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Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality

The relationship between environmental change and hominin evolution remains obscure. For the most part, this stems from the difficulty of reconstructing ancient hominin habitats. Bovids are among the most frequently utilized paleoenvironmental indicators, but little is known about the habitat preferences of extinct taxa. It is generally assumed that fossil bovids both ate the same things and occupied the same habitats as their closest extant relatives. We test the first part of this assumption by reconstructing the diets of seven bovids from Makapansgat Limeworks, South Africa. Since diet and habitat are linked, these reconstructions have implications for our understanding of fossil bovid habitat tolerances. Ecomorphological and stable carbon isotope analyses are employed, allowing us to take advantage of the strengths and overcome the weaknesses of both. In most cases, fossil bovids did have similar diets to their extant relatives, and probably occupied similar habitats. *Gazella vanhoepeni* and *Aepyceros* sp., however, were almost exclusive browsers, and not mixed feeders like their living counterparts.

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Introduction

Environmental change has been considered an important force behind hominin evolution since Darwin's publication of *The Descent of Man* in 1871 (e.g., Dart, 1925; Robinson, 1963; Coppens, 1975; Howell, 1978; Brain, 1981; Vrba, 1985; Tobias, 1991; Stanley, 1992; Potts, 1996). While researchers disagree as to how environmental shifts affected the development of the human lineage, most agree that they did exert some influence, even if in poorly understood ways. To some degree, this

ambiguity results from the difficulty of reconstructing early hominin habitats, despite the panoply of faunal, geological and geochemical techniques now available, making it difficult to test hypotheses about the relationship between evolutionary and environmental change. If this situation is to improve, we must find ways to refine our paleoenvironmental reconstructions.

Bovids are particularly useful paleoenvironmental indicators (e.g., Gentry, 1970; Kappelman, 1984; Vrba, 1985; Shipman & Harris, 1988; Harris, 1991; Plummer & Bishop, 1994; Spencer, 1997)

due partly to their ubiquity at Pliocene sites. In addition, they are a speciose group subsuming species adapted to diverse habitats from rainforest to desert (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Since the habitat preferences of extant bovids are well-known, bovids recovered from recently accumulated assemblages should enable sound environmental reconstructions (barring irrevocable taphonomic distortion). For instance, if a Holocene faunal assemblage is dominated by the arid-adapted springbok (*Antidorcas marsupialis*), we might infer that the area was like the shrublands of the Kalahari or Karoo during the site's accumulation. But when trying to reconstruct more ancient environments, how can we know the habitats of bovid taxa which, in some cases, have been extinct for millions of years? The most widely used method for determining a fossil bovid's habitat is taxonomic uniformitarianism: fossil species are assumed to have the same habitat tolerances as their closest extant relatives (e.g., Gentry, 1970; Vrba, 1980; Shipman & Harris, 1988; Harris, 1991; WoldeGabriel *et al.*, 1994). This method is problematic, however, as not all closely related taxa inhabit similar environments. Tragelaphines, for instance, range in habitats as diverse as forests, wooded grasslands, and wetlands (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Moreover, habitat tolerances within bovid lineages may have altered as community ecology changed through time. Therefore, other means are necessary to test habitat reconstructions suggested by taxonomic affinity (Plummer & Bishop, 1994; Kappelman *et al.*, 1997; Reed, 1998).

One way to accomplish this is to reconstruct the diets of fossil taxa, since diet and habitat tolerance are linked *perforce*. For example, if a fossil bovid was a grazer, it did not prefer forests, but existed in habitats with abundant grasses, such as woodlands and grasslands. On top of this direct

evidence of habitat, dietary reconstruction allows us to address subtle questions regarding the validity of ecological uniformitarianism. Specifically, if a fossil bovid did not have the same diet as its closest extant relatives, it becomes increasingly difficult to assume that it preferred the same habitats as its living relations. Thus, accurate reconstruction of ancient bovid diets can be a crucial step in improving paleoenvironmental reconstructions of early hominin sites. It is therefore desirable to use as many lines of evidence as possible to insure accurate bovid dietary reconstruction. Here, we use ecomorphology and stable carbon isotope analysis to make dietary assessments for seven Pliocene bovids from Makapansgat Limeworks, South Africa. Although isotope data have been used in conjunction with morphological data to reconstruct diets (MacFadden & Shockey, 1997), this is the first attempt to use these methods in tandem to reconstruct the trophic behavior of Pliocene bovids.

