass on habitat prediction, Degusta & Vrba (2003) found a strong correlation (R^2 = 0.91) between astragalus measurements and body mass. In addition, Weinand (2005) used a log-transformed method to convert the raw measurements of

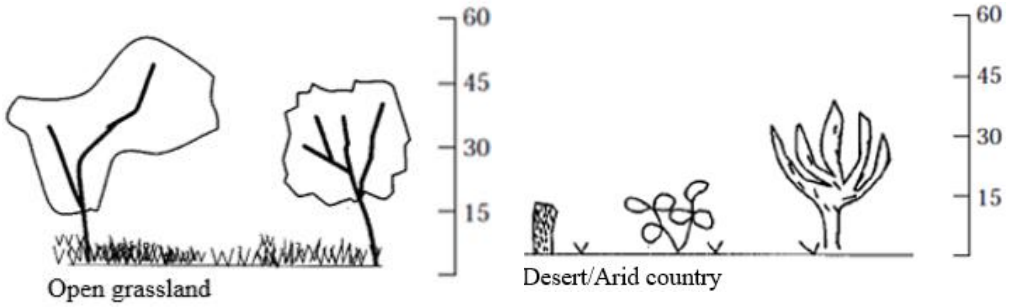
Southeast Asian astragalus specimens to log-scaled values after Darroch & Mosimann's (1985) work and confirmed Degusta & Vrba's (2003) argument. Body size effects can be minimized by excluding bovids that exceed 250 kg (isometric scaling) (Kappelman 1991). My sample for this current study does not contain bovids bigger than 250 kg, and all sizes range from 0-250 kg. Therefore, no statistical method will be used for eliminating body size.

3.2.3 Habitat classifications

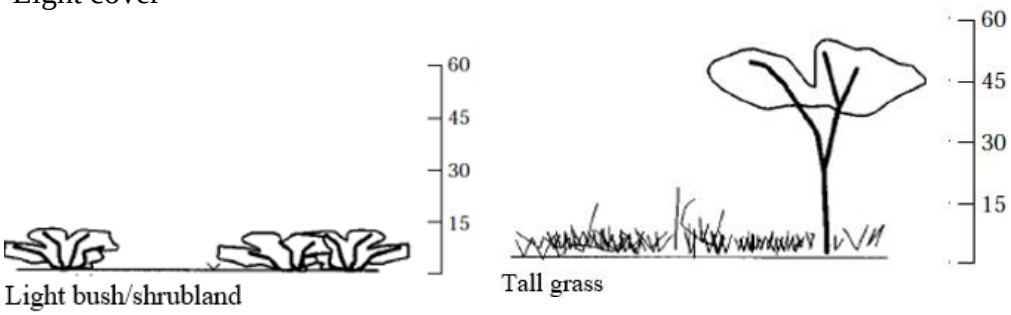
To predict habitats for the unknown cases, previous ecomorphological studies have provided habitat classifications that produce an "arbitrary finite sample of a continuous range of habitats encountered by the taxonomic group being studied" (Weinand 2005:22). Earlier habitat classifications employed a three-habitat grouping (e.g., open/plains, intermediate/broken cover, and closed/forest) (Kappelman 1986, 1988, 1991; Plummer & Bishop 1994). Subsequently this was refined in recent studies to a four-habitat grouping scheme namely: open, light cover, heavy cover, and forest (Scott 1979, 1985; Kappelman 1986, 1988, 1991; Kappelman *et al.* 1997; Scott *et al.* 1999; Degusta & Vrba 2003). Most recently, a fifth habitat scheme (mountain habitat) was also created (Weinand 2005, 2007). For a study of this kind, an ideal categorization of habitats would be based on extensive field behavioural observations (independent of statistical analysis) to accurately characterize specific habitat preferences of individual bovids to be included in the sample before collection (Kappelman *et al.* 1997). However, during the time when early ecomorphological studies were conducted, it was difficult to collect such data or even reconstruct this amount of details "because in most cases museums did not record enough information for each specimen at the time that it was collected to determine where the individual lived, i.e., parts or exact habitat of the specific individual" (Kappelman *et al.* 1997:231). Hence today, habitat classifications are based on a large body of published literature on extant species habitats as well as literature describing modern bovid habitat preferences (Skinner & Smithers 1990; Skinner & Chimimba 2005; Degusta & Vrba 2003).

In this study, a four-habitat grouping scheme adapted from Degusta & Vrba (2003) for modern African specimens is utilized as well as those from Southeast Asia (Weinand 2005). The detailed breakdown simplifying these habitat categories are as follows (see Fig 3.4): open cover (grassland, open country, arid country), light cover (light bush, tall grass with some occasional trees), heavy cover (bush, woodland, swamp, close to water), and forest which is a continuous tree canopy. As bovids manoeuver across a mosaic of habitats, the assignment of bovid taxa to these categories is a "best fit designation rather than an exclusive one" (Degusta & Vrba 2003:1014). These classifications take into consideration "the kinds of selection pressures on locomotion and body mass that are specific to each species in its particular habitat" (Kappelman *et al.* 1997:232; see Kappelman 1988; Plummer & Bishop 1994). For example, an African species like kob (*Kobus kob*) generally inhabits open cover habitat. Still, it also relies on woodlands where manoeuvrability is important, and thus, it is classified as a light cover species. The same applies to the Southeast Asian species bateng (*Bos javanicus*) as noted by (Weinand 2005). This species is usually found in dry and more open environments, as well as in dense thickets and forest settings for shelter, and therefore this complex substrate is considered an ecotone. Therefore, bateng (*Bos javanicus*) is classified *as* an open habitat species Weinand (2005).

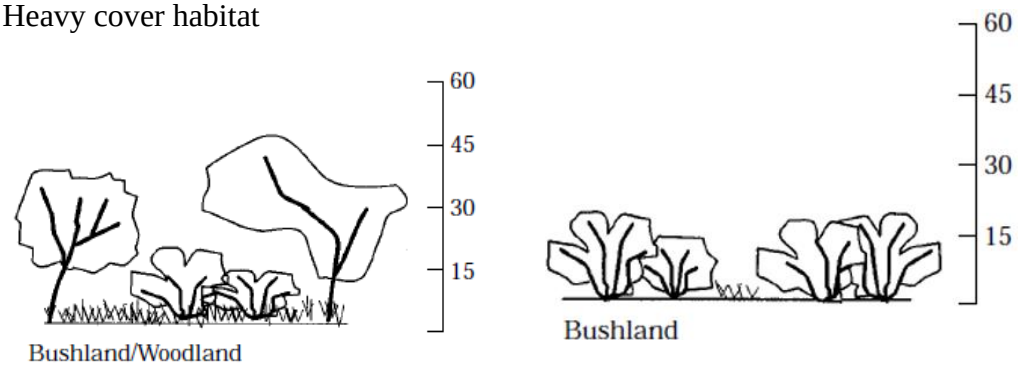
Open habitat



Light cover



Heavy cover habitat



Forest cover habitat

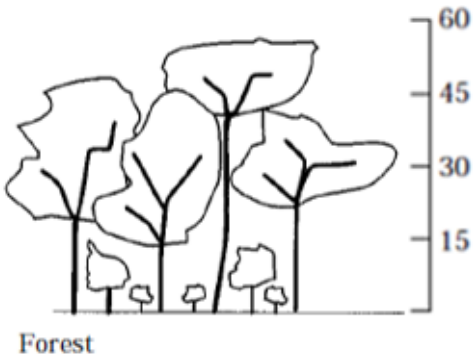


Figure 3.4: Examples of habitat types within each habitat categories used in this study (images from Reed 1997:295).

3.2.4 Linear Discriminant Analysis

Having obtained astragalus measurements for the fossil sample and raw measurements for the African and Southeast Asian modern specimens and the habitat preference information from the modern sample, the next step was to apply a method to assess the degree to which habitat could be predicted from these measurements. The method used in this study as in most ecomorphological studies, as mention earlier, is a Linear Discriminant Analysis (LDA) a parametric statistic method (Weinand 2005). In ecomorphological studies, LDA is designed to create a linear combination that best "characterizes the relationship between a set of predictor variables or measurements taken from the bones and grouping variables being the constructed habitat classification scheme, hence the name Linear Discriminant Analysis" (Weinand 2005:24). This methodology was employed here following Degusta & Vrba's (2003) work that uses African bovid astragali, as well as Weinand (2005, 2007) with Southeast Asian bovid astragali. The discriminant analysis was run in the 'Statistical Package for the Social Science' (SPSS v.25.0. In SPSS a discriminant function was used to calculate the probabilities describing the likelihood that an individual case or specimen correlated with a specific habitat. To achieve this, a discriminant model was constructed by analyzing all seven measurements (e.g., LM, LI, LL, WI, WD, TI, TD) of the fossil sample of unknown group membership or ecology in conjunction with the four-habitat scheme extracted from the modern sample for which group membership is known (Weinand 2005, 2007). All the discriminant functions produced by this model uses the following mathematical formula employed by Weinand (2005, 2007).

$$F_K = D_0 + D_1X_1 + D_2X_2 + \ldots + D_pX_p$$

F_K is the score on function K and D_1 stands for the discriminant coefficients, whereas X_1 are the predictor variables. In LDA, "the maximum number of functions K that can be derived is equal to the minimum number of predictors (p) or the quantity (number of groups-1)" (Weinand 2005:25). There are generally more predictor variables than grouping variables when conducting ecomorphological studies, which restrict the number of functions by the latter value (Weinand 2005, 2007). For example, for a four-habitat model, three classifications functions (four groups-

1) are constructed, and discriminant scores for each function are calculated by LDA. The calculated score is, therefore "used to classify the cases into one of the group variable categories" (Weinand 2007:1776). The following methods are used in classifying cases into groups: (1) the maximum likelihood methods; (2) linear classification functions; and (3) distance functions. However, for the present study, the maximum likelihood method is applied following the Bayesian statistics that create a rule to classify cases. This method is simply based on the "principle that a case is assigned to a group if its probability of membership to that group is greater than the probability of belonging to any other group" (Weinand 2005:25). This is achieved by using two probability estimates, namely: prior probability and posterior probability. Prior probability estimates the likelihood of a case belonging to a group without predictors information by using the number of cases in each category of the grouping variable or by assuming equality of prior probabilities (Weinand 2005, 2007). The posterior probability is concerned with obtaining a discriminant score that determines the likelihood that a case belongs to a specific group and the confidence of the calculated predictions.

Furthermore, in addition to the above-mentioned prediction probabilities, cross-validation tests are conducted to ensure that the constructed model is accurate. This is done based on a classification system knows as 'leave-one-out' (Weinand 2005, 2007), which means that LDA constructs a model by leaving-out one specimen from the analysis which is held-out to be tested against a new model. This process continues until all the specimens in the dataset have been held-out and tested. Therefore, "the overall cross-validated accuracy of the model is based on the number of correct classifications, divided by the total specimens in the sample" (Weinand 2005:25).

Most importantly, the accuracy of the LDA model depends on the adherence to two principal assumptions about the dataset relating to the population to be studied. The first assumption is that data should be normally distributed, but this is often violated and problematic particularly when groups selected from a multivariate normal population do not demonstrate normality in the space of predictor variables

(Weinand 2005, 2007). The second assumption suggests that there should be equality in the covariance matrices of different groups, an assumption mainly tested with Box's M test in the Equality of Covariances procedures. This is, however, true for small sample sizes but not often true in the case of large sample sizes (Manly 1986). If covariances for a discriminant model are not equal (e.g., $p<0.001$), the confidence of the classifications for that test will be minimized. An examination of the data selected for used in this study, however, shows that both these assumptions were not met. For instance, Wilk's lambda (multivariate test) demonstrates that the data was not normally distributed because $p>.05$, and we can say that the model is not a good fit for the data. Furthermore, Box's M test of covariance equality indicates that the covariance matrices are not equal ($p<0.001$). As mentioned earlier, this is deemed problematic for studies of this kind and in this current study, it is acknowledged as a potential limitation, and thus the results should be treated with caution. The group sample sizes for this study are nearly equal; hence the assumption of covariance equality does not strictly restrict the use of LDA. However, one obvious explanation for Box's M test results not being equal is possibly the small sample size for Swartkrans Member 2 (SKX-M2).

Furthermore, most LDA tests are conducted using large datasets, typically with group samples of over a hundred to ensure the above assumptions are met. Previous studies have shown that "if normality can be assumed, the issue of unequal covariance matrices can be solved" Weinand (2007:1775), this can be done by using another statistical method (Manly 1986)-- for example, Quadratic Discriminant Analysis (QDA), a method applied by Plummer & Bishop (1994), or recursive partitioning (rpart), a nonparametric method utilized by Steinberg & Colla (1995), Feldesman (2002), and Weinand (2005, 2007). When comparing LDA and recursive partitioning (rpart) for Southeast Asian and African specimens, Weinand (2005, 2007) found that these methods produce the highest accuracy results when combined, which was better than the two individual models. However, regardless of its robust violations of normality and equal covariance is proven by rpart, the LDA is a good model to use because on its own, it produced a high accuracy rate for a four-habitat model. Therefore, with this result, I consider it safe to continue

using the LDA in this current study without having to use another statistical method to determine if this method is robust to the violation of the above-mentioned assumptions or test if it is the best classification model for predicting palaeoenvironments.

Chapter 4: Results

The constructed LDA model adopted from previous studies of the astragalus ecomorphology for modern bovids indicates that there is at least two times better than a chance for predicting habitat from measurements taken, thus, making the astragalus morphology suitable for inferring palaeoenvironments. This chapter is divided into two sections. The first section presents briefly the results produced by LDA for a four-habitat grouping scheme for modern sample of bovids selected from a previous study of the astragalus morphology. The second section, 'Fossil Results', presents the LDA results of the fossil sample from Sterkfontein and Swartkrans caves for a four-habitat grouping scheme.

4.1 Four-habitat model for modern samples

The statistics summary for the raw measurements obtained from Weinand's (2005, 2007) modern specimens and the fossil samples of this current study is shown in Appendix A.3. Similar to Degusta & Vrba (2003), Weinand (2005, 2007) observed an increase for the raw measurement values for the four-habitat model for Southeast Asian and African bovid astragali. In the majority of cases, and as it appears in the current study, the order of the variables ranged from least to highest as follows: forest, light cover, heavy cover, and open cover. In two cases, metrics (WI and WD) show a reversed pattern between open cover and heavy cover, in this case heavy cover had the highest value. In this study, open cover and heavy cover for metrics (WI and WD) have similar values. It is only one case (LL), that open and heavy cover means were the same, but in all cases the variables of these two habitat categories are comparable (see Appendix A.3).

4.1.1 Raw measurements-Discriminant Function Analysis

The discriminant function produced by SPSS accurately predicted habitat group for 55 fossil bovid specimens using a comparative dataset of 61 modern bovids of known environments for overall accuracy (or representative estimate) of 68.9% (nominally 2.1 times than expected by chance=25%) for a four-habitat model; (see Table 4.1). The four habitats vary from a low of 36.4% accuracy for heavy cover to

a high of 64.7% for open cover, with forest at 78.6% and light cover at 84.2%. Three discriminant functions (Functions 1-3) were calculated in the analysis and accounted for the variance of F1:83.3%, F2:12.6%, and F3:4.1% respectively (Table 4.2). The structure matrix of the pooled within-group correlations indicated that all the variables are strongly correlated with F2. The visual representation of the habitat group separations in discriminant space is shown in Fig 4.1, with a scatterplot of canonical function 1 versus function 2. The cross-validation test is done only for those cases in the analysis to estimate the error rate of the model used and helps to determine if the model used is the best fit. In this case, the cross-validated test correctly predicted 50.8% of the held-out specimens to habitat class (see Table 4.1). This result (50.8%) is lower than the classification rate for correctly classified habitat groups (68.9%). Therefore, the validation test indicates that 68.9% accuracy of the model is a best fit and a good representative estimate.

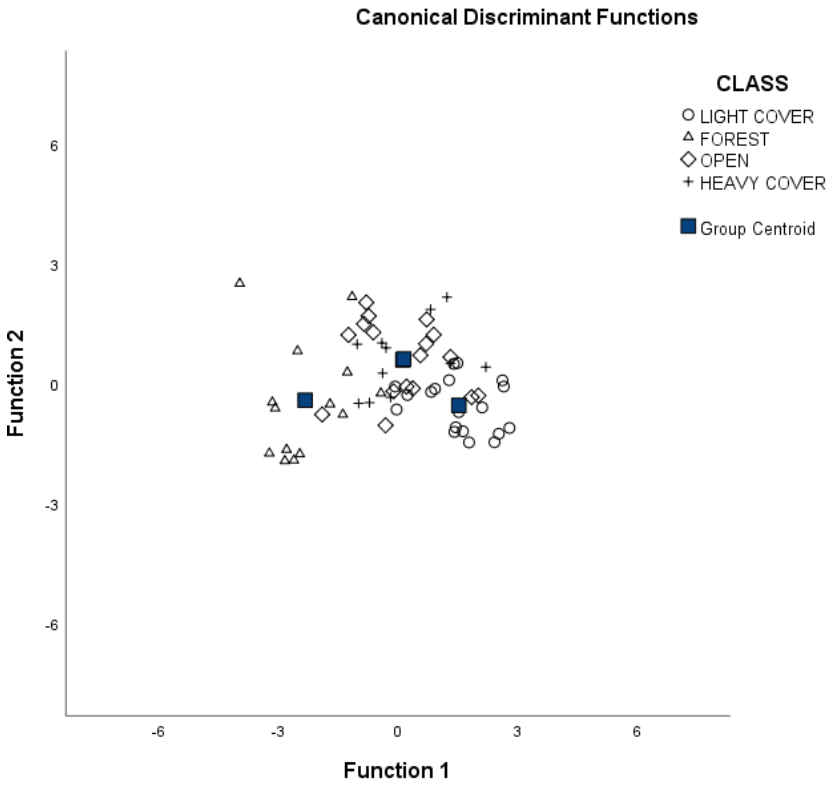


Figure 4.1: Scatterplot of canonical function 1 versus function 2 of the Group Centroid showing a visual representation of the habitat group separations.

Table 4.1: Predicted group membership classification results for the four-habitat model.

		Classified as:				
Actual group	**n**	**Open cover**	**Light cover**	**Heavy cover**	**Forest cover**	**accuracy (actual)**
Open cover	17	11	3	2	1	64.7%
Light cover	19	3	16	0	0	84.2%
Heavy cover	11	4	2	4	1	36.4%
Forest cover	14	2	0	1	11	78.6%

68.9% of original grouped cases correctly classified.

50.8% cross-validation results

Table 4.2: Structure Matrix discriminant functions.

Metric	**Function 1**	**Function 2**	**Function 3**
LL	-0.071	0.001	-0.244
LM	-0.252	0.129	-0.117
LI	-0.097	0.122	0.118
WD	0.481	-0.244	-0.094
WI	-0.162	-0.157	-0.201
TD	0.472	-0.019	-0.123
TI	0.048	0.210	0.807
% Variance	83.3	12.6	4.1

Pooled within-group correlations between functions and variables. (*) Indicates largest absolute correlation between variable and function

4.2 Fossil Samples

This section presents the results of the fossil analysis **(**see Appendix A.4). The results differ for the faunas in all archaeological members, but a similar trend is notable. In all cases, there is an increase over time in the percentage of open and light cover, and a decrease in the percentage of heavy cover and forest cover

specimens at Swartkrans and Sterkfontein caves. More details on these trends will be examined below. It is significant to note that in addition to a prediction of habitat group, the discriminant function "also provides an associated percentage probability known as confidence cut-off value for that prediction" (Degusta & Vrba 2003:1015). The confidence cut-off value for the astragalus dataset used in this study is 66%. This applies only to those values in the discriminant function that fall below the 66% value, and these values are indicated by boldface type for all the archaeological members (see Appendix A.4). These values are significant because they highlight specimens in the assemblage that have been reclassified into another closest habitat group in the second most-likely habitat classification. For example, a discriminant function can provide an estimate of the probability that two astragali specimens belong to an open cover habitat group, the fact that one specimen has high confidence value of, i.e., 75% and another 49% does not necessarily mean that the two specimens are of equal reliability (Degusta &Vrba 2003). However, "the confidence cut-off value determines which predictions generated by a discriminant function are statistically significant" (Degusta &Vrba 2003:1015). In most cases, predictions with higher confidence values are statistically significant, while those with less statistical significance should not be ruled out but rather accorded less weight. Confidence values will also be explored in more detail for each one of the four archaeological members with reference to the results of the fossil analyses.

4.2.1 Sterkfontein M4--Four-habitat model, raw measurements

The DFA model produced habitat classifications as well as probability assignments to habitat groups for Sterkfontein Member 4 (STK-M4) specimens (see Table 4.3). For this sample, the most abundant habitat prediction is open cover (44.4%), followed by light cover (33.3%) as the second-highest habitat category. Forest cover (6.7%) and heavy cover (6%) are the least categories. This model shows that 11 specimens from M4 did not succeed in meeting the 66% confidence cut-off value. Of these 11, five were open cover specimens, three of which when classified in the second classification of habitat categories fell in the light cover category, one under heavy cover and another one under forest cover. Of the same 11, three light cover specimens failed the cut-off value; two of these specimens are open cover

specimens and one heavy cover in the second classification of habitat groups. One heavy cover specimen of the 11 cut-off values was reassigned to open cover in the second classification. Lastly, two forest cover specimens of the total 11 did not meet the cut-off value and were both assigned as open cover specimens in the second classification of habitat groups.

Table 4.3: Sterkfontein M4, Results: Raw measurements four-habitat model.

Taxon	Deposit/Member	Kibii's collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	STK M4	S94-11276	6 (Forest cover)	0.753
Bovidae	STK M4	S94-12077	7 (Open cover)	0.876
Bovidae	STK M4	S94-12030	7 (Open cover)	0.187
Bovidae	STK M4	S94-12492	7 (Open cover)	0.813
Bovidae	STK M4	S94-13716	8 (Heavy cover)	0.607
Bovidae	STK M4	UKNOWN	5 (Light cover)	0.258
Bovidae	STK M4	S94-14305	5 (Light cover)	0.668
Bovidae	STK M4	S94-14454	7 (Open cover)	0.148
Bovidae	STK M4	S94-14458	7 (Open cover)	0.080
Bovidae	STK M4	S94-14499	6 (Forest cover)	0.590
Bovidae	STK M4	S94-15046	6 (Forest cover)	0.301
Bovidae	STK M4	S94-14177	5 (Light cover)	0.766
Bovidae	STK M4	S94-10766	7 (Open cover)	0.775
Bovidae	STK M4	S94-10749	5 (Light cover)	0.771
Bovidae	STK M4	S94-9145	7 (Open cover)	0.085
Bovidae	STK M4	S94-12064	5 (Light cover)	0.000
Bovidae	STK M4	S94-8859	7 (Open cover)	0.394
Bovidae	STK M4	S94-11004	5 (Light cover)	0.190

[1]P(D>d | G=g) is the probability of an individual belonging to the assigned group.

[2]Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

4.2.2 Sterkfontein M5E, Oldowan Infill--Four-habitat model, raw measurements

The habitat classifications produced by DFA model for the Sterkfontein Member 5 East, Oldowan Infill (STK-M5E Oldowan) specimens and their probability assignment to a habitat group are given in Table 4.4. It appears that STK-M5E Oldowan Infill has open cover specimens (40%) that are relatively more abundant than those in heavy cover and forest cover category. For STK-M5E, Oldowan Infill, seven predictions did not meet the 66% confidence cut-off value. Of these, four were originally open cover specimens; however, three of the four were reclassified as forest cover specimens and the last one of the four assigned as a heavy cover specimen in the second classification of habitat categories. From the seven, two forest cover specimens did not meet the cut-off, and both assigned as open cover specimen in the second classification. Lastly, one of the seven specimens that did not meet the 66% cut-off value was light cover and was classified as a heavy cover specimen in the secondary classification.

Table 4.4: Sterkfontein M5E, Oldowan Infill Results: Raw measurements four-habitat model.

Taxon	Deposit/Member	Pickering's collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	STK M5E	S94-3098	6 (Forest cover)	0.513
Bovidae	STK M5E	S94-13356	6 (Forest cover)	0.264
Bovidae	STK M5E	S94-13433	5 (Light cover)	0.762
Bovidae	STK M5E	S94-13474	6 (Forest cover)	0.731
Bovidae	STK M5E	S94-6111	7 (Open cover)	0.805
Bovidae	STK M5E	S94-2755	7 (Open cover)	0.365
Bovidae	STK M5E	S94-6905	7 (Open cover)	0.566
Bovidae	STK M5E	S94-13346	8 (Heavy cover)	0.744
Bovidae	STK M5E	BP/3/19962	5 (Light cover)	0.134
Bovidae	STK M5E	S94-3620	5 (Light cover)	0.714
Bovidae	STK M5E	S94-2923	7 (Open cover)	0.536
Bovidae	STK M5E	S94-13300	7 (Open cover)	0.500
Bovidae	STK M5E	S94-13426	5 (Light cover)	0.914
Bovidae	STK M5E	S94-3726	7 (Open cover)	0.826
Bovidae	STK M5E	S94-13497	5 (Light cover)	0.729

[1]P(D>d | G=g) is the probability of an individual belonging to the assigned group.

[2]Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

4.2.3 Swartkrans M1 Lower Bank, Oldowan--Four-habitat model, raw measurements

The predicted habitats for Swartkrans Member 1 Lower Bank (SKX-M1 LB) and their associated probability assignments appear in Table 4.5. Light cover specimens (78.57%) are more than twice as abundant for this collection, thus making light cover a more prominent habitat category than open cover (14.29%), forest cover (7%) and heavy cover (0%). Six specimens that did not succeed in meeting the confidence cut-off value (66%). Five of these were primarily light cover specimens,

all of which were classified as heavy cover in the second classification of habitat groups. The last one of the six that failed the cut-off value is a forest cover specimen, which was predicted to fall under open cover in the second most-likely category.

Table 4.5: Swartkrans M1 LB, Oldowan Results: Raw measurements four-habitat model.

Taxon	Deposit/Member	Brain's collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	SKX M1 LB	13790	5 (Light cover)	0.372
Bovidae	SKX M1 LB	5687	7 (Open cover)	0.845
Bovidae	SKX M1 LB	5846	5 (Light cover)	0.884
Bovidae	SKX M1 LB	9809	5 (Light cover)	0.458
Bovidae	SKX M1 LB	6703	6 (Forest cover)	0.084
Bovidae	SKX M1 LB	6309	5 (Light cover)	0.468
Bovidae	SKX M1 LB	13949	5 (Light cover)	0.951
Bovidae	SKX M1 LB	5687	7 (Open cover)	0.845
Bovidae	SKX M1 LB	5846	5 (Light cover)	0.884
Bovidae	SKX M1 LB	9809	5 (Light cover)	0.458
Bovidae	SKX M1 LB	12730	5 (Light cover)	0.824
Bovidae	SKX M1 LB	13640	5 (Light cover)	0.318
Bovidae	SKX M1 LB	7991	5 (Light cover)	0.824
Bovidae	SKX M1 LB	13640	5 (Light cover)	0.840

[1]P(D>d | G=g) is the probability of an individual belonging to the assigned group.

[2]Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

4.2.4 Swartkrans M2, Acheulean--Four-habitat model, raw measurements

Habitat classifications and probability assignments for Swartkrans Member 2, Acheulean (SKX-M2) are given in Table 4.6. The classifications show that the most abundant specimens in the sample are those from the light cover category (50%).

Open cover (25%) and forest cover (25%) specimens making up half of the assemblage are tied for the second most abundant category, and heavy cover (0%) is absent. Seven specimens did not meet the 66% cut-off value in the probability of habitat assignment. Four of the seven were primarily predicted as light cover; three predicted to be open cover and one as heavy cover in the second classification of habitat categories. Two forest cover specimens of the seven that did not meet the cut-off value and was reclassified as open cover specimens in the second prediction category. One open cover specimen was reclassified as light cover in the second classification.

Table 4.6: Swartkrans M2, Results: Raw measurements four-habitat model.

Taxon	Deposit/Member	Brain's collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	SKX M2	3852	5 (Light cover)	0.403
Bovidae	SKX M2	990	5 (Light cover)	0.328
Bovidae	SKX M2	916	6 (Forest cover)	0.176
Bovidae	SKX M2	3775	7 (Open cover)	0.811
Bovidae	SKX M2	792	5 (Light cover)	0.526
Bovidae	SKX M2	3061	7 (Open cover)	0.326
Bovidae	SKX M2	3189	6 (Forest cover)	0.359
Bovidae	SKX M2	12337/1237	5 (Light cover)	0.303

[1]P(D>d | G=g) is the probability of an individual belonging to the assigned group.

[2]Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%)

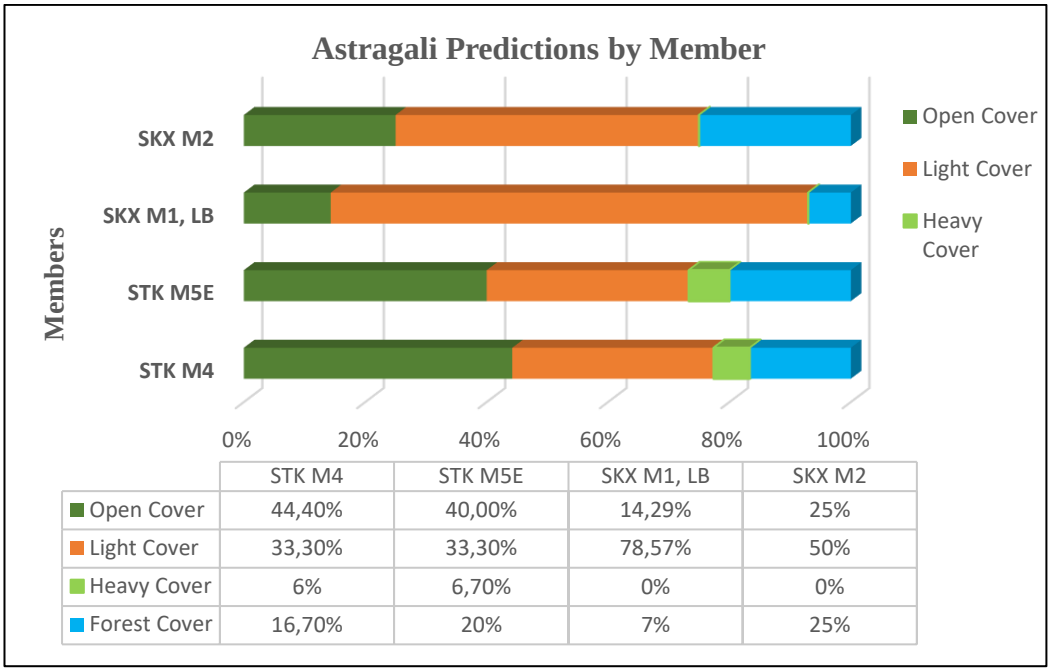
4.3 Summary of results

A summary of the fossil results to habitat groups is presented in Table 4.7, and the proportion of astragali habitat predictions for all the deposits (Sterkfontein M4 and M5E Oldowan infill and Swartkrans M1 LB, Oldowan and M2 Acheulean) is presented in Fig 4.2. Trends observed in habitats and bovid morphology revealed

by these results will be discussed in greater detail in Chapter 5 (Discussion and Conclusion).

Table 4.7: Fossil Results: All Members/Deposits.

	Raw measurements	
	LDA	
4 Habitats:		
Sterkfontein Member 4	Open cover	44.4%
	Light cover	33.3%
	Heavy cover	6%
	Forest cover	16.7%
Sterkfontein Member 5 East, Oldowan Infill	Open cover	40%
	Light cover	33.3%
	Heavy cover	6.7%
	Forest cover	20%
Swartkrans Member 1 Lower Bank	Open cover	14.29%
	Light cover	78.57%
	Heavy cover	0%
	Forest cover	7%
Swartkrans Member 2, Acheulean	Open cover	25%
	Light cover	50%
	Heavy cover	0%
	Forest cover	25%



	STK M4	STK M5E	SKX M1, LB	SKX M2
Open Cover	44,40%	40,00%	14,29%	25%
Light Cover	33,30%	33,30%	78,57%	50%
Heavy Cover	6%	6,70%	0%	0%
Forest Cover	16,70%	20%	7%	25%

Figure 4.2: The proportions of astragali habitat predictions by member: Sterkfontein M4, M5E, Oldowan Infill, and Swartkrans M1 Lower, Bank Oldowan and M2 Acheulean.

Chapter 5: Discussion & Conclusions

A taxon-free ecomorphological approach was conducted to investigate palaeoenvironmental changes at Sterkfontein and Swartkrans caves between 2.8 and 1.5 Ma through the functional morphology of well-preserved bovid astragali. This was conducted by testing the discriminant function model for its applicability in predicting and interpreting habitats for bovid astragali to search for similarities and differences between the two sites, and to clarify their respective environmental conditions. In using this model, this approach revealed some differences and similarities between the sites and provided another perspective on their palaeoenvironment contexts. This chapter is divided into five sections. The first section presents an interpretation of the results presented in Chapter 4 and their contribution to the palaeoenvironmental reconstructions of Sterkfontein and Swartkrans. The second section presents the palaeoenvironmental implications of each deposit in question for the two sites based on environmental changes revealed by the results, as well as a brief discussion on the issue of animal migration and seasonality changes. The third section is a discussion on the degree to which these results fit into the major theoretical framework of regional and global palaeoclimatic shifts that significantly influenced environments, mammalian and early human evolution during the Plio-Pleistocene period in Africa. The fourth section addresses the issues of time-averaging and taphonomy briefly when interpreting faunal assemblages, as well as a summary on the geomorphological implications for the two sites. The fifth section presents conclusions and future avenues of this research.

5.1 Observable trends, Four-habitat model, Fossil measurements

5.1.1 Sterkfontein faunas

As shown in Chapter 4, Table 4.7 and Fig. 4.2, the fossil analyses reveal a similar trend through time in the selected Sterkfontein bovid faunas for the Member 4 and Member 5 East, Oldowan Infill habitats for open cover from 44.4% in M4 to 40% in M5E Oldowan. The percentage of light cover habitats (33.3%) is the same between the two members. There is an increase in the number of forest cover (16.7

to 20%) and heavy cover (6 to 6.7%) specimens from M4 to M5E Oldowan. Overall, the percentage of heavy cover specimens is relatively low between these two deposits.

5.1.2 Swartkrans faunas

Results of the fossil analyses as it appears in Table 4.7, show a different trend between Sterkfontein and Swartkrans faunas. Swartkrans Member 1 Lower Bank (Oldowan) and Acheulean-bearing Member 2 have high percentages of light cover specimens representing a significant decrease from M1 LB, Oldowan (78.57%) to M2 Acheulean (50%). A substantial increase in both open cover specimens (14.29 to 25%) and forest cover specimens (7 to 25%) from M1 LB, Oldowan to M2 Acheulean is notable. As shown in Table 4.7, the two Swartkrans members do not have any heavy cover bovid specimens whatsoever, in contrast with Sterkfontein.

5.2 Palaeoenvironmental implications of the site's deposits

A comparison of Sterkfontein and Swartkrans faunal assemblages highlights patterns of environmental change for the two site's deposits over a time span of approximately 2.8 to 1.5 Ma. The results, clearly show that the environment at Sterkfontein during the deposition of Member 4 ~2.8-2.4 Ma (Vrba 1974b, 1980) was favourable to bovids of varied morphological adaptations particularly those that require easy manoeuvrability in less complex environmental settings such as open plains, grasslands, tall grasses, light bushes, as well as heavy cover environments such as bushlands, woodlands, and a forest (continuous tree cover canopy). Tall grasses indicate the presence of edaphic grasslands or reeds (associated with seasonal swamps) for fresh grass grazers, while woodland, bushland and forest suggest a riparian environment in the vicinity. Similarly, open and medium-density woodland and bushland environments persisted with more tree cover until the deposition of Member 5 East, Oldowan Infill ~2.18 Ma (Granger *et al.* 2015). The results show a significant difference between the Sterkfontein and Swartkrans environments which provided preferable habitats for suitably adapted bovids. This is apparent at Swartkrans during the deposition of Member 1 Lower Bank, Oldowan ~2.2 Ma (Kuman *et al.* in prep.). Although the environment was

somewhat still open with riparian forest, M1 LB, Oldowan bovids mainly reflect a lighter cover environment dominated by light bushes, tall grasses (reeds or edaphic grass), and one which would have been suitable for grazers. At ~1.5 Ma (Vrba 1985b; Churcher & Watson 1993; Brain 1993) in Swartkrans M2, Acheulean, the same conditions are evident, showing more light cover and open environments and forest adapted bovids compared to Sterkfontein deposits.

This study shows that the reconstruction of STK-M4 and M5E Oldowan is similar, the presence over 25% bovids adapted to woodlands, bushlands and forest in the two deposits, suggest that the environment between ~2.8 and ~2.18 Ma was a mix of somewhat closed, and more open environmental conditions, as indicated by the high frequency of bovids displaying adaptions for locomotion in open cover and light cover habitats. This is in general agreement with previous interpretations (see Table 5.1 below for comparison) that indicate a mosaic of habitats, including forest, medium-density bushland/woodland, open grassland with more tree cover for STK-M4 (Bamford 1999; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Reynolds & Kibii 2011; Leichliter *et al.* 2017) and an open or wooded grassland for STK-M5E Oldowan (Vrba 1975, 1980; Reed 1997; Bishop *et al.* 1999; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Reed & Rector 2007; Reynolds & Kibii 2011). Micromammal assemblages analysed by Avery (2001), indicate that these two deposits are variable, with a high frequency of riverine grassland species represented in M4. This result corresponds well with Bamford's (1999) reconstruction based on fossilized lianas (*Dichapetalum mombuttense*), which suggest a moist environment nearby a riparian forest with large canopy trees during M4 times. Furthermore, locomotor and habitat reconstructions of cercopithecoid postcranial bones (Old World monkeys) by Elton (2001) and a new student paper submitted by Moswara in 2019 for Sterkfontein M4 also agree with these reconstructions, suggesting that *Cercopithecoidea* inhabited a variety of habitats ranging from forest, open woodland/bushland and grassland habitats. Previously, STK-M4 has been compared with Makapansgat M3 because of their similar closed environmental settings (Vrba 1995; Reed 1997; Sponheimer *et al.* 1999; Lee-Thorp *et al.* 2007; Sponheimer & Lee-Thorp 2009). Although these members overlap in

age, results of the current study agree with this comparison because STK-M4 (2.8-2.4 Ma) shows elements of woodland and bushland, which is slightly less dense compared to that of Makapansgat M3 ~2.9-3.0 Ma (Brain 1993; Partridge 2000; Kuman & Clarke 2000; Clarke & Partridge 2002; Sponheimer & Lee-Thorp 2009).

The absence of woodlands and bushlands adapted bovids within Swartkrans (M1 LB, Oldowan to M2 Acheulean) between ~2.2-1.5 Ma, as shown by the results, could simply indicate a period of the expansion of open environments supporting bovids adapted to open cover and light cover habitats. However, the relatively small sample size, particularly for M2 Acheulean assemblages, could have biased these reconstructions. Previous reconstructions using larger sample sizes for these deposits suggest that in addition to moderately open savanna, tree cover, and riverine grassland or wetlands, there was also an element of open woodlands or wooded savanna grasslands around this period (Vrba 1975, 1980; Brain 1981; Watson 1993; Reed 1997; Avery 1998, 2001; Kuman & Clarke 2000; Lee-Thorp *et al.* 2007; Reed & Rector 2007; Leichliter *et al.* 2017). Details on taphonomic biases and time-averaging as another option for assemblage biasing will be discussed later in this chapter.

The increase in forest-adapted bovids up to 25% from Swartkrans (M1 LB, Oldowan to M2 Acheulean) can possibly be interpreted as an indication that despite the environment opening up and drying, the river could have been much closer to Swartkrans during the deposition of these deposits and thus attracting more forest-dwelling bovids. At Swartkrans, the transition to more open environments is more evident during M2 Acheulean times when conditions were drier with relatively less riverine grassland represented compared to M1 LB, Oldowan (Avery 2001), and during this time, cercopithecoids exploited relatively open environments rather than heavy or closed cover environments such as forest, and woodland/bushland (Elton 2001).

There is indeed as previously proposed and as shown by the current results, an ecological difference between the two Oldowan deposits, STK-M5E and SKX-M1 LB (~2.2 Ma) that can be explained by the different site contexts. It seems that a

medium density woodland/ bushland along with riparian forest, and edaphic grasslands and open grassland existed at Sterkfontein during the Oldowan. In contrast, the Swartkrans Oldowan deposit is reconstructed as a lighter cover environment dominated by light bushes, tall grasses (reeds or edaphic grass), and open grassland with a riparian forest. The new interpretation that the current study provides when comparing the two deposits is that a river was also in closer proximity to Sterkfontein, because the vegetation that was present during Oldowan times, e.g., woodland, bushland, a riparian forest and edaphic grasslands, would have required nearby water supply. Taxonomically, this would have accommodated species inhabiting a variety of open and closed (heavy cover and forest cover) habitats near a water source, such as: southern African wildebeest (*Connochaetes sp.*), hartebeest (*Alcelaphus buselaphus*), African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), bushbuck *(Tragelaphus scriptus*), and kudu (*Tragelaphus strepsiceros*) to mention a few.

Based on the results presented in this study, the best supported interpretation is that at approximately ~2.8 to 1.5 Ma, Sterkfontein M4 and younger deposits at Sterkfontein (M5E Oldowan) and Swartkrans (M1 LB, Oldowan and M2 Acheulean) appear to have been generally more open with light tree cover and light bushes, tall grasses, and riparian forest. It is only the Sterkfontein deposits that show the moderate presence of woodlands and bushlands. When taking M4 out of the equation, it is clear that environmental reconstructions between ca. 2.2 and 1.5 Ma are consistent with stable carbon isotope results which indicate the abundance of C4 grazers in these younger deposits (Lee-Thorp *et al.* 2007). According to Lee Thorp's (*et al.* 2007) supplementary material for their carbon isotope study, STK M5E has over 33% C_4 grazers, with some grazers falling under the mixed-feeding category at 40%. Given this, I can confidently compare results of the current study to theirs, because my results show that there is 40% open cover and 33.3% light cover adapted bovids at STK M5E. If dietary preferences are concerned, these bovids are most likely to feed on C_4 grasses.

5.2.1 Migration and seasonality changes in Sterkfontein and Swartkrans habitats

A recent study by Hodgkins (*et al.* 2020) highlights the role of animal migration as a result of seasonal changes in rainfall (e.g., winter vs. summer rainfall) and vegetation structure (C_3 and C_4) in southern African coastal sites. Due to the variation in rainfall seasonality which strongly influences the distribution of green plants, it is likely that animals moved between rainfall zones across the Paleo-Agulhas Plain from the west coast (winter rainfall zone) with C_3 plants and lower $\delta^{18}O$ values to the east coast (summer rainfall zone) with C_4 plants and higher $\delta^{18}O$ values conversely for greener pastures. Although their study (Hodgkins *et al.* 2020) does not discuss Sterkfontein and Swartkrans caves, it is evident that these Cradle sites are located in the summer rainfall regime where the distribution of C_4 grasses is prominent during high rainfall seasons. A possible scenario would be: during the hot summer months, the C_3 grasses of the winter rainfall zone became moribund and unpalatable (with low-quality nutrients) so that these grazing animals were unable to consume large quantities, and this would have compelled them to migrate east in search of fresh grass with summer rains, and vice versa (Faith & Thompson 2013). Therefore, it is possible that the over-representation of bovids adapted to open and light cover habitats as indicated by the fauna from Sterkfontein and Swartkrans caves could be due to a seasonal abundance of these animals around the sites when they died, probably during the time when C_4 plants were abundant in the region.

5.3 Plio-Pleistocene African palaeoclimatic shifts and faunal evolution

Environmental theories of African faunal evolution document that important evolutionary changes during the Plio-Pleistocene period were mediated by shifts in African climate variability (Vrba 1995; Bobe *et al.* 2002; Hopley *et al.* 2007). These theories are mainly based on evidence of marine sediment sequences (aeolian dust) (Tiedemann & Shackleton 1994; Shackleton 1995; de Menocal & Bloemendal 1995; de Menocal 2004; de Menocal 1995, 2011; Potts 1998a, b). These demonstrate that "subtropical African climate periodically oscillated between markedly wetter and drier conditions, paced by earth orbital variations, with

evidence for step-like (±0.2 Ma) increases in African climate variability and aridity near 2.8 Ma, 1.7 Ma, and 1.0 Ma, coincided with the onset and intensification of high latitude glacial cycles" (de Menocal 2004:3; and see Tiedemann & Shackleton 1994; Shackleton 1995; de Menocal & Bloemendal 1995; de Menocal 1995, 2011; Potts 1998a, b; Bobe & Behrensmeyer 2004; Hernandez Fernandez & Vrba 2006; Maslin & Christen 2007; Hopley *et al.* 2007; Reed & Russak 2009; Hopley & Maslin 2010; Potts 2013; Maslin 2014).

Analysis of the best dated African mammal fossils from hominin sites in southern and eastern Africa indicate that, in response to these extreme precessional cycles, there were events of faunal speciation, migration, and adaptation, following shifts from woodland-dominated to savanna-dominated mammalian communities, and thus suggesting a shift from more closed woodland environments to a more varied and open environment in Africa during this time (Vrba 1980, 1995, 2000; Reed 1997). A series of hypotheses has been proposed linking these events. The environmental hypotheses of African faunal evolution are habitat-specific and commonly linked to the emergence of grassland savanna during the Plio-Pleistocene (Vrba 1974a, 1975, 1980, 1985a, 1995, 2000; Cerling 1992, 1997; Spencer 1997; Bobe *et al.* 2002; Bobe &; Behrensmeyer 2004; Bobe & Leakey 2009). Vrba (1988, 1995), who studied fossil bovids from the largest African collections, proposed a 'turnover pulse hypothesis' (a variant of the savanna hypothesis) which suggests that bovid species turnover first occurred near ca. 2.7-2.5 Ma with a dramatic increase in the proportions of grazing bovids and other mammals, linking faunal changes to aridity and expansion of grasslands (Bobe & Eck 2001; Bobe *et al.* 2002). The second appearance is recorded near ca. 1.8 Ma and 1.7 Ma. However, Vrba's (1988, 1995) claims of a taxonomic shift have been challenged by researchers who argue that grazing adaptations (especially in South Africa) did not increase substantially until the second appearance at 1.8 and 1.7 Ma (Reed 1997; Bobe & Behrensmeyer 2004; Bobe & Leakey 2009). What happened during the first appearance would have been the fluctuation of grazing mammals from East African sites from 15 to 25% and 45% at approximately 1.8 Ma, "caused by either continuous, gradual climate aridification or an increase in seasonality"

(Reed 1997:314) as "supported by evidence for high-latitude glacial cycles that developed gradually between 3.1 and 2.6 Ma" (de Menocal 1995:53). According to Reed (1997), change to more pronounced dry seasons, and the great expansion of grazing mammals exceeding 30% occurred at 1.8 Ma in East African hominin sites. This view supports Cerling's (1992) carbon isotope study of soil carbonates from East African sites (Turkana Basin and in Olduvai-Laetoli region) which suggests that the first evidence of the significant expansion of C_4 grasslands at about 60 to 80% and major environmental change (to open environments) occurred about 1.8-1.7 Ma. Other records of the shift towards open environments dominated by C_4 grasslands at 1.7 Ma in East Africa are documented by Plummer & Bishop (1994) and Kappelman *et al.* (1997). The greater dominance of C_4 vegetation and open landscapes for South African hominin localities also occurs about 1.7 Ma (Luyt 2001; Luyt & Lee-Thorp 2003; Sponheimer *et al.* 2005a, b; Lee-Thorp *et al.* 2007; Sponheimer & Lee-Thorp 2009).

Given these records, it is evident that Sterkfontein and Swartkrans caves straddle a large-part of the Plio-Pleistocene and show trends consistent with this period elsewhere in Africa. A 'medium density bushland and woodland' and a forest cover that existed during Sterkfontein M4 and M5E Oldowan times ~2.8 and 2.2 Ma possibly suggest a time when climatic conditions were warmer and more humid, supporting more closed habitats which were possibly inhabited by less cursorial animals. However, it was also around this time that M4 and M5E Oldowan conditions became progressively cool and arid/dry, accompanied by the appearance of more open cover and light cover habitats conducive for highly cursorial animals. The major expansion of open cover and light cover habitats occurred between 1.7 and 1.5 Ma at Swartkrans, and this agrees with previous reconstructions (see Cerling 1992; Luyt & Lee Thorp 2003; Sewell *et al.* 2018). This is recorded at Sterkfontein in Member 5 West Acheulean deposit (Luyt & Lee-Thorp 2003), and also documented for Swartkrans M2, Acheulean and onwards. Around this time, a wide range of mammals developed morphologies adapted to more arid conditions in open environments for easy and fast manoeuvrability.

Furthermore, the records of climatic and environmental shifts also coincided with important key junctures in hominin evolution; hence investigating palaeoenvironments using faunal assemblages associated with hominins from Sterkfontein and Swartkrans offers a rare opportunity to indirectly study palaeoenvironments associated with *Australopithecus*, *Paranthropus* and *Homo* species. Based on the reconstructions presented by the current study, *Australopithecus* found at STK-M4 (2.8-2.4 Ma) seems to have existed during moist conditions when the environment was still relatively closed with a medium-density woodland, bushland and riparian forest, and around this time, the environment was also gradually becoming drier and more open, with such conditions probably less conducive for *Australopithecus.* This agrees with the previous construction of STK-M4 by Reed (1997:316): "perhaps a gradual change to drier, more open habitats and/or a more pronounced dry season forced these australopithecines across an environmental tolerance limit around 2.8-2.5 Mya, and resulted in their extinction". When more open environments with edaphic grasslands and small elements of woodlands, bushlands and forest persisted as the landscape became more arid and open around 2.0 to 1.5 Ma, species like *Paranthropus robustus* which was specialised in tough fallback foods, and the larger-brained *Homo* became common at Sterkfontein and Swartkrans during Oldowan and Acheulean times. The two hominin lineages are thought to be sympatric, with *Paranthropus robustus* in both wooded and more open environments but consistently foraging edaphic grasslands or wetlands (Reed 1997; Kuman & Clarke 2000), and *Homo* also was found near edaphic grasslands, open and dry shrublands (Reed 1997). Both *Paranthropus* and early *Homo* lineages are associated with the appearance of stone tools, the 'Oldowan Industry' (a core-flake technology), suggesting tool use for one or possibly both species (Reed 1997).

As the environment was changing, however, some form of adaptive transition took place in hominin behavioural development, which led to the extinction of *Paranthropus* (Plummer 2004). Evidence of tool cut marks on large animal bones dating ca. 2.58 Ma (Pobiner & Blumenschine 2003; Domínguez-Rodrigo *et al*. 2005) and possibly earlier (McPherron *et al.* 2010), suggest an important dietary

shift of early *Homo* species with regards to the acquisition and consumption of animal tissue (Pickering 2001; Pobiner & Blumenschine 2003; Domínguez-Rodrigo *et al*. 2005; Braun *et al.* 2010; Pickering & Domínguez-Rodrigo 2006; Pickering & Brain 2010; Ungar 2012; Ferraro *et al.* 2013; Lemorini *et al.* 2014). A dietary shift to tool-assisted meat consumption would have required some form of foraging behaviour with increased competition in carnivory for shared limited resources (e.g., carcasses) and interactions with the carnivore palaeoguild (Pobiner & Blumenschine 2003). This would have been more prominent, particularly, during times of seasonal plant food shortages (Foley 1987). Other adaptive implications for the Oldowan hominins (*early Homo),* was the exploitation of terrestrial and marine resources. Tool-edge wear and dental morphology indicated their incorporation of tough-plant food such as ground tubers and roots (Domínguez-Rodrigo *et al*. 2005; Braun *et al.* 2010; Ungar 2012; Aiello & Antón 2012; Ferraro *et al.* 2013; Lemorini *et al.* 2014). They also developed flexible and energetic traits as they transported stone tools from source as far as 12 km (Braun *et al*. 2008; Antón *et al.* 2014).

It is only around 1.76 Ma that we see a transition from the Oldowan to the production of Acheulean technology (e.g., large bifacial cutting tools) as well as the appearance of the later species *Homo erectus*/*ergaster* (Kuman 2014). Because of its enhanced adaptive potential during the expansion of grasslands and open environments, *Homo erectus*/*ergaster* utilized arid and open environments (Ruff 1991; Reed 1997). In such conditions, their adaptation to open environments inevitably selected new biological traits for this *Homo* lineage, which was characterized by increased cognitive ability, larger brain size and larger body size (Stout *et al.* 2008; Antón 2012; Antón & Snodgrass 2012; Antón *et al.* 2014), as well as a shift towards efficient bipedal locomotion and endurance running, similar to modern humans (Shipman & Walker 1989; Ruff & Walker 1993; Aiello & Wheeler 1995). In addition, these species would have required an increase in the consumption of a calorie-rich diet and animal tissue to sustain their larger brains and body size (Shipman & Walker 1989; Ruff & Walker 1993; Aiello & Wheeler

1995; Bramble & Lieberman 1995; Bramble & Lieberman 2004; Aiello & Anton 2012; Antón *et al.* 2014).

With these changes, it is clear that the results for the current study fit well and address broader theoretical framework about the influence of Plio-Pleistocene shifts in the environment, and mammalian and early human evolution in the Cradle of Humankind, South Africa and Africa in general.

5.4 Time-Averaging and Taphonomy

The issue of 'time-averaging' could possibly be another source of environmental biasing within the selected sample in this study. "The process of time-averaging can be caused in the primary sedimentation deposit as a result of the great periods of accumulation time, or by the mixing of sediments during resedimentation" Stratford (2011:360); and see Olszewsky (2004). This is, however, a typical scenario for cave deposits in the Cradle, particularly Sterkfontein and Swartkrans deposits (O'Regan & Reynolds 2009; Stratford 2011). Consequently, time-averaging should be carefully examined and borne in mind when analyzing faunal assemblages because it influences palaeoenvironmental and taphonomic interpretations (O'Regan & Reynolds 2009).

Results presented in this study indicate a clear diversity of bovid species associated with different or mosaic habitats within the Sterkfontein and Swartkrans deposits. However, the presence of these key faunal indicators within these deposits cannot only be considered a sound palaeoenvironmental indication but most likely represent time-averaging. Due to the consistent mosaic environmental interpretations this study reveals, it is likely that these deposits have been intensely time-averaged in that at the time of death of each selected specimen, certain environmental conditions may have prevailed. Control of time-averaging is ultimately dependent on stratigraphic and chronological resolution, an aspect of research that continues to be contentious in these sites. Despite the inevitability of time-averaging as a conflating process in these deposits, where compression and deflation have brought fossils together that represent potentially distinct periods and

prevailing environmental conditions, the representation of those specimens in these deposits is still indicative of palaeoenvironmental conditions within the temporal control of the deposits. It is hoped that through the improvement of stratigraphic control in these sites that palaeoenvironmental resolution may also increase.

Time-averaging will also coalesce signals from taphonomic agents involved in the accumulation of fauna identified at Sterkfontein and Swartkrans deposits as mentioned in Chapter 1. It is most likely that the larger Plio-Pleistocene carnivore guild (the major accumulating agents at both sites) may have selected different prey animals at different times and from different habitats (O'Regan & Reynolds 2009). For example, "carnivores or predators prefer to prey upon animals that are approximately half to twice their own body mass and also considering the habitat favoured for hunting" (Owen-Smith and Mills 2008:173). It is also most likely that the over-representation of open cover and light cover species at Sterkfontein and Swartkrans is due to the predation of size classes II and III bovids (mainly grazers) by cursorial carnivores concentrated in open environments, while ambush hunters living in more wooded regions and thicker vegetation at Sterkfontein near the Bloubank River preyed upon size class I browsing bovids (but these are not represented in the selected faunal assemblage). The diversity of prey species (bovids) and different habitats identified in this study for the two site's deposits serve as a good indication that these faunal assemblages were potentially admitted into these deposits over a long period by different taphonomic agents (particularly predators that targeted bovids from a variety of habitats), thus representing tens of thousands of years of accumulation. It is important to mention that the reason for the variety of the accumulation agents identified in these deposits does not necessarily mean they were all contributing for the whole duration of deposition, however, because of the generally low stratigraphic and temporal resolution it is therefore, challenging to tease out more nuanced associations between specific accumulation agent (both geogenic and biogenic), and accumulated fauna and through this exercise propose with greater confidence the prevailing conditions at specific, even relative, times.

Similar to time-averaging, reworking and redeposition of older fossil material into younger deposits is another feature which has been noted and published for both Sterkfontein (Reynolds *et al.* 2003) and Swartkrans (de Ruiter 2003). Therefore, we must be cautious when interpreting faunal material as contemporaneous within these deposits.

5.5 Geomorphological implications for Sterkfontein and Swartkrans

The geographic location and proximity of Sterkfontein and Swartkrans caves contributed to bovids from the two sites having similar locomotor adaptations. The analysis of the faunal assemblages shows that bovids from the two sites both inhabited a mosaic of habitats, (e.g., open cover, light cover, heavy cover, and forest). However, the selected faunal assemblages indicate that there were no heavy cover dependant bovids at Swartkrans, which provides a more detailed interpretation of past environments than previously proposed from taxonomic studies. Originally the lack of heavy cover bovids at Swartkrans would be thought to be the result of the extreme skewness in bovid size-types, for example, the Swartkrans assemblages range from size classes II to III, whereas the Sterkfontein bovid assemblage has bovids ranging from size classes I to III. This is possibly due to taphonomic reasons as mentioned above, suggesting that carnivore and hominin prey selection at Swartkrans was based on animal size, particularly size I bovids. Because Sterkfontein M4 and M5 Oldowan are also death trap, assemblages (as well as a mix of slope wash, carnivore accumulation and little porcupine action), small or size 1 bovids are mostly likely found there. However, this is not the case here, as it seems that the lack of bovid class I at Swartkrans does not bias the reconstructions. This study reveals that the pattern is the same when comparing only bovid size classes II and III across the two sites. Alternatively, the relatively small sample size of Swartkrans assemblages in contrast with that from Sterkfontein could possibly have biased representative samples for Swartkrans and in turn influenced the reconstructions. Furthermore, this could simply be an indication of ecomorphology in general without any sample size biases.

Overall, it is logical to expect bovids with different habitat preferences and adaptations between the two sites because of the different geographic contexts, as suggested by previous reconstructions--e.g., Swartkrans is wetter due to the presence of the flooded grassland and reedbeds and has water-dependent species such as otter (*Aonyx capensis*) and hippopotamus (Hippopotamus sp.) (Watson 1993). Sterkfontein has no water-dependent species (but hippopotamus may be found from MSA-aged deposits) and is slightly further from the river (Kuman 1996; Kuman & Clarke 2000; Martini *et al.* 2003; Reynolds *et al.* 2007; Kuman *et al.* 2018). However, this study shows that a swamp or a river could have been present close to the two sites to support woodlands and bushlands at Sterkfontein, as well as a riparian forest and tall grasses that were present at both sites. The Bloubank river is known to have been much larger and wider in the past (Kuman 1996; Kuman & Clarke 2000; Martini *et al.* 2003; Kuman *et al.* 2018), based on mapping of terrace gravels by T.C Partridge and as noted by Kuman (1996), in the past the river was wider in size with an estimated distance of 300 m from Sterkfontein, and today the estimated distance is 500 m making it small in size and far away from Sterkfontein (measurements courtesy of L. Bruxelles pers. comm. 2017 to Kuman *et al.* 2018.).

According to (Bruxelles pers. comm. to K. Kuman) it could have been too wide for people and animals to cross back and forth. However, the author's view is that the suggested larger size and width of the river perhaps indicate that the river was not far from Sterkfontein as previously thought, and this is logical because the element of woodlands, bushlands, a forest and tall grasses (edaphic) proposed to have been present at Sterkfontein by the current study would have required a nearby water source. Therefore, bovids from Sterkfontein and Swartkrans had access to the river but it is unlikely that they could have crossed between the two sites, and the only way they could have manoeuvered across was probably at another location along the course of the river than the one close to the sites. Because riparian vegetation grows along banks of a waterway channel where water flows permanently or seasonally, the author's view is that the estimated distance between the vegetation and the river was 50 m to 450m. However, due to lack of evidence on the evolution

and migration of the river the author cannot emphatically state the actual distance from the river or say which site the river was closest to during that period.

The pattern revealed by the current study indicates improved details of the habitats for the two sites compared to previous taxonomic studies. For example, heavy cover dependent species at Swartkrans are only those found in riparian forest and tall grasses (possibly edaphic grasslands or reedbeds) and not in woodlands or bushlands as previously proposed, and this study justifies the presence of water-dependent species at the site. This study indicates that Sterkfontein bovids inhabited environment types that suggest the presence of a water source in the vicinity e.g., bushlands, woodlands, riparian forest, and tall grasses, thus adding a new interpretation that is somewhat different to previous reconstructions.

There is a comparable pattern of change over time in the locomotor adaptations of bovids from the two sites, signifying a lapse of tens of thousands of years between the accumulations (as typical for cave deposits). The Sterkfontein and Swartkrans deposits accumulated during a significant period ~2.8-1.5 Ma (Plio-Pleistocene) which coincided with gradual global climatic shifts and environmental change; hence we see this pattern of change in the selected faunal assemblages.

Table 5.1: Comparison of previous and current palaeoenvironmental reconstructions for Sterkfontein and Swartkrans members

Site, Member, and Age	Previous reconstructions	References	Taxon-free ecomorphological reconstruction
Sterkfontein Member 4, (~2.8-2.4 Ma).	Mosaic of habitats, including forest, open woodland/bushland and grassland.	(Vrba 1975,1980; Reed 1997; Bamford 1999; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Leichliter *et al.* 2017).	Mosaic of habitats including open plains, grasslands, tall grasses, light bushes, medium-density bushland/ woodland and riparian forest in the vicinity.
Sterkfontein Member 5 East, Oldowan Infill (~2.18 Ma).	drier and more open habitat with tree cover.	(Vrba 1975; Reed 1997; Bishop et al. 1999; Kuman & Clarke 2000; Luyt & Lee-Thorp 2003; Reynolds & Kibii 2011).	Mosaic of habitats, including open plains, grasslands, tall grasses, light bushes, medium-density bushland, woodland and riparian forest in the vicinity.
Swartkrans Member 1 Lower Bank (2.2 Ma).	a moderately open savanna, grassland with tree cover, savanna woodland.	(Vrba 1975,1980; Brain 1991; Watson 1993; Reed 1997; Avery 1998; Lee-Thorp *et al.* 2007; Reed & Rector 2007; de Ruiter *et al.* 2008; Leichliter *et al.* 2017).	Mosaic of habitats, including, moderate open plains and grassland, prominent light cover constituted by tall grass, light bushes, and tree cover represented by a riparian forest in the vicinity.

Swartkrans Member 2, Acheulean (1.5 Ma).	wooded grasslands with wetlands and open savanna.	(Vrba 1975; Watson 1993; Reed 1997; Lee-Thorp *et al.* 2007).	Mosaic of habitats, including, moderate open plains and dominant light cover constituted by tall grass, light bushes, and tree cover represented by a riparian forest or swamps in the vicinity.

5.6 Conclusions

Samples of fossil bovid astragali were collected, measured, analysed and presented by the author in the Results chapter. The analysis does provide somewhat conclusive answers to the research questions for this project. Based on the analysis, it appears that around 2.8-1.5 Ma bovids from Sterkfontein and Swartkrans caves responded to the global climatic shifts that had a significant influence on the habitats they inhabited, and that they had varied morphological and locomotor adaptation specific to their mixed habitats. Some bovids from these two sites are highly cursorial, adapted to running fast and straight over level open country terrain, while others, particularly those from Sterkfontein, were laterally dodging over uneven closed habitats which includes forest, woodlands and bushlands.

As mentioned in Chapter 3, the use of LDA for ecomorphology in this study should be treated with caution due to the LDA assumptions not being met. However, this does not strictly restrict the use of LDA, hence it was safe to continue using this test without having to use another statistical method to determine if this method is robust to the violation of LDA's primary assumptions namely: normality and equality of covariance metrices. Regardless of these limitations, the method of predicting palaeohabitats from measurements of bovid astragali has proven to be accurate and applicable, thus making it another useful technique for investigating

palaeoenvironments. It does have some advantages over traditional taxon-based faunal methods, as it only requires that specimens be identified to family level rather than species level. Instead of assuming behavioural stasis between fossil taxa and their modern relatives (taxonomic uniformitarianism), ecomorphological reconstructions focus more on how the morphology of a species is shaped by its evolutionary history. In essence, it takes into account the unique adaptations of fossil taxa and compare with that of modern taxa that share similar adaptations (Plummer & Bishop 1994; Forrest 2017).

Future avenues of research

In future, a taxon-free ecomorphological analysis of bovid astragali will be conducted using more advanced and recent scanning methods (e.g., Next Engine laser scanner) or 3D geometric morphometrics, rather than the traditional digital caliper measuring method. The traditional method had to be used in this research for two reasons. First, this is the first study in Cradle of Humankind World Heritage Site to use this method on bovid astragali and the author needed to explore the traditional method that was used in early ecomorphological studies. Secondly, the author's primary source of learning the method was via published literature, so it was important that the author grasps the traditional method before exploring other methods. Another interesting future research focus would be a comparison of the advanced and traditional (caliper) methods, as this would be ideal for testing whether both methods produce any differences and to determine which one is best applicable for analysing the functional morphology of bovid astragali in relation to habitat. However, studies by Barr (2014,2015) suggest that although laser scanning is a better protocol because it includes the smoothing and merging of multiple scan families and digital alignments of bone elements compared to caliper measurements, there is no major source of measurement imprecision between the two methods. For comparative purposes, the author plans to construct her own comparison using measurements of modern bovids from South Africa. The author also plans to use a large sample size (as in most LDA tests) in order to ensure that LDA's primary assumptions are met.

In future, a taxon-free ecomorphological analysis could be conducted on other postcranial bones, e.g., femora and metapodials as previously used in other studies, as this would allow for better palaeoenvironmental reconstruction of Sterkfontein and Swartkrans environments. However, due to the fragmented nature or limited preservation of these elements in the fossil record and particularly at the two sites, these elements would require complete bones. Other postcranial elements that can be used for this analysis are: calcaneus, carpals, phalanges, radii, and tali to mention a few. These elements also have morphologies adapted to locomotion and are well preserved and found complete at Sterkfontein and Swartkrans caves and in the palaeontological record in general.

The study presented here was aimed at expanding the application of taxon-free ecomorphology by including bovids from the Cradle of Humankind in South Africa. The application of this method to the fossil record of Sterkfontein and Swartkrans caves has provided insights into the palaeoenvironment associated with *Australopithecus, Paranthropus,* and *Homo* species. The applicability of this method to reconstructing palaeoenvironments strengthens the idea that our understanding of hominin behavioural and morphological adaptations can be improved through the examination of the environments they inhabited. As part of a wider discussion on Plio-Pleistocene environments, this research provides a testable method that palaeoanthropologists can use when addressing the issue of evolution and environmental change.

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Appendix A

TABLES

Table A.1: Sterkfontein (STK) Member 4 (M4): Seven caliper raw-measurements in (mm).

Site	Member	Specimen	Square	Depth	Element	size class	Side	LM	LL	TI	TD	LI	WI	WD
STK	M4	S94-11276	U41	8'5"-9'8"	Ast	1	L	22.3	24.6	11.65	11.05	20.1	14.6	14.75
STK	M4	S94-12077	P/44	25'7"-26'7"	Ast	3	L	53.5	57.65	29.65	27.85	47.2	35.2	36.55
STK	M4	S94-12030	P/43	26'0"-27'0"	Ast	3	R	53.1	55.6	30.15	27.55	45.4	32.75	33.45
STK	M4	S94-12492	P/44	29'7"-30'7"	Ast	3	R	50.05	51.85	26.5	26.45	40.75	32.1	33.8
STK	M4	S94-13716	O/43	12'6"-13'9"	Ast	3	L	49.35	55.9	27.65	27.5	39.05	32.4	35.25
STK	M4	UKNOWN	S/55	19'8"-20'8"	Ast	1	L	30.45	31.9	16.55	17.45	25.95	19.05	19.75
STK	M4	S94-14305	S/43	27'2"-28'2"	Ast	3	R	50.25	54.55	31.6	29.65	42.85	32.65	34.6
STK	M4	S94-14454	U45	23'2"-24'9"	Ast	3	R	52.6	58.65	30.6	29.1	45.65	36	34.5
STK	M4	S94-14458	U45	23'2"-24'9"	Ast	3	L	50.3	58.4	29.75	30.45	45.5	34.05	33.4
STK	M4	S94-14499	U/52	N/A	Ast	1	R	28.05	30.2	15.6	14.7	24.2	17.7	17.55
STK	M4	S94-15046	Q/50	13'111"-14'11"	Ast	1	L	31.45	31.5	16.35	16.2	26.2	19.35	19.5
STK	M4	S94-14177	U61	19"11"-20'11	Ast	2	R	37	38.4	21.25	20.25	30.15	24.2	24.75
STK	M4	S94-10766	S/63	9'1"-10'1"	Ast	2	R	40.15	40.1	22.15	21.3	31.8	24.95	25.4
STK	M4	S94-10749	S/63	8'1"-9'1"	Ast	2	R	40.35	44.15	23.2	21.65	34.05	29.2	27.1
STK	M4	S94-9145	V/43	26'2"-27'2"	Ast	3	R	53	53.15	29.75	28.75	43.2	29.05	31.85

Table A.1: Continued. Sterkfontein (STK) Member 5 East, Oldowan Infill (M5 East, Oldowan): Seven caliper raw-measurements in (mm).

Site	Member	Specimen	Square	Depth	Element	Size class	Side	LM	LL	TI	TD	LI	WI	WD
STK	M5 East, Oldowan	S94-3098	Q/56	27'2"-28'2"	Ast	2	R	33.1	36.15	18.65	18.3	28.05	20.4	21.4
STK	M5 East, Oldowan	S94-13356	Q/54	23'0"-24'0"	Ast	1	L	28.45	29.7	15	14.75	23.85	17.55	16.75
STK	M5 East, Oldowan	S94-13433	Q/54	27'0"-28'0"	Ast	2	L	33.7	35	21.65	19.25	27.45	22.85	22.95
STK	M5 East, Oldowan	S94-13474	Q/57	24'8"-25'8"	Ast	1	R	22.4	24.35	13.2	11.7	19.1	14.25	14.25
STK	M5 East, Oldowan	S94-6111	R/55	28'4"-29'4"	Ast	3	R	40.35	42.2	21.75	21.65	33.7	26.3	26.6
STK	M5 East, Oldowan	S94-2755	Q/55	25'4"-26'4"	Ast	2	R	31.65	33.55	18	16.9	26.2	20.45	19.55
STK	M5 East, Oldowan	S94-6905	P/53/54	32'10"-36'10"	Ast	2	R	32.8	34	19.15	17.25	27.1	20.9	21.45
STK	M5 East, Oldowan	S94-13346	Q/54	22'0"-23'0"	Ast	2	L	32.05	35.85	18.55	17.75	28.05	22.05	22.7
STK	M5 East, Oldowan	BP/3/19962	R/57	22'4"-23'4"	Ast	2	L	33.45	35.3	16.5	19.25	30.5	21.55	21.55
STK	M5 East, Oldowan	S94-3620	R/56	29'4"-30'4"	Ast	2	R	33.3	37.55	18.6	19.35	28.5	23.4	24
STK	M5 East, Oldowan	S94-2923	Q/55	26'4"-27'4"	Ast	2	R	33.2	33.75	18.7	16.35	26.35	20.7	20.8
STK	M5 East, Oldowan	S94-13300	Q/53	22'2"-23'2"	Ast	3	R	40.5	40.85	22.7	22.15	33.15	22.7	25.45
STK	M5 East, Oldowan	S94-13426	Q/54	25'0"-26'0"	Ast	2	R	33.6	36.55	20.65	20.25	28.45	23.05	23.2
STK	M5 East, Oldowan	S94-3726	R/56	31'4"-32'4"	Ast	3	L	40.9	42.05	22.15	21.85	34.65	26.3	27.35
STK	M5 East, Oldowan	S94-13497	Q/57	28'8"-29'8"	Ast	2	L	33.45	34.7	17.05	17.6	26.5	22.35	21.95

Table A.1: Continued. Swartkrans (SKX) Member 1 Lower Bank, Oldowan (M1 LB): Seven caliper raw-measurements in (mm).

Site	Member	Specimen	Square	Depth	Element	Size class	Side	LM	LL	TI	TD	LI	WI	WD
SKX	M1 LB, Oldowan	13790	N/A	N/A	Ast	2	R	27.6	29.75	16.6	16.1	24.45	19.1	18.15
SKX	M1 LB, Oldowan	5687	E4/N5	650-660	Ast	3	R	42.75	45.05	24.15	22	35.2	27.85	27.4
SKX	M1 LB, Oldowan	5846	E3/N5	570-580	Ast	3	L	40.25	42.7	22.65	22.05	33.7	27.25	27.65
SKX	M1 LB, Oldowan	9809	N/A	N/A	Ast	2	R	28.85	30.7	17.1	16.55	24.45	20.05	18.25
SKX	M1 LB, Oldowan	6703	N/A	N/A	Ast	2	L	30.85	30.6	15.55	14.65	25.45	18.35	16.9
SKX	M1 LB, Oldowan	6309	N/A	N/A	Ast	2	L	34.25	36.4	20.35	19.6	29.35	22.45	22.15
SKX	M1 LB, Oldowan	13949	E3/N5	510-520	Ast	3	R	43.3	45.2	26.4	25.05	37	29.6	29.95
SKX	M1 LB, Oldowan	5687	E4/N5	650-660	Ast	3	R	42.75	45.05	24.15	22	35.2	27.85	27.4
SKX	M1 LB, Oldowan	5846	E3/N5	570-580	Ast	3	L	40.25	42.7	22.65	22.05	33.7	27.25	27.65
SKX	M1 LB, Oldowan	9809	N/A	N/A	Ast	2	R	28.85	30.7	17.1	16.55	24.45	20.05	18.25
SKX	M1 LB, Oldowan	12730	E3/N5	560-570	Ast	3	L	40.15	41.25	23.35	22.6	33.65	26.4	26.1
SKX	M1 LB, Oldowan	13640	E5/N4	490-500	Ast	3	L	42.5	43.95	24.45	24.05	35	27.35	26.45
SKX	M1 LB, Oldowan	7991	E4/N5	660-670	Ast	3	R	40.15	41.25	23.35	22.6	33.65	26.4	26.1
SKX	M1 LB, Oldowan	13640	E5/N5	490-500	Ast	3	L	43.4	45.6	24.1	23.75	36.65	28.6	30

Table A.1: Continued. Swartkrans (SKX) Member 2, Acheulean (M2, Acheulean): Seven caliper raw-measurements in (mm).

Site	Member	Specimen	Square	Depth	Element	Size class	Side	LM	LL	TI	TD	LI	WI	WD
SKX	M2, Acheulean	3852	N/A	N/A	Ast	3	R	43.15	46.35	26.75	25.4	37.1	30.85	31.6
SKX	M2, Acheulean	990	N/A	N/A	Ast	2	R	30.25	31.1	17.15	17.35	25.4	19.25	19.1
SKX	M2, Acheulean	916	N/A	N/A	Ast	2	L	29.05	30.8	15.05	15.45	24.85	17.15	16.85
SKX	M2, Acheulean	3775	N/A	N/A	Ast	3	R	44.45	47.8	25.2	24.7	36.25	28.75	29.05
SKX	M2, Acheulean	792	N/A	N/A	Ast	2	L	28.35	29.2	17.1	16.65	25.35	19.5	19.45
SKX	M2, Acheulean	3061	N/A	N/A	Ast	2	L	29.1	29.2	15.7	15.35	23.75	18.65	18.6
SKX	M2, Acheulean	3189	N/A	N/A	Ast	2	L	27.85	28.8	14.35	15.2	24.2	16.75	17.55
SKX	M2, Acheulean	12337/1237	N/A	N/A	Ast	2	R	29.25	30.45	17.25	16.6	24.6	19.05	18.45

Table A.2: Modern Astragali Raw measurements by species selected from Weinand (2005).

Individual/ Genus	Species	Habitat	Body mass (kg)	Size class	LM	LI	LL	WI	WD	TI	TD
Hemitragus (*tahr*) 1	*Hylocrius*	Light Cover	85	1	33.3	28.6	35.9	26.7	24.2	19.7	16.8
Hemitragus (*tahr*) 2	*Hylocrius*	Light Cover	85	1	33.8	28.7	26.1	25.4	23	18.4	15.5
Hemitragus (*tahr*) 3	*Hylocrius*	Light Cover	85	1	32.6	27.6	34.8	24.4	22	18.5	15.2
Hemitragus (*tahr*) 4	*Hylocrius*	Light Cover	85	1	32.7	28.3	35.4	26.2	22.8	19	16.1
Cephalophus monticola (*duiker*) 1	*Monticola*	Forest	6	1	15.1	12.8	16.6	8.9	9.7	7.7	6.7
Cephalophus monticola (*duiker*) 2	*Monticola*	Forest	6	1	14.5	12.5	15.2	8.4	9.2	7.2	6.6
Cephalophus monticola (*duiker*) 3	*Monticola*	Forest	6	1	15.5	13.3	16.4	9.6	9.6	8.5	7
Madoqua (*dik-dik*) 1	*Kirk*	Forest	5	1	16.3	13.9	17	9.1	9.2	8.6	6.6
Madoqua (*dik-dik*) 2	*Kirk*	Forest	5	1	14.8	12.7	15.1	8.5	8.7	7.5	6.2
Capricornis (*japanese*) 1	*Crispus*	Heavy Cover	30	2	28.9	24.4	29	21	19.9	13.3	11.7
Capricornis 2	*Crispus*	Heavy Cover	30	2	30.7	26.4	32.1	22.4	21.3	17.5	14.7
Capricornis (*formosan serow*) 1	*Swinhoei*	Heavy Cover	30	2	30.2	26.5	32.8	20.8	20.6	17	14.9

Table A.2: Continued. Modern Astragali Raw measurements by species selected from Weinand (2005).

Individual/ Genus	Species	Habitat	Body mass (kg)	Size class	LM	LI	LL	WI	WD	TI	TD
Naemorhedus goral 1	*Goral*	Forest cover	30	2	29.7	24.6	30.1	19.4	18.4	15.3	13.2
Naemorhedus goral 2	*Goral*	Forest cover	30	2	29.8	26	32.4	19.5	20.2	15.1	13.9
Naemorhedus goral 3	*Goral*	Forest cover	30	2	31.7	28.2	33.7	18.7	20.6	14.9	13.3
Naemorhedus goral 4	*Goral*	Forest cover	30	2	30.6	26.9	32.2	17.5	19.8	14.8	13.3
Naemorhedus goral 5	*Goral*	Forest cover	30	2	29.2	25.5	31.8	22	21.1	15.4	13.5
Ovis (*asiastic*) 1	*Orientalis mounflon*	Light cover	30	2	29.6	24.8	31.2	21.3	19.7	17.1	15
Procapra 2	*Gutturosa*	Open cover	30	2	25.9	21.3	28.1	16.2	15.9	13.7	11.6
Pseudois (*bharal*) 1	*Nayaur*	Open cover	50	2	33.6	29.1	35.9	23.8	23.2	19.9	17.1
Pseudois 2	*Nayaur*	Open cover	50	2	34.3	29.3	37.4	25.1	23.7	19.7	17.7
Pseudois 3	*Nayaur*	Open cover	50	2	33.2	27.8	35.7	24	23.4	18.1	16.6
Boselaphus (*nilgal*) 1	*Tragocamelus*	Heavy cover	250	3	49.1	41.8	52.5	34.3	36.3	29.4	24.6

Table A.2: Continued. Modern Astragali Raw measurements by species selected from Weinand (2005).

Individual/ Genus	Species	Habitat	Body mass (kg)	Size class	LM	LI	LL	WI	WD	TI	TD
Bubalus (*lowland anaoa*) 1	*Depressicorns*	Forest cover	225	3	40.3	35.2	43.9	25.8	27.1	21.5	17.3
Bubalus 2	*Depressicorns*	Forest cover	225	3	36.7	31.1	39.5	25.6	23.8	19	15.7
Bubalus (*tamaraw*) 3	*Mindorensis*	Forest cover	225	3	51.8	43.9	55.5	31.7	34.4	27.1	19.6
Bubalus 4	*Mindorensis*	Forest cover	225	3	53.6	46.2	57.9	37.7	35.9	27.5	21.8
Capricornis (*sumatran*) 1	*Sumatraensis*	Heavy cover	30	3	42.6	38.2	46.2	30.9	31.8	24.2	22.9
Capricornis 2	*Sumatraensis*	Heavy cover	30	3	45.6	38.8	47.8	30.9	30.9	24.6	21.2
Capricornis 3	*Sumatraensis*	Heavy cover	30	3	40.6	24.5	42	28.3	27.8	21.4	18
Capricornis 4	*Sumatraensis*	Heavy cover	30	3	44.9	37.6	48.1	30	29.5	23.8	20.2
Capricornis 5	*Sumatraensis*	Heavy cover	30	3	44	37.9	46.4	32.8	31.5	24.1	23.1
Capricornis 6	*Sumatraensis*	Heavy cover	30	3	42.9	37.1	46.5	30.4	29.9	23.5	19.7
Capricornis 7	*Sumatraensis*	Heavy cover	30	3	40	36.4	44.5	27.5	28.2	23.8	21.1
Capra (markhor) 8	*Sibrica*	Light cover	30	3	34.2	28.8	37.8	26	24.9	19.2	17.9
Capra	*Sibrica*	Light cover	30	3	37.6	32	40.6	28	26.4	21.1	19.6
Capra	*Sibrica*	Light cover	30	3	39.7	32.9	40.9	25.2	26.7	20.7	20.1
Capra	*Sibrica*	Light cover	30	3	33.7	27.9	35.2	23.4	22.5	18	16.2
Capra	*Sibrica*	Light cover	30	3	37.7	31.5	39.7	26.7	25.9	19.5	18

Table A.2: Continued. Modern Astragali Raw measurements by species selected from Weinand (2005).

Individual/ Genus	Species	Habitat	Body mass (kg)	Size class	LM	LI	LL	WI	WD	TI	TD
Capra	*Sibrica*	Light cover	30	3	34.8	30	35.8	23.6	23.9	19.7	16.6
Capra	*Sibrica*	Light cover	30	3	40.6	35.1	42..6	28.6	24.7	21.1	18.4
Ovis (*argali*)	*Ammon*	Light cover	180	3	32.8	27.9	36.2	24.4	22.9	19	19.4
Ovis	*Ammon*	Light cover	180	3	39.7	34	43.3	29	29.8	24.6	24.4
Ovis	*Ammon*	Light cover	180	3	36.3	30.4	39.1	27.6	27	22.6	21.8
Ovis	*Ammon*	Light cover	180	3	38.5	32.7	39.6	26.5	25.3	20.2	18.9
Ovis	*Ammon*	Light cover	180	3	38.8	32.9	42.2	28.7	28.7	22.2	20.7
Ovis	*Ammon*	Light cover	180	3	41.7	34.5	43.9	30.5	29.1	23	21.1
Wildebeest (*connochaetes*)	*Taurinus*	Open cover	180	3	43.1	36.5	44.6	29.2	29.9	22.2	17.7
Connochaetes	*Taurinus*	Open cover	180	3	50.6	43	53.2	35.1	33.6	27.7	24.5
Connochaetes	*Taurinus*	Open cover	180	3	53.7	45.8	56.2	36.3	36.2	30.1	23.4
Connochaetes	*Taurinus*	Open cover	180	3	47.9	41.6	51.8	36.2	33.6	27	21.7
Connochaetes	*Taurinus*	Open cover	180	3	48.6	41.8	52.9	34.8	33.9	27.2	24.2
Connochaetes	*Taurinus*	Open cover	180	3	48.8	40.4	50.7	32.3	32.4	25.4	21.7
Connachaetes	*Taurinus*	Open cover	180	3	53.5	45	56.7	35	35.6	29	24.6

Table A.2: Continued. Modern Astragali Raw measurements by species selected from Weinand (2005).

Individual/ Genus	Species	Habitat	Body mass (kg)	Size class	LM	LI	LL	WI	WD	TI	TD
Damaliscus (topi)	*Lunatus*	Open cover	136	3	44.4	36.6	47.1	28.6	31.7	24.7	23.9
Damaliscus	*Lunatus*	Open cover	136	3	45.1	36.5	48.5	30	30.8	24.3	20.4
Damaliscus	*Lunatus*	Open cover	136	3	43.9	35.9	46.9	28.4	29.7	24.4	20.6
Damaliscus	*Lunatus*	Open cover	136	3	43.9	36.8	47	28.6	30.3	24.6	20.5
Damaliscus	*Lunatus*	Open cover	136	3	45.7	38.3	49.3	31.8	31.4	26.8	24.7

Table A.3: The summary statistics for the raw measurements taken for bovid sizes 1-3 astragali obtained from Weinand (2005,2007) are presented for the four-habitat grouping scheme.

Metric habitat		n	X	SD
LM	Open cover	17	42.6	8.6
	Light cover	19	35.5	3.9
	Heavy cover	11	39.96	6.9
	Forest cover	14	29.3	13.2
LI	Open cover	17	34.7	8.3
	Light cover	19	27.7	3.9
	Heavy cover	11	33.6	6.6
	Forest cover	14	25.2	11.4
LL	Open cover	17	42.5	10.2
	Light cover	19	34.1	5.8
	Heavy cover	11	42.5	7.7
	Forest cover	14	31.2	14.4
WI	Open cover	17	28.3	6.7
	Light cover	19	23.5	4.2
	Heavy cover	11	28.1	4.7
	Forest cover	14	18.7	9.3
WD	Open cover	17	27.6	7.2
	Light cover	19	21.9	4.5
	Heavy cover	11	27.9	5.2
	Forest cover	14	19.1	9.2
TI	Open cover	17	27.0	8.5
	Light cover	19	27.8	9.4
	Heavy cover	11	22.1	4.5
	Forest cover	14	15.0	6.9
TD	Open cover	17	21.4	4.5
	Light cover	19	21.4	4.4
	Heavy cover	11	19.3	4.0
	Forest cover	14	12.5	5.2

[1]n, Sample size; X, mean; SD, standard deviation.

Table A.4: Fossil results: Sterkfontein and Swartkrans raw measurements four-habitat model.

Taxon	Deposit/Member	Fossil collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	STK M5E	S94-3098	6(Forest cover)	**0.513**
Bovidae	STK M5E	S94-13356	6(Forest cover)	**0.264**
Bovidae	STK M5E	S94-13433	5(Light cover)	0.762
Bovidae	STK M5E	S94-13474	6(Forest cover)	0.731
Bovidae	STK M5E	S94-6111	7 (Open cover)	0.805
Bovidae	STK M5E	S94-2755	7 (Open cover)	**0.365**
Bovidae	STK M5E	S94-6905	7 (Open cover)	**0.566**
Bovidae	STK M5E	S94-13346	8(Heavy cover)	0.744
Bovidae	STK M5E	BP/3/19962	5(Light cover)	**0.134**
Bovidae	STK M5E	S94-3620	5(Light cover)	0.714
Bovidae	STK M5E	S94-2923	7 (Open cover)	**0.536**
Bovidae	STK M5E	S94-13300	7 (Open cover)	**0.500**
Bovidae	STK M5E	S94-13426	5(Light cover)	0.914
Bovidae	STK M5E	S94-3726	7 (Open cover)	0.826
Bovidae	STK M5E	S94-13497	5(Light cover)	0.729
Bovidae	SKX M1 LB	13790	5(Light cover)	**0.372**
Bovidae	SKX M1 LB	5687	7 (Open cover)	0.845
Bovidae	SKX M1 LB	5846	5(Light cover)	0.884
Bovidae	SKX M1 LB	9809	5(Light cover)	**0.458**
Bovidae	SKX M1 LB	6703	6(Forest cover)	0.084
Bovidae	SKX M1 LB	6309	5(Light cover)	**0.468**
Bovidae	SKX M1 LB	13949	5(Light cover)	0.951
Bovidae	SKX M1 LB	5687	7 (Open cover)	0.845
Bovidae	SKX M1 LB	5846	5(Light cover)	0.884
Bovidae	SKX M1 LB	9809	5(Light cover)	**0.458**
Bovidae	SKX M1 LB	12730	5(Light cover)	0.824
Bovidae	SKX M1 LB	13640	5(Light cover)	**0.318**
Bovidae	SKX M1 LB	7991	5(Light cover)	0.824

Table A.4: Continued. Fossil results: Sterkfontein and Swartkrans raw measurements four-habitat model.

Taxon	Deposit/Member	Fossil collection number	LDA most likely/predicted group	P(D>d | G=g)
Bovidae	SKX M1 LB	13640	5(Light cover)	0.840
Bovidae	STK M4	S94-11276	6(Forest cover)	0.753
Bovidae	STK M4	S94-12077	7 (Open cover)	0.876
Bovidae	STK M4	S94-12030	7 (Open cover)	**0.187**
Bovidae	STK M4	S94-12492	7 (Open cover)	0.813
Bovidae	STK M4	S94-13716	8(Heavy cover)	0.607
Bovidae	STK M4	Unknown	5 (Light cover)	**0.258**
Bovidae	STK M4	S94-14305	5 (Light cover)	0.668
Bovidae	STK M4	S94-14454	7 (Open cover)	**0.148**
Bovidae	STK M4	S94-14458	7 (Open cover)	**0.080**
Bovidae	STK M4	S94-14499	6(Forest cover)	**0.590**
Bovidae	STK M4	S94-15046	6(Forest cover)	**0.301**
Bovidae	STK M4	S94-14177	5 (Light cover)	0.766
Bovidae	STK M4	S94-10766	7 (Open cover)	0.775
Bovidae	STK M4	S94-10749	5 (Light cover)	0.771
Bovidae	STK M4	S94-9145	7 (Open cover)	0.085
Bovidae	STK M4	S94-12064	5 (Light cover)	**0.000**
Bovidae	STK M4	S94-8859	7 (Open cover)	**0.394**
Bovidae	STK M4	S94-11004	5 (Light cover)	**0.190**
Bovidae	SKX M2	3852	5 (Light cover)	**0.403**
Bovidae	SKX M2	990	5 (Light cover)	**0.328**
Bovidae	SKX M2	916	6(Forest cover)	**0.176**
Bovidae	SKX M2	3775	7 (Open cover)	0.811
Bovidae	SKX M2	792	5 (Light cover)	**0.526**
Bovidae	SKX M2	3061	7 (Open cover)	**0.326**
Bovidae	SKX M2	3189	6(Forest cover)	**0.359**
Bovidae	SKX M2	12337/1237	5 (Light cover)	**0.303**

[1]P(D>d | G=g) is the probability of an individual belonging to the assigned group.

[2]Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).