



Quantitative morphological analysis of bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng Province, South Africa



Juliet K. Brophy^{a,b,*}, Darryl J. de Ruiter^{b,c}, Sheela Athreya^c, Thomas J. DeWitt^d

^a Department of Anthropology, Loyola University Chicago, USA

^b Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

^c Department of Anthropology, Texas A&M University, USA

^d Department of Wildlife and Fisheries Sciences, Texas A&M University, USA

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ABSTRACT

Fossil bovids are widely recognized as valuable ecological indicators, useful for reconstructing paleoenvironments associated with the hominins of Africa. Taxonomic identification of bovid remains in the Plio-Pleistocene fossil deposits of South Africa is based predominantly on dental remains, usually isolated teeth. However, factors such as age and degree of occlusal attrition of teeth often render taxonomic identification difficult. In addition, teeth of closely related bovid taxa can be particularly difficult to diagnose at the species level. Given that closely related bovid species often have differing ecological requirements, imprecise identification of bovids recovered from fossil sites can have significant ramifications when reconstructing environments. This study tests a method for accurately identifying bovid teeth using Elliptical Fourier Function Analysis in order to standardize their identification. The occlusal surfaces of maxillary and mandibular molars of bovid teeth from twenty extant species were digitized and the quantified tooth forms (size and shape) were statistically compared to other closely related bovids. Results indicated that all upper and lower teeth classified correctly using discriminant function analysis $\geq 85\%$ of the time, suggesting that occlusal surface form can reliably differentiate between closely related, morphologically similar bovids.

This method was applied to a sample of fossil bovid teeth previously identified as “medium-sized alcelaphine” from Plovers Lake, Gauteng Province, South Africa. Precise taxonomic identification of these alcelaphines result in the earliest recorded presence of *Alcelaphus buselaphus* and *Connochaetes gnou* in Gauteng Province, as well as potentially the earliest documented co-occurrence of these taxa alongside *Connochaetes taurinus* and *Damaliscus dorcas* in South Africa. Revising the paleoenvironment reconstructed for Plovers Lake suggests that it was likely not much more densely wooded than the area today. This contradicts the paleoenvironment previously inferred for the site, suggesting that overreliance on rare and/or small-bodied taxa in the initial report on Plovers Lake overemphasized the extent of woodlands that were indicated.

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1. Introduction

Paleoanthropologists often rely upon associated animals, particularly those of the Family Bovidae, to reconstruct past hominin environments (Gentry, 1970, 1978; Vrba, 1975; Watson, 1993b; Spencer, 1997; Reed, 1998; Bobe and Eck, 2001; Bobe et al., 2002;

Alemseged, 2003; de Ruiter et al., 2008b). Bovids are especially useful for paleoenvironmental reconstructions owing to their well-documented ecological tendencies, including diet, habitat, and water dependence (Jarman, 1974). In addition, bovids have dominated the African fauna for the past 3.5 Ma (Bobe et al., 2002), including the faunal assemblages from the hominin fossil-bearing caves of South Africa (Vrba, 1976, 1995; Brain, 1981; de Ruiter et al., 2008b). Several recent studies have demonstrated that changes in relative abundances of bovid taxa in fossil assemblages correspond to fluctuations in environmental conditions, as bovids appear to be particularly responsive to environmental changes

* Corresponding author. Department of Anthropology, 1032 W Sheridan Rd., Chicago, IL 60660, USA. Tel.: +1 773 508 2981.

E-mail address: jbrophy1@luc.edu (J.K. Brophy).

(Bobe and Eck, 2001; Alemseged, 2003; de Ruiter et al., 2008b). Thus, bovids are important sources of information for reconstructing paleoenvironments associated with fossil hominins.

Isolated bovid teeth are overwhelmingly the most common fossil elements found in the fossil cave infills of South Africa (Brain, 1981; de Ruiter, 2004; de Ruiter et al., 2008b). While relatively complete fossil bovid cranial remains, in particular those bearing horns, can generally be identified to species (e.g. Gentry, 2011), they are exceedingly rare and highly comminuted in South Africa (Brain, 1981; Watson, 1993a; de Ruiter, 2004), and only factor into questions of taxonomic abundance under limited circumstances (e.g. Vrba, 1971). As a result, the majority of research into bovid abundances in the hominin-bearing cave assemblages of South Africa is based on isolated fossil teeth, even though taxonomic identification of such isolated teeth is often imprecise and subjective. Bovid teeth can be morphologically differentiated at the level of the tribe, because at this level they differ rather consistently in morphological features (Gentry, 1978). However, more precise taxonomic diagnoses below the tribal level can be elusive, as biasing factors such as age and degree of occlusal wear complicate identifications among animals of similar body size, and often result in considerable overlap in the size and shape of teeth within the same tribe (Adams et al., 2007; Brophy, 2011). In addition, patterns of attrition in hypsodont teeth differ from those seen in more brachyodont teeth (Fortelius and Solounias, 2000), further complicating taxonomic identification. Because subtle distinctions in tooth shape of closely related species are difficult for the human eye to perceive or quantify, faunal analysts often rely upon the size of a tooth to help distinguish between bovids within a given tribe. However, tooth size alone is not an accurate indicator of a species, as there is often considerable overlap in the absolute and relative body size, and thus dental size, of animals within a tribe (Adams et al., 2007; Brophy, 2011).

Owing to this, identification of bovid teeth in the fossil record is particularly challenging and can lead to misidentifications, which in turn can lead to erroneous paleoenvironmental reconstructions. Alternatively, researchers can adopt a more conservative approach and lump together closely related species with similar looking teeth into higher taxonomic categories, despite their notably different habitat preferences. For example, blue wildebeest (*Connochaetes taurinus*) and red hartebeest (*Alcelaphus buselaphus*) are often grouped together as “medium-sized alcelaphines”, obscuring the subtle ecological differences between the two. Different approaches utilized by different researchers lead to the problem of inter-observer error, thus faunal analysts often encounter difficulty when comparing faunal lists of sites produced by different analysts owing to quality of fossil preservation, access to comparative materials, differences in levels of experience, and relative confidence of identifications (e.g. see Watson, 1993b contra Adams, 2006). By way of example, using different techniques to study essentially the same faunal assemblage, Wells and Cooke (1956), Vrba (1995), and Reed (1998) have all proposed contrasting environmental reconstructions for Makapansgat Member 3 (gray breccia). Wells and Cooke (1956) suggested a shrub-like terrain with nearby open grasslands, Vrba (1995) a woodland, and Reed (1998) a bushland with riparian woodland and nearby limited wetlands, highlighting the contradictory outcomes can result even when the same assemblage is being analyzed. At Swartkrans, Watson (1993a) concluded that the faunas, and therefore environments, were relatively consistent across Members 1–3, whereas de Ruiter (2004) revised the relative abundance estimates for these same Members and found that the faunas were not consistent throughout the depositions, concluding that the paleoenvironment at Swartkrans had changed over time. And, Adams (2006) reanalyzed the faunal assemblage from Gondolin and recognized several previously undocumented

Table 1
Extant bovid species analyzed in this study.