Makapansgat Limeworks is located about 325 km north of Johannesburg in Northern Province, South Africa. Well over 50,000 mammalian specimens have been recovered from the site since work began there in 1945. Although the Limeworks has been divided into 5 Members, we will only discuss specimens from the highly fossiliferous Member 3, which has been dated to about 3 Ma using both biostratigraphic and paleomagnetic evidence (Brock *et al.*, 1977; Harris & White, 1979; McFadden *et al.*, 1979; Vrba, 1982, 1987; Delson, 1984). Previous environmental reconstructions for the Member 3 assemblage have ranged from sub-tropical forest (Rayner *et al.*, 1993) to woodland (Vrba, 1985) to fairly shrub-like with open grasslands nearby (Wells & Cooke, 1956). A recent ecomorphological study suggests that the vegetation at the time of the Member 3 deposits was bushland with riparian woodland, and nearby limited wetlands (Reed, 1998).

Methods

Bovid species from Member 3 were analyzed both morphologically and isotopically. Previous research demonstrated that a bovid's craniodental morphology and feeding behavior are linked (Janis, 1988; Spencer, 1995a,b, 1997; Reed, 1996). For instance, grazers tend to have more hypsodont teeth and shorter premolar rows than browsers. The study commenced with the measurement of mandibles and dentition of 215 extant bovid specimens from 23 species, the feeding behaviors of which were compiled from the literature (e.g., Hofmann & Stewart, 1972; Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). These measurements were used to create four morphological indices (Table 1), and discriminant function analysis (DFA) of these successfully classified individual bovid specimens into five feeding behaviors: grazing (eating grasses from secondary grasslands), fresh grass grazing (eating floodplain or wetland grasses), mixed feeding-preferring leaves, mixed feeding-preferring grass, and browsing groups (Table 2; Figure 1) with 91.7% accuracy. The DFA was performed stepwise using Mahalanobis distance (D^2) with SPSS (SPSS, 1996), as this method produces the largest D^2 between the two closest groups. The mean index values for each species classified the bovinds into feeding type with 100% accuracy. Index values for bovinds from Makapansgat (Table 1) were then incorporated into the DFA, and classified to one of the dietary groups with percentage posterior probability of belonging to that group and distance from group centroid (Table 2; Figure 1). The mean index values for each fossil species were also calculated whenever possible. When all indices were not measurable for a fossil taxon, diet was estimated using remaining indices by the DFA program if possible.

The foundation for reconstructing the diets of fossil taxa with stable carbon isotope

analysis is our knowledge of photosynthesis in plants. In African savannas, trees, bushes, shrubs, and herbs (C_3 plants) discriminate more markedly against the "heavy" ^{13}C isotope during fixation of CO_2 than do grasses and sedges (C_4 plants). As a result, the ratios of ^{13}C to ^{12}C (expressed as δ values in parts per thousand relative to the PDB standard) are always lower in C_3 plants than in C_4 plants (Smith & Epstein, 1971; Vogel *et al.*, 1978; Deines, 1980). When plants are consumed by large herbivores, the plants' carbon is incorporated into their bone and tooth mineral with some additional fractionation (Lee-Thorp *et al.*, 1989; Ambrose & Norr, 1993; Cerling *et al.*, 1997). We can then analyze these biological minerals using mass spectrometry to determine the relative amounts of C_3 and C_4 vegetation in an animal's diet. Animals that eat C_3 vegetation (including fruits, leaves, and roots of trees, bushes, and forbs) have $\delta^{13}\text{C}$ values between about -10‰ and -16‰ , animals that eat C_4 vegetation (including tropical grass blades, seeds, and roots) have $\delta^{13}\text{C}$ values between $+2\text{‰}$ and -2‰ , and mixed feeders that eat both fall in between these two extremes (Lee-Thorp, 1989; Lee-Thorp *et al.*, 1989). While both bones and teeth often fossilize, empirical and theoretical studies show that tooth enamel is less susceptible to diagenesis than bone because of enamel's greater inorganic content, density, and crystallinity (Lee-Thorp & van der Merwe, 1991; Wang & Cerling, 1994; Sponheimer & Lee-Thorp, 1999). Hence, we analyzed only enamel from permanent molars for this study.

