Dental mesowear and the palaeodiets of bovids from Makapansgat Limeworks Cave, South Africa

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The palaeodiet of seven bovids from Makapansgat Limeworks Cave are analysed using dental mesowear. Results suggest that *Tragelaphus pricei* had a highly attritional diet and was thus a browser. *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. were also browsers, having diets similar in texture to the extant mule deer (*Odocoileus hemionus*). *Gazella vanhoepeni* had an intermediate attrition-abrasion wear signal and groups most closely with extant mixed feeders. *Redunca darti* and *Makapania broomi* are at the abrasion end of the wear continuum and cluster with living grazers, such as the hippotragines and reduncines. *Parmularius braini* had a highly abrasive diet similar to extreme grazers like the American bison (*Bison bison*) and topi (*Damaliscus lunatus*). The bovid mesowear data were compared to previous palaeodietary studies using taxonomic uniformitarianism, ecomorphology (hypsodonty), and stable carbon isotopes on the same Makapansgat taxa. This comparison showed that the mesowear results are most closely in-line with the isotope data, both of which are non-genetic signals that reflect diet during an extended portion of an animal's life.

Keywords: Makapansgat, Plio-Pleistocene, bovids, mesowear, palaeodiets.

INTRODUCTION

Makapansgat Limeworks Cave is a well known Plio-Pleistocene site located northeast of Johannesburg, approximately 15–20 km east-northeast of the town of Mokopane in Limpopo Province, South Africa (24°12′S, 29°12′E). The vertebrate assemblage is extensive and includes a wide variety of taxa, ranging from sabre-toothed cats to chalicotheres and hominins (*Australopithecus africanus*) (Maguire *et al.* 1980; Reed 1996). Bovids are the most abundant large mammal from the site and have been studied by a number of researchers (e.g. Wells & Cooke 1956; Vrba 1987; Reed 1996; Sponheimer *et al.* 1999).

Palaeoenvironmental reconstructions of Makapansgat are numerous and vary widely (Rayner *et al.* 1993; Reed 1996; Sponheimer *et al.* 1999; McKee 1999). The driving force behind these palaeoecological reconstructions has been to better understand the ecology of *A. africanus.* Such environmental reconstructions have focused on Member 3, the main fossil-bearing unit of the deposit. Member 3 dates to about 2.5–3.2 Ma based on biostratigraphic (Harris & White 1979; Vrba 1982; Delson 1984) and palaeomagnetic evidence (Partridge *et al.* 2000; Herries 2003).

Bovids are often used as palaeoenvironmental indicators because they are common in Plio-Pleistocene sites and they can be divided into dietary groupings that are closely linked to habitat types. Browsers are those taxa that eat primarily dicots and typically occur in more densely vegetated habitats, grazers eat mostly monocot grasses and are generally associated with open habitats, and mixed feeders are a large group that vary their diets between graze and browse (Fortelius & Solounias 2000).

In this paper the palaeodiets of seven bovids from the Member 3 fauna are reconstructed using the attrition-abrasion wear gradient, also known as dental mesowear. These results are compared to previously published studies on the diets of these bovids using taxonomic uniformitarianism, ecomorphology (hypsodonty), and isotopic studies (Sponheimer *et al.* 1999), in an attempt to further evince the dietary classifications of these taxa. Schubert *et al.* (in press) compare the results of these data with dental microwear on the same Makapansgat bovids, further elucidate the strengths and weaknesses of the proxy measures, and discuss the palaeoenvironmental implications for Makapansgat.

METHODOLOGICAL BACKGROUND

Mesowear, described by Fortelius & Solounias (2000), is a relatively new technique for reconstructing the diet of ungulates. This method is based on the degree of facet development (cusp height and shape) on the buccal cutting edges of cheek teeth. Wear on teeth can be divided into two categories: attrition (tooth-on-tooth contact) and abrasion (food-on-tooth contact). The difference between a diet that is high in abrasives and one that is not correlates well with traditional dietary categories (Fortelius & Solounias 2000). For example, grazers eat mostly grasses that are composed of silica phytoliths which cause abrasion (McNaughton *et al.* 1985). This results in high percentages of rounded or blunt cusps. Browsers focus on foods that cause less abrasion, resulting in sharper cusps. Some relatively high cusps are found in all dietary categories, but a high percentage of low cusps is a diagnostic feature of extreme grazers (Fortelius & Solounias 2000).

Mesowear has been utilized extensively in ungulate palaeodietary studies (e.g. Franz-Odendaal 2002; Kaiser & Fortelius 2003; Franz-Odendaal & Kaiser 2003; Kaiser & Croiter 2004; Semprebon *et al.* 2004). The original mesowear method was based on the analysis of the upper second molar (M2) only (Fortelius & Solounias 2000). This method has now been extended to include other upper

Table 1. Mesowear and hypsodonty data for Makapansgat bovid taxa. Hypsodonty indices and categories are from Sponheimer *et al.* (1999) and are based on the technique of Janis (1988). Hyp-ind = hypsodonty index, Hyp = hypsodonty index categories, b = brachydont, m = mesodont, h = hypsodont. % high = percentage of high cusps, % low = percentage of low cusps, % sharp = percentage of sharp cusps, % round = percentage of round cusps, % blunt = percentage of blunt cusps.

Taxon	*n*	% high	% low	% sharp	% round	% blunt	Hyp-ind	Hyp
Tragelaphus pricei	13	1.000	0.000	0.846	0.154	0.000	2.50	b
Tragelaphus sp. aff. *T. angasii*	8	1.000	0.000	0.625	0.375	0.000	2.11	b
Aepyceros sp.	8	1.000	0.000	0.625	0.375	0.000	3.59	h
Gazella vanhoepeni	27	1.000	0.000	0.480	0.520	0.000	3.16	m
Makapania broomi	23	0.739	0.261	0.000	0.957	0.043	3.42	m
Redunca darti	23	0.727	0.273	0.000	0.864	0.182	2.93	m
Parmularius braini	5	0.000	1.000	0.000	0.600	0.400	5.11	h

tooth positions in equids (Kaiser & Solounias 2003).

Kaiser & Fortelius (2003) explored differential mesowear in upper and lower equid molars and found a shift in the mesowear towards the grazing end of the spectrum in lowers. To adjust for this, they introduced a calibration factor that allowed comparable mesowear results between upper and lower teeth (Kaiser & Fortelius 2003). Unfortunately, extension of the original method to other teeth in non-equid groups has met with little success (Fortelius & Solounias 2000; Franz-Odendaal & Kaiser 2003). Franz-Odendaal & Kaiser (2003) tested other teeth in ruminants and found that while upper M3s gave the same mesowear signature as upper M2s, lower cheek teeth score significantly different than uppers.

Fortelius & Solounias (2000) compare mesowear to morphology and microwear. They note that morphology (e.g. hypsodonty) is genetic, reflecting deep time and long-term adaptation. Dental microwear is at the other extreme, recording only the last few meals of an animal (Teaford & Oyen 1989). Like microwear, mesowear is a non-genetic signal that reflects the cumulative diet of an animal during its life. The difference is it records diet over an extended period of the animal's lifetime, and thus falls between microwear, which provides a dietary snapshot, and ecomorphology, which reflects adaptation and phylogeny over deep time (Fortelius & Solounias 2000).

MATERIALS AND METHODS

One hundred and seven maxillary bovid teeth from Makapansgat Member 3 were included in the analysis (Appendix I). All utilized specimens are housed at the University of Witwatersrand, Johannesburg, South Africa.

Methods follow Fortelius & Solounias (2000) and Fortelius (pers. comm., 2004). In sum, two variables are scored in mesowear analysis: cusp relief (high or low) and cusp shape (sharp, round, or blunt). The sharper of the two cusps, either the paracone or mesocone is used. Cusps are considered 1) sharp if they come to a distinct point at the apex where mesial and distal facets meet (Fig. 1A–C), round if the cusp is rounded between the mesial and distal facets (Fig. 1D–F), and 3) blunt when this area is flattened and lacks distinct facets. Cusp relief is based on the height of cusps relative to the valley between them. A relief index was calculated for specimens where this was not clear. For this index, the vertical distance between a line connecting the cusp tips and the shallowest point between them is measured and divided by the length of the tooth. Those with a value at or above 0.1 are considered to be high while those below are considered to be low (Fortelius & Solounias 2000). Note, in the original description of the method, Fortelius & Solounias (2000) make an erroneous statement when describing occlusal relief as the 'vertical distance between a line connecting two adjacent cusp tips and two adjacent valley bottoms'(Fortelius, pers. comm., 2004). It should also be noted that some of the figures in this paper are incorrect (e.g. Fortelius & Solounias 2000, fig. 20A,B,G). Thus, while general methodological directions in the text are reliable, some of the figures are not.

Individual Makapansgat bovid teeth were scored for both variables with a ×10 hand lens. Following Franz-Odendaal & Kaiser (2003), both upper M2s and M3s were used. Only teeth with the entire occlusal surface in-wear were included. Excessively worn teeth were not used in the analysis (Fortelius & Solounias 2000).

The mesowear of nineteen extant ruminant artiodactyls (bovids, giraffids and cervids) were used for comparison in this study. The mesowear results for this baseline are from Fortelius & Solounias (2000, table 1). These taxa were chosen because they were considered to be 'typical' feeders within conservative dietary categories (Fortelius & Solounias 2000, table 1).

Percentages of each category were tabulated and hierarchical cluster analyses were used to group taxa into dietary categories based on mesowear variables, $\delta^{13}C$ values and hypsodonty. These cluster analyses were run using complete linkage (furthest neighbors) and Euclidean distance in SYSTAT 7.0. Complete linkage was used to enhance the distinctness of clusters (following Fortelius & Solounias 2000).

MESOWEAR RESULTS

The mesowear results are summarized in Table 1 and Figs 2 and 3. These data show clear differences in the types of wear on the bovid teeth, separating them into two broad groups. *Tragelaphus pricei, T.* sp. aff. *T. angasii, Aepyceros* sp. and *Gazella vanhoepeni* have high percentages of sharp cusps and 100% high cusps, while *Makapania broomi, Redunca darti* and *Parmularius braini* lack sharp cusps and have at least some low cusps.

Hierarchical cluster analysis of mesowear data from the 19 extant ruminant artiodactyls (from Fortelius & Solounias 2000) separated the taxa into distinct dietary categories, with attrition dominated browsers like the

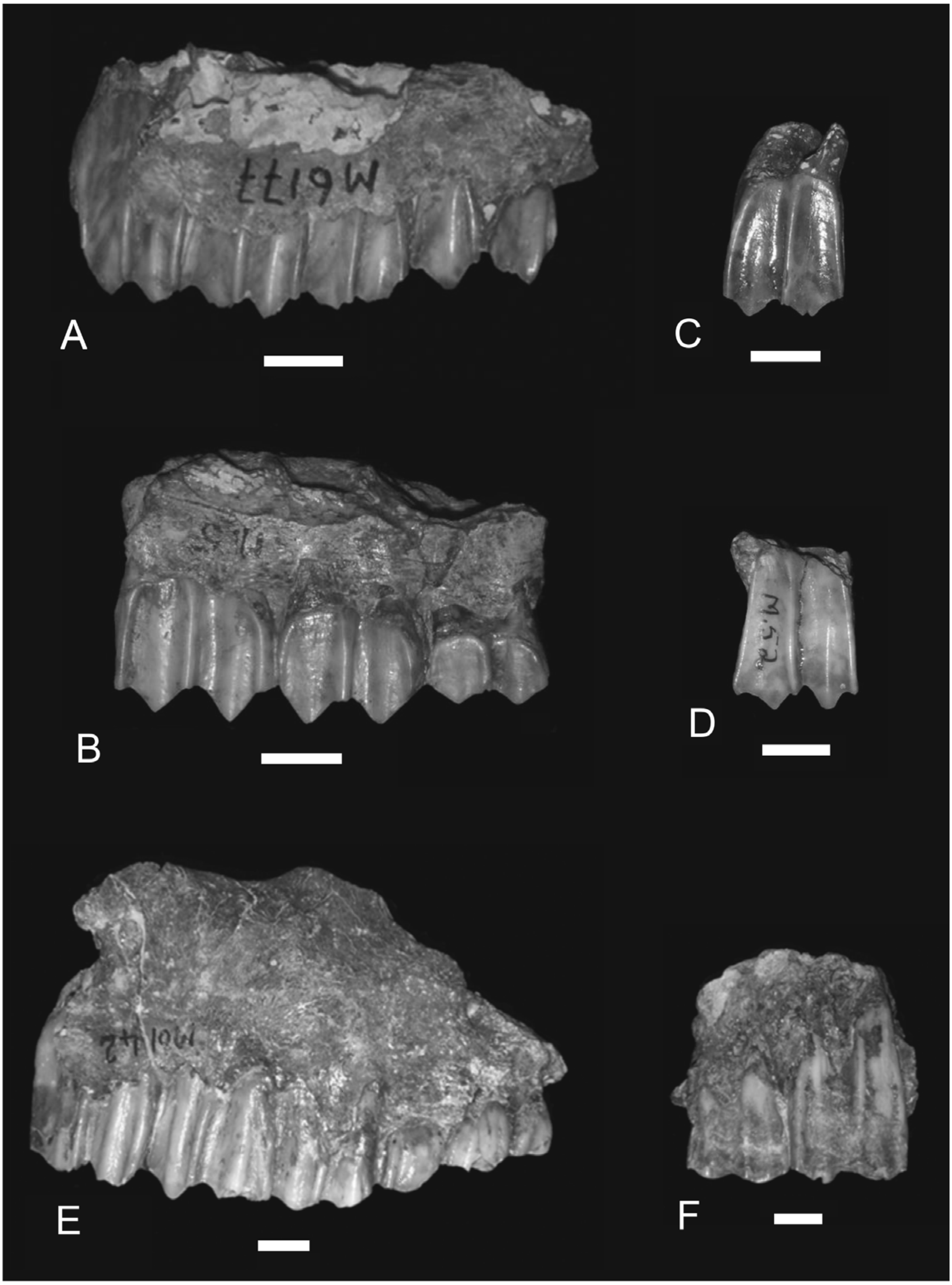

Figure 1. Examples of Makapansgat specimens used in the mesowear analysis. **A**, *Tragelaphus pricei* right P3–M3 (M6177); **B**, *Tragelaphus* sp. aff. *T. angasii* right M1–M3 (M5); **C**, *Aepyceros* sp. left M2 (M7502); **D**, *Gazella vanhoepeni* right M2 (M52); **E**, *Makapania broomi* right P2–M3 (M6142); **F**, *Parmularius braini* left M1–M2 (M6171).

moose (*Alces alces*) at one end of the spectrum, and extreme grazers such as the American bison (*Bison bison*) at the other (Fig. 4). This cluster analysis separates the taxa into four primary groups.

The first group is attrition dominated and contains one Makapansgat bovid, *Tragelaphus pricei*. This species groups most closely with two extreme browsers, the giraffid *Okapia johnstoni* and the cervid *Odocoileus virginiana.*

The second group divides into three subgroups, ranging from browsers to mixed feeders. Two Makapansgat taxa, *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. cluster with the browsing mule deer (*Odocoileus hemionus*). The other two subgroups are composed of extant mixed feeders. The

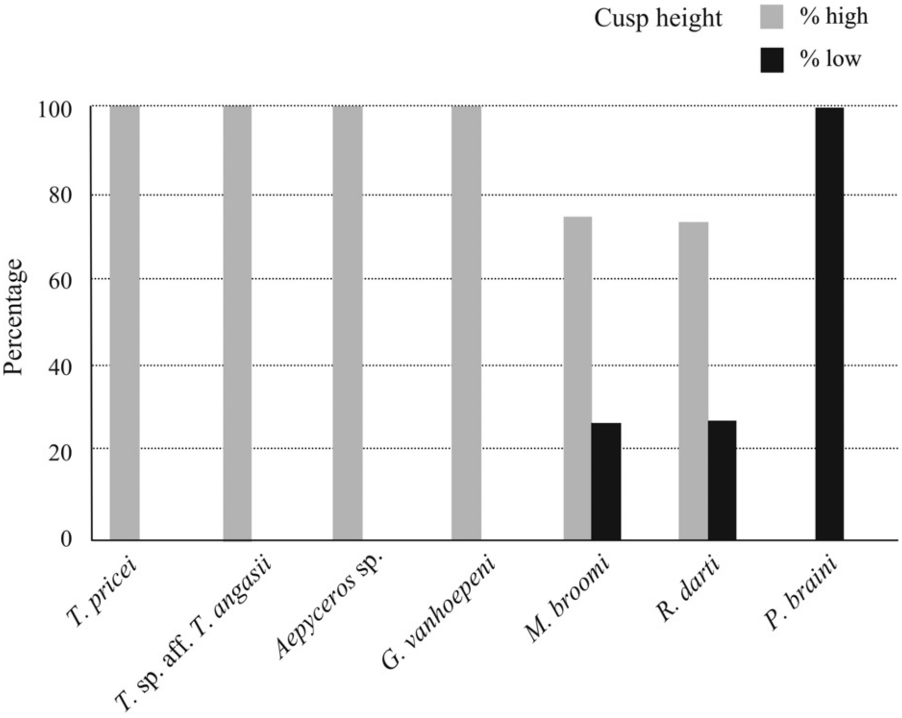

Figure 2. Histogram of mesowear variables % high cusps and % low cusps for the Makapansgat bovids.

Makapansgat gazelle, *Gazella vanhoepeni* has higher and rounder cusps than its congeners *G. thomsoni* and *G. granti,* both of which are mixed feeders. This species (*G. vanhoepeni*) groups most closely with the attrition/abrasion levels of *Taurotragus oryx* and *Tragelaphus scriptus.* While *T. oryx* is considered to be a mixed feeder, there is disagreement over whether or not *T. scriptus* is a browser (Gagnon & Chew 2000) or a seasonal-regional mixed feeder (Fortelius & Solounias 2000; Solounias & Semprebon 2002; Merceron *et al.* 2004). Here the latter interpretation is followed because the species is known for eating tender young grasses when available (Estes 1991) and microwear evidence clearly suggests browsing and grazing populations (Merceron *et al.* 2004).

The third group is composed of three extant grazers, one hypotragine (*Hippotragus niger*) and two reduncines (*Redunca redunca* and *Kobus ellipsiprymnus*). Two Makapansgat taxa are in this cluster, *Makapania broomi* and *Redunca darti. Redunca darti* has lower cusps than the compared extant members of its tribe. In terms of abrasion, the

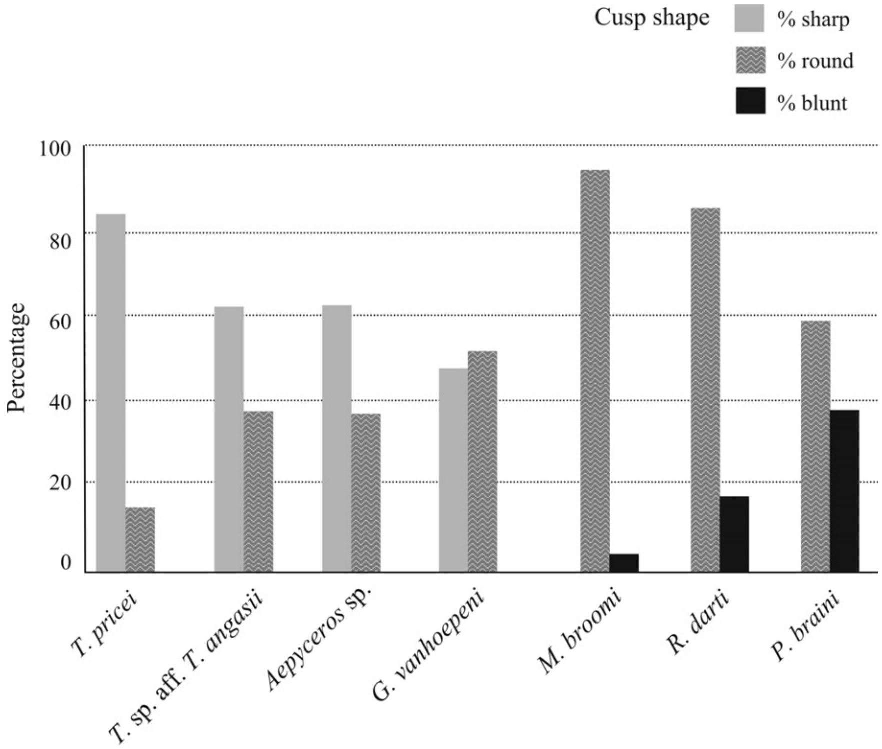

Figure 3. Histogram of mesowear variables % sharp cusps, % round cusps and % blunt cusps for the Makapansgat bovids.

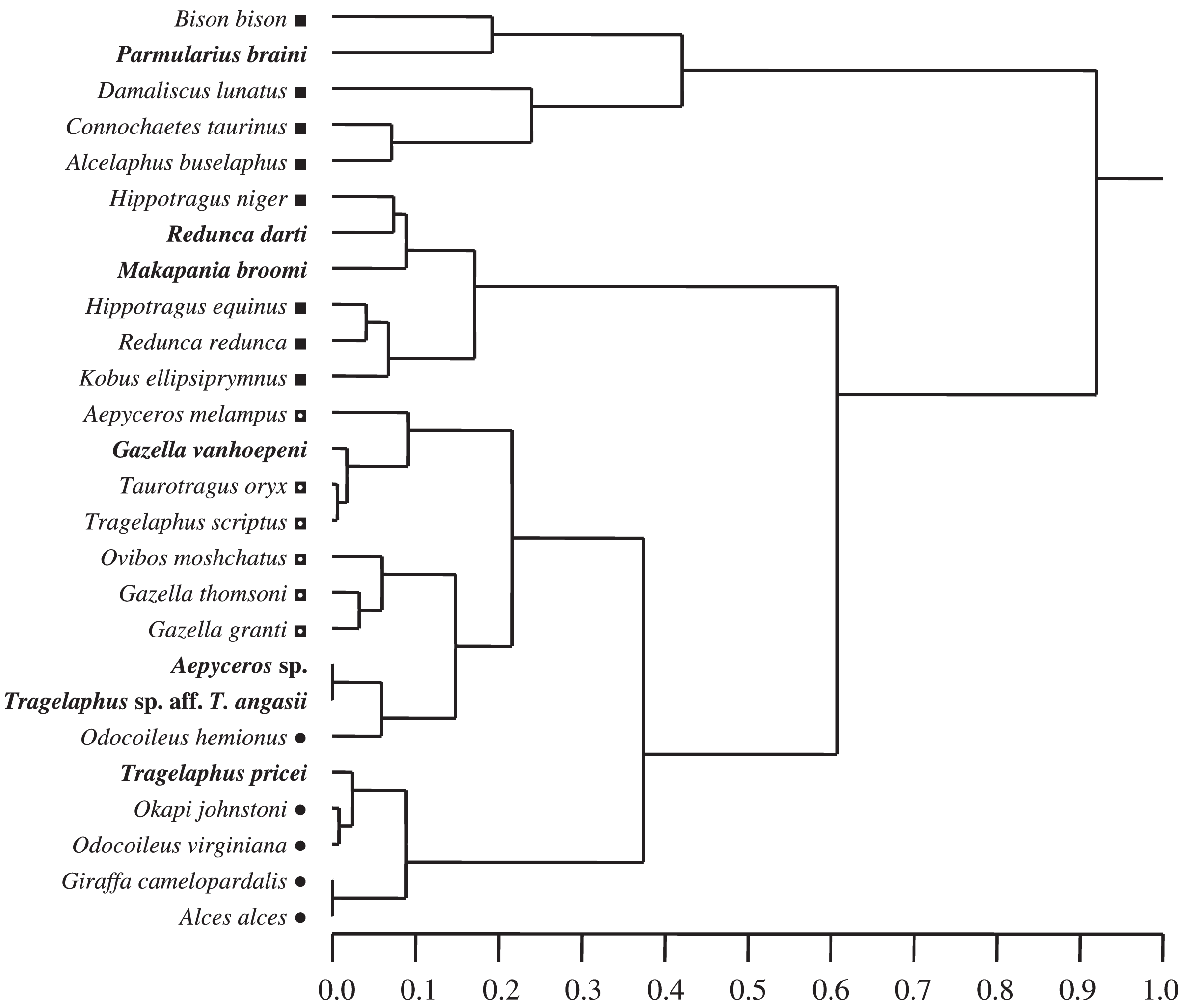

Figure 4. Hierarchical cluster diagram of % high, % sharp and % blunt cusps. Clusters are based on the mesowear data for nineteen 'typical' extant ruminant artiodactyls (from Fortelius & Solounias 2000) and the seven Makapansgat taxa. The extant grazers are represented by solid squares, mixed feeders by circles in squares, and browsers by solid circles. The Makapansgat bovids are in bold. The scale is Euclidean distance (root-mean-squared difference).

Makapansgat *R. darti* seems to be more closely aligned with hippotragines than to the extant reduncines.

The final primary grouping contains those taxa with highly abrasive diets and includes one Makapansgat species, the alcelaphine *Parmularius braini.* This taxon has abrasion features most similar to *Bison bison* and extant members of the alcelaphine tribe (*Connochaetes taurinus, Damaliscus lunatus, Alcelaphus buselaphus*), all of which are relatively pure grazers (Kingdon 1997).

DISCUSSION OF MESOWEAR RESULTS

Mesowear results suggest that the Makapansgat bovids ranged from browsers to extreme grazers. *Tragelaphus pricei* had the most attritional diet and probably did more browsing than the other taxa. *Tragelaphus* sp. aff. *T. angasii* and *Aepyceros* sp. group most closely with each other and an extant browser and are considered to have had a similar diet. Extant tragelaphines range in diet from mixed feeders to browsers (Kingdon 1997; Fortelius & Solounias 2000), while the only living member of the genus *Aepyceros* (*A. melampus*) is a mixed feeder. Thus, the Makapansgat *Aepyceros* sp. had a more attritional diet than its extant relative. *Gazella vanhoepeni* had intermediate attrition-abrasion levels, and based on mesowear alone, is considered to be a mixed feeder like extant members of the genus.

Makapania broomi and *R. darti* nested within a group of grazing taxa in the multivariable cluster analysis (Fig. 4). *Makapania broomi* is an ovibovine and its closest living relatives are mixed feeders. Fortelius & Solounias (2000) note that the reduncines, unlike other grazers, have a low percentage of blunt cusps and a high percentage of rounded cusps and they attribute this to fresh grass grazing. However, hippotragines also have similar mesowear variables and are not fresh grass grazers. Further, *R. darti* groups more closely to the hippotragines in terms of abrasion than to the extant reduncines. Based on mesowear, *R. darti* is certainly considered to have been a grazer, but not necessarily a specialized fresh grass grazer. The mesowear of *Parmularius braini* indicates it was an extreme grazer like living members of its tribe, the alcelaphines.

COMPARISONS

Hypsodonty

The crown height of teeth has been used extensively as a dietary signal and is best understood in terms of a measurement called the hypsodonty index (Janis 1988).

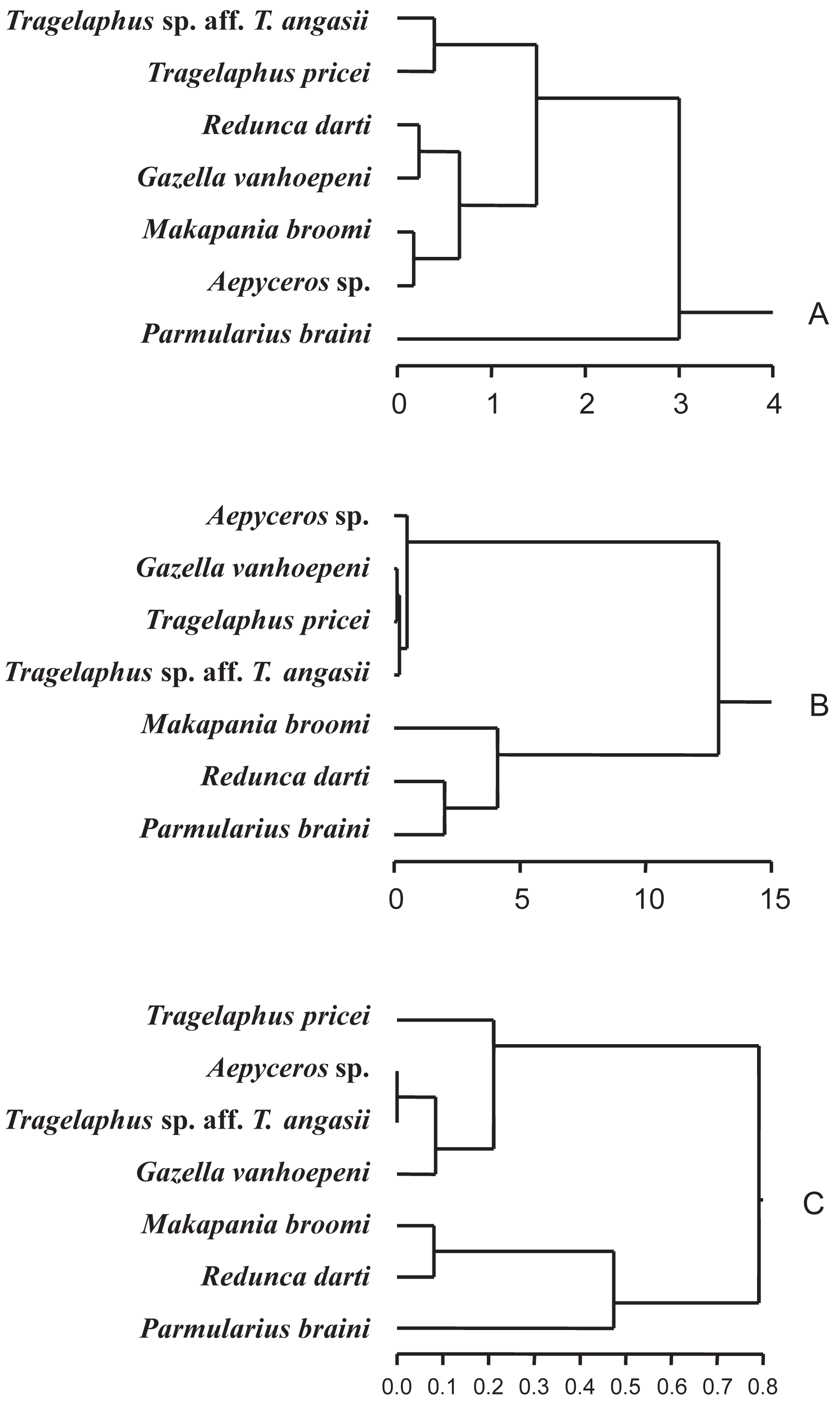

Figure 5. Hierarchical cluster diagrams based on (**A**) hypsodonty indexes [data from Fortelius & Solounias (2000) and Sponheimer *et al.* (1999)], (**B**) δ^{13}C values from Sponheimer *et al.* (1999) and (**C**) mesowear variables % high, % sharp and % blunt cusps for the Makapansgat bovids. The scales are Euclidean distance (root-mean-squared difference).

This index is calculated by dividing the width of an unworn third lower molar by its length. For ruminant artiodactyls, high-crowned or hypsodont teeth are generally those of grazers and usually have indices of 3.5 or higher, mesodont teeth typically belong to mixed feeders and have indices between 2.6 and 3.4, and brachydont teeth are generally those of browsers, with an index of 2.5 or lower (Janis 1988).

This method is often considered to be one of the best morphological predictors of diet in ungulates (Janis 1988; Fortelius & Solounias 2000), and it is the only ecomorphological character that is readily available for all taxa used in this comparative analysis. Fortelius & Solounias (2000) made comparisons between hypsodonty and mesowear variables and found that hypsodonty was the best single variable for correctly calculating the diet of all 64 of their extant taxa (65% correct). When only including the conservative typical taxa, 81% of these were correctly classified (Fortelius & Solounias 2000, table 3).

Makapansgat hypsodonty indices from Sponheimer *et al.* (1999) are shown in Table 1. A hierarchical cluster analysis of these data divides the bovids into four groups, with distinct separation between the hypsodont *Parmularius braini* and brachydont *Tragelaphus* species (Fig. 5). *Redunca darti* and *Gazella vanhoepeni*, which fall in the mesodont category, group together in the middle while

Makapania broomi (considered to be mesodont) and *Aepyceros* sp. (hypsodont) cluster towards the hypsodont end of the spectrum.

Stable carbon isotopes

This method is based on the fact that C_4 plants (grasses and sedges) accumulate more of the heavier ^{13}C isotope during fixation of CO_2 than do C_3 plants (e.g. trees, shrubs and bushes). Consequently, C_4 consumers have a higher level of $\delta^{13}C$ in their teeth and bones than do C_3 feeders. Mixed feeders that incorporate various amounts of C_3 and C_4 vegetation vary greatly in their $\delta^{13}C$ values but typically fall between the browser and grazer ranges (Lee-Thorp *et al.* 1989; Sponheimer *et al.* 1999). While isotope analysis is certainly a powerful tool for determining whether or not an animal was a C_4 grazer, C_3 consumer, or something in between, it provides limited dietary discrimination. It does not, for example, distinguish whether or not an animal with a C_3 diet was a C_3 browser or C_3 grazer.

The $\delta^{13}C$ values for the Makapansgat bovids (from Sponheimer *et al.* 1999) divide into two major groups (Fig. 5B). The C_3 consumers (*Aepyceros* sp., *Gazella vanhoepeni* and the *Tragelaphus* species) cluster together tightly, while the second major group is divided into C_4 consumers (*Redunca darti* and *Parmularius braini*) and a mixed C_4/C_3 consumer (*Makapania broomi*) that falls towards the C_4 end of the spectrum. Based on these values, *Aepyceros* sp., *Gazella vanhoepeni* and the *Tragelaphus* species are considered to be browsers, *Redunca darti* and *Parmularius braini* are grazers, and *Makapania broomi* is labelled as a mixed feeder preferring grass (Sponheimer *et al.* 1999).

Comparative summary

Hypsodonty is an ecomorphological character that reflects long-term adaptation, and does not necessarily indicate the diet of a given animal or population. The discrepancies between the morphological data (Fig. 5A) and the non-genetic data (stable carbon isotopes and mesowear) suggest that hypsodonty (at least in this case) is a poor indicator of actual diet. In contrast, the non-genetic results produce hierarchical clusters that are very similar and divide the taxa into two primary groups (Fig. 5B ,C). A close association between these non-genetic methods was expected since both measure diet over an extended period of an animal's life.

Using these two non-genetic methods in tandem results in more accurate reconstructions of dietary behavior. As noted above, an animal with a C_3 diet could either be a C_3 browser or a C_3 grazer. However, *Tragelaphus pricei, T.* sp. aff. *T. angasii* and *Aepyceros* sp. from Makapansgat had C_3 diets that were highly attritional (based on mesowear) and therefore they were browsers and not C_3 grazers. Similarly, *Parmularius braini* and *Redunca darti* had primarily C_4 diets and this is reflected in the amount of abrasion on their teeth. These species were most likely grazers. *Makapania broomi* was placed in a grass-dominated mixed feeder category based on stable carbon isotopes (Sponheimer *et al.* 1999) but mesowear (Fig. 4) groups the taxon most closely with grazers. This discrepancy is minor though because the isotope data (Sponheimer *et al.* 1999) comes very close to placing this species in a grazing category. The only large outlier is *Gazella vanhoepeni,* which is nested with extant mixed feeders in the multivariable mesowear cluster analysis (Fig. 4), however, its carbon isotope signal indicates it was primarily a C_3 consumer. One possible explanation for this is that *G. vanhoepeni* included C_3 grass in its diet. This inclusion would have increased abrasion while at the same time raising $\delta^{13}C$ values in the bones and teeth. A combined mesowear/isotope investigation of extant taxa that eat C_3 grasses may help answer this question and provide a means for distinguishing C_3 grass consumption in the fossil record.

CONCLUSION

Mesowear analysis was conducted on seven bovids from Makapansgat Limeworks Cave, Limpopo Province, South Africa. A hierarchical cluster analysis that included the mesowear data of the Makapansgat bovids and a baseline of extant artiodactyls divided the taxa into browsing, mixed feeding and grazing categories.

Comparison of the mesowear results with other dietary proxy measures indicates a poor relationship between the dietary predictions of this method and that of taxonomic uniformitarianism and hypsodonty. This is not surprising since these genetic signals of diet reflect long term adaptations while mesowear, a non-genetic signal, is a measure of diet during an extended period of an animal's life. The stable carbon isotope results, another non-genetic signal, divided the Makapansgat taxa into nearly identical dietary categories. Combination of these measures results in more accurate dietary assessments because these two non-genetic signals provide information about different aspects of diet. In this case the following can be concluded about the Makapansgat bovids: *Parmularius braini* was an extreme grazer with a highly abrasive C_4 diet, *Redunca darti* had an abrasive C_4 diet and was a grazer, *Makapania broomi* was a grazer or mixed feeder with an abrasive diet, *Tragelaphus pricei, T.* sp. aff. *T. angasii* and *Aepyceros* sp. had attritional C_3 diets and were browsers, and *Gazella vanhoepeni* had an enigmatic C_3 diet that was somewhat abrasive.

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REFERENCES

DELSON, E. 1984. Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forschungs Institute, Senckenberg* **69**, 199–218.

ESTES, R.D. 1991. *The Behavior Guide to African Mammals.* Berkeley, University of California Press.

FORTELIUS, M. & SOLOUNIAS, N. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* **3301**, 1–36.

FRANZ-ODENDAAL, T.A. 2002. *Analysis of dental pathologies in the Pliocene herbivores of Langebaanweg and their palaeoenvironmental implications.* Unpublished Ph.D. thesis, University of Cape Town.

FRANZ-ODENDAAL, T.A. & KAISER, T.M. 2003. Differential mesowear in the maxillary and mandibular dentition of some ruminants (Artiodactyla). *Annales Zoologici Fennici* **40**, 395–410.

GAGNON, M & CHEW, A.E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy* **81**, 490–511.

HARRIS, J.M. & WHITE, T.D. 1979. Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society* **69**, 1–128.

HERRIES, A.I.R. 2003. *Magnetostratigraphic seriation of South African hominin paleocaves.* Unpublished Ph.D. thesis, Department of Archaeology, University of Liverpool, Liverpool.

JANIS, C.M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. **In**: Russell, D.E., Santoro, J. & Sigogneau-Russell, D. (eds), *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology,* 367–387. Muséum National d'Histoire Naturelle Memoir sér. C 53.

KAISER, T.M. & CROITOR, R. 2004. Ecological interpretations of early Pleistocene deer (Mammalia, Cervidae) from Ceyssaguet (Haute-Loire, France). *Geodiversitas* **26**, 661–674.

KAISER, T.M. & FORTELIUS, M. 2003. Differential mesowear in occluding upper and lower molars-opening mesowear analysis for lower molars and premolars in hypsodont equids. *Journal of Morphology* **258**, 67–83.

KAISER, T. M. & SOLOUNIAS, N. 2003. Extending the tooth mesowear method to extinct and extant equids. *Geodiversitas* **25**, 321–345.

KINGDON, J. 1997. *The Kingdon Field Guide to African Mammals.* New York, Academic Press.

LEE-THORP, J.A., STEALY, J.C. & VAN DER MERWE, N.J. 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science* **16**, 585–599.

MAGUIRE, J.M, PEMBERTON, D. & COLLETT, M.H. 1980. The Makapansgat Limeworks grey breccia: hominids, hyaenas, hystricids or hillwash? *Palaeontologia africana* **23**, 75–98.

McKEE, J.K. 1999. The autocatalytic nature of hominid evolution in African Plio-Pleistocene environments. **In**: Bromage, T.G. & Schrenk, F. (eds), *African Biogeography, Climate Change, and Human Evolution,* 57–75. New York, Oxford.

McNAUGHTON, S.J., TARRANTS, J.L., McNAUGHTON, M.M. & DAVIS, R.H. 1985. Silica as a defense against herbivory and a growth promoter in African grasses. *Ecology* **66**, 528–535.

MERCERON, G., BLONDEL, C., BRUNET, M. SEN, S., SOLOUNIAS, N., VIRIOT, L. & HEINTZ, E. 2004. The late Miocene paleoenvironments of Afghanistan as inferred from dental microwear in artiodactyls. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**, 143–163.

PARTRIDGE, T.C., LATHAM, A.G. & HESLOP, D. 2000. Appendix on magnetostratigraphy of Makapansgat, Sterkfontein, Taung and Swartkrans. **In**: Partridge T.C. & Maud R.R. (eds), *The Cenozoic of Southern Africa,* 126–129. New York, Oxford.

RAYNER, R.J., MOON, B.P. & MASTERS, J.C. 1993. The Makapansgat australopithecine environment. *Journal of Human Evolution* **24**, 219–231.

REED, K.E. 1996. *The paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities.* Unpublished Ph.D. thesis, State University of New York at Stony Brook, New York.

SCHUBERT, B.S., UNGAR, P.S., SPONHEIMER, M. & REED, K.E. In press. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology.*

SEMPREBON, G., JANIS, C. & SOLOUNIAS, N. 2004. The diets of the Dromomerycidae (Mammalia: Artiodactyla) and their response to Miocene vegetational change. *Journal of Vertebrate Paleontology* **24**, 427–444.

SOLOUNIAS, N. & SEMPREBON, G. 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *American Museum Novitates* **3366**, 1–49.

SPONHEIMER, M., REED, K.E. & LEE-THORP, J.A. 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *Journal of Human Evolution* **36**, 705–718.

TEAFORD, M.F. & OYEN, O.J. 1989. *In vivo* and *in vitro* turnover in dental microwear. *American Journal of Physical Anthropology* **80**, 447–460.

VRBA, E.S. 1982. Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. **In**: *Proceedings of the 1st International Congress on Human Palaeontology,* 707–752. Volume 2, Paris, CNRS.

VRBA, E.S. 1987. A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeontologia africana* **26**, 33–46.

WELLS, L.H. & COOKE, H.B.S. 1956. Fossil Bovidae from the Limeworks quarry, Makapansgat, Potgietersrust. *Palaeontologia africana* **4**, 1–55.

APPENDIX 1

Dental specimens used in this study. L = left, R = right, M2 = second upper molar, M3 = third upper molar.

Makapania broomi: M7776 LM2, M8873 LM2, M8609 RM2, M7674 LM3, M8520 RM2, M971 RM3, M7681 RM3, M7764 LM2, M7655 RM3, M8490 LM2, M7668 RM3, M7765 RM2, M8425 RM2, M7680 LM3, M7117 LM3, M6142 RM2, M7654 RM2, M2940 RM2, M8347 RM2, M7675 LM2, M8827 LM3, M974 LM3, M30 RM2.

Redunca darti: M8838 RM2, M6060 RM2, M881 RM2, M6097 RM2, M6079 LM2, M808 RM3, M812 RM2, M6043 LM2, M6059 LM2, M822 RM3, M852 RM3, M7242 RM2, M7250 RM2, M7246 RM2, M6974 RM2, M7169 RM2, M7260 RM2, M7591 RM2, M8483 LM2, M8601 LM2, M7153 LM2, M8177 RM3, M1329 LM2.

Tragelaphus pricei: M6177 RM2, M609 RM2, M7489 LM2, M1694 LM2, M662 RM2, M1678 LM2, M1373 LM3, M7488 LM3, M7797 LM3, M7736 LM3, M7461 LM3, M7388 RM3, M1611 RM3.

Tragelaphus sp. aff. *T. angasi*: M6187 LM3, M195 RM3, M7780 LM3, M7597 RM3, M7716 LM3, M7141 LM3, M5 RM2, M6175 RM2.

Parmularius braini: M8351 RM2, M774 RM3, M6171 LM2, M1061 LM2, M2943 RM2.

Gazella vanhoepeni: M600 LM2, M612 RM2, M613 RM2, M611 RM2, M602 LM2, M615 RM2, M2955 RM2, M7261 RM2, M7615 RM2, M7598 RM2, M8549 RM2, M7369 RM2, M7370 RM2, M7614 RM2, M55 RM2, M7140 RM2, M7577 RM2, M657 RM2, M7144 RM2, M52 RM2, M7605 RM2, M7604 RM2, M51 LM2, M7477 LM2, M1622 LM2, M7506 LM2, M7735 LM2.

Aepyceros sp.: M7088 LM2, M7502 LM2, M7733 LM2, M8652 RM2, M7758 RM2, M763 RM3, M44 LM3, M1643 LM3.