Tribe	Species	# Specimens
Alcelaphini	<i>Connochaetes taurinus</i>	180
	<i>Connochaetes gnou</i>	180
	<i>Alcelaphus buselaphus</i>	180
	<i>Damaliscus dorcas</i>	180
Tragelaphini	<i>Taurotragus oryx</i>	162
	<i>Tragelaphus strepsiceros</i>	162
	<i>Tragelaphus scriptus</i>	180
Bovini	<i>Syncerus caffer</i>	153
Reduncini	<i>Redunca arundinum</i>	171
	<i>Redunca fulvorifula</i>	180
Hippotragini	<i>Kobus leche</i>	141
	<i>Kobus ellipsiprymnus</i>	180
	<i>Hippotragus niger</i>	141
	<i>Hippotragus equinus</i>	96
Neotragini	<i>Oryx gazella</i>	102
	<i>Raphicerus campestris</i>	180
	<i>Oreotragus oreotragus</i>	75
	<i>Pelea capreolus</i>	64
Antilopini	<i>Ourebia ourebi</i>	60
	<i>Antidorcas marsupialis</i>	180

Redunca sp. specimens, resulting in a considerably different paleoenvironmental than Watson (1993b) had reconstructed.

With these problems in mind, this study presents a new morphometric-based system for reliably and consistently identifying bovid teeth using the outline of the occlusal form (size and shape). We test the hypothesis that extant bovid dentitions can be reliably distinguished as belonging to discrete species, separate from morphologically similar, closely related species. This study also tests the hypothesis that the occlusal outline of a given tooth does not change over its lifespan, despite alteration resulting from attrition. The goal is to assess whether fossil teeth are recognizably similar to modern forms, and whether it is appropriate to use modern bovid teeth as a reference sample to make genus/species level identifications of fossil bovids. This new identification methodology is applied to a sample of bovid teeth recovered from Plovers Lake, South Africa that were previously identified as “medium-sized alcelaphine” (de Ruiter et al., 2008a) to investigate whether more precise taxonomic identifications will substantially influence the paleoenvironment reconstructed.

2. Materials and methods

This research was conducted in three stages: 1) we examined a large sample of modern bovids to test whether they could be reliably sorted into discrete taxonomic categories (genus and/or species) based on occlusal size and shape; 2) we examined a subset of modern bovid teeth to test whether or not dental attrition alters occlusal size and shape such that increasingly worn teeth no longer sort into their respective taxonomic categories; and 3) we examined a sample of imprecisely identified fossil bovid teeth from Plovers Lake to investigate whether they group with modern forms, thus facilitating more precise taxonomic identifications.

2.1. Extant bovid sample

Data collection for the modern sample involved photographing a large number of modern bovid teeth at the National Museum, Bloemfontein and the Ditsong Museum (formerly Transvaal Museum), Pretoria, South Africa. Table 1 lists the species that were photographed and examined in this project. These species were chosen because they are the most abundant bovids in South Africa today, and because they have dominated the South African fauna

for the past 3.5 Ma (Greenacre and Vrba, 1984). Rarer South African bovids such as gazelles and duikers were not included because so few complete, modern, non-zoo specimens were available in the museum collections studied here that they could not comprise statistically viable reference samples.

Separate images were taken of the occlusal surface of the three molars from the upper and lower dentitions for each extant 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 leveled and positioned with a tripod directly above the occlusal surface of the tooth. Each cranium/mandible was situated in a uniform manner so that the teeth were vertical, the occlusal surface could be seen clearly, and each tooth was photographed in the same plane. Specimens were leveled and balanced using bean bags and props. A scale bar was placed directly next to each tooth at the level of the occlusal surface in order to account for any scale differences between photographs. A minimum of 10 individuals per tooth position, per species were used in order to encompass normal variation, but 30 individuals were typically used when sufficient specimens were available. All extant bovid teeth were photographed regardless of their level of attrition, provided that the teeth exhibited complete or mostly complete lobes. If a majority, or approximately 85% or more, of the enamel around the occlusal surface of the tooth could be distinguished, the tooth was included in this study. A majority of the occlusal outline means that if some of the occlusal outline enamel of the tooth was worn away, the tooth was still photographed, but if the overall form of the occlusal surface could not be distinguished, it was not included in this study.

The occlusal surface outlines of the bovid teeth were captured and analyzed using Elliptical Fourier Function Analysis (EFFA) and an associated digitizing program, MLmetrics (Lestrel, 1989; Wolfe et al., 1999). EFFA is a curve-fitting function particularly suited to the characterization of boundary outline data of complex, irregular morphologies (Lestrel, 1974). The use of EFFA allows for 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 two-dimensional morphometric method has previously been applied to the study of primate teeth and other 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; Ginter et al., 2012). EFFA has been shown to be useful in defining detailed differences between ostensibly similar shapes and is an established method for differentiating among taxa. This research is the first time EFFA has been applied to the quantification and identification bovid teeth.

The EFFA approach in this study involved documenting 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 form can be described by a trigonometric function. The sum of the sine and cosine terms in the series makes up a harmonic, or a quantitative descriptor of the form. As the number of terms in the series increases, the difference, or residual, between forms decreases and the series can be shown to converge onto, or redescribe, any shape under consideration. How well the function redescribes the form 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 two-dimensional form being measured.

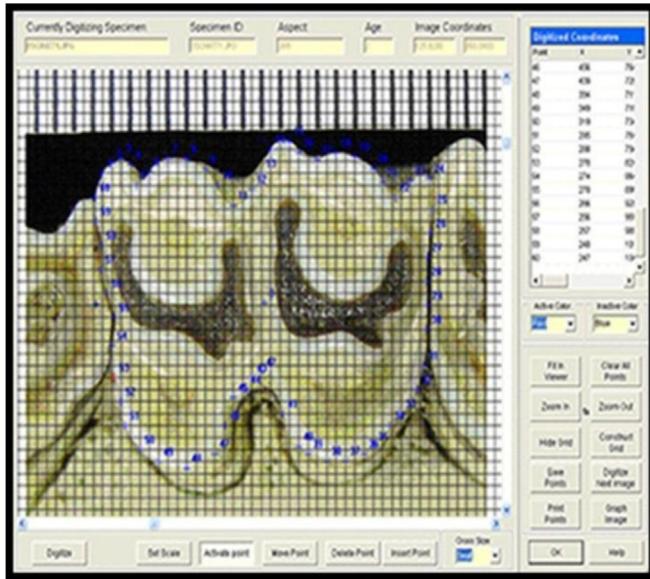
Form comparisons in EFFA are typically made by analyzing the amplitudes of the harmonics. The amplitudes are the maximum height of the sine wave measured from the x-axis (Lestrel, 1974). These measurements are orthogonal and non-cumulative. Thus, these features allow a term by term analysis of the shape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

The digitization process involved creating two-dimensional bounded outline tracings of the occlusal surface of the same tooth type (e.g. M³) from a given species. This step relied on the program MLmetrics, a virtual digitizer developed to function specifically with EFF23 v.4 (Wolfe et al., 1999). Each picture was opened in MLmetrics and a line grid was overlain on the tooth by defining the left and right most point of the tooth and then the top and bottom most points. This step created a square around the tooth and a grid whose middle lines cross directly through the center of the tooth. A standardized, rectangular grid was placed on the image using that center of the tooth as a reference. Teeth were digitized according to a template ensuring that each tooth has the same number of points and that the points were placed in homologous positions. After experimentation, sixty points were found to capture adequately the invaginations and convolutions of each tooth (see Fig. 1). Elliptical Fourier analysis (unlike conventional Fourier analysis) does not require that the points are evenly spaced; therefore, digitized points were concentrated in areas of the tooth that were more complex. Sixty points were placed around the outline of the tooth using the grid and template for orientation. The first point, point 1, was always the upper most, left most spot where the grid crosses the tooth (Fig. 1). MLmetrics produced X,Y coordinates for each of the sixty points on the tooth. The outline defined by these points was then quantified using EFFA.

In order to analyze the data, the harmonic amplitudes of each tooth type generated by EFFA were compared statistically across species in the same tribe. For example, only the M³ teeth from species in the tribe Alcelaphini were compared with each other, and the M³ teeth from species in the tribe Hippotragini, etc. A tribe that had only one representative species in its tribe was combined with the tribe to which it was most closely evolutionarily related; for instance, Antilopini (in South Africa, only *Antidorcas marsupialis* were available for study) was subsumed into Neotragini while Bovini was combined with Tragelaphini. Members of the same tribe were analyzed in order to maintain similar sample sizes. The number of individuals per species available for study in modern reference samples varied. For example, a large number of modern Alcelaphini existed in the collections but a relatively small number of Neotragini; therefore, the number of individuals in each tribe differed. By analyzing species in the same tribe, sample sizes were more consistent.

First, a multivariate analysis of variance (MANOVA) was calculated using JMP statistical software (version 8.0.1, SAS Institute, Inc., Cary, NC) and Wilks' lambda was evaluated to determine whether there were significant shape differences for a given a tooth type (e.g. M³) among the means of each bovid species within a tribe. The means of the occlusal surface for each bovid species were considered significantly different among the species if the Wilks' lambda results were $p < 0.01$. Next, principal component analyses were conducted using a between group covariance matrix. A principal component analysis was done because 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 principal components (PCs) were then used to perform a linear discriminant function analysis (DFA). Thirty PCs were used following the results of a pilot study, where this number of

A)



B)

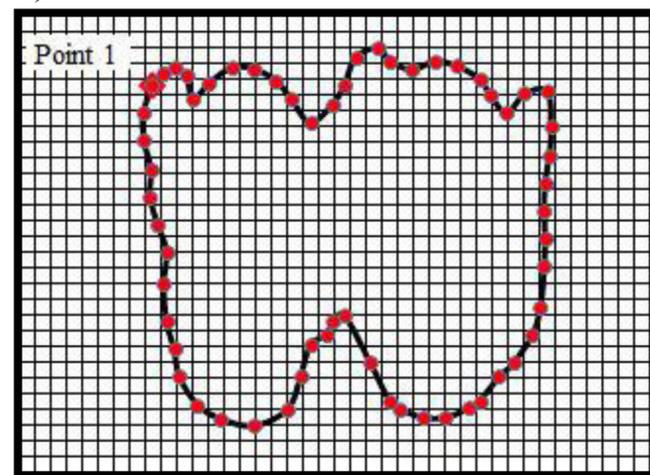


Fig. 1. The images illustrate the grid and point placement about each tooth. Screen capture of tooth digitization using the program MLmetrics (Wolfe et al., 1999) (A). An outline of the tooth using the x,y coordinates generated in MLmetrics (B). Point one, the upper most, left most point, is indicated with a \blacklozenge .

variables most successfully discriminated among species in the same tribe; in other words, the least number of misclassifications resulted. This suggests that the higher order PCs contributed significantly towards discriminating among the groups.

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 were compiled into a database. MANOVA and PCA were run on the amplitudes and group membership was predicted using DFA. This study considers an *a priori* reliable rate of classification to be 85%. If the modern bovids classify correctly $\geq 85\%$ of the time, then the results were considered reliable enough to apply this methodology to fossil specimens (see Reyment et al., 1984; Bailey and Lynch, 2005; Cucchi et al., 2008).

2.2. Occlusal attrition test

Before examining fossil specimens, it must first be demonstrated that the shape of the occlusal outline of a tooth remains

Table 2

Results of the Tukey–Kramer test for the tribe Hippotragini.

Comparison		p Value
<i>H. niger</i>	<i>O. gazella</i>	<0.001
<i>H. equinus</i>	<i>O. gazella</i>	0.0003
<i>H. niger</i>	<i>H. equinus</i>	0.993

consistent throughout the lifespan of an animal. Age and attrition could potentially cause changes in the morphology and size of a tooth throughout the course of the animal's life, potentially invalidating the results obtained above. For example, the possibility exists that a change in occlusal shape or size is occurring as hypsodont teeth wear down. The occlusal shape or size of brachydont teeth could also change over time. Thus, it is important to ensure that the outline of the tooth remains consistent regardless of age and attrition. This test assesses intra-tooth variation using computed tomography (CT) scans of a sample of bovid teeth (see Adams, 2005, for a similar study using Suidae teeth).

Specimens were borrowed from The Field Museum in Chicago and CT scanned at Mercy Hospital and Medical Center, Chicago. A sample of bovids was carefully chosen to include four different tribes: Alcelaphini, Antilopini, Tragelaphini and Reduncini (Table 4). These four tribes were chosen because they encompass a wide range of variation in shape and relative hypsodonty/brachydonty, and are common in the South African fossil assemblages. 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 the attrition accrued during an animal's life. The specimens were scanned using a Phillips Brilliance 64 CT Scanner, with images taken at 0.67 mm intervals. Every third image was digitized for this study, approximately every 2 mm, starting from the first image where the entire occlusal surface was in view and ending when at least 85% of the occlusal surface could no longer be discerned.

The digitized CT scans were analyzed using MLmetrics and EFA. The same protocol used on the extant teeth was applied to the CT scans to ensure standardization. The teeth were digitized according to a template ensuring that each tooth has the same 60 points, and that the points were placed in homologous positions. The X and Y coordinates for each of the sixty points on the tooth were exported and used in EFA where the harmonics and amplitudes were generated (Lestrel, 1989; Wolfe et al., 1999). The amplitudes of those scans were placed as “unknowns” in a dataset of known, modern teeth and PCs were obtained. During the calculation of the PCs, the CT scans were excluded; this method allows the CT scans to have PCs without introducing bias. A DFA was performed using the PCs to test whether each CT scan, or “wear stage”, classified correctly when compared with the set of known teeth. DFA was used to predict to what tribe the tooth belonged, and then to predict to which species each scan belonged. This procedure allows for each tooth to be considered as an unknown taxon in the Family Bovidae. This procedure tests whether the occlusal outline defined for each species changes significantly throughout the life of the animal in various stages of attrition, and that the occlusal outline still groups with members of its species.

2.3. Plovers Lake fossil sample

Plovers Lake is located in the Gauteng Province, South Africa, approximately 45 km northwest of Johannesburg (Fig. 2). The internal deposits of the cave were excavated from 2002 to 2004, and a large faunal assemblage and archeological sample of a Middle Stone Age (MSA) character was recovered, dating to between 62.9 and

Table 3
Percentage of teeth that classified correctly using discriminant function analysis. Results are broken down by tribe.

	M ³	n	M ²	n	M ¹	n	M ₃	n	M ₂	n	M ₁	n
Alcelaphini												
<i>Damaliscus dorcas</i>	100	30	100	30	100	30	100	30	100	30	100	30
<i>Alcelaphus buselaphus</i>	96.7	30	100	30	100	30	100	30	96.7	30	100	30
<i>Connochaetes gnou</i>	96.7	30	100	30	100	30	100	30	96.7	30	100	30
<i>Connochaetes taurinus</i>	100	30	96.8	30	100	30	100	30	100	30	100	30
Tragelaphini												
<i>Taurotragus oryx</i>	100	30	100	30	100	30	100	24	100	24	100	24
<i>Tragelaphus strepsiceros</i>	100	30	100	30	100	30	100	24	100	24	100	24
<i>Tragelaphus scriptus</i>	100	30	100	30	100	30	100	30	100	30	100	30
Bovini												
<i>Syncerus caffer</i>	100	25	100	25	100	25	100	26	100	26	100	26
Neotragini												
<i>Raphicerus campestris</i>	100	30	100	30	100	30	100	30	100	30	100	30
<i>Oreotragus oreotragus</i>	100	13	100	13	100	13	100	12	100	12	100	12
<i>Ourebia ourebi</i>	100	10	100	10	100	10	100	10	100	10	100	10
<i>Pelea capreolus</i>	100	11	100	10	100	10	100	11	100	11	100	11
Antilopini												
<i>Antidorcas marsupialis</i>	100	30	100	30	100	30	100	30	100	30	100	30
Hippotragini												
<i>Hippotragus niger</i>	100	30	100	30	100	30	100	17	100	17	100	17
<i>Hippotragus equinus</i>	100	16	100	16	100	16	100	16	100	16	100	16
<i>Oryx gazella</i>	100	17	100	17	100	17	100	17	100	17	100	17
Reduncini												
<i>Redunca arundinum</i>	96.7	30	96.6	30	100	30	100	27	95.5	27	100	27
<i>Redunca fulvorufula</i>	100	30	96.7	30	100	30	95.7	30	100	30	100	30
<i>Kobus leche</i>	95.8	24	89.3	24	100	24	100	23	100	23	100	23
<i>Kobus ellipsiprymnus</i>	100	30	100	30	100	30	100	30	100	30	100	30

88.7 ka (de Ruiter et al., 2008a). The animal paleocommunity of the Plovers Lake assemblage was interpreted as indicating a predominantly grassland environment. The presence of browsers and mixed feeders suggest some form of woodland in the vicinity. The water dependent taxa including Cape clawless otter, water mongoose, reedbuck, and possibly hippopotamus indicate the presence of a nearby permanent water source such as a lake or, more likely, a perennial river. The environment is reconstructed as being predominantly made up of grasslands, but more densely wooded, colder, and moister than the area is today (de Ruiter et al., 2008a).

Thirteen bovid species were identified at the site, including a variety of alcelaphines. In addition to alcelaphines that could be diagnosed to species, de Ruiter et al. (2008a) included a broad taxonomic category of “medium-sized alcelaphine”, which was mainly comprised of isolated teeth that could not be visually

identified to species with any certainty. Medium sized alcelaphines potentially includes species such as *Damaliscus dorcas*, *Damaliscus niro*, *Alcelaphus buselaphus*, *Connochaetes gnou*, and possibly even smaller individuals of *C. taurinus*. Teeth in this category overlapped in shape and size with more than one species in the modern and fossil alcelaphine comparative collection, thus preventing de Ruiter et al. (2008a) from making genus/species identifications. As a result, de Ruiter et al. (2008a) were only able to reconstruct the paleoenvironment in relatively broad terms.

Using the same protocols as for the extant bovids, two dimensional images were taken of the occlusal surface outline of the “medium-sized alcelaphine” teeth from Plovers Lake at the University of Witwatersrand, Johannesburg. Table 5 lists the fossil specimens examined in this study. The outlines of the occlusal surface of the bovid teeth were captured and analyzed using the same procedure as the extant teeth and CT scans. The X and Y coordinates were exported and used in EFFA to generate the harmonics and amplitudes (Lestrel, 1989; Wolfe et al., 1999). The amplitudes of the harmonic that were calculated for each fossil tooth type were placed as unknowns in the database of the modern reference sample of the same tooth type (e.g. M³) and PCs were obtained. As described above in the CT scan protocol, the fossil amplitudes were excluded when the PCs were calculated in order to obtain PCs for the fossils without introducing any bias. Linear DFA was performed relying on 30 PCs and was used to predict to what tribe each fossil most likely belonged. Analyzing the fossils first at this broad level ensures that there are no preconceived assumptions about their taxonomic identification. Once the tribe affiliation was predicted, the extant and fossil teeth were divided up by tooth type into their respective tribes and DFA was performed again in order to determine the species identification of each fossil specimen. For example, an unidentified fossil M³ is first compared to all of the extant bovid M³s to determine its tribe. After the tribe is predicted, e.g. Alcelaphini, the fossil is compared with the species in the tribe Alcelaphini. Fossils that classify with ≥ 0.15 typicality probability are considered a member of that group. A typicality probability demonstrates whether the fossil falls within the

Table 4
Percentage of CT scans of extant teeth that classified correctly using DFA.

	Tooth type	# Scans per tooth	% Correct classification
Alcelaphini			
<i>Connochaetes gnou</i>	M ¹	4	100
<i>Connochaetes gnou</i>	M ²	4	100
<i>Connochaetes gnou</i>	M ³	4	85
<i>Connochaetes gnou</i>	M ₂	4	100
<i>Connochaetes taurinus</i>	M ₃	5	100
Antilopini			
<i>Antidorcas marsupialis</i>	M ¹	4	100
<i>Antidorcas marsupialis</i>	M ²	4	100
<i>Antidorcas marsupialis</i>	M ³	4	100
<i>Antidorcas marsupialis</i>	M ₁	4	100
<i>Antidorcas marsupialis</i>	M ₂	4	100
<i>Antidorcas marsupialis</i>	M ₃	4	100
Tragelaphini			
<i>Tragelaphus scriptus</i>	M ²	4	100
<i>Tragelaphus strepsiceros</i>	M ₂	4	100
Reduncini			
<i>Redunca arundinum</i>	M ²	4	100

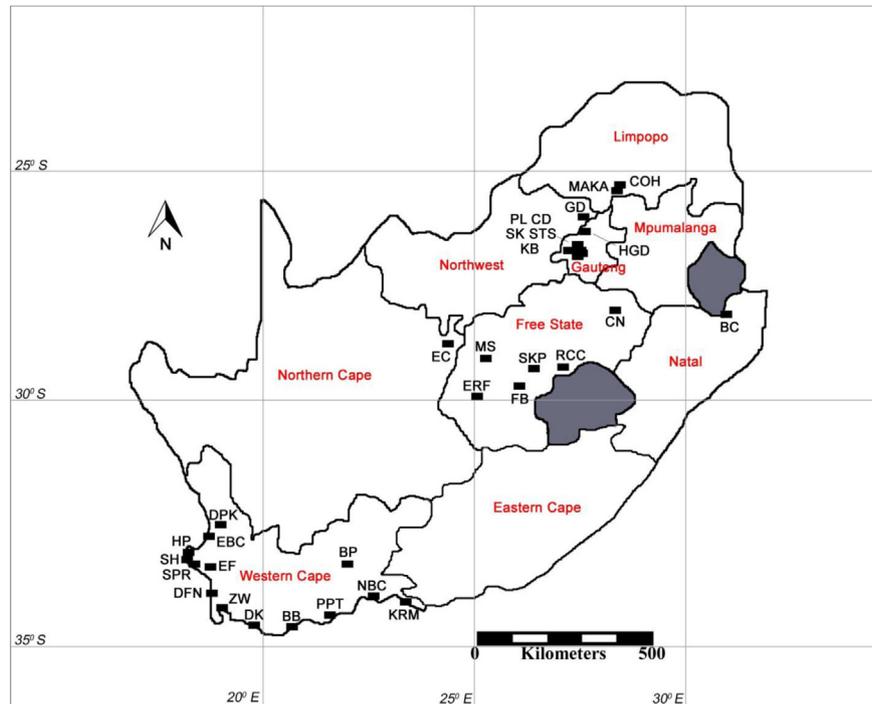


Fig. 2. Map of fossil localities in South Africa mentioned in the text. **Gauteng Province:** PL = Plovers Lake, SK = Swartkrans, STS = Sterkfontein, KB, Kromdraai B, CD = Coopers Cave D, HGD = Haasgat; **Northwest Province:** GD = Gondolin; **Limpopo Province:** MAKA = Makapansgat, COH = Cave of Hearths; **Natal Province:** BC = Border Cave; **Northern Cape:** EC = Equis Cave; **Free State Province:** FB = Florisbad, ERF = Erfkroon, CN = Cornelia, RCC = Rose Cottage Cave, MS = Mahemspan, SKP = Spitskop; **Western Cape:** DFN = Duinefontein, EBC = Elands Bay Cave, DPK = Diepkloof, HP = Hoedjies Punt, SH = Sea Harvest, SPR = Spreeuwal, EF = Elandsfontein, ZW = Swartklip, BP = Boomplaas, DK = Die Kelders, PPT = Pinnacle Point, NBC = Nelson Bay Cave, KRM = Klasies River Mouth, BB = Blombos Cave.

multivariate normal distribution of one of the reference groups. This probability is based on the generalized distances between a fossil and each group centroid (Albrecht, 1992). A typicality probability of ≥ 0.15 means that no more than 85% of the individuals in a group lie closer to the group centroid than the unknown specimen (Albrecht, 1992). The typicality probability is not limited to the choice of one of the reference groups, however; 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. However, teeth that belong to taxa not included in the reference groups are not classified. While the use of typicality probabilities can result in a smaller dataset of identified fossils, there is a high amount of confidence in the classification of those fossils.

A fossil that classifies with a typicality probability of ≤ 0.15 does not fall within the multivariate normal distribution of one of the reference groups. This fossil could be an extinct species, an outlier of form (size and shape) of an extant species, or a modern species not previously thought to be in South Africa at this time. While some fossils may not be classified if they belong to a taxa not included in the reference groups, as this study and methodology

expands the unknown specimens will be diagnosed with more confidence. Future research will be aimed at expanding the modern reference sample, as well as documenting statistically viable extinct samples.

3. Results

3.1. Extant bovid sample

Results of the MANOVA suggest that the means of the occlusal surface for each tooth type differ significantly among almost all of the species (all values $p < 0.001$). In fact, only one tooth had a non-significant result: the M_1 of the Hippotragini was not significant with a p value of 0.0781. This result indicates that the average means of the occlusal surface of the M_1 from the three species in the tribe Hippotragini are not significantly different from each other; the M_2 , M_3 , M^1 , M^2 , and M^3 of the Hippotragini are significantly different from each other. In other words, this technique can readily identify the M_2 , M_3 , M^1 , M^2 , and M^3 respectively of the three Hippotragini species. In order to determine which of the M_1 of the three Hippotragini species were significantly different from each other, a MANOVA post hoc test, the Tukey–Kramer, was performed on the data (Table 2). The results of this test indicate that *Oryx gazella* is significantly different from *Hippotragus niger* ($p < 0.001$) and *Hippotragus equinus* ($p < 0.001$), but *H. niger* and *H. equinus* are not different from each other ($p = 0.993$). This finding is not surprising given the fact that *H. niger* and *H. equinus* belong to the same genus and are evolutionarily closely related; thus, some overlap in the means of the occlusal surface outline form exists between the *H. niger* and *H. equinus*.

Table 3 illustrates the percentage of teeth that classified correctly per species, per tooth. DFA classified all of the teeth above the *a priori* rate of 85%. These results suggest that the occlusal

Table 5

Plovers Lake specimens that were examined in this study. These teeth were previously identified as “Medium-sized Alcelaphine”.

Tooth	Plovers Lake specimen number (PV)
M_1	17719, 19084a, 5917
M_2	14561, 17706, 10681
M_3	10917, 10943, 16322, 9954, 11077, 14546, 17713
M^1	18940, 17761, 3401, 3475, 5861
M^2	17727, 4609
M^3	14586, 17754

Table 6
New identifications of Plovers Lake specimens. All specimens classified with a ≥ 0.15 typicality probability.

Tooth	Side	Accession number (PV)	Tribe	Species	Typicality probability
M ₁	Left	17719	Alcelaphini	<i>Connochaetes gnou</i>	0.538
	Left	19084a	Alcelaphini	<i>Connochaetes gnou</i>	0.82
	Left	5917	Alcelaphini	<i>Damaliscus dorcas</i>	0.147 ^a
M ₂	Left	14561	Alcelaphini	<i>Alcelaphus buselaphus</i>	0.557
	Left	17706	Alcelaphini	<i>Alcelaphus buselaphus</i>	0.396
M ₃	Right	10681	Alcelaphini	<i>Alcelaphus buselaphus</i>	0.372
	Left	10917	Alcelaphini	<i>Damaliscus dorcas</i>	0.335
	Left	10943	Alcelaphini	<i>Damaliscus dorcas</i>	0.97
	Left	16322	Alcelaphini	<i>Damaliscus dorcas</i>	0.937
	Left	9954	Alcelaphini	<i>Damaliscus dorcas</i>	0.863
	Right	11077	Alcelaphini	<i>Connochaetes gnou</i>	0.462
	Right	14546	Alcelaphini	<i>Damaliscus dorcas</i>	0.597
	Right	17713	Alcelaphini	<i>Damaliscus dorcas</i>	0.555
M ¹	Left	18940	Alcelaphini	<i>Connochaetes gnou</i>	0.428
	Right	17761	Alcelaphini	<i>Damaliscus dorcas</i>	0.838
	Left	3401	Alcelaphini	<i>Damaliscus dorcas</i>	0.173
	Left	3475	Alcelaphini	<i>Damaliscus dorcas</i>	0.331
M ²	Right	5861	Alcelaphini	<i>Connochaetes gnou</i>	0.192
	Right	17727	Alcelaphini	<i>Damaliscus dorcas</i>	0.525
M ³	Left	4609	Alcelaphini	<i>Alcelaphus buselaphus</i>	0.837
	Left	14586	Alcelaphini	<i>Damaliscus dorcas</i>	0.886
	Right	17754	Alcelaphini	<i>Damaliscus dorcas</i>	0.873

^a The typicality probability of specimen 5917 was rounded to 0.15.

outline of extant bovid teeth is indicative of species; i.e. an isolated, extant bovid tooth can be classified to species based on an analysis of its occlusal outline. The high classification rates of the extant teeth support the application of this method to the identification of fossil bovids in order to test whether fossil bovid forms are recognizably similar to modern forms.

The results of the MANOVA for the M₁ of the Hippotragini demonstrated that there was overlap in the means of teeth in this group; however, these teeth were discriminated from each other when DFA was performed. This result occurred because MANOVA and DFA assess the variables of the groups differently. A MANOVA assesses whether the mean of a tooth type (e.g. M³) from one species differs from the mean of the same tooth type from another species, while DFA compares the variables of one specimen to the means of the groups and calculates to which group the specimen best aligns (Campbell, 1984). DFA does not calculate whether the group means are statistically different from each other. Therefore, a MANOVA may show that the means of a tooth of one species are not significantly different from the means of a tooth of another species in the same tribe, as seen in the M₁ of the Hippotragini, but this result would not necessarily affect its ability to discriminate one tooth type from another.

As this identification methodology expands, the number of individuals in each species and number of species will increase. The possibility exists that the percentages of correct classifications could increase or decrease with a larger sample size and/or more species; in particular, the results could change when more congeners are examined. The results of the methodology using the current sample demonstrate that if there are differences in the form (size and shape) between the teeth of closely related species, this approach will be able to discriminate between them.

3.2. Occlusal attrition test

All of the individuals in the sample classified above the *a priori* rate of 85% (Table 4). The misclassifications that did result tend to be from the layers closest to the roots of the tooth. While only teeth with >85% of the enamel around the tooth were digitized, the enamel outline of the tooth becomes more rounded and less distinct at the layers closest to the roots, i.e. as teeth become very worn. The results of this age and attrition test suggest that the form

of the teeth tested in this sample does not change significantly enough during dental attrition to impede precise species identification of teeth. The lack of intra-tooth variation suggests that a sample of bovid teeth has a similar occlusal outline regardless of its level of ontogenetic development or attrition. Furthermore, the results of this test indicate that bovid teeth at different wear stages can be used reliably to test if the occlusal outline of a given tooth can be distinguished from other closely related bovid species.

3.3. Plovers Lake fossil sample

Table 6 lists the new identifications of the Plovers Lake specimens that were previously identified as “medium-sized alcelaphine”. Thirteen specimens were identified as *D. dorcas*, four as *A. buselaphus*, and five as *C. gnou*. All fossils analyzed had a typicality probability of ≥ 0.15 . These results increase the number of *D. dorcas* recovered and add *A. buselaphus*, the red hartebeest, and *C. gnou*, the black wildebeest, to the Plovers Lake faunal list (de Ruiter et al., 2008a).

It is important to note that the extinct species *D. niro* was not one of the reference samples when DFA was performed, despite the fact that it is considered a medium-sized alcelaphine and was previously identified at Plovers Lake from a single horn core (de Ruiter et al., 2008a). All thirteen fossils analyzed resulted in a typicality probability of ≥ 0.15 , suggesting that there is a high degree of confidence that these fossils *do* belong to one of the reference groups and not an unknown or extinct species. However, several of the *D. dorcas* teeth are identified as such with typicality probabilities very close to the threshold value of 0.15, raising the possibility that they might represent a closely allied form, perhaps even *D. niro*. Future research using this methodology will incorporate extinct taxa for which reliable reference samples can be identified, i.e. samples based on horn cores with directly associated dentition, allowing us to revisit the *D. niro* issue.

4. Discussion and conclusions

The results of the extant bovid sample and the occlusal attrition test substantiate the use of form (size and shape) of the occlusal surface of bovid teeth as a reliable indicator of a species. The methodology will help standardize the way bovids are taxonomically identified. This approach is not meant to replace previous identification methods but to be used as a quantifiable supplement to other methods (see Ginter et al., 2012), in particular where ambiguity exists in their identification. This research provides a database of occlusal surface outlines of extant bovids and will expand as the number of individuals increases for each species and the number of species (extant and fossil) in the reference sample grows. Most importantly, this research demonstrates that the database generated in this study can be used as a reference for analysts to identify bovids in the fossil record.

The results of the Plovers Lake analysis suggest that *A. buselaphus* and *C. gnou* should be added to the faunal list presented by de Ruiter et al. (2008a), resulting in a great diversity of alcelaphines at Plovers Lake. However, the broad temporal span identified for Plovers Lake (62.9–88.7 ka) raises the possibility of time-averaging in the assemblage, suggesting that multiple habitats might have been sampled. While time-averaging remains a potentially confounding factor, several points argue against such a bias. A single ESR date of 75.6 (± 5.6) ka possibly constrains the age of the fossils to a greater degree than the wider U-series dates produced for the overlying and underlying flowstones (de Ruiter et al., 2008a). The probable source of the fossils is a vertically restricted deposit of less than 0.75 m thickness which shows no internal stratification or geomorphological heterogeneity. Given

Table 7
Alcelaphines identified at Plio-Pleistocene sites in South Africa. The sites are divided up by province.

	<i>Damaliscus dorcas</i>	<i>Damaliscus</i> sp.	<i>Damaliscus</i> cf. <i>dorcas</i>	<i>Damaliscus dorcas</i> or <i>D. niro</i>	<i>Damaliscus pygargus</i>	<i>Damaliscus niro</i>	? <i>Damaliscus niro</i>	cf. <i>Damaliscus</i> sp. or <i>Parmularius</i> sp.
Gauteng Province								
Plovers Lake Internal	X					X		
Plovers Lake External								
Swartkrans Member 1		X ²						X ¹
Swartkrans Member 2		X ²	X ¹				X ¹	
Swartkrans M3		X						
Sterkfontein		X	X					
Cooper's D		X						
Kromdraai B								
Haasgat HGD	X	X						
Northwest Province								
Gondolin (GD1 and GD2)		X						
Limpopo Province								
Makanpansgat Limeworks								
Cave of Hearths Makapansgat								
Northern Cape Province								
Equus Cave	X							
Free State Province								
Florisbad					X	X		
Erfkroon	X					X		
Cornelia						X		
Rose Cottage Cave	X							
Mahemspan					X	X		
Spitskop					X	X		
Natal Province								
Border Cave			X					
Western Cape Province								
Klasies River Mouth		X						
Die Kelders Cave	X							
Blombos Cave								
Elandsfontein		X				X		
Duinefontein 2								
Spreeuwal	X							
Swartklip I								
Diepkloof Rock Shelter								
Elands Bay Cave								
Nelson Bay Cave			X					
Pinnacle Point					X		X	
Boomploas Cave				X	X			
Sea Harvest	X							
Hoedjies Punt								

Superscripts indicate that only the corresponding author identified that species. While research suggests that some of the above species can be taxonomically combined (e.g. *D. pygargus*, see Vrba, 1979; Plug and Badenhorst, 2001), the list highlights the current confusion over alcelaphines and emphasizes the need for a quantifiable way of identifying alcelaphines in the fossil record.

the lack of evidence of human occupation, the homogeneous nature of the sediments from which the fossils were extracted suggests rapid sedimentation. More particularly, this argues against any major environmental fluctuations, as these would likely appear in the geomorphology of the deposit. As a result, there is no clear indication that multiple habitats have been sampled.

The identification of *A. buselaphus* at Plovers Lake is not atypical for the geographical area. In southern Africa, historical and archaeological records document this species in Botswana, Namibia, southern Angola, and South Africa (Skinner and Smithers, 1990; Estes, 1992). On the coast of South Africa, Klein (1976, 1983) identifies *A. buselaphus* from the upper and lower part of the MSA sequence at Klasies River Mouth, which broadly spans the period from 50 to 115 ka (Feathers, 2002), and Rector and Reed (2010) report *A. buselaphus* from Pinnacle Point at 151 ka. Evidence for *A. buselaphus* at non-coastal sites in South Africa was recovered from the Florisbad spring site dating to between 100 and 300 ka (Brink, 1987; Grün et al., 1996). Chronologically, the next evidence of *A. buselaphus* in the interior of South Africa comes from Rose Cottage Cave which dates to 11.8–15 ka (Plug and Engela, 1992;

Pienaar et al., 2008). The identification of *A. buselaphus* at Plovers Lake, dating to ~75 ka, therefore fills a short chronological gap for inland sites (Table 7).

Connochaetes gnou, the black wildebeest, currently tends to occur only in protected areas and reserves; however, historical and archaeological records indicate that the distribution of this species consisted largely of the central plateau of southern Africa extending from south of Pretoria in the north down to the central Karoo and from the Botswana border in the west to the Swaziland border in the east (Brink, 2005; Plug and Badenhorst, 2001). Brink (2005) proposes that the earliest evidence of *C. gnou* in southern Africa comes from Cornelia-Uitzoek in the Free State Province approximately 1.07–0.99 Ma (Brink et al., 2012). This species has been recovered from several other sites in the Free State including Florisbad (100–300 ka) and Erfkroon (~25–125 ka) (Brink, 1987; Grün et al., 1996; Churchill et al., 2000) but has only identified at two sites in the Gauteng Province, Haasgat and Plovers Lake (Table 7) (Adams, 2012). While Haasgat has deposits that date to ~2 Ma, the *ex situ* assemblage has some time averaging and the approximate dates of *C. gnou* are still under analysis (Adams, 2012).

	<i>Alcelaphus</i> <i>cf. helmei</i>	<i>Alcelaphus</i> <i>cf. caama</i>	<i>Alcelaphus</i> <i>buselaphus/</i> <i>C. gnou</i>	<i>Connochaetes</i> <i>gnou</i>	<i>Connochaetes</i> <i>cf. gnou</i>	<i>Connochaetes</i> <i>gnou</i> and/or <i>A. buselaphus</i>	<i>Connochaetes/</i> <i>Alcelaphus</i>	<i>Connochaetes</i> <i>taurinus</i>	<i>Connochaetes</i> <i>cf. taurinus</i>	<i>Connochaetes</i> sp.
Gauteng Province										
Plovers Lake Internal			X					X		
Plovers Lake External										X
Swartkrans Member 1									X ²	
Swartkrans Member 2									X ²	
Swartkrans M3									X	
Sterkfontein								X	X	X
Cooper's D									X	X
Kromdraai B									X	
Haasgat HGD			X							X
Northwest Province										
Gondolin (GD1 and GD2)										X
Limpopo Province										
Makanpansgat Limeworks X									X	
Cave of Hearths										
Makapansgat										
Northern Cape Province										
Equus Cave						X		X		
Free State Province										
Florisbad			X							
Erfkroon			X							
Cornelia			X							
Rose Cottage Cave			X				X		X	
Mahemspan			X					X		
Spitskop			X					X		
Natal Province										
Border Cave								X		
Western Cape Province										
Klasies River Mouth										X
Die Kelders Cave			X							
Blombos Cave						X				
Elandsfontein			X							
Duinefontein 2			X							
Spreeuwal			X							
Swartklip I			X							
Diepkloof Rock Shelter			X							
Elands Bay Cave										
Nelson Bay Cave		X			X					
Pinnacle Point			X							
Boomploos Cave			X				X			
Sea Harvest							X			
Hoedjies Punt							X			

Badenhorst, 2001; Brink, 2005) and their social behaviors help to refine the paleoenvironment reconstruction. *C. gnou*, black wildebeest, require open spaces for their specialized territorial mating behavior, while *C. taurinus*, blue wildebeest, require nearby woodlands (Skinner and Smithers, 1990; Brink, 2005). Since both species are specialized short grass grazers, the coexistence of these two species at the site suggests that at least a component of the habitat at Plovers Lake likely consisted of open grasslands with unobstructed vision for the black wildebeest territorial mating behavior and peripheral areas of shade for the blue wildebeest.

D. dorcas, *A. buselaphus*, *C. gnou*, and a majority of the other bovines substantiate a predominately secondary grassland

paleoenvironment at Plovers Lake (de Ruiter et al., 2008a). While the presence of certain fauna such as *Papio ursinus*, *Chlorocebus aethiops*, *Genetta tigrina*, *Tragelaphus strepsiceros*, and to an extent, *C. taurinus*, support the existence of some form of woodland component at Plovers Lake, the natural abundance of woodland at the site should not be overestimated. The addition of two more secondary grassland adapted species suggests that Plovers Lake at the time of deposition was probably only marginally more densely wooded than the present area today. Moreover, the diversity of the grazing ungulates suggests that the late Pleistocene grasslands of Plovers Lake were different from the sour-veld grassland habitats in the region today (Acocks, 1988; Brink and Lee-Thorp, 1992). These grasslands may have

cf. <i>Connochaetes</i> sp.	<i>Megalotragus priscus</i>	<i>Megalotragus eucornutos</i>	cf. <i>Megalotragus priscus</i>	cf. <i>Megalotragus</i> sp.	<i>Megalotragus</i> sp.	Medium sized alcelaphines	Alcelaphini indet	Reference
	X				X	X		de Ruiter et al., 2008a McKee et al., 1995;
X ¹			X ¹		X ²	X		Thackeray and Watson, 1994
X ¹			X ¹		X ²	X		Vrba, 1976 ¹ ; de Ruiter 2004 ²
					X	X		Vrba, 1976 ¹ ; de Ruiter 2004 ²
X ¹			X ¹		X	X	X	de Ruiter et al., 2008b
					X	X		Vrba, 1976 ¹ ; de Ruiter et al., 2008b; Reynolds and Kibii, 2011 ³
					X	X		de Ruiter et al., 2008b;
								de Ruiter et al., 2009
					X			de Ruiter et al., 2008b;
								de Ruiter et al., 2009
							X	Adams, 2012
							X	Adams et al., 2007; Adams and Conroy, 2005
						X	X	Cooke, 1968; McKee et al., 1995
	X							McKee et al., 1995
	X							Klein et al., 1991
	X							Brink, 1987; Brink, 2005
	X							Churchill et al., 2000
		X						Brink et al., 2012
	X						X	Plug and Engela, 1992;
	X							Wadley, 1997
	X							Brink, 2005
	X							Brink, 2005
								Klein, 1977
								Klein, 1976
								Marean et al., 2000
	X							Henshilwood et al., 2001
								Klein et al., 2007
	X							Cruz-Urbe et al., 2003;
								Klein et al., 2007
								Klein et al., 2007
							X	Klein et al., 2007
							X	Klein and Cruz-Urbe, 1987;
					X			Klein et al., 2007
								Klein, 1972
	X		X				X	Rector and Reed, 2010
							X	Klein, 1978, 1983; Faith, 2012
								Klein, 1983
	X							Klein, 1983

been more productive, less seasonal, and able to sustain more grazing species (Brink and Lee-Thorp, 1992).

In sum, the paleoenvironment of Plovers Lake likely consisted largely of secondary grasslands and some open woodlands with ≤20% of tree cover, and was colder and moister than it is today. This contradicts evidence gleaned from the woodland adapted taxa listed in de Ruiter et al. (2008a), which initially prompted them to reconstruct the environment of Plovers Lake as having been more wooded than today. This suggests that an overreliance on rare and/or small-bodied taxa in the initial report on Plovers Lake overemphasized the extent of woodlands that were indicated. This highlights the importance of precise taxonomic identifications, as the addition of *C. gnou*, for example, an animal

that relies on significant open spaces for its mating practices, forces us to rethink previous interpretations of the environment that the Plovers Lake humans encountered.

The final product of this research is a reliable, standardized, and replicable methodology for identifying fossil bovid teeth, both in isolated form and embedded in crania and mandibles. This method minimizes the impact of biasing factors that often cause overlap in the size and shape of bovid teeth, and helps reduce the degree of subjectivity involved in analyzing faunal lists compiled by different researchers. Future research is aimed at expanding the number of modern taxa included in the comparative sample, and at incorporating extinct taxa based on dentitions directly associated with more identifiable cranial, horn core, and mandibular remains.

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