Early stable carbon isotope work required samples weighing approximately 0.25–0.5 g (Lee-Thorp, 1989; Quade *et al.*, 1992), but recent experimental work demonstrates that reliable data can be obtained from <3 mg samples (Lee-Thorp *et al.*, 1997). The protocol involves removal of a fine layer of enamel from a small cleaned area of the tooth's surface using a 2.0 mm

Table 1 Indices for modern and fossil bovids

Species	Diet	Mean	N	S.D.	Range	Species	Diet	Mean	N	S.D.	Range
Modern bovids											
<i>Redunca redunca</i>	FG					<i>Litocranius walleri</i>	B				
PMR		0.53	10	0.067	0.22	PMR		0.53	11	0.029	0.09
MD/MR		0.63	10	0.065	0.18	MD/MR		0.47	11	0.034	0.11
DD/MR		0.39	10	0.038	0.11	DD/MR		0.29	11	0.030	0.09
HI		3.63				HI		1.32			
<i>Redunca arundinum</i>	FG					<i>Tragelaphus imberbis</i>	B				
PMR		0.53	7	0.051	0.14	PMR		0.63	8	0.016	0.04
MD/MR		0.65	7	0.071	0.23	MD/MR		0.47	8	0.026	0.07
DD/MR		0.41	7	0.036	0.11	DD/MR		0.26	8	0.029	0.08
HI		3.63				HI		1.95			
<i>Kobus leche</i>	FG					<i>Tragelaphus scriptus</i>	B				
PMR		0.53	10	0.083	0.32	PMR		0.64	9	0.042	0.12
MD/MR		0.72	10	0.055	0.19	MD/MR		0.51	9	0.053	0.15
DD/MR		0.43	10	0.038	0.12	DD/MR		0.30	9	0.031	0.10
HI		3.63				HI		2.51			
<i>Kobus ellipsiprymnus</i>	FG					<i>Tragelaphus strepsiceros</i>	B				
PMR		0.51	10	0.021	0.06	PMR		0.64	7	0.033	0.11
MD/MR		0.62	10	0.047	0.17	MD/MR		0.51	7	0.043	0.12
DD/MR		0.37	10	0.029	0.09	DD/MR		0.28	7	0.033	0.09
HI		3.47				HI		2.29			
<i>Kobus kob</i>	FG					<i>Sylvicapra grimmia</i>	B				
PMR		0.56	17	0.091	0.30	PMR		0.67	10	0.047	0.16
MD/MR		0.69	17	0.042	0.16	MD/MR		0.59	10	0.042	0.15
DD/MR		0.40	17	0.027	0.09	DD/MR		0.31	10	0.020	0.06
HI		3.72				HI		2.95			
<i>Syncerus caffer</i>	FG					<i>Boocercus euryceros</i>	B				
PMR		0.57	7	0.032	0.10	PMR		0.59	8	0.030	0.07
MD/MR		0.70	7	0.068	0.17	MD/MR		0.49	8	0.020	0.07
DD/MR		0.38	7	0.037	0.11	DD/MR		0.30	8	0.020	0.06
HI		3.02				HI		1.91			
<i>Oryx gazella</i>	MF-G					<i>Aepyceros melampus</i>	MF-G				
PMR		0.51	7	0.029	0.09	PMR		0.45	10	0.065	0.22
MD/MR		0.66	7	0.040	0.11	MD/MR		0.61	10	0.127	0.44
DD/MR		0.33	7	0.027	0.08	DD/MR		0.32	10	0.085	0.30
HI		3.39				HI		4.90			
<i>Tragelaphus spekei</i>	MF-B					<i>Raphicerus campestris</i>	MF-B				
PMR		0.57	4	0.027	0.06	PMR		0.59	10	0.016	0.05
MD/MR		0.53	4	0.034	0.08	MD/MR		0.54	10	0.034	0.11
DD/MR		0.28	4	0.017	0.04	DD/MR		0.25	10	0.027	0.08
HI		2.88				HI		3.47			
<i>Taurotragus oryx</i>	MF-B					<i>Cephalophus natalensis</i>	B				
PMR		0.55	9	0.0300	0.09	PMR		0.58	2	0.011	0.02
MD/MR		0.52	9	0.0253	0.08	MD/MR		0.56	2	0.020	0.03
DD/MR		0.28	9	0.0188	0.06	DD/MR		0.28	2	0.005	0.00
HI		2.88				HI		2.24			
<i>Gazella granti</i>	MF-B					<i>Damaliscus lunatus</i>	G				
PMR		0.45	9	0.026	0.09	PMR		0.47	10	0.025	0.07
MD/MR		0.51	9	0.027	0.07	MD/MR		0.77	10	0.043	0.13
DD/MR		0.25	9	0.017	0.06	DD/MR		0.43	10	0.031	0.11
HI		3.47				HI		5.13			
<i>Gazella soemmerringi</i>	MF-B					<i>Alcelaphus buselaphus</i>	G				
PMR		0.47	6	0.027	0.07	PMR		0.48	9	0.022	0.07
MD/MR		0.56	6	0.035	0.09	MD/MR		0.75	9	0.053	0.14
DD/MR		0.27	6	0.017	0.04	DD/MR		0.45	9	0.049	0.17
HI		3.24				HI		5.25			

Table 1 Continued

Species	Diet	Mean	N	S.D.	Range	Species	Diet	Mean	N	S.D.	Range
Modern bovids											
<i>Gazella thomsoni</i>	MF-G					<i>Redunca fulvorufula</i>	G				
PMR		0.48	9	0.012	0.04	PMR		0.45	7	0.018	0.06
MD/MR		0.58	9	0.035	0.12	MD/MR		0.62	7	0.054	0.14
DD/MR		0.28	9	0.024	0.07	DD/MR		0.41	7	0.016	0.05
HI		3.80				HI		3.80			
Fossil bovids											
<i>Tragelaphus pricei</i>	?					<i>T. sp. aff. T. angasi</i>	?				
PMR		0.54	9	0.04	0.10	PMR		0.62	1		
MD/MR		0.52	9	0.06	0.13	MD/MR		0.58	1		
DD/MR		0.32	3	0.03	0.08	DD/MR		NA			
HI		2.5	4	0.247	0.52	HI		2.11	1		
<i>Redunca darti</i>	?					<i>Parmularius braini</i>	?				
PMR		0.53	8	0.029	0.08	PMR		0.39	3	0.015	0.025
MD/MR		0.58	8	0.06	0.19	MD/MR		0.77	3	0.050	0.08
DD/MR		0.37	5	0.05	0.11	DD/MR		NA			
HI		2.93	5	0.73	1.62	HI		5.11	1		
<i>Gazella vanhoepeni</i>	?					<i>Aepyceros sp.</i>	?				
PMR		0.45	9	0.075	0.25	PMR		NA			
MD/MR		0.53	9	0.06	0.21	MD/MR		NA			
DD/MR		0.27	4	0.045	0.16	DD/MR		NA			
HI		3.16	3	0.28	0.55	HI		3.59	1		
<i>Makapania broomi</i>	?										
PMR		0.5	1								
MD/MR		0.64	2	0.051	0.07						
DD/MR		0.32	1								
HI		3.42	1								

PMR (lower premolar row/lower molar row); MD/MR (depth of mandible at M_2/M_3 /lower molar row); DD/MR (depth of diastema at P_2 /lower molar row); HI (unworn height of M_3 /width of M_3); NA (not available). HI from Janis, 1988. Feeding types (diets): FG, fresh grass; G, grass; B, browse (leaves); MF-B, mixed feed—preferring leaves; MF-G, mixed feed—preferring grass.

diamond-tipped bit. A 1.5% sodium hypochlorite solution is then added to the powdered enamel for 30 min to remove organic material, followed by a thorough rinsing with distilled water. Next, the powder is subjected to 1 ml of 0.1 M acetic acid for 15 min to remove labile carbonates and followed again by a thorough rinse. The remaining sample is introduced into an individual reaction cup in an automated Kiel carbonate device attached to a Finnigan MAT 252 mass spectrometer, in which clean, dry CO_2 is obtained by reaction with phosphoric acid at 70°C and cryogenic distillation. Precision is better than 0.1‰ as determined from replicate measurements. $\delta^{13}C$ values for

bovids from Makapansgat are shown in Table 3.

Results

Dietary reconstructions of seven Makapansgat bovids using taxonomic uniformitarianism, ecomorphology, and stable carbon isotope analysis are provided in Table 4. A final reconstruction that combines morphological and isotopic data is also included. We discuss these reconstructions for each species below.

Parmularius braini

The extant Alcelaphini, such as wildebeests (*Connochaetes*) and hartebeests (*Alcelaphus*),

Table 2 (a)–(e)

(a)		G	MF-B	B	MF-G
Feeding type					
Fresh grass (FG)	F	6.84	35.78	43.99	14.06
	Sig.	0.003	0.000	0.000	0.000
Grass (G)	F		44.45	62.06	18.02
	Sig.		0.000	0.000	0.000
Mixed feed—browse (MF-B)	F			13.90	4.68
	Sig.			0.000	0.015
Browse (B)	F				21.52
	Sig.				0.000
Mixed feed—grass (MF-G)					
3,17 ? degrees of freedom					
(b)		% of		Canonical	
Function	Eigenvalue	variance	Cumulative %	correlation	
1	15.604	79.9	79.9	0.969	
2	3.926	20.1	100	0.893	
3	0.008	0.00	100	0.089	
(c)		Function			
	1	2	3		
Diastema depth	0.826	0.546	−0.141		
Mandible depth	0.531	0.280	0.441		
Premolar row	−0.239	0.502	0.831		
Hypsodonty index	0.368	−0.475	0.799		
Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions					
(d)		Function			
Feeding	1	2	3		
Fresh grass	3.14	1.24	0.103		
Grass	6.15	−0.281	−0.145		
Mixed feed—browse	−2.57	−2.14	0.004		
Browse	−3.60	1.73	−0.005		
Mixed feed—grass	0.271	−2.67	−0.001		
Unstandardized canonical discriminant functions evaluated at group means					

Results of discriminant function. (a) F-tests among feeding types all groups significantly different. (b) Eigenvalues, % variance and canonical correlations for each function. (c) Correlations between each function and morphological indices. (d) Group centroids for functions and feeding type.

are grazers. Their habitats range from more open woodlands through grasslands (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Morphological criteria (Tables 1 and 2; Figure 1) suggest that *P. braini* was a mixed feeder preferring grass: although diastema depth was not

available for this species, DFA assigned a mean value for that index based on the other variables and classified it as a mixed feeder with 99% posterior probability. However, it is extremely distant from the MF-G centroid. Stable carbon isotope analysis supports a grazing dietary reconstruction as

Table 2 (a)-(e) continued

Species	AFT	PFT1	PROB 1	MDC	PFT2	PROB 2	MDC2	DF1	DF2	DF3
<i>Redunca redunca</i>	FG	FG	0.9962	0.2733	2	0.0038	11.4358	2.9396	0.7597	0.1029
<i>Redunca arundinum</i>	FG	FG	0.9906	0.1060	2	0.0094	9.4229	3.3829	1.0365	0.0633
<i>Redunca fulvorifula</i>	G	G	0.9086	2.1089	1	0.0914	6.7025	4.9883	-0.1780	-1.0132
<i>Kobus leche</i>	FG	FG	0.8513	2.9153	2	0.1487	6.4055	4.7392	1.8178	-0.0181
<i>Kobus elipsipygmnus</i>	FG	FG	0.9871	2.3738	5	0.0115	11.2785	2.2309	0.0445	-0.2371
<i>Kobus kob</i>	FG	FG	0.9979	0.3018	2	0.0020	12.6814	3.0794	0.6402	-0.2371
<i>Oryx gazella</i>	MF-G	MF-G	0.9641	3.0707	3	0.0266	10.2500	0.3884	-0.9329	-0.1772
<i>Boercerus euryceros</i>	B	B	0.9998	0.6223	3	0.0002	18.1392	-3.3061	1.9886	-0.7306
<i>Tragelaphus imberbis</i>	B	B	0.9999	2.2410	3	0.0001	20.8318	-5.0922	1.6689	0.0842
<i>Tragelaphus spekei</i>	MF-B	MF-B	0.8115	3.7375	4	0.1611	6.9718	-1.9430	-0.3140	0.1986
<i>Tragelaphus scriptus</i>	B	B	0.9989	1.1791	3	0.0011	14.7940	-3.2903	1.5257	0.9723
<i>Tragelaphus strepsiceros</i>	B	B	0.9995	1.3226	3	0.0005	16.6005	-4.4221	1.4327	0.7030
<i>Taurotragus oryx</i>	MF-B	MF-B	0.9688	1.2259	4	0.0255	8.5042	-2.6924	-1.0394	0.1369
<i>Sylvicapra grinnia</i>	B	B	0.9985	4.4246	3	0.0015	17.3862	-2.8647	1.5760	1.9157
<i>Cephalophus natalensis</i>	B	B	0.9966	1.7116	3	0.0034	13.0555	-2.3795	1.4436	-0.4194
<i>Damaliscus lanatus</i>	G	G	0.9988	0.2785	1	0.0012	13.6637	6.3187	-0.6319	0.2105
<i>Alcelaphus buselaphus</i>	G	G	0.9997	1.3011	1	0.0003	17.7048	7.1357	-0.0338	0.3684
<i>Aepyceros melampus</i>	MF-G	MF-G	0.9998	3.0882	3	0.0002	20.2101	1.6008	-3.8029	0.1995
<i>Litocranius walleri</i>	B	B	1.0000	8.5113	3	0.0000	31.0280	-3.8604	2.4401	-2.8652
<i>Raphicerus campestris</i>	MF-B	MF-B	0.9972	4.4253	4	0.0027	16.2651	-4.1436	-1.9888	1.4277
<i>Gazella granti</i>	MF-B	MF-B	0.9130	4.8190	5	0.0870	9.5211	-2.3276	-4.1898	-0.6963
<i>Gazella soemmerringi</i>	MF-B	MF-B	0.7785	2.5324	5	0.2215	5.0459	-1.7481	-3.1453	-0.8759
<i>Gazella thomsoni</i>	MF-G	MF-G	0.5998	2.4688	3	0.4002	3.2779	-1.1754	-3.2848	-0.0596
<i>Syncerus caffer</i>	FG	FG	0.9999	1.9611	2	0.0001	21.2960	2.4414	2.4601	0.0694
<i>Tragelaphus pricei</i>	?	B	0.9998	6.4415	3	0.0002	24.0274	-2.0611	2.3020	-1.9809
<i>Redunca darti</i>	?	FG	0.9988	2.8626	5	0.0012	16.3469	1.5643	-1.1245	-0.5124
<i>Gazella vanhoepeni</i>	?	MF-B	0.7302	3.2513	5	0.2698	5.2423	-1.6712	-3.2032	-1.1027
<i>Makapania broomi</i>	?	MF-G	0.9550	1.6209	3	0.0444	7.7556	0.1091	-1.4315	-0.2405
* <i>Tragelaphus</i> sp. aff. <i>T. angasi</i>	?	B	1.0000	4.3368	3	0.0000	27.0343	-1.9791	3.0276	-0.1244
* <i>Parnularius braini</i>	?	MF-G	0.9996	12.0159	2	0.0004	27.7125	3.1169	-4.5603	-0.6109

(c) Predicted diets of extant and fossil taxa.

Key: AFT = actual feeding type; PFT1 = predicted feeding type; PROB 1 = probability of belonging to PFT1; MDC = Mahalanobis D2 to group centroid; PFT2 = predicted feeding type 2; PROB 2 = second predicted feeding type; MDC2 = Mahalanobis D2 to group centroid; DF1-DF4 = discriminant function scores for each taxon.

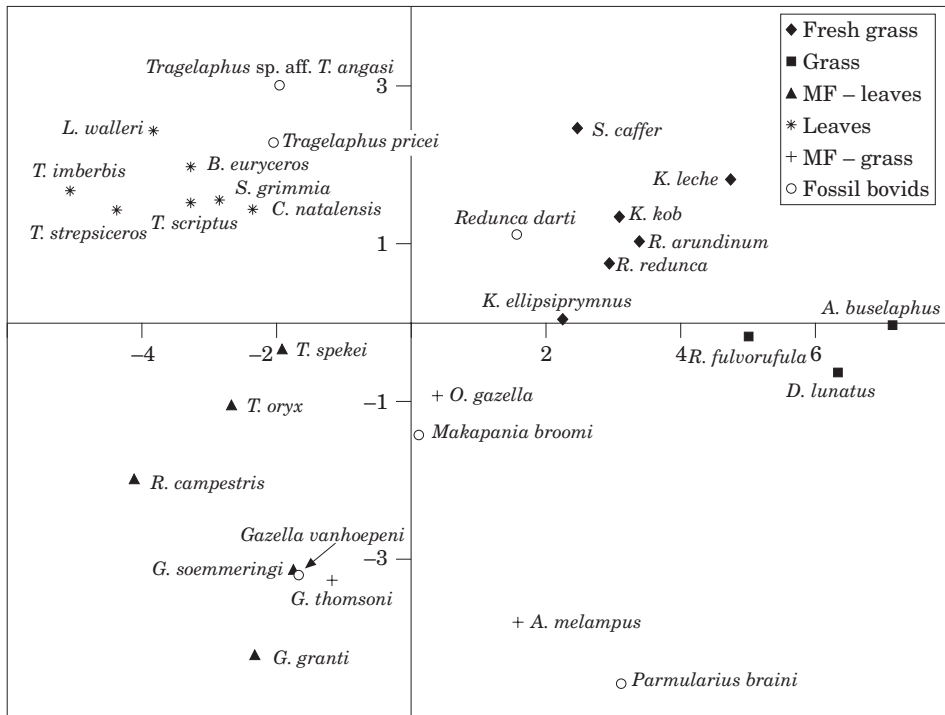


Figure 1. First two discriminant functions of extant Bovidae with Makapansgat fossil taxa based on mandibular and hypsodonty mean indices. The first two functions account for 100% of the variance seen among these bovid taxa, and both functions are significant. In general, browsers are located in the upper left quadrant, fresh grass grazers in the upper right quadrant, grazers are in the lower right quadrant, and mixed feeders are in the lower part of the graph. All bovids from Table 1.

$\delta^{13}\text{C}$ values for this species ($x=0.7\text{‰}$, $s.d.=0.7$, $x=4$) are within the expected grazer range. In this case, taxonomic uniformitarianism and stable carbon isotope analysis concur that *P. braini* was a grazing herbivore.

Redunca darti

Reduncini, the reedbucks and waterbucks (e.g., *Redunca arundinum*, *Kobus ellipsiprymnus*), are grazers with a preference for the grasses of edaphic grasslands or wetlands. Most of the extant members of the tribe stay close to both water and vegetation suitable for cover. One extant relative, however, prefers to graze on tall grasses in more open, rocky country (*Redunca fulvorufula*) (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Morphological criteria (Tables

1 and 2; Figure 1) indicate that *R. darti* was a fresh grass grazer favoring grasses from wetlands and edaphic grasslands with a 99.8% posterior probability. Stable carbon isotope analysis supports this reconstruction as the mean $\delta^{13}\text{C}$ value for this species ($x=-1.3\text{‰}$, $s.d.=2.4$, $x=4$) falls within the expected grazer range. In this case, it was important to use both morphological and isotopic data as the carbon isotope data do not differentiate between various types of grasses, while the morphological data appear to do so.

Tragelaphus sp. aff. T. angasi

The Tragelaphini [e.g., kudu, nyala, and bushbuck (*T. strepsiceros*, *T. angasi*, *T. scriptus*)] tend to browse in a wide variety of habitats ranging from forests through open

Table 3 $\delta^{13}\text{C}$ values (‰) of bovids from Makapansgat Limeworks

Specimen	Species	$\delta^{13}\text{C}$
M1642	<i>Aepyceros</i> sp.	-12.7
M7504	<i>Aepyceros</i> sp.	-11.0
M8876	<i>Aepyceros</i> sp.	-13.0
Mean		-12.2
S.D.		1.1
M7805	<i>Gazella vanhoepeni</i>	-12.4
M7811	<i>Gazella vanhoepeni</i>	-12.8
M8823	<i>Gazella vanhoepeni</i>	-10.9
M9014	<i>Gazella vanhoepeni</i>	-11.5
Mean		-11.9
S.D.		0.9
M1398	<i>Makapania broomi</i>	-3.6
M6274	<i>Makapania broomi</i>	-1.0
M6528	<i>Makapania broomi</i>	-3.5
M978	<i>Makapania broomi</i>	-5.3
Mean		-3.4
S.D.		1.8
M6272	<i>Parmularius braini</i>	1.2
M774	<i>Parmularius braini</i>	1.2
M8351	<i>Parmularius braini</i>	-0.2
M8835	<i>Parmularius braini</i>	0.6
Mean		0.7
S.D.		0.7
M6269	<i>Redunca darti</i>	-4.7
M6280	<i>Redunca darti</i>	0.9
M6609	<i>Redunca darti</i>	-0.9
M8897	<i>Redunca darti</i>	-1.7
Mean		-1.3
S.D.		2.4
M6325	<i>Tragelaphus</i> sp. aff. <i>T. angasi</i>	-12.7
M7689	<i>Tragelaphus</i> sp. aff. <i>T. angasi</i>	-11.8
M9053	<i>Tragelaphus</i> sp. aff. <i>T. angasi</i>	-12.6
M183	<i>Tragelaphus</i> sp. aff. <i>T. angasi</i>	-9.5
Mean		-11.7
S.D.		1.5
M6769	<i>Tragelaphus pricei</i>	-12.5
M19	<i>Tragelaphus pricei</i>	-12.0
M6477	<i>Tragelaphus pricei</i>	-10.9
Mean		-11.8
S.D.		0.8

woodland. The sitatunga (*T. spekei*), however, is a wetland mixed feeder (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Despite this diversity, fossil tragelaphines are generally considered browsers with predilections for heavily wooded habitats (e.g., WoldeGabriel *et al.*, 1994). Morphological criteria (Tables 1 and 2; Figure 1) indicate that *T. sp. aff. T. angasi* was a browser. The

DFA assigned this taxon to the browsing category with 100% posterior probability although the diastema depth index was not available. This finding is supported by the isotope data as the taxon has $\delta^{13}\text{C}$ values ($x = -11.7\text{‰}$, $s.d. = 1.5$, $x = 4$) within the expected browser range. Stable carbon isotