RECONSTRUCTING THE HABITAT MOSAIC ASSOCIATED WITH *Australopithecus robustus*: EVIDENCE FROM QUANTITATIVE MORPHOLOGICAL ANALYSIS OF BOVID TEETH

A Dissertation

by

JULIET KRUEGER BROPHY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2011

Major Subject: Anthropology

Reconstructing the Habitat Mosaic Associated with *Australopithecus robustus*: Evidence from a Quantitative Morphological Analysis of Bovid Teeth

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Approved by:

Chair of Committee,	Darryl de Ruiter
Committee Members,	Sheela Athreya
	Thomas DeWitt
	C. Wayne Smith
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ABSTRACT

Reconstructing the Habitat Mosaic Associated with *Australopithecus robustus*: Evidence from a Quantitative Morphological Analysis of Bovid Teeth. (December 2011)

Juliet Krueger Brophy, B.S., University of Michigan, 2002; B.A., University of Michigan; M.A., University of Tennessee

Chair of Advisory Committee: Dr. Darryl de Ruiter

This research better resolves the environmental mosaic that is typically reconstructed for the *A. robustus*-bearing faunal assemblages of South Africa and evaluates whether *A. robustus* were habitat specialists or habitat generalists by testing whether they are associated with numerous, different reconstructed habitats, or if they can be associated with a single, more homogeneous habitat type. Determining the habitat preferences of *A. robustus* holds important implications for understanding the behavior of these hominins and, potentially, for understanding whether their ultimate extinction might have been climatically influenced, as fluctuations in the environments associated with the robust australopiths provide direct evidence about the responses of hominins to environmental change. To achieve this, a 2-dimensionsal morphometric tool was developed for accurately identifying the abundant bovid teeth that are found in direct association with the hominins using Elliptical Fourier Function Analysis. More accurate taxonomic identifications facilitate more precise estimates of the relative abundance of ecologically sensitive bovids, allowing for finer resolution when segmenting the various components of the reconstructed habitat mosaics. The fossil bovids from Cooper's D and Swartkrans HR, LB, M2 and M3 were identified and their relative

abundances were compared across the assemblages over time in order to define the environmental mosaic in each assemblage and to determine if environmental heterogeneity existed across the assemblages. The relative abundances of the bovid fossil assemblages and *A. robustus* were compared to assess the habitat preferences of these hominins. *A. robustus* were not consistently associated with a particular habitat type suggesting that perhaps they were habitat generalists, capable of surviving in multiple types of habitats.

DEDICATION

This dissertation is dedicated to all the people who believed in me. Without your love and/or support, none of this would be possible. I dedicate this dissertation to the Brophy Family in their entirety, and, of course, to Darryl.

ACKNOWLEDGEMENTS

I would like to start by thanking my committee chair, Darryl de Ruiter, and my committee members: Sheela Athreya, Thom DeWitt and Wayne Smith. Their time, patience and guidance were invaluable for the completion of this dissertation. Sheela always responded to frantic emails, questions about EFFA and statistics and, importantly, always helped keep me focused. Thom and I would spend long hours in his office brainstorming about forms of objects, shapes and statistics. From him, I learned about things I did not think I would ever be dealing with for a dissertation in anthropology. Wayne helped me finalize my data collection methods and taught me that simply "playing around" and experimenting with cameras/lighting can be an important way of learning.

No one deserves greater acknowledgement for this dissertation than Darryl de Ruiter. Behind his back, I tell people that deciding to work with him was the best decision of my academic career. He undertook the arduous task of molding me into a researcher, writer, professor and colleague. While I know it took quite a bit of work, he taught me invaluable lessons. (BE PRECISE!) I wanted to do well in academia for my own personal goals, but also so he could be proud of me. Darryl is like a dad in that I want him to respect me and be proud of me, like a brother who gives you a hard time and pushes you to be your absolute best, going beyond where you thought you could go, and like a best friend you can always count on. I will always cherish the countless football Saturdays that, while not directly related to my dissertation, helped pull me away from the digitizing and writing and maintain my sanity. Dual and sometimes tri- projection of games whilst enjoying grilled cheese buns for crack burgers, bath tub Sparks, Orange whips and bacon burgers will go down as epic in the history

books. I would be neglect if I did not include the important dissertation time at the PG, the Keg and O'Bannon's. Often, more work got done here than anywhere else. I look forward to many more meetings of this sort in our future collaborative research endeavors.

My dissertation involves the processing and digitizing of an enormous sample of bovid teeth. I would not have been able to have the large sample sizes I did have without the help of several people. Suzy Billington, my anal retentive, nocturnal, hardworking, student, digitized for me for three semesters. I really appreciate all of her long nights and valiant efforts. I would also like to thank Megan Stewart, Tu Nguyen and Lauren Butaric for all of their hard efforts in digitizing.

I thank James Brink and the National Museum Bloemfontein for access to modern and fossil collections. I learned more about bovids and bovid identifications from talking to James at the Mystic, Florisbad and his lovely home than I have learned from most books. I appreciate the time he took to talk bovids, or as I like to call it- bovid brainstorm, with me. I would also like to thank him and his family for their amazing hospitality including but not limited to Windhoek, braais and warthog ribs. Thanks are also given to Theresa Kierney, Stephany Potze, Tersia Perregil and the Transvaal (Ditsong) National Museum of Natural History, Pretoria, South Africa. This museum is a treasure trove of modern bovids and South African fossil assemblages. I spent so much time there that at one point I was introduced as "practically museum furniture". I really appreciate all of the accommodations that they have made for me over the years and I look forward to working there again the future. I would like to thank Lee Berger and Bernhard Zipfel for access to the collections at the University of Witwatersrand. In addition, Lee has been extremely generous to me over the years. When funds were low, he was always willing to help out with beverages and meals. To this end, I

think I should also thank the PG Club, Café Fino and, of course, the Keg for allowing Darryl, Lee, Steve and me a place for academic discussion/banter and helping us maintain our sanity.

The Field Museum graciously allowed me to borrow bovid skulls in order to CT scan them. The scanning was done at Mercy Hospital with the assistance of Fernando Pedroza. He was very generous in his time by CT scanning the bovid teeth and organizing them into usable formats. I could not have accomplished that phase of the dissertation without his help.

This research would not be possible without the love and support (physically, psychologically and financially!) from my family: James III, Shirley, Anne, Jim IV, Shannon, Karin, Phil, Sue, Ted and my 10 nieces and nephews. There were good days and bad days, and they stood by me every step of the way. Specifically, I would like to thank my Mum for being my biggest cheerleader and always having an ear and shoulder for me when I needed someone. She helped give me the strength to make it to that finish line and I am eternally indebted to her for it. Dad ignited and continually fueled my research interests. My sisters Anne and Susan merit special attention for their constant encouragement and support, while Karin helped keep me beautiful when I was stressed. Having a similar career trajectory, Susan could not have been more helpful in the academic process. Jim and Shan provided the warmth of their home and family when I needed love and encouragement. I give special thanks to everyone in the family who helped make this document possible.

While I initially fell in love with paleoanthropology (and Mrs Ples!) at Michigan, I coin Steve Churchill to be the first person to ever believe in me as a biological anthropologist. After corresponding with him in 2003, I became a Teaching Assistant for him at Plover's Lake, South Africa; subsequently, I did my Masters research at this site. Late night cigars and numerous Castle and Namibia's Finest with him about paleoanthropology

and I knew in my heart and soul that this was the field for me. I cannot express how much I learned on our (almost) daily runs around Wits and time spent around a bonfire or at the Keg, about anthropology, research and life in general. He has always helped me see things from multiple perspectives and I think I am a better scientist/anthropologist and person because of it. I sincerely value all of the time I have had to spend with him.

This dissertation could not have been achieved without the support of my friends. I will genuinely miss the brainstorming that occurred in the 310 office area of the Anthropology building. Lauren, Bonny, Nanda, Heather and from afar, Lauren Cox, Drew, Jason and Victoria, have been a rock for me both academically and personally. I thank them for all of their encouragement over the years. I would also like to thank Christopher. While he only got tangled up in this dissertation in the final months, he had to go through the most dramatic emotional roller coasters. He had the opportunity to deal with both of my most current life situations: stressed out and uber stressed out. I appreciate all of the zen he brought to my life in the final months using his calming personality and craft beverages. With that said, I would also like to thank TABC and the New Republic. I regret that I did not get more time to spend with the club but I appreciate the friendship and knowledge I learned from them as well!

I would not be the anthropologist I am today without the education I received from the Department of Anthropology and Texas A&M University. While I chose this university to work with Darryl, I was continually impressed with the other faculty in the department and learned an incredible amount from them. Thank you to Texas A&M University for my education and the use of the facilities during my dissertation. While I am a Wolverine for life, Texas A&M University and the Aggies, will always hold a special place in my heart.

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CHAPTER I

INTRODUCTION

1.1 Introduction

The primary objective of this dissertation is to help advance the understanding of the nature and timing of the responses of early human ancestors to environmental changes in South Africa. Thus, this research involves documenting past environments associated with *Australopithecus robustus* and determining if changes in those environments influenced the behavior of these hominins.

The purpose of this research is to test the recurrent suggestion that *Australopithecus robustus* were habitat specialists, preferring an environment consisting of predominately open to lightly wooded grasslands situated within a larger habitat mosaic (Vrba, 1985a; Brain et al., 1988; Shipman and Harris, 1988; McKee, 1991; Watson, 1993a; Reed, 1997; Avery, 2001). To achieve this, the research project will produce highly accurate taxonomic diagnoses of fossil bovid teeth associated with the South African robust australopithecines in order to retrieve bio-ecological data preserved in these bovid faunal assemblages. Several recent studies have demonstrated that fluctuations in the relative abundance of bovid taxa are particularly responsive to environmental changes (Bobe and Eck, 2001; Bobe et al., 2002; Alemseged, 2003; de Ruiter et al., 2008). However, taxonomic identification of fossil bovid teeth is often imprecise and subjective, a difficulty exacerbated by the fragmentary nature of the South African faunal assemblages. Biasing factors such as age and degree of occlusal attrition further complicate identifications, as they often result in considerable overlap in absolute and relative size of teeth. Bovids in *A. robustus*-bearing cave infills are

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This dissertation follows the style of the Journal of Human Evolution.

overwhelmingly represented by isolated teeth. The horn cores and associated crania that are commonly identified in east African localities are especially rare (Brain, 1981a; Watson, 1993a; de Ruiter, 2004), and only factor into questions of taxonomic abundance under very limited circumstances (Vrba, 1971). By way of example, in the Swartkrans Member 3 assemblage, of the 19 845 identified specimens, 453 (2.3%) are horn cores; of these, 88 (0.4%) can be identified to genus, while only 22 (0.1%) can be identified to species. This enforced reliance on teeth, alongside a handful of more complete maxillas and mandibles, results in taxonomic diagnoses that often cannot go beyond such broad taxonomic levels as the Tribe or even Family. Faunal lists typically contain Tribe level categories such as "Medium-sized alcelaphines", or "?Hippotragini", etc. (Vrba, 1975, 1995; Brain, 1981a, 1985; Watson, 1993a; Klein et al., 2007; de Ruiter et al., 2008). Such inexact identifications will mask the more subtle ecological traces that might otherwise be detected through more precise taxonomic diagnoses. The subjective nature of bovid identifications is potentially compounded by inter-observer error when attempting to compare faunal lists compiled by different researchers. As a result, one researcher's faunal identifications and, therefore, paleoenvironmental reconstructions, might differ from another's. Examples of this can be seen in the different paleoenvironmental reconstructions that have been produced using faunal remains from the sites of Makapansgat (Wells and Cooke, 1956; Vrba, 1985a, 1985b; Reed, 1998), Swartkrans (Vrba, 1975; Brain, 1985; Watson, 1993a; de Ruiter, 2003; de Ruiter et al., 2008), and Gondolin (Watson, 1993b; Adams and Conroy, 2005).

The initial goal of this project is to quantitatively assess bovid dental morphology in order to facilitate greater precision and reliability when examining the faunal assemblages

associated with *A. robustus*. Ultimately, the purpose of this research project is to produce more precise paleoenvironmental reconstructions than are presently available by more accurately identifying the bovid taxa that numerically dominate all of the assemblages recovered from the *A. robustus*-bearing cave infills of South Africa. Increased taxonomic control will allow for more fine-grained resolution of paleoenvironments within the reconstructed habitat mosaics that are reflected in the relative abundances of the different bovids recorded in the assemblages. The results of this study will indicate whether greater environmental heterogeneity for *A. robustus* exists than is presently recognized, and will allow the habitat mosaics associated with these hominins to be more precisely constrained. The aim is to move beyond the broad environmental category of "grassland", for example, to more precise sub-categories, such as those recognized in modern vegetational studies in South Africa (e.g. Acocks, 1988). In addition, fluctuations in environmental conditions over time will be compared to fluctuations in the proportions of *A. robustus* in order to determine if they correspond. This latter aspect will test if *A. robustus* is consistently associated with any particular set of environmental conditions, or if they appear to be more of a habitat generalist; i.e. capable of occupying a variety of environments. This study relies on a taxonomic uniformitarian approach by assuming that fossil representatives of extant taxa shared equivalent ecological adaptations as their modern counterparts. In addition, one of the nested aims of this study is to test if fossil representatives can or cannot be accommodated within extant species. If extinct specimens are recognized, i.e. ones that cannot be assigned to a modern taxon, the fossils will be assessed using ecological functional morphological techniques developed by Reed (1996, 1997) and Schubert (2007) to test if they represent

such a radical departure that they warrant alternative ecological reconstructions than their nearest living relatives.

1.2 Significance and application

To identify fossil bovid remains, researchers currently rely on fossil and modern comparative collections, though several biasing factors, for example age and degree of occlusal attrition, have the potential to make this approach subjective. Additionally, the near complete lack of associated, identifiable horn cores in the robust australopithecine faunal assemblages adds to the difficulty encountered when attempting to identify bovid taxa in the fossil record. Due to these circumstances, faunal studies are susceptible to two main concerns in South Africa. The first issue involves misidentified bovids, which could lead to erroneous paleoenvironmental reconstructions due to the fact that bovid species have different ecological requirements. By way of example, the closely related blue wildebeest (*Connochaetes taurinus*) and red hartebeest (*Alcelaphus buselaphus*) have notably different habitat preferences, yet their teeth appear remarkably similar. In a fossil assemblage, teeth of these animals are difficult to distinguish visually, thus they are often lumped together at the tribal level, Alcelaphini, obscuring the ecological differences between them. Blue wildebeest are typically associated with savanna woodlands, and shade and sufficient amounts of drinking water represent essential habitat requirements (Skinner and Smithers, 1990). Conversely, red hartebeest are found mostly in open country, often in semi-desert conditions, avoiding wooded cover and relying on more ephemeral surface waters such as pans. Recognizing one versus the other would have a major influence on the habitat reconstructed for a fossil assemblage, especially in terms of levels of tree coverage and potential water

sources. Currently, the necessarily broad taxonomic categories are problematic in that recent studies have relied on fluctuations in the abundance of bovid tribes over time to reconstruct past environments, necessitating broad ecological divisions (Shipman and Harris, 1988; Bobe et al., 2002; Alemseged, 2003; de Ruiter et al., 2008). A standardized methodology for identifying fossil bovids has the potential to improve the practice of reconstructing past environments, as researchers will be freed from the constraints of more subjective analytical studies, and will be able to base their reconstructions on increasingly precisely documented faunal assemblages.

The second major issue in paleoecological research involves inter-observer error. Researchers often cannot reliably compare the faunal lists of sites produced by different analysts owing to quality of fossil preservation, differences in experience, confidence of identifications, and access to comparative materials. This extends to comparisons of minimum numbers of individuals computed, as these form the basis for calculating relative abundance estimates. This issue can potentially confound paleoanthropologists' ability to generate accurate interpretations of faunal assemblages and paleoenvironments over space and time. By way of example, these concerns can be illustrated in the analyses of the South African cave site, Makapansgat. Wells and Cooke (1956), Vrba (1995), and Reed (1998) have all proposed paleoenvironmental reconstructions for Member 3 of Makapansgat. Despite the fact that all of the researchers relied upon the same bovid assemblage for their reconstructions, three varying types of environments have been suggested: shrub-like with nearby open grasslands (Wells and Cooke, 1956); woodland (Vrba, 1995); and bushland with riparian woodland and nearby limited wetlands (Reed, 1998). A second example involves the fauna from Swartkrans (Watson, 1993a; de Ruiter, 2004). Watson's (2004) research at

Swartkrans concluded that the fauna and, therefore, environment, were relatively consistent throughout the depositions of the cave and consisted of primarily open savannah with a woodland component and nearby water source. de Ruiter (2004) revised the relative abundance estimates of the fauna from Swartkrans, which resulted in the numbers of some taxa increasing, others decreasing, and a subsequent inconsistency between these researchers in the proportion of bovids at Swartkrans. A third example involves the analysis of the site Gondolin by Watson (1993b). In a revised faunal list, Adams (2006) identified several fossil specimens as *Redunca* sp., whereas Watson (1993b) had originally classified them as *Antidorcas* cf. *marsupialis/australis*. These and other identification differences translated into considerably different paleoenvironmental reconstructions. While Watson (1993b) concluded that Gondolin consisted of edaphic grassland with rocky and open-country paleohabitats, Adams (2006) suggested an open to wooded grasslands on rocky hills, with localized patches of bush and light tree cover. These examples illustrate the need for a standardized method for identifying bovids. This approach would allow more accurate reconstructions and more precise interpretations of environmental change across space and time.

1.3 Project outline

Chapter II provides an in depth background to the problems addressed in the dissertation. A history of the Family Bovidae is presented including what their characteristics are and where they originated. A description of *A. robustus* is discussed alongside a historical review of where and when they were recovered. In addition, previous paleoenvironmental

reconstructions of the assemblages associated with the robust australopithecines were described.

Chapter III presents the first phase of the project and involves developing a standardized system for accurately identifying bovid teeth using the occlusal morphology of modern dentitions in order to distinguish between closely related bovid taxa. The following hypothesis is tested:

Hypothesis 1: Modern bovid dentitions can be reliably distinguished as belonging to discrete species, separate from morphologically similar, closely related species, based on analyses of the outlines of occlusal surfaces of their teeth.

This hypothesis will test whether the outlines of occlusal surfaces of bovid teeth exhibit distinct, reliable shapes that can be used to differentiate one bovid species from another. If so, then an extant, isolated bovid tooth could be identified to the level of the species based on a comparison of its occlusal morphology with the occlusal morphology of a dataset of known species. If, however, the teeth from closely related bovid taxa cannot reliably be distinguished from each other, then the taxonomic level of identification for an unknown tooth must be reconsidered. In this case, bovid tooth identification would involve classifying them only to the taxonomic level of genus or tribe and not species, whichever is supported by the morphological analysis.

To test H1, Elliptical Fourier Function Analysis (EFFA), a curve-fitting function particularly suited for the characterization of boundary outline data of complex irregular morphologies, will be employed. The outlines of the modern bovid teeth will be compared using discriminant function analysis (DFA) to determine if they consistently classify

correctly. If the teeth classify correctly ≥ 85% of the time, the methodology will be considered reliable and will be applied to the fossil record.

Chapter III also involves ensuring that the occlusal morphology is maintained throughout the life of the animal through the use of computed tomography (CT) scans. The CT scanner produces a series of slices of the tooth that will be used as a proxy for occlusal attrition; the morphology of the tooth at each layer will be analyzed using EFFA in order to assess any changes in shape over ontogenetic development.

The second phase of the dissertation is presented in Chapter IV. This research involves applying the outline data of the modern teeth to the fossil record. The following hypothesis is tested:

Hypothesis 2: A. Extant bovid teeth can be used to accurately identify representatives of modern taxa in the fossil record;

Hypothesis 2: B. The occlusal outline of the teeth of extinct bovid species can be quantitatively documented, thus allowing precise identifications of fossil species for whom there are no modern counterparts.

If the occlusal outlines of modern comparative teeth are identified as being diagnostic of extant bovid species, then the methods can be applied to the fossil record. A fossil bovid tooth can be identified by comparing its occlusal morphology to the occlusal morphology of a dataset of modern bovid teeth previously established by EFFA (Chapter III). A database of the occlusal surface outlines of each tooth for the extant and, if identified, extinct species will be created. This database will be used as a reference for analysts to identify bovids in the fossil record. Alternatively, if a rigorous shape analysis cannot differentiate between the teeth of closely related bovid taxa in the fossil record, then the identification of an unknown tooth

might involve classifying them only to the taxonomic level of genus or tribe, with a corresponding loss of precision in paleoecological reconstruction.

The EFFA results of the modern specimens are compared to the bovid assemblages from two robust australopith fossil localities, consisting of 5 assemblages: Cooper's D and Swartkrans Member 1 Lower Bank, Member 1 Hanging Remnant, Member 2 and Member 3, in order to reliably identify fossil representatives of modern bovid species. The results of the DFA identifications of the fossil teeth are presented using the posterior probability and the typicality probability. The identifications using the typicality and posterior probabilities are compared in order to test whether the different classification methods yield different results.

Chapter V uses the relative abundances of the bovids identified by the typicality probabilities to reconstruct the environments from the five assemblages of Cooper's D and Swartkrans. Hypothesis 3 is tested in Chapter V.

Hypothesis 3: Fossil bovids accurately identified based on EFFA of their occlusal outlines can be used to detect environmental heterogeneity at robust australopithecine sites in South Africa.

Once accurate diagnostic tools for identifying bovid teeth have been established, the bovid assemblages associated with *A. robustus* will be compared to each other in their probable chronological order to detect any changes over time in the environment. Fluctuations in the proportions of bovid taxa will be documented across the robust australopithecine assemblages in order to determine whether any environmental heterogeneity is reflected within the respective habitat mosaics, or if they demonstrate a relatively homogeneous set of reconstructed paleoenvironments. Changes in the bovid fauna are compared to changes in the proportions of *A. robustus*, with the goal of testing for

particular habitat associations. If *A. robustus* were habitat specialists, they would consistently be associated with a particular set of environmental conditions. On the contrary, if the robust australopithecines were habitat generalists, they would not consistently associate with any particular set of environmental conditions.

1.4 Expected outcomes

This study represents the first time occlusal surface morphometric quantification has been applied to bovid tooth identification. While previous methods have been very successful in paleoecological analyses, this research will change the way that paleoenvironments are reconstructed by reducing reliance on subjective visual comparisons, and instead developing a quantifiable method for the identification of bovid fossils. The final product will be a reliable, standardized, and replicable methodology for identifying fossil bovid teeth that will minimize the impact of biasing factors such as age and attrition that often cause overlap in the size and shape of bovid teeth, as well as help reduce the degree of subjectivity involved in analyzing faunal lists compiled by different researchers. Since individual bovid species, even closely related species, have very particular habitat requirements, establishing a tool for accurately identifying these bovid remains will result in significantly greater precision in taxonomic diagnoses, and in turn the environmental reconstructions based upon these remains. Thus, the methodology established in this project will allow anthropologists to use bovids as a direct and accurate proxy for environmental change across the Plio-Pleistocene of South Africa. Furthermore, this methodology will establish a foundation for future investigations of teeth where ambiguity in their identification exists.

This research will be used to evaluate whether *A. robustus* were habitat specialists or habitat generalists. Determining the habitat preferences of these hominins has important implications for understanding their behavior and, potentially, for understanding why they went extinct. Fluctuations in the environments associated with the robust australopithecines provide direct evidence about the responses of hominins to environmental change. Ultimately, this approach will help improve our knowledge of the relationship between hominin evolution and ecological change in southern Africa.

CHAPTER II

BACKGROUND TO THE PROBLEM

2.1 Introduction

This chapter presents a literature review on the description and evolutionary history of the Family Bovidae in order to better understand what characteristics an individual in the Family Bovidae has and why they are so important in the fossil record. Next, this chapter outlines a general description of *A. robustus* and a historical review of the sites where they have been recovered. The purpose of this section is to appreciate the morphological attributes of the robust australopithecines and where and when these fossils have been found. Finally, this chapter presents a review of previous paleoenvironmental reconstructions of robust australopith sites.

2.2 Family Bovidae

2.2.1 *Characteristics of the Family Bovidae*

The Family Bovidae is a diverse group of ungulates that are native to Africa, Europe, Asia, and North America (Gentry, 1978). The family includes cattle, sheep, goats, and antelopes. Bovids are characterized by their permanent and un-branched horn cores and sheaths, and by their diagnostic teeth (Gentry, 1978; Janis and Scott, 1988). Bovid teeth are described as being hyposodont, or high crowned (Hillson, 2005). The molars are selenodont, meaning the cusps are coalesced into crescentric folds with the long axis running primarily mesiodistally (Gentry, 1978; Hillson, 2005). Styles, or minor cusps, and ribs, expansions of the cusps between the styles, can be seen on the buccal side of the upper molars and lingual

side of the lower molars (Hillson, 2005) (Figure 2.1). Each molar lobe exhibits an infundibulum, or central cavity, which varies from simple to complicated depending on the Tribe to which the animal belongs. Gentry (1978) describes how the upper molar mesial lobe is often more constricted than the distal molar lobe and a transverse "goat fold" located at the mesial edge of lower molars is variably common in Hippotragini and Reduncini. Mandibular, and occasionally maxillary, third molars exhibit a hypoconulid, a smaller, extra lobe distal to the two main lobes (Figure 2.1).

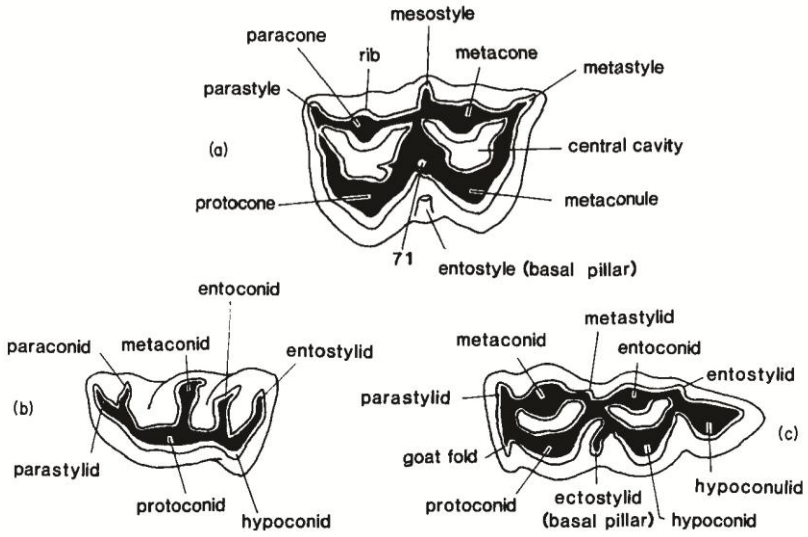


Figure 2.1 Picture adapted from Gentry (1992: 6) illustrating the characteristics of bovid teeth.

In profile, the upper and lower third molars often flare distally towards the root of the tooth due the fact that they are the last teeth in the row to erupt (Figure 2.2). The second molars are frequently U-shaped in profile above the roots with the mesial and distal outlines of the tooth being parallel, while the outline of the first molar is often V-shaped when viewed in profile (Figure 2.2).

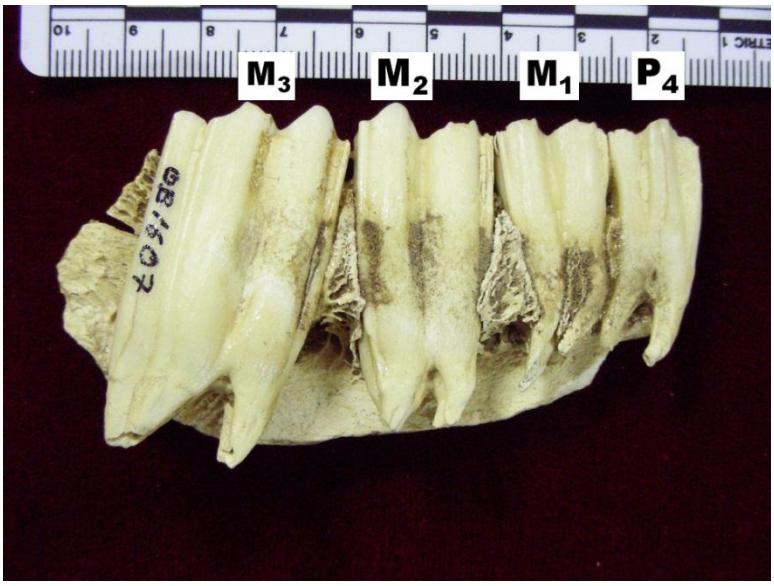


Figure 2.2 Left mandibular tooth row in profile.

2.2.2 *Evolutionary history of Family Bovidae*

Perhaps the oldest known Bovidae in the fossil record is *Eotragus* which is found across Eurasia in the Early Miocene (Ginsburg and Heintz, 1968; Bibi et al., 2009). It has been suggested that the teeth and cranial characteristics of some species of *Eotragus* represent the last common ancestor to all of the Bovidae and that *Eotragus* or an *Eotragus*-like ancestor migrated to Africa early in the Miocene (Gentry, 1978; Bibi et al., 2009). No pre-Miocene ruminants have been recovered from Africa (Gentry, 2010).

Evidence of early Miocene bovids in Africa is scant. Stromer (1926) and Hopwood (1929) describe two bovid specimens from the Namib desert area of southwest Africa dating to the early Miocene. Whitworth (1958) identified early ruminants from East Africa and named them *Walangania gracilis* and *Palaeomeryx africanus*. Hamilton (1973) found similar material in Libya and allocated all of the fossils to *Walangania africanus*. While this species is considered to be one of the earliest ruminants in Africa, it is controversial as to whether it

is the ancestor to the Family Bovidae or to the Superfamily Cervoidae (Janis and Scott, 1988; Gentry, 1994).

Evidence of bovids from the middle Miocene of Africa comes from four main sites: Gebel Zelten, Egypt, and Maboko, Kenya, date to approximately 16 Ma; Fort Ternan, Kenya dates to ~14 Ma; and sediments of the Ngorora Formation in Baringo, Kenya, range from 12-8 Ma in age (Bishop et al., 1969; Gentry, 1970, 2010). Five bovid species are recognized from Fort Ternan: *Oioceros tanyceras*, *Gazella* sp., *Kipsigicerus labidotus*, *Capratragoides potwaricus* and ?*Eotragus* sp. (Shipman, 1986). Gentry (1970, 1978) highlight the similarities between contemporaneous boselaphines and caprines (two primitive groups of bovids) in Eurasia and the Fort Ternan bovids in Kenya, and suggest that these bovids strongly resemble Eurasian bovids and/or the earliest descendants of the Eurasian bovids in Africa. The Ngorora Formation also contains boselaphines and caprines similar to the bovids at Fort Ternan. Gentry (1978) states that the likeness between the Fort Ternan and the Ngorora Formation bovids indicates an ancestor-descendant relationship, respectively.

The next documented chronologically younger site also lies in Baringo, Kenya. The Mpesida Beds date to ~ 7 Ma and contain tragelaphines, antilopines and [likely] alcelaphines (Gentry, 1978). While bovids have been recovered from localities such as Beni Mellal, Morocco, and Marceau, Algeria, the dating of these sites as Miocene or Pliocene is controversial (Cooke, 1968; Gentry, 1978).

Widespread cooling in the late Miocene led to a major adaptive radiation of the bovids, and they began to increasingly exploit more open environments (Maglio, 1978; Vrba, 1988a, 1988b). Thus, by approximately 3.5 Ma, bovids came to dominate the African fauna, replacing the previously abundant suids (White and Harris, 1977; Greenacre and Vrba, 1984;

Bobe et al., 2002). The current distribution of bovids extends across the African continent in myriad environments that differ significantly in proportions of wood and grass cover. The bovids have developed distinct ecological adaptations including diet, habitat, water dependence and seasonal movement patterns that vary according to their respective environments. Gentry (1978) suggests that the varied ecological adaptations of the bovids explain why they are such a successful Family.

2.2.3 *Bovidae taxonomy*

Several taxonomic configurations have been suggested for the Family Bovidae (Simpson, 1945; Ansell, 1971; Kingdon, 1997; Gentry, 1978, 1992). The taxonomic arrangement of bovids is difficult due to morphological convergence and gaps in the fossil record prior to 3.5 Ma (Gentry, 1992). The classification system proposed by Gentry (1992) resulted from cladistic and phenetic analyses using 112 skeletal characteristics. He proposed five subfamilies and thirteen tribes (Table 2.1). The indeterminate tribe consists of non-African bovids (Gentry, 1992). The present study relies on Gentry's (1992) classification scheme and focuses on the seven most common tribes in the southern African fossil record and the twenty most common species from these tribes (Table 2.2).

Table 2.1 Classification proposed by Gentry (1992).

Subfamily	**Tribe**
Bovinae	Tragelaphini*
	Boselaphini
	Bovini*
	Cephalopini
Antilopinae	Neotragini*
	Antilopini*
Hippotraginae	Reduncini*
	Hippotragini*
Alcelaphinae	Aepycerotini
	Alcelaphini*
Caprinae	Ovibovini
	Caprini
	indeterminate

*indicates Tribes examined in this study

Table 2.2 Extant bovid species analyzed in this study.

Tribe	Species List
Alcelaphini	*Connochaetes taurinus*
	Connochaetes gnou
	Alcelaphus buselaphus
	Damaliscus dorcas
Tragelaphini	*Taurotragus oryx*
	Tragelaphus strepsiceros
	Tragelaphus scriptus
Bovini	*Syncerus caffer*
Reduncini	*Redunca arundinum*
	Redunca fulvorufula
	Kobus leche
	Kobus ellipsiprymnus
Hippotragini	*Hippotragus niger*
	Hippotragus equinus
	Oryx gazella
Neotragini	*Raphicerus campestris*
	Oreotragus oreotragus
	Pelea capreolus
	Ourebia ourebi
Antilopini	*Antidorcas marsupialis*

2.3 Australopithecus robustus

2.3.1 *Description of* A. robustus

Australopithecus robustus, often referred to as a "robust" australopith, is defined by a suite of unique craniodental characteristics. The cranium exhibits an anteriorly placed sagittal crest, extreme post orbital constriction, flaring zygomatic arches, and a highly prognathic face (Wood and Strait, 2004). Remains from this species also demonstrate anterior pillars and a thick palate (Wood and Strait, 2004). Dentally, these hominins had small anterior teeth and large premolars and molars. The premolars are considered to be molarized, or smaller versions of molars that function similar to molars in mastication (Wood and Strait, 2004). The cranial capacity of this hominin is estimated at 500-550 cc and the body size is suggested to be 70-90 pounds (McHenry, 1994).

2.3.2 *History of the discovery of* A. robustus

Robert Broom recovered the first robust australopithecine from Kromdraai in 1937. Broom considered the large cranial and dental features of these finds to be too dramatically different from the previously recovered *Australopithecus africanus* (formerly "*Plesianthropus transvaalensis*") fossils from Sterkfontein that he named a new genus and species, "*Paranthropus" robustus* (Broom, 1938). The Kromdraai fossil TM 1517 is the holotype of *Australopithecus robustus* (formerly "*Paranthropus*"). Some authors prefer the nomen "*Paranthropus" robustus* (Broom, 1937), though the generic attribution of this species is beyond the scope of the present research.

In 1948, Broom began excavation of the *in situ* material at Swartkrans at the request of Wendell Phillips of the University of California-Berkeley's Africa Expedition. During this

time he recovered additional hominin fossils which he assigned to a new species "*Paranthropus crassidens*". In 1950, local miners began blasting operations at Swartkrans. Broom and his assistant John Robinson took advantage of the operations and collected the fossiliferous breccia that the miners were extracting from the cave (de Ruiter, 2001). In this *ex situ* material, Broom and Robinson (1952) recovered numerous fossils including such notable specimens as SK 48 and SK 23. Broom also placed these specimens in the species "*Paranthropus crassidens*". "*Paranthropus crassidens*" fossils have since been subsumed into the genus and species *Australopithecus robustus*, though with some debate (Robinson, 1954; Grine, 1988; Howell, 1978; Moggi-Cecchi et al., 2010). For this thesis I will refer to these fossils as *A. robustus*.

To date, robust australopiths have been recovered from a total of six sites: Kromdraai, Swartkrans, Cooper's Cave, Sterkfontein, Gondolin and Drimolen (Figure 2.3) (de Ruiter et al., 2009). Herries et al. (2009) suggest that *A. robustus* existed from approximately, 2.5-0.3 Ma, while Pickering et al. (2011) propose a much more constrained date of approximately, 1.9-1.4 Ma. Although *A. robustus* fossils are known from 6 localities, the fossil assemblages from Gondolin and Drimolen are either poorly provenienced, or unavailable for study, thus these latter two sites are not discussed further. Due to preservational issues and small sample sizes, Kromdraai and Sterkfontein faunal assemblages were not assessed. This study will focus on the bovid fossils from Swartkrans Members 1-3 and Cooper's Cave.

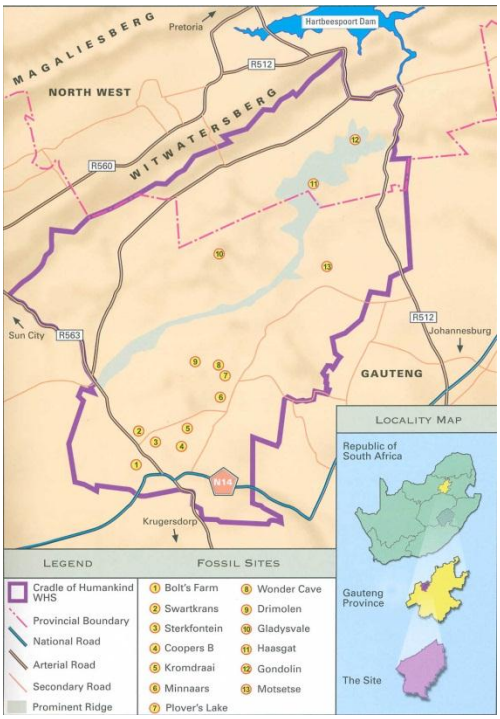


Figure 2.3. Map showing the locations of sites where *Australopithecus robustus* has been recovered. These localities are located in the Bloubank Valley, Gauteng Province, South Africa (from Hilton-Barber and Berger, 2002).

2.4 Australopithecus robustus *sites*

2.4.1 *Kromdraai*

The Kromdraai Formation consists of two discrete, non-contemporaneous depositional units represented by narrow solution cavities: Kromdraai A and B (Brain, 1981a). In 1937, Broom was notified that a school boy named Gert Terblanche had found some teeth on a hill near Sterkfontein cave (Broom, 1938). The teeth were ultimately found to be part of a skull and lower jaw from what is now referred to as Kromdraai B. After examining the fossils the boy had found, Broom decided to excavate at Kromdraai. He extracted the rest of the fossil Terblanche had located and named it the first robust australopith. The skull was the holotype of *A. robustus*, TM 1517 (Broom, 1938). Subsequent excavations at Kromdraai B have revealed additional hominin fossils (Broom, 1948; Brain,

1981a; Vrba, 1981; Berger et al., 1994; Thackeray et al. 2001). Thackeray et al. (2002) suggested that Kromdraai B dates to ~1.9 Ma based on paleomagnetic dating. de Ruiter et al. (2008) support a date of 1.9 Ma for Kromdraai B based on the presence of *Hexaprotodon protamphibius*, which disappears in East Africa about this time. Herries et al. (2009) suggest a date of 2.11-1.6 Ma for Kromdraai B using biochronology and paleomagnetism dating techniques. Hominin fossils have not been recovered from Kromdraai A.

2.4.2 *Swartkrans*

The largest concentration of robust australopith fossils comes from Swartkrans. Swartkrans is divided up into Members 1-5. Member 1 is the largest deposit and consists of two separate sub-deposits: the Lower Bank and the Hanging Remnant (Brain, 2004). Broom supervised excavations of the *in situ* deposits of Member 1 from1948 to the end of 1949. In 1950, local miners moved onto the site and mined the cave for limestone until 1951. Broom and Robinson (1952) examined the *ex situ* fossiliferous breccia that the miners extracted from the cave. Brain (1981a) resumed excavations of the *in situ* and *ex situ* deposits in 1965. Excavations ceased at Swartkrans in 1986 in order to organize and analyze the backlog of material from the site.

The first robust australopithecine from Swartkrans was found in what came to be known as the Hanging Remnant of Member 1 (Broom, 1949). Subsequent excavations have recovered additional robust australopithecines from Members 1 (both the Lower Bank and the Hanging Remnant), 2 and 3 (Brain, 1981a). The oldest Swartkrans deposit, the Lower Bank of Member 1, was dated to approximately 1.7 Ma based on biostratigraphy (de Ruiter, 2003; Brain, 2004) while the Hanging Remnant was dated to approximately 1.6 Ma (Delson,

1984; de Ruiter, 2003). More recently, U-Pb dating reveals that the Hanging Remnant of Member 1 is likely between 1.9-1.8 Ma (Pickering et al., 2011). Using biostratigraphy and U-Pb dating, Member 2 dates to ~1.65-1.07 Ma (Herries et al., 2009; Delson, 1984). U-Pb dating of bovid tooth enamel provides the only absolute dates for Swartkrans Member 3 (Albarè et al., 2006; Balter et al., 2008). Albarè et al. (2006) suggest a date of 0.988 ± 0.003 for Swartkrans Member 3 while Balter et al. (2008) concluded an age of 1.04-0.62 for Member 3. Vrba (1995) suggests a date of ~<0.78 Ma for Swartkrans M3 based on first appearance data of five bovids: *Ourebia ourebi*, *Oreotragus oreotragus*, *Antidorcas marsupialis*, *Damaliscus lunatus* and *Hippotragus niger*. Herries et al. (2009), assessing all of the dating techniques for Swartkrans Member 3, suggests a date range or 1.04-0.62 Ma.

2.4.3 *Cooper's Cave*

Cooper's Cave is composed of three spatially distinct infills: Cooper's A, B and D. Excavations began at Cooper's A and B in 1955 (Brain, 1958). While three hominin specimens have been recovered from Cooper's A and B, the fossils lack secure provenience (Steininger et al., 2008). In 2001, *in situ* excavations were undertaken at Cooper's D (de Ruiter et al., 2009). This large, well-documented assemblage has yielded robust australopith fossils including several isolated teeth, two mandible fragments and a lumbar vertebra. The site was initially biostratigraphically dated to 1.9-1.6 Ma (Berger et al., 2003), though U-Pb dating resulted in a revised estimate of 1.5-1.4 Ma (de Ruiter et al., 2009).

2.4.4 *Sterkfontein*

The Sterkfontein cave system was originally divided into six successive Members based on sedimentological and stratigraphic analyses (Partridge, 1978). However, more recent research could not retrieve all of the members recognized by Partridge (Pickering and Kramers, 2010), and presently fossils are known from Members 2, 4 and 5. Recent research has led Kuman and Clarke (2000) to divide Sterkfontein Member 5 into three separate sub-components: the Oldowan Infill, the Acheulean and the Stw 53 infill.

The first fossils from the Sterkfontein cave system were recovered by Broom in 1936 when the site was being quarried for lime by local miners (Broom, 1936). From 1936-1939, Broom found numerous hominin remains from an area that is now termed the "Type Site". This deposit is now referred to as Member 4, and the fossils are widely considered to belong to *A. africanus* (Broom et al., 1950; Lockwood and Tobias, 2002; though see Clarke, 2008). In 1947, Broom and Robinson resumed activities at Sterkfontein (Broom et al., 1950). The site was ultimately abandoned in 1953, two years after Broom died. Systematic excavation of the Sterkfontein cave system recommenced in 1966, and the cave has been excavated continuously ever since (Tobias and Hughes, 1969; Reed, 1996).

Three robust australopith dental specimens were recovered from the Oldowan Infill of Sterkfontein Member 5 (Clarke, 1994). Kuman and Clarke (2000) date this member to approximately 2.0-1.7 Ma using the occurrence of Oldowan tools as a reference while Herries et al. (2009) suggest a younger date of 1.38-1.07 based on electron spin resonance (ESR) dates. The Sterkfontein Member 5- Oldowan Infill is the only stratum at this site that yielded robust australopithecine remains.

2.5 Taphonomic factors

The purpose of this research is to investigate the potential habitat preferences of *A. robustus* using bovids as ecological indicators of the surrounding environment. In order to achieve this, the assumption is made that the proportions of bovids in the assemblages associated with *A. robustus* are an accurate reflection of the proportions in the original paleocommunity, and that these proportions are in turn accurate reflections of this surrounding environment. However, numerous studies describe different taphonomic factors that can bias assemblages that include hominins, carnivores and rodents (Brain, 1981a, 1989; Capaldo and Blumenschine, 1994; Cruz-Uribe, 1991; Lam, 1992; de Ruiter and Berger, 2001; Pickering et al., 2004; de Ruiter et al., 2008). de Ruiter et al. (2008) investigated the influence of taphonomy on faunal assemblage composition for the *A. robustus*-bearing assemblages of South Africa. Although carnivore damage is rare, de Ruiter et al. (2008) documented a variety of bone accumulating agents in the robust australopithecine assemblages, with no single collector standing out as predominant. They concluded that the combined impact of numerous agents over long spans of time would minimize the idiosyncratic influence of any individual accumulating agent, in agreement with Brain (1980). They did note a potential bias in the depositional matrix, as hard-breccia deposits tended to have an overabundance of isolated teeth. However, they documented a relatively even distribution of dental remains across the assemblages, which are the focus of the present study. In addition, chord distance values (a measure of faunal assemblage dissimilarity) indicated there was no relationship between taphonomic conditions and taxonomic composition, thus the two factors vary independently. They concluded that fluctuations in taxonomic abundance represent reasonable reflections of original animal paleocommunities;

thus, changes in taxonomic composition over time signaled animal paleocommunity responses to fluctuating environmental conditions. The present study will utilize the same faunal assemblage data in an attempt to more accurately identify the bovids in the assemblages, accepting the conclusions of de Ruiter et al. (2008) that taphonomic biases have not irretrievably masked the underlying biological signals relating to animal paleocommunity composition.

2.6 Previous paleoenvironmental reconstructions of sites with A. robustus

Numerous studies have presented interpretations of the environment associated with *A. robustus* from the sites of Kromdraai, Swartkrans, Sterkfontein and Cooper's (Table 2.3). These studies have changed over time due to the recovery of more material from the sites, different techniques being used to reconstruct the environment and reanalysis of collections by different researchers. Thus, these studies are presented in chronological order and broken up into three major time frames: 1938-1970, 1970-2002 and 2002-2011.

Table 2.3 Summary of previous paleoenvironmental reconstructions for *A. robustus*

	Swartkrans	Kromdraai B
Broom (1938; 1943)	open grassland	open grassland
Cooke (1952, 1963)	open grassland	open grassland
Robinson (1963)	open grassland	open grassland
Vrba (1975, 1976, 1980, 1981, 1985a, 1985b, 1988a, 1989, 1995)	open grassland with low bushcover	open grassland with some dense woodland
Brain (1981b)	open, arid environment	
Brain (1988a); Brain et al (1988)	SK M1-3: open-country grassland with a nearby river lined with trees	
Shipman and Harris (1988)	SK M1, 2: open habitats	
McKee (1991)		
Watson (1993a)	SK M1LB, 2, 3, 5: predominately open savannah with a savannah woodland component lining the Bloubank River	
Reed (1997)	SK M1: open habitat with a river that likely supported a woodland or forest as well as areas of edaphic grasslands; SK M2: wooded grassland with nearby wetlands; SK M3: open grassland with a river or stream nearby supporting edaphic grasslands	open grassland with patches of riparian woodland
Avery (2001)	SK M1-3:environment consisted of a mosaic including riverine grassland and plains with open savannah woodland	
de Ruiter (2003)	SK M1-3:open grasslands, a large permanent water source and some extensive woodlands in the vicinity of this site	
de Ruiter *et al*. (2008)	woodland, grassland and a nearby permanent water source	woodland, grassland and a nearby permanent water source
de Ruiter *et al* . (2009)		

Table 2.3 continued

	Sterkfontein	Cooper's D
Broom (1938; 1943)		
Cooke (1952, 1963)		
Robinson (1963)		
Vrba (1975, 1976, 1980, 1981, 1985a, 1985b, 1988a, 1989, 1995)	open grassland with low bushcover	
Brain (1981b)		
Brain (1988a); Brain et al (1988)		
Shipman and Harris (1988)	STS M5: open habitats	
McKee (1991)	M5 included open grasslands in the near vicinity of the cave	
Watson (1993a)		
Reed (1997)		
Avery (2001)	STS M5E-O: environment consisted of a mosaic including riverine grassland and plains with open savannah woodland	
de Ruiter (2003)		
de Ruiter *et al.* (2008)	woodland, grassland and a nearby permanent water source	woodland, grassland and a nearby permanent water
de Ruiter *et al* . (2009)		woodland, grassland and a nearby permanent water

2.6.1 Reconstructions from 1938-1970

Early researchers reconstructed the environments of robust australopithecines as being similar to the present day (Broom, 1938, 1943; Cooke, 1963; Robison, 1963). The current environment is referred to as a false grassveld type known as the central variation of

the Bankenveld (Acocks, 1988). According to Acocks (1988), the summer includes rainfalls of approximately 700-750 mm per annum and cold winters that produce sour, ungrazable grassveld. In Broom's (1938, 1943) analyses of the faunal assemblage associated with the robust australopithecines, he interpreted the conditions at the time of these hominins as consisting of rocky outcroppings and plains. Later, Cooke (1963) concurred with Broom that the robust australopith deposits corresponded to the current climate and suggested that these hominins were open grassland dwellers. In Robinson's (1963) study on the adaptive radiation of the australopithecines, he described the changes in dentition and cognitive developments of *A. robustus* as being due to the expansion of open grassland habitats throughout the Plio-Pleistocene.

2.6.2 *Reconstructions from 1970-1997*

With the recovery and analysis of more faunal collections from the Bloubank Valley, previous paleoenvironment interpretations of *A. robustus* were modified. Vrba (1975, 1976, 1980, 1981, 1985a, 1985b, 1988a, 1989, 1995) played a pivotal role in the discussion of the paleoecology of the robust australopithecines. Vrba (1975) employed fossil bovid remains to assess the chronology and paleoecology of Sterkfontein, Swartkrans and Kromdraai. Specifically, she listed the minimum number of individuals (MNI) of bovids from the three sites. She combined the MNIs of Alcelaphini and Antilopini, as these tribes consist of animals that are indicative of open plains and grasslands. She calculated the proportional abundance of these bovids as ≥51% of the assemblage at each site. The high percentage of these bovid tribes at the sites during the time of the robust australopiths suggested that an open grassland environment predominated. Furthermore, the high percentage of

Alcelaphini+Antilopini suggested a corresponding low percentage of bush cover. Thus, Vrba (1975) agreed with the early researchers than an open grassland environment predominated at Sterkfontein, Swartkrans and Kromdraai (Vrba, 1975).

Using a different technique to reconstruct the past environments, Vrba (1980) again concluded that an open grassland environment existed during the time of the robust australopiths. This article focused on the importance of bovids as environmental indicators when reconstructing past environments using modern ecology and fossil faunal assemblages (Vrba, 1980). She illustrated the distribution of bovids by tribe and weight classes from Sterkfontein, Swartkrans Members 1 and 2 and Kromdraai A, again combining the proportions of Alcelaphini and Antilopini. She compared percentages of body size and species distribution from the fossil cave sites to percentages of bovid prey availability and predator sampling from the Kruger National Park (Vrba, 1980). She concluded that the fossil sites sampled consisted of very little bush cover, and were probably comparable to the current environmental conditions (Vrba, 1980; see Acocks, 1988).

While reanalyzing Kromdraai B faunal materials, Vrba (1981) reassigned a fossil identified as *Connochaetes* to an extinct buffalo species, and reclassified two bovid horn cores as reduncine, a bovid tribe highly dependent on water. She stated that she disregards her earlier paleoenvironmental reconstructions, and suggested that Kromdraai B consisted of more dense woodland, especially along the nearby Bloubank River, than previously proposed (Vrba, 1981: 19). This was the first time a significant woodland component had been mentioned in the reconstructions of a robust australopith site. In addition, she concluded that the Bloubank River was a permanent presence and that there was likely a higher average annual rainfall than current conditions (Vrba, 1981).

Brain's research also contributed greatly to the understanding of past environments associated with robust australopiths (1981b; 1988a; 1988b). The results of his study agreed with those of Vrba (1975, 1980, 1981) and other earlier researchers that an open, arid environment existed at the time of *A. robustus*. Brain (1981b) discussed the effect of temperature changes on African climates and environments. He demonstrated that the temperature rose at the end of the Miocene before falling approximately 3 Ma when the northern hemisphere ice cap developed. The subsequent alterations of glacial/interglacial cycles affected African faunas. These changes led to more open habitats and rapid evolution of fauna such as Alcelaphini (Brain 1981b). Brain (1981b) suggested that the appearance of the robust australopiths (and *Homo*) in South Africa was the result of an adaptation for surviving in the more arid environment.

Later, Vrba (1985a) concluded again that *A. robustus* was associated with an open, arid environment in her paper on the habitat preferences of early Hominidae, though she did not specifically emphasize a woodland component other than to say that they had decreased. In this study, she used phylogenetic and temporal distributions of bovid morphologies as indicators of paleoenvironments and paleoenvironmental change (Vrba, 1985a). She again employed the proportion of Alcelaphini+Antilopini as an indicator of the gross vegetation cover at hominin-bearing fossil sites to reach her conclusions (Vrba, 1985a). Approximately 2.5-2.0 Ma, environmental change was evident in the bovids across south and east Africa which led to an expansion of open grasslands and a decrease in woodlands and forests (Vrba, 1985a). This environmental fluctuation, according to Vrba (1985a: 67), "caused" changes in hominin evolution. She reiterated these conclusions in her 1985b paper. Again, Vrba (1985b)

stated that an environmental change occurred between 2.5-2.0 Ma which led to a more arid and open environment during the time of early *Homo* and *A. robustus* in South Africa.

Brain et al. (1988) and Brain (1988a) examined the fossil assemblages from Swartkrans Members 1, 2 and 3. They concluded that the three Members were similar in species composition and habitat indications. Furthermore, they concluded that the species composition and habitat indications were similar to that of present day. They depicted the habitat at Swartkrans as being open-country grassland with a nearby river lined with trees (Brain et al., 1988; Brain, 1988a).

Shipman and Harris (1988) assessed both eastern and southern African robust australopith sites. Specifically, Shipman and Harris (1988) evaluated the habitat preferences of *A. boisei* from East Africa and compared their results with habitat preferences developed for *A. robustus* sites. These researchers relied upon proportions of different bovid tribes in the fossil assemblages as a measure for reconstructing the environment. The study stated that the six localities analyzed in South Africa, including Sterkfontein Members 4, 5, Sterkfontein West Pit and Sterkfontein Dumps, and Swartkrans Members 1 and 2, were "quite open habitats" (Shipman and Harris, 1988: 374), though they did include a cautionary statement that some taphonomic and depositional issues may have played a role in their results. .

Using bovid data from sub-Saharan Africa, Vrba (1988a) discussed an environmental change which she called a turnover pulse of evolution of African mammals at ~2.5 Ma. This article presented a series of hypotheses concerning how environmental changes relate to biotic evolution. She concluded that the environment changed becoming colder, more arid and more vegetationally open, and that this change correlated with evolutionary events (Vrba, 1988a).

Vrba (1989) further discussed climactic changes and their relationship to evolutionary changes in hominid morphological and cultural evolution. Again, she concluded that there is a causal relationship between climactic change and hominin and bovid evolution; in particular, she emphasized how the shift to a cold, dry, and vegetationally open environment caused changes in hominin evolution and manifestations in culture (Vrba, 1989).

McKee (1991) investigated the paleoecology of Sterkfontein Member 4 and 5 by reviewing and interpreting recent paleoenvironmental work from these sites (McKee, 1991). While no robust hominins have been recovered from Member 4, McKee (1991) suggested that the environment was richer and more wooded than Sterkfontein Member 5, from which robust australopiths had been recovered. McKee's (1991) research indicated that the habitat of the robust australopithecines at Member 5 included open grasslands in the near vicinity of the cave, a result consistent with previous reconstructions (Vrba, 1975, 1980, 1981; Brain et al. 1988; Shipman and Harris, 1988; Vrba, 1988a, 1989).

When Watson (1993a) examined the identifiable fossils from Member 1 – Lower Bank, Member 2, Member 3 and Member 5 of Swartkrans, she concluded that the fauna were relatively consistent throughout the depositional history of the cave. Watson (1993a) stated that open savannah grazers dominated the assemblage, with a paucity of bovids preferring savannah woodland and rocky hillsides; these results were consistent with Brain et al. (1988). She reconstructed the past environment of these four members as predominately open savannah with a savannah woodland component lining the Bloubank River (Watson, 1993a). She also suggested that the Bloubank River in the past was larger, more permanent, and supported a riparian woodland environment, a result similar to Vrba (1981).

Vrba (1995) related the evolutionary history of bovids to human evolution. This paper supported previous conclusions (Vrba, 1988a; 1989) that climactic changes, particularly to a cooler more arid environment, caused evolutionary changes in fauna and humans (Vrba, 1995).

2.6.3 *Reconstructions from 1997-present*

The last section spans the time period from 1997-present. These results represent a turning point in the paleoenvironmental reconstructions of robust australopith sites, as these more recent reconstructions consistently include a significant woodland component and describe a more mosaic type environment. The greater environmental heterogeneity recognized in these later studies had a dramatic impact on the presumed habitat associations of the robust australopiths, and formed part of the impetus of the current study.

Investigating the relationship between hominin evolution and ecological change, Reed (1997) relied upon functional morphology and ecological structure analyses of mammalian assemblages associated with hominins in South and East Africa to reconstruct paleoenvironments. Her results differ from previous paleoenvironmental reconstructions in the amount of woodland she recognized. Reed (1997) analyzed Kromdraai B and Swartkrans Members 1-3 from South Africa, and concluded that a mosaic of habitats existed in the Bloubank Valley. Kromdraai B was an open grassland with patches of riparian woodland. Swartkrans Member 1 included an open habitat with a river that likely supported a woodland or forest as well as areas of edaphic grasslands. Swartkrans Member 2 fauna indicated a wooded grassland with nearby wetlands while Swartkrans Member 3 habitat indicators suggested an open grassland with a river or stream nearby supporting edaphic grasslands

(Reed, 1997). Reed suggested that *A. robustus* preferred an environment with a water component such as a river or stream. Due to this preference of nearby water, the gradual increase in arid and open environments and decrease in water sources in the early Pleistocene may have contributed to the extinction of this hominin (Reed, 1997). This study presented a more thorough and more diverse reconstruction of the environment at the robust sites than had previously been indicated.

Avery (2001) studied the vegetation and climate from Sterkfontein Member 5E-O (Oldowan Infill), Member 5E-A (early Acheulean), a small sample from Member 4 and Swartkrans Members 1-3, via micromammal remains. She concluded that an unusually low level of variation of species existed across the strata of these sites and a majority of the species inhabited both savannah and grassland (Avery, 2001). She stated that while all stratigraphic layers represented approximately the same vegetation elements, they all followed a vegetational succession. Furthermore, Avery (2001) concluded that all of the analyzed samples represent interglacial conditions. Based on her research, she suggested that the environment of these sites consisted of a mosaic including riverine grassland and plains with open savannah woodland (Avery, 2001). The Sterkfontein Valley is likely positioned on the "ecotone between Grassland and Savannah Biomes, and the arid and moist Savannah" (Avery, 2001: 130). The surrounding area would have consisted of a vegetational succession of riverine grassland, to plains with open savannah woodland (Avery, 2001). The results of this study overlap most closely with Reed's (1997) and provide a detailed reconstruction of the environment at these sites.

de Ruiter's (2003) results also suggest a more varied environment for the robust australopiths. He proposed reconstructed environments for *A. robustus* after examining,

revising and updating the faunal assemblage for Members 1-3 of Swartkrans. He provided fossil evidence of a predominance of grazers which suggested nearby open grasslands. de Ruiter (2003) also identified water dependent mammals and very large mammals such as elephant, giraffe and large bovids which indicated a large permanent water source and some extensive woodlands in the vicinity of this site.

de Ruiter et al. (2008) examined the habitat associations of *A. robustus*. In this study, they investigated indicators of habitat association of *A. robustus* preserved in the faunal assemblages at four robust hominin localities: Kromdraai A and B, Sterkfontein Member 5-Oldowan Infill, Cooper's Cave D and Swartkrans Members 1-3. Fluctuations in the abundance of *A. robustus* were documented and compared to fluctuations in a series of ecologically sensitive taxa. Animal communities from modern African nature reserves were compared to the paleocommunities associated with these robust australopithecines in order to determine the habitat association(s) of these hominins (de Ruiter et al., 2008). Habitat indicators associated with the robust australopiths suggested that these hominins were most similar to that of woodland adapted taxa. In addition, these researchers found a negative correlation between these hominins and grassland adapted taxa in their data set; this result means that as the proportion of grassland adapted taxa decreased, the proportions of hominins increased. Thus, while a majority of the paleoenvironments associated with the robust australopithecines have been reconstructed as open grassland, they do not necessarily indicate the habitat preferences of these hominins (de Ruiter et al., 2008).

According to de Ruiter et al. (2009), the faunal assemblage from Cooper's Cave D represented similar environmental conditions to Members 1-3 of Swartkrans (de Ruiter, 2003). These researchers described a faunal list consisting of ungulates indicative of

grassland habitats such as Alcelaphini, Antilopini, *Equus* and *Metridiochoerus*. de Ruiter et al. (2009) also report the presence of woodland-adapted animals, and water dependent animals requiring a nearby permanent water source, thus indicating a mosaic habitat structure.

2.7 Summary and conclusions

Early researchers broadly characterized the environment associated with the robust australopiths of South Africa as open grassland, open habitat and open country (Broom, 1938; 1943; Cooke, 1963; Robinson, 1963). The reconstructions made by these researchers were based largely on presence/absence of fauna in an assemblage. With the use of different techniques, the reconstructions became more specific; while a grassland environment still dominated, a woodland component was introduced that varied across the sites (Vrba, 1980, 1995; Brain, 1988a, 1988b; Brain et al., 1988; Watson, 1993a). More specific information about the environment was obtained; however, these studies c9ontinued to look at the environment in broad ecological categories such as grassland and woodland. Vrba (1980; 1985a) even combined species in the tribes Alcelaphini and Antilopini and discussed them as a being collectively indicative of grasslands. These studies were assessing the bovids with more detail but were not obtaining all of the ecological information out of them. Furthermore, the results of these studies were consistent and largely all came up with the same conclusion for the environment of the robust australopiths: open to lightly wooded grasslands.

The most recent research refined and enhanced the techniques for reconstructing past environments, and concluded that a mosaic of environments likely existed at the robust

australopithecine sites. These studies broadly range in the amount of woodland suggested at the sites (Reed, 1997; Avery, 2001; de Ruiter 2003; de Ruiter et al., 2008; 2009). These studies used techniques that tried to assess the faunal assemblages more critically, quantifiably and less subjectively (Reed, 1997; de Ruiter et al., 2008). These methods produced more refined and more objective environmental reconstructions.

The purpose of this research is to advance the field of paleoenvironmental reconstruction further and obtain the specific details of that environmental mosaic. This method relies on much more sophisticated identification techniques with associated probability statements that will dramatically reduce the amount of bias in fossil bovid classification. Furthermore, increased taxonomic control will allow for more fine-grained resolution of paleoenvironments within the reconstructed habitat mosaics. The result of this study will be an objective, replicable, in depth analysis of the environment associated with the robust australopiths.

CHAPTER III

DOCUMENTATION OF MODERN BOVID TEETH

3.1 Introduction and hypothesis

The purpose of this phase of the dissertation is to quantitatively assess bovid dental morphology in order to facilitate greater precision and reliability when identifying bovids recovered in the faunal assemblages associated with *A. robustus* in South Africa. Isolated bovid teeth are the most common type of fossil found in the cave infills of South Africa. Several recent studies have demonstrated that changes in the relative abundance of bovid taxa reflected in fossil assemblages are indicative of fluctuations in environmental conditions, as bovids appear to be particularly responsive to environmental changes (Bobe and Eck, 2001; Alemseged, 2003; de Ruiter et al., 2008). Thus, bovid teeth are important sources of information for reconstructing the paleoenvironments associated with the fossil hominins. Taxonomic identification of fossil bovid teeth, however, is often imprecise and subjective. Biasing factors such as age and degree of wear complicate identifications and often result in considerable overlap in the shape and size of teeth. To identify fossil bovid remains, researchers currently rely on fossil and modern comparative collections. Thus, faunal studies are susceptible to issues involving misidentified bovids which can lead to erroneous paleoenvironmental reconstructions, as well as to issues involving inter-observer error. Comparing faunal lists produced by different researchers can be problematical, owing to differences in experience, confidence of identifications and access to comparative materials. This issue can potentially confound paleoanthropologists' ability to generate accurate interpretations of faunal assemblages and paleoenvironments over space and time.

Thus, this phase includes developing a standardized system for accurately identifying bovid teeth using the occlusal morphology form (size and shape) of modern dentitions in order to distinguish between closely related bovid taxa. A standard method of identifying bovids would allow more accurate reconstructions and more precise interpretations about environmental change across space and time to be made.

The following hypothesis will be tested in this phase of the study: *H1: Modern bovid dentitions can be reliably distinguished as belonging to discrete species, separate from morphologically similar, closely related species, based on analysis of the outlines of occlusal surfaces of their teeth.* This hypothesis will test whether the outlines of occlusal surfaces of bovid teeth exhibit distinct, reliable shapes that can be used to differentiate one bovid species from another. If so, then an extant, isolated bovid tooth could be identified to the level of the species based on a comparison of its occlusal morphology with the occlusal morphology of a known species. If, however, the teeth from closely related bovid taxa cannot be reliably distinguished from each other, the taxonomic level (e.g. tribe, genus, species) of identification for an unknown tooth must be reconsidered. In this case, bovid tooth identification would involve classifying them only to the taxonomic level of genus or tribe and not species.

3.2 Materials, methods and Elliptical Fourier Function Analysis

3.2.1 Obtaining photographs of bovid teeth

Photographs of modern bovid teeth were obtained at the National Museum, Bloemfontein and the Transvaal Museum, Pretoria in June-August, 2008. These institutions have the largest collection of wild shot, non-zoo specimens in southern Africa. Table 3.1 lists

the species that were photographed and examined in this project. These species were chosen because they are the most abundant bovids in Africa today, and because they have dominated the African fauna for the past 3.5 Ma (Greenacre and Vrba, 1984; Bobe et al., 2002). Bovids were excluded from this list if they are not native to Africa or if they are not known to be in South African circa 2 Ma (e.g. the Boselaphini) (Gentry, 2010). Bovids such as gazelles and duikers were not included because so few complete, modern specimens exist in museum collections that they could not comprise a statistically viable reference sample.

Separate images were taken of the three molars from the upper and lower dentitions for each bovid specimen. Whenever possible, the left side of the jaw was photographed. When teeth from the right side were used, the images were flipped horizontally in Adobe Photoshop® in order to artificially remake them as left teeth. This process ensured that all teeth were analyzed in the exact same orientation.

A digital camera was positioned with a tripod directly above the occlusal surface of the tooth and leveled using a bubble level. Each cranium/mandible was situated so that the teeth were vertical and the occlusal surface could be clearly seen. The specimens were leveled and balanced using a bubble level, bean bags and props. A stand with an adjustable clamp held a scale bar which was leveled, and placed directly next to the tooth at the height of the occlusal surface. Each picture was taken using the self-timer in order to assure that the camera was still while taking the picture. Pictures were taken at 300 megapixels resolution.

Documentation of a minimum of 15 individuals per species (6 teeth per individual X 15 individuals = 90 images per species) is recommended to perform the shape analysis (Sokal and Rohlf, 1994). This study used 30 individuals per species when enough specimens were available. All bovid teeth were photographed regardless of their level of attrition, provided

that the teeth exhibited complete or mostly complete lobes; if a majority of the occlusal surface of the tooth could be distinguished, the tooth was included in this study.

Table 3.1 Extant bovid species analyzed in this study.

Tribe	**Species List**
Alcelaphini	*Connochaetes taurinus*
	Connochaetes gnou
	Alcelaphus buselaphus
	Damaliscus dorcas
Tragelaphini	*Taurotragus oryx*
	Tragelaphus strepsiceros
	Tragelaphus scriptus
Bovini	*Syncerus caffer*
Reduncini	*Redunca arundinum*
	Redunca fulvorufula
	Kobus leche
	Kobus ellipsiprymnus
Hippotragini	*Hippotragus niger*
	Hippotragus equinus
	Oryx gazella
Neotragini	*Raphicerus campestris*
	Oreotragus oreotragus
	Pelea capreolus
	Ourebia ourebi
Antilopini	*Antidorcas marsupialis*

3.2.2 Elliptical Fourier Function Analysis

The outlines of the occlusal surface of the bovid teeth were captured and analyzed using Elliptical Fourier Functional Analysis (EFFA) and an associated digitizing program,

MLmetrics (Lestrel, 1989). EFFA is a curve-fitting function particularly suited for the characterization of boundary outline data of complex, irregular morphologies. The use of EFFA allows for the actual quantification of the traits on the occlusal surface of the tooth and enables a multivariate statistical assessment of their distribution both intra- and inter-specifically. This 2-dimensional morphometric method has previously been applied to the study of other primate species and anatomical regions in order to differentiate between both intra- and inter-specific morphologies (Daegling and Jungers, 2000; Bailey and Lynch, 2005; Athreya, 2006; Schmittbuhl et al., 2007). It has been shown to be useful in defining detailed differences between ostensibly similar shapes, and is an established method for differentiating between taxa. This project is the first time EFFA has been applied towards the identification of bovid teeth.

Specifically, this approach involves documenting the coordinates of points around a 2-D closed contour and detecting the presence of repeated elements in sets of data, also known as periodicity. In EFFA, a series consists of these periodic elements, or sinusoidal wave forms, which are the trigonometric relations sine and cosine (Lestrel, 1974). The underlying principle of EFFA is that the form can be described by a trigonometric curve. The sum of the sine and cosine terms in the series makes up a harmonic, or a quantitative descriptor of the form. As the terms in the series increase, the difference, or residual, between forms decreases. The series can be shown to converge onto any shape under consideration as the terms in the series increases. How well the terms fit the data depends on the number of terms in the series and how irregular the shape under consideration is. Essentially, EFFA is measuring the amount of distortion between an original circle and the object being measured. In the end, the data is converted from the spatial domain to the frequency domain.

Shape comparisons in EFFA are made by analyzing the harmonics or the amplitudes of the harmonics. The amplitudes are the maximum height of the sine wave measured from the x-axis (Lestrel, 1974). These measurements are orthogonal, non-cumulative and independent of each other. Thus, these features allow a term by term analysis of the shape in question. Either the harmonics or the amplitudes can then be used to identify shape and/or compare shapes using multivariate statistics. This study relies upon the amplitudes of the bovid teeth outlines to analyze and compare the teeth across species.

The digitization process for this project involves creating two-dimensional bounded outline tracings of the occlusal surface of the same tooth type (e.g. mandibular first molar) from ≥15 individuals of a species. This step relies on the program MLmetrics, a virtual digitizer developed to function specifically with EFF23 v.4 (Wolfe et al., 1999). Each picture is opened in the program and a line grid is made on the tooth by defining the left and right most point of the tooth and then the top and bottom most points. This step creates a square around the tooth and a grid whose middle lines cross directly through the center of the tooth. After clicking on where these lines cross, a standardized, rectangular grid is placed on the image using that center of the tooth as a reference. The teeth are digitized according to a template ensuring that each tooth has the same number of points, and that the points are placed in homologous positions. Sixty points are laid down around the outline of the tooth using the grid and template for orientation. The first point, point 1, is always the upper most, left most spot where the grid crosses the tooth (Figure 3.1). The outline will include important diagnostic features of the tooth including ribs and styles. MLmetrics produces X,Y coordinates for each of the sixty points on the tooth. These points are then exported and used in EFFA.

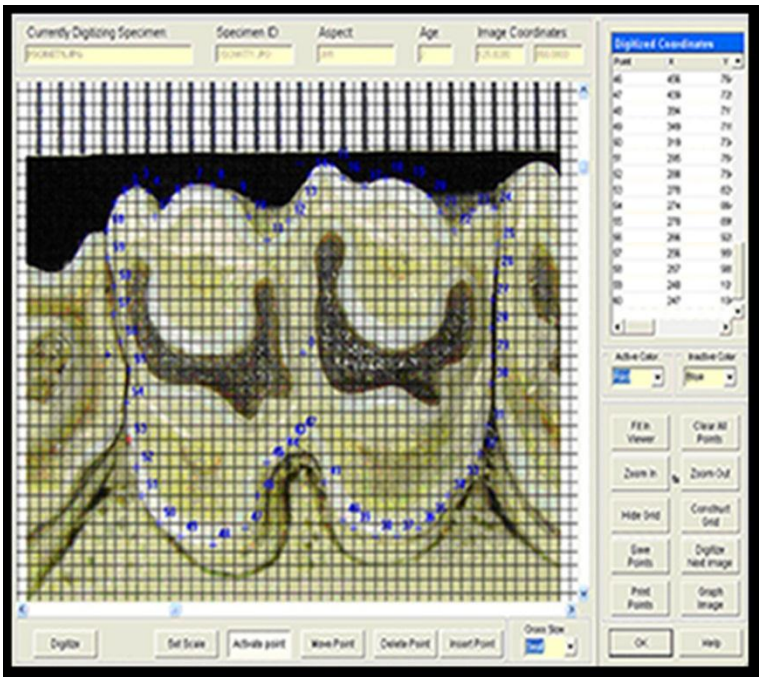


Figure 3.1 Example picture of a digitized tooth demonstrating the grid and points around the tooth. This screen shot was taken in the digitizing program MLmetrics.

The points of the image outline are imported into EFF23 v. 4 where the harmonics and amplitudes are generated (Wolfe et al., 1999). The amplitudes of the harmonic that are calculated for each tooth type were compared across species in the same tribe using JMP statistical software. For example, only the M^3 teeth from species in the tribe Alcelaphini were compared with each other, and the M^3 teeth from species in the tribe Neotragini, etc. First, a multivariate analysis of variance (MANOVA) is calculated and a Wilks' lambda test statistic is reported demonstrating whether there are significant shape differences of a tooth type (i.e. M_2) between the means of each bovid species within a tribe. Next, principal component analyses on covariances (PCA) are calculated. This test converts and organizes the data from a set of potentially correlated variables into a set of uncorrelated and correlated variables so that the maximum differences between the groups can be seen (Jolliffe, 2002). The first

principal component reveals the maximum amount of variability between the groups, and each subsequent component accounts for the remaining variability until little or no variability exists in the components i.e. the groups are very similar for those components. The principal component analysis on covariance, as opposed to correlation, is appropriate to use due to the fact that the data are in the same scale, and all of the data consist of the amplitudes of the harmonics (Jolliffe, 2002). Jolliffe (2002) states that standardizing data already in the same scale in order to make a correlation matrix is unnecessary. Additionally, PCA of covariance is more sensitive to detecting differences between the variances in similar data.

The principal components (PCs) were used to perform a linear discriminant function analysis (DFA). Linear DFA calculates the means of each of the original variables within a group and finds whether the groups differ with regard to the means of the variables. The analysis deciphers which variables maximize the differences between groups, relative to the within-group variation (Campbell, 1984). In order to predict group membership, DFA compares the variables of that specimen to the group means and calculates to which group the specimen best aligns. In this instance, DFA was used to investigate the relationships between *a priori* taxonomic groups of bovids.

In addition to predicting group membership, DFA produces posterior probability values. These values indicate the probability that an individual belongs to the group it was predicted. This probability is based on the Mahalanobis distance of the specimen to the group centroid (Albrecht, 1992). The higher the posterior probability, the more likely it is that the specimen belongs to that reference group. The posterior probabilities are reported for all of the extant bovid data.

DFA results include a discriminant plot. While only illustrated in 2-D (See Figure 3.2 for an example), this plot shows where each bovid specimen is situated in relation to each other in multivariate data space (Albrecht, 1992). Each group has an associated ellipse on the graphs which represents its 95% confidence ellipse, or confidence interval. This ellipse represents a range of variables around the mean where the "true" (group) mean is located, e.g. 95% of the time, the true mean is located within the circle (Snedecor and Cochran, 1989). Accordingly, the size of the circle corresponds to a 95% confidence limit for the mean. A large ellipse is indicative of a wide range of variation within a group while a small ellipse denotes a more restricted range of variation around the mean. Groups whose variables overlap or are very similar will have confidence ellipses closer together than groups that differ greatly from each other. Overlapping circles suggest a lot of overlap between the two groups though it is important to keep in mind that the graph is only in 2-D and that the circles may appear differently in 3-D space. Each ellipse has a centroid. This centroid is the mean of the entire sample.

In order to document the modern bovid teeth, thirty PCs were used. This number was chosen because the number of *a priori* groups that classified correctly increased with the addition of principal components up to 30 (Figure 3.2). Figure 3.2 demonstrates that 30 principal components appear to provide some contribution towards differentiating between the species. While the eigenvalues of the upper principal components are small and do not account for as much of the variation as the first and second principal components, they do provide important information for species recognition. Thirty principal components were not used when the sample sizes were less than thirty (Jackson, 1991). In these instances, less principal components were used than samples so as not to violate any statistical principles.

Since the purpose of this phase of the project is to correctly classify the known groups, 30 principal components were used. The following process was repeated for all of the teeth within the same tribe: all of the amplitudes of the same type of tooth from species within the same tribe are compiled into a database, MANOVA and PCA are run on the amplitudes and group membership is predicted using DFA.

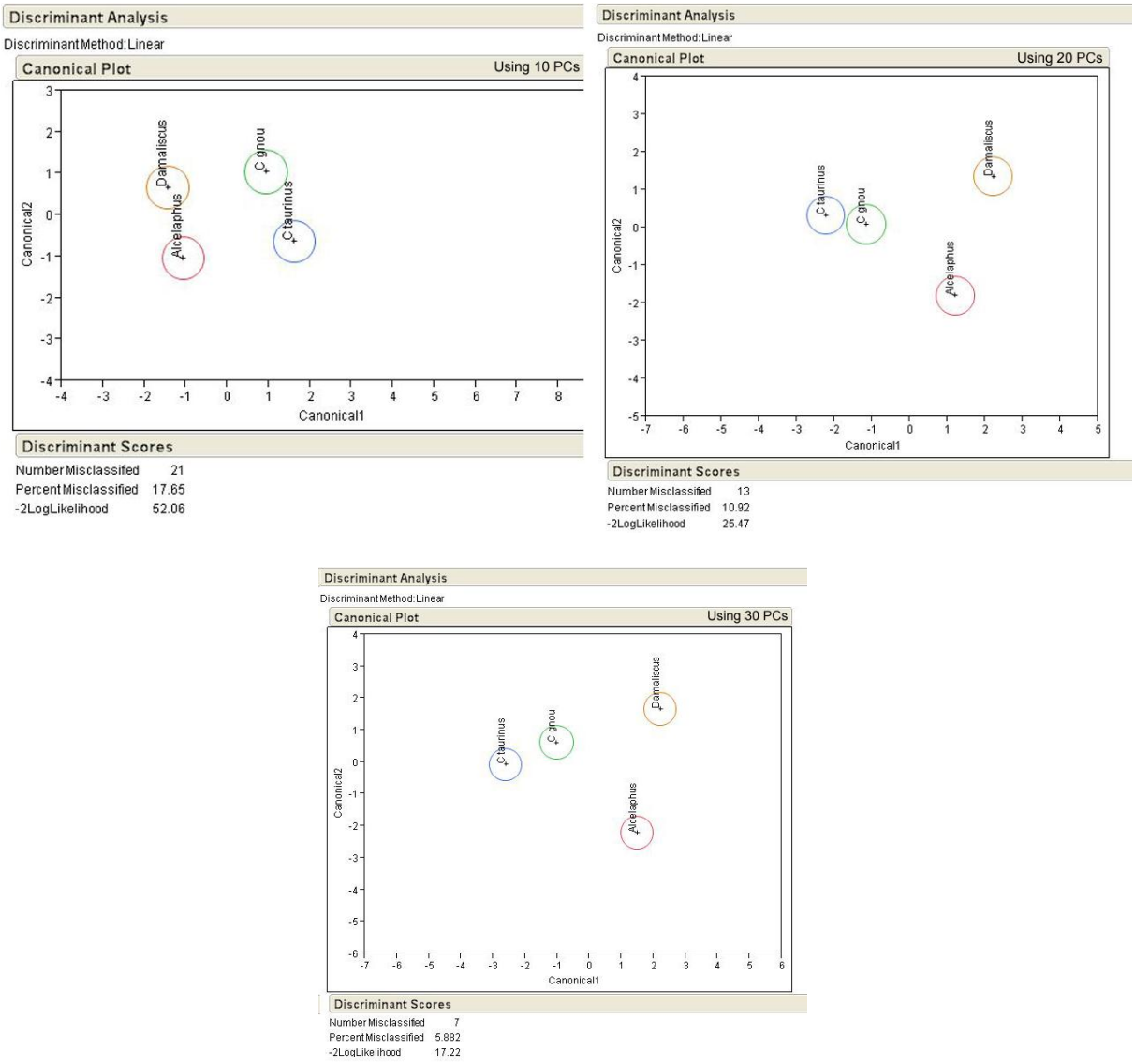


Figure 3.2 Graphs showing that the percentage of individuals classified correctly increased as the number of principal components increased.

3.2.3 Pilot study

In 2008, the protocol for taking pictures was finalized, and the amount of time it took to set up equipment, orient the specimen, obtain the image and replace the specimen was documented. Using a sample of the images obtained, several different morphometric programs were tested and a pilot study was performed to test the methodology and statistical approach. A sample of three species from the tribe Alcelaphini were chosen for the pilot study because of the noteworthy overlap in shape and size of the teeth within the tribe and because this tribe is so prolific in South African fossil assemblages. The three species included *Damaliscus dorcas*, *Alcelaphus buselaphus* and *Connochaetes gnou*.

First, I experimented with different morphometric programs, including a landmark based approach, namely thin-plate spline (TPS) and the above-mentioned outline based approach, EFFA (Rohlf and Marcus, 1993). While both EFFA and TPS are able to differentiate between closely-related bovid taxa, EFFA was chosen because it is designed specifically to analyze outlines of biological data. In addition, Baylac and Frieβ (2005) performed a morphometric analysis on cranial shape that demonstrated how both TPS and EFFA yielded comparable results.

Next, the pilot study allowed me to establish my methodological protocol and statistics. The study involved digitizing the M^3, M^2 and M^1 teeth of the three aforementioned species (30 individuals/per species). I performed a MANOVA and PCA on the amplitudes of the digitized teeth and calculated group membership using DFA. Both the MANOVA and DFA demonstrated fundamental shape differences between the three groups. I also tested whether using the PCs or using the raw amplitude data for the DFA yielded better results. The groups classified correctly at a higher rate when the PCs were used with the DFA. Thus,

30 principal components were used for the remaining samples. When the discriminant scores were used to calculate group membership, the molars classified correctly 86+% of the time: M^3 93% correct, M^2 93% and M^1 95% (Table 3.2). The M^1 of *Damaliscus* classified the best at 100% while the M^2 of *Alcelaphus* classified at 86.7%. This pilot study demonstrated the viability of using this approach for identifying closely related bovids.

Table 3.2 Results of the discriminant function analysis on the pilot study material.

	M^3	M^2	M^1
Alcelaphini			
Damaliscus	**96.67%**	**96.67%**	**100%**
Alcelaphus	**93.3%**	**86.7%?**	**96.77%**
C. gnou	**90%**	**96.67%**	**89.28%**
Total correct	**93%**	**93%**	**95%**

The goal of this phase of the dissertation is to use the shape of the surface of the tooth to differentiate between closely related bovids, which the pilot study demonstrated was successful. The *Alcelaphus* M^2 classified at the lowest rate, 86.7%; this rate was used as a guide for determining an *a priori* classification rate for the dissertation. Thus, this study will consider an *a priori* reliable rate of classification to be 85%. If the modern bovids continue to classify correctly ≥85% of the time, then the results will be considered reliable enough to apply this methodology to fossil specimens. While a classification rate of ≥85% is considered to be biologically informative (see Reyment et al., 1984; Bailey and Lynch, 2005; Cucchi et al., 2008), a complete profile of probabilities including posterior and typicality probabilities, by species and specimen, will be performed for each classification study. Thus, every intra- and inter-specific classification test will be judged individually on its empirical merits.

3.2.4 Age and attrition test

In order for the occlusal surface of a tooth to be a reliable indicator of a bovid species in this study, its shape must remain consistent throughout the life span of the animal. Age and attrition could potentially cause changes in the morphology of a tooth throughout the course of the animal's life. For example, bovid teeth are hyposodont, or high crowned; while the teeth may appear to maintain the same occlusal shape throughout the height of the tooth, the possibility exists that shape change is occurring. Another example involves the profile of the tooth, as discussed in Chapter II. M^1 and M_1 molars are "V" shaped in profile. This profile shape suggests that there is size change in the tooth; accordingly, the occlusal shape of the tooth may change as well. Thus, it is important to ensure that the outline of the tooth remains stable regardless of age and attrition, in order to be considered indicative of that species and to reliably differentiate between closely related bovids. This test assesses intra-tooth variation by taking computed tomography (CT) scans of a sample of bovid teeth (see Adams, 2005, for a similar study using Suidae teeth).

Specific increments of CT scan slices from the same tooth were digitized and analyzed using MLmetrics and EFFA. The amplitudes of those scans were placed as "unknowns" in a dataset of known, modern teeth and principal components were obtained. During the calculation of the principal components, the CT scans were excluded; this method allows the fossils to have PCs without introducing bias by including them. A linear DFA was performed using the principal components to test whether each CT scan, or "wear stage" classified correctly when compared with the set of known teeth. These procedures will ensure that the occlusal outline defined for each species does not change significantly throughout the

life of the animal in various stages of attrition and the occlusal outline still groups with members of its species.

In November 2008, permission was received from The Field Museum in Chicago to CT scan a selection of bovid specimens at the Mercy Hospital and Medical Center. Only a limited number of specimens were allowed to leave the Field Museum; time was also constrained on the CT scanner. Thus, a sample of bovids was carefully chosen to encompass 4 different tribes: Alcelaphini, Antilopini, Tragelaphini and Reduncini (Table 3.1). These four tribes were chosen because they encompass a wide range of variation in shape and relative hypsodonty, and are common in the South African fossil assemblages. Also, using different tribes eliminates bias in the results at the tribe level. The species were also chosen specifically to encompass a lot of variation and what was available in the Museum collection. Maxillary and mandibular molars were digitized to avoid any biasing in the tooth type. Essentially, the sample of species and tooth type analyzed in this study were chosen to maximize the chance of observing a change in the shape of a tooth throughout an animal's life. The specimens were scanned using a Phillips Brilliance 64 CT Scanner. Images were taken at 0.67 mm intervals. Every third image was digitized in this study, approximately every 2 mm., starting from the first image where the entire occlusal surface was in view and ending when the entire occlusal surface could no longer be discerned. The scans were digitized using MLmetrics and EFFA and PCA and DFA were run on the data. Table 3.3 illustrates the results of this study.

Table 3.3. Percentage of CT scans of teeth that classified correctly using DFA.

Tribe	Species	Tooth Type	Percentage
Alcelaphini	*Connochaetes gnou* 34550	UM1	100
		UM2	100
		UM3	85
	Connochaetes gnou 34484	LM2	100
	Connochaetes taurinus 34560	LM3	90
Antilopini	*Antidorcas marsupialis* 34482	UM1	100
		UM2	100
		UM3	100
		LM1	100
		LM2	100
		LM3	100
Tragelaphini	*Tragelaphus scriptus* 38159	UM2	100
	Tragelaphus strepsiceros 34430	LM2	100
Reduncini	*Redunca arundinum* 7233	UM2	100

As seen in Table 3.3, all of the individuals in the sample classified above the *a priori* rate of 85%. The results of this age and attrition test suggest that the shape of the teeth tested in this sample does not change significantly enough during dental attrition to impede the species identification of that tooth. The lack of intra-tooth variation suggests that a sample of bovid teeth has a similar occlusal outline shape regardless of its level of ontogenetic development. Furthermore, the results of this test indicate that a sample of bovid teeth at various wear stages is an appropriate sample for testing if the occlusal outline of a tooth can be distinguished from other closely related bovid species.

3.3 Results of analyses of the modern bovid teeth by tribe

3.3.1 Alcelaphini

Four species of Alcelaphini were tested: *Damaliscus dorcas, Alcelaphus buselaphus*, *Connochaetes gnou* and *Connochaetes taurinus*. The results of the MANOVA suggest that the means of each tooth type differ between the species; the Wilks' lambda results were significant, $p<0.001$, between the species for all of the teeth. These results indicate that true differences in the means of the form exist between the species when analyzing outlines of their occlusal surfaces. These results are supported by the DFA results highlighted in Table 3.4 and Figures 3.3-3.8. Table 3.4 illustrates the percentage of teeth that classified correctly per species, per tooth. DFA correctly classified Alcelaphini ≥ 86.7% of the time. The M^3 teeth classified at the lowest percentage, while the M_2 classified with the highest percentage (Table 3.4). The DFA demonstrates that the occlusal surface form of a bovid tooth is indicative of a species. In fact, the results show that the occlusal surface form of a bovid tooth is so particular to a species that even when other closely related, morphologically similar bovid teeth are in the database, the teeth classify correctly at a high rate. Thus, teeth from the same bovid species are more similar in shape and size than teeth from closely related bovids.

Figures 3.3-3.8 illustrate the graphical results of the DFA for each tooth type (i.e. upper and lower M1, M2, and M3). The centroids, or the means of the groups, are plotted in the 95% confidence ellipses. The distance between the circles demonstrates that fundamental form differences exist between the groups based on the fact that no overlap exists in the confidence ellipses between these groups.

These results support Hypothesis H1; the Alcelaphini classified at a rate higher than the previously established 85%. Thus, modern bovid dentitions from the tribe Alcelaphini were reliably distinguished as discrete species based on the outlines of the occlusal surface of their teeth, when compared with closely related bovid species. The results of these analyses also suggest that this approach is appropriate to test on unknowns such as fossils in the faunal assemblage.

Table 3.4 Percentage of Alcelaphini teeth that classified correctly in the discriminant function analysis.

Alcelaphini	M^3	M^2	M^1	M_3	M_2	M_1
Damaliscus	**96.67%**	**96.67%**	**100%**	**96.77%**	**93.33%**	**100%**
Alcelaphus	**93.3%**	**86.7%**	**96.77%**	**96.77%**	**96.55%**	**95.45%**
C. gnou	**90%**	**96.67%**	**89.28%**	**96.67%**	**96.67%**	**93.33%**
C. taurinus	**90%**	**96.77%**	**96.55%**	**96%**	**100%**	**95.83%**

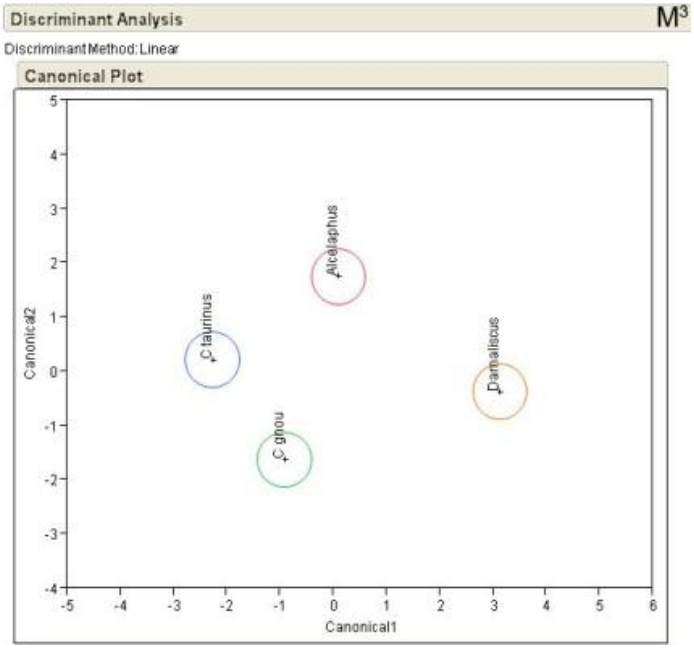


Figure 3.3 DFA results for the M^3 teeth in the tribe Alcelaphini.

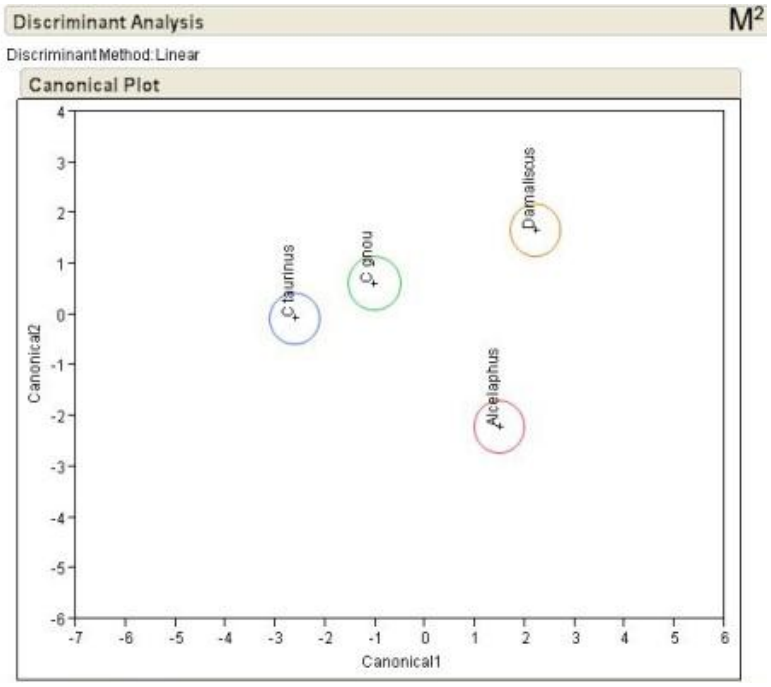


Figure 3.4 DFA results for the M^2 teeth in the tribe Alcelaphini.

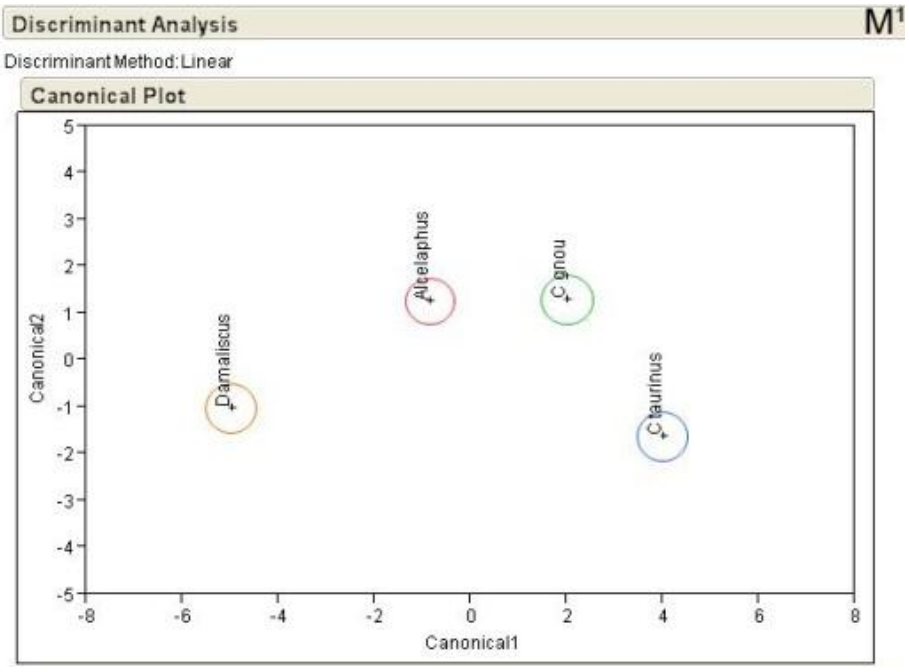


Figure 3.5 DFA results for the M^1 teeth in the tribe Alcelaphini.

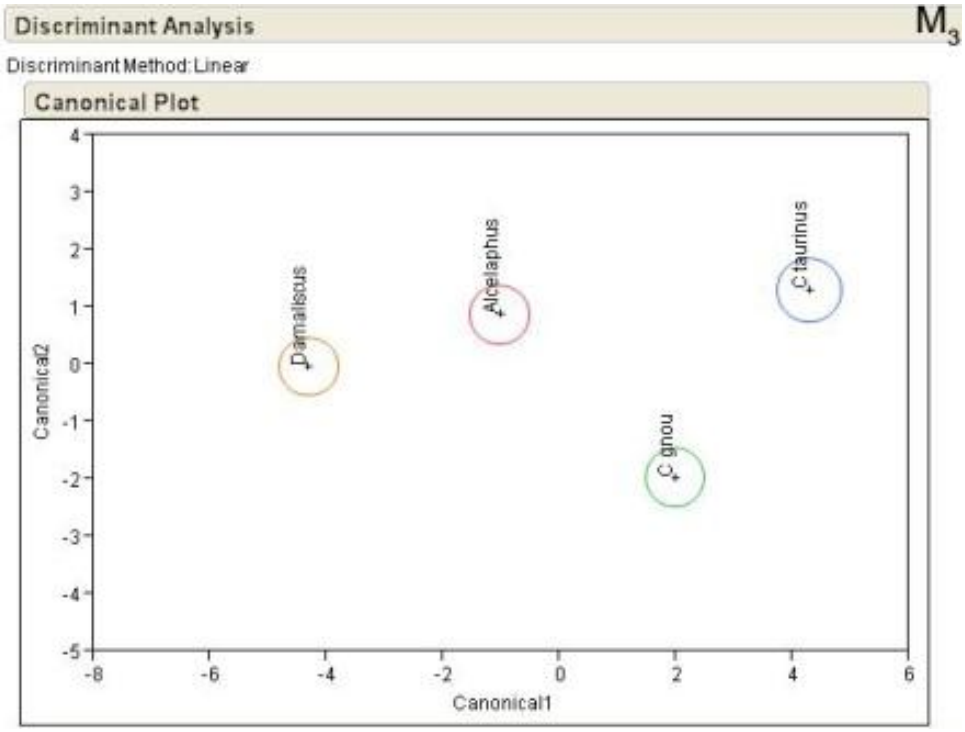


Figure 3.6 DFA results for the M_3 teeth in the tribe Alcelaphini.

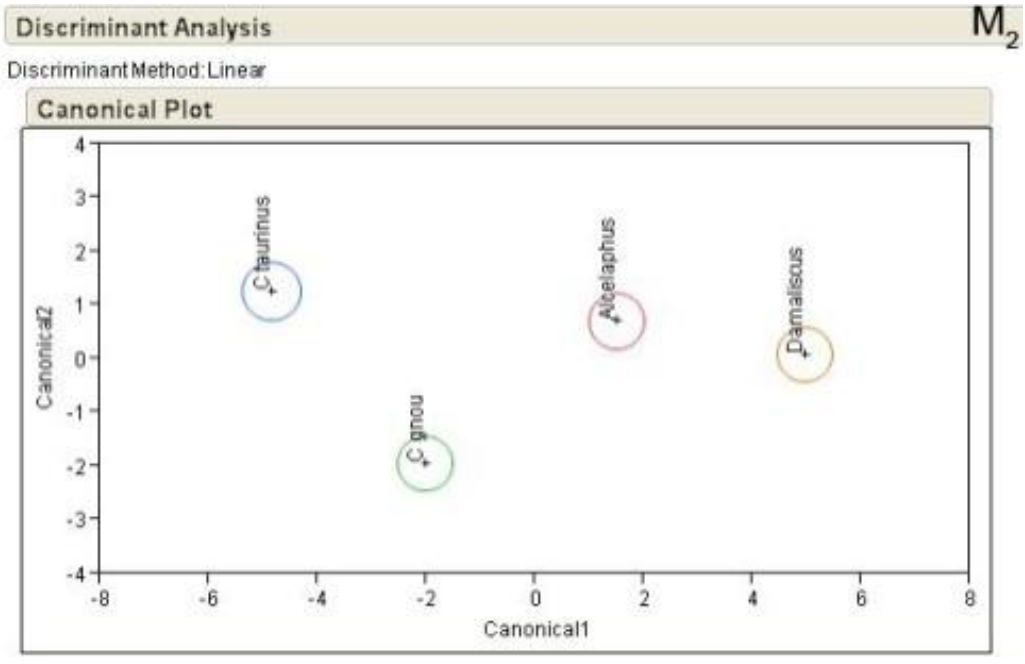


Figure 3.7 DFA results for the M_2 teeth in the tribe Alcelaphini.

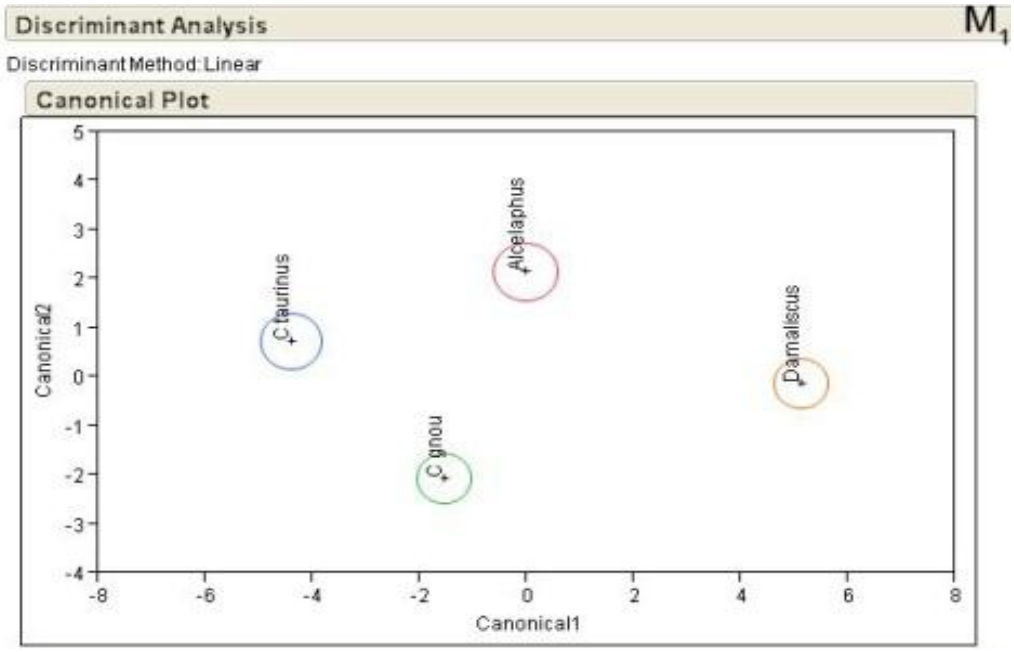


Figure 3.8 DFA results for the M_1 teeth in the tribe Alcelaphini.

3.3.2 Tragelaphini

Three Tragelaphini species were analyzed in this study, including *Taurotragus oryx*, *Tragelaphus strepsiceros* and *Tragelaphus scriptus*. According to the MANOVA, the Wilks' lambda yielded significant results for all of the teeth, yielding a $p<0.001$ for each tooth type. This result shows that the means of the shape and size of the each tooth is different than the shape and size of teeth of closely related bovid species in the same tribe.

Differences between the species can also be seen in the results of the DFA (Table 3.5 and Figures 3.9-3.14). DFA classified the teeth correctly at a high percentage with no classifications below 85%. In fact, only two of the samples did not classify correctly 100% of the time. These results indicate that the form of occlusal surface outline of tooth within the tribe Tragelaphini can reliably be distinguished at the species level.

Tragelaphini teeth separate into discrete groups based on the shape and size of the occlusal surface of their teeth (Figures 3.9-3.14). These three species have large distances between the centroids in all of the Figures. In particular, the centroids of the mandibular molars are widely disparate from each other (Figures 3.12-3.14). These illustrations highlight the substantial differences between the occlusal surface outlines of these three Tragelaphini species.

The results of the MANOVA, Wilks' lambda and DFA demonstrate that species in the tribe Tragelaphini can be reliably differentiated as separate species based on the outlines of the occlusal surface of their teeth, even when compared with closely related bovid species. All of the teeth in this tribe classified at a rate higher than the *a priori* classification rate of 85%. Thus, these results support Hypothesis H1. These results, in accordance with the Alcelaphini conclusions, support the use of this approach on fossils from faunal assemblages.

Table 3.5 Percentage of Tragelaphini teeth that classified correctly in the discriminant function analysis.

Tragelaphini	M^3	M^2	M^1	M_3	M_2	M_1
T. oryx	**96.50%**	**100%**	**100%**	**100%**	**100%**	**100%**
Tr. strep	**100%**	**93.54%**	**100%**	**100%**	**100%**	**100%**
Tr. scriptus	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**

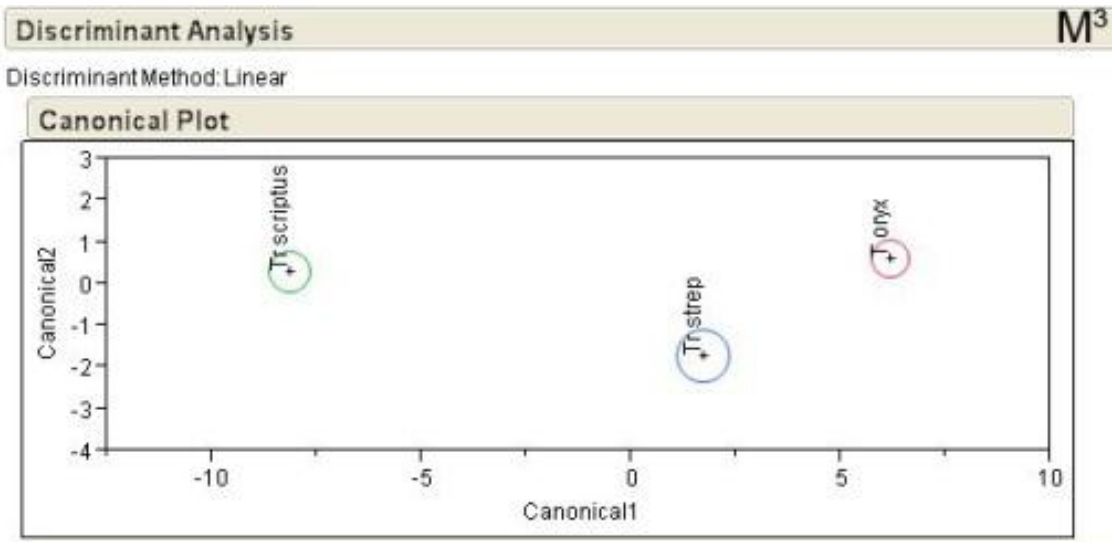


Figure 3.9 DFA results for the M^3 teeth in the tribe Tragelaphini.

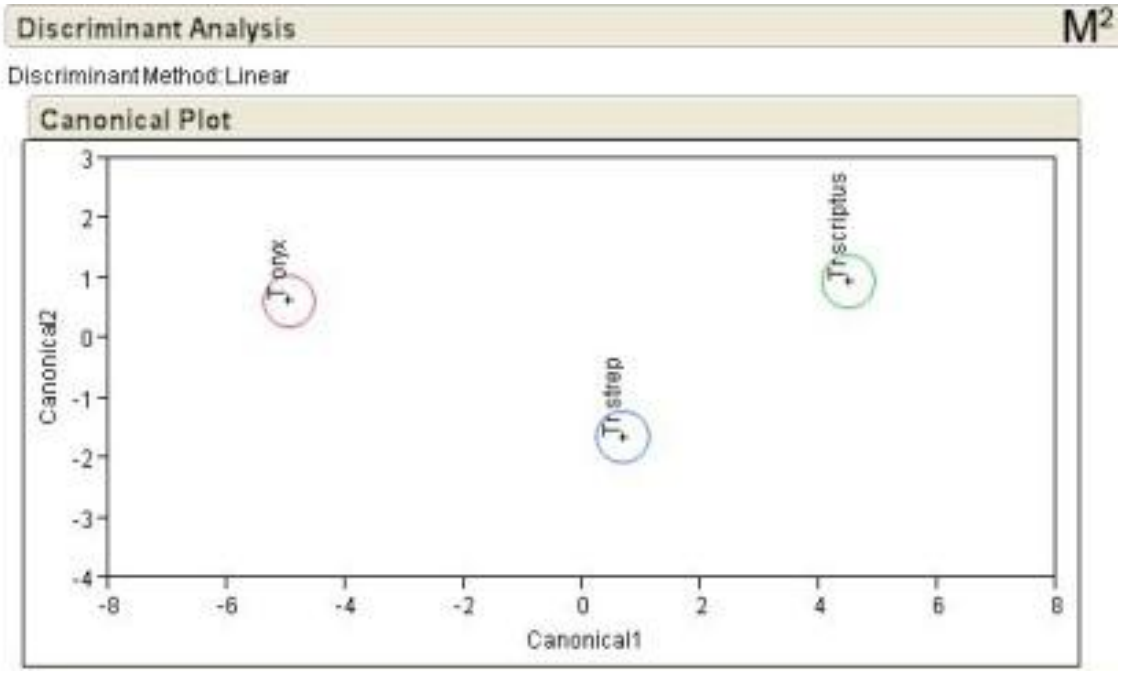


Figure 3.10 DFA results for the M^2 teeth in the tribe Tragelaphini.

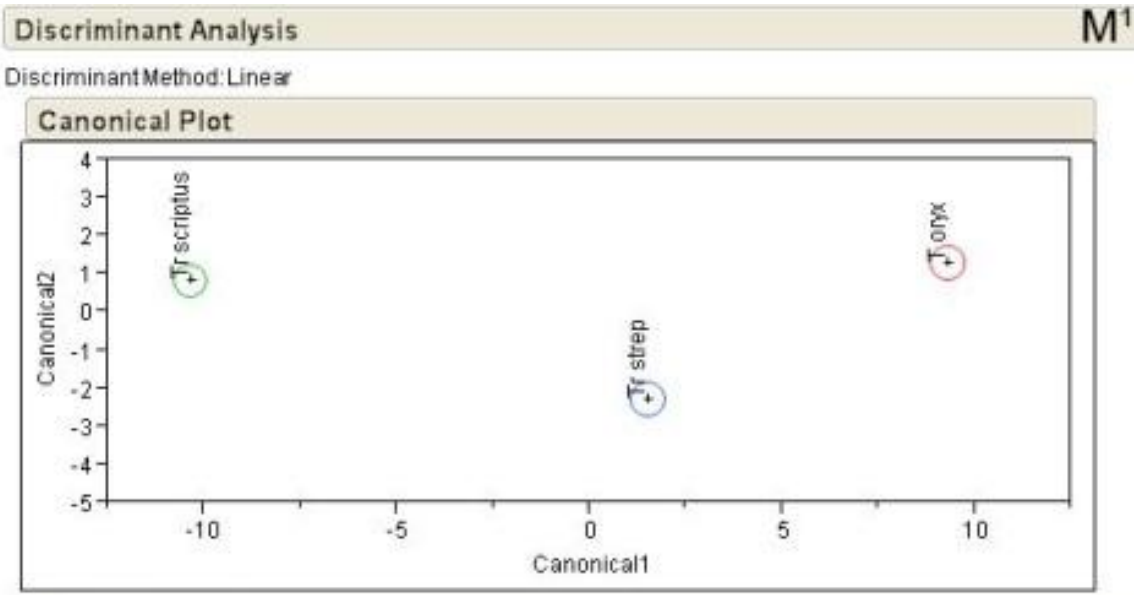


Figure 3.11 DFA results for the M^1 teeth in the tribe Tragelaphini.

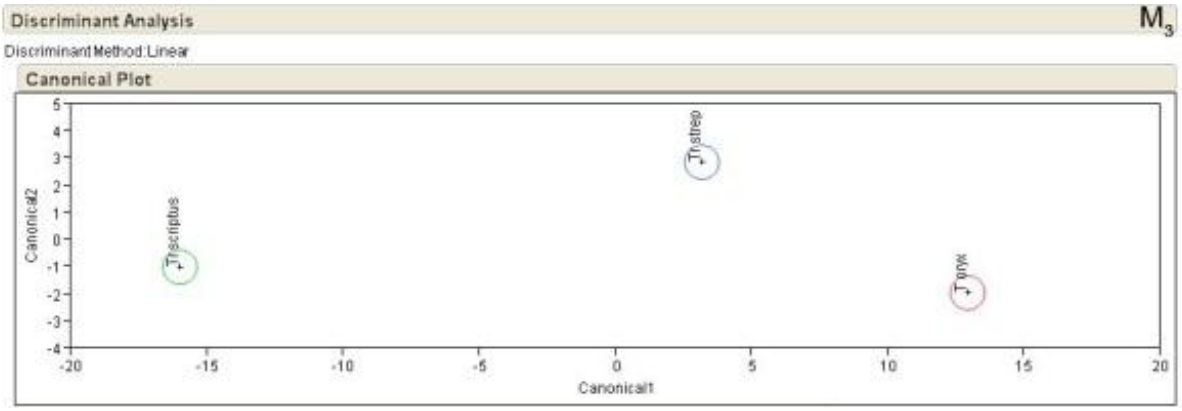


Figure 3.12 DFA results for the M_3 teeth in the tribe Tragelaphini.

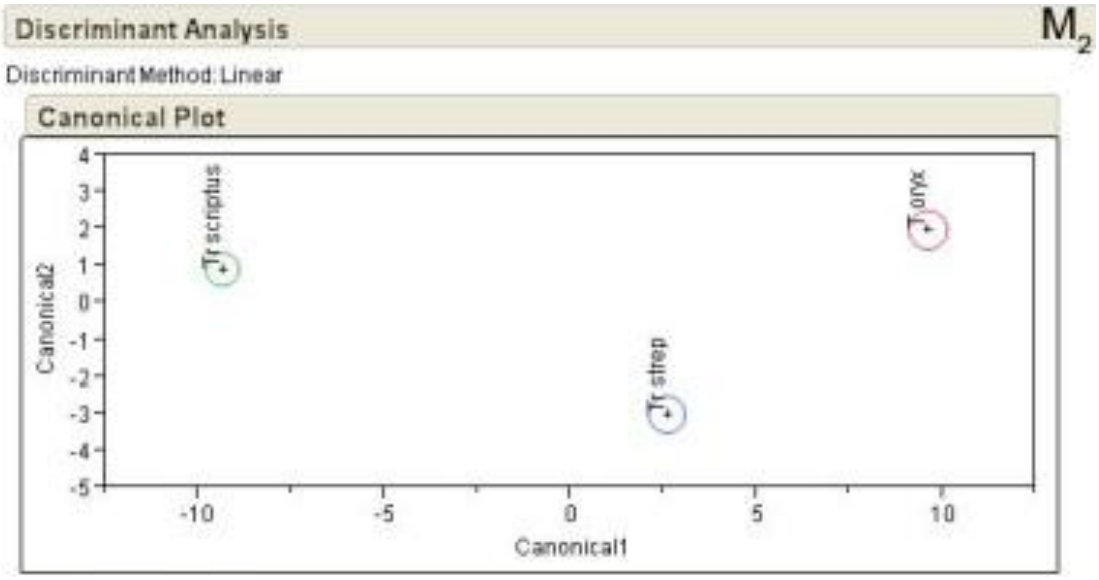


Figure 3.13 DFA results for the M_2 teeth in the tribe Tragelaphini.

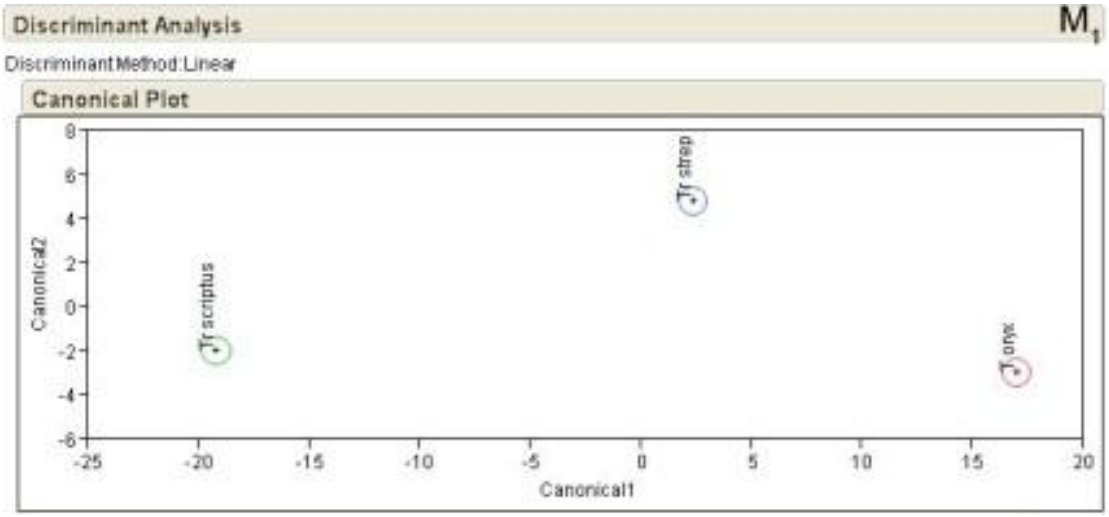


Figure 3.14 DFA results for the M_1 teeth in the tribe Tragelaphini.

3.3.3 Bovini

Only one species in the tribe Bovini was analyzed, *Syncerus caffer*. This species is the only living, wild representative of the Bovini in southern Africa, thus it is the only extant one

that might be found in the fossil assemblage at robust australopith sites. Because it has no modern congeners, the teeth of *Syncerus caffer* were compared with the three Tragelaphini species, as these tribes are evolutionarily more closely related to each other than to any other bovid tribe (Gentry, 2010). The Wilks' lambda from the MANOVA analysis yielded significant results for all of the teeth in this sample; the means of each tooth per species is significantly different from each other with a p value of <0.001. The MANOVA results are supported by the DFA results highlighted in Table 3.6 and Figures 3.15-3.20.

Each Bovini molar classified correctly 100% of the time when the DFA was calculated (Table 3.6). These results reveal that clear form differences exist between the occlusal surface outlines of *Syncerus* and Tragelaphini. Having a clear separation from Tragelaphini is important for the classification of unknown fossils. If a *Syncerus* exists in the fossil record, it will clearly classify as a *Syncerus* with no chance to misclassify as a Tragelaphini, despite the close evolutionary relationship.

Figures 3.15-3.20 show the graphical results of the DFA. Each Figure represents the results of a different molar. In each graph, *S. caffer* is a clear outlier from the Tragelaphini. This distinction is evident by the large distance between the *S. caffer* centroid and the centroid of each of the Tragelaphini species.

The results of this analysis support Hypothesis H1. The occlusal surface outlines of the teeth of *Syncerus caffer* are reliably identified as a discrete species, when compared with the outlines of closely related bovids. These results support the application of this method towards unknown Bovini fossils in the fossil record.

Table 3.6 Percentage of Bovini teeth that classified correctly in the discriminant function analysis.

Bovini	M^3	M^2	M^1	M_3	M_2	M_1
S. caffer	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**

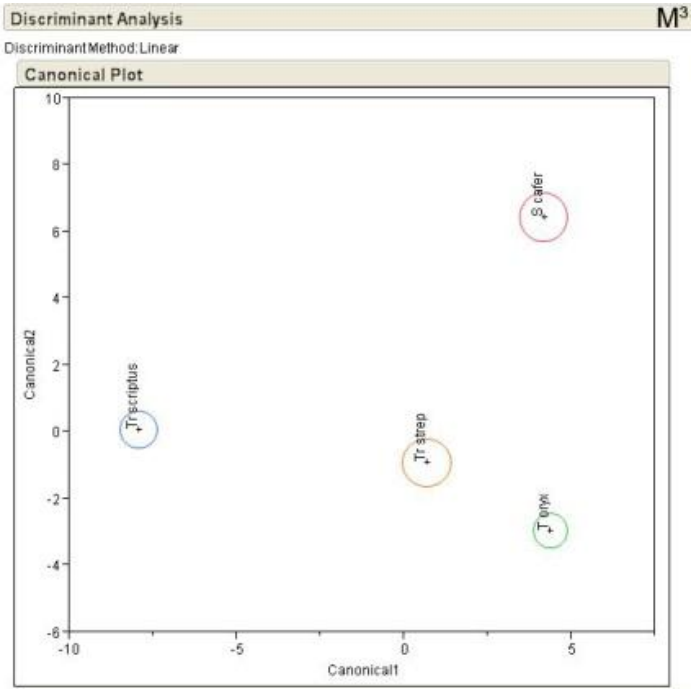


Figure 3.15 DFA results for the M^3 teeth in the tribe Bovini.

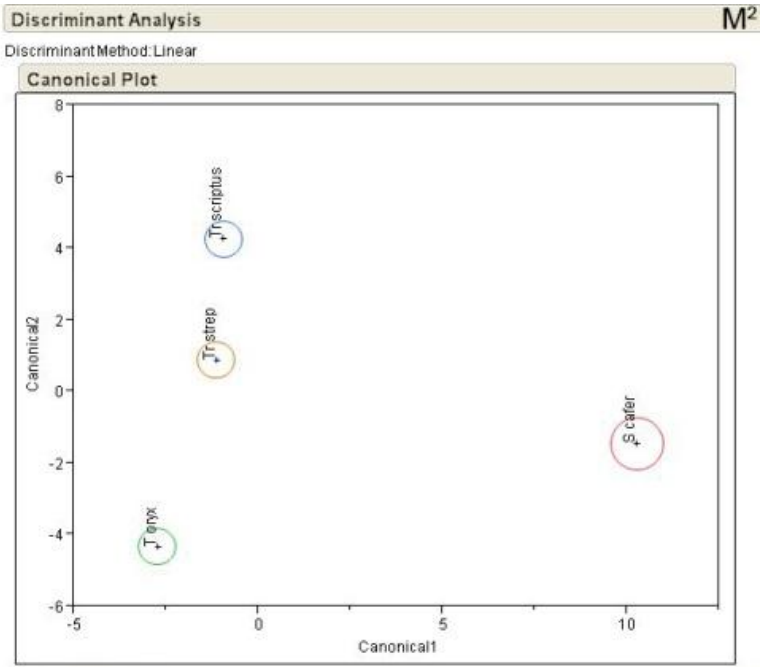


Figure 3.16 DFA results for the M^2 teeth in the tribe Bovini.

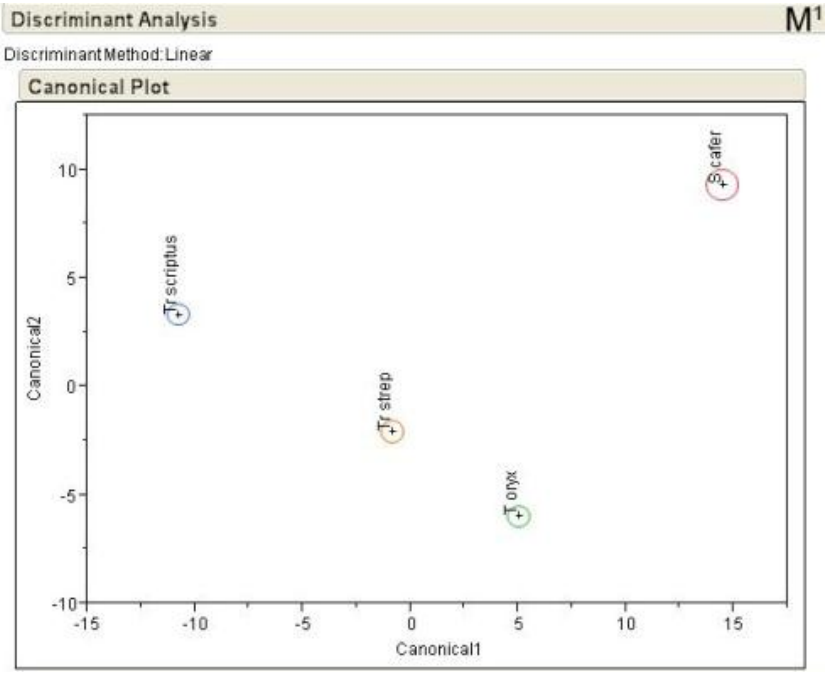


Figure 3.17 DFA results for the M^1 teeth in the tribe Bovini.

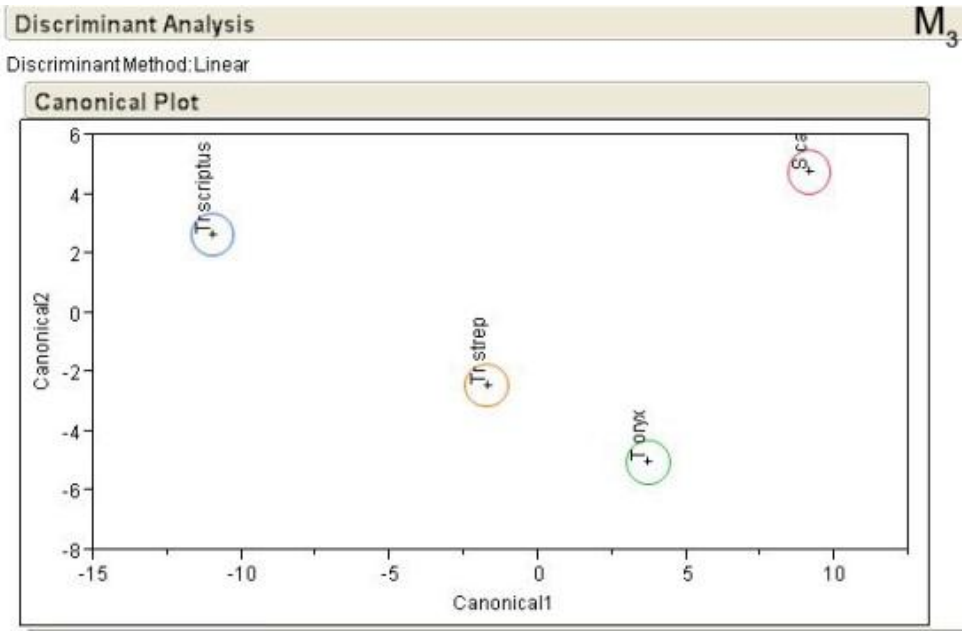


Figure 3.18 DFA results for the M_3 teeth in the tribe Bovini.

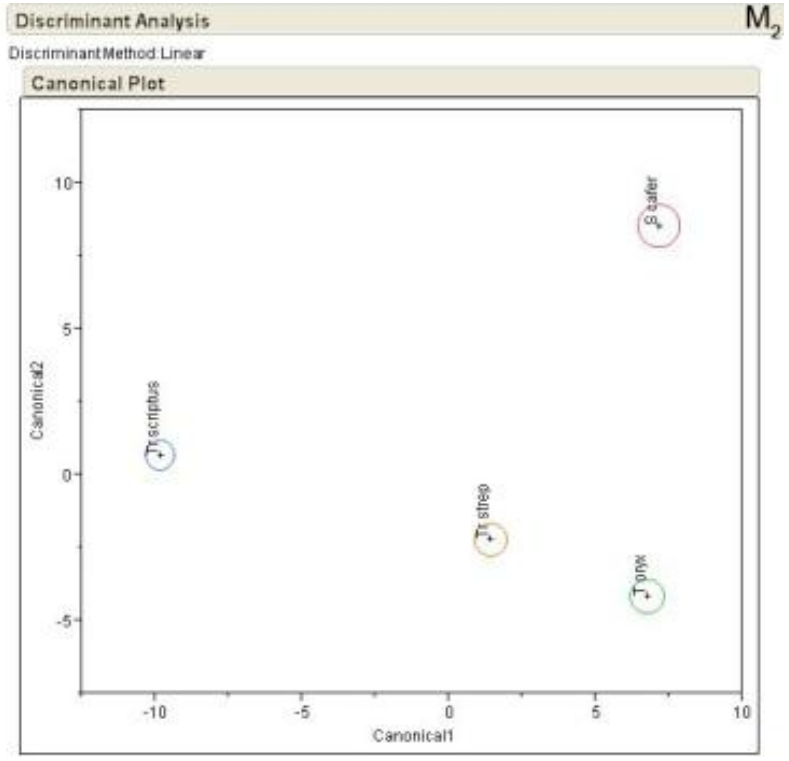


Figure 3.19 DFA results for the M_2 teeth in the tribe Bovini.

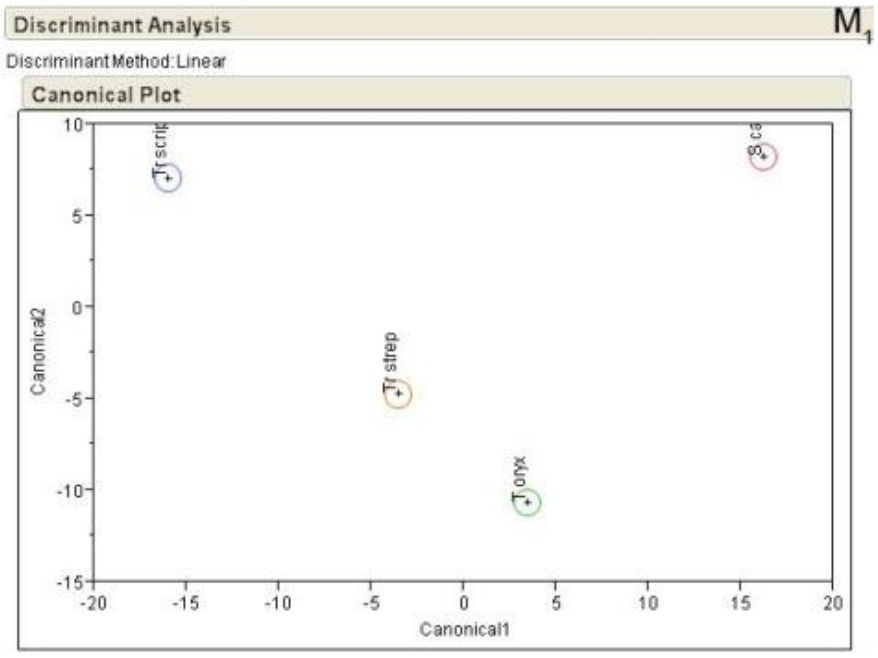


Figure 3.20 DFA results for the M_1 teeth in the tribe Bovini.

3.3.4 Reduncini

Redunca arundinum, *Redunca fulvorufula*, *Kobus leche* and *Kobus ellipsiprymnus* were analyzed from the Tribe Reduncini. The Wilks' lambda test from the MANOVA yielded significant results when all of the teeth from the four species were compared to each other. The *p* values for all of the teeth were $p<0.001$ demonstrating that the means of occlusal surface of the teeth are significantly different between the species within the tribe Reduncini.

The results of the DFA are shown in Table 3.7. The teeth from Reduncini classified correctly at a relatively high classification rate with M^1, M_3 and M_2 classifying correctly 100% of the time across all species within Reduncini. The M^3 teeth classified the weakest with *Redunca arundinum* classifying correctly only 83.3% of the time. The 83.3% classification result is due to the fact that 5 of the 30 *R. arundinum* specimens misclassified as *R.fulvorufula*. This means that there is some overlap in the form between these two

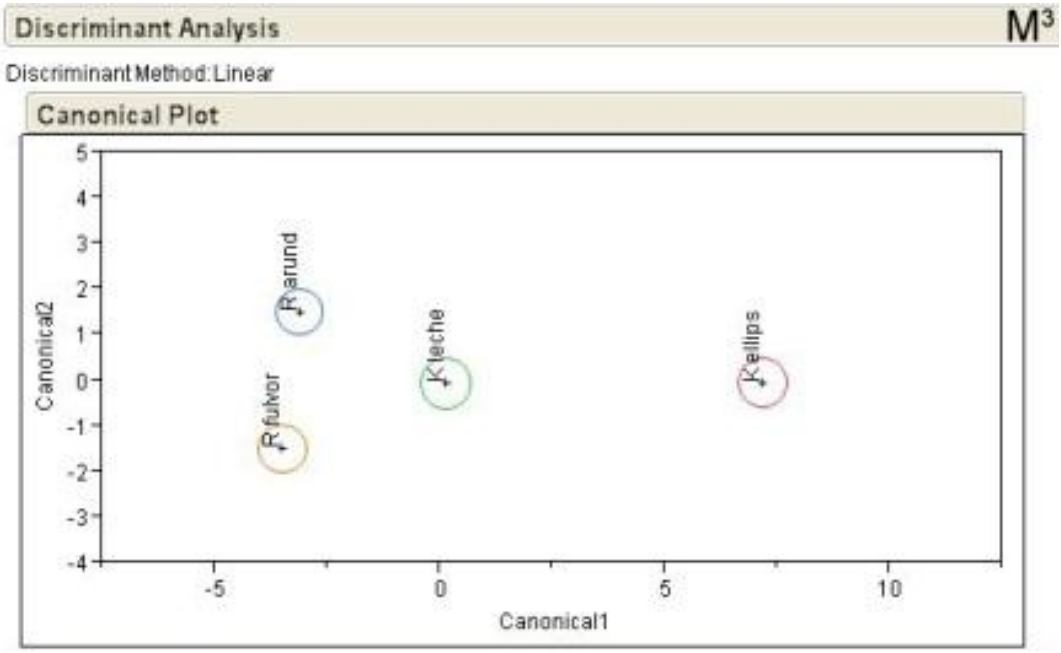
congeners. While the classification rate is close to 85%, these results suggest that caution should be taken when a tooth is identified as a *R. arundinum* due to the fact that the classification rate is not as robust as the other teeth.

Graphical representations of the DFA results of Reduncini are in Figures 3.21-3.26. Despite the M^3 of *Redunca arundinum* classifying at only 83.3%, the DFA results from Figures 3.21-3.26 illustrate that the 95% confidence ellipses do not overlap in this 2D illustration. However, the group centroids of *R. arundinum* and *R.fulvorufula* consistently plot close to each other in the graphs, in particular in Figures 3.21, 3.22, 3.23 and 3.26. This result suggests that there are some similarities between the species.

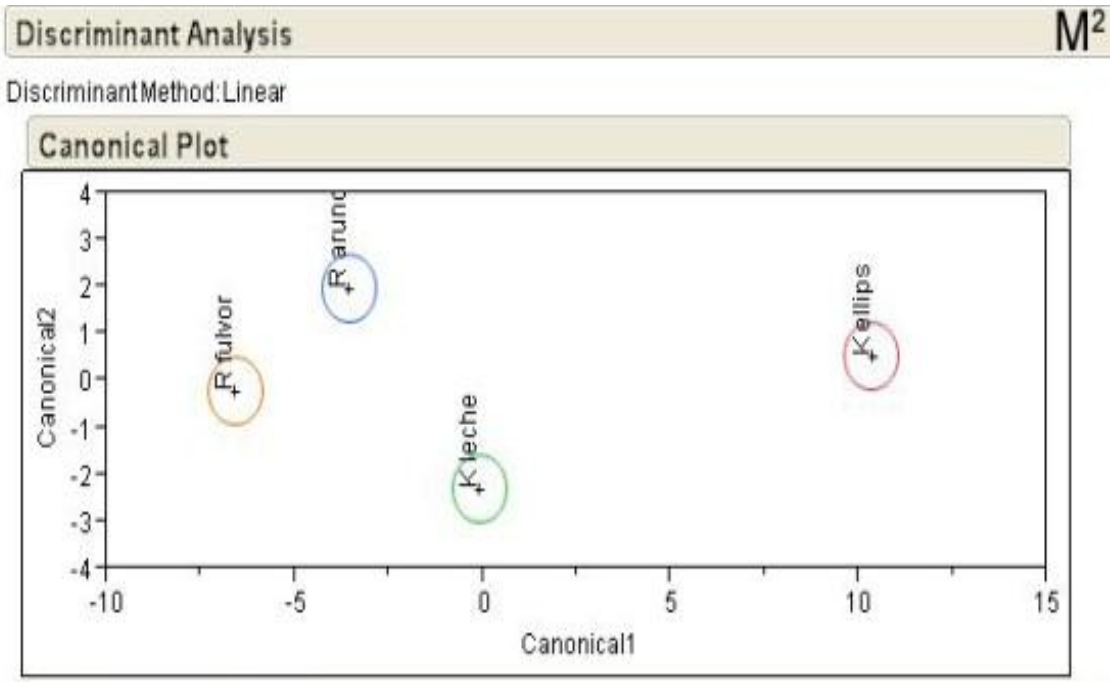
Overall, the results support Hypothesis H1 and suggest that this is an appropriate methodology to correctly identify Reduncini in the fossil record. The modern bovid Reduncini dentitions were reliably distinguished as discrete species based on the outlines of the occlusal surface of their teeth, when compared with closely related bovid species. All of the teeth except M^3 of *Redunca arundinum* classified at a percentage above the *a priori* rate of ≥85% and the M^3 of *Redunca arundinum* classified at a high percentage, 83.30%. The correct classification rate of for *Redunca arundinum* is slightly less robust than it is for the other species and other teeth in the tribe Reduncini. As a result, caution must be used when identifying fossil representatives of these closely related species.

Table 3.7 Percentage of Reduncini teeth that classified correctly in the discriminant function analysis.

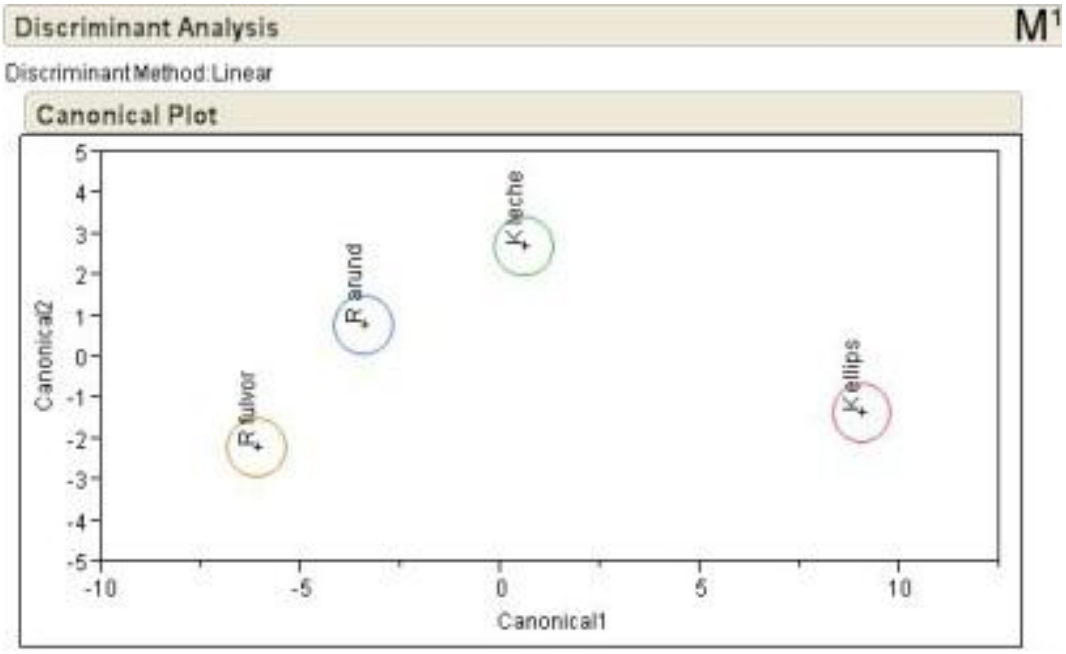
Reduncini	M^3	M^2	M^1	M_3	M_2	M_1
R. arund	**83.30%**	**93.30%**	**100%**	**100%**	**100%**	**94%**
R. fulvor	**96.50%**	**100%**	**100%**	**100%**	**100%**	**100%**
K. leche	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**
K. ellips	**96.29%**	**100%**	**100%**	**100%**	**100%**	**100%**



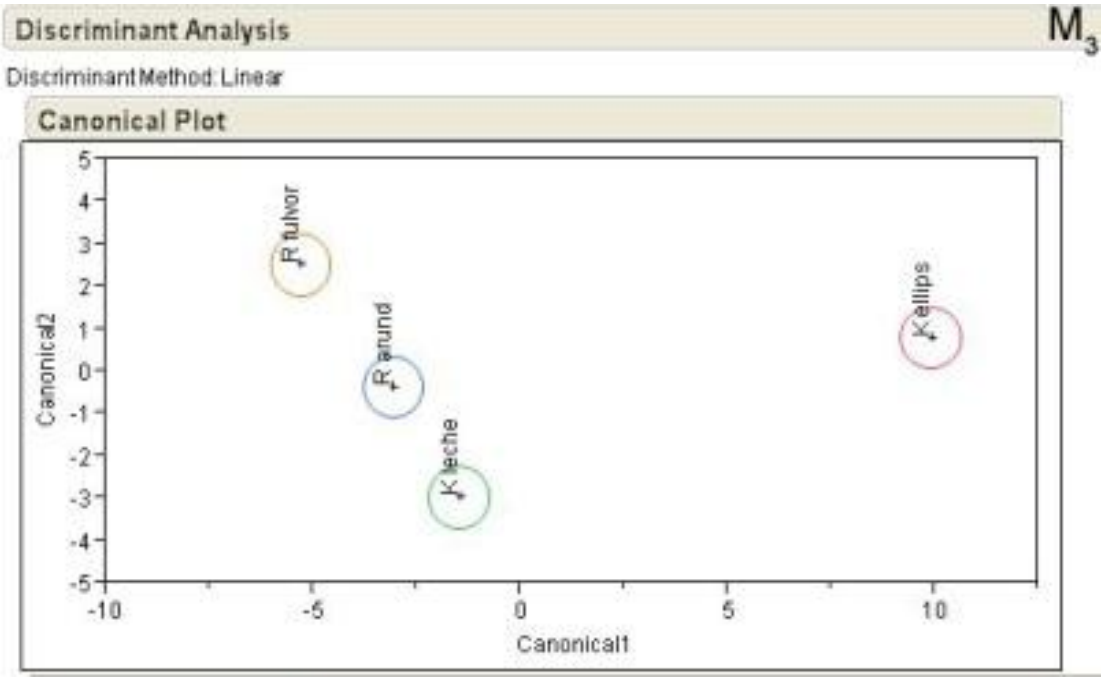
Figures 3.21 DFA results for the M^3 teeth in the tribe Reduncini.



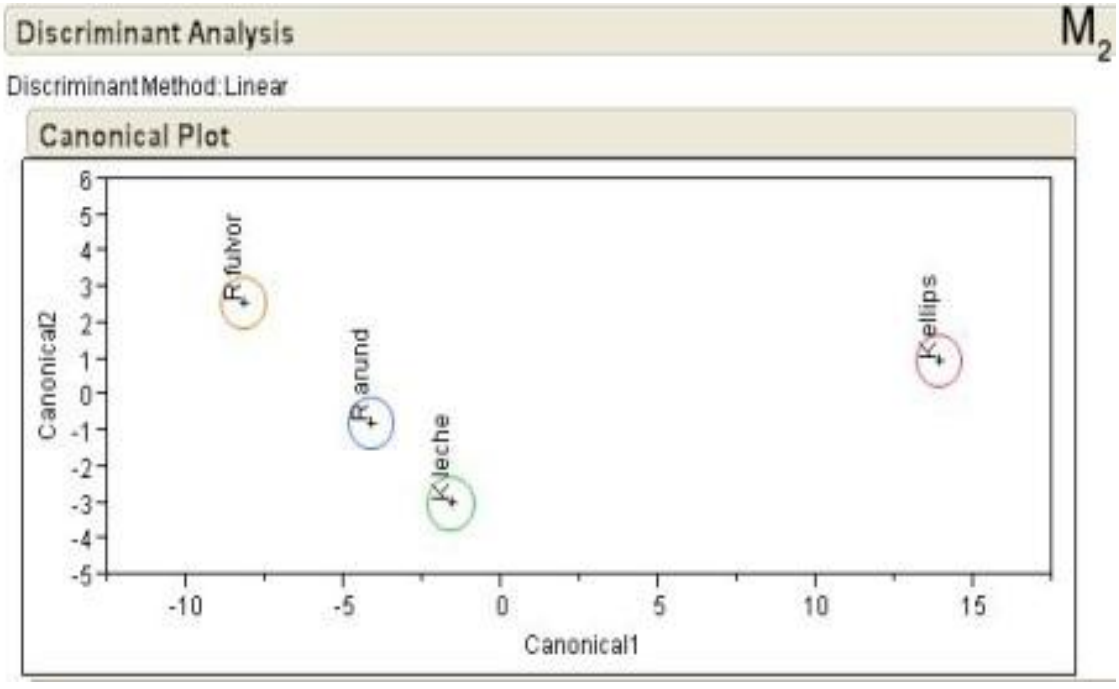
Figures 3.22 DFA results for the M^2 teeth in the tribe Reduncini.



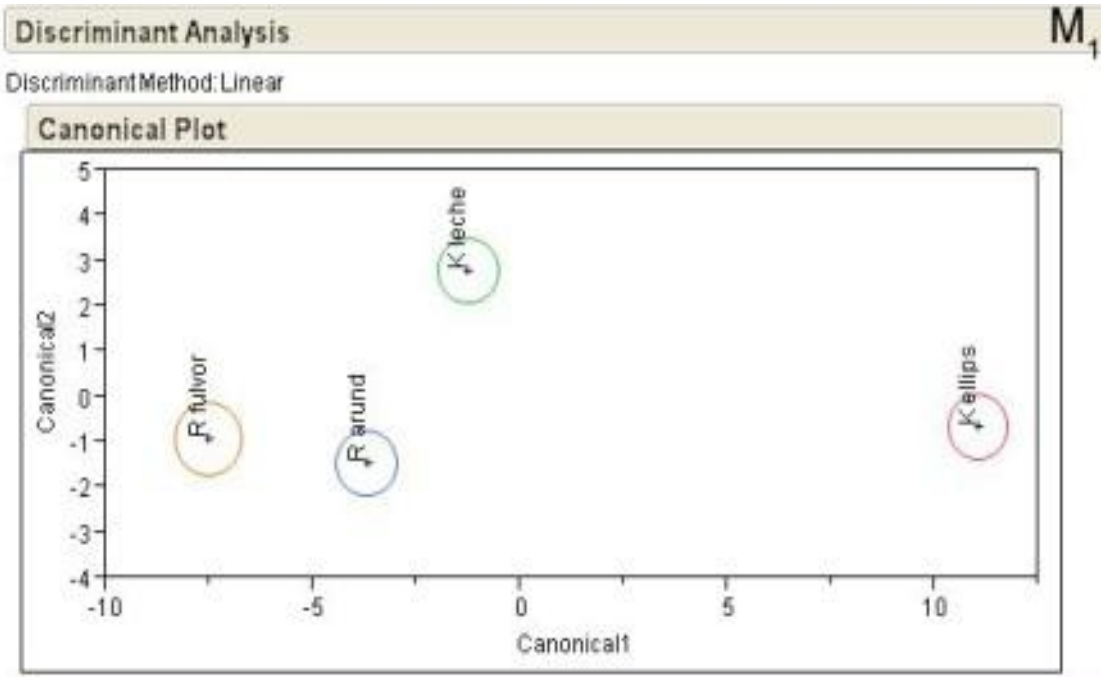
Figures 3.23 DFA results for the M^1 teeth in the tribe Reduncini.



Figures 3.24 DFA results for the M_3 teeth in the tribe Reduncini.



Figures 3.25 DFA results for the M_2 teeth in the tribe Reduncini.



Figures 3.26 DFA results for the M_1 teeth in the tribe Reduncini.

3.3.5 Hippotragini

Three Hippotragini species were analyzed in this study: *Hippotragus niger*, *Hippotragus equinus* and *Oryx gazella*. A MANOVA test was performed and the Wilks' lambda statistic obtained. Since this is the first time the Wilks' lambda was not $p<0.001$, a Table of the results is presented (Table 3.8). The M_1 is the only tooth not significant with a *p* value as 0.0781, indicating that the average means of the M_1 from the three Hippotragini species are not significantly different from each other. The other five teeth are significantly different from each other (Table 3.8), though with lower probabilities than other Tribes.

Table 3.8 Results of the MANOVA Wilks' lambda test for three species of Hippotragini.

	M^3	M^2	M^1	M_3	M_2	M_1
Hippotragini	**0.0005**	**0.0033**	**0.0307**	**0.0108**	**0.0022**	0.0781*

In order to determine which groups were significantly different from each other, a MANOVA post hoc test, the Tukey-Kramer, was performed on the data (Table 3.9). A Tukey-Kramer test is performed after a MANOVA and is used to decipher, specifically, which of the groups MANOVA analyzed are different from each other. The results of this test indicate that *H. niger* and *H. equinus* are not significantly different from each other while *O. gazella* is significantly different than both *H. niger* and *H. equinus*. This result means that there is some overlap in the means of the two species *H. niger* and *H. equinus*. This finding is not surprising given to the fact that these two are congeners and overlap in body size; thus, some overlap in the means of the occlusal surface outline exists between the *H. niger* and *H. equinus*. The fact that the means are not significantly different did not affect their ability to discriminate from each other (Table 3.10). The maxillary third molars classified the weakest with *H. niger* classifying at 96.56% rate and *H. equinus* classifying correctly at 92.86%. The remainder of the teeth, including M_1, classified correctly 100% of the time.

DFA calculates the means of each of the original variables within the group and finds whether the groups differ with regard to these means, similar to the Wilks' lambda statistic; however, DFA also calculates which variables maximize the differences between groups and uses that to predict group membership. In addition, DFA was run on the PCs which organize the data in order to maximize the differences between the groups. Thus, when the raw means are compared to each other, some overlap exists in the occlusal surface outlines of M_1 of *H. niger* and *H. equinus*. When a test statistic such as DFA is used that is attempting to discriminate between the species, it is able to discriminate between the two congeners. This means that while the raw means of the original variables might not be statistically different from each other, when the data is reorganized (PCs) and the variables maximized to find the

differences between the groups (DFA), *H. niger* and *H. equinus* are able to be distinguished from each other.

Table 3.9 Results of the Tukey-Kramer test for the tribe Hippotragini.

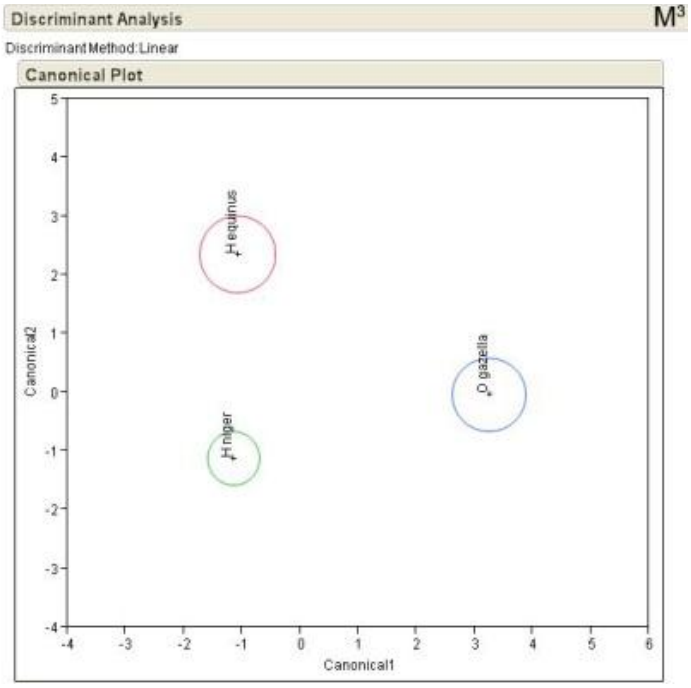
Comparison		p value
H. niger	*O. gazella*	<0.001
H. equinus	*O. gazella*	0.0003
H niger	*H. equinus*	0.993

The graphical DFA results for the tribe Hippotragini suggest that the occlusal surface of the teeth are significantly different from each other based on the large distances between the centroids of the groups on the graphs (Figures 3.27-3.32). Specifically, the distances between the centroids in Figure 3.30 and 3.31, M_3 and M_1, respectively, are extreme.

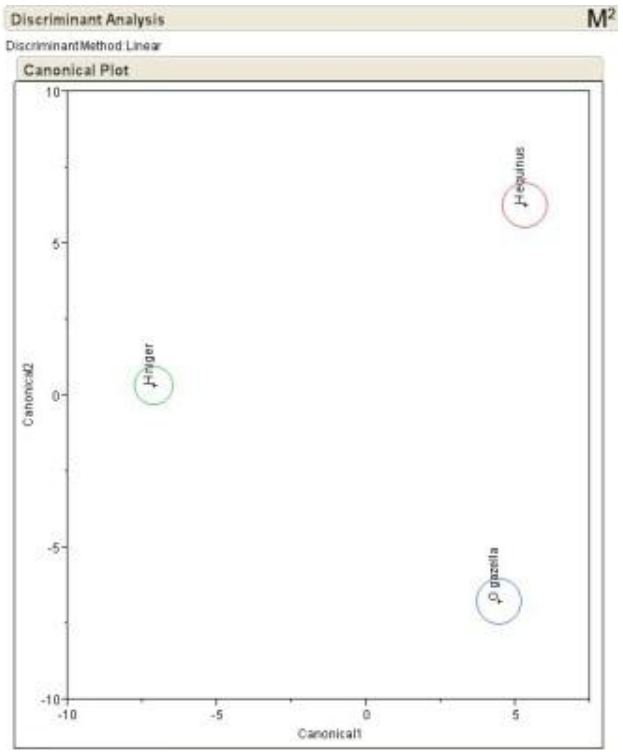
The Hippotragini results support Hypothesis H1. All of the teeth in this tribe classified above the *a priori* rate of 85%. Hippotragini teeth can be distinguished as discrete species based on the outlines of their occlusal surface of their teeth when compared with closely related bovids, using DFA. The results of these analyses also suggest that this approach is appropriate to apply to unknown fossils in faunal assemblages.

Table 3.10 Percentage of Hippotragini teeth that classified correctly in the discriminant function analysis.

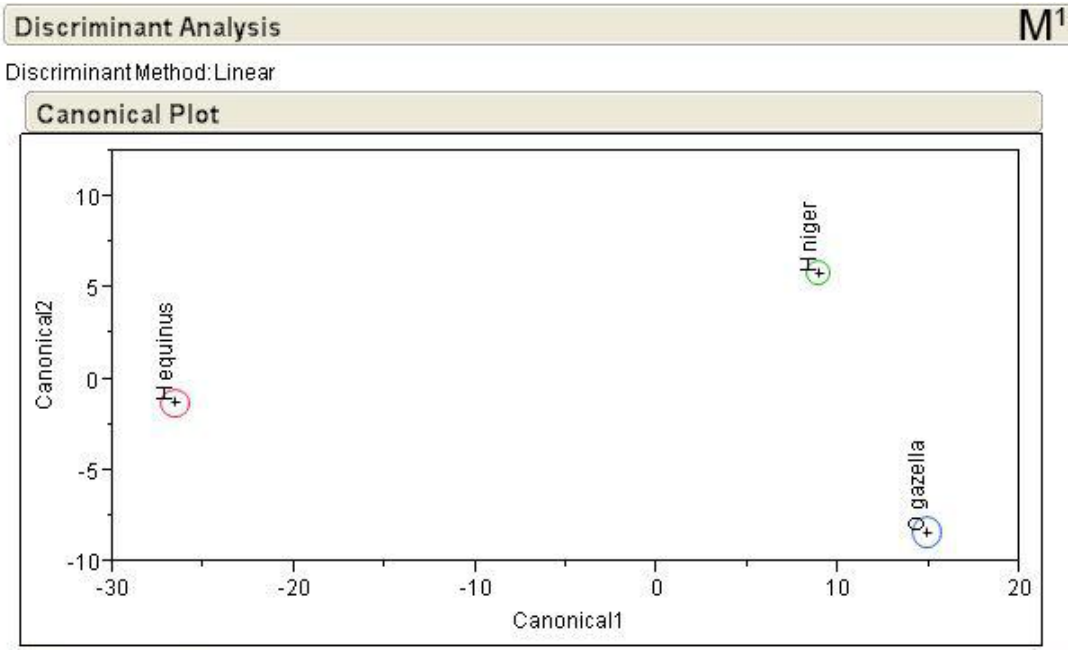
Hippotragini	M^3	M^2	M^1	M_3	M_2	M_1
H. niger	**96.56%**	**100%**	**100%**	**100%**	**100%**	**100%**
H. equinus	**92.86%**	**100%**	**100%**	**100%**	**100%**	**100%**
O. gazella	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**



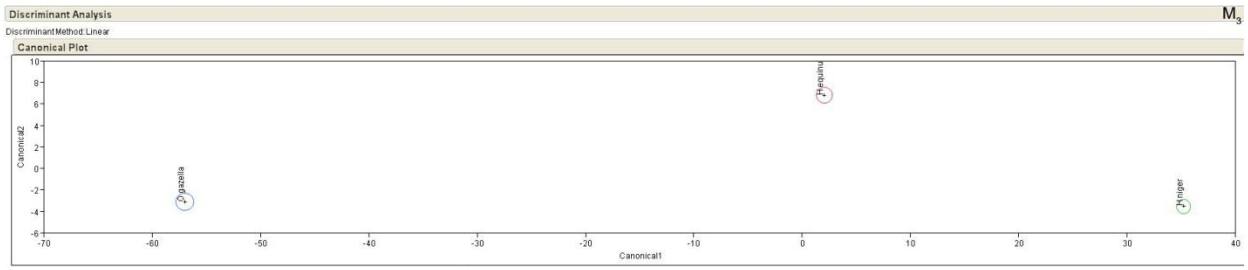
Figures 3.27 DFA results for M^3 teeth in the tribe Hippotragini.



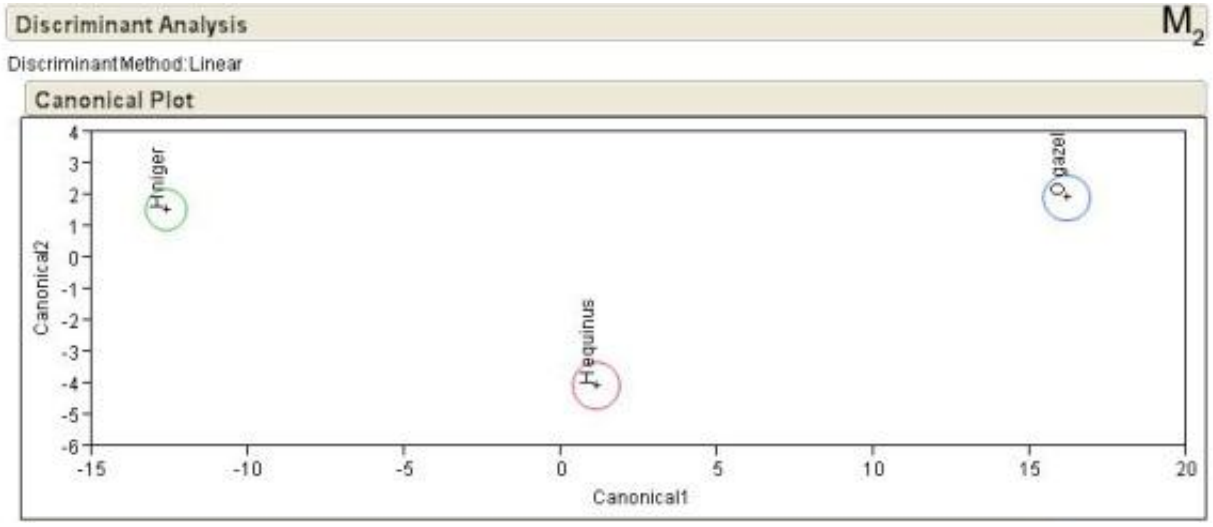
Figures 3.28 DFA results for M^2 teeth in the tribe Hippotragini.



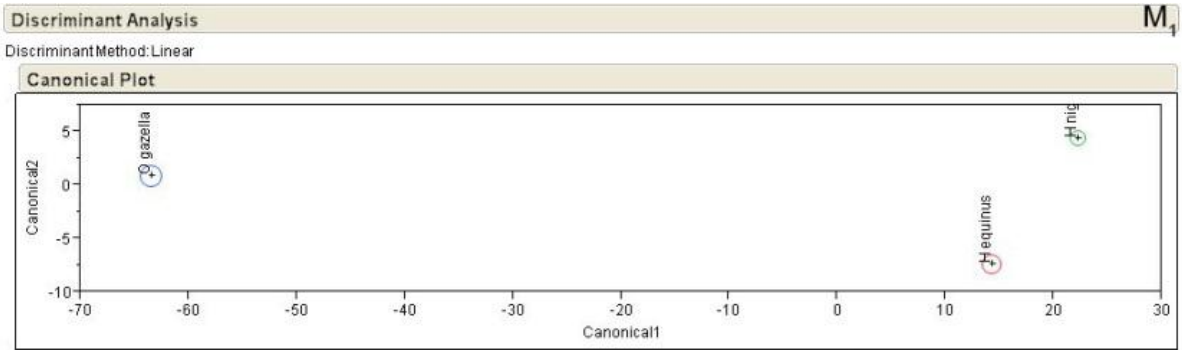
Figures 3.29 DFA results for M^1 teeth in the tribe Hippotragini.



Figures 3.30 DFA results for M_3 teeth in the tribe Hippotragini.



Figures 3.31 DFA results for M_2 teeth in the tribe Hippotragini.



Figures 3.32 DFA results for M_1 teeth in the tribe Hippotragini.

3.3.6 Neotragini

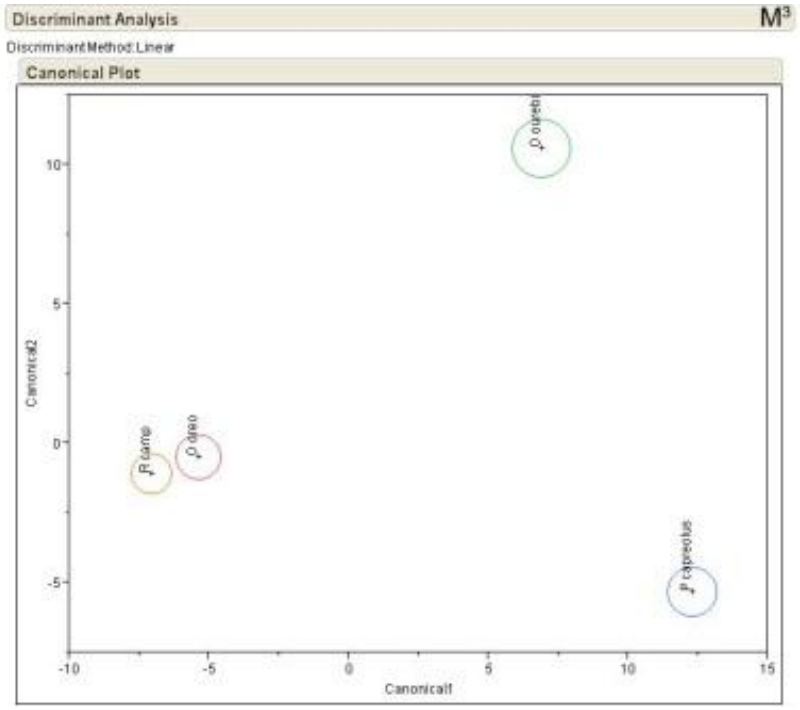
The Neotragini sample consisted of the following four species: *Raphicerus campestris*, *Oreotragus oreotragus*, *Pelea capreolus* and *Ourebia ourebi*. The Wilks' lambda test from the MANOVA yielded significant results when all of the teeth from the four species were compared to each other; the means for all of the teeth were significantly different from each other, $p<0.001$. These results indicate that true differences in the means of the outlines of the occlusal surface exist between species in the tribe Neotragini. The DFA results also suggest differences at the species level in the upper and lower molars (Table 3.11 and Figures 3.33-3.38). Table 3.11 lists the percentage of teeth that classified correctly in the DFA. All of the maxillary teeth classified 100% correctly. The M_3 and M_2 molar had some misclassifications for *Oreotragus oretragus* and *Raphicerus campestris*, respectively. All of the teeth classified correctly at a rate above the *a priori* classification rate. Thus, teeth from the same bovid species are more similar in shape and size than teeth from closely related bovids.

Table 3.11 Percentage of Neotragini teeth that classified correctly in the discriminant function analysis.

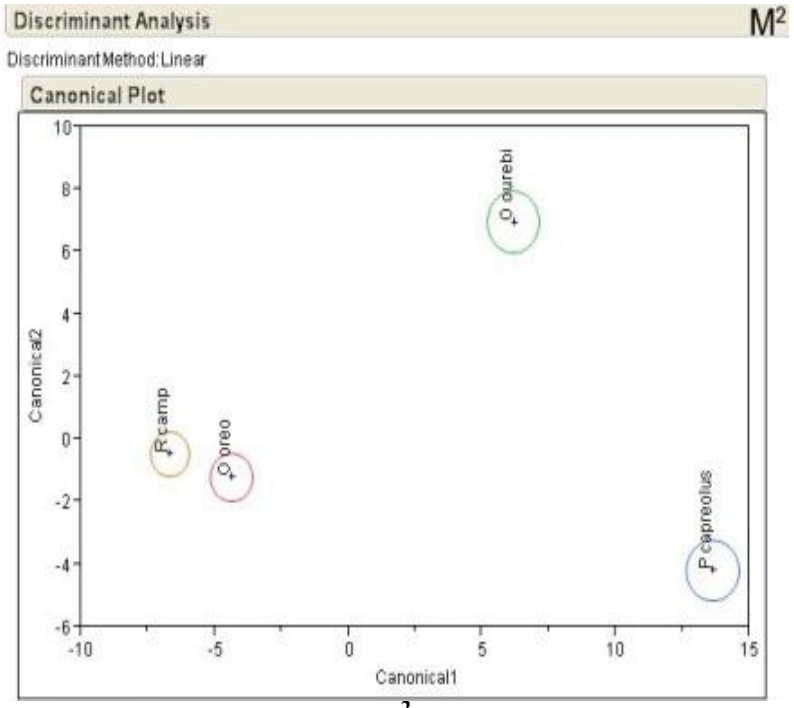
Neotragini	M^3	M^2	M^1	M_3	M_2	M_1
R. camp	**100%**	**100%**	**100%**	**100%**	**94%**	**100%**
O. oreo	**100%**	**100%**	**100%**	**91.70%**	**100%**	**100%**
P. capre	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**
O. ourebi	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**

The graphical results for the DFA are shown in Figures 3.33-3.38. The confidence ellipses do not overlap for any of the species in this 2D illustration (Figures 3.33-3.38). All of

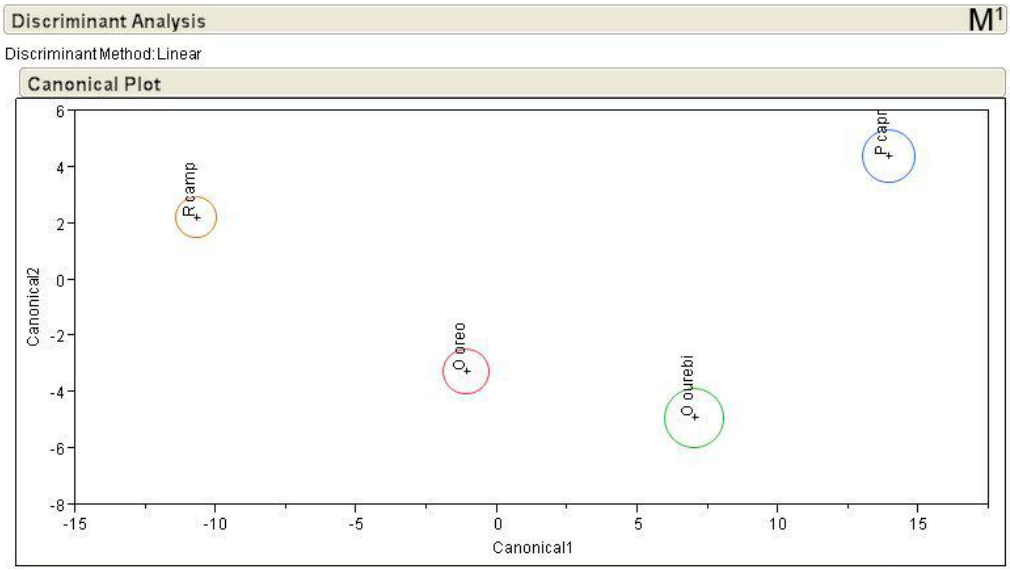
the Neotragini teeth classified above the *a priori* rate of 85%. These results support Hypothesis H1, that outlines of the occlusal surface of Neotragini teeth can reliably be distinguished from closely related bovid species. Thus, this approach can be used to test for Neotragini species in fossil assemblages.



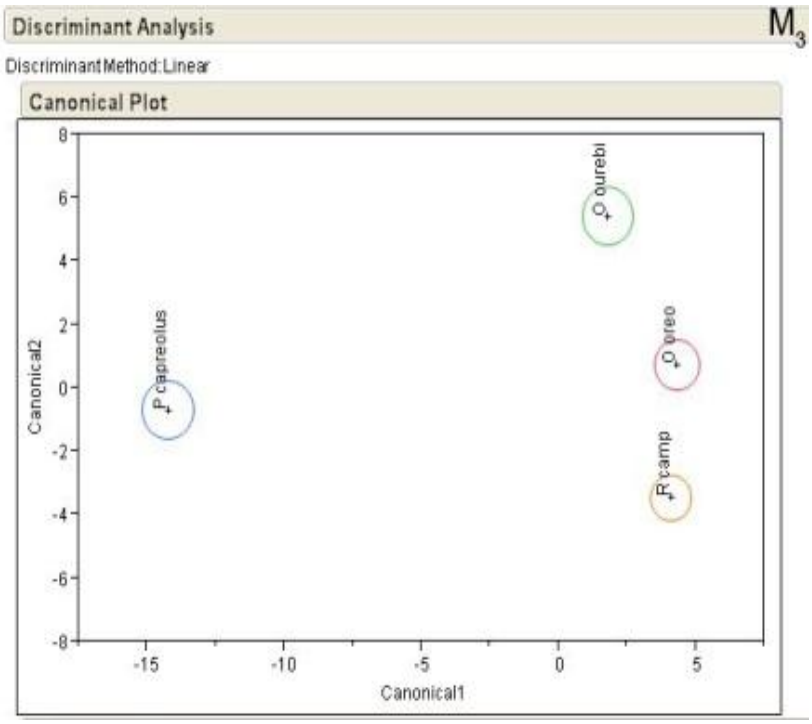
Figures 3.33 DFA results for M^3teeth in the tribe Neotragini.



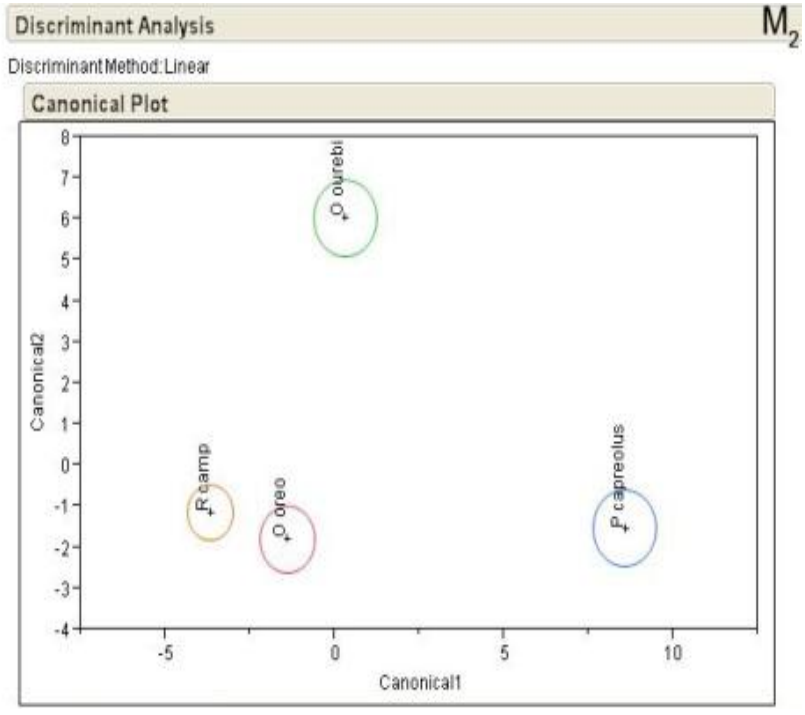
Figures 3.34 DFA results for M^2teeth in the tribe Neotragini.



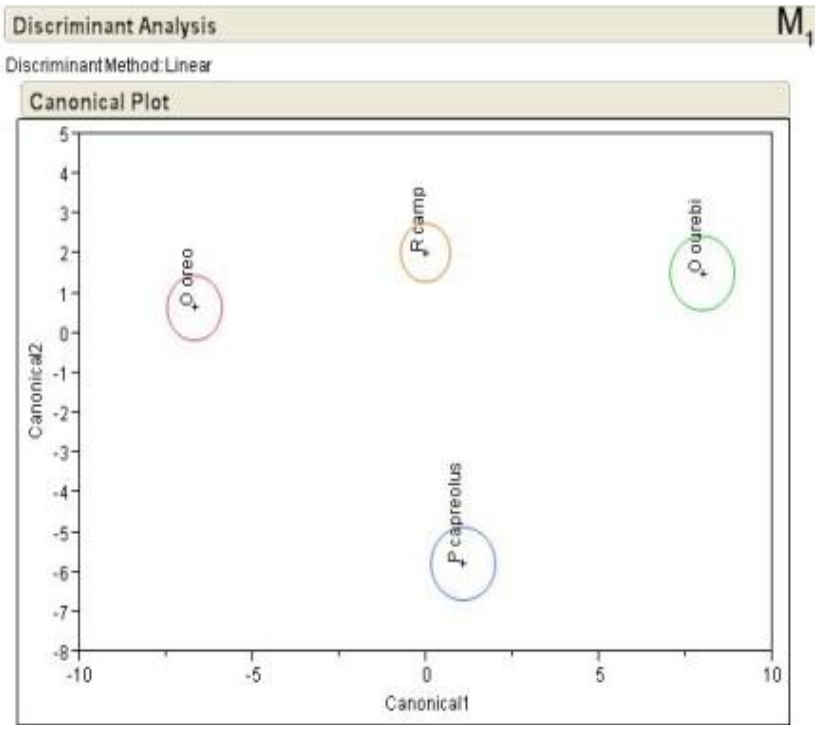
Figures 3.35 DFA results for M^1teeth in the tribe Neotragini.



Figures 3.36 DFA results for M_3 teeth in the tribe Neotragini.



Figures 3.37 DFA results for M_2 teeth in the tribe Neotragini.



Figures 3.38 DFA results for M_1 teeth in the tribe Neotragini.

3.3.7 Antilopini

One species in the tribe Antilopini was analyzed, *Antidorcas marsupialis*. This species was the only Antilopini available that had a sufficient sample size to be used in this study. Therefore, each molar tooth type was compared to the same tooth in the tribe Neotragini, as these two tribes have a close evolutionary relationship (Gentry, 2010). The MANOVA and Wilks' lambda tests yielded $p<0.001$ for all of the *A. marsupialis* teeth. This result indicates that the means of the occlusal surface outlines of *A. marsupialis* and Neotragini teeth are significantly different from each other. In addition, all of the teeth classified correctly at a 100% classification rate (Table 3.12), suggesting that distinct form differences exist between the occlusal surface outlines of *A. marsupialis* and Neotragini. Figures 3.39-3.44 graphically illustrate the DFA results. These Figures demonstrate that

Antidorcas marsupialis is consistently separate from the four species of Neotragini, further suggesting distinct differences in the occlusal outlines of these teeth.

A future goal of the project is to find another Antilopini species with sufficient sample size to be used in the study. Regardless, it is important to test Antilopini against Neotragini since they are in the same Subfamily and overlap in the occlusal outline of teeth between these two tribes would not be unexpected. Thus, it is important to test that a fossil can be distinguished between *A. marsupialis* and the four Neotragini species.

The results of this analysis support Hypothesis H1. The occlusal surface outlines of the teeth of *Antidorcas marsupialis* are reliably identified as a discrete species, when compared with the outlines of closely related bovids in the same Subfamily. These results support the application of this method towards unknown Antilopini fossils in faunal assemblages.

Table 3.12 Percentage of Antilopini teeth that classified correctly in the discriminant function analysis.

Antilopini	M^3	M^2	M^1	M_3	M_2	M_1
A. marsupialis	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**

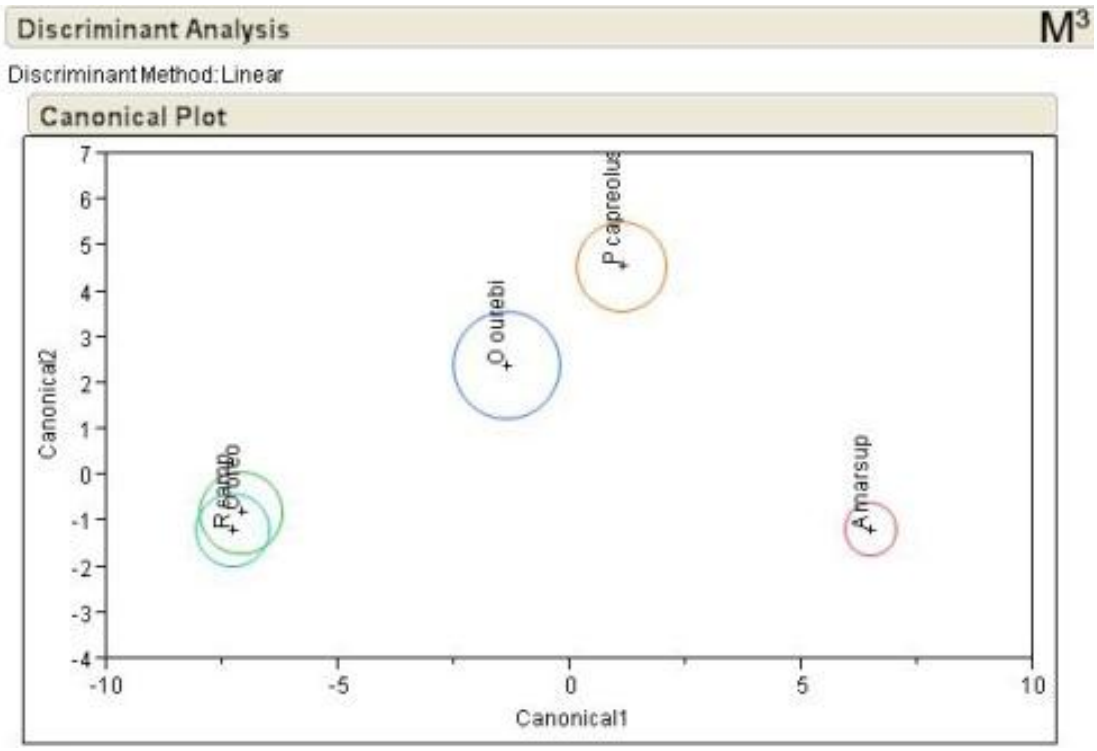


Figure 3.39 DFA results for M^3 teeth in the tribe Antilopini.

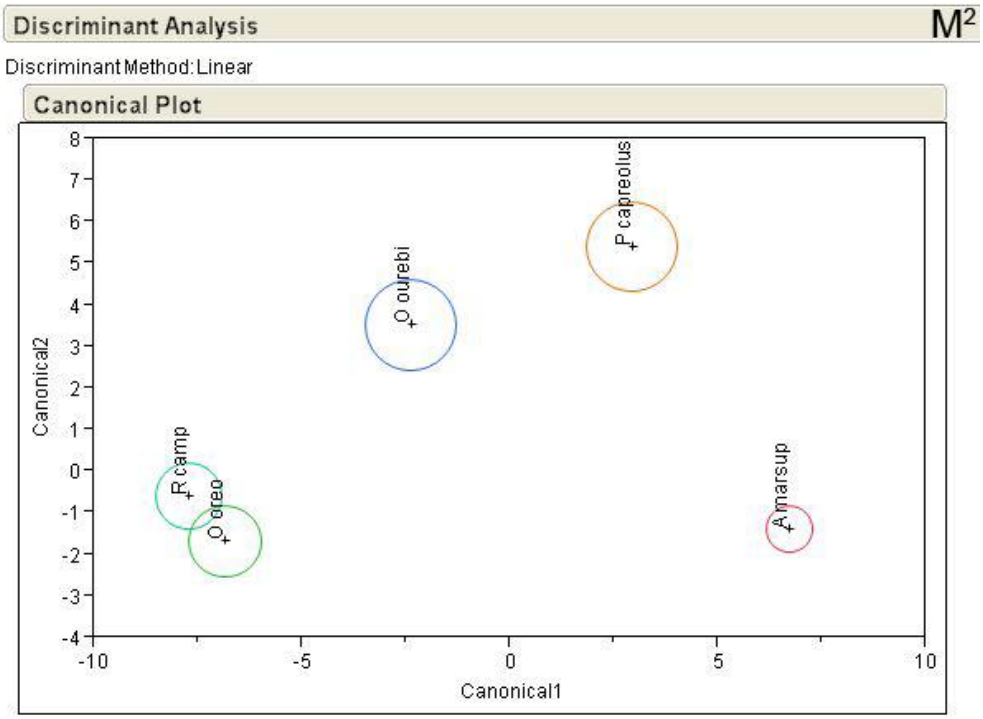


Figure 3.40 DFA results for M^2 teeth in the tribe Antilopini.

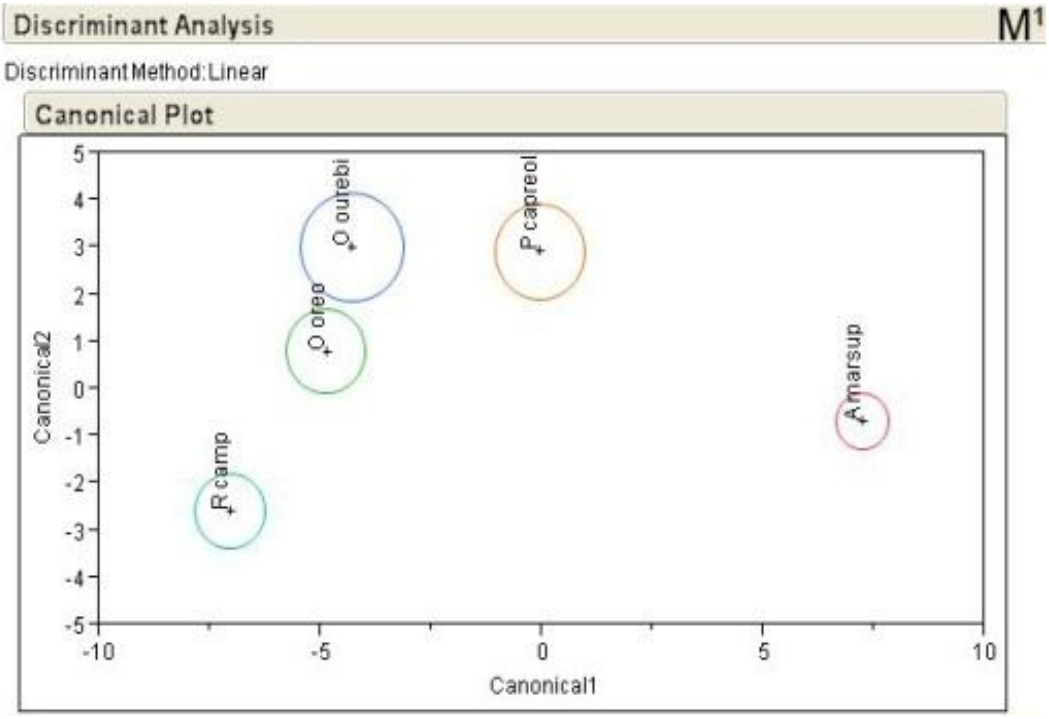


Figure 3.41 DFA results for M^1 teeth in the tribe Antilopini.

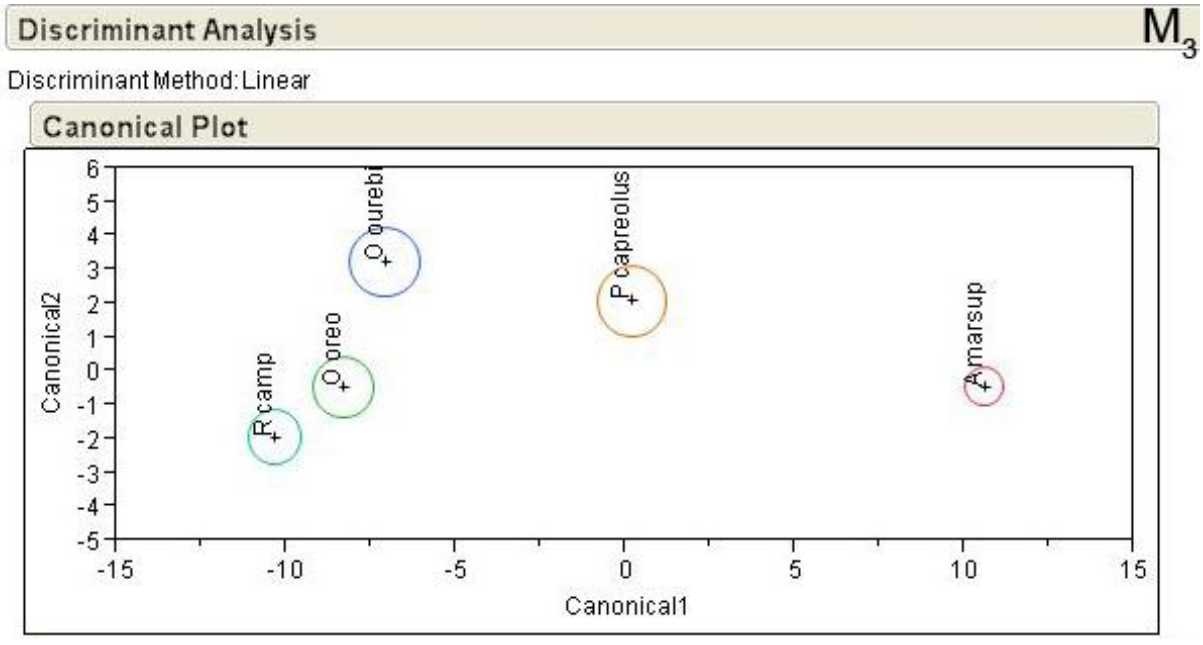


Figure 3.42 DFA results for M_3 teeth in the tribe Antilopini.

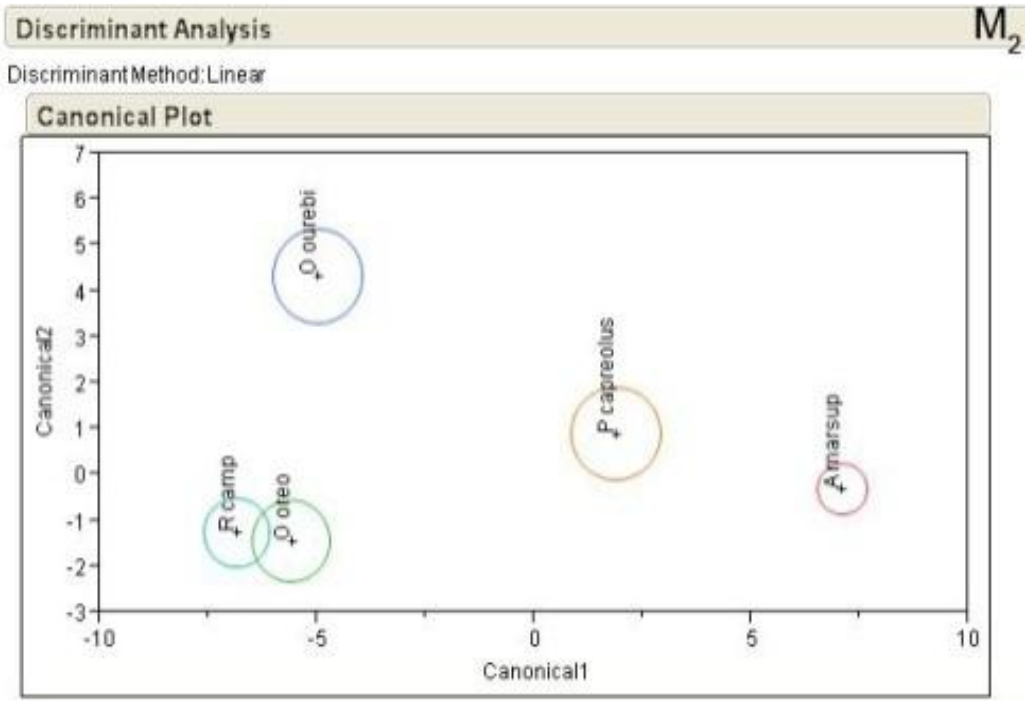


Figure 3.43 DFA results for M_2 teeth in the tribe Antilopini.

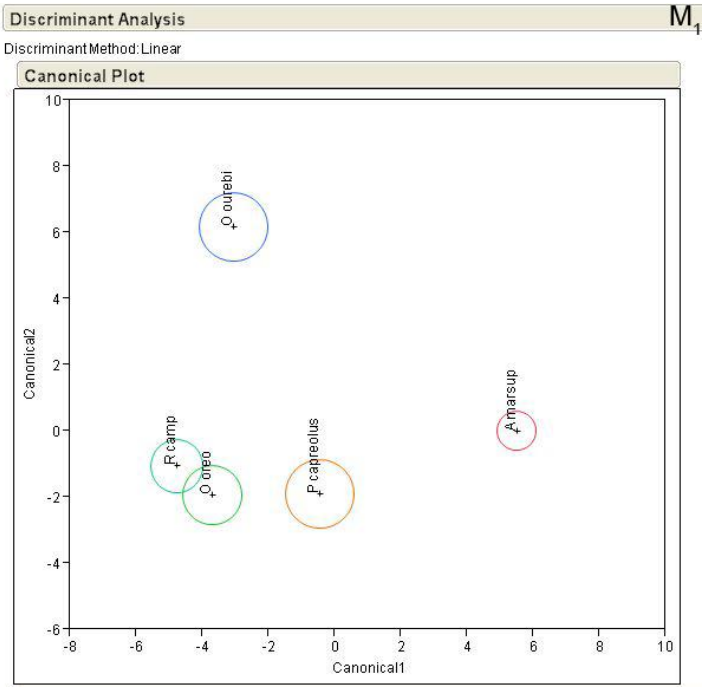


Figure 3.44 DFA results for M_1 teeth in the tribe Antilopini.

3.4 Discussion

The goal of this phase of the dissertation is to test whether modern bovid dentitions can be distinguished between closely related species based on an analysis of the occlusal surface outlines of their teeth (Hypothesis H1). To test this hypothesis, analyses were run on samples of three maxillary and three mandibular molars from twenty species across seven tribes (Table 3.1). If the modern bovids classified correctly ≥85% of the time when DFA was performed, then the results would be considered reliable enough to apply this methodology to fossil specimens. Of the 120 analyses that were performed, all but one tooth classified above this *a priori* rate. *Redunca arundinum* M^3 had 5 misclassifications as its congener, *Redunca fulvorufula*; therefore, the classification for this species was just slightly below the *a priori* classification rate at 83.3%. While the classification rate is close to 85%, these results suggest that the classification rate is not as robust as the other teeth in the analysis and that caution should be taken when a tooth is identified as a *R. arundinum*. The rest of the analyses yielded a correct classification rate of ≥85%. These results indicate that DFA was able to use the means of each of the variables in the sample to correctly predict group membership at a high classification rate. Thus, teeth from the same bovid species are more similar in shape and size than teeth from closely related bovid species.

Graphical results of the DFA also demonstrate the dissimilarity between bovid species in the same tribe. While the graph is only plotted in 2D, none of the confidence ellipses overlap with each other, suggesting little overlap in the variation between the specimens. The results of some of the specimens also illustrate large distances between the centroids of the groups, signifying that a lot of variation exists between those samples.

Thus, the results of the analysis support Hypothesis H1: *Modern bovid dentitions can be reliably distinguished as belonging to discrete species, separate from morphologically similar, closely related species, based on analysis of the outlines of occlusal surfaces of their teeth.* The outlines of occlusal surfaces of bovid teeth exhibit distinct, reliable shapes that can be used to differentiate one bovid species from another. An extant, isolated bovid tooth could be identified to the level of species based on a comparison of its occlusal morphology with the occlusal morphology of a known species. The results of these analyses suggest that this approach is appropriate to test on an unknown bovid tooth in the fossil record.

3.5 Conclusions

Taxonomic identification of fossil bovid teeth is often imprecise and subjective. Biasing factors such as age and degree of occlusal attrition complicate identifications, as they often result in considerable overlap in absolute and relative size of teeth. Due to these biasing factors, faunal studies could contain misidentified bovids which, in turn, could lead to erroneous paleoenvironmental reconstructions. In addition, these biasing factors could lead to inter-observer error where the identification of the same bovids varies depending on the researcher. Subsequently, the paleoenvironment that is reconstructed using those bovid identifications will be different.

This phase of the dissertation presents and tests a methodology which standardizes the way bovids are taxonomically identified. The results of this study substantiate the use of the shape of the occlusal surface of bovid teeth as a reliable indicator of a species. The high success rates of MANOVA and Wilks' lambda tests suggest that the means of the shape of the occlusal surface of extant bovid teeth differ between species within the same tribe. These

tests support the hypothesis that differences do exist in the shape of the occlusal surface of bovid teeth. Furthermore, the high classification rates resulting from DFA indicate that the shape of the occlusal surface of these bovid teeth can be used to taxonomically identify bovid species to the species level.

This study represents the first time occlusal surface morphometric quantification has been applied to bovid tooth identification. The purpose of testing this quantification method is an attempt to standardize the way bovids are identified in the fossil record. This chapter represents the first step in that endeavor. Samples of three maxillary and three mandibular molars from twenty species across seven tribes were used to test this method. The results indicate that bovid identification can be quantified and standardized. Ultimately, the final product is a reliable, standardized, and replicable methodology for identifying fossil bovid teeth that will minimize the impact of biasing factors such as age and attrition that often cause overlap in the size and shape of their teeth, as well as help reduce the degree of subjectivity involved in analyzing faunal lists complied by different researchers.

CHAPTER IV

DOCUMENTATION OF THE FOSSIL TEETH

4.1 Introduction and hypothesis

This phase of the dissertation involves identifying the fossil bovid teeth from Swartkrans and Cooper's D using a standardized method in order to test whether fossil forms are recognizably similar to modern forms. It is hypothesized that this standardized method will produce highly accurate taxonomic diagnoses of fossil bovid teeth, providing classifications that go beyond broad taxonomic levels such as Tribe or Family. More precise identifications will allow more subtle ecological traces to be detected and more accurate paleoenvironmental reconstructions to be made. The bovid teeth from Swartkrans and Cooper's D will be used to reconstruct the environment associated with *A. robustus*. The following hypothesis will be tested in this phase of the dissertation:

> *H2: A. Extant bovid teeth can be used to accurately identify representatives of modern taxa in the fossil record;*
>
> *H2: B. The occlusal outline of the teeth of extinct bovid species can be quantitatively documented, thus allowing precise identifications of fossil species for whom there are no modern counterparts.*

The results of Chapter III demonstrated that the occlusal outlines of modern comparative teeth are diagnostic of extant bovid species; therefore, the next step is to apply this methodology to fossil faunal assemblages. A fossil bovid tooth can be identified by comparing its occlusal morphology to the occlusal morphology of modern bovid teeth previously established by EFFA. Teeth that do not classify as one of the modern references

will undergo further statistical testing to determine if it can be identified as an extinct species or a species not previously thought to be in South Africa at the time.

4.2 Materials and methods

This study includes fossils from Swartkrans and Cooper's D. Photographs were taken of the occlusal surface of fossil bovid teeth at the University of Witwatersrand, Johannesburg, where the Cooper's D fossils are housed, and the Transvaal Museum, Pretoria, in South Africa where the Swartkrans fossils are housed in June-August, 2009. Appendix I lists the specimens that were photographed and examined in this project. All bovid teeth in the collections were photographed regardless of their level of attrition, provided that the teeth exhibited complete or mostly complete lobes; if a majority of the occlusal surface of the tooth could be distinguished, the tooth was included in this study.

The same protocols were used for obtaining the fossils bovid images as the modern bovid images. A digital camera was positioned with a tripod directly above the occlusal surface of the tooth and leveled using a bubble level. Each tooth was situated vertically in a box of sand. A stand with an adjustable clamp held a scale bar which was leveled using a bubble level, and placed directly next to the tooth at the height of the occlusal surface. Separate images were taken of each molar tooth. Images of right teeth were flipped horizontally in Adobe Photoshop® in order to make them left teeth, since only left teeth (or teeth flipped to be left) were used in the modern bovid teeth analysis.

The outlines of the occlusal surface of the bovid teeth were captured and analyzed using MLmetrics and Elliptical Fourier Functional Analysis (EFFA) (Lestrel, 1989). Each picture is opened in MLmetrics and a line grid is overlain on the tooth by defining the left

and right boundaries of the tooth and the top and bottom boundaries. The grid creates a cross in the middle of the tooth defining the center. After marking where these lines cross, a standardized, rectangular grid is placed on the image using that center of the tooth as a reference. As was done with the modern sample, the teeth are digitized according to a template ensuring that each tooth has the same number of points, and that the points are placed in homologous positions. Sixty points are laid down around the outline of the tooth using the grid and template for orientation. The first point, point 1, is always the upper most, left most spot where the grid crosses the tooth. The X and Y coordinates for each of the sixty points on the tooth are exported and used in EFFA where the harmonics and amplitudes are generated (Wolfe et al., 1999).

The amplitudes of the harmonic that are calculated for each fossil tooth type were compared to the entire modern reference sample of the same tooth type (e.g. M^2) using SPSS and JMP statistical software. Linear DFA was performed on the amplitudes of the teeth and was used to predict to what group each fossil most appropriately belonged. DFA reports both posterior probabilities and typicality probabilities. The posterior probability values indicate the probability that an individual belongs to one of the reference groups in the analysis (Albrecht, 1992). This probability is based on the Mahalanobis distance of the specimen to the group centroid. Posterior probabilities are the result of a restricted approach, where the unknown specimen is forced into one of the *a priori* reference groups and the probabilities of group membership must equal one (Albrecht, 1992). Typicality probabilities result from an unrestricted approach. This probability determines whether the fossil falls within the multivariate normal distribution of one of the reference groups. These probabilities are based on the generalized distances between a fossil and each group centroid (Albrecht, 1992).

Typicality probabilities estimate the number of *a priori* specimens in a group that lie farther away from the centroid than the unknown specimen. High typicality probabilities suggest that the fossil lies within the normal distribution of that group; low typicalities indicate that the fossil likely does not belong to that group. While the use of typicality probabilities is rare, it is most frequently used in craniometric studies of living and fossil primates (Campbell, 1984; Albrecht, 1992; Jantz and Owsley, 2001; Brace et al., 2006). With that said, researchers tend to not disclose a strict typicality threshold on which they based their classifications. A high or low typicality is described as being relative to the results of their sample. In this study, group membership was determined using DFA for all six of the tooth types. The posterior and typicality probabilities were reported and their classifications were used in the analysis

According to Albrecht (1992), the possibility exists that group membership can be misinterpreted if only the posterior probability is relied upon. DFA classifies an unknown fossil specimen into the group to which it is closest based on the distance of the fossil to a group centroid. The posterior probability of the DFA reports how likely it is that the unknown specimen belongs to one of the reference groups. However, posterior probabilities are limited to the available reference groups; therefore, a tooth that in reality does not belong to a reference group will be forced into the closest matching group. The typicality probability is unrestricted and not limited to the choice of one of the reference groups; therefore, it reports how likely it is that the fossil specimen actually belongs to the group it is closest to, or if it is possible that the specimen does not belong to any of the reference groups. As such, typicality probabilities are less likely to mistakenly classify a tooth, though teeth that belong to taxa not included in the reference groups cannot be classified, and therefore cannot be

included in further analysis. Thus, typicality probabilities used in this study are by nature more exclusionary, resulting in smaller available datasets that are limited to fossils that plot within the normal multivariate distribution of the groups. While the use of typicality probabilities does result in a smaller dataset of identified fossils, there is a high amount of confidence in the classification of those fossils. An unknown fossil could have a high posterior probability and a high typicality probability, meaning the fossil is closest to that *a priori* group and is within the normal multivariate distribution of that group. However, the possibility also exists that the fossil has a high posterior probability and a low typicality. In this situation, the fossil is closest to the *a priori* reference group it classified as, but does not lie within its normal distribution. In such a case, there is an enhanced probability that such a tooth has been misclassified by the posterior probability.

In order to test whether the different classification methods yield different results, the findings of the DFA using both the posterior and typicality probabilities were compared. It is important to test for any discrepancies between these classification methods because they determine the bovid identifications which are used to reconstruct past environments. Misidentified bovids will lead to erroneous paleoenvironmental reconstructions. If the classification methods yield the same results, then all of the fossils are in the normal multivariate space of one of the reference groups. If, on the other hand, the classification methods yield different results, the likelihood exists that a fossil was classified as a particular species, though it does not lie in the normal multivariate space of that species. In other words, the fossil had a high posterior probability and a low typicality probability. Therefore, the more robust typicality probability needs to be relied upon to ensure that the fossils identified as one of the reference species plot within in the normal multivariate space of that

species. This will provide the most accurate identifications possible of fossil bovid teeth, and will highlight specimens that do not belong to any of the modern reference species as either being representatives of modern species not currently known in South Africa, or representatives of extinct taxa (see below for further discussion).

Hereafter, the classifications made using DFA relying on the posterior probability will be referred to as the posterior probability approach and the classifications made relying on the typicality probability will be referred to as the typicality probability approach. The classifications that result from these approaches are used to compile a faunal assemblage list per fossil deposit. The faunal lists and the paleoenvironmental reconstructions based on the posterior probability approach and typicality probability approach are compared.

Posterior probabilities will force the fossils into one of the 20 reference groups. Therefore, this classification scheme uses all of the data, though it must be remembered that the teeth can and must be forced into one of the reference groups, thus the possibility exists that specimens might be incorrectly grouped with a reference sample. The results are computed based upon the minimum number of individuals (MNI) calculation. The MNI is the smallest number of individuals necessary to account for all of the teeth in a sample identified as belonging to a particular species. For this study, this calculation is made by assessing how many left and right teeth of each tooth type there are in the assemblage and then determining which tooth type and side (e.g. left M^2) is the most common. The highest number of tooth type and side is the MNI.

A second set of results shows the DFA classifications of fossils using the typicality probability approach. This study uses a typicality probability threshold at or above 0.15. If the DFA calculated a typicality of $\geq$0.15, then the fossil was considered to be a member of

that group. A threshold of ≥0.15 means that no more than 85% of the individuals in a group fall closer to the centroid than the unknown specimen. The unknown specimen could be on the margins of the group, but not so far as to be an outlier with no possibility of being in the group. The use of a typicality threshold of 0.15 was used because it is statistically robust in that there is a high amount of confidence in the classification results of that fossil. Fossils that do not classify above the typicality probability threshold of 0.15 should be excluded from paleoenvironmental reconstructions. Therefore, using a typicality threshold is less inclusive than using the posterior probability but yields classification results with more confidence. Those fossils with typicality probabilities < 0.15 underwent two more tests to determine if they could yet be identified and included in paleoenvironmental reconstructions.

Follow up analysis 1: This analysis involves giving the fossils that classified with a <0.15 typicality *a priori* designations based on the identifications determined by the posterior probability approach. These provisionally identified fossils were put back into the database with the known modern specimens and a DFA was performed. Because the fossils were given an *a priori* classification, DFA will calculate group membership *assuming* the specimen is a part of that group. This approach tests whether the unknown fossil specimen is an outlier of the modern species to which it classified, or if does not represent any of the modern reference species. If the specimen is actually a member of the group to which it initially classified using the posterior probability approach, it will classify with a higher typicality rate than in the original analysis because DFA is operating under the assumption that the specimen is a member of that group. If the fossil misclassifies or classifies with a typicality rate <0.15, the identification of the tooth cannot be verified and it will not be used to reconstruct the past environment.

Follow up analysis 2 was also used to test for outliers. This analysis involves taking only the fossils that classified with a typicality ≥0.15, organizing them into the groups/species defined by the posterior probability approach, and placing them in their own database. As a result, the fossils with a ≥0.15 typicality were given *a priori* distinctions. The fossils that classified with <0.15 typicality were then added to this database as "unknowns". DFA was performed using the fossils with a high typicality as the reference sample. This approach only compares fossils with fossils. If an "unknown" classifies with a typicality of ≥0.15, then the specimen will be considered to be a member of that species. If an "unknown" classifies with a typicality of <0.15, the tooth might be an example of either an extinct species or a species not previously identified in South Africa.

The faunal lists developed as a result of the posterior probability approach and the typicality probability approach are compared to each other. That is, the results of the classifications using the posterior probabilities and the fossils that classified with a ≥0.15 typicality are compared to each other. If follow up analyses 1 or 2 classifies a fossil with a ≥0.15, then the fossil will be used in the comparisons and the paleoenvironmental reconstructions.

A chord distance measure was used to assess differences between the faunal lists. Chord distance is a measure of faunal dissimilarity that compares the taxonomic composition of the faunal lists and determines if the species composition and proportions of the assemblages are dissimilar (Ludwig and Reynolds, 1988; Bobe et al., 2002; de Ruiter et al., 2008). Chord distances measure the degree of dissimilarity between assemblage j and assemblage k using the following formula:

CRDjk¼ SQRT[2(1–ccosjk)]

with ccosjk ¼SS(Xij*Xik)/SQRT[SSX2ijSSX2ik]

In this analysis, Xij represents the abundance of the ith species in the jth assemblage and Xik represents the abundance of the ith species in the kth assemblage. S is the total number of species shared in the two assemblages. Chord distance results range from 0 to the square of 2 (~1.414); 0 means the assemblages are identical while ~1.414 means the assemblages have no similarities. These tests were performed in order to determine if any differences exist between the posterior probability approach results and the typicality probability approach results.

A paleoenvironmental reconstruction for each assemblage from Swartkrans and Cooper's D is presented in two ways: using the MNI data from the Posterior probability approach and the MNI data of the Typicality probability approach. The paleoenvironments reconstructed from the faunal lists developed via the two classifications schemes were compared to each other to see if differences exist. In specific, the species composition and relative abundance of the species are assessed between the two datasets. The presence/absence of a species in an assemblage will affect a paleoenvironmental reconstruction as the reconstruction is largely based on the species identified in an assemblage. The relative abundance of bovids is important because faunal assemblage composition is compared between temporally ordered sites in order to assess change over time. Thus, in order to obtain a precise paleoenvironmental reconstruction and confidently assess change over time, it is important to have an accurate species presence/absence and relative abundance data.

The environment was reconstructed for each assemblage using the ecological requirements of the bovids that were identified based on the procedures outlined above. The ecological requirements are defined below and were obtained from Skinner and Smithers (1990), Estes (1992), Reed (1996), Spencer (1997), Sponheimer et al. (1999, 2003) and de Ruiter et al. (2008).

Animals in the Family Bovidae fall into three different types of feeding categories: grazer, browser and mixed feeder. A grazer is an herbivore that eats mainly grass while a browser is an herbivore that feeds on plants other than grass such as foliage (Estes, 1992). A mixed feeder grazes and browses eating foods from both of these categories (Estes, 1992). Lee-Thorp et al. (1989) defined these terms more precisely using the relative amount of C_3 and C_4 grasses vegetation in an animal's diet. They concluded that browsers consuming C_3 vegetation such as a leaves, fruits, tree roots, bushes and forbs have a $\delta^{13}C$ values that range between -10% to -16%. Grazers consuming C_4 vegetation such as tropical grass blades, seeds and roots, have $\delta^{13}C$ values between +2% and -2%. Mixed feeder animals that graze and browse and have $\delta^{13}C$ values between -2% and -10% (Lee-Thorp et al., 1989). The $\delta^{13}C$ values were used to determine what feeding category a bovid belongs to (Sponheimer et al., 2003).

The following habitat types were used in this study:

Forest

Forests are defined as containing columnar trees ranging from 10-80 m high with a complex, closed canopy. Usually, several vegetation layers exist and the tree crowns are interwoven with vines. The forest typically contains a shrub layer, although the ground vegetation is commonly sparse and absent.

Woodlands

A woodland habitat is characterized by having deciduous trees ranging from 8-20 m in height. Greater than 20% of the land cover must be made up of trees to be considered a woodland habitat. The ground cover consists of herbs and grasses and an understory of small trees or large bushes may exist. The habitat is considered a closed woodland when greater than 40% of the land cover is made up of trees and tall grasses. When the land cover consists of only ~20% of trees, herbs and grasses, the habitat is an open woodland.

Bushland and thicket

This habitat is a cross between a bushland and woodland with tree species no more than 3 m tall. A bushland and thicket habitat means that at least 40% of the ground cover consists of bushes which are defined as a woody plant intermediate between a shrub and a tree. The bushes are often densely interwoven in thickets. This habitat is frequently interspersed within woodland habitats.

Grassland savannahs

A grassland savannah is defined as a vegetation community that has a continuous layer of arid adapted plants and which is scattered with shrubs and trees in varying concentrations (Reed, 1996). Bush fires occasionally occur in these habitats. The main growth patterns of the plants in the grassland savannahs coincide with seasonality. Several different types of grassland savannah variants exist including grasslands/plains, edaphic grasslands, secondary grasslands and wooded grasslands. The grasslands/plains habitat is dominated by grasses and herbs with widely scattered or grouped trees and shrubs. Trees and

shrubs comprise ≤ 2% of the ground cover. Edaphic grasslands consist of grasslands associated with water logged soils such as wetlands and vleis, which are marshy areas with waterlogged soils. Aquatic sedges and grasses are usually associated with edaphic grasslands. Secondary grasslands are grassland savannahs that result when fire or constant grazing prevents woody growth from becoming prevalent, though with varying concentrations of trees and shrubs (Spencer, 1997). A wooded grassland environment is similar to a grassland/plains environment but with more groups of woody plants.

4.3 Results of the analyses by assemblage

4.3.1 Cooper's Cave

4.3.1.1 Results of the DFA using the posterior probability approach

Ninety-six Cooper's D fossils were digitized and analyzed. The posterior and typicality probabilities for all of the fossil specimens are listed in Appendix II. Figure 4.1 illustrates the classification results produced by DFA based on the posterior probability approach. These results suggest a diverse assemblage including fifteen of the twenty modern reference species. The most common tribe found at the site is Alcelaphini comprising approximately 35% of the assemblage. *C. taurinus* is the most abundant Alcelaphini making up 15% of the assemblage. *A. buselaphus* comprises 11%, *C. gnou* makes up 6%, and *D. dorcas* comprises 3%. Antilopini is represented by the species *A. marsupialis* and comprises 11% of the assemblage. Three Tragelaphini species comprise 23% of the assemblage and are represented by *T. oryx*, *Tr. strepsiceros* and *Tr. scriptus*. *T. oryx* and *Tr. strepsiceros* each represent 9% while *Tr. scriptus* makes up 5%. The Bovini species *S. caffer* makes up 3% of the faunal assemblage. Three Neotragini species were identified in the assemblage and

comprise 20%: *R. campestris*, *P. capreolus* and *O. ourebi*. *R. campestris* makes up 3%, *P. capreolus* makes up 11% and *O. ourebi* comprises 6%. Two Hippotragini species make up 6% of the assemblage. *H. equinus* and *O. gazella* each comprise 3% of the assemblage. Finally, the tribe Reduncini is represented by one species, *K. ellipsiprymnus* and makes up 3% of the assemblage at Cooper's D.

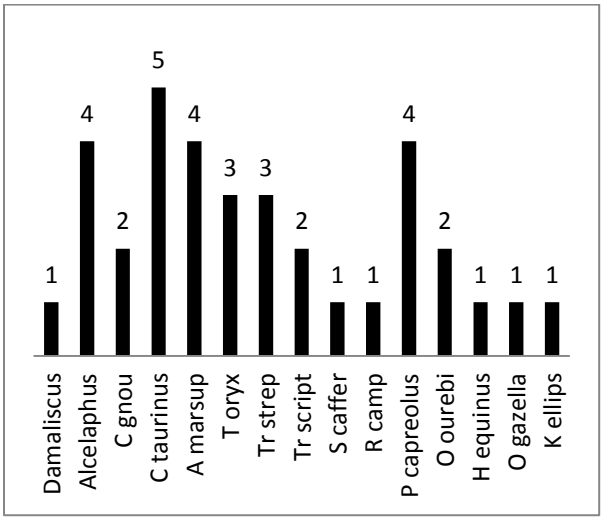


Figure 4.1 DFA results for Cooper's D using all fossils (MNI).

4.3.1.2 Results of DFA using the typicality probability approach

Fifty-four of the 96 digitized Cooper's D fossils classified with a typicality ≥0.15. Figure 4.2 graphically demonstrates the MNIs of the species that were predicted using DFA. Ten species were found at the site consisting of 19 individuals. The tribe Alcelaphini comprises 37% of the assemblage. *D. dorcas* makes up 5% while *A. buselaphus*, *C. gnou* and *C. taurinus* each comprise 11% of the assemblage. Antilopini is represented at this site by *A. marsupialis* and comprises 22% of the assemblage. Tragelaphini make up 5% of the assemblage with one species: *Tr. scriptus*. Three Neotragini species were identified including

R. campestris, *P. capreolus* and *O. ourebi*. The tribe comprises 32% of the assemblage. *R. campestris* and *O. ourebi* make up 5% each while *P. capreolus* comprises 22%. One species of Reduncini, *K. ellipsiprymnus*, was classified at Cooper's D making up 5%.

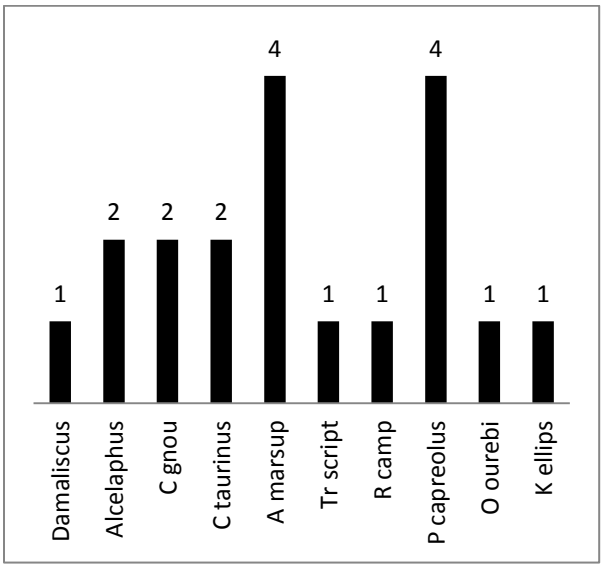


Figure 4.2 DFA results for Cooper's D using fossils with a typicality of ≥0.15 (MNI).

Forty-two fossils did not classify above the ≥0.15 typicality threshold. These specimens were analyzed using the two follow up analyses. Follow up analysis 1 involves putting fossils with <0.15 typicality back into the database with the modern specimens and giving the fossils an *a priori* identification using the identifications the posterior probability approach produced. A DFA was performed to test whether the typicality probabilities change when the fossil is given an *a priori* distinction. In this analysis, fossils with a <0.15 typicality revealed two results. They either misclassified as a different species than their a *priori* grouping, or they classified correctly as the *a priori* group, but still had a <0.15 typicality. This test suggests that these fossils are not members of one of the 20 reference modern

groups. These fossils are likely extinct specimens or a modern species not currently known in South Africa.

Follow-up analysis 2 consisted of using the fossils that classified above the 0.15 threshold as the "known" reference groups with *a priori* identifications, and using the fossils with a <0.15 typicality as "unknowns" in a DFA. Fossils with a <0.15 typicality did not classify above the 0.15 typicality probability when this supplementary DFA was performed. The results of this test suggest that these fossils are not members of the fossils groups and are likely either extinct species of a modern species not previously identified in South Africa.

4.3.1.3 Comparison of the assemblages resulting from the posterior probability approach and the typicality probability approach

The results of the faunal lists using the posterior probability approach and the typicality probability approach are presented above. In order to test for differences between the results, a chord distance test was performed. With a distance of 0.489, the chord distance test results suggest that some differences exist between the two MNI faunal lists. This measure means that while overlap in the proportions of species exists in the lists, some important differences exist as well (Table 4.1). Only ten species were identified when the typicality approach was employed versus fifteen species using the posterior probability approach. *T. oryx*, *Tr. strepsiceros*, *S. caffer*, *H. equinus* and *O. gazella* were recognized when the posterior probability approach data were used.

Additionally, the abundance of some of the bovid species changed when the typicality probability approach was used to classify the fossils. The relative abundance increased for the following species: *D. dorcas*, *C. gnou*, *A. marsupialis*, *R. campestris*, *P. capreolus* and *K.*

ellipsiprymnus (Table 4.1). In fact, the relative abundance of *A. marsupialis* and *P. capreolus* each almost doubled, increasing from 11% to 21% when the typicality probability approach was used. On the other hand, the relative abundance of *C. taurinus*, *Tr. scriptus* and *O. ourebi* decreased when the typicality probability approach was used to classify the fossils. The proportions of *A. buselaphus* remained the same.

	Table 4.1 Cooper's Cave D MNI results of DFA															
	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	S caffer	R camp	P capreolus	O ourebi	H equinus	O gazella	K ellips	Total
MNI of all data-posterior	1	4	2	5	4	3	3	2	1	1	4	2	1	1	1	35
%MNI of all data-posterior	3	11	6	14	11	9	9	6	3	3	11	6	3	3	3	
MNI of data with >0.15 typ	1	2	2	2	4			1		1	4	1			1	19
%MNI of data with >0.15 typ	5	11	11	11	21			5		5	21	5			5	

Table 4.1 highlights how the species composition and relative abundances change depending on the classification method. The absence of several species in the typicality probability approach faunal list would have a substantial effect on the reconstructed environment. Differences in the proportions of bovids will have a dramatic effect on determining if change over time has occurred when this site is compared to other sites. This comparison of the two classification methods using the Cooper's D fauna highlights how paleoenvironmental reconstruction is highly dependent on methods of the analysis.

4.3.1.4 Paleoenvironmental implications using the posterior probability approach

4.3.1.4.1 Alcelaphini

The Alcelaphini are the most common tribe identified at Cooper's D when the MNIs of the posterior probability approach is used. Four Alcelaphini species were classified: *D.*

dorcas, *A. buselaphus*, *C. gnou* and *C. taurinus*. *D. dorcas* comprises 3% of the data. This species is a grazer that prefers secondary grassland habitats. *A. buselaphus* typically inhabits secondary grasslands, though it will also occupy open woodland with sufficient grasses. Eleven percent of the assemblage is made up of *A. buselaphus*, This species is an almost exclusive grazer whose diet consists of about 98% C_4 grasses, (Sponheimer et al., 2003), specifically leafy perennial grasses. *C. gnou* comprises 6% of the assemblage and is a grazer that obtains 94% of its diet from C_4 grasses. This species also prefers a secondary grassland habitat. *C. taurinus* is the most abundant Alcelaphini and comprises 15% of the assemblage. Ninety-four percent of the diet of this grazer consists of C_4 grasses. *D. dorcas* is the most water dependent of the four Alcelaphini, though *C. taurinus* is also water dependent and needs to drink water daily. *A. buselaphus* and *C. gnou* are only somewhat water dependent, requiring water every few days. Comprising 35% of the assemblage, the tribe Alcelaphini indicate that the environment of Cooper's D included an abundant secondary grassland habitat with a permanent water source in the vicinity.

4.3.1.4.2. Antilopini

A. marsupialis comprises 11% of the assemblage. This species is a browser subsisting on foods such as shrubs and succulents, maintaining a diet consisting of only 23% of C_4 grasses (Sponheimer et al., 2003). *A. marsupialis* typically occupies secondary grassland habitats with abundant amounts of shrubs and succulents. This bovid avoids hills/mountains and woodlands with dense vegetation. The high relative abundance of this bovid suggests that an abundant secondary grassland habitat in the vicinity of Cooper's D.

4.3.1.4.3 Tragelaphini

The tribe Tragelaphini makes up 23% of the assemblage and is represented by *T. oryx*, *Tr. strepsiceros* and *Tr. scriptus*. *T. oryx* is a browser that obtains some 92% of its diet from C_3 resources (Sponheimer et al., 2003). Similarly, Watson and Owen-Smith (2000) suggest that this species consumes ~94% browse in South Africa. Spencer (1997) states that *T. oryx* prefers secondary grassland habitats with sufficient concentrations of trees and shrubs, while Estes (1992) suggests that this bovid is adaptable and capable of living in a variety of environments, including grassland savannah, woodland and floodplain. *T. oryx* tends to avoid desert and dense forest. *Tr. strepsiceros* is a browser subsisting on foods such as herbs, fallen fruits, succulents and tubers; only 4% of the diet of this species is C_4 grasses (Sponheimer et al., 2003). *Tr. strepsiceros* is a woodland species that does not venture into open grasslands or forests. The third Tragelaphini, *Tr. scriptus*, comprises 5% of the assemblage. Sponheimer et al. (2003) determined that this species had no C_4 grasses in its diet. Thus, this species subsists entirely on browse such as herbs, shrubby legumes and fruits. Reed (1996) states that *Tr. scriptus* occupies thick bushy areas, or a bushland and thicket habitat. *Tr. scriptus* is usually found near water, *Tr. strepsiceros* needs to drink every few days and *T. oryx* is water independent. The Tragelaphini species suggest that an environment appropriate to strict browsers was available in the area, and likely consisted of an open woodland habitat with an understory of thick bushes and a water source nearby.

4.3.1.4.4 Bovini

Three percent of the assemblage is made up of the one species of Bovini, *S. caffer*. This species is a grazer that feeds on fresh grasses, obtaining about 88% of its diet from C_4

grasses. This species tends to prefer a habitat with dense cover of thickets or reeds such as a bushland and thicket habitat. Additionally, *S. caffer* requires shade during the day, thus the habitat they occupy must be extensive enough, and be comprised of sufficient vegetational coverage, to provide protection for often large herds. These animals are water dependent and, therefore, usually found near water. The environmental indicators of *S. caffer* overlap with those of Tragelaphini in that a woodland is signaled, with an understory of thick bushes and a nearby water source in the vicinity.

4.3.1.4.5 Neotragini

The tribe Neotragini comprises 20% of the assemblage and is made up of three species: *R. campestris*, *P. capreolus* and *O. ourebi*. *R. campestris* is a browser that feeds on leaves and shoots of low shrubs and trees. Sponheimer et al. (2003) demonstrate that only 10% of their diet is made up of C_4 grasses. This species occupies open woodlands, where about 20% of the land is covered by trees, and bushland such as bushland and thicket habitat. *P. capreolus* is a browser subsisting on herbs, leaves and green shoots. The habitat of *P. capreolus* is best described as grassland savannah with an associated hill or mountainside and is scattered with shrubs and trees in varying concentrations. *O. ourebi* is a fresh grass grazer, with 82% of its diet consisting of C_4 grasses. Spencer (1997) and Estes (1992) suggests that this species prefers edaphic grasslands. This species tends to avoid woodland and bush and steep slopes. All of the Neotragini species are water independent. These species suggest that an open to lightly wooded grassland with a nearby water source predominated at the time of deposition for Cooper's D.

4.3.1.4.6 Hippotragini

Two species of Hippotragini were identified at Cooper's D making up a total of 6% of the assemblage: *H. equinus* and *O. gazella*. *H. equinus* is a grazer whose diet consists of about 91% C_4 grasses, including perennial grasses. This species occupies secondary grasslands. *O. gazella* is also a grazer, obtaining about 81% of its diet from C_4 grasses (Sponheimer et al., 2003). This bovid prefers a grassland/plains habitat. *H. equinus* is also a grazer, with 100% of its diet consisting of C_4 grasses (Sponheimer et al., 2003). This species occupies woodland habitats where >20% of the land cover consists of trees. Both of these species are water dependent, suggesting a nearby water source. These species suggest that the environment consisted of both grasslands and woodlands in the vicinity, perhaps in the form of a relatively open woodland habitat.

4.3.1.4.7 Reduncini

One species was identified from the tribe Reduncini, *K. ellipsiprymnus*, making up 3% of the assemblage at Cooper's D. The diet of this species consists entirely of C_4 grasses. This species lives in edaphic grasslands where the soils become waterlogged either seasonally or permanently. *K. ellipsiprymnus* is highly water dependent, indicating a nearby permanent water source in the form of a wetland or continuously flowing river.

4.3.1.4.8 Summary

The bovids classified using the posterior probability approach, i.e. the larger assemblage, suggest a predominantly grassland habitat at Coopers D, bordered by a nearby open woodland with a relatively thick bushland component. A more densely wooded

component is also indicated in the vicinity, as is some form of permanent water, perhaps in the form of a wetland or vlei. The grasslands must have had sufficient quantities of forbs and shrubs to support low level browsers, and it is probable that fire and continuous grazing combined to maintain the grasslands by preventing woodland encroachment. All indications are of more substantial water supply in the past, with denser and more extensive vegetational coverage than is seen in the area today.

4.3.1.5 Paleoenvironmental implications using the typicality probability approach

4.3.1.5.1 Alcelaphini

When the results of the typicality probability approach are examined, the Alcelaphini comprises 37% of the assemblage. *D. dorcas* and *A. buselaphus* are grazers whose diet consists almost entirely of C_4 grasses. While both of these species inhabit secondary grasslands, *A. buselaphus* will also occupy open woodlands where there is sufficient grass for it to subsist. *C. gnou* and *C. taurinus* obtain 94% of their diet from C_4 grasses in secondary grassland habitats. *D. dorcas* and *C. taurinus* are water dependent and require water daily. *A. buselaphus* and *C. gnou* are only somewhat water dependent and require water every few days. The ecological requirements of these bovids suggest that abundant secondary grasslands and a permanent water source were in the vicinity of the site.

4.3.1.5.2 Antilopini

The predominantly browsing, water independent *A. marsupialis* represents about 22% of the assemblage in the restrictive approach. This suggests that a secondary grassland with sufficient forbs and succulents was available at Cooper's D.

4.3.1.5.3 Tragelaphini

Tragelaphini make up 5% of the assemblage with one species: *Tr. scriptus*. This species is a browser whose diet consists entirely of herbs, legumes and fruits. *Tr. scriptus* is usually found near water and in a bushland and thicket habitat with dense thickets and sufficient food.

4.3.1.5.4. Neotragini

The three Neotragini species identified using the typicality probability approach comprise 32% of the assemblage. As a browser, *R. campestris* occupies open woodlands and bushlands, and takes only about 10% graze in its diet. *O. ourebi*, in contrast, is a fresh grass grazer preferring edaphic grasslands with waterlogged soils. Each of these species accounts for 5% of the assemblage. At 22% of the assemblage, *P. capreolus* is the most abundant Neotragini, and its fondness for grasslands associated with mountains or hills suggests considerable topography at Cooper's D. The Neotragini are all water independent, though their combined numbers indicate an ample grassland savanna with nearby trees and dene cover, as well as some form of permanent water source.

4.3.1.5.5 Reduncini

Only one species of Reduncini was classified at Cooper's D making up 5%, *K. ellipsiprymnus*. *K. ellipsiprymnus* is a strict grazer obtaining all of its diet from C_4 grasses. Inhabiting edaphic grasslands and requiring water daily, the ecological indicators of this species suggests that a permanent water source was in the vicinity.

4.3.1.5.6 Summary

The bovids that were classified with the typicality probability approach indicate that secondary grasslands predominated at the site, with sufficient quantities of forbs and shrubs for the low level browsers. Continuous grazing and regular burning likely worked to maintain the grasslands and prevent woodlands from dominating. The suite of bovids also suggests that a nearby open woodland component with relatively thick bushland was evident in the vicinity of the site. A permanent, more substantial water source existed in the past providing water logged soils for an edaphic grassland habitat. Thus, the environment largely consisted of grasslands with areas of denser vegetational cover than is currently found in the area today.

4.3.1.6. Comparison between paleoenvironmental implications using the posterior probability approach and the typicality probability approach

Fewer species were identified when the typicality approach was used. Specifically, *T. oryx*, *Tr. strepsiceros* and *H. equinus* did not classify above the 0.15 typicality threshold, thus reducing the shrubs and woodland components in the typicality probability approach reconstruction. The amount of dense bushland, thicket and woodlands also changed since *S. caffer* was not identified in the typicality probability approach. The absence of *O. gazella* reduces the amount of grasslands necessary in the reconstruction.

The proportions of the species also changed when the posterior and typicality probability approach data sets were compared. Using the posterior probability approach, 74% of the assemblage consists of grazers while ninety percent of the assemblage consists of grazers when the typicality probability approach was used.

Both reconstructions suggest a more substantial water source was in the area in the past than is there today. Both reconstructions also support that a secondary grassland habitat comprised a considerable amount of the environment and that a denser vegetation was also evident at Coopers D. However, when the posterior probability approach data is used, the environment is reconstructed as having more dense vegetation than when the typicality probability approach is used. Furthermore, these results demonstrate that if the results of the paleoenvironmental reconstructions using the posterior probability approach and the typicality probability approach were compared with other sites in order to test for change over time and/or habitat preferences, they would lead to different conclusions.

4.3.2 Swartkrans Member 1- Hanging Remnant, SKHR

4.3.2.1 Results of the DFA using the posterior probability approach

One hundred eighty five bovid fossils from Swartkrans Member 1 Hanging Remnant (SKHR) were digitized for this analysis. The MNIs of the SKHR assemblage are shown in Figure 4.3, with a total of 51 individuals identified. Sixteen of the twenty modern reference species are represented. Comprising approximately 55%, Alcelaphini makes up a significant component of the assemblage. *A. buselaphus* is the most abundant Alcelaphini making up 20% of the assemblage while *C. taurinus* and *C. gnou* also contribute significantly to the assemblage making up 18% and 12%, respectively. Comprising 6%, *D. dorcas* contributes the smallest amount of the Alcelaphini. The Antilopini *A. marsupialis* makes up 2% of the assemblage. Three species of Tragelaphini were identified. *T. oryx* and *Tr. strepsiceros* each comprise 2% while *Tr. scriptus* comprises 4%. Four Neotragini species were identified comprising 20% of the assemblage. *R. campestris* makes up 6% of the assemblage while *O.*

oreotragus comprises 4%. *P. capreolus* makes up 2% and *O. ourebi* makes up 8%. Four percent of the assemblage contains *O. gazella*. Three Reduncini species were identified comprising 12% of the assemblage: *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*.

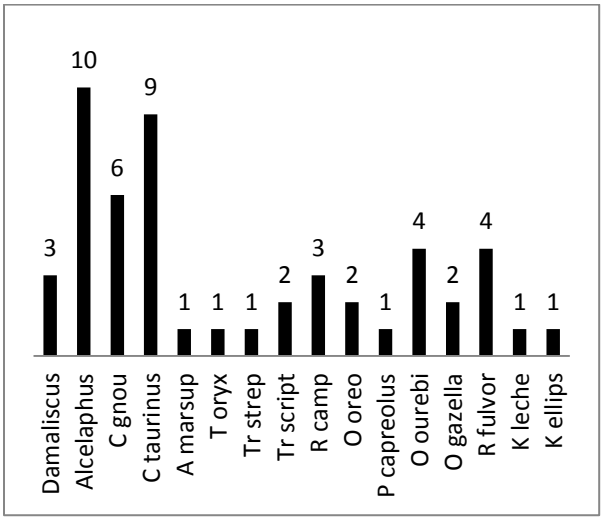


Figure 4.3 DFA results for SKHR using all fossils (MNI).

4.3.2.2 Results of DFA using the typicality probability approach

Of the 185 fossils, 118 yielded typicalities ≥0.15. Figure 4.4 shows the data converted to MNIs. A total of 37 individuals were recognized from the site. This site is taxonomically diverse with 14 species represented. The Alcelaphini predominate, making up 46% of the assemblage. *D. dorcas* comprises 5% of the assemblage. *A. buselaphus* is the most abundant bovid identified and makes up 22%. *C. gnou* comprises 8% of the assemblage while *C. taurinus* is 11%. *A. marsupialis* makes up 3% of the assemblage. Only one species of Tragelaphini was identified, *Tr. scriptus*, comprising 2% of the assemblage. Four Neotragini species are represented. *R. campestris* comprises 8%, *O. oreotragus* is 5%, *P. capreolus* makes up 3% while *O. ourebi* is 11%. Eleven percent of the assemblage is made up of *O.*

gazella. Three Reduncini species classified above the 0.15 typicality: *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*. These species comprise 11%, 3% and 3% of the assemblage, respectively.

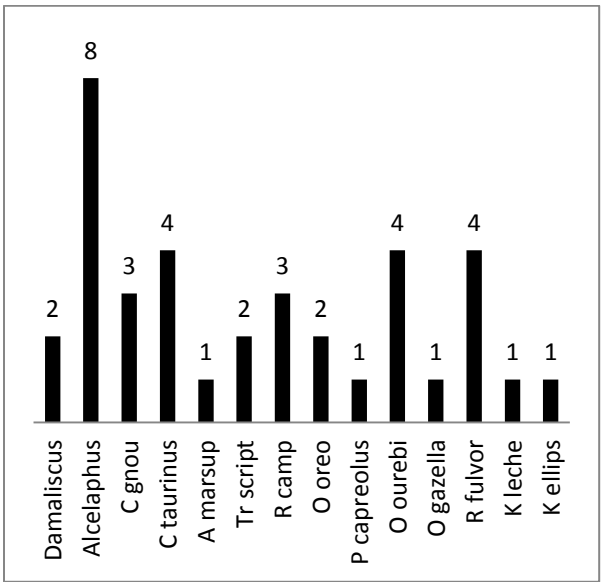


Figure 4.4 DFA results for SKHR using fossils with a typicality of ≥0.15 (MNI).

Sixty seven fossils classified with a <0.15 typicality, thus two additional DFA tests were run on the data. Follow up analysis 1 was performed on a database consisting of the known modern specimens and all of the fossils with a <0.15 typicality. The fossils were given an *a priori* identification based on the posterior probability approach. The goal of this analysis is to see if the fossils will classify above the 0.15 threshold when they are given an *a priori* designation. None of the fossils classified above the 0.15 threshold when Follow up analysis 1 was performed. Therefore, these results suggest that these fossils are not members of one of the reference groups.

Follow up analysis 2 involved a database where the fossils that classified above the 0.15 typicality have an *a priori* designation from the posterior probability approach. They are

treated as the known reference sample in the DFA. The fossils with a typicality of <0.15 were designated as unknowns in the database. When a DFA was performed on the database, none of the unknown fossils classified above the 0.15 typicality probability. Thus, these fossils are likely not members of one of the modern reference groups. The possibility exists that these are either fossil representatives of bovid species not known in South Africa today, or that they are representatives of extinct species. The information from these fossils will be retained for future study but will not be used in this analysis.

4.3.2.3 Comparison of the classification results using the posterior probability approach and the and typicality probability approach

The faunal lists developed using the posterior probability approach and the typicality probability approach were compared to assess differences between the assemblages. The chord distance yielded a measure of 0.3021. This value suggests that differences exist between the lists. This measure means that while there is overlap in the proportions of species in the lists, there are also some important differences (Table 4.2). Two species did not classify above the 0.15 typicality probability: *T. oryx* and *Tr. strepsiceros*.

The proportions of bovids are different between the lists. The proportions of four of the species decreased relative to the typicality threshold: *D. dorcas*, *C. gnou*, *C. taurinus* and *O. gazella*. The proportions of the remaining nine species increased when the typicality probability approach was used. In particular, the proportions of *O. ourebi* and *R. fulvorufula* each increased significantly from 8% to 11%.

	Table 4.2 SKHR MNI results of DFA																
	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	R camp	O oreo	P capreolus	O ourebi	O gazella	R fulvor	K leche	K ellips	Total
SK M1 HR MNI of all data-posterior	3	10	6	9	1	1	1	2	3	2	1	4	2	4	1	1	51
%SK M1 HR MNI of all data-posterior	6	20	12	18	2	2	2	4	6	4	2	8	4	8	2	2	
MNI of data with >0.15 typ	2	8	3	4	1			2	3	2	1	4	1	4	1	1	37
%MNI of data with >0.15 typ	5	22	8	11	3			5	8	5	3	11	3	11	3	3	

4.3.2.4 Paleoenvironmental implications using the posterior probability approach

4.3.2.4.1 Alcelaphini

Sixteen species were classified at Swartkrans Member 1 Hanging Remnant (Figure 4.3). The environment has a strong component of secondary grasslands, based on the high proportions of Alcelaphini including *D. dorcas*, *A. buselaphus*, *C. gnou* and *C. taurinus*. The Alcelaphini collectively make up more than half of the assemblage, 56%. In fact, *A. buselaphus* comprises a significant 20% of the assemblage and *C. taurinus* comprises 18%. *C. gnou* is represented by 12% while *D. dorcas* is represented by 6%. According to Sponheimer et al. (2003), these species are almost exclusively grazers and obtain 94+ % of their diet from C_4 grasses. Thus, the environmental indicators from these four Alcelaphini play a strong role in the overall environment for SKHR and suggest that secondary grasslands, likely with some patchy woodland dominated the site, and a permanent water source to fulfill the water requirements of *D. dorcas* and *C. taurinus*.

4.3.2.4.2 Antilopini

Two percent of the assemblage is made up of *A. marsupialis*. This species is a browser that subsists on the shrubs and succulents that are available in secondary grassland

habitats. Thus, the ecological indicators of this species support the Alcelaphini indicators that a strong secondary grassland habitat existed at SKHR.

4.3.2.4.3 Tragelaphini

T. oryx, *Tr. strepsiceros* and *Tr. scriptus* were identified when the posterior probabilities were used. *T. oryx* and *Tr. strepsiceros* both comprise 2% of the assemblage while *Tr. scriptus* represents 4%. These browsers suggest that trees and shrubs existed in the environment at the time of deposition. *T. oryx* tends to occupy secondary grassland habitats with sufficient concentrations of trees and shrubs, *Tr. strepsiceros* prefers woodlands and *Tr. scriptus* is usually found in a bushland and thicket habitat. Thus, all of these species suggest that the environment was more than just secondary grasslands but there was a considerable component of shrubs and trees in the vicinity.

While *T. oryx* is water independent, *Tr. scriptus* is usually found near water, *Tr. strepsiceros* needs to drink every few days. Thus, the ecological indicators of these species suggest that a permanent water source was also in the vicinity of SKHR.

4.3.2.4.4 Neotragini

All four Neotragini species were identified at SKHR. *R. campestris* represents 6% of the assemblage, *O. oreotragus* makes up 4% while *P. capreolus* comprises 2% and *O. ourebi* makes up 8% of the assemblage. *R. campestris*, *O. oreotragus* and *P. capreolus* are browsers while *O. ourebi* is a fresh grass grazer. *R. campestris occupies* open woodlands habitats with bushland and thickets. *O. oreotragus* prefers the woodland and rocky habitats. *P. capreolus* is usually found in the grassland savannahs while *O. ourebi* prefers edaphic grasslands. The

environment that best describes the ecological indicators of these four species consists of a grassland savannah with sufficient quantities of shrubs and trees as well as a permanent water source with edaphic grasslands in the vicinity.

4.3.2.4.5 Hippotragini

One Hippotragini, *O. gazella*, was identified when the typicality threshold was used. This grazer comprises 4% of the assemblage, prefers to live in grassland/plains and is not dependent on water. Thus, this species contributes a grassland component to the reconstruction of the environment.

4.3.2.4.6 Reduncini

Three Reduncini species were identified at this site: *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*. *R. fulvorufula* is a grazer whose diet consists of 99% of C_4 grasses. This species usually prefers grassland/plains that are associated near hills/mountains. *K. leche* and *K. ellipsiprymnus* are both highly water dependent and occupy edaphic grasslands though *K. leche* is a mixed feeder and *K. ellipsiprymnus* is a grazer. These species suggest that a grassland and likely some woodland habitat components existed at the site with a permanent water source.

4.3.2.4.7 Summary

Overall, the secondary grassland component predominates in this assemblage. It is likely that a secondary grassland existed in the vicinity with sufficient trees and shrubs for the browsers as well as varying degrees of open woodland. *O. oreotragus* indicates that a

nearby hill or mountain existed during the time of deposition. The ecological indicators of the species also indicate that a permanent, more substantial water source existed in the vicinity of the site.

4.3.2.5 Paleoenvironmental implications using the typicality probability approach

4.3.2.5.1 Alcelaphini

Four Alcelaphini at the site compose 46% of the assemblage. The abundance of these four grazers suggests that a secondary grassland habitat prevailed. In addition, both *D. dorcas* and *C. taurinus* are water dependent and require water daily while *A. buselaphus* and *C. gnou* are only somewhat water dependent and require water every few days. Thus, the ecological requirements of these bovids suggest that abundant secondary grasslands were in the vicinity of the site with a nearby permanent water source.

4.3.2.5.2 Antilopini

Three percent of the assemblage consists of *A. marsupialis*. This species is a browser that also lives in secondary grasslands. The ecological requirements of *A. marsupialis* build on the secondary grasslands proposed by the Alcelaphini by suggesting that a sufficient component of shrubs and forbs must have also been available in the secondary grassland habitat.

4.3.2.5.3 Tragelaphini

Five percent of the assemblage is made up of the Tragelaphini *Tr. scriptus*. The presence of this browser suggests that a dense vegetation with bushland and thickets was also

available at the site in addition to the grasslands. This species is usually found near water. Thus, the ecological requirements of this species likely indicate that a permanent water source was available.

4.3.2.5.4 Neotragini

Four Neotragini species were identified at SKHR when the typicality threshold was used. *R. campestris* comprises 8% of the assemblage. Five percent of the assemblage is represented by *O. oreotragus*, 3% by *P. capreolus* and 11% by *O. ourebi*. These species suggest that a mosaic environment existed at SK M1 consisting of open woodlands with nearby grassland savannah, possibly on a hill or mountainside as both *O. oreotragus* and *P. capreolus* prefer a rocky, mountainous habitat. A permanent water source with water-logged soils was also available at the site as *O. ourebi* tends to occupy edaphic grasslands.

4.3.2.5.5 Hippotragini

O. gazella comprises 3% of the assemblage. This species is a grazer and suggests that a grassland/plains component was evident at the site. *O. gazella* is not dependent on water. Thus, this species provides further evidence for a grassland component at the site during the time of deposition.

4.3.2.5.6 Reduncini

Eleven percent of the assemblage is made up of *R. fulvorufula*. This species is almost entirely a C_4 grassland grazer and is predominately found in grassland/plains situated on hills

and mountains. *K. leche* and *K. ellipsiprymnus* each represent 3% of the assemblage and indicate that a permanent water source, such as a wetland or vlei, was likely in the area.

4.3.2.5.7 Summary

Using the typicality threshold, the reconstructed environment for SKHR has a significant grassland savannah component that has sufficient herbs and shrubs for low level browsers. The margins of the area consisted of a denser vegetation than previously thought was prevalent at the site. A larger, more substantial water source was also in the area probably contributing to a wetland habitat. Thus, these species suggest that they likely lived in a grassland savannah with an open woodland component and a permanent water source.

4.3.2.6 Comparison between paleoenvironmental implications using the posterior probability approach and the typicality probability approach

The reconstructed environments for SKHR differ depending on which classification scheme is used. To start, two species of Tragelaphini are missing from the typicality MNI data. The absence of these species reduces the amount of tree and shrub vegetation required in the reconstructed environment. The reconstructions also differ in that the proportions of species from one list to the next differ. For example, when the posterior probability was used, *C. taurinus* comprised 18% of the assemblage but when the typicality probability threshold was used, the species comprises 11% of the assemblage. The results of this analysis demonstrate that the classification schemes used by an analyst can affect the paleoenvironmental reconstructions.

4.3.3 Swartkrans Member 1- Lower Bank, SKLB

4.3.3.1 Results of the DFA using posterior probabilities

Only 45 fossils from the Lower Bank of Member 1 could be digitized for this study. Twenty individuals were found in the assemblage, representing 10 different species (Figure 4.5). The Alcelaphini represent 45% of the sample. *C. taurinus* is the one of the most abundant bovids making up 20% of the assemblage. *C. gnou* and *A. buselaphus* each represent 10% while *D. dorcas* makes up 5% of the assemblage. The Antilopini *A. marsupialis* is also very abundant in the assemblage making up 20%. The other most abundant bovid is *P. capreolus* comprising 15%. The remaining bovids, *Tr. strepsiceros*, *O. oreotragus*, *K. leche* and *K. ellipsiprymnus* each contribute to 5% to the assemblage.

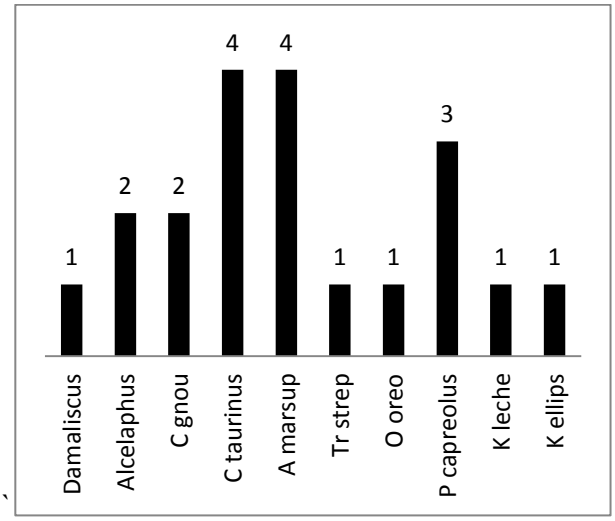


Figure 4.5 DFA result for SKLB using all fossils (MNI).

4.3.3.2 Results of the DFA using typicality probability approach

When the typicality threshold is employed, 24 of the 45 fossils had a typicality probability high enough to be used. Nine individuals were recovered representing six species

(Figure 4.6). Three species of Alcelaphini are represented: *A. buselaphus*, *C. gnou* and *C. taurinus*. *C. taurinus* makes up 22% of the assemblage while *A. buselaphus* and *C. taurinus* each represent 11% of the assemblage. Twenty-two percent of the assemblage was also made up of *A. marsupialis* and *P. capreolus*. *O. oreotragus* comprises 11% of the assemblage.

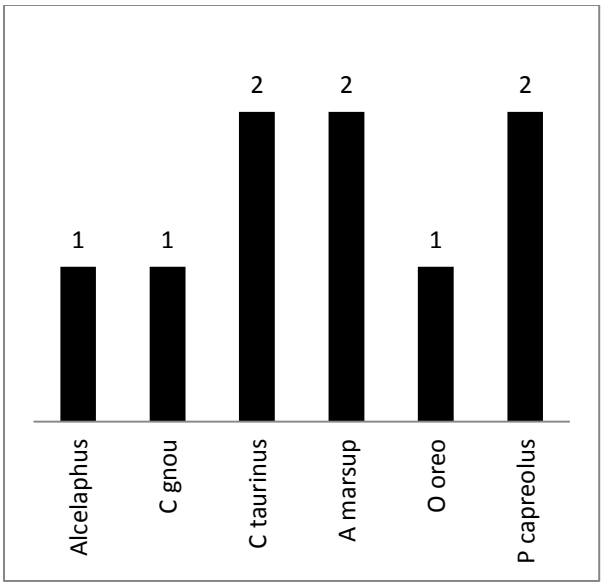


Figure 4.6 DFA results for SKLB using the fossils with a typicality of ≥0.15 (MNI).

The remaining 21 fossils that classified with a <0.15 typicality underwent two additional DFA analyses. The fossils with <0.15 typicality were not able to be identified accurately when the fossils were assigned an *a priori* name in Follow up analysis 1. Follow up analysis 2 also did not produce results useful for identifying these fossils. When the fossils that had a ≥0.15 typicality were used as the known groups and the fossils with a <0.15 typicality were the unknowns in the DFA, none of the fossils classified above the 0.15 typicality probability.

4.3.3.3 Comparison of the classification results using posterior probability approach and the typicality probability approach

The classification results reveal that differences exist between the assemblages depending on which classification method is used (Table 4.3). The chord distance measure, establishing how dissimilar two faunal lists are, resulted in a distance of 0.4158. A chord distance measure of 0.4158 suggests that important differences exist between the assemblages. Four of the species recognized when the posterior probabilities are used did not classify with a ≥0.15 typicality: *A. buselaphus*, *Tr. strepsiceros*, *K. leche* and *K. ellipsiprymnus*. The absence of these species means that only 6 species are represented in the assemblage. The omission of the four species will have a dramatic effect on the reconstruction of the environment. In addition, the proportions of the species change depending on which classification scheme is used. The proportions of bovids increased for all six species when the typicality probabilities are used. In fact, the proportions of the *D. dorcas* and *O. oreotragus* more than doubled. These results indicate that substantial differences exist between these reconstructed assemblages depending on the classification scheme used.

Table 4.3 SKLB results of DFA

	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	Tr strep	O oreo	P capreolus	K leche	K ellips	Total
SKX M1 LB MNI of all data-posterior	1	2	2	4	4	1	1	3	1	1	20
%SKX M1 LB MNI of all data-posterior	5	10	10	20	20	5	5	15	5	5	
MNI of data with >0.15 typ	1		1	2	2		1	2			9
%MNI of data with >0.15 typ	11		11	22	22		11	22			

4.3.3.4 Paleoenvironmental implications using posterior probabilities

4.3.3.4.1 Alcelaphini

The Alcelaphini dominate the assemblage comprising 45% of the assemblage. These four species indicate the strong presence of secondary grasslands were present at the site, with perhaps some open woodland habitat for *A. buselaphus*. *D. dorcas* is water dependent and *A. buselaphus* also required regular water. Thus, these species suggest an abundance of grassland, possibly with some tree coverage and a permanent water source.

4.3.3.4.2 Antilopini

A. marsupialis represents 22% of the assemblage. This species is indicative of extensive, open grasslands such as a secondary grassland habitat, though it requires browse foods such as shrubs and forbs.

4.3.3.4.3 Tragelaphini

One species of Tragelaphini was identified at the site: *Tr. strepsiceros.* This species is a browser subsisting on foods such as herbs and fallen fruit. *Tr. strepsiceros* is a woodland species that does not venture into open grasslands, nor into denser forests. Thus, the ecological indicators of that species suggest an open woodland habitat was in the nearby vicinity.

4.3.3.4.4 Neotragini

Two species of Netograni were recognized at the site comprising 5% and 15%, respectively: *O. oreotragus* and *P. capreolus*. Both of these species prefer rocky habitats with grasslands, some tree cover and sufficient C_4 foods in the vicinity.

4.3.3.4.5 Reduncini

K. leche and *K. ellipsiprymnus* were classified at the site. Each species represents 5% of the assemblage and require daily water. The ecological indicators of these species indicate that a permanent water source, such as a wetland or vlei, was likely in the area.

4.3.3.4.6 Summary

The Alcelaphini share a preference for secondary grasslands, though *A. buselaphus* often prefers more wooded areas. The presence of *A. marsupialis*, an animal with a distinct preference for open grassy areas, combined with *C. gnou* and *C. taurinus*, indicate that secondary grasslands are a predominant component of this environment, though *Tr. strepsiceros* indicates the presence of some level of relatively wooded habitat. *P. capreolus* and *O. oreotragus* prefer rocky areas with some cover, leading to a reconstruction of a mosaic environment. A permanent water source is demonstrated by the two species of *Kobus*, either in the form of an edaphic grassland or perhaps a standing body of water.

4.3.3.5 Paleoenvironmental implications using the typicality probability approach

4.3.3.5.1 Alcelaphini

Three Alcelaphini species identified when the typicality probabilities were used. The species are all grazers and indicate that a significant secondary grassland component existed at the site. The water requirements of *D. dorcas* and *C. taurinus* suggest that a water source was in the vicinity of the site.

4.3.3.5.2 Antilopini

A. marsupialis represents 20% of the assemblage. This species is a browser subsisting on shrubs and succulents. This species also suggests that secondary grassland was prevalent at the site but further suggests that low level shrubs and trees were there at the time of deposition.

4.3.3.5.3 Neotragini

O. oreotragus was identified at the site and makes up 11% while *P. capreolus* was also found at the site and makes up 22%. Both of these species are browsers and prefer rocky habitats. The ecological indicators of these species suggest a habitat of grassland with scattered groups of trees. The resultant environment would likely appear similar to a lightly wooded grassland in a rocky habitat.

4.3.3.5.4 Summary

When the typicality probability approach is employed, only 6 species are used to reconstruct the environment. The three Alcelaphini species and one Antilopini species

suggest that secondary grassland habitats predominated with scattered groups of low level trees and shrubs for *A. marsupialis*. The bovids also indicate that a rocky hillside covered in grasses with sufficient concentrations of trees and shrubs. The water requirements of *D. dorcas* and *C. taurinus* indicate that water was present in the vicinity. In sum, open, secondary grasslands with varying concentrations of trees and shrubs likely dominated the environment. A grassy hillside with some tree cover was also likely evident at the site.

4.3.3.5.5 Comparison between paleoenvironmental implications using the posterior probability approach and the typicality probability approach

The greatest difference between the two paleoenvironmental reconstructions is the amount of tree cover indicated by the bovids. Specifically, more dense habitats with tree coverage are evident when the posterior probabilities are used than when a typicality threshold is used. *A. buselaphus* and *Tr. strepsiceros* suggest a denser environment when the posterior probabilities were used. These two species did not classify above the 0.15 typicality probability and therefore were not used in the reconstruction. Another major difference is the lack of Reduncini in the assemblage when the typicalities were used. These results demonstrate that waterlogged soils such as floodplains or vleis would not be reconstructed in the environment if typicality probabilities were used. The paleoenvironmental reconstructions highlight how different the results can be depending on what classification methods are used.

4.3.4 Swartkrans Member 2- SKM2

4.3.4.1 Results of the discriminant function analysis using the posterior probability approach

Swartkrans Member 2 consists of the largest sample digitized in this study with 563 dental specimens. Figure 4.7 illustrates the MNI data of the DFA results when the posterior probabilities are relied upon to identify all of the fossils from Member 2. A total of 132 individuals from 17 of the 20 modern reference species were identified for this site. The Alcelaphini comprise 11% of the assemblage. *D. dorcas*, *A. buselaphus* and *C. taurinus* each comprise 3% while *C. gnou* comprised 2% of the assemblage. *A. marsupialis* is well represented at the site and makes up 22%. Two species of Tragelaphini were identified though *Tr. strepsiceros* represents 1% of the assemblage while *Tr. scriptus* represents a significant 23% of the assemblage. All four Neotragini are represented at the site. The relative abundance of *R. campestris* is 4%, *O. oreotragus* is 8%, *P. capreolus* is 15% and *O. ourebi* is 6%. Two Hippotragini were classified each comprising only 1% of the assemblage: *H. niger* and *H. equinus*. Four Reduncini species were represented: *R. arundinum*, *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*. *R. arundinum*, *K. leche*, and *K. ellipsiprymnus* each represent 2% of the assemblage while *R. fulvorufula* represents 4%.

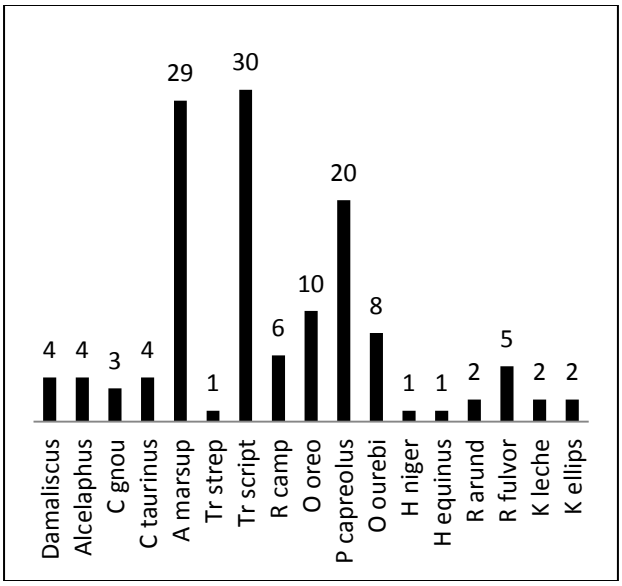


Figure 4.7 DFA results of SKM2 using all fossils (MNI).

4.3.4.2 Results of the discriminant function analysis using typicality probability approach

Four hundred twenty fossils classified with a typicality of ≥0.15. Figure 4.8 displays the results of the MNI of the DFA of these fossils. A total of 114 individuals from 14 species were calculated. While all four Alcelaphini are represented, they contribute a small amount. *D. dorcas*, *A. buselaphus* and *C. gnou* each comprise 2% each of the assemblage while *C. taurinus* makes up 3%. *A. marsupialis*, on the other hand, represents a significant portion of the assemblage, 23%. *Tr. scriptus* makes up another significant component of the assemblage, 24%. *R. campestris* is the least represented Neotragini at 4% while *O. oreotragus* is 8%, *P. capreolus* is 18% and *O. ourebi* is 6%. All four Reduncini species were identified at Member 2. *R. arundinum* comprises 1% of the assemblage, *R. arundinum* makes up 4% and *K. leche* and *K. ellipsiprymnus* each comprise 2% of the assemblage.

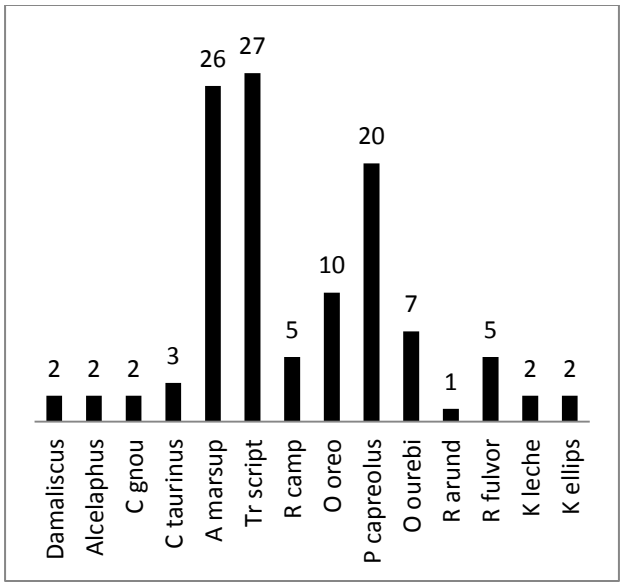


Figure 4.8 DFA results of SKM2 using the fossils with a typicality of ≥0.15 (MNI).

The remaining 143 fossils that classified with a <0.15 typicality were analyzed again using two different types of DFA. In Follow up analysis 1, the fossils were reanalyzed in the database of known fossils using the classifications from the posterior probability approach. The results of this DFA showed the fossils either misclassified or classified with a <0.15 typicality probability. The identifications of these teeth could not be determined and they were not used in the reconstruction of the environment.

Follow up analysis 2 involved using the fossil bovid species that classified above the threshold as the known groups, while the fossils with a <0.15 typicality were the unknowns in the DFA. None of the fossils classified above the 0.15 typicality probability when the DFA was performed. These fossils will be reassessed in the future but were not used to reconstruct the environments in this study.

4.3.4.3 Comparison of the classification results using posterior probability approach and the typicality probability approach

The results of the classifications using the posterior probability approach and the typicality probability approach indicate that some differences exist between the two assemblages. The chord distance measure showing whether faunal dissimilarity exists at the sites, yielded a measure of 0.07898. While this number is relatively low, it still suggests that there are subtle differences between the assemblages. To start, three species did not classify with a ≥0.15 typicality that did classify when the posterior probabilities were used: *Tr. strepsiceros*, *H. niger* and *H. equinus* (Table 4.4). The absence of these species in the assemblage using the typicality probability will cause the paleoenvironmental reconstruction to be different than the reconstruction using the posterior probability.

Another difference between the results is the proportions of the species, as many of them changed depending on which approach was used. In fact, the proportions of grazers changed from 49% to 45% when the typicality approach was used.

Table 4.4 SK M2 results of DFA

	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	Tr strep	Tr script	R camp	O oreo	P capreolus	O ourebi	H niger	H equinus	R arund	R fulvor	K leche	K ellips	Total
SK M2 MNI of all data-posterior	4	4	3	4	29	1	30	6	10	20	8	1	1	2	5	2	2	132
%SK M2 MNI of all data-posterior	3	3	2	3	22	~1	23	5	10	15	6	~1	~1	2	4	2	2	
MNI of data with >0.15 typ	2	2	2	3	26		27	5	10	20	7			1	5	2	2	114
%MNI of data with >0.15 typ	2	2	2	3	23		24	4	9	18	6			~1	4	2	2	

4.3.4.4 Paleoenvironmental implications using the posterior probability approach

4.3.4.4.1 Alcelaphini

Four species of Alcelaphini are represented at Member 2. These species indicate that a portion of the environment consisted of a type of grassland savanna, specifically, secondary grasslands with widely scattered groups of trees, as *A. buselaphus* often occupies an open woodland habitat. *D. dorcas* and *C. taurinus* suggest that a water source was available in the vicinity.

4.3.4.4.2 Antilopini

A large number of *A. marsupialis* was identified at SK M2, 22%. This result suggests that the environment at SK M2 likely consisted of an abundance of open secondary grasslands with sufficient amounts of shrubs and succulents for subsistence.

4.3.4.4.3 Tragelaphini

Two species of Tragelaphini were identified: *Tr. strepsiceros* and *Tr. scriptus*. Both of these species are browsers that subsist on foods such as herbs, fruits and legumes. These species indicate that a woodland habitat with areas of dense bushes and thickets existed at the site. *Tr. scriptus* is usually found in dense thickets near water while *Tr. strepsiceros* needs to drink every few days. Thus, these species also suggest that a permanent water source was in the area at the time of deposition.

4.3.4.4.4 Neotragini

Four species of Neotragini were identified at SK M2 when the posterior probabilities were used. *R. campestris* comprises 5% of the assemblage. Ten percent of the assemblage is

represented by *O. oreotragus*, 15% by *P. capreolus* and 6% by *O. ourebi*. The ecological indicators of these species suggest that a mosaic environment existed consisting of open woodlands with nearby grassland savannah, possibly on a hill or mountainside. A permanent water source with water-logged soils was also available at the site as *O. ourebi* tends to occupy edaphic grasslands.

4.3.4.4.5 Hippotragini

H. niger and *H. equinus* represent the Hippotragini at SK M2 but they each only comprise about 1% of the assemblage. These species suggest that a habitat of lightly wooded secondary grassland was found at the site. Both of these species are water dependent, suggesting a nearby water source.

4.3.4.4.6 Reduncini

Four Reduncini species were identified at SK M2 when the posterior probabilities were relied upon for classification. *R. fulvorufula* represents 4% of the assemblage while *R. arundinum*, *K. leche* and *K. ellipsiprymnus* each comprise 2% of the assemblage. SK M2 is the first time *R. arundinum* was classified at a site in this study. This species is a grazer and, according to Sponheimer et al. (2003), 96% of its diet consists of C_4 grasses. This Reduncini likes to frequent tall grasses for protection. Often, these bovids inhabit tall grasses near drainage lines such as edaphic grasslands. *R. arundinum* needs to drink water every few days. The ecological indicators of the Reduncini at this site suggest that a grasslands/plains habitat was prevalent at the site with a small component of scattered groups of trees. A nearby, substantial water source saturating the soils and allowing aquatic sedges and grasses to grow

also probably existed at the site, as *R. arundinum*, *K. leche* and *K. ellipsiprymnus* tend to inhabit edaphic grasslands. It is likely that some grassy hills were also in the vicinity.

4.3.4.4.7 Summary

The assemblage suggests that a mosaic environment existed at the site where three main habitats likely overlapped to make the ecological community at SK M2. The environment consisted of open grasslands with nearby open woodlands and areas of bushes and thickets. Grassland savannahs associated with a hill existed with scattered areas of shrubs and low level trees sufficient for browsing. A permanent water source existed in the environment causing a wetland, or some form of water logged soils, to also occur in the environment.

4.3.4.5 Paleoenvironmental implications using the typicality probability approach

4.3.4.5.1 Alcelaphini

All four Alcelaphini species were identified when the typicality threshold was used to classify the fossils. *D. dorcas*, *A. buselaphus* and *C. gnou* each represent 2% of the assemblage while *C. taurinus* represents 3%. These species subsist almost entirely on C_4 grasses and prefer to occupy secondary grasslands with some wooded component. Thus, the environment based on these species suggests that a secondary grassland habitat existed at the site with scattered areas of open woodlands. In addition, the water requirements of these bovids suggest that a permanent and more substantial water source existed during the time of deposition than exists in the area today.

4.3.4.5.2 Antilopini

A. marsupialis also comprise a significant part of the assemblage when the typicality probability approach is used. The MNI of *A. marsupialis* is 26 and represents 23% of the entire assemblage. The ecological indicators of this species suggest that an open grassland with sufficient vegetational coverage of shrubs and succulents predominated at SK M2.

4.3.4.5.3 Tragelaphini

Tr. scriptus was also abundant at SK M2 and represents 24% of the assemblage. The ecological indicators of this species suggest that dense coverage of bushes and interwoven thickets, likely near water, were prevalent at the site.

4.3.4.5.4 Neotragini

Four species of Neotragini classified above the 0.15 typicality threshold. Four percent of the assemblage is made up of *R. campestris*. *O. oreotragus* comprises 9% of the assemblage. *P. capreolus* was prevalent at the site representing 18% of the assemblage. *O. ourebi* represents 6% of the assemblage. These species indicate that a mosaic of habitats likely existed at the site. The site consisted of an open woodland habitat interspersed with grassland savannah probably on a hill or a rocky habitat in the area. The open woodlands likely had some dense areas of low shrubs, bushes and thickets. *O. ourebi* tends to prefer edaphic grasslands; therefore, this species suggests that a permanent water source was available water-logging the soils and providing aquatic sedges and grasses.

4.5.4.5.5 Reduncini

All four Reduncini species were classified when the 0.15 typicality threshold was used. *R. arundinum* is evident at the site, though its proportion of the assemblage is barely 1%. *R. fulvorufula* is the most common Reduncini found at the site and comprises 4% of the assemblage. *K. leche* and *K. ellipsiprymnus* each comprise 2% of the assemblage.

These species indicate that a grassland habitat existed on the plains and hills in the vicinity of the site with tall grasses sufficient for coverage. This grassland habitat would have been interspersed with groups of trees and low shrubs for browsing. Furthermore, edaphic grasslands would have been represented at the site based on the fact that *R. arundinum, K. leche and K. ellipsiprymnus* tend to inhabit edaphic grasslands. Edaphic grassland habitats suggest a permanent water source in the area of the site.

4.3.4.5.6 Summary

The ecological indicators of the species identified using the typicality probability approach at SK M2 signify that a mosaic of habitats existed in the past. The environment consists of an area rich in grasses with varying concentrations of woodlands across the habitat. Sections of the environment with higher tree coverage also exhibit some dense, interwoven bushlands and shrubs. A permanent water source is surrounded by aquatic sedges and grasses indicating an edaphic grassland is present.

4.3.4.5.7 Comparison between paleoenvironmental implications using the posterior probability approach and the typicality probability approach

The paleoenvironments for Member 2 using the posterior probability approach and the typicality probability approach illustrate that some overlap occurs between the assemblages but that enough differences exist between the two faunal lists that the environments would be reconstructed differently. For example, both assemblages indicate a strong grassland habitat interspersed with patches of shrubs and succulents that gets denser and more concentrated, becoming bushlands and thickets. A hill or small mountainside covered in tall grasses with some small trees and shrubs is indicated by each assemblage. Both assemblages suggest a permanent water source provided saturated soils and edaphic grasslands. However, the reconstruction using the typicality probability has a reduced amount of woodlands. The absence of *H. equinus* further indicates that while open woodlands and secondary grasslands with open woodlands existed in the environment, the same concentrations of woodlands and not required in the reconstruction.

While the relative abundances of the bovids from each probability approach are comparable, some differences exist. The abundance of *P. capreolus* increased in proportion by 3% when the typicality probability approach was used. The proportion of Alcelaphini also decreased when the typicality probability approach was used, suggesting that there were changes in the grassland coverage. Thus, while the differences between the two assemblages using the posterior probability and the typicality probability might not appear dramatic, they can be important when assessing the overall picture of the ecosystem and when assessing change over time.

4.3.5 Swartkrans Member 3- SKM3

4.3.5.1. Results of the discriminant function analysis using the posterior probability approach

One hundred forty five fossils were digitized from Swartkrans Member 3. A total of 41 individuals from 16 species were calculated for this Member (Figure 4.9). Appendix II displays the MNI results of the posterior probability approach for all of the fossils. Alcelaphini dominate the assemblage making up 37% of the assemblage. *D. dorcas* comprises 5% of the assemblage and *A. buselaphus* comprises 7%. *C. gnou* makes up 10% while *C. taurinus* makes up 15% of the assemblage. The Antilopini *A. marsupialis* also makes up 15% of the assemblage. Three species of Tragelaphini were identified at the site. *Tr. strepsiceros* comprises 2% of the assemblage while *T. oryx* and *Tr. scriptus* each comprise 5%. All four Neotragini species are represented. *R. campestris* and *O. oreotragus* each make up 2% of the assemblage. *P. capreolus* is abundant at the site representing 10%. *O. ourebi* makes up 5%. The two Hippotragini species at the site, *H. niger* and *O. gazella* represent 2% and 5% of the assemblage, respectively. Two Reduncini species were identified: *R. arundinum* and *K leche*. Both of these species represent 2% of the assemblage.

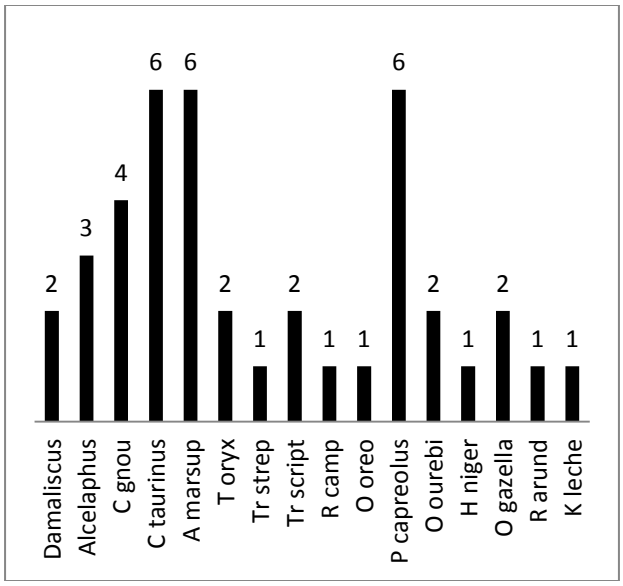


Figure 4.9 DFA results for SKM3 using all fossils (MNI).

4.3.5.2 Results of the discriminant function analysis using the typicality probability approach

Eighty-seven of the Swartkrans M3 fossils had a typicality of ≥0.15 and were used in this analysis. SK M3 consists of 31 individuals from 14 different species (Figure 4.10). *D. dorcas* and *A. buselaphus* each represent 6% of the assemblage. *C. gnou* comprises 3% and *C. taurinus* makes up 16% of the assemblage. The two Tragelaphini, *Tr. strepsiceros* and *Tr. scriptus*, each comprise 3% of the assemblage. Four Neotragini were classified using the typicality probability. *R. campestris* and *O. oreotragus* each comprise 3% of the assemblage while *P. capreolus* makes up 19% and *O. ourebi* represents 6%. One Hippotragini species was identified at Swartkrans M3, *O. gazella*, and makes up 3% of the assemblage. Two Reduncini species, *R. arundinum* and *K. leche*, were identified and each comprise 3% of the assemblage.

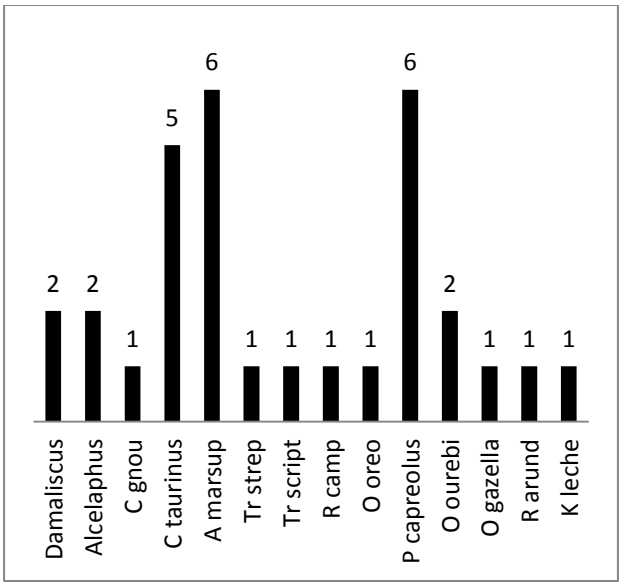


Figure 4.10 DFA results for SKM3 using the fossils with a typicality of ≥0.15 (MNI).

Fossils that classified with a <0.15 typicality were analyzed further using two Follow up analyses. In Follow up analysis 1, DFA was performed with all of the modern specimens and all of the fossils with a <0.15 typicality using the classifications previously assigned to the fossils by the first DFA. Two results emerged: the fossils misclassified as other bovids or classified correctly but with a typicality <0.15. This test demonstrates that the fossils that classified <0.15 are likely not members of one of the 20 modern references species used in this study.

In follow up analysis 2, the fossils that classified above the 0.15 threshold were used as the known groups, and the fossils with a <0.15 typicality were the unknowns in a DFA. None of the fossils classified above the 0.15 typicality probability when the DFA was performed. These fossils will be reexamined in the future but were not used to reconstruct the environment.

4.3.5.3 Comparison of the classification results using the posterior probability approach and the typicality probability approach

The results of the classification schemes using the posterior and typicality probabilities are shown in Table 4.5. A chord distance measure was used to determine how much faunal dissimilarity exists between assemblages. The results of this test reveal a distance of 0.2791. This result means that while there is substantial overlap between the lists, some important differences exist as well. Two major differences exist between the faunal lists: species composition and species proportions. First, two species did not classify above the *a priori* typicality rate of 0.15: *T. oryx* and *H. niger*. These species were identified when the posterior probabilities were used but did not have a high enough typicality to be presented with the typicality results. Thus, the composition of species differs between the lists. Since the faunal lists are used to reconstruct the past environment, different faunal lists will result in different paleoenvironmental reconstructions.

The second major difference between the assemblages is that the abundance of bovids changes depending on which probability approach is used. Specifically, the abundance of *D. dorcas*, *C. taurinus*, *A. marsupialis*, *Tr. strepsiceros*, *R. campestris*, *O. oreotragus*, *P. capreolus*, *O. ourebi*, *R. arundinum* and *K. leche* increased when the typicality probability approach was used as compared to the list from the posterior probability approach. Conversely, the proportions of *C. gnou*, *Tr. scriptus* and *O. gazella* decreased when the typicality probability approach was used as compared to the posterior probability approach data.

	Table 4.5 SKX M3 results of DFA																
	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	R camp	O oreo	P capreolus	O ourebi	H niger	O gazella	R arund	K leche	Total
SKX M3 MNI of all data	2	3	4	6	6	2	1	2	1	1	6	2	1	2	1	1	41
%SKX M3 MNI of all data	5	7	10	15	15	5	2	5	2	2	15	5	2	5	2	2	
MNI of data with >0.15 typ	2	2	1	5	6		1	1	1	1	6	2		1	1	1	31
%MNI of data with >0.15 typ	7	7	3	16	19		3	3	3	3	19	7		3	3	3	

4.3.5.4 Paleoenvironmental implications using posterior probabilities

4.3.5.4.1 Alcelaphini

The Alcelaphini have a strong presence in this assemblage. *D. dorcas* comprises 5% of the assemblage and *A. buselaphus* comprises 7%. *C. gnou* makes up 10% while *C. taurinus* makes up 15% of the assemblage. The four species of Alcelphini at the site suggest that a strong grassland habitat component, specifically, secondary grassland habitats predominated at the site with small patches of open woodlands and a permanent water source.

4.3.5.4.2 Antilopini

A. marsupialis represents an abundant part if the assemblage making up 15%. Thus, a strong component exists for the habitat required for *A. marsupialis* which overlaps with the Alcelaphini requirements. This species prefers to stay in the open grasslands but requires areas of shrubs and succulents for subsistence.

4.3.5.4.3 Tragelaphini

The tribe Tragelaphini makes up 12% of the assemblage and is represented by *T. oryx*, *Tr. strepsiceros* and *Tr. scriptus*. The Tragelaphini species suggest that an environment sufficient to sustain strict browsers was available in the area, and likely consisted of an open woodland habitat with an understory of thick bushes and a water source nearby.

4.3.5.4.4 Neotragini

Four Neotragini species were represented in varying concentrations. *R. campestris* and *O. oreotragus* each make up 2% of the assemblage. *O. ourebi* makes up 5% and *P. capreolus* is the most abundant Neotragini at the site representing 10%. These species suggest that an open to lightly wooded grassland with a nearby water source and a grassy hill predominated at the time of deposition.

4.3.5.4.5 Hippotragini

Two species of Hippotragini were identified at the SK M3 including *H. niger* representing 2% and *O. gazella* representing 5%. These two species are water dependent suggesting a nearby permanent water source in the vicinity. These species suggest that the environment included grasslands and woodlands in the vicinity, perhaps in the form of a relatively open woodland habitat.

4.3.5.4.6 Reduncini

R. arundinum and *K. leche* represent the Reduncini at the site, each comprising 2% of the assemblage. The ecological indicators of these species suggest that a permanent water

source with poor drainage existed at SK M3 allowing water-logged, saturated soils at the site, appropriate for edaphic grasslands.

4.3.5.4.7 Summary

These species suggest that the environment included an open, arid grassland, scattered with varying concentrations of trees and shrubs. The Alcelaphini indicate the strong presence of a grassland habitat, perhaps with some open woodlands. *A. marsupialis* also indicates that a grassland was in the vicinity but with sufficient browse for its survival, thus adding more vegetational coverage of shrubs and succulents to the overall environmental picture. The three Tragelaphini browser species also suggest that more vegetational coverage was at the site and indicate that an open woodland with some dense thickets existed. This suggested environment is appropriate for most of the Neotragini species identified here though indicators from *O. oreotragus* and *P. capreolus* also suggest that rocky hills were in the vicinity. The species indicate that a permanent water source was at the site in the past. Thus, the environment at SK M3 was a complex mosaic with ecological indicators of grasslands with scattered shrubs and trees. Denser vegetation including open woodlands and bushes and thickets were also likely in the area.

4.3.5.6 Paleoenvironmental implications using typicality probabilities

4.3.5.6.1 Alcelaphini

The Alcelaphini still have a strong presence when the typicality threshold is used. *D. dorcas* and *A. buselaphus* represent 7% of the assemblage, *C. gnou* makes up 3% while *C. taurinus* is the most abundant Alcelaphini representing 16%. The ecological indicators of the

species suggest that secondary grasslands predominated at the site, likely with small areas of open woodlands and a permanent water source.

4.3.5.6.2 Antilopini

A. marsupialis also plays a strong role in determining the environment as 19% of the assemblage is comprised of this species. This Antilopini indicates that an open grasslands with areas of shrubs and succulents were abundant at the site.

4.3.5.6.3 Tragelaphini

Tr. strepsiceros and *Tr. scriptus* each represent 3% of the assemblage and indicate that a strong woodland and bushland and thicket component existed at the site to sustain these strict browsers. These species also suggest that a water source was nearby.

4.3.5.6.4 Neotragini

Four Neotragini species were represented in varying concentrations. *R. campestris* and *O. oreotragus* each comprise 3% of the assemblage, *O. ourebi* makes up 7% and *P. capreolus* is the most abundant Neortagini at the site representing 19%. The Neotragini species suggest that a grassland savannah habitat with lightly wooded grassland, a nearby water source and a grassy hill predominated at the time of deposition.

4.3.5.6.5 Hippotragini

One species, *O. gazella* is identified at the site representing 3% of the assemblage. This grazer species indicates that open grasslands/plains habitat existed at the site.

4.3.5.6.6 Reduncini

R. arundinum and *K. leche* represent the Reduncini at the site and each comprises 3% of the assemblage, respectively. The ecological indicators of these species suggest that a permanent water source existed at SK M3 allowing water-logged, saturated soils such as floodplains at the site, appropriate for edaphic grasslands.

4.3.5.6.7 Summary

The species from SK M3 that classified with a ≥0.15 typicality threshold indicate that a significant component of the environment consists of grasslands including grasslands/plains and secondary grasslands with abundant shrubs and succulents and hills covered with grasses and interspersed with shrubs. Edaphic grasslands were also abundant at the site suggesting that a permanent water source creating water logged soils such as floodplains existed at SK M3. The species identified at the site indicate that a woodland with some bushland and thicket existed at the site enough to sustain browsers.

4.3.5.6.8 Comparison between paleoenvironmental implications using the posterior and typicality probabilities

The paleoenvironmental reconstructions for SK M3 differ depending on whether the posterior probability or a typicality probability threshold is used. First, two species are missing from the typicality MNI data: *T. oryx* and *H. niger*. The absence of these species reduces the amount of woodland coverage required in the environment.

The reconstructions also differ in that the proportions of species from one list to the next fluctuate. For example, when the posterior probability approach was used, *A.*

marsupialis and *P. capreolus* each comprised 15% of the assemblage but when the typicality probability approach was used, the species comprised 19% of the assemblage.

While both assemblages indicate that a grassland environment dominated, they differ in their amount of vegetational coverage that is reconstructed due to the differences in species composition and relative abundance between the two assemblages. These results further support that the paleoenvironmental reconstructions differ depending on the methods of classification an analyst chooses to run in an analysis.

4.3.6 Chord distances

Chord distances were used to statistically assess faunal dissimilarity. This test measures how different the assemblages are when using the MNI of bovids that were classified using the posterior probability approach against the MNI of bovids that were classified using the typicality probability approach. Table 4.6 illustrates the chord distance measures between the sites.

Table 4.6 Chart listing the chord distance measures from each site when the posterior probability results and the typicality probability results are compared to each other. An A after the site name means the posterior data was used and a T indicates the typicality data was used.

Locality comparisons	Chord distances
COD P-COD T	0.489335
SKHR P-SKHR T	0.3020927
SKLB P-SKLB2 T	0.41581
SKM2 P-SKM2 T	0.0789848
SKXM3 P-SKXM3 T	0.27918

A comparison of the posterior and typicality data from SKM2 yielded the lowest chord distance, 0.07898. The highest chord distance was the measure between Coopers D posterior and typicality data 0.489335. These results suggest that SKM2 posterior and typicality datasets are the most similar assemblages while Cooper's D posterior and typicality data are the least similar. The chord distances reflect the differences in species composition and relative abundance of the bovids. While some chord distances are larger than others, they all indicate that there are quantitative differences between the two assemblages that resulted from the two different classification schemes.

4.4 Discussion

4.4.1 Discriminant function analysis

Two sets of results were presented for each site: the classification results of the DFA using the posterior probability approach and using the typicality probability approach. The classifications from each probability approaches were compiled to make a faunal list for the assemblages. The environment was reconstructed for each assemblage, using both of the faunal lists. The side-by-side comparison of these two approaches highlights how the methods of classification can play a role in affecting the paleoenvironmental reconstruction.

The classification methods were compared to each other to see if differences existed between the two resulting data sets. Differences between the assemblages can be seen in the species composition, species proportions and the chord distances. The species composition changed at every locality when the typicality probability approach was used; specifically, the number of different of species decreased (Tables 4.1-4.5). The posterior probability approach identifies more species because it forces the fossils into one of the modern reference groups.

The typicality probability approach only incorporated the fossils that were within 85% of the variation of that species i.e. within the normal multivariate space of the species. Therefore, the number of species used to reconstruct an environment can change depending on which classification method a researcher chooses.

The proportion of each species also frequently changed depending on the classification approach. While the exact proportions of bovid species at a site are not considered a direct correlation to the past environment, the proportions are extremely important when assessing relative change in the proportion of bovid species over time across sites. In this study, some of the species proportions doubled depending on which probability was used (e.g. Table 4.1, *A. marsupialis*). The fact that the proportion of species frequently changes depending on the classification approach used further highlights how the methods an analyst chooses can have dramatic effects on the results.

The chord distances were also used to assess differences between the assemblages. When the results of the posterior probability approach and the typicality probability approach were statistically compared to each other, the distance measures demonstrated that differences existed between the datasets.

Therefore, the species composition, proportions and chord distance measures demonstrate that the classification systems yielded different results. This discrepancy means that not all of the fossils identified in the posterior probability approach and subsequently used in the reconstructed environment lie in the normal multivariate space of its modern reference species. Even though the assemblage from the posterior probability approach has more specimens and more species, there is not as much confidence in the classifications of the bovids as there is when the typicality probability approach is used. The results of the

typicality probability approach consist of less overall specimens and less species diversity to reconstruct the environment. However, there is a high amount of confidence in the identification of those species. Thus, if a researcher only includes the posterior probability DFA data, without taking into account the typicalities, they might incorrectly reconstruct an environment. The more robust typicality probability approach needs to be applied towards bovid classifications in order to ensure that the fossils identified as one of the reference species are in the normal multivariate space of that species. Precise bovid identifications are necessary because they are used to reconstruct past environments; accordingly, misidentified bovids lead to inaccurate paleoenvironmental reconstructions.

This study suggests that a typicality probability should be used when classifying unknown fossils. In this study, a threshold of 0.15 was used to classify the unknown fossils due to the fact that this threshold allows no more than 85% of the individuals in a group to classify closer to the group centroid than the fossil. The use of a typicality of 0.15 was chosen because it is statistically robust and reliable, meaning that there is a high amount of confidence in the classification results of that fossil. A conservative typicality probability is necessary when trying to assess unknown specimens in the fossil record if the analyst wants to identify them with a high amount of confidence.

This study has shown that the classification methods an analyst uses can play an important role in affecting the species composition and proportions of bovids found in an assemblage. A standardized approach will help eliminate analyst bias in the classification methods used after a tooth has been digitized. In turn, this approach will allow faunal lists from different researchers who use this standardized approach to be compared more confidently.

4.4.2 Fossils with a <0.15 typicality

A total of 282 fossils did not classify above the 0.15 typicality probability threshold. These fossils underwent additional analyses in order to try to determine the identification of the fossil. In Follow up analysis 1, a DFA test was performed where all specimens with a <0.15 typicality were given an *a priori* distinction. However, all of the fossils either misclassified, or classified at an unacceptably low typicality rate. This result means that these individuals are likely not one of the species in the reference sample. Thus, this test was inconclusive for helping to identify the unknown fossils.

Follow up analysis 2 involved a DFA analysis using only fossils. This test was performed in order to identify outliers. The possibility exists that the <0.15 typicality fossil might not fall in the normal multivariate range for the modern reference sample, but it does fall within the normal multivariate range of the fossil sample of that same species. The fossils with a ≥0.15 typicality probability were assessed against the fossils with a <0.15 probability. However, the results of this test were also inconclusive. None of the fossils classified with a typicality ≥0.15. This result means that these individuals are not fossil representatives of the modern species in the reference sample.

The inconclusive results of these tests are unfortunate as this means that the fossils with a <0.15 typicality cannot be reliably identified and, therefore, cannot be used to reconstruct the past environments. The exclusion of these fossils will undoubtedly affect the paleoenvironmental reconstructions presented in this study. At this time, this will likely result in discrepancies between the results from this study and previous studies. However, as this study and methodology expands, the unknown specimens will be identified with more

confidence. Future studies will reexamine these fossils in order to classify them with more confidence.

Appendix III lists the fossils that did not classify above the 0.15 threshold and their previous identifications from the literature (de Ruiter, 2003; de Ruiter et al., 2008; de Ruiter et al. 2009). The number of discrepancies between the identifications produced in this study and the ones from de Ruiter (2003), de Ruiter et al. (2008) and de Ruiter et al. (2009) is low. These results mean that while it is possible to identify a fossil using the comparative method, the methodology presented in this study can provide better, more accurate results. In addition, some of the classifications in Appendix III are only to the tribe or genus level, and not to the species level. This classification means that the analyst was not certain of the classification of the bovid below the tribe or genus taxonomic level. While these classifications are not incorrect, this study allows the fossils to be more precisely identified to the genus and species taxonomic level. Also, some of the previous identifications do not match the identifications predicted in this study. This discrepancy supports the need for a study where the process of identifying bovid teeth in the fossil record is standardized, reliable and replicable.

Researchers examining fauna from a site will differ in the amount of experience they have in identifying bovids in the fossil record and in the amount of confidence they have in their identifications. A standardized, reliable method towards identification will ensure that all faunal lists are identified with the same amount of detail and robust levels of confidence. Thus, this study concludes that a typicality threshold should be used when classifying unknown fossils.

4.5 Summary and conclusions

This study demonstrated that modern bovid teeth could be reliably distinguished from closely related bovids at a high classification rate (Chapter III). Therefore, this method was applied to the fossil record to identify unknown fossils bovid specimens. The purpose of this phase of the dissertation was to test Hypothesis H2: *A. Extant bovid teeth can be used to accurately identify representatives of modern taxa in the fossil record; H2: B. The occlusal outline of the teeth of extinct bovid species can be quantitatively documented, thus allowing precise identifications of fossil species for whom there are no modern counterparts.* The results of this study support H2A, a majority of the fossil specimens classified as one of the modern species with a statistically robust typicality of ≥0.15. A robust classification threshold combined with a standardized approach towards the identification of bovids indicates that there is a high amount of confidence in the identification of that fossil. The results of this phase of the dissertation neither support nor reject H2B, as the occlusal outlines of extinct species could not be quantitatively identified at present. Follow up analysis 2 was used to look for outliers of the modern species but also to see if the low typicality fossils clustered, thereby suggesting a consistent morphotype. The fact that they did not cluster suggests that they are representatives of multiple species, likely a mix of extant species not found in South Africa alongside extinct animals. Future research will be aimed at expanding the modern reference sample by documenting East African fossils, as well as identifying extinct critters in East Africa. One of the purposes of the study was to identify the extinct species to genus/species. While their taxonomic designation cannot be currently defined, their occlusal surfaces were captured and will continually be analyzed in

order to assess their identifications. Their occlusal outlines will be used to help identify unknown fossils into groups and, ultimately, identify their extinct species designation.

This study provides a way to identify fossil bovids that helps eliminate misclassifications, classify them to the genus/species level and incorporate a high amount of confidence into the identifications. Replicable, confident identifications are important since it is these identifications that are used to create the paleoenvironmental reconstruction and to assess environmental change over time.

CHAPTER V

ASSESSING ENVIRONMENTAL HETEROGENEITY

5.1 Introduction and hypothesis

The final phase of the dissertation uses the taxonomic abundance data of the bovids associated with robust australopiths from Cooper's D and Swartkrans Members 1 (Lower Bank and Hanging Remnant), 2 and 3 in order to document changes in environmental conditions over time. This approach will allow the components of a reconstructed habitat mosaic to be defined more precisely by analyzing proportions of bovids associated with particular environments. This study will allow subtle alterations that occurred in the environment across the sites to be identified. The goal is to detect whether a suite of bovids, therefore a set of particular environmental characteristics, consistently associates with the robust australopiths over time and to thus move beyond the necessarily broad ecological categories to which faunal analyses are currently restricted (e.g. de Ruiter et al., 2008).

Fluctuations in the relative abundance of bovid taxa will be compared across the assemblages in order to detect whether environmental heterogeneity is evident between robust australopithecine sites over time; i.e. whether the robust australopithecines are associated with numerous different reconstructed habitats, or if they can be associated with a single, more homogeneous habitat type. This phase of the research tests the following Hypothesis H3: *Fossil bovids accurately identified based on EFFA of their occlusal surface outlines can be used to detect environmental heterogeneity at robust australopith sites in South Africa.*

The relative abundances of the fossil assemblages will be compared with the proportions of the robust australopithecines, and organized according to their probable chronological order: Swartkrans Member 1 Lower Bank (SKLB), Swartkrans Member 1Hanging Remnant (SKHR), Swartkrans Member 2 (SK M2), Coopers D (COD), and Swartkrans Member 3 (SK M3) (Pickering et al., 2011; Herries et al. 2009). The goal of this investigation is to test for particular habitat associations. If *A. robustus* were habitat specialists, they should consistently be associated with a particular set of environmental conditions. On the contrary, if the robust australopithecines were habitat generalists, they will not consistently associate with any particular set of environmental conditions.

5.2 Materials and methods

The fossil bovids that were identified using EFFA and classified using a ≥0.15 typicality probability were used in this analysis (see Chapter IV). Before the assemblages were compared to each other, several analyses including rarefaction, species richness, and species evenness were performed in order to test whether taxonomic biases are affecting the assemblages. This step is important for this study because the sample size of the five assemblages vary widely. These analyses ensure that the taxonomic abundance data of the assemblages can be considered accurate reflections of the animal communities at the time of the robust australopiths.

Diversity indices are used to measure the variety of different species in an assemblage. Using the relative abundance of species, these tests provide information about rarity and dominance of a species in a community. Quantifying the diversity of an assemblage allows the structure of the animal community to be examined. Diversity indices

are often dependent on sample size and can skew the results when comparing assemblages of different sizes (Sanders, 1968; Magurran, 1988). Therefore, a rarefaction analysis is used to compare multiple assemblages by reducing the number of species in the larger samples to the same size as that of the smallest sample (Gart et al., 1982). The rarefaction curve estimates the number of species that would have been identified if a smaller number of fossils were recovered (Gart et al., 1982). The test shows how similar the diversity is when all of the assemblages are rarified, or scaled to the same size. The samples are scaled to the assemblage with the smallest sample size; in this study, all of the assemblages are scaled to SKLB.

The results produce a rarefaction curve for each assemblage. If the rarefaction curves from each assemblage are highly divergent from each other when the curves are scaled to the smallest sample size, then there is a sample size bias and the assemblages cannot reliably be compared to each other. If the curves are not highly divergent from each other when the curves are scaled to the smallest sample size, then no sample size bias exists and the assemblages can reliably be compared to each other.

Species richness and species evenness are examined in order to determine if sample size is affecting the composition of the animal paleocommunity (Ludwig and Reynolds, 1988). Species richness is the number of species found in an assemblage relative to sample size. Large sample sizes tend to have more species relative to their sample size because there is a greater chance of detecting rare animals. This test will demonstrate if the sample size is affecting the number of species in the assemblage. Species richness is measured using the Fisher's log series α (Magurran, 1988). Fisher's log series α predicts the number of species at different levels of abundance (*n* individuals) with the formula:

$$S_n = \frac{\alpha x^n}{n}$$

In this formula, S = the number of species with an abundance of *n* while *x* = a positive constant ($0 < x < 1$) derived from the sample data set and generally approaches 1 in value.

The number of species with 1, 2, …, *n* individuals are therefore defined by this formula:

$$\alpha, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \ldots, \frac{\alpha x^n}{n}$$

If Fisher's log series α is similar across the sites, then the species richness is considered to be comparable across the sites. This means the number of species relative to sample size in one assemblage is similar to the number of species relative to sample size in another. If Fisher's log series α is widely divergent across the sites, then the species richness is not the same across the sites; i.e. the number of species relative to sample size in one assemblage is not comparable to the number of species relative to sample size in another assemblage.

Species evenness, also referred to as equitability, identifies how the abundance of species is distributed across the species. This measure is estimated using the Berger-Parker index. This index measures the relative dominance of the most abundant species in the assemblage to determine if the distribution of species across the assemblages is dramatically different. Berger-Parker indices are reported as reciprocal values (1/d). A high Berger-Parker index indicates that that the most common species is not dominating an assemblage, while a low index suggests that the most common species in an assemblage is dominating that assemblage.

A species evenness test is important because assemblages consisting of a few common species are distributed different than assemblages consisting of many species with similar abundances. This test will determine what effect the differences in abundances will

have on the assemblages. An increase in the value of the index means there is an increase in diversity and a decrease in dominance. For this study, the Berger-Parker Index was performed for each assemblage and the results were compared to each other. If the indices are similar across the assemblages, then the distribution of species is similar across the assemblages. If the indices are widely divergent, then the distribution of species is not similar across the assemblages and the assemblages cannot reliably be compared.

Once it has been established that the assemblages are not affected by a taxonomic bias, the assemblages can reliably be compared to each other. A chord distance test will be performed to test for differences between the localities. Faunal dissimilarity is measured using a chord distance measure that compares the taxonomic composition and proportion of species across sites (Ludwig and Reynolds, 1988), according to their probable chronological order. Chord distances measure the differences between assemblage *j* and assemblage *k* using the following formula:

CRDjk¼ SQRT[2(1–ccosjk)]

with ccosjk ¼SS(Xij*Xik)/SQRT[SSX2ijSSX2ik]

In this analysis, Xij represents the abundance of the ith species in the jth assemblage and Xik represents the abundance of the ith species in the kth assemblage. S is the total number of species shared in the two assemblages (Ludwig and Reynolds, 1988; Bobe et al., 2002; de Ruiter et al., 2008). The results of the chord distance measure range from 0- the square root of 2 (~1.414); 0 means the assemblages are identical while ~1.414 means the assemblages do not have any similarities. These tests were performed in order to determine if any differences exist between the assemblages.

The relative abundances of the bovids over time were compared to the relative abundances of *A. robustus* to determine if any correlations are evident between the groups. The MNIs of the robust australopith taxa from each of the assemblages were obtained from de Ruiter et al. (2008). The relative abundance percentages of *A. robustus* and the bovid taxa were calculated and the abundances of *A. robustus* were plotted. The bovids were grouped according to their dietary categories of grazer and browser and their relative abundances were summed and plotted. The relative abundances of *A. robustus* and the grazers and the browsers were compared to each other using a Spearman's rank order correlation coefficient. This non-parametric test will assess whether the two groups are correlated. While this analysis will not reveal whether *A. robustus* preferred the habitat of a grazer or browser, it will help indicate the habitat that the hominins are most closely associated.

5.3 Results of the analyses

5.3.1 Rarefaction

Rarefaction analysis produces a predicted number of species curve for each locality (Figure 5.1). The black vertical line represents where the curve for the smallest assemblage ends. In this case, SKLB has the smallest sample size. The figure illustrates that the curves are very similar to each other when they are scaled to the smallest sample size, i.e. the curves to the left of the black line overlap significantly. The curve for SKM2 is the most divergent line of the assemblages. This divergence is due to the fact that SKM2 has the largest sample size. However, if the sample size of SKM2 was biasing the species composition, the species diversity would increase. The species diversity decreased for SKM2, indicating that the sample size is not biasing the composition. The scaled sample sizes are not widely divergent

from each other across the sites, meaning the diversity of species is similar across the sites. Therefore, the rarefaction evidence suggests that no sample size bias exists and the assemblages can reliably be compared to each other.

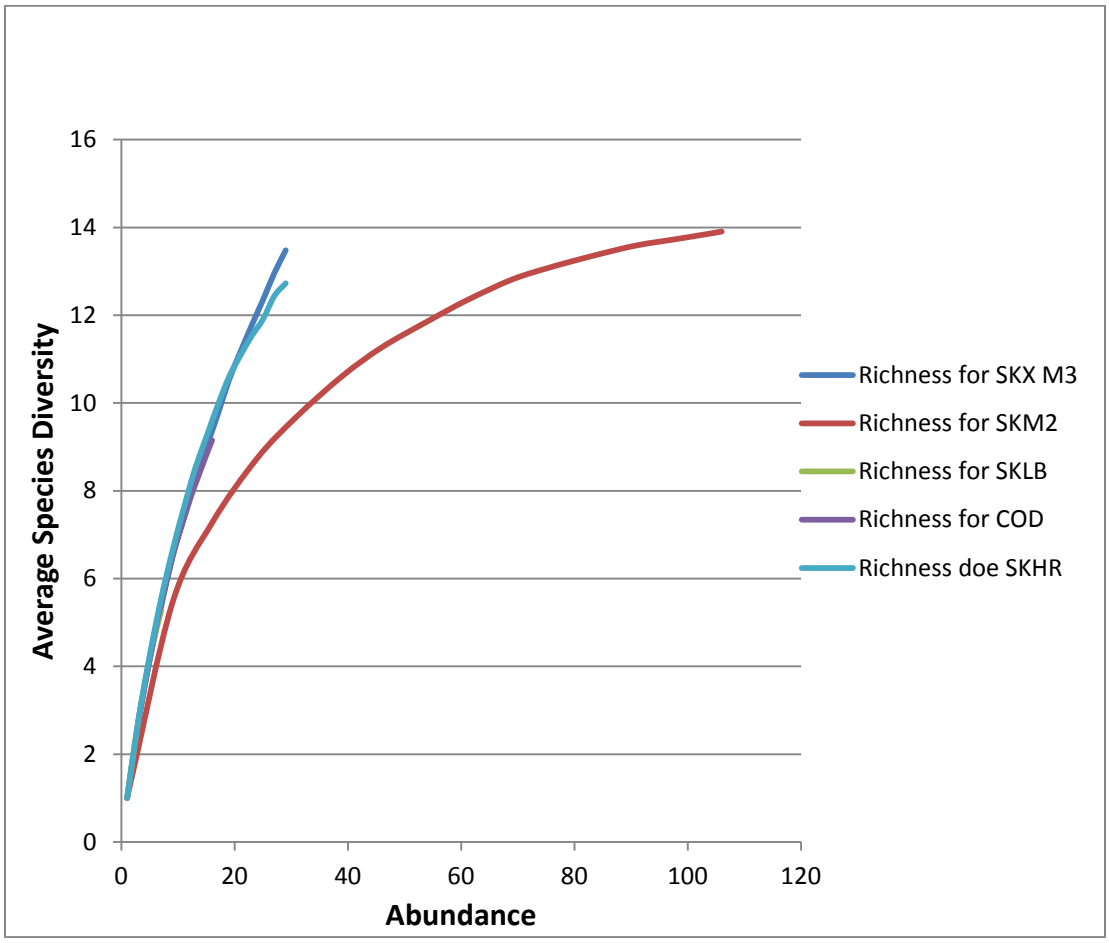


Figure 5.1 Rarefaction curves for each locality.

5.3.2 Species richness and species evenness

Species richness was examined using the Fisher's log series α. Table 5.1 shows the results of this analysis. These results suggest that sample size is not significantly biasing the number of species in the assemblages as all of the α's are comparable to each other (Table

5.1). The α for SKM2 is slightly lower than the other assemblages and this outcome is likely due to the fact that it has a larger sample size (Figure 5.2). Species richness measures the number of species in an assemblages *relative* to sample size. While the large sample sizes tend to have more species relative to their sample size, there are usually more of each species so the richness tends to decrease as the sample size increases. However, the rarefaction analysis demonstrated that there was not a significant sample size bias when the data was scaled to the smallest sample. Therefore, Fisher's log series α suggests that the assemblages are not biased in their species composition. This analysis indicates that the assemblages can reliably be compared to each other.

Table 5.1 Measures of species richness and diversity

	SKM1 LB	SKM1 HR	SK M2	COD	SKX M3
MNI	9	37	114	19	31
# species	6	14	14	10	14
Fisher's log series (α)	7.868147	8.177045	4.195956	8.536232	9.843215
Berger-Parker Index	4.5	4.625	4.222222	4.75	5.166667

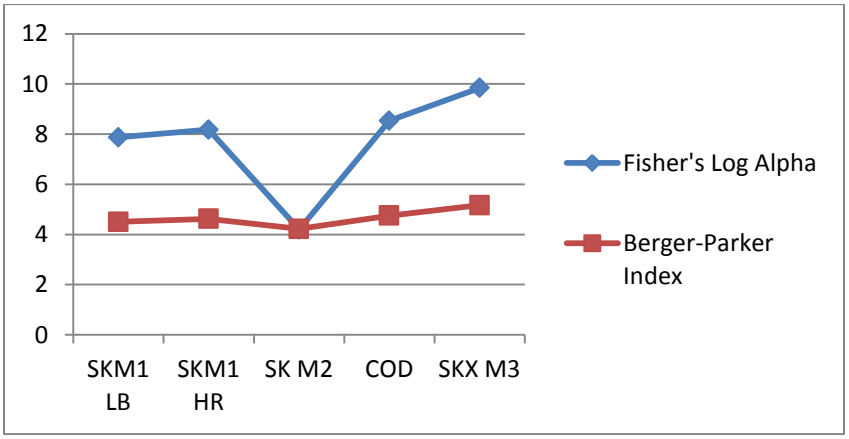


Figure 5.2 Species Diversity

The Berger-Parker Index assesses the species evenness in the assemblages (Table 5.1). The results of the Index show that the assemblages are not dominated by the most abundant species as all of the indices are comparable (Figure 5.2). In addition, these results show that the distribution of species across the assemblages is not dramatically different.

5.3.3. Chord distances

The rarefaction, species richness and species diversity analyses indicate that differences in sample size between the assemblages do not affect the ecological composition of the assemblages. Therefore, these assemblages can be considered reflections of the animal paleocommunity. The assemblages are compared to each other in order to determine if any changes in the environment have occurred over time by assessing them in their probable chronological order: SKLB, SKHR, SKM2, COD and SK M3. The relative abundance percentages of the bovids from each assemblage calculated using the typicality probability derived MNIs are shown in Table 5.2. Differences in the assemblages are assessed using a chord distance measure to see how different the assemblages are from each other. Due to possible uncertainty in the dating of some of the sites used in this study, a matrix of chord distances is presented comparing all sites in the event that a change in the age estimation of a site occurs. The results of the chord distances illustrate that there is substantial faunal dissimilarity between the assemblages (Table 5.3). The biggest differences were found between the assemblages of SKM1 LB and SKM1 HR. These two assemblages are not very similar in terms of their relative faunal representation. The smallest differences occurred between COD and SK M3 suggesting that these assemblages are more similar than the other

comparisons. These distance results indicate that differences exist between the assemblages which are chronologically closest to each other, suggesting changes in bovid faunal representation occurred over time (Figure 5.3).

Table 5.2 Relative abundance (%) of bovids from each assemblage calculated using the MNIs

	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	S caffer	R camp	O oreo	P capreolus	O ourebi	H niger	H equinus	O gazella	R arund	R fulvor	K leche	K ellips
SKLB	11		11	22	22						11	22								
SKHR	5	22	8	11	3			5		8	5	3	11			3		11	3	3
SK M2	2	2	2	3	23			24		4	9	18	6				1	4	2	2
COD	5	11	11	11	21			5		5		21	5							5
SKX M3	7	7	3	16	19		3	3		3	3	19	7			3	3		3	

Table 5.3 Matrix of chord distances computed between pairs of assemblages. Bold results indicate the distances between the sites in chronological order.

Deposit	SKM1 LB	SKM1 HR	SKM2	COD	SMX M3
SKM1 LB	0				
SKM1 HR	**1.091217**	0			
SKM2	0.8471068	**1.084915**	0		
COD	0.550694	0.9065	**0.687917**	0	
SMX M3	0.431094	0.949725	0.72393	**0.3885863**	0

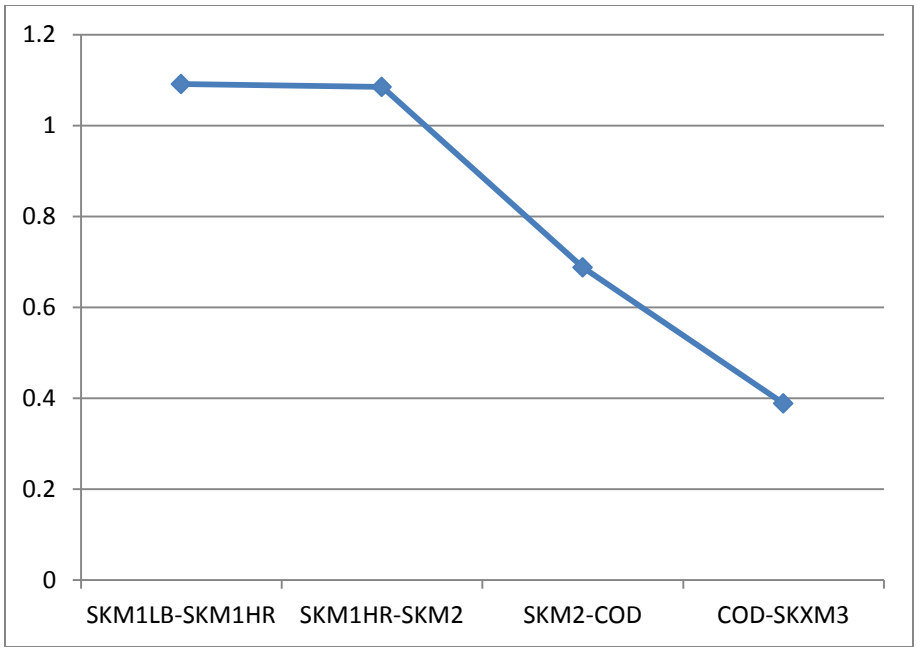


Figure 5.3 Chord distances between the sites.

5.3.4 Correlations between relative abundances

The MNI data of the bovids and *A. robustus* are presented in Table 5.4. Table 5.5 represents the relative abundance percentages of the bovids and *A. robustus*. The relative abundance percentage of *A. robustus* was plotted (Figure 5.4). The number of bovids from the assemblages that are grazers and browsers were summed and their relative abundance percentage data was also plotted for each locality (Figure 5.5 and 5.6).

Table 5.4 MNIs of bovids and *A. robustus* from each assemblage

	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	S caffer	R camp	O oreo	P capreolus	O ourebi	H niger	H equinus	O gazella	R arund	R fulvor	K leche	K ellips	A. robustus
SKLB	1		1	2	2						1	2									9
SKHR	2	8	3	4	1			2		3	2	1	4			1		4	1	1	58
SK M2	2	2	2	3	26			27		5	10	20					1	5	2	2	8
COD	1	2	2	2	4			1		1		4	1							1	2
SKX M3	2	2	1	5	6		1	1		1	1	6	2			1	1		1		6

	Table 5.5 Relative abundnace (%) of bovids and *A. robustus* from each assemblage																				
	Damaliscus	Alcelaphus	C gnou	C taurinus	A marsup	T oryx	Tr strep	Tr script	S caffer	R camp	O oreo	P capreolus	O ourebi	H niger	H equinus	O gazella	R arund	R fulvor	K leche	K ellips	A. robustus
SKLB	5		5	11	11						5	11									50
SKHR	2	8	3	4	1			2		3	2	1	4			1		4	1	1	61
SK M2	2	2	2	3	23			23		4	9	17					1	4	2	2	7
COD	5	10	10	10	19			5		5		19	5							5	10
SKX M3	5	5	3	14	16		3	3		3	3	16	5			3	3		3		16

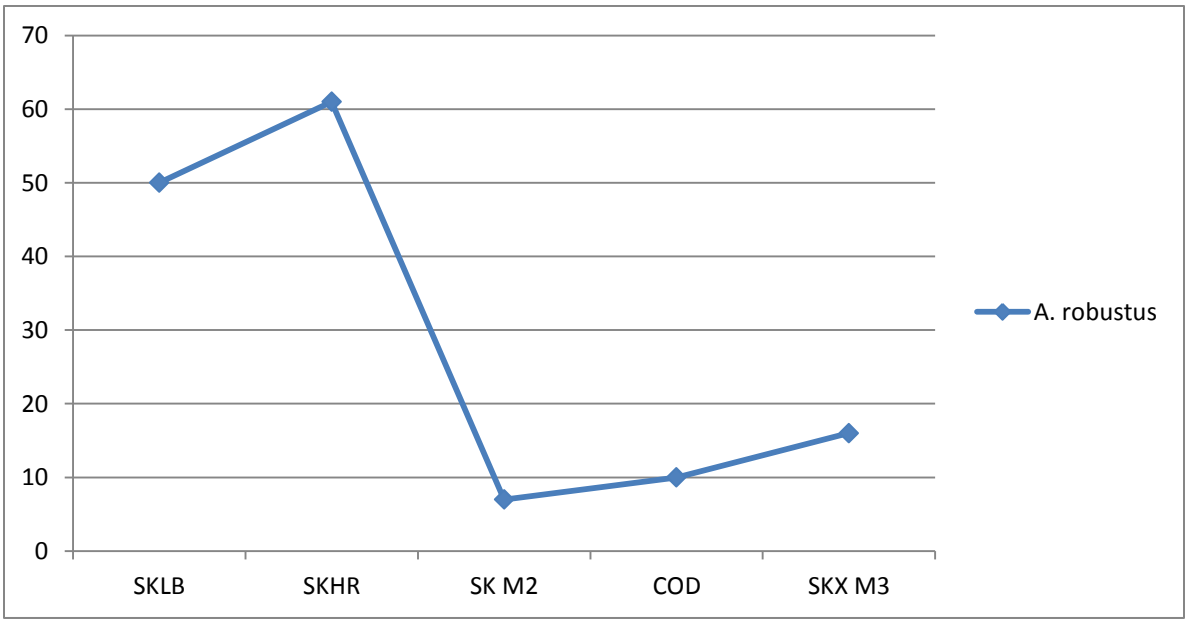


Figure 5.4 Relative abundance of *A. robustus*.

Figure 5.5 Relative abundance of grazers.

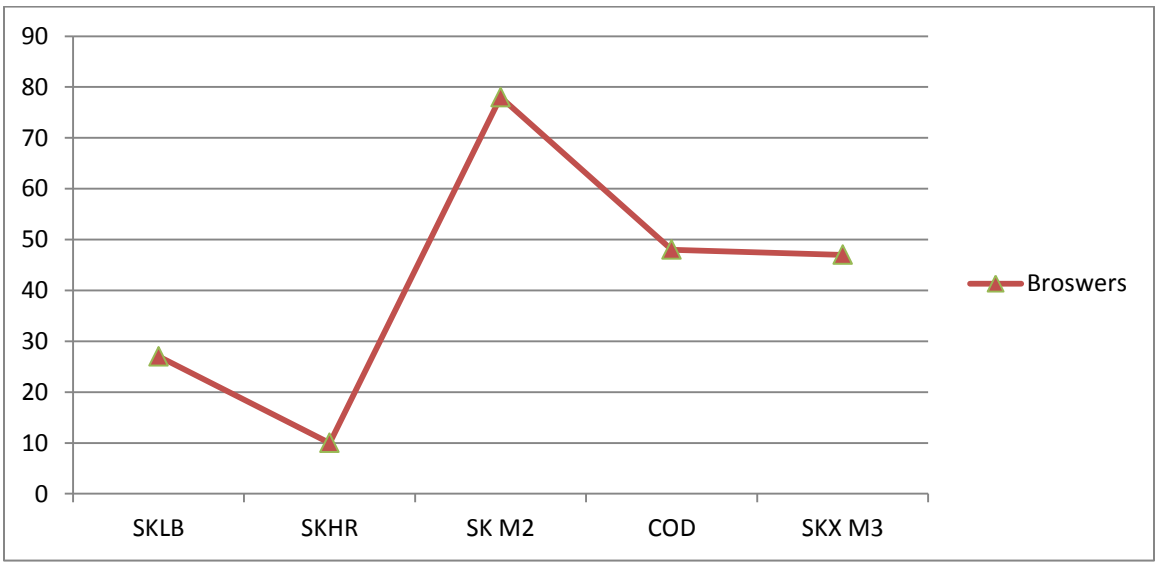


Figure 5.6 Relative abundance of broswers.

The Spearman's rank correlation coefficient results suggest that *A. robustus* are not significantly correlated with either of the grazers or browsers (Table 5.6). Thus, there does not appear to be a consistent relationship between *A. robustus* and the grazers and browsers.

Subsequent Spearman's rank tests were performed comparing the relationship between *A. robustus* and each of the bovid tribes, and between *A. robustus* and each of the bovid species in order to determine if there were any relationships between these groups and *A. robustus*. The results of these tests showed that *A. robustus* was not significantly correlated with any of the bovid tribe or species.

Table 5.6 Results of the Spearman's rank order correlation coefficient.

	Spearman's ρ	p-value
A. robustus and Grazers	0.2	0.7471
A. robustus and Browsers	-0.31	0.6144

5.4 Discussion

5.4.1 Assessing environmental heterogeneity

The results of de Ruiter et al. (2008) suggest that taphonomic biases are not acting on the assemblages from Swartkrans and Cooper's D. The rarefaction, species richness and species diversity analyses indicate that there is no bias in taxonomic composition acting on the assemblages. Therefore, any distortion in the relative representation of ecological signals is likely to be minimized. The assemblages can be considered a reflection of the animal community that existed at the time of the robust australopiths and can be compared to each other to examine fluctuations in the environment over time.

The sites are discussed in chronological order and the factors driving the differences between the assemblages are outlined. The chord distance measures are used as a guideline for assessing change over time.

5.4.1.2 SKLB and SKHR

5.4.1.2.1 Differences between the assemblages of SKLB and SKHR

The two oldest sites are SKLB and SKHR. The chord distance between these two assemblages is the largest at 1.091217 (Table 5.3). This result suggests that these assemblages are not very similar and that a change in the animal community took place between the times when these assemblages were deposited. The differences in species composition and relative abundance resulted in a high chord distance. SKLB consists of 6 species while SKHR consists of 14. The species represented at SKHR and not at SKM1 LB include *A. buselaphus*, *Tr. scriptus*, *R. campestris*, *O. ourebi*, *O. gazella*, *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*. In addition, the proportions of all six species common to the two assemblages significantly decreased by the time of the SKHR assemblage.

5.4.1.2.2 The paleoenvironmental implications

The paleoenvironment of SKLB consisted primarily of secondary grasslands with scattered groups of low level trees and shrubs and a nearby associated hill. The species preferences indicate that a nearby permanent water source was also in the vicinity.

By the time SKHR was deposited, the environment changed opening up new habitats. The environment at SKHR still has a grassland component with sufficient herbs and shrubs and an associated hill in the area, as in the time of the SKLB environment. However, the SKHR environment had significantly more dense vegetation than at SKLB in the form of bushlands and open woodlands. Furthermore, while both assemblages suggest a permanent water source was in the area, the environment at SKHR also included wetlands sustaining edaphic grasslands.

While SKLB has a smaller sample size than SKHR, the rarefaction, species richness and species evenness analyses demonstrated that indications of taxonomic biases in the assemblages are minimal. Thus, the changes in the composition and proportions of bovids in the assemblages are interpreted as responses to actual shifts in the environment between the SKLB deposits and the SKHR deposits. Therefore, the results support Hypothesis *H3* that fossil bovids can be used to detect environmental heterogeneity at robust australopith sites.

5.4.1.3 SKHR and SKM2

5.4.1.3.1 Differences between the assemblages of SKHR and SKM2

The next two assemblages that were compared were SKHR and SK M2. The chord distance measure was 1.084915, suggesting that substantial differences exist between the assemblages (Table 5.3). The assemblages differ in composition by two species (Table 5.2). *O. gazella* was only identified at SKHR while *R. arundinum* was only identified at SK M2. The remaining differences between the two assemblages are due to changes in the relative proportions of the bovids between the assemblages (Table 5.2).

The proportions of four species increased from SKHR to SKM2: *A. marsupialis*, *Tr. scriptus*, *O. oreotragus* and *P. capreolus*. The proportions of nine species decreased from SKHR to SK M2: *D. dorcas*, *A. buselaphus*, *C. gnou*, *C. taurinus*, *R. campestris*, *O. ourebi*, *R. fulvorufula*, *K. leche* and *K. ellipsiprymnus*.

5.4.1.3.2 The paleoenvironmental implications

The paleoenvironment of SKHR consisted largely of secondary grasslands and open woodlands with areas of bushland and thickets. A substantial water source was in the area that provided waterlogged soils for edaphic grasslands.

The environment at SKM2 appears to have had similar habitat components to SKHR, as the species composition between the two assemblages is quite similar. However, the discrepancies in the proportions of the bovids suggest a shift in the availability of certain habitats, some receding and others expanding. While open, secondary grasslands existed in the SK M2 environment, the availability of that habitat in the environment decreased. The amount of edaphic grasslands also decreased, perhaps suggesting that the water source was not as substantial as it had been during the time of SKHR.

The amount of dense vegetation expanded at SK M2 as compared to SKHR. Shrubs and succulents became more prevalent in the grasslands, the amount of bushy areas and thickets dramatically increased, and areas of open woodlands became expanded at SK M2. Interestingly, the amount of grassland/savannahs expanded due to the increase in proportion of *P. capreolus*.

These results suggest that significant changes in the paleocommunity took place at the time between SKHR and SK M2. In particular, the amount of vegetational coverage such as bushes, thickets and trees increased. Thus, the comparison of these assemblages suggests that the environment did change between SKHR and SK M2.

5.4.1.4 SK M2 and COD

5.4.1.4.1 Differences between the assemblages of SK M2 and COD

The next two sites to be compared are SK M2 and Cooper's D. These two assemblages had a chord distance of 0.6879 and differ in both their species compositions and proportions (Table 5.3). Four species which are known in the SKM2 assemblage are absent from the COD assemblage: *O. oreotragus*, *R, arundinum*, *R. fulvorufula* and *K. leche*.

The proportions of three species decreased between SK M2 and COD: *A. marsupialis*, *Tr. scriptus* and *O. ourebi* (Table 5.2). However, *A. marsupialis* and *O. ourebi* only decreased marginally while *Tr. scriptus* decreased significantly in its proportion, shifting from 24% to 5%. The remaining 7 species increased their representation from SK M2 to COD. An increase in the abundance of species is especially apparent in the Alcelaphini. *D. dorcas* increased from 2%-5%, *A. buselaphus* increased from 2%-22%, *C. gnou* also increased from 2%-11% and *C. taurinus* increased in abundance from 3%-11%. Overall, the Alcelaphini shifted significantly from comprising 9% of SK M2 to 38% of COD.

5.4.1.4.2 The paleoenvironmental implications

The environment at SK M2 consisted of a mosaic of habitats including grasslands with areas of increasing vegetational cover such as shrubs and succulents, interwoven bushes and open woodlands. A permanent water source was available resulting in water-logged soils that sustained edaphic grasslands.

The environment at COD shifted to contain a more significant grassland component, including grassland savannahs and open secondary grasslands with some low browse. A minor habitat of edaphic grasslands still existed at COD, though it was likely marginalized

based on the reduction of species requiring this habitat. COD consisted of less vegetational coverage i.e. bushes and trees than SK M2. The purpose of the analysis was to test whether bovids from the fossil record could be used to determine if there is environmental heterogeneity between the robust australopith sites.

5.4.1.5 COD and SK M3

5.4.1.5.1 Differences between the assemblages of COD and SK M3

The last two assemblages to be compared to each other are COD and Swartkrans Member 3. These two assemblages have the lowest chord distances suggesting they are more similar to each other than the other assemblages (Table 5.3). However, important differences between these assemblages exist.

One species was identified at COD and not in the SK M3 assemblage, *K. ellipsiprymnus* (Table 5.2). Five species are represented at SK M3 that are not found at COD: *Tr. strepsiceros*, *O. oreotragus*, *O. gazella, R. arundinum* and *K. leche*. In addition, the proportions of bovids changed dramatically between the assemblages from COD and SK M3. *D. dorcas*, *A. buselaphus*, *C. gnou*, *A. marsupialis*, *Tr. scriptus*, *R. campestris* and *P. capreolus* decreased in their relative proportions from COD to SK M3. Only *C. taurinus* and *O. ourebi* increased in their proportions from COD to SK M3.

5.4.1.5.2 The paleoenvironmental implications

The paleoenvironment for COD can be described as having predominately secondary grasslands, with sufficient quantities of forbs and shrubs for the low level browsers. A small

component of the habitat consisted of edaphic grasslands. There was likely a nearby open woodland with some scattered peripheral areas of denser vegetation in the vicinity of the site.

With the addition of five species and a change in the proportions of the shared species, the animal community changed at SK M3 changed. While grassland savannah and secondary grasslands still exist at the site, the amount of secondary grasslands slightly reduced. Edaphic grasslands were more abundant at SK M3 than at COD suggesting perhaps that the water source expanded between the time of the sites. An expansion of habitats with more vegetational coverage also occurred at SK M3.

These results suggest that changes took place in the paleocommunity at the time of deposition between COD and SK M3. Specifically, the amount of secondary grasslands appears to have reduced slightly while edaphic grasslands expanded.

5.4.2 Implications for A. robustus

The results of this study indicate that the robust australopiths are not consistently found with the same suite of bovids across the sites. The robust australopiths are found at sites that vary significantly in the amount of grassland, vegetational coverage and the availability of water. In addition, the Spearman's rank correlation coefficient results indicate that the robust australopiths are not significantly correlated with either the grazers or browsers or with any of the individual species in the study. Thus, the analyses demonstrate that more environmental heterogeneity exists between the robust australopith sites than previously thought. The results support Hypothesis H3 that fossil bovids can be used to detect environmental heterogeneity at robust australopith sites.

While the species composition and relative abundances change across the sites, there are trends in the animal community. The Alcelaphini including *D. dorcas*, *A. buselaphus*, *C. gnou* and *C. taurinus* were identified rather consistently across all of the sites and often in considerable proportion. This suggests that a secondary grassland habitat with varying concentrations of open woodlands was a persistent component of the environment over time. While the proportion of the environment consisting of this type of habitat fluctuated over time, the presence of Alcelaphini suggests it was constantly available. *A. marsupialis* also consistently classified at the sites, and usually comprised a substantial part of the environment. The fact that *A. marsupialis* is consistently identified at these sites indicates that its preferred environment of secondary grasslands with associated shrubs and succulents was likely available at all of the sites.

Tr. scriptus and all four of the Neotragini, *R. campestris*, *O. oreotragus*, *P. capreolus* and *O. ourebi,* also were regularly identified in the assemblages, though not usually in as high of abundance as the Alcelaphini and Antilopini. *Tr. scriptus*, *R. campestris* and *O. oreotragus* indicate more vegetational coverage in the environment. *P. capreolus* inhabits grassland savannahs and *O. ourebi* requires edaphic grasslands. While these bovid species might not have been as abundant over time as the Alcelaphini or Antilopini, the results of this study indicate that their preferred habitat was also a consistent part of the environment.

The habitats of *O. gazella* and the Reduncini were not consistently found at the sites and usually not in any significant proportions. While these habitats might not have always been in the environment of the robust australopiths, they provide extremely important information about the subtleties of the environment at a given point in time such as the availability of open grasslands/plains or of edaphic grasslands.

The relative abundance percentages of the robust australopiths changed across the sites (Table 5.5). If *A. robustus* preferred one type of environment such as an open grassland habitat with shrubs and succulents, as would be indicated by the abundance of Alcelaphini and Antilopini, then the relative abundances of all of these species would correspond. The Spearman's rank order correlation tests indicate that *A. robustus* is not consistently associated with the Alcelaphini or Antilopini. In fact, the results of this study suggest that the robust australopiths are not found associated with any one particular species, tribe or specific suite of bovids over time, but that the species composition and abundance of bovids is different in each habitat. This outcome indicates that the robust australopiths were not habitat specialists, particularly associated with a unique set of environmental conditions. Instead, the data suggest that the robust australopiths were habitat generalists capable of inhabiting different types of environments over time. Thus, this phase of the dissertation indicates that the common reconstruction of the habitat preferences of the robust australopiths as *open to lightly wooded grasslands with a nearby water component* needs to be modified to include more subtle ecological indicators, and analysts should focus on the more precise paleoenvironmental reconstructions that can be obtained.

The continuous and relatively abundant identification of the Alcelaphini and Antilopini at the sites may appear to support the recurrent suggestion that the robust australopithecines were habitat specialists preferring *open to lightly wooded grasslands with a nearby water component*. However, when the specific habitats are examined more closely and the abundances of all of the bovid species are considered, a more detailed and more accurate paleoenvironmental reconstruction can be obtained. The paleoenvironmental

reconstructions of the sites associated with the robust australopiths are dynamic and change over time in species composition and relative abundance.

5.5 Summary and conclusions

The Swartkrans and Cooper's D bovid assemblages associated with *A. robustus* were examined using the identifications produced by EFFA. While de Ruiter et al. (2008) tested the Swartkrans and Cooper's D assemblages for taphonomic bias, this study tested the sites for taxonomic bias. Sample size can affect the taxonomic abundance of bovids at a site; therefore, a series of ecological tests were performed on the bovid assemblages in order to determine if the sample sizes were skewing the results and causing a taxonomic bias. The assemblages were compared to each other using rarefaction, species richness and species evenness. The results suggest that these assemblages are not affected by sample size or taxonomic biases, is affecting the assemblages. This outcome means that the faunal assemblages are likely to be relatively accurate reflections of the animal community, which in turn are relatively accurate reflections of the paleoenvironment. Therefore, the assemblages can be compared to each other according to their chronological order, in an effort to assess change in the environment over time.

Chord distance measures, or measures of faunal dissimilarity, suggest that the assemblages changed over time. The bovid fauna changed in species composition and proportion across the sites. Accordingly, the reconstructed environments which are based on the assemblages changed over time. Fluctuations in the bovid assemblages suggest that more environmental heterogeneity exists at these sites than previously thought. A comparison of the abundances of the robust australopiths and the bovids in each of the assemblages indicate

that this hominin is not consistently found with any one particular type of habitat. In fact, the suite of bovids associated with the robust australopiths is different at each site. This study suggests that it is possible that one particular habitat reconstruction does not exist for the robust australopithecines because they were able to occupy multiple types of habitats. This result indicates that these hominins were not habitat specialists preferring one specific environment. The robust australopiths were capable of surviving in myriad environments and might more accurately be called habitat generalists.

CHAPTER VI

CONCLUSIONS

This dissertation advances the understanding of the habitat preferences of the robust australopithecines in South Africa. Using a standardized, reliable and replicable approach for identifying bovids in the fossil record, this research was better able to resolve the environmental mosaic that is typically reconstructed for the *A. robustus*-bearing faunal assemblages of South Africa.

This research began by digitizing photographs of modern bovid teeth using EFFA and statistically analyzing them to determine if their shape and size (form) are reliable enough to distinguish them from closely related bovids. The teeth classified correctly at a high classification rate. In fact, all of the modern teeth classified correctly >83% of the time. While examining the modern teeth, a separate test involved ensuring that the shape of a tooth maintains itself throughout the life of the animal. Thus, teeth were CT scanned and the slices of the CT scans were compared to each other to determine if any intra-tooth variation existed. The results of this test suggest that the outline of the occlusal surface morphology does not change significantly over the course of a lifetime. The success of the classifications of the modern bovid teeth indicates that the methodology is reliable enough to apply to the fossil record.

Fossil bovid teeth from five assemblages of Cooper's Cave and Swartkrans were digitized and statistically compared to the modern bovid reference sample using discriminant function analysis. The results of the classifications using the posterior probability and the typicality probability were presented and compared side by side to determine if there were

differences between the classifications of the fossil bovid teeth. Reconstructions of the environment were also presented using the classifications from the posterior probability and the typicality probability. This research concludes that a typicality threshold should be used when identifying unknown bovids in the fossil record in order to obtain highly confident classifications. This study employed a robust ≥ 0.15 typicality probability threshold. If the fossils classified with a ≥ 0.15 typicality probability, then the fossils were considered members of that modern reference group. Fossils that classified with a <0.15 typicality probability were examined further using two follow up analyses in order to determine if the fossils were members of an extinct species, or a modern species not previously thought to be in South Africa. While the identifications of the fossils with a <0.15 typicality could not be confidently established, future studies including expanding the modern reference sample to include East African bovids will reexamine these fossils in order to classify them with more confidence.

The fossils bovids that classified with a ≥ 0.15 typicality probability from Cooper's Cave and Swartkrans were used to assess environmental heterogeneity. Several diversity index analyses were performed to ensure that no taxonomic biases were affecting the assemblages and that they could reliably be compared. The fossil assemblages were organized according to their probable chronological order, Swartkrans Member 1 Lower Bank, Swartkrans Member 1 Hanging Remnant, Swartkrans Member 2, Cooper's Cave and Swartkrans Member 3, and compared over time. The species composition and relative abundances of the bovids differed in the assemblages, suggesting that changes in the environment occurred. The results also indicate that environmental heterogeneity exists at robust australopith sites. The relative abundances of the fossil assemblages and the robust

australopiths were compared to determine if any correlations were evident. The goal was to see if the robust australopiths consistently associated with a particular habitat. The robust australopiths were not statistically correlated with the bovid grazers or with the browsers. In fact, the robust australopiths were not statistically correlated with any of the bovid tribes or with any of the bovid species. This study suggests that one particular habitat preference was not found for the robust australopiths because one does not exist. The robust australopiths likely occupied multiple types of habitats and were not limited to one type.

Determining that *A. robustus* are habitat generalists holds important implications for understanding why these hominins went extinct. It has been suggested that *A. robustus* went extinct because they were highly specialized for one type of environment. As the environment started to fluctuate, the hominins were not able to adapt quickly enough to the new environment. *A. robustus* are commonly considered habitat specialists due to their specialized dietary adaptations for hard object feeding, an assumption that likely has its origins in Robinson's Dietary Hypothesis (Robinson, 1954). Intuitively, this conclusion is logical because of their suite of unique cranial characteristics that is thought to be an efficient way of producing force on the molars. However, this conclusion assumes that these adaptations exist because the entire diet of *A. robustus* consisted of hard object foods only found in a certain types of environments. If these adaptations developed as a way of surviving only when higher quality food was not available, then these hominins would not be considered habitat or dietary specialists. Lee-Thorp et al. (1994) and Sponheimer et al. (2006) describe how *A. robustus* was not a strict vegetarian and likely varied its diet seasonally and inter-annually. This dissertation demonstrates that the hominins were not consistently associated with one type of environment. *A. robustus* were neither dietary nor

habitat specialists. Therefore, the hypothesis that these hominins went extinct due to being habitat specialists should no longer be considered a viable option.

Suggesting that the robust australopiths are habitat generalists is not a novel conclusion. Several other lines of research have come to similar results (Lee-Thorp et al., 1994; Sponheimer et al., 2006; de Ruiter et al. 2008). However, reconstructions of past environments using the fauna from *A. robustus* sites, in particular, animals from the Family Bovidae, have shown that these hominins are consistently found with a particular set of environmental conditions, while this study demonstrates that *A. robustus* were not significantly correlated with any particular habitat. The difference in the results is due to the techniques utilized in the studies. Previous studies are frequently limited by subjectivity in bovid identifications, taxonomic diagnoses that cannot go beyond broad taxonomic levels such as Tribe or Family, and the use of presence/absence of bovids to assess past environments. The use of inexact identifications and presence/absence of species for generating paleoenvironmental reconstructions leads to broad scale ecological descriptions. This study presents more precise paleoenvironmental reconstructions by combining two technologies that offer qualitative and quantitative faunal analyses: morphometric analysis of bovid teeth and relative abundance. Therefore, it is not surprising that this dissertation yields different results. This study presents an analysis of the faunal material associated with *A. robustus* that agrees with Lee-Thorp et al. (1994), Sponheimer et al. (2006), and de Ruiter et al. (2008) that *A. robustus* were habitat generalists.

This research produced more precise paleoenvironmental reconstructions than are presently available by more accurately identifying the bovid taxa that dominate all of the assemblages recovered from the robust australopith-bearing cave infills of South Africa. The

results of this study demonstrate that greater environmental heterogeneity for robust australopiths existed than is presently recognized. Furthermore, the robust australopiths do not consistently associate with a particular type of habitat. The robust australopithecines were not habitat specialists, consistently associated with a particular set of environmental conditions; instead the robust australopiths were more likely habitat generalists, capable of occupying a variety of environments.

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APPENDIX I

Appendix I. List of fossil specimens analyzed in this study	
Site	**Accession Number**
Coopers D	COD 8181
Coopers D	COD 492
Coopers D	COD 8164
Coopers D	COD 5430
Coopers D	COD 6187
Coopers D	COD 7381
Coopers D	COD 7478
Coopers D	COD 3122
Coopers D	COD 6213
Coopers D	COD 5426
Coopers D	COD 6181
Coopers D	COD 8182
Coopers D	COD 3123
Coopers D	COD 314
Coopers D	COD 294/295
Coopers D	COD 3096
Coopers D	COD 5405
Coopers D	COD 1928
Coopers D	COD 5441
Coopers D	COD 6180
Coopers D	COD 3689
Coopers D	COD 7481
Coopers D	COD 1247
Coopers D	COD 11062
Coopers D	COD 3193
Coopers D	COD 7445
Coopers D	COD 6190
Coopers D	COD 7387
Coopers D	COD 7491
Coopers D	COD 6167
Coopers D	COD 5445
Coopers D	COD 3707
Coopers D	COD 7490
Coopers D	COD 7383
Coopers D	COD 5450
Coopers D	COD 1227
Coopers D	COD 7492
Coopers D	COD 8185
Coopers D	COD 8582

Coopers D	COD 7441
Coopers D	COD 3699
Coopers D	COD 309
Coopers D	COD 3152
Coopers D	COD 9127Ba
Coopers D	COD 3183
Coopers D	COD 7463
Coopers D	COD 6178
Coopers D	COD 9433
Coopers D	COD 1219
Coopers D	COD 5398
Coopers D	COD 10919
Coopers D	COD 15682
Coopers D	COD 6171
Coopers D	COD 8672a
Coopers D	COD 9986
Coopers D	COD 11740
Coopers D	COD 8184
Coopers D	COD 3709
Coopers D	COD 7380
Coopers D	COD 3092
Coopers D	COD 3103
Coopers D	COD 6179
Coopers D	COD 1231
Coopers D	COD 3119
Coopers D	COD 5410
Coopers D	COD 9127Bb
Coopers D	COD 1220
Coopers D	COD 5399
Coopers D	COD 1255
Coopers D	COD 1235
Coopers D	COD 7392A
Coopers D	COD 10828
Coopers D	COD 6209
Coopers D	COD 3149
Coopers D	COD 3160
Coopers D	COD 8672b
Coopers D	COD 6193
Coopers D	COD 5417
Coopers D	COD 17009
Coopers D	COD 1216
Coopers D	COD 1218
Coopers D	COD 1226
Coopers D	COD 7398
Coopers D	COD 3194

Coopers D	COD 7409
Coopers D	COD 3090
Coopers D	COD 8161
Coopers D	COD 3095
Coopers D	COD 19962
Coopers D	COD 2823
Coopers D	COD 8672c
Coopers D	COD 19952
Coopers D	COD 8694
Coopers D	COD 5475
Coopers D	COD 9042
Coopers D	COD 1223
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SK M1	SK 2239b
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SK M1	SK 1936
SK M1	SK 3008
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SK M1	SK 3128a
SK M1	SK 2048
SK M1	SK 3118c
SK M1	SK 3142b
SK M1	SK 2982c
SK M1	SK 2114b
SK M1	SK 2049
SK M1	SK 3102
SK M1	SK 2068
SK M1	SK 2061
SK M1	SK 3111a
SK M1	SK 3053
SK M1	SK 1616b
SK M1	SK 2438
SK M1	SK 2314
SK M1	SK 3080c
SK M1	SK 2987c
SK M1	SK 3123e
SK M1	SK 2686c
SK M1	SK 3108e
SK M1	SK 2097b
SK M1	SK 14124
SK M1	SK 14063i
SK M1	SK 2269
SK M1	SK 3012a
SK M1	SK 3012f
SK M1	SK 3126c

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SK M1	SK 3087b
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SK M1	SK 3533
SK M1	SK 2448
SK M1	SK 3005b
SK M1	SK 225
SK M1	SK 2966a
SK M1	SK 2989
SK M1	SK 1624b
SK M1	SK 3081
SK M1	SK 2302
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SK M1	SK 2886b
SK M1	SK 2987b
SK M1	SK 3080b
SK M1	SK 3118b
SK M1	SK 3123d
SK M1	SK 3033a
SK M1	SK 3041
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SK M1	SK 3111b
SK M1	SK 3047
SK M1	SK 2982b
SK M1	SK 2107d
SK M1	SK 2457
SK M1	SK 3126b
SK M1	SK 3107b
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SK M1	SK 3087a
SK M1	SK 1616a
SK M1	SK 3108d
SK M1	SK 3012b
SK M1	SK 14063h
SK M1	SK 2278
SK M1	SK 2225
SK M1	SK 3066
SK M1	SK 5941
SK M1	SK 2109
SK M1	SK 4244
SK M1	SK 3005a
SK M1	SK 3018
SK M1	SK 3111c

SK M1	SK 2032a
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SK M1	SK 3056b
SK M1	SK 2987a
SK M1	SK 3128c
SK M1	SK 3108c
SK M1	SK 2950b
SK M1	SK 1652
SK M1	SK 2982a
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SK M1	SK 3123c
SK M1	SK 14063b
SK M1	SK 3261d
SK M1	SK 3185a
SK M1	SK 3126a
SK M1	SK 3025
SK M1	SK 3134a
SK M1	SK 2992a
SK M1	SK 2358
SK M1	SK 3125c
SK M1	SK 2054
SK M1	SK 3100b
SK M1	SK 2957a
SK M1	SK 3151b
SK M1	SK 1944
SK M1	SK 2985
SK M1	SK 3019e
SK M1	SK 3141d
SK M1	SK 3010e
SK M1	SK 3156
SK M1	SK 6073e
SK M1	SK 3213Da
SK M1	SK 10440e
SK M1	SK 3068
SK M1	SK 2352b
SK M1	SK 2986
SK M1	SK 3131a
SK M1	SK 3104a
SK M1	SK 3099
SK M1	SK 3040
SK M1	SK 3045
SK M1	SK 2064
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SK M1	SK 3052b
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SK M1	SK 3019d
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SK M1	SK 3094b
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SK M1	SK 1931
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SK M2	SK 11084a
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SK M2	SK 1980
SK M2	SK 4574
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SK M2	SK 6032
SK M2	SK 14049b

SK M2	SK 2072
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SK M2	SK 4040b
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SK M2	SK 6052b
SK M2	SK 10663b
SK M2	SK 14241c
SK M2	SK 4042b
SK M2	SK 4071

SK M2	SK 3062b
SK M2	SK 3035b
SK M2	SK 5988b
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SK M2	SK 11003
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SK M2	SK 4021
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SK M2	SK 4074a
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SK M2	SK 11167
SK M2	SK 12531
SK M2	SK 2113
SK M2	SK 2998
SK M2	SK 1957
SK M2	SK 2375b
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SK M2	SK 12472b
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SK M2	SK 2958c
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SK M2	SK 3035a
SK M2	SK 3049c
SK M2	SK 6088
SK M2	SK 5130
SK M2	SK 10489b
SK M2	SK 2578
SK M2	SK 2977c
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SK M2	SK 12324
SK M2	SK 4041b
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SKX M1	SKX 8891
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SKX M1	SKX 40387
SKX M1	SKX 13630
SKX M1	SKX 45553
SKX M1	SKX 4829
SKX M1	SKX 12067
SKX M1	SKX 17239b
SKX M1	SKX 40561
SKX M1	SKX 16247
SKX M1	SKX 10621
SKX M1	SKX 21113
SKX M1	SKX 14250

SKX M1	SKX 4991a
SKX M1	SKX 13511
SKX M1	SKX 7207
SKX M1	SKX 7955
SKX M1	SKX 6194
SKX M1	SKX 5360
SKX M1	SKX 13337
SKX M1	SKX 6331
SKX M1	SKX 7066
SKX M1	SKX 13159
SKX M1	SKX 13389
SKX M1	SKX 6195
SKX M1	SKX 13822
SKX M1	SKX 4988c
SKX M1	SKX 14147
SKX M1	SKX 8455
SKX M1	SKX 4936/32
SKX M1	SKX 4191
SKX M1	SKX 6608
SKX M1	SKX 4988b
SKX M2	SKX 1326
SKX M2	SKX 607
SKX M2	SKX 2830
SKX M2	SKX 3250
SKX M2	SKX 1263
SKX M2	SKX 281
SKX M2	SKX 3018/5
SKX M2	SKX 280
SKX M2	SKX 50049f
SKX M2	SKX 357
SKX M2	SKX 3907
SKX M2	SKX 2285
SKX M2	SKX 1462
SKX M2	SKX 670
SKX M2	SKX 3302
SKX M2	SKX 50049e
SKX M2	SKX 50049g
SKX M2	SKX 2620
SKX M2	SKX 1491
SKX M2	SKX 906
SKX M2	SKX 2526
SKX M2	SKX 848
SKX M2	SKX 4021
SKX M2	SKX 893
SKX M2	SKX 107

SKX M2	SKX 1075
SKX M2	SKX 2901
SKX M2	SKX 50049d
SKX M2	SKX 2528
SKX M2	SKX 12391
SKX M2	SKX 946
SKX M2	SKX 106
SKX M2	SKX 370
SKX M2	SKX 12390
SKX M2	SKX 50049h
SKX M2	SKX 952
SKX M2	SKX 2286
SKX M2	SKX 17336b
SKX M2	SKX 2520
SKX M2	SKX 2404
SKX M2	SKX 2677
SKX M2	SKX 466
SKX M2	SKX 907
SKX M2	SKX 895
SKX M2	SKX 17336a
SKX M2	SKX 4034
SKX M2	SKX 1230
SKX M2	SKX 1697
SKX M2	SKX 3264
SKX M2	SKX 198
SKX M2	SKX 3134
SKX M2	SKX 465
SKX M2	SKX 2487
SKX M2	SKX 954 (?)
SKX M2	SKX 284
SKX M2	SKX 2853
SKX M2	SKX 415
SKX M2	SKX 803
SKX M2	SKX 2633
SKX M2	SKX 2527
SKX M2	SKX 1707
SKX M2	SKX 908
SKX M2	SKX 909
SKX M3	SKX 28176
SKX M3	SKX 22135
SKX M3	SKX 22284
SKX M3	SKX 38593
SKX M3	SKX 27483
SKX M3	SKX 32552

SKX M3	SKX 31611
SKX M3	SKX 28175
SKX M3	SKX 29110
SKX M3	SKX 30135
SKX M3	SKX 29147
SKX M3	SKX 35066
SKX M3	SKX 19696
SKX M3	SKX 37041
SKX M3	SKX 24831
SKX M3	SKX 40083
SKX M3	SKX 39709
SKX M3	SKX 35248
SKX M3	SKX 28381
SKX M3	SKX 36477
SKX M3	SKX 35384
SKX M3	SKX 34972
SKX M3	SKX 22236
SKX M3	SKX 19540
SKX M3	SKX 21911
SKX M3	SKX 28492
SKX M3	SKX 3240
SKX M3	SKX 38858
SKX M3	SKX 34949
SKX M3	SKX 35320
SKX M3	SKX 30334
SKX M3	SKX 25040
SKX M3	SKX 26844
SKX M3	SKX 34586
SKX M3	SKX 34492
SKX M3	SKX 30874
SKX M3	SKX 32887
SKX M3	SKX 34987
SKX M3	SKX 36720
SKX M3	SKX 37215
SKX M3	SKX 22280
SKX M3	SKX 29769
SKX M3	SKX 29091
SKX M3	SKX 38182
SKX M3	SKX 39708
SKX M3	SKX 33628
SKX M3	SKX 26049
SKX M3	SKX 37102
SKX M3	SKX 46244
SKX M3	SKX 27876
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SKX M3	SKX 22287
SKX M3	SKX 37055
SKX M3	SKX 29770
SKX M3	SKX 30524
SKX M3	SKX 22252
SKX M3	SKX 32493
SKX M3	SKX 35319
SKX M3	SKX 35318
SKX M3	SKX 22625
SKX M3	SKX 40018
SKX M3	SKX 39718
SKX M3	SKX 32703
SKX M3	SKX 38140
SKX M3	SKX 30332
SKX M3	SKX 36722
SKX M3	SKX 29278
SKX M3	SKX 32624
SKX M3	SKX 39101a
SKX M3	SKX 37809
SKX M3	SKX 36347
SKX M3	SKX 28560
SKX M3	SKX 24305
SKX M3	SKX 33284
SKX M3	SKX 21944/45/46
SKX M3	SKX 32888/89
SKX M3	SKX 26736
SKX M3	SKX 29323
SKX M3	SKX 30211
SKX M3	SKX 21807
SKX M3	SKX 37649
SKX M3	SKX 39102
SKX M3	SKX 35851a
SKX M3	SKX 3710
SKX M3	SKX 31660a
SKX M3	SKX 27338
SKX M3	SKX 34249
SKX M3	SKX 32790
SKX M3	SKX 35037
SKX M3	SKX 34926
SKX M3	SKX 22239
SKX M3	SKX 40216
SKX M3	SKX 31550
SKX M3	SKX 28655/56
SKX M3	SKX 27822
SKX M3	SKX 34211

SKX M3	SKX 32005
SKX M3	SKX 28654
SKX M3	SKX 39872
SKX M3	SKX 28055
SKX M3	SKX 28832
SKX M3	SKX 38590c
SKX M3	SKX 19645b
SKX M3	SKX 24762
SKX M3	SKX 40230
SKX M3	SKX 22281
SKX M3	SKX 32494
SKX M3	SKX 27701
SKX M3	SKX 22088
SKX M3	SKX 19781
SKX M3	SKX 35177
SKX M3	SKX 19832
SKX M3	SKX 39208
SKX M3	SKX 39601
SKX M3	SKX 35041
SKX M3	SKX 29705
SKX M3	SKX 35753
SKX M3	SKX 37508
SKX M3	SKX 30806
SKX M3	SKX 39541
SKX M3	SKX 26880
SKX M3	SKX 32588
SKX M3	SKX 28028
SKX M3	SKX 38591
SKX M3	SKX 36803b
SKX M3	SKX 29541
SKX M3	SKX 20101
SKX M3	SKX 28393
SKX M3	SKX 37821
SKX M3	SKX 37198
SKX M3	SKX 46727a
SKX M3	SKX 35038
SKX M3	SKX 39908
SKX M3	SKX 30878
SKX M3	SKX 28467
SKX M3	SKX 28027
SKX M3	SKX 34290
SKX M3	SKX 29420
SKX M3	SKX 38590b
SKX M3	SKX 21826a
SKX M3	SKX 32176

SKX M3	SKX 34250
SKX M3	SKX 19645a
SKX M3	SKX 27061
SKX M3	SKX 22254

APPENDIX II

Appendix II. Typicality and posterior probabilities of all fossil specimens

Site	Accession Number	Tooth type	Picture Number	Predicted Species	Species Typicality	Species Posterior
Coopers D	COD 5426	UM3	9479	Ctaurinus	.930	.991
Coopers D	COD 6187	UM3	9480	Ctaurinus	.072	.985
Coopers D	COD 8182	UM3	9484	Kellips	.256	.397
Coopers D	COD 3122	UM3	9519	Alcelaphus	.854	.489
Coopers D	COD 7478	UM3	9550	Alcelaphus	.718	.997
Coopers D	COD 8164	UM3	9554	Damaliscus	.000	.606
Coopers D	COD 6181	UM3	9587	Ctaurinus	.959	.887
Coopers D	COD 6213	UM3	9588	Ctaurinus	.353	.795
Coopers D	COD 7381	UM3	9592	Alcelaphus	.297	.619
Coopers D	COD 8181	UM3	9645	Toryx	.000	1.000
Coopers D	COD 492	UM3	9655	Toryx	.000	1.000
Coopers D	COD 5430	UM3	9672	Toryx	.007	1.000
SKX M1	SKX 4996a	UM3	3221	Ctaurinus	.682	.966
SKX M1	SKX 21121	UM3	3224	Ctaurinus	.715	.785
SKX M1	SKX 17239a	UM3	3154	Pcapreolus	.393	.779
SKX M2	SKX 2830	UM3	3385	Ctaurinus	.205	.959
SKX M2	SKX 3250	UM3	3397	Ctaurinus	.336	.786
SKX M2	SKX 281	UM3	3351	Damaliscus	.957	.974
SKX M2	SKX 1326	UM3	3356/57	Ctaurinus	.000	.993
SKX M2	SKX 3018/5	UM3	3369	Kellips	.166	.503
SKX M2	SKX 1263	UM3	3393	Ctaurinus	.435	.990
SKX M2	SKX 607	UM3	3407	Ctaurinus	.137	.526
SKX M2	SKX 50049f	UM3	3300	Pcapreolus	.910	.574
SKX M2	SKX 280	UM3	3406	Kleche	.829	.890
SKX M3	SKX 40083	UM3	3447	Kleche	.897	.528
SKX M3	SKX 30135	UM3	3470	Alcelaphus	.897	.853
SKX M3	SKX 29110	UM3	3481	Alcelaphus	.636	.458
SKX M3	SKX 35384	UM3	3638	Rcamp	.998	.658
SKX M3	SKX 28381	UM3	3644	Pcapreolus	.782	.806
SKX M3	SKX 35248	UM3	3783/84	Pcapreolus	.773	.962
SKX M3	SKX 37041	UM3	3448	Damaliscus	.496	.624
SKX M3	SKX 24831	UM3	3479	Damaliscus	.914	.930
SKX M3	SKX 28176	UM3	3535/36	Ogazella	.002	.418
SKX M3	SKX 36477	UM3	3588	Pcapreolus	.998	.917
SKX M3	SKX 35066	UM3	3611	Amarsup	.995	.994

SKX M3	SKX 29147	UM3	3643	Amarsup	.984	.999
SKX M3	SKX 22135	UM3	3659	Toryx	.002	1.000
SKX M3	SKX 39709	UM3	3704	Ogazella	.665	.652
SKX M3	SKX 19696	UM3	3705	Ctaurinus	.743	.970
SKX M3	SKX 22284	UM3	3708	Toryx	.003	.914
SKX M3	SKX 27483	UM3	3710	Alcelaphus	.085	.918
SKX M3	SKX 28175	UM3	3713	Alcelaphus	.631	.706
SKX M3	SKX 32552	UM3	3716	Ctaurinus	.106	.968
SKX M3	SKX 38593	UM3	3718	Ctaurinus	.008	.994
SKX M3	SKX 31611	UM3	3723	Alcelaphus	.175	.994
SK M1	SK 3008	UM3	1755	Ctaurinus	.089	.929
SK M1	SK 1634a	UM3	1760	Alcelaphus	.125	.880
SK M1	SK 3128a	UM3	1772	Alcelaphus	.196	.976
SK M1	SK 2068	UM3	1946	Alcelaphus	.728	.687
SK M1	SK 2314	UM3	1948	Cgnou	.667	.545
SK M1	SK 2426	UM3	1951	Ctaurinus	.006	.657
SK M1	SK 2438	UM3	1953	Cgnou	.266	.968
SK M1	SK 2269	UM3	1963	Rcamp	.999	.534
SK M1	SK 2048	UM3	1965	Alcelaphus	.330	.512
SK M1	SK 3111a	UM3	1987	Alcelaphus	.849	.990
SK M1	SK 3012a	UM3	2044	Rcamp	1.000	.666
SK M1	SK 3038a	UM3	2156	Rfulvor	.939	.585
SK M1	SK 3053	UM3	1975	Alcelaphus	.964	.997
SK M1	SK 3080c	UM3	1767	Ctaurinus	.789	.876
SK M1	SK 2686c	UM3	1778	Kellips	.666	.705
SK M1	SK 2982c	UM3	1781	Alcelaphus	.501	.905
SK M1	SK 3013c	UM3	1804	Ogazella	.000	1.000
SK M1	SK 2097b	UM3	1806	Ogazella	.368	.991
SK M1	SK 2061	UM3	1818	Alcelaphus	.805	.704
SK M1	SK 3102	UM3	1820	Alcelaphus	.691	.778
SK M1	SK 3123e	UM3	1923	Damaliscus	.829	.852
SK M1	SK 3118c	UM3	1937	Alcelaphus	.440	.922
SK M1	SK 2114b	UM3	1939	Alcelaphus	.592	.991
SK M1	SK 2049	UM3	1954	Alcelaphus	.652	.907
SK M1	SK 2239b	UM3	1978	Alcelaphus	.000	.997
SK M1	SK 3142b	UM3	1983	Alcelaphus	.495	.619
SK M1	SK 2987c	UM3	1986	Ctaurinus	.824	.486
SK M1	SK 3108e	UM3	1995	Kleche	.649	.687
SK M1	SK 3087b	UM3	1999	Rfulvor	.951	.624
SK M1	SK 1616b	UM3	2001	Amarsup	.919	.454
SK M1	SK 3126c	UM3	2009	Rfulvor	.620	.348

SK M1	SK 14124	UM3	2016	Pcapreolus	.903	.522
SK M1	SK 1991	UM3	2017	Rfulvor	.625	.924
SK M1	SK 3107a	UM3	2030	Rfulvor	.907	.721
SK M1	SK 3012f	UM3	2049	Rcamp	1.000	.711
SK M1	SK 14063i	UM3	2061	Rcamp	.999	.645
SK M1	SK 1936	UM3	2158	Alcelaphus	.029	.790
SK M2	SK 14218a	UM3	2338	Damaliscus	.351	.474
SK M2	SK 11391	UM3	2384	Ctaurinus	.740	.550
SK M2	SK 5942	UM3	2389	Damaliscus	.971	.977
SK M2	SK 4065	UM3	2391	Damaliscus	.120	.831
SK M2	SK 10841	UM3	2396	Rfulvor	.016	.639
SK M2	SK 10555	UM3	2943	Tr script	.950	.770
SK M2	SK 5172	UM3	2382	Damaliscus	.575	.825
SK M2	SK 3616	UM3	2868	Tr script	.908	.623
SK M2	SK 5069 ?	UM3	3011	Tr script	.671	.666
SK M2	SK 4626	UM3	3012	Tr script	.959	.914
SK M2	SK 11168	UM3	3013	Amarsup	.680	.789
SK M2	SK 12671	UM3	3019	Tr script	.945	.916
SK M2	SK 5731	UM3	3025	Tr script	.959	.782
SK M2	SK 5918	UM3	2869	Amarsup	.919	.994
SK M2	SK 5427	UM3	2870	Amarsup	.985	.970
SK M2	SK 4633	UM3	2944	Amarsup	.958	.885
SK M2	SK 4080	UM3	2958	Rarund	.442	.326
SK M2	SK 10520	UM3	2994	Amarsup	.882	.622
SK M2	SK 2393	UM3	2995	Amarsup	.962	.635
SK M2	SK 4285	UM3	3003	Amarsup	.490	.388
SK M2	SK 11514	UM3	3007	Pcapreolus	.652	.797
SK M2	SK 2465	UM3	3008	Amarsup	.388	.661
SK M2	SK 11600	UM3	3010	Tr script	.872	.873
SK M2	SK 3117c	UM3	3056	Rfulvor	.603	.385
SK M2	SK 2010	UM3	2322	Rcamp	.959	.470
SK M2	SK 3152a	UM3	2563	Rcamp	.946	.320
SK M2	SK 5892a	UM3	2624	Tr script	.987	.495
SK M2	SK 2387	UM3	2936	Oourebi	.837	.801
SK M2	SK 11899	UM3	2940	Pcapreolus	.924	.787
SK M2	SK 2292	UM3	2962	Rfulvor	.977	.509
SK M2	SK 3048	UM3	2980	Pcapreolus	.946	.999
SK M2	SK 5902	UM3	2996	Pcapreolus	.641	.924
SK M2	SK 11122	UM3	2998	Tr script	.960	.304
SK M2	SK 2414	UM3	3014	Kleche	.626	.325
SK M2	SK 10611	UM3	3015	Tr script	.941	.352

SK M2	SK 11036	UM3	3021	Tr script	.937	.870
SK M2	SK 2067	UM3	3024	Pcapreolus	.842	.621
SK M2	SK 11031a	UM3	3034	Tr script	.599	.461
SK M2	SK 7079a	UM3	3061	Tr script	.993	.401
SK M2	SK 4044	UM3	2361	Ooreo	.984	.662
SK M2	SK 2423b	UM3	2724	Tr script	.877	.494
SK M2	SK 4022	UM3	2872	Pcapreolus	.863	.757
SK M2	SK 6106	UM3	2946	Pcapreolus	.978	.870
SK M2	SK 4064	UM3	2957	Rfulvor	.755	.399
SK M2	SK 4083	UM3	2959	Rfulvor	.944	.477
SK M2	SK 5882	UM3	2960/61	Tr script	.982	.453
SK M2	SK 5910d	UM3	2977	Amarsup	.555	.694
SK M2	SK 10804	UM3	3004	Rfulvor	.994	.505
SK M2	SK 6084	UM3	3006	Pcapreolus	.767	.964
SK M2	SK 2417	UM3	3026	Tr script	.785	.649
SK M2	SK 12578d	UM3	3044	Rfulvor	.995	.761
SK M2	SK 3055d	UM3	3052	Rarund	.122	.901
SK M2	SK 5990	UM3	2942	Pcapreolus	.855	.574
SK M2	SK 6014	UM3	2381	Kellips	.272	.801
SK M2	SK 5893a	UM3	2627	Tr script	.988	.867
Coopers D	COD 1247	UM2	9476	Rcamp	.869	.488
Coopers D	COD 3689	UM2	9478	Oourebi	.999	.823
Coopers D	COD 5405	UM2	9483	Alcelaphus	.340	.756
Coopers D	COD 1928	UM2	9485	Alcelaphus	.642	.812
Coopers D	COD 294/295	UM2	9500	Oourebi	.004	.786
Coopers D	COD 314	UM2	9503	Cgnou	.001	.984
Coopers D	COD 3096	UM2	9514	Alcelaphus	.095	.554
Coopers D	COD 3123	UM2	9520	Ctaurinus	.000	.917
Coopers D	COD 5441	UM2	9528	Alcelaphus	.735	.686
Coopers D	COD 6180	UM2	9586	Ctaurinus	.941	.961
Coopers D	COD 7481	UM2	9646	Pcapreolus	.994	.892
SKX M1	SKX 4996b	UM2	3222	Alcelaphus	.033	.636
SKX M1	SKX 6200	UM2	3228	Alcelaphus	.710	.503
SKX M1	SKX 4299	UM2	3169	Alcelaphus	.001	.983
SKX M1	SKX 12839a	UM2	3179	Pcapreolus	.174	.381
SKX M1	SKX 13507	UM2	3185	Kellips	.012	.682
SKX M1	SKX 21112	UM2	3225	Ctaurinus	.559	.831
SKX M1	SKX 4560	UM2	3229	Kleche	.009	.877
SKX M2	SKX 906	UM2	3278	Ooreo	.812	.643
SKX M2	SKX 50049g	UM2	3301	Amarsup	.984	.809
SKX M2	SKX 2526	UM2	3320	Pcapreolus	.962	.782

SKX M2	SKX 3302	UM2	3354	Alcelaphus	.929	.919
SKX M2	SKX 1491	UM2	3384	Ctaurinus	.299	.960
SKX M2	SKX 357	UM2	3388	Ctaurinus	.019	.964
SKX M2	SKX 3907	UM2	3389	Ctaurinus	.041	.967
SKX M2	SKX 2285	UM2	3390	Ctaurinus	.072	1.000
SKX M2	SKX 1462	UM2	3275	Rcamp	.095	.605
SKX M2	SKX 50049e	UM2	3299	Amarsup	.713	.885
SKX M2	SKX 2620	UM2	3392	Cgnou	.759	.583
SKX M2	SKX 670	UM2	3400	Alcelaphus	.572	.880
SKX M3	SKX 28492	UM2	3475	Alcelaphus	.710	.850
SKX M3	SKX 34972	UM2	3543	Cgnou	.000	.992
SKX M3	SKX 25040	UM2	3622	Amarsup	.934	.567
SKX M3	SKX 34586	UM2	3717	Oourebi	.754	.521
SKX M3	SKX 38858	UM2	3468	Amarsup	.150	.965
SKX M3	SKX 34949	UM2	3471	Amarsup	.570	.582
SKX M3	SKX 21911	UM2	3480	Alcelaphus	.366	.735
SKX M3	SKX 19540	UM2	3493	Amarsup	.047	.695
SKX M3	SKX 35320	UM2	3609	Amarsup	.723	1.000
SKX M3	SKX 30334	UM2	3617	Amarsup	.815	.816
SKX M3	SKX 26844	UM2	3625	Ooreo	.984	.484
SKX M3	SKX 32887	UM2	3627	Pcapreolus	.941	.407
SKX M3	SKX 34492	UM2	3709	Oourebi	.823	.831
SKX M3	SKX 22236	UM2	3715	Damaliscus	.002	.931
SKX M3	SKX 30874	UM2	3725	Oourebi	.962	.715
SKX M3	SKX 3240	UM2	3735	Alcelaphus	.773	.949
SK M1	SK 3047	UM2	1754	Ctaurinus	.261	.995
SK M1	SK 2966a	UM2	1762	Alcelaphus	.117	.994
SK M1	SK 2448	UM2	1955	Ctaurinus	.047	.674
SK M1	SK 2989	UM2	1979	Alcelaphus	.132	.540
SK M1	SK 3111b	UM2	1988	Ctaurinus	.187	.655
SK M1	SK 2302	UM2	2014	Alcelaphus	.432	.499
SK M1	SK 2457	UM2	2015	Oourebi	.599	.616
SK M1	SK 3012b	UM2	2045	Rcamp	.992	.589
SK M1	SK 2053	UM2	2179	Oourebi	.864	.477
SK M1	SK 3080b	UM2	1766	Alcelaphus	.680	.976
SK M1	SK 2686b	UM2	1776	Alcelaphus	.525	.493
SK M1	SK 2982b	UM2	1780	Ctaurinus	.281	.960
SK M1	SK 3013b	UM2	1803	Alcelaphus	.517	.972
SK M1	SK 2097a	UM2	1805	Ctaurinus	.183	.999
SK M1	SK 2224	UM2	1817	Ogazella	.000	.998
SK M1	SK 3041	UM2	1822	Cgnou	.313	.932

SK M1	SK 3005b	UM2	1854	Alcelaphus	.069	.998
SK M1	SK 3123d	UM2	1922	Alcelaphus	.795	.987
SK M1	SK 2107d	UM2	1932	Damaliscus	.540	.604
SK M1	SK 1624b	UM2	1934	Cgnou	.138	.879
SK M1	SK 3118b	UM2	1936	Alcelaphus	.789	.993
SK M1	SK 225	UM2	1945	Ctaurinus	.112	.978
SK M1	SK 2987b	UM2	1985	Alcelaphus	.609	.925
SK M1	SK 3108d	UM2	1994	Rcamp	.921	.547
SK M1	SK 3087a	UM2	1998	Oourebi	.887	.431
SK M1	SK 1616a	UM2	2000	Oourebi	.934	.423
SK M1	SK 3126b	UM2	2008	Oourebi	.698	.356
SK M1	SK 3081	UM2	2011	Alcelaphus	.323	1.000
SK M1	SK 3107b	UM2	2032	Oourebi	.812	.582
SK M1	SK 14063h	UM2	2060	Rcamp	.993	.545
SK M1	SK 3533	UM2	2102	Pcapreolus	.005	.605
SK M1	SK 3033a	UM2	2104	Amarsup	.378	.998
SK M2	SK 5978	UM2	2311	Alcelaphus	.902	.899
SK M2	SK 6064b	UM2	2333	Oourebi	.977	.685
SK M2	SK 14218b	UM2	2339	Oourebi	.629	.746
SK M2	SK 1523d	UM2	2347	Rcamp	.974	.625
SK M2	SK 2116	UM2	2373	Pcapreolus	.058	.589
SK M2	SK 10906	UM2	2387	Oourebi	.983	.689
SK M2	SK 1515c	UM2	2612	Rcamp	.969	.753
SK M2	SK 5892b	UM2	2625	Oourebi	1.000	.599
SK M2	SK 5893c	UM2	2628	Pcapreolus	.841	.472
SK M2	SK 2530	UM2	2932	Oourebi	.076	.739
SK M2	SK 2046	UM2	2939	Oourebi	.555	.968
SK M2	SK 10670a	UM2	2983	Pcapreolus	.844	.605
SK M2	SK 4059a	UM2	2988	Oourebi	.942	.418
SK M2	SK 2115a	UM2	3027	Amarsup	.989	.980
SK M2	SK 3112b	UM2	3031	Amarsup	.952	.714
SK M2	SK 5938a	UM2	3036	Pcapreolus	.997	.576
SK M2	SK 7079b	UM2	3062	Oourebi	.836	.644
SK M2	SK 5949	UM2	2312	Alcelaphus	.001	.369
SK M2	SK 5967	UM2	2315	Oourebi	.869	.747
SK M2	SK 6090	UM2	2320	Oourebi	.631	.903
SK M2	SK 10917c	UM2	2337	Oourebi	.955	.703
SK M2	SK 1523c	UM2	2346	Rcamp	.915	.586
SK M2	SK 7791	UM2	2386	Alcelaphus	.143	.601
SK M2	SK 4015	UM2	2390	Alcelaphus	.505	.829
SK M2	SK 5954d	UM2	2415	Cgnou	.050	.560

SK M2	SK 1515b	UM2	2611	Rcamp	1.000	.575
SK M2	SK 5909	UM2	2614	Tr strep	.092	.976
SK M2	SK 1960b	UM2	2930	Oourebi	.535	.378
SK M2	SK 2366b	UM2	2954	Oourebi	.442	.459
SK M2	SK 3014c	UM2	2966	Ooreo	.652	.394
SK M2	SK 5910c	UM2	2976	Oourebi	.677	.909
SK M2	SK 5975b	UM2	2982	Pcapreolus	.886	.610
SK M2	SK 10350b	UM2	2991	Amarsup	.608	.639
SK M2	SK 3055c	UM2	3050	Pcapreolus	.995	.821
SK M2	SK 3117b	UM2	3055	Amarsup	.640	.369
SK M2	SK 3122a	UM2	3059	Oourebi	.736	.432
Coopers D	COD 6190	UM1	9481	Ctaurinus	.006	1.000
Coopers D	COD 3193	UM1	9524	Tr script	.000	.582
Coopers D	COD 5450	UM1	9530	Ctaurinus	.674	.863
Coopers D	COD 6167	UM1	9534	Ctaurinus	.130	.883
Coopers D	COD 7383	UM1	9538	Ctaurinus	.560	.876
Coopers D	COD 7445	UM1	9548	Pcapreolus	.004	.988
Coopers D	COD 7491	UM1	9551	Ctaurinus	.092	.998
Coopers D	COD 7387	UM1	9593	Ctaurinus	.050	.991
Coopers D	COD 7490	UM1	9597	Ctaurinus	.405	1.000
Coopers D	COD 1227	UM1	9604	Damaliscus	.316	.998
Coopers D	COD 3707	UM1	9609	Amarsup	.662	.651
Coopers D	COD 8185	UM1	9644	Pcapreolus	.887	.791
Coopers D	COD 7492	UM1	9647	Pcapreolus	.566	.840
Coopers D	COD 5445	UM1	9654	Amarsup	.412	.956
Coopers D	COD 11062	UM1	9668	Scaffer	.000	1.000
Coopers D	COD 7441	UM1	9673	Pcapreolus	.917	.957
Coopers D	COD 8582	UM1	9675	Pcapreolus	.895	.492
SKX M1	SKX 45553	UM1	3206	Ctaurinus	.070	.944
SKX M1	SKX 45499	UM1	3215	Ctaurinus	.009	1.000
SKX M1	SKX 40387	UM1	3231	Ctaurinus	.059	.997
SKX M1	SKX 16247	UM1	3265	Ctaurinus	.235	.614
SKX M1	SKX 5688	UM1	3149	Amarsup	.001	.940
SKX M1	SKX 17239b	UM1	3155	Amarsup	.689	.813
SKX M1	SKX 14250	UM1	3157	Pcapreolus	.899	.871
SKX M1	SKX 12067	UM1	3165	Amarsup	.613	.941
SKX M1	SKX 4829	UM1	3177	Amarsup	.430	1.000
SKX M1	SKX 10698	UM1	3196	Ctaurinus	.003	.995
SKX M1	SKX 8891	UM1	3205	Tr strep	.008	1.000
SKX M1	SKX 40561	UM1	3208	Cgnou	.333	.887
SKX M1	SKX 13630	UM1	3209	Ctaurinus	.066	.594

SKX M1	SKX 21113	UM1	3226	Ctaurinus	.802	1.000
SKX M1	SKX 10621	UM1	3230	Ctaurinus	.236	.999
SKX M2	SKX 50049h	UM1	3302	Pcapreolus	.984	.897
SKX M2	SKX 12390	UM1	3321	Pcapreolus	.860	.490
SKX M2	SKX 2528	UM1	3326	Amarsup	.786	.998
SKX M2	SKX 2901	UM1	3328	Amarsup	.646	.878
SKX M2	SKX 1075	UM1	3395	Cgnou	.103	.526
SKX M2	SKX 848	UM1	3396	Ctaurinus	.000	.982
SKX M2	SKX 107	UM1	3398	Ctaurinus	.078	.828
SKX M2	SKX 952	UM1	3281	Pcapreolus	1.000	.592
SKX M2	SKX 370	UM1	3282	Pcapreolus	.180	.486
SKX M2	SKX 50049d	UM1	3298	Amarsup	.778	.896
SKX M2	SKX 12391	UM1	3319	Amarsup	.901	.997
SKX M2	SKX 106	UM1	3350	Ctaurinus	.200	.961
SKX M2	SKX 893	UM1	3391	Damaliscus	.003	.836
SKX M2	SKX 4021	UM1	3409	Ctaurinus	.000	.998
SKX M2	SKX 946	UM1	3410	Cgnou	.452	.970
SKX M3	SKX 34987	UM1	3544	Amarsup	.000	.670
SKX M3	SKX 36347	UM1	3606	Pcapreolus	.918	.735
SKX M3	SKX 37809	UM1	3613	Pcapreolus	.849	.887
SKX M3	SKX 46244	UM1	3629	Amarsup	.821	.646
SKX M3	SKX 29278	UM1	3630	Pcapreolus	.594	.984
SKX M3	SKX 30332	UM1	3639	Pcapreolus	.386	.675
SKX M3	SKX 22287	UM1	3640	Amarsup	.976	.999
SKX M3	SKX 37102	UM1	3641	Pcapreolus	.116	.925
SKX M3	SKX 27876	UM1	3645	Amarsup	.876	.997
SKX M3	SKX 26049	UM1	3741	Cgnou	.097	.970
SKX M3	SKX 37215	UM1	3743	Amarsup	.004	.566
SKX M3	SKX 33284	UM1	3754	Tr strep	.172	.995
SKX M3	SKX 22252	UM1	3756	Ctaurinus	.295	.936
SKX M3	SKX 29769	UM1	3757	Ctaurinus	.005	.987
SKX M3	SKX 29091	UM1	3759	Ctaurinus	.015	.994
SKX M3	SKX 30524	UM1	3760	Ctaurinus	.285	.721
SKX M3	SKX 37055	UM1	3763	Cgnou	.347	.999
SKX M3	SKX 22280	UM1	3765	Cgnou	.005	.958
SKX M3	SKX 39708	UM1	3799	Cgnou	.073	.975
SKX M3	SKX 32493	UM1	3439	Ctaurinus	.362	.998
SKX M3	SKX 38140	UM1	3458	Pcapreolus	.287	.917
SKX M3	SKX 38182	UM1	3476	Tr strep	.030	.596
SKX M3	SKX 40018	UM1	3485	Ctaurinus	.711	.924
SKX M3	SKX 33628	UM1	3490	Cgnou	.094	.999

SKX M3	SKX 35319	UM1	3492	Ctaurinus	.512	1.000
SKX M3	SKX 24305	UM1	3579	Pcapreolus	1.000	.801
SKX M3	SKX 36722	UM1	3589	Pcapreolus	.507	.630
SKX M3	SKX 28560	UM1	3597	Pcapreolus	.986	.472
SKX M3	SKX 32624	UM1	3607	Pcapreolus	.599	.841
SKX M3	SKX 32703	UM1	3608	Pcapreolus	.176	.586
SKX M3	SKX 35326	UM1	3628	Amarsup	.894	.999
SKX M3	SKX 39718	UM1	3734	Damaliscus	.317	.564
SKX M3	SKX 35318	UM1	3737	Ctaurinus	.537	1.000
SKX M3	SKX 22625	UM1	3746	Ctaurinus	.584	1.000
SKX M3	SKX 29770	UM1	3755	Ctaurinus	.282	1.000
SKX M3	SKX 36720	UM1	3761	Ctaurinus	.002	.992
SKX M3	SKX 39101a	UM1	3801	Pcapreolus	.806	.859
SK M1	SK 1652	UM1	1753	Ctaurinus	.656	1.000
SK M1	SK 2966b	UM1	1764	Ctaurinus	.758	.847
SK M1	SK 3128c	UM1	1774	Ctaurinus	.369	1.000
SK M1	SK 3018	UM1	1821	Ctaurinus	.067	.946
SK M1	SK 2109	UM1	1823	Ctaurinus	.000	.996
SK M1	SK 4244	UM1	1824	Ctaurinus	.035	1.000
SK M1	SK 2278	UM1	1894	Tr strep	.000	.998
SK M1	SK 5941	UM1	1952	Ctaurinus	.000	1.000
SK M1	SK 2032a	UM1	1961	Ctaurinus	.109	.998
SK M1	SK 3056b	UM1	1969	Cgnou	.322	.988
SK M1	SK 3111c	UM1	1989	Cgnou	.072	.992
SK M1	SK 2950b	UM1	1997	Ctaurinus	.460	.744
SK M1	SK 14063b	UM1	2052	Ooreo	.481	.584
SK M1	SK 3185a	UM1	2081	Ooreo	.998	.698
SK M1	SK 3066	UM1	1751	Ctaurinus	.000	.488
SK M1	SK 2225	UM1	1768	Ctaurinus	.000	1.000
SK M1	SK 2982a	UM1	1779	Ctaurinus	.754	1.000
SK M1	SK 3005a	UM1	1853	Ctaurinus	.049	.533
SK M1	SK 3123c	UM1	1921	Damaliscus	.511	.969
SK M1	SK 2326b	UM1	1950	Cgnou	.211	.924
SK M1	SK 2987a	UM1	1984	Cgnou	.825	.997
SK M1	SK 3108c	UM1	1993	Ctaurinus	.395	.986
SK M1	SK 3126a	UM1	2007	Oourebi	.859	.830
SK M1	SK 3261d	UM1	2065	Ooreo	.932	.763
SK M2	SK 12000	UM1	2321	Ooreo	.828	.639
SK M2	SK 3219b	UM1	2341	Oourebi	.999	.869
SK M2	SK 1523e	UM1	2348	Oourebi	.994	.834
SK M2	SK 4036	UM1	2351	Rcamp	.613	.498

SK M2	SK 14205	UM1	2385	Ooreo	.971	.504
SK M2	SK 4572	UM1	2388	Amarsup	.001	.620
SK M2	SK 4075	UM1	2394	Damaliscus	.243	.979
SK M2	SK 11404	UM1	2395	Damaliscus	.019	.809
SK M2	SK 9341	UM1	2429	Damaliscus	.961	1.000
SK M2	SK 10941	UM1	2430	Tr script	.022	.437
SK M2	SK 12363	UM1	2598	Ooreo	1.000	.549
SK M2	SK 1515d	UM1	2613	Rcamp	.995	.588
SK M2	SK 8010	UM1	2615	Hequinus	.000	.999
SK M2	SK 5993	UM1	2632	Amarsup	.037	.605
SK M2	SK 11287	UM1	2873	Amarsup	.227	.999
SK M2	SK 2531b	UM1	2935	Tr script	.750	.895
SK M2	SK 12596	UM1	2937	Pcapreolus	.044	.498
SK M2	SK 2264	UM1	2963	Pcapreolus	.618	.755
SK M2	SK 10670b	UM1	2984	Pcapreolus	.915	.950
SK M2	SK 1930b	UM1	2987	Pcapreolus	.950	.917
SK M2	SK 4059b	UM1	2989	Pcapreolus	.888	.707
SK M2	SK 3931	UM1	3018	Pcapreolus	.986	.544
SK M2	SK 5938b	UM1	3037	Pcapreolus	.381	.840
SK M2	SK 3147a	UM1	3065	Pcapreolus	.986	.836
SK M2	SK 2923	UM1	3090	Oourebi	.198	.602
SK M2	SK 3251	UM1	2313	Ctaurinus	.004	.994
SK M2	SK 10917b	UM1	2336	Ooreo	.414	.833
SK M2	SK 1523b	UM1	2345	Oourebi	.995	.707
SK M2	SK 5999	UM1	2383	Oourebi	.902	.557
SK M2	SK 11178	UM1	2392	Damaliscus	.083	.899
SK M2	SK 11244	UM1	2399	Ctaurinus	.003	.673
SK M2	SK 10521	UM1	2402	Amarsup	.005	.610
SK M2	SK 5954c	UM1	2414	Ctaurinus	.735	.840
SK M2	SK 6037	UM1	2425	Damaliscus	.269	.645
SK M2	SK 12003	UM1	2426	Pcapreolus	.000	.844
SK M2	SK 5996	UM1	2427	Damaliscus	.012	.783
SK M2	SK 14111	UM1	2428	Pcapreolus	.011	.577
SK M2	SK 11271	UM1	2431	Tr script	.087	.779
SK M2	SK 1515a	UM1	2610	Rcamp	.999	.744
SK M2	SK 2366a	UM1	2953	Pcapreolus	.607	.909
SK M2	SK 11073	UM1	2956	Amarsup	.757	.997
SK M2	SK 3014b	UM1	2965	Pcapreolus	.987	.466
SK M2	SK 5910b	UM1	2975	Pcapreolus	.688	.951
SK M2	SK 2984a	UM1	2978	Pcapreolus	.956	.936
SK M2	SK 10350a	UM1	2990	Pcapreolus	.950	.825

SK M2	SK 5992b	UM1	2993	Pcapreolus	.956	.874
SK M2	SK 4240	UM1	2999	Tr script	.975	.546
SK M2	SK 14066	UM1	3000	Pcapreolus	.966	.923
SK M2	SK 10601	UM1	3016	Pcapreolus	.935	.562
SK M2	SK 11068	UM1	3017	Pcapreolus	.988	.722
SK M2	SK 2051	UM1	3022	Oourebi	.987	.760
SK M2	SK 2506	UM1	3023	Pcapreolus	.816	.955
SK M2	SK 12578b	UM1	3042	Pcapreolus	.955	.572
SK M2	SK 3055b	UM1	3049	Amarsup	.565	.795
Coopers D	COD 3699	LM3	9489	Alcelaphus	.000	.523
Coopers D	COD 6178	LM3	9535	Alcelaphus	.005	.941
Coopers D	COD 7463	LM3	9549	Ctaurinus	.003	.467
Coopers D	COD 10919	LM3	9564	Alcelaphus	.255	.996
Coopers D	COD 15682	LM3	9566	Alcelaphus	.473	.480
Coopers D	COD 8184	LM3	9615	Amarsup	.914	.933
Coopers D	COD 9986	LM3	9639	Amarsup	.752	.558
Coopers D	COD 8672a	LM3	9649	Amarsup	.654	.990
Coopers D	COD 309	LM3	9680	Alcelaphus	.000	.926
Coopers D	COD 3103	LM3	9515	Cgnou	.462	.872
Coopers D	COD 3152	LM3	9522	Ctaurinus	.000	.560
Coopers D	COD 5398	LM3	9525	Ctaurinus	.018	.989
Coopers D	COD 9127Ba	LM3	9556	Alcelaphus	.001	.881
Coopers D	COD 9433	LM3	9560	Cgnou	.011	.698
Coopers D	COD 3092	LM3	9579	Cgnou	.280	.876
Coopers D	COD 3183	LM3	9608	Amarsup	.002	.897
Coopers D	COD 6171	LM3	9612	Amarsup	.248	.538
Coopers D	COD 7380	LM3	9614	Amarsup	.997	1.000
Coopers D	COD 3709	LM3	9623	Amarsup	.935	1.000
Coopers D	COD 11740	LM3	9640	Amarsup	.797	.977
Coopers D	COD 1219	LM3	9670	Damaliscus	.011	.643
SKX M1	SKX 6331	LM3	3146	Amarsup	.734	1.000
SKX M1	SKX 13511	LM3	3158	Amarsup	.010	.850
SKX M1	SKX 13337	LM3	3161	Amarsup	.480	.797
SKX M1	SKX 7207	LM3	3181	Amarsup	.029	.800
SKX M1	SKX 6194	LM3	3183	Alcelaphus	.089	.499
SKX M1	SKX 5360	LM3	3184	Alcelaphus	.161	.701
SKX M1	SKX 7955	LM3	3211	Alcelaphus	.050	.501
SKX M1	SKX 4991a	LM3	3246	Damaliscus	.001	.890
SKX M1	SKX 13159	LM3	3218	Cgnou	.243	.998
SKX M1	SKX 7066	LM3	3235	Amarsup	.822	1.000
SKX M2	SKX 907	LM3	3337	Amarsup	.888	.994

SKX M2	SKX 466	LM3	3338	Amarsup	.869	.965
SKX M2	SKX 895	LM3	3339	Amarsup	.932	.999
SKX M2	SKX 2677	LM3	3340	Amarsup	.420	.963
SKX M2	SKX 2404	LM3	3349	Alcelaphus	.167	.686
SKX M2	SKX 17336b	LM3	3368	Alcelaphus	.043	.846
SKX M2	SKX 2520	LM3	3374	Alcelaphus	.088	.987
SKX M2	SKX 2286	LM3	3376	Ctaurinus	.000	.942
SKX M3	SKX 34249	LM3	3634	Amarsup	.834	1.000
SKX M3	SKX 39102	LM3	3697	Ctaurinus	.092	.999
SKX M3	SKX 30211	LM3	3682	Alcelaphus	.006	.998
SKX M3	SKX 27338	LM3	3633	Amarsup	.774	.725
SKX M3	SKX 21807	LM3	3670	Cgnou	.021	.927
SKX M3	SKX 29323	LM3	3673	Cgnou	.001	.728
SKX M3	SKX 35037	LM3	3674	Ctaurinus	.373	.781
SKX M3	SKX 32790	LM3	3684	Ctaurinus	.218	.999
SKX M3	SKX 21944-6	LM3	3688	Ctaurinus	.000	.509
SKX M3	SKX 35851a	LM3	3451	Damaliscus	.106	.870
SKX M3	SKX 3710	LM3	3529	Alcelaphus	.146	.405
SKX M3	SKX 26736	LM3	3669	Ctaurinus	.000	.999
SKX M3	SKX 34926	LM3	3672	Ctaurinus	.446	.987
SKX M3	SKX 37649	LM3	3679	Ctaurinus	.042	.470
SKX M3	SKX 31660a	LM3	3686	Alcelaphus	.323	.980
SKX M3	SKX 32888/89	LM3	3689	Cgnou	.000	.603
SK M1	SK 3131a	LM3	1788	Ctaurinus	.437	.986
SK M1	SK 3156	LM3	1791	Cgnou	.137	.709
SK M1	SK 3104a	LM3	1793	Ctaurinus	.604	.992
SK M1	SK 3100b	LM3	1799	Ctaurinus	.012	.727
SK M1	SK 3099	LM3	1852	Ctaurinus	.624	1.000
SK M1	SK 1944	LM3	1858	Ctaurinus	.065	.999
SK M1	SK 3213Da	LM3	1874	Alcelaphus	.562	.881
SK M1	SK 2992a	LM3	1879	Damaliscus	.001	.827
SK M1	SK 3040	LM3	1882	Ctaurinus	.813	.895
SK M1	SK 2985	LM3	1898	Cgnou	.102	.575
SK M1	SK 2957a	LM3	1901	Cgnou	.018	.796
SK M1	SK 2064	LM3	1909	Damaliscus	.152	.919
SK M1	SK 3127a	LM3	1913	Damaliscus	.811	1.000
SK M1	SK 3134a	LM3	1925	Ctaurinus	.000	.460
SK M1	SK 2495	LM3	2079	Ooreo	.212	.712
SK M1	SK 2665	LM3	2094	Ooreo	.982	.884
SK M1	SK 2054	LM3	1756	Ctaurinus	.010	.959
SK M1	SK 2352b	LM3	1771	Ctaurinus	.191	.820

SK M1	SK 3068	LM3	1807	Cgnou	.261	.626
SK M1	SK 2358	LM3	1808	Cgnou	.001	1.000
SK M1	SK 2986	LM3	1810	Ctaurinus	.295	.710
SK M1	SK 3045	LM3	1811	Ctaurinus	.838	1.000
SK M1	SK 6073e	LM3	1816	Alcelaphus	.170	1.000
SK M1	SK 3010e	LM3	1834	Alcelaphus	.133	.849
SK M1	SK 3125c	LM3	1857	Damaliscus	.002	.769
SK M1	SK 3141d	LM3	1873	Cgnou	.120	.736
SK M1	SK 3151b	LM3	1904	Alcelaphus	.033	1.000
SK M1	SK 10440e	LM3	2088	Amarsup	.878	1.000
SK M1	SK 3019e	LM3	2093	Tr script	.108	.956
SK M1	SK 3025	LM3	2095	Toryx	.000	1.000
SK M2	SK 2024a	LM3	2596	Ooreo	1.000	.820
SK M2	SK 14212	LM3	2323	Oourebi	.968	.907
SK M2	SK 11827a	LM3	2355	Oourebi	.697	.945
SK M2	SK 4016a	LM3	2358	Oourebi	.988	.776
SK M2	SK 2242	LM3	2365	Ooreo	.996	.518
SK M2	SK 7716	LM3	2380	Damaliscus	.033	.917
SK M2	SK 14054a	LM3	2406	Alcelaphus	.669	.956
SK M2	SK 10867a	LM3	2408	Damaliscus	.913	.989
SK M2	SK 4042a	LM3	2434	Amarsup	.694	.969
SK M2	SK 11084a	LM3	2438	Tr script	.963	.880
SK M2	SK 14226	LM3	2442	Amarsup	.101	.968
SK M2	SK 5929a	LM3	2448	Tr script	.906	.985
SK M2	SK 10577a	LM3	2451	Tr script	.872	.818
SK M2	SK 5904	LM3	2456	Amarsup	.486	.596
SK M2	SK 4441 (?)	LM3	2474	Amarsup	.573	.495
SK M2	SK 10278	LM3	2478	Pcapreolus	.948	.924
SK M2	SK 6109	LM3	2481	Tr script	.402	.782
SK M2	SK 5890	LM3	2483	Amarsup	.920	.930
SK M2	SK 11933a	LM3	2498	Amarsup	.063	.915
SK M2	SK 10663a	LM3	2501	Pcapreolus	.531	.595
SK M2	SK 2952a	LM3	2504	Amarsup	.661	.946
SK M2	SK 3073a	LM3	2507	Amarsup	.702	.918
SK M2	SK 4046a	LM3	2510	Amarsup	.479	.774
SK M2	SK 2963a	LM3	2513	Amarsup	.722	.987
SK M2	SK 1965a	LM3	2515	Tr script	.509	.882
SK M2	SK 14225a	LM3	2517	Pcapreolus	.559	.571
SK M2	SK 3030	LM3	2519	Amarsup	.942	.567
SK M2	SK 2720	LM3	2540	Tr script	.317	.802
SK M2	SK 4023	LM3	2544	Amarsup	.501	.926

SK M2	SK 4062	LM3	2548	Amarsup	.888	.996
SK M2	SK 6044	LM3	2554	Amarsup	.049	.967
SK M2	SK 6995a	LM3	2622	Ooreo	.482	.847
SK M2	SK 6002	LM3	2633	Hniger	.012	1.000
SK M2	SK 4261	LM3	2637	Pcapreolus	.306	.622
SK M2	SK 6052a	LM3	2642	Amarsup	.905	.922
SK M2	SK 11389a	LM3	2646	Amarsup	.607	.539
SK M2	SK 5922	LM3	2672	Amarsup	.980	.997
SK M2	SK 5988a	LM3	2694	Pcapreolus	.767	.978
SK M2	SK 2977a	LM3	2696	Pcapreolus	.831	.652
SK M2	SK 2289	LM3	2707	Pcapreolus	.561	.866
SK M2	SK 2367	LM3	2708	Pcapreolus	.953	.778
SK M2	SK 3049a	LM3	2731	Tr script	.694	.802
SK M2	SK 7521a	LM3	2736	Amarsup	.738	.512
SK M2	SK 5974	LM3	2845/46	Oourebi	.877	.587
SK M2	SK 14051	LM3	2848	Pcapreolus	.786	.636
SK M2	SK 3054a	LM3	2849	Ooreo	.981	.532
SK M2	SK 10417a	LM3	2856	Amarsup	.180	.589
SK M2	SK 14126a N?	LM3	2864	Amarsup	.897	.977
SK M2	SK 2253a	LM3	2890	Amarsup	.651	.998
SK M2	SK 4081a	LM3	2892	Amarsup	.569	.981
SK M2	SK 3138b	LM3	2898	Amarsup	.925	.985
SK M2	SK 3057a	LM3	2903	Amarsup	.860	1.000
SK M2	SK 4006a	LM3	2906	Amarsup	.989	.991
SK M2	SK 12125	LM3	2916	Amarsup	.165	.954
SK M2	SK 14070	LM3	2955	Amarsup	.505	.999
SK M2	SK 11221a	LM3	3085	Tr script	.834	.755
SK M2	SK 6087a	LM3	3101	Tr script	.019	.946
SK M2	SK 4040a	LM3	3103	Tr script	.002	.999
SK M2	SK 2341	LM3	2314	Damaliscus	.332	.521
SK M2	SK 5961	LM3	2318	Cgnou	.051	.599
SK M2	SK 6008	LM3	2319	Oourebi	.927	.718
SK M2	SK 3306	LM3	2374	Damaliscus	.089	.972
SK M2	SK 2003	LM3	2398	Damaliscus	.032	.905
SK M2	SK 6108	LM3	2476	Amarsup	.910	.850
SK M2	SK 3248	LM3	2477	Tr script	.226	.705
SK M2	SK 12669	LM3	2479	Tr script	.956	.462
SK M2	SK 4061	LM3	2485	Amarsup	.718	.499
SK M2	SK 4063	LM3	2486	Amarsup	.374	1.000
SK M2	SK 3140d	LM3	2497	Amarsup	.842	1.000
SK M2	SK 2705b	LM3	2528	Tr script	.697	.700

SK M2	SK 1628b	LM3	2531	Pcapreolus	.424	.464
SK M2	SK 4086b	LM3	2533	Amarsup	.903	.995
SK M2	SK 5880c	LM3	2536	Amarsup	.207	.796
SK M2	unnumbered	LM3	2537	Amarsup	.096	.862
SK M2	SK 2532	LM3	2546	Amarsup	.474	.812
SK M2	SK 12630	LM3	2549	Amarsup	.968	.964
SK M2	SK 14205b	LM3	2636	Tr script	.966	.763
SK M2	SK 3009b	LM3	2659	Amarsup	.724	.758
SK M2	SK 2085b	LM3	2662	Tr script	.936	.644
SK M2	SK 2250b	LM3	2664	Amarsup	.819	.472
SK M2	SK 3841	LM3	2669	Tr script	.783	.542
SK M2	SK 5956d	LM3	2692	Oourebi	.178	.564
SK M2	SK 5934	LM3	2702	Pcapreolus	.947	.920
SK M2	SK 4049	LM3	2704	Pcapreolus	.911	.750
SK M2	SK 6101	LM3	2706	Ooreo	.762	.556
SK M2	SK 5155b	LM3	2730	Amarsup	.486	.871
SK M2	SK 3062c	LM3	2827	Amarsup	.806	.549
SK M2	SK 3144d	LM3	2832	Pcapreolus	.681	.852
SK M2	SK 4074c	LM3	2835	Pcapreolus	.398	.434
SK M2	SK 3075b	LM3	2837	Pcapreolus	.677	.827
SK M2	SK 2970c	LM3	2840	Tr script	.880	.483
SK M2	SK 12628	LM3	2844	Pcapreolus	.919	.960
SK M2	SK 3079b	LM3	2855	Pcapreolus	.850	.520
SK M2	SK 5175b	LM3	2878	Pcapreolus	.832	.952
SK M2	SK 2953	LM3	2949	Amarsup	.783	1.000
SK M2	SK 5982c	LM3	2970	Amarsup	.764	.998
SK M2	SK 3116b	LM3	2972	Amarsup	.490	.994
SK M2	SK 2090	LM3	3071/72	Pcapreolus	.000	.610
SK M2	SK 2311	LM3	3073	Pcapreolus	.989	.914
SK M2	SK 2308	LM3	3091	Pcapreolus	.235	.908
SK M2	SK 4029	LM3	3092	Pcapreolus	.018	.937
Coopers D	COD 1255	LM2	9507	Alcelaphus	.017	.952
Coopers D	COD 3149	LM2	9521	Cgnou	.881	.999
Coopers D	COD 7392A	LM2	9540	Ctaurinus	.078	.994
Coopers D	COD 9127Bb	LM2	9557	Tr strep	.000	1.000
Coopers D	COD 10828	LM2	9562	Alcelaphus	.144	.541
Coopers D	COD 1231	LM2	9576	Ogazella	.000	.982
Coopers D	COD 1235	LM2	9577	Cgnou	.025	.516
Coopers D	COD 3160	LM2	9607	Pcapreolus	.311	.942
Coopers D	COD 6209	LM2	9613	Amarsup	1.000	.943
Coopers D	COD 5417	LM2	9638	Tr script	.992	.574

Coopers D	COD 8672b	LM2	9650	Pcapreolus	.768	.793
Coopers D	COD 6193	LM2	9657	Pcapreolus	.997	.771
Coopers D	COD 1220	LM2	9671	Tr script	.002	.385
Coopers D	COD 5399	LM2	9681	Tr strep	.005	1.000
Coopers D	COD 5410	LM2	9682	Tr strep	.000	1.000
Coopers D	COD 3119	LM2	9677	Hequinus	.000	.998
Coopers D	COD 6179	LM2	9678	Cgnou	.000	.998
SKX M1	SKX 8455	LM2	3148	Pcapreolus	.992	.988
SKX M1	SKX 14147	LM2	3166	Pcapreolus	.869	.876
SKX M1	SKX 13389	LM2	3170	Pcapreolus	.000	.998
SKX M1	SKX 6195	LM2	3232	Cgnou	.044	.996
SKX M1	SKX 13822	LM2	3233	Cgnou	.055	.846
SKX M1	SKX 4988c	LM2	3242	Ooreo	1.000	.911
SKX M2	SKX 198	LM2	3329	Pcapreolus	.564	.721
SKX M2	SKX 3134	LM2	3333	Pcapreolus	.904	.765
SKX M2	SKX 465	LM2	3334	Pcapreolus	.941	.809
SKX M2	SKX 2487	LM2	3331	Pcapreolus	.995	.918
SKX M2	SKX 1230	LM2	3363	Alcelaphus	.000	.955
SKX M2	SKX 1697	LM2	3364	Pcapreolus	.001	.942
SKX M2	SKX 17336a	LM2	3366	Alcelaphus	.000	.913
SKX M2	SKX 3264	LM2	3380	Ctaurinus	.378	.908
SKX M2	SKX 4034	LM2	3382	Alcelaphus	.000	.849
SKX M3	SKX 32005	LM2	3454	Damaliscus	.011	.744
SKX M3	SKX 34211	LM2	3477	Cgnou	.000	.960
SKX M3	SKX 31550	LM2	3525	Hniger	.000	.968
SKX M3	SKX 28655/56	LM2	3698	Alcelaphus	.000	.892
SKX M3	SKX 39872	LM2	3731	Alcelaphus	.488	.831
SKX M3	SKX 28654	LM2	3489	Alcelaphus	.013	.867
SKX M3	SKX 28055	LM2	3494	Alcelaphus	.492	.593
SKX M3	SKX 19645b	LM2	3587	Pcapreolus	.539	.802
SKX M3	SKX 38590c	LM2	3593	Oourebi	.978	.556
SKX M3	SKX 24762	LM2	3596	Rarund	.567	.999
SKX M3	SKX 27822	LM2	3696	Ogazella	.000	.925
SKX M3	SKX 22239	LM2	3699	Ogazella	.000	.969
SKX M3	SKX 28832	LM2	3720	Cgnou	.315	.805
SKX M3	SKX 40216	LM2	3724	Cgnou	.000	.934
SK M1	SK 3131b	LM2	1790	Ctaurinus	.268	.994
SK M1	SK 3104b	LM2	1794	Cgnou	.009	.926
SK M1	SK 3091	LM2	1797	Ctaurinus	.040	1.000
SK M1	SK 3100c	LM2	1800	Alcelaphus	.453	.382
SK M1	SK 2081	LM2	1847	Ctaurinus	.001	1.000

SK M1	SK 3213Db	LM2	1875	Cgnou	.971	.993
SK M1	SK 3146a	LM2	1891	Alcelaphus	.001	.650
SK M1	SK 2957b	LM2	1902	Cgnou	.558	.951
SK M1	SK 3127b	LM2	1914	Damaliscus	.196	.659
SK M1	SK 3134b	LM2	1926	Ctaurinus	.168	.997
SK M1	SK 3759	LM2	2103	Rcamp	1.000	.660
SK M1	SK 2320	LM2	2166	Rcamp	.990	.434
SK M1	SK 2565	LM2	2174	Tr script	.143	.724
SK M1	SK 2352a	LM2	1770	Damaliscus	.001	.770
SK M1	SK 3137b	LM2	1783	Cgnou	.051	.842
SK M1	SK 2069	LM2	1785	Cgnou	.082	.975
SK M1	SK 3052b	LM2	1787	Ctaurinus	.448	.842
SK M1	SK 2697	LM2	1796	Tr strep	.000	1.000
SK M1	SK 6073d	LM2	1815	Ctaurinus	.031	.999
SK M1	SK 3010d	LM2	1833	Ctaurinus	.026	1.000
SK M1	SK 3105d	LM2	1838	Ctaurinus	.002	.994
SK M1	SK 2964b	LM2	1840	Alcelaphus	.104	.639
SK M1	SK 3125b	LM2	1856	Cgnou	.188	.583
SK M1	SK 3213Ac	LM2	1868	Cgnou	.122	.993
SK M1	SK 3141c	LM2	1872	Alcelaphus	.413	.883
SK M1	SK 3151a	LM2	1903	Alcelaphus	.593	.446
SK M1	SK 3094b	LM2	2072	Rcamp	.968	.953
SK M1	SK 3501c	LM2	2076	Rcamp	.998	.668
SK M1	SK 2235b	LM2	2078	Rcamp	.789	.845
SK M1	SK 10440d	LM2	2086	Amarsup	.201	1.000
SK M1	SK 3019d	LM2	2092	Pcapreolus	.965	.977
SK M2	SK 2978	LM2	2328	Oourebi	.566	.711
SK M2	SK 14211a	LM2	2330	Oourebi	.280	.983
SK M2	SK 6059	LM2	2350	Pcapreolus	.185	.808
SK M2	SK 5180	LM2	2353	Ooreo	.923	.769
SK M2	SK 11827b	LM2	2356	Oourebi	.816	.911
SK M2	SK 4016b	LM2	2359	Rcamp	.661	.523
SK M2	SK 5208	LM2	2366	Oourebi	.658	.740
SK M2	SK 6032	LM2	2370	Alcelaphus	.000	.985
SK M2	SK 5023	LM2	2371	Alcelaphus	.000	.975
SK M2	SK 10867b	LM2	2409	Damaliscus	.328	.897
SK M2	SK 4574	LM2	2419	Alcelaphus	.000	.539
SK M2	SK 5143	LM2	2433	Tr script	.793	.555
SK M2	SK 4042b	LM2	2435	Tr script	.929	.438
SK M2	SK 6075b	LM2	2446	Ooreo	.989	.940
SK M2	SK 5929b	LM2	2449	Ooreo	.990	.820

SK M2	SK 10577b	LM2	2452	Ooreo	.997	.591
SK M2	SK 5984a	LM2	2453	Rcamp	.372	.497
SK M2	SK 11272b	LM2	2460	Pcapreolus	.999	.930
SK M2	SK 10489a	LM2	2463	Ooreo	.998	.694
SK M2	SK 4071	LM2	2490	Tr script	.946	.441
SK M2	SK 12677	LM2	2491	Pcapreolus	.994	.778
SK M2	SK 6080	LM2	2492	Pcapreolus	.971	.795
SK M2	SK 11933b	LM2	2499	Ooreo	.850	.880
SK M2	SK 10663b	LM2	2502	Tr script	.900	.525
SK M2	SK 2952b	LM2	2505	Ooreo	.997	.952
SK M2	SK 3073b	LM2	2508	Tr script	.581	.526
SK M2	SK 4046b	LM2	2511	Ooreo	.997	.957
SK M2	SK 2963b	LM2	2514	Tr script	.388	.906
SK M2	SK 1965b	LM2	2516	Ooreo	.512	.892
SK M2	SK 14225b	LM2	2518	Ooreo	.999	.828
SK M2	SK 10038a	LM2	2521	Pcapreolus	.997	.659
SK M2	SK 2072	LM2	2618	Kleche	.000	.998
SK M2	SK 1980	LM2	2621	Hniger	.000	1.000
SK M2	SK 6995b	LM2	2623	Oourebi	.861	.955
SK M2	SK 11297	LM2	2638	Ctaurinus	.000	.817
SK M2	SK 6052b	LM2	2643	Tr script	.897	.488
SK M2	SK 2958b	LM2	2650	Pcapreolus	.996	.835
SK M2	SK 3092a	LM2	2652	Pcapreolus	.963	.635
SK M2	SK 2375a	LM2	2674	Oourebi	.274	.730
SK M2	SK 4497	LM2	2683	Pcapreolus	.207	.906
SK M2	SK 5988b	LM2	2695	Tr script	.994	.864
SK M2	SK 2977b	LM2	2699	Pcapreolus	.999	.951
SK M2	SK 6081a	LM2	2725	Tr script	.833	.481
SK M2	SK 3049b	LM2	2732	Tr script	.211	.519
SK M2	SK 7521b	LM2	2737	Tr script	.885	.932
SK M2	SK 3054b	LM2	2850	Pcapreolus	.968	.672
SK M2	SK 10417b	LM2	2857	Pcapreolus	.692	.940
SK M2	SK 4041a	LM2	2859	Pcapreolus	.668	.949
SK M2	SK 14126b N?	LM2	2865	Pcapreolus	.930	.571
SK M2	SK 9201a	LM2	2887	Pcapreolus	.922	.664
SK M2	SK 2253b	LM2	2891	Amarsup	.999	.978
SK M2	SK 4081b	LM2	2893	Amarsup	.949	.994
SK M2	SK 2956a	LM2	2895	Damaliscus	.013	.998
SK M2	SK 2979a	LM2	2901	Amarsup	.968	.938
SK M2	SK 3057b	LM2	2904	Amarsup	.798	.918
SK M2	SK 14169a	LM2	2910	Pcapreolus	.301	.668

SK M2	SK 2702	LM2	2928	Amarsup	.430	.976
SK M2	SK 3941	LM2	3002	Pcapreolus	.382	.557
SK M2	SK 14055b	LM2	3079	Pcapreolus	.656	.672
SK M2	SK 11221b	LM2	3086	Pcapreolus	.862	.799
SK M2	SK 2455	LM2	3089	Oourebi	.628	.768
SK M2	SK 6087b	LM2	3102	Tr script	.002	.809
SK M2	SK 4040b	LM2	3104	Tr script	.002	.979
SK M2	SK 14049b	LM2	3107	Tr script	.000	.965
SK M2	SK 12472c	LM2	2473	Pcapreolus	.964	.817
SK M2	SK 3140c	LM2	2496	Ooreo	.600	.805
SK M2	SK 2705a	LM2	2527	Tr script	.795	.493
SK M2	SK 1628a	LM2	2529	Ooreo	.969	.992
SK M2	SK 4086a	LM2	2532	Ooreo	.966	.544
SK M2	SK 5880b	LM2	2535	Ooreo	.864	.977
SK M2	SK 14060b	LM2	2601	Rcamp	.999	.521
SK M2	SK 14205a	LM2	2634	Pcapreolus	.446	.619
SK M2	SK 2250a	LM2	2663	Pcapreolus	.863	.772
SK M2	SK 2490b	LM2	2666	Pcapreolus	.940	.903
SK M2	SK 2409	LM2	2677	Pcapreolus	.112	.624
SK M2	SK 11986b	LM2	2679	Pcapreolus	.060	.931
SK M2	SK 5908b	LM2	2682	Rfulvor	.003	.819
SK M2	SK 6045b	LM2	2687	Damaliscus	.001	.927
SK M2	SK 5956c	LM2	2690	Pcapreolus	.866	.545
SK M2	SK 5899b	LM2	2728	Ooreo	.734	.650
SK M2	SK 5155a	LM2	2729	Ooreo	.961	.370
SK M2	SK 3062b	LM2	2826	Tr script	.971	.503
SK M2	SK 3144c	LM2	2831	Pcapreolus	.968	.813
SK M2	SK 4074b	LM2	2834	Pcapreolus	.963	.939
SK M2	SK 3075a	LM2	2836	Pcapreolus	.789	.568
SK M2	SK 2970b	LM2	2839	Pcapreolus	.984	.661
SK M2	SK 2999c	LM2	2843	Pcapreolus	.971	.674
SK M2	SK 3079a	LM2	2854	Pcapreolus	.857	.826
SK M2	SK 5175a	LM2	2877	Pcapreolus	.936	.840
SK M2	SK 2961d	LM2	2884	Amarsup	.860	.980
SK M2	SK 2535	LM2	2885	Pcapreolus	.254	.853
SK M2	SK 5958b	LM2	2952	Amarsup	.999	.996
SK M2	SK 5982b	LM2	2968	Pcapreolus	.999	.894
SK M2	SK 3035b	LM2	3096	Tr script	.988	.912
SK M2	SK 14241c	LM2	3100	Tr script	.909	.541
SKX M1	SKX 6608	LM1	3204	Ctaurinus	.402	1.000
SKX M1	SKX 4191	LM1	3237	Pcapreolus	.001	.834

SKX M1	SKX 4936/32	LM1	3150	Damaliscus	.000	.993
SKX M1	SKX 4988b	LM1	3240	Ooreo	.599	.487
SKX M2	SKX 954 (?)	LM1	3288	Rfulvor	.000	.786
SKX M2	SKX 908	LM1	3335	Pcapreolus	.914	.788
SKX M2	SKX 909	LM1	3336	Pcapreolus	.943	.947
SKX M2	SKX 415	LM1	3413	Alcelaphus	.071	.994
SKX M2	SKX 803	LM1	3285	Damaliscus	.072	.581
SKX M2	SKX 2527	LM1	3330	Amarsup	.561	.635
SKX M2	SKX 2853	LM1	3341	Tr script	.065	.819
SKX M2	SKX 1707	LM1	3365	Cgnou	.311	1.000
SKX M2	SKX 284	LM1	3424	Cgnou	.038	.694
SKX M2	SKX 2633	LM1	3428	Damaliscus	.106	.759
SKX M3	SKX 38591	LM1	3472	Damaliscus	.134	.988
SKX M3	SKX 29705	LM1	3473	Ctaurinus	.008	.803
SKX M3	SKX 28467	LM1	3474	Cgnou	.197	1.000
SKX M3	SKX 27061	LM1	3582	Rcamp	.998	.769
SKX M3	SKX 29541	LM1	3583	Amarsup	.583	.707
SKX M3	SKX 30806	LM1	3601	Pcapreolus	.018	.796
SKX M3	SKX 20101 ?	LM1	3602	Amarsup	.676	.690
SKX M3	SKX 37198	LM1	3616	Amarsup	.923	.985
SKX M3	SKX 22254	LM1	3618	Tr script	.419	.748
SKX M3	SKX 30878	LM1	3620	Amarsup	.999	.998
SKX M3	SKX 35038	LM1	3631	Amarsup	.986	.773
SKX M3	SKX 34250	LM1	3632	Pcapreolus	.968	.584
SKX M3	SKX 46727a	LM1	3662	Amarsup	.956	.739
SKX M3	SKX 21826a	LM1	3665	Pcapreolus	.834	.575
SKX M3	SKX 39541	LM1	3727	Cgnou	.029	.985
SKX M3	SKX 26880	LM1	3729	Tr script	.048	.903
SKX M3	SKX 32494	LM1	3732	Cgnou	.000	.995
SKX M3	SKX 28027	LM1	3736	Ctaurinus	.250	1.000
SKX M3	SKX 22088	LM1	3752	Ctaurinus	.000	.842
SKX M3	SKX 39208	LM1	3753	Ctaurinus	.000	1.000
SKX M3	SKX 35177	LM1	3437	Amarsup	.000	1.000
SKX M3	SKX 28028	LM1	3488	Cgnou	.079	.981
SKX M3	SKX 34290	LM1	3491	Damaliscus	.713	.997
SKX M3	SKX 22281	LM1	3495	Damaliscus	.000	1.000
SKX M3	SKX 19645a	LM1	3585	Pcapreolus	.986	.963
SKX M3	SKX 38590b	LM1	3592	Pcapreolus	.739	.960
SKX M3	SKX 37821	LM1	3603	Amarsup	.913	.997
SKX M3	SKX 32176	LM1	3610	Pcapreolus	.962	.994
SKX M3	SKX 29420	LM1	3615	Pcapreolus	.309	.394

SKX M3	SKX 36803b	LM1	3624	Amarsup	.441	.999
SKX M3	SKX 28393	LM1	3626	Amarsup	.902	.999
SKX M3	SKX 37508	LM1	3636/37	Rcamp	.018	.819
SKX M3	SKX 19781	LM1	3726	Cgnou	.000	.996
SKX M3	SKX 35041	LM1	3728	Ctaurinus	.007	1.000
SKX M3	SKX 27701	LM1	3733	Ctaurinus	.000	1.000
SKX M3	SKX 40230	LM1	3742	Ctaurinus	.000	.648
SKX M3	SKX 35753	LM1	3745	Ctaurinus	.009	1.000
SKX M3	SKX 39601	LM1	3749	Ctaurinus	.004	.748
SKX M3	SKX 19832	LM1	3750	Ctaurinus	.000	1.000
SKX M3	SKX 32588	LM1	3751	Cgnou	.060	.889
SKX M3	SKX 39908	LM1	3790	Amarsup	.992	.999
SK M1	SK 3104c	LM1	1795	Cgnou	.518	.553
SK M1	SK 3100d	LM1	1801	Cgnou	.345	1.000
SK M1	SK 2082	LM1	1841	Damaliscus	.000	.904
SK M1	SK 2693	LM1	1845	Ctaurinus	.083	.619
SK M1	SK 2983a	LM1	1850	Cgnou	.022	.993
SK M1	SK 3213Dc	LM1	1876	Alcelaphus	.729	.979
SK M1	SK 2992c	LM1	1881	Damaliscus	.000	.690
SK M1	SK 3146b	LM1	1892	Cgnou	.278	.966
SK M1	SK 2478b	LM1	1906	Cgnou	.018	.810
SK M1	SK 3064	LM1	2024	Tr script	.000	.499
SK M1	SK 2545b	LM1	2068	Rcamp	.315	.906
SK M1	SK 14059a	LM1	2097	Ooreo	.998	.697
SK M1	SK 2967	LM1	2172	Cgnou	.000	.881
SK M1	SK 3570	LM1	2173	Ooreo	.958	.459
SK M1	SK 7216	LM1	1757	Ctaurinus	.010	.657
SK M1	SK 3010c	LM1	1832	Ctaurinus	.356	1.000
SK M1	SK 3105c	LM1	1837	Ctaurinus	.195	1.000
SK M1	SK 2964a	LM1	1839	Damaliscus	.720	.999
SK M1	SK 3125a	LM1	1855	Cgnou	.287	1.000
SK M1	SK 3213Ab	LM1	1867	Cgnou	.023	.510
SK M1	SK 3141b	LM1	1870	Cgnou	.022	.970
SK M1	SK 2971b	LM1	1889	Cgnou	.286	.977
SK M1	SK 1999b	LM1	1912	Damaliscus	.175	.992
SK M1	SK 10500	LM1	1916	Damaliscus	.000	.999
SK M1	SK 1972b	LM1	2039	Kleche	.000	.999
SK M1	SK 3094a	LM1	2069	Rcamp	.842	.938
SK M1	SK 3501b	LM1	2074	Rcamp	.983	.828
SK M1	SK 2235a	LM1	2077	Tr script	.938	.875
SK M1	SK 10440c	LM1	2084	Tr script	.927	.572

SK M1	SK 1931	LM1	2100	Ctaurinus	.000	1.000
SK M1	SK 1950	LM1	2167/68	Alcelaphus	.050	.924
SK M2	SK 1957	LM1	2437	Tr script	.667	.681
SK M2	SK 4013a	LM1	2325	Rcamp	.915	.909
SK M2	SK 14211b	LM1	2331	Ooreo	.706	.582
SK M2	SK 6004	LM1	2349	Tr script	.053	.495
SK M2	SK 2540	LM1	2354	Ooreo	.500	.576
SK M2	SK 4016c	LM1	2360	Rcamp	.968	.600
SK M2	SK 604 B	LM1	2367	Oourebi	.792	.545
SK M2	SK 11117	LM1	2368	Rfulvor	.437	.912
SK M2	SK 6029	LM1	2369	Rfulvor	.317	.897
SK M2	SK 5979a	LM1	2376	Ooreo	.571	.420
SK M2	SK 7050	LM1	2400/01	Amarsup	.000	.995
SK M2	SK 11003	LM1	2403	Damaliscus	.000	.977
SK M2	SK 10867c	LM1	2410	Damaliscus	.288	.991
SK M2	SK 11939	LM1	2421	Damaliscus	.300	.845
SK M2	SK 11889	LM1	2423	Alcelaphus	.044	.951
SK M2	SK 10421	LM1	2424	Damaliscus	.001	.963
SK M2	SK 11084c	LM1	2440	Ooreo	.978	.824
SK M2	SK 5929c	LM1	2450	Ooreo	1.000	.599
SK M2	SK 5984b	LM1	2454	Pcapreolus	.774	.562
SK M2	SK 4032b	LM1	2458	Pcapreolus	.896	.714
SK M2	SK 10489b	LM1	2464	Tr script	.994	.546
SK M2	SK 12135b	LM1	2470	Ooreo	.970	.454
SK M2	SK 5354	LM1	2487	Tr script	.996	.947
SK M2	SK 6117	LM1	2489	Tr script	.817	.914
SK M2	SK 11933c	LM1	2500	Ooreo	.971	.617
SK M2	SK 10663c	LM1	2503	Tr script	.949	.505
SK M2	SK 2952c	LM1	2506	Ooreo	.994	.652
SK M2	SK 3073c	LM1	2509	Ooreo	.998	.700
SK M2	SK 10038b	LM1	2522	Pcapreolus	.924	.522
SK M2	SK 5130	LM1	2525	Tr script	.994	.993
SK M2	SK 11345	LM1	2552	Tr script	.425	.944
SK M2	SK 12324	LM1	2559	Tr script	.997	.966
SK M2	SK 2578	LM1	2560/61	Tr script	.995	.943
SK M2	SK 6052c	LM1	2644	Tr script	.999	.736
SK M2	SK 11389c	LM1	2648	Tr script	.972	.491
SK M2	SK 2958c	LM1	2651	Tr script	.977	.885
SK M2	SK 3092b	LM1	2653	Ooreo	.960	.796
SK M2	SK 6021	LM1	2654	Tr script	.854	.794
SK M2	SK 6088	LM1	2655	Tr script	.992	.676

SK M2	SK 6116	LM1	2656	Pcapreolus	.822	.418
SK M2	SK 2113	LM1	2657	Tr script	.656	.591
SK M2	SK 5962	LM1	2670	Amarsup	.832	.740
SK M2	SK 2375b	LM1	2675	Tr script	.672	.942
SK M2	SK 6093	LM1	2676	Tr script	.814	.855
SK M2	SK 2998	LM1	2684	Tr script	.657	.500
SK M2	SK 10622	LM1	2685	Tr script	.695	.721
SK M2	SK 2977c	LM1	2700	Tr script	.995	.926
SK M2	SK 3049c	LM1	2733	Tr script	.990	.857
SK M2	SK 7521c	LM1	2738	Pcapreolus	.931	.588
SK M2	SK 2020a	LM1	2851	Tr script	.906	.956
SK M2	SK 10417c	LM1	2858	Tr script	.966	.795
SK M2	SK 4041b	LM1	2860	Tr script	.998	.808
SK M2	SK 2962	LM1	2863	Tr script	.480	.870
SK M2	SK 3138c	LM1	2900	Amarsup	.416	.839
SK M2	SK 2979b	LM1	2902	Amarsup	.744	.896
SK M2	SK 3057c	LM1	2905	Amarsup	.953	.860
SK M2	SK 4006c	LM1	2908	Amarsup	.932	.923
SK M2	SK 14169b	LM1	2913	Amarsup	.363	.953
SK M2	SK 2381	LM1	2917	Amarsup	.972	.604
SK M2	SK 2685	LM1	2924	Pcapreolus	.000	.905
SK M2	SK 2547	LM1	2925	Amarsup	.989	1.000
SK M2	SK 14064	LM1	2926	Pcapreolus	.792	.547
SK M2	SK 3042	LM1	3083	Tr script	.371	.967
SK M2	SK 11221c	LM1	3087	Pcapreolus	.970	.982
SK M2	SK 9911	LM1	3093	Pcapreolus	.877	.637
SK M2	SK 12531	LM1	3094	Tr script	.599	.937
SK M2	SK 4040c	LM1	3105	Tr script	.008	.446
SK M2	SK 14049c	LM1	3108	Kleche	.000	.997
SK M2	SK 6057	LM1	2324	Tr script	.029	.524
SK M2	SK 3083	LM1	2327	Rcamp	.524	.742
SK M2	SK 3003	LM1	2329	Rcamp	.661	.969
SK M2	SK 5920	LM1	2352	Rcamp	.325	.987
SK M2	SK 4219	LM1	2375	Rcamp	.500	.511
SK M2	SK 11238a	LM1	2404	Damaliscus	.004	.992
SK M2	SK 4056	LM1	2418	Damaliscus	.000	.706
SK M2	SK 5397	LM1	2420	Cgnou	.468	.977
SK M2	SK 12472b	LM1	2472	Tr script	.759	.647
SK M2	SK 5905	LM1	2488	Tr script	.846	.954
SK M2	SK 3140b	LM1	2495	Tr script	.857	.943
SK M2	SK 5880a	LM1	2534	Ooreo	.999	.954

SK M2	SK 11561	LM1	2550	Tr script	.001	.543
SK M2	SK 7920	LM1	2551	Tr script	.875	.972
SK M2	SK 11412	LM1	2553	Ooreo	.727	.665
SK M2	SK 11167	LM1	2556	Tr script	.590	.943
SK M2	SK 11637	LM1	2558	Pcapreolus	.581	.540
SK M2	SK 14060a	LM1	2600	Rcamp	.989	.924
SK M2	SK 11986a	LM1	2678	Tr script	.150	.813
SK M2	SK 5908a	LM1	2681	Tr script	.424	.959
SK M2	SK 5956b	LM1	2689	Pcapreolus	.250	.636
SK M2	SK 5899a	LM1	2727	Pcapreolus	.987	.645
SK M2	SK 3062a	LM1	2825	Tr script	.984	.911
SK M2	SK 3144b	LM1	2830	Tr script	.780	.720
SK M2	SK 4074a	LM1	2833	Tr script	.483	.980
SK M2	SK 2970a	LM1	2838	Tr script	.976	.713
SK M2	SK 2999b	LM1	2842	Tr script	.960	.878
SK M2	SK 12051	LM1	2879	Pcapreolus	.951	.532
SK M2	SK 2961c	LM1	2883	Amarsup	.965	.875
SK M2	SK 4021	LM1	2886	Tr script	.000	.602
SK M2	SK 4039	LM1	2938	Rcamp	.000	.901
SK M2	SK 14123	LM1	2950	Tr script	.101	.633
SK M2	SK 5958a	LM1	2951	Amarsup	.985	.991
SK M2	SK 5982a	LM1	2967	Tr script	.266	.910
SK M2	SK 11683	LM1	3001	Pcapreolus	.418	.510
SK M2	SK 2468	LM1	3068	Tr script	.010	.948
SK M2	SK 3015	LM1	3069	Tr script	.012	.526
SK M2	SK 1429	LM1	3070	Tr script	.586	.970
SK M2	SK 3035a	LM1	3095	Tr script	.988	.918
Coopers D	COD 3090	LM1	9512	Ctaurinus	.072	.727
Coopers D	COD 3095	LM1	9513	Cgnou	.276	.995
Coopers D	COD 7398	LM1	9544	Damaliscus	.000	.988
Coopers D	COD 17009	LM1	9567	Amarsup	.000	.962
Coopers D	COD 8161	LM1	9603	Amarsup	.263	.916
Coopers D	COD 2823	LM1	9605	Pcapreolus	.583	.880
Coopers D	COD 8672c	LM1	9651	Pcapreolus	.938	.691
Coopers D	COD 9042	LM1	9653	Tr script	.348	.665
Coopers D	COD 8694	LM1	9656	Pcapreolus	.992	.700
Coopers D	COD 19952	LM1	9674	Pcapreolus	.971	.790
Coopers D	COD 3194	LM1	9477	Ctaurinus	.001	1.000
Coopers D	COD 1216	LM1	9504	Amarsup	.000	.905
Coopers D	COD 1218	LM1	9505	Damaliscus	.000	.962
Coopers D	COD 19962	LM1	9569	Cgnou	.563	.996

Coopers D	COD 7409	LM1	9596	Ctaurinus	.025	.903
Coopers D	COD 5475	LM1	9611	Pcapreolus	.997	.858
Coopers D	COD 1226	LM1	9641	Tr script	.000	.591
Coopers D	COD 1223	LM1	9659	Tr script	.576	.621

APPENDIX III

Appendix III. Fossils that identified with a typicality <0.15 and their original identifications. Bold identifications means the previous identification matches the predicted species. * means that the species was originally classified as an extinct species

Site	Tooth type	Picture Number	Predicted Species	Species Typicality	Species Posterior	Previous Identification
Coopers D	LM1	9477	Ctaurinus	.001	1.000	Megalotragus*
Coopers D	UM3	9480	Ctaurinus	.072	.985	Megalotragus*
Coopers D	UM1	9481	Ctaurinus	.006	1.000	Megalotragus*
Coopers D	LM3	9489	Alcelaphus	.000	.523	Damaliscus
Coopers D	UM2	9500	Oourebi	.004	.786	Med alcel
Coopers D	UM2	9503	Cgnou	.001	.984	Connochaetes sp
Coopers D	LM1	9504	Amarsup	.000	.905	Med alcel
Coopers D	LM1	9505	Damaliscus	.000	.962	Med alcel
Coopers D	LM2	9507	Alcelaphus	.017	.952	Med alcel
Coopers D	LM1	9512	Ctaurinus	.072	.727	Med alcel
Coopers D	UM2	9514	Alcelaphus	.095	.554	Med alcel
Coopers D	UM2	9520	Ctaurinus	.000	.917	Med alcel
Coopers D	LM3	9522	Ctaurinus	.000	.560	Med alcel
Coopers D	UM1	9524	Tr script	.000	.582	Med alcel
Coopers D	LM3	9525	Ctaurinus	.018	.989	Med alcel
Coopers D	UM1	9534	Ctaurinus	.130	.883	Med alcel
Coopers D	LM3	9535	Alcelaphus	.005	.941	Med alcel
Coopers D	LM2	9540	Ctaurinus	.078	.994	Med alcel
Coopers D	LM1	9544	Damaliscus	.000	.988	Med alcel
Coopers D	UM1	9548	Pcapreolus	.004	.988	Med alcel
Coopers D	LM3	9549	Ctaurinus	.003	.467	Med alcel
Coopers D	UM1	9551	Ctaurinus	.092	.998	Med alcel
Coopers D	UM3	9554	Damaliscus	.000	.606	Med alcel
Coopers D	LM3	9556	Alcelaphus	.001	.881	Med alcel
Coopers D	LM2	9557	Tr strep	.000	1.000	Med alcel
Coopers D	LM3	9560	Cgnou	.011	.698	Med alcel
Coopers D	LM2	9562	Alcelaphus	.144	.541	Med alcel
Coopers D	LM1	9567	Amarsup	.000	.962	Med alcel
Coopers D	LM2	9576	Ogazella	.000	.982	Connochaetes sp
Coopers D	LM2	9577	Cgnou	.025	.516	Connochaetes sp
Coopers D	UM1	9593	Ctaurinus	.050	.991	Connochaetes sp
Coopers D	LM1	9596	Ctaurinus	.025	.903	Connochaetes sp
Coopers D	LM3	9608	**Amarsup**	.002	.897	**A marsup**
Coopers D	LM1	9641	Tr script	.000	.591	A recki*
Coopers D	UM3	9645	Toryx	.000	1.000	A recki*

Coopers D	UM3	9655	Toryx	.000	1.000	A recki*
Coopers D	UM1	9668	**Scaffer**	.000	1.000	**S caffer**
Coopers D	LM3	9670	Damaliscus	.011	.643	R fulvorufula
Coopers D	LM2	9671	Tr script	.002	.385	R fulvorufula
Coopers D	UM3	9672	Toryx	.007	1.000	Pelea
Coopers D	LM2	9677	Hequinus	.000	.998	Hippotragus sp
Coopers D	LM2	9678	Cgnou	.000	.998	Hippotragus sp
Coopers D	LM3	9680	Alcelaphus	.000	.926	T strep
Coopers D	LM2	9681	**Tr strep**	.005	1.000	**T strep**
Coopers D	LM2	9682	**Tr strep**	.000	1.000	**T strep**
SK M1	UM1	1751	Ctaurinus	.000	.488	Connochaetes sp
SK M1	UM3	1755	Ctaurinus	.089	.929	Connochaetes sp
SK M1	LM3	1756	Ctaurinus	.010	.959	Connochaetes sp
SK M1	LM1	1757	Ctaurinus	.010	.657	Connochaetes sp
SK M1	UM3	1760	Alcelaphus	.125	.880	Connochaetes sp
SK M1	UM2	1762	Alcelaphus	.117	.994	Connochaetes sp
SK M1	UM1	1768	Ctaurinus	.000	1.000	Connochaetes sp
SK M1	LM2	1770	Damaliscus	.001	.770	Connochaetes sp
SK M1	LM2	1783	Cgnou	.051	.842	Connochaetes sp
SK M1	LM2	1785	Cgnou	.082	.975	Connochaetes sp
SK M1	LM3	1791	Cgnou	.137	.709	Connochaetes sp
SK M1	LM2	1794	Cgnou	.009	.926	Connochaetes sp
SK M1	LM2	1796	Tr strep	.000	1.000	Connochaetes sp
SK M1	LM2	1797	Ctaurinus	.040	1.000	Connochaetes sp
SK M1	LM3	1799	Ctaurinus	.012	.727	Connochaetes sp
SK M1	UM3	1804	Ogazella	.000	1.000	Connochaetes sp
SK M1	LM3	1808	Cgnou	.001	1.000	Connochaetes sp
SK M1	LM2	1815	Ctaurinus	.031	.999	Connochaetes sp
SK M1	UM2	1817	Ogazella	.000	.998	Connochaetes sp
SK M1	UM1	1821	Ctaurinus	.067	.946	Connochaetes sp
SK M1	UM1	1823	Ctaurinus	.000	.996	Connochaetes sp
SK M1	UM1	1824	Ctaurinus	.035	1.000	Connochaetes sp
SK M1	LM2	1833	Ctaurinus	.026	1.000	Connochaetes sp
SK M1	LM3	1834	Alcelaphus	.133	.849	Connochaetes sp
SK M1	LM2	1838	Ctaurinus	.002	.994	Connochaetes sp
SK M1	LM2	1840	Alcelaphus	.104	.639	Connochaetes sp
SK M1	LM1	1841	Damaliscus	.000	.904	Connochaetes sp
SK M1	LM1	1845	Ctaurinus	.083	.619	Makapania sp*
SK M1	LM2	1847	Ctaurinus	.001	1.000	Megalotragus*
SK M1	LM1	1850	Cgnou	.022	.993	Alcelaphini
SK M1	UM1	1853	Ctaurinus	.049	.533	Makapania sp*
SK M1	UM2	1854	Alcelaphus	.069	.998	Makapania sp*
SK M1	LM3	1857	Damaliscus	.002	.769	Alcelaphini

SK M1	LM3	1858	Ctaurinus	.065	.999	Megalotragus*
SK M1	LM1	1867	Cgnou	.023	.510	Rabaticerus porrocornutus*
SK M1	LM2	1868	Cgnou	.122	.993	Rabaticerus porrocornutus*
SK M1	LM1	1870	Cgnou	.022	.970	Rabaticerus porrocornutus*
SK M1	LM3	1873	Cgnou	.120	.736	Rabaticerus porrocornutus*
SK M1	LM3	1879	Damaliscus	.001	.827	Alcelaphini
SK M1	LM1	1881	Damaliscus	.000	.690	Alcelaphini
SK M1	LM2	1891	Alcelaphus	.001	.650	Alcelaphini
SK M1	UM1	1894	Tr strep	.000	.998	Alcelaphini
SK M1	LM3	1898	Cgnou	.102	.575	Rabaticerus porrocornutus*
SK M1	LM3	1901	Cgnou	.018	.796	Damaliscus niro*
SK M1	LM3	1904	Alcelaphus	.033	1.000	Alcelaphini
SK M1	LM1	1906	Cgnou	.018	.810	Alcelaphini
SK M1	LM1	1916	Damaliscus	.000	.999	Damaliscus niro*
SK M1	LM3	1925	Ctaurinus	.000	.460	Connochaetes sp
SK M1	UM2	1934	Cgnou	.138	.879	Rabaticerus porrocornutus*
SK M1	UM2	1945	Ctaurinus	.112	.978	Connochaetes sp
SK M1	UM3	1951	Ctaurinus	.006	.657	Alcelaphini
SK M1	UM1	1952	Ctaurinus	.000	1.000	Alcelaphini
SK M1	UM2	1955	Ctaurinus	.047	.674	Alcelaphini
SK M1	UM1	1961	Ctaurinus	.109	.998	Rabaticerus porrocornutus*
SK M1	UM3	1978	Alcelaphus	.000	.997	Alcelaphini
SK M1	UM2	1979	Alcelaphus	.132	.540	Rabaticerus porrocornutus*
SK M1	UM1	1989	Cgnou	.072	.992	Alcelaphini
SK M1	LM1	2024	Tr script	.000	.499	Syncerus
SK M1	LM1	2039	Kleche	.000	.999	Syncerus
SK M1	LM3	2093	Tr script	.108	.956	Antilopini
SK M1	LM3	2095	Toryx	.000	1.000	Antilopini
SK M1	LM1	2100	Ctaurinus	.000	1.000	A. bondi*
SK M1	UM2	2102	Pcapreolus	.005	.605	R arundinum
SK M1	UM3	2158	Alcelaphus	.029	.790	Alcelaphini
SK M1	LM1	2172	Cgnou	.000	.881	Connochaetes sp
SK M1	LM2	2174	Tr script	.143	.724	Megalotragus*
SK M1	LM1	2167/68	Alcelaphus	.050	.924	Damaliscus sp
SK M2	UM2	2312	Alcelaphus	.001	.369	Alcelaphini
SK M2	UM1	2313	Ctaurinus	.004	.994	Alcelaphini
SK M2	LM3	2318	Cgnou	.051	.599	Alcelaphini

SK M2	LM1	2324	Tr script	.029	.524	Alcelaphini
SK M2	LM1	2349	Tr script	.053	.495	Connochaetes sp
SK M2	LM2	2370	Alcelaphus	.000	.985	Damaliscus niro*
SK M2	LM2	2371	Alcelaphus	.000	.975	Damaliscus niro*
SK M2	UM2	2373	Pcapreolus	.058	.589	Damaliscus sp
SK M2	LM3	2374	Damaliscus	.089	.972	Damaliscus sp
SK M2	LM3	2380	Damaliscus	.033	.917	Damaliscus sp
SK M2	UM2	2386	Alcelaphus	.143	.601	Damaliscus sp
SK M2	UM1	2388	Amarsup	.001	.620	Damaliscus sp
SK M2	UM3	2391	Damaliscus	.120	.831	Damaliscus sp
SK M2	UM1	2392	Damaliscus	.083	.899	Damaliscus sp
SK M2	UM1	2395	Damaliscus	.019	.809	Damaliscus sp
SK M2	UM3	2396	Rfulvor	.016	.639	Damaliscus sp
SK M2	LM3	2398	Damaliscus	.032	.905	Damaliscus sp
SK M2	UM1	2399	Ctaurinus	.003	.673	Damaliscus sp
SK M2	UM1	2402	Amarsup	.005	.610	Damaliscus sp
SK M2	LM1	2403	**Damaliscus**	.000	.977	**Damaliscus cf dorcas**
SK M2	LM1	2404	**Damaliscus**	.004	.992	**Damaliscus cf dorcas**
SK M2	UM2	2415	Cgnou	.050	.560	Damaliscus cf dorcas
SK M2	LM1	2418	**Damaliscus**	.000	.706	**Damaliscus cf dorcas**
SK M2	LM2	2419	Alcelaphus	.000	.539	Damaliscus cf dorcas
SK M2	LM1	2423	Alcelaphus	.044	.951	Damaliscus cf dorcas
SK M2	LM1	2424	**Damaliscus**	.001	.963	**Damaliscus cf dorcas**
SK M2	UM1	2426	Pcapreolus	.000	.844	Damaliscus cf dorcas
SK M2	UM1	2427	**Damaliscus**	.012	.783	**Damaliscus cf dorcas**
SK M2	UM1	2428	Pcapreolus	.011	.577	Damaliscus cf dorcas
SK M2	UM1	2430	Tr script	.022	.437	Damaliscus cf dorcas
SK M2	UM1	2431	Tr script	.087	.779	Damaliscus cf dorcas
SK M2	LM3	2442	Amarsup	.101	.968	A. bondi*
SK M2	LM3	2498	Amarsup	.063	.915	A. bondi*
SK M2	LM3	2537	Amarsup	.096	.862	A. bondi*
SK M2	LM1	2550	Tr script	.001	.543	A. bondi*
SK M2	LM3	2554	Amarsup	.049	.967	A. bondi*
SK M2	UM2	2614	Tr strep	.092	.976	Hippotragus cf niger
SK M2	UM1	2615	Hequinus	.000	.999	Hippotragus cf niger
SK M2	LM2	2618	Kleche	.000	.998	Hippotragus cf niger
SK M2	LM2	2621	**Hniger**	.000	1.000	**Hippotragus cf niger**
SK M2	UM1	2632	Amarsup	.037	.605	Hippotragus cf niger
SK M2	LM3	2633	**Hniger**	.012	1.000	**Hippotragus cf niger**
SK M2	LM2	2638	Ctaurinus	.000	.817	K ellipsiprymnus
SK M2	LM2	2677	Pcapreolus	.112	.624	A. bondi*
SK M2	LM2	2679	Pcapreolus	.060	.931	A. bondi*
SK M2	LM2	2682	Rfulvor	.003	.819	A. bondi*

SK M2	LM2	2687	Damaliscus	.001	.927	A. bondi*
SK M2	LM1	2886	Tr script	.000	.602	A.marsup
SK M2	LM2	2895	Damaliscus	.013	.998	A.marsup
SK M2	LM1	2924	Pcapreolus	.000	.905	A.marsup
SK M2	UM2	2932	Oourebi	.076	.739	A. bondi*
SK M2	UM1	2937	Pcapreolus	.044	.498	A. bondi*
SK M2	LM1	2938	Rcamp	.000	.901	A. bondi*
SK M2	LM1	2950	Tr script	.101	.633	A.marsup
SK M2	UM3	3052	Rarund	.122	.901	Antidorcas
SK M2	LM1	3068	Tr script	.010	.948	P.capreolus
SK M2	LM1	3069	Tr script	.012	.526	P.capreolus
SK M2	LM3	3092	**P.capreolus**	.018	.937	**P.capreolus**
SK M2	LM3	3101	Tr script	.019	.946	P.capreolus
SK M2	LM2	3102	Tr script	.002	.809	P.capreolus
SK M2	LM3	3103	Tr script	.002	.999	P.capreolus
SK M2	LM2	3104	Tr script	.002	.979	P.capreolus
SK M2	LM1	3105	Tr script	.008	.446	P.capreolus
SK M2	LM2	3107	Tr script	.000	.965	P.capreolus
SK M2	LM1	3108	Kleche	.000	.997	P.capreolus
SK M2	LM1	2400/2401	Amarsup	.000	.995	Damaliscus
SK M2	LM3	3071/72	**P.capreolus**	.000	.610	**P.capreolus**
SKX M1	UM1	3149	Amarsup	.001	.940	Alcelaphus
SKX M1	LM1	3150	Damaliscus	.000	.993	Alcelaphus
SKX M1	LM3	3158	**A.marsup**	.010	.850	**A.marsup**
SKX M1	UM2	3169	Alcelaphus	.001	.983	Damaliscus sp
SKX M1	LM2	3170	Pcapreolus	.000	.998	Damaliscus sp
SKX M1	LM3	3181	Amarsup	.029	.800	Damaliscus sp
SKX M1	LM3	3183	Alcelaphus	.089	.499	Connochaetes sp
SKX M1	UM2	3185	Kellips	.012	.682	Connochaetes sp
SKX M1	UM1	3196	**Ctaurinus**	.003	.995	**C.taurinus**
SKX M1	UM1	3205	Tr strep	.008	1.000	C.taurinus
SKX M1	UM1	3206	**Ctaurinus**	.070	.944	**C.taurinus**
SKX M1	UM1	3209	**Ctaurinus**	.066	.594	**C.taurinus**
SKX M1	LM3	3211	Alcelaphus	.050	.501	C.taurinus
SKX M1	UM1	3215	Ctaurinus	.009	1.000	Syncerus
SKX M1	UM2	3222	Alcelaphus	.033	.636	Connochaetes sp
SKX M1	UM2	3229	Kleche	.009	.877	C.taurinus
SKX M1	UM1	3231	**C.taurinus**	.059	.997	**C.taurinus**
SKX M1	LM2	3232	Cgnou	.044	.996	Alcelaphini
SKX M1	LM2	3233	Cgnou	.055	.846	C.taurinus
SKX M1	LM1	3237	Pcapreolus	.001	.834	A.marsup
SKX M1	LM3	3246	Damaliscus	.001	.890	Alcelaphus

SKX M2	UM2	3275	Rcamp	.095	.605	Reduncini
SKX M2	LM1	3285	**Damaliscus**	.072	.581	**Damaliscus**
SKX M2	LM1	3288	Rfulvor	.000	.786	Damaliscus
SKX M2	LM1	3341	Tr script	.065	.819	Antidorcas
SKX M2	LM2	3363	**Alcelaphus**	.000	.955	**Alcelaphus**
SKX M2	LM2	3364	Pcapreolus	.001	.942	Alcelaphus
SKX M2	LM2	3366	**Alcelaphus**	.000	.913	**Alcelaphus**
SKX M2	LM3	3368	**Alcelaphus**	.043	.846	**Alcelaphus**
SKX M2	LM3	3374	Alcelaphus	.088	.987	Connochaetes sp
SKX M2	LM3	3376	Ctaurinus	.000	.942	Connochaetes sp
SKX M2	LM2	3382	Alcelaphus	.000	.849	Connochaetes sp
SKX M2	UM2	3388	Ctaurinus	.019	.964	Connochaetes sp
SKX M2	UM2	3389	Ctaurinus	.041	.967	Connochaetes sp
SKX M2	UM2	3390	Ctaurinus	.072	1.000	Connochaetes sp
SKX M2	UM1	3391	Damaliscus	.003	.836	Connochaetes sp
SKX M2	UM1	3395	Cgnou	.103	.526	Connochaetes sp
SKX M2	UM1	3396	Ctaurinus	.000	.982	Connochaetes sp
SKX M2	UM1	3398	Ctaurinus	.078	.828	Connochaetes sp
SKX M2	UM3	3407	Ctaurinus	.137	.526	Connochaetes sp
SKX M2	UM1	3409	Ctaurinus	.000	.998	Connochaetes sp
SKX M2	LM1	3413	Alcelaphus	.071	.994	Damaliscus sp
SKX M2	LM1	3424	Cgnou	.038	.694	Damaliscus sp
SKX M2	LM1	3428	Damaliscus	.106	.759	Damaliscus sp
SKX M2	UM3	3356/57	Ctaurinus	.000	.993	Megalotragus
SKX M3	LM1	3437	Amarsup	.000	1.000	Alcelaphus
SKX M3	LM3	3451	Damaliscus	.106	.870	Damaliscus
SKX M3	LM2	3454	Damaliscus	.011	.744	Damaliscus
SKX M3	LM1	3472	Damaliscus	.134	.988	Damaliscus
SKX M3	LM1	3473	Ctaurinus	.008	.803	Damaliscus
SKX M3	UM1	3476	Tr strep	.030	.596	Alcelaphus
SKX M3	LM2	3477	Cgnou	.000	.960	Alcelaphus
SKX M3	LM1	3488	Cgnou	.079	.981	Alcelaphus
SKX M3	LM2	3489	**Alcelaphus**	.013	.867	**Alcelaphus**
SKX M3	UM1	3490	Cgnou	.094	.999	Alcelaphus
SKX M3	UM2	3493	Amarsup	.047	.695	Alcelaphus
SKX M3	LM1	3495	Damaliscus	.000	1.000	Alcelaphus
SKX M3	LM2	3525	Hniger	.000	.968	Syncerus
SKX M3	LM3	3529	Alcelaphus	.146	.405	Megalotragus*
SKX M3	UM2	3543	Cgnou	.000	.992	T.oryx
SKX M3	UM1	3544	Amarsup	.000	.670	T.oryx
SKX M3	LM1	3601	Pcapreolus	.018	.796	A.marsup
SKX M3	UM1	3641	Pcapreolus	.116	.925	A.marsup
SKX M3	UM3	3659	Toryx	.002	1.000	A.marsup

SKX M3	LM3	3669	Ctaurinus	.000	.999	Connochaetes sp
SKX M3	LM3	3670	Cgnou	.021	.927	Connochaetes sp
SKX M3	LM3	3673	Cgnou	.001	.728	Connochaetes sp
SKX M3	LM3	3679	Ctaurinus	.042	.470	Connochaetes sp
SKX M3	LM3	3682	Alcelaphus	.006	.998	Connochaetes sp
SKX M3	LM3	3688	Ctaurinus	.000	.509	Connochaetes sp
SKX M3	LM3	3689	Cgnou	.000	.603	Connochaetes sp
SKX M3	LM2	3696	Ogazella	.000	.925	Connochaetes sp
SKX M3	LM3	3697	Ctaurinus	.092	.999	Connochaetes sp
SKX M3	LM2	3698	Alcelaphus	.000	.892	Connochaetes sp
SKX M3	LM2	3699	Ogazella	.000	.969	Connochaetes sp
SKX M3	UM3	3708	Toryx	.003	.914	C.taurinus
SKX M3	UM3	3710	Alcelaphus	.085	.918	Connochaetes sp
SKX M3	UM2	3715	Damaliscus	.002	.931	Connochaetes sp
SKX M3	UM3	3716	Ctaurinus	.106	.968	Connochaetes sp
SKX M3	UM3	3718	Ctaurinus	.008	.994	Connochaetes sp
SKX M3	LM2	3724	Cgnou	.000	.934	Connochaetes sp
SKX M3	LM1	3726	Cgnou	.000	.996	Connochaetes sp
SKX M3	LM1	3727	Cgnou	.029	.985	Connochaetes sp
SKX M3	LM1	3728	Ctaurinus	.007	1.000	Connochaetes sp
SKX M3	LM1	3729	Tr script	.048	.903	Connochaetes sp
SKX M3	LM1	3732	Cgnou	.000	.995	Connochaetes sp
SKX M3	LM1	3733	Ctaurinus	.000	1.000	Connochaetes sp
SKX M3	UM1	3741	Cgnou	.097	.970	Connochaetes sp
SKX M3	LM1	3742	Ctaurinus	.000	.648	Connochaetes sp
SKX M3	UM1	3743	Amarsup	.004	.566	Connochaetes sp
SKX M3	LM1	3745	Ctaurinus	.009	1.000	Connochaetes sp
SKX M3	LM1	3749	Ctaurinus	.004	.748	Connochaetes sp
SKX M3	LM1	3750	Ctaurinus	.000	1.000	Connochaetes sp
SKX M3	LM1	3751	Cgnou	.060	.889	Connochaetes sp
SKX M3	LM1	3752	Ctaurinus	.000	.842	Connochaetes sp
SKX M3	LM1	3753	Ctaurinus	.000	1.000	Connochaetes sp
SKX M3	UM1	3757	Ctaurinus	.005	.987	Connochaetes sp
SKX M3	UM1	3759	Ctaurinus	.015	.994	Connochaetes sp
SKX M3	UM1	3761	Ctaurinus	.002	.992	Connochaetes sp
SKX M3	UM1	3765	Cgnou	.005	.958	Connochaetes sp
SKX M3	UM1	3799	Cgnou	.073	.975	Damaliscus sp
SKX M3	UM3	3535/36	Ogazella	.002	.418	Syncerus
SKX M3	LM1	3636/37	Rcamp	.018	.819	A.marsup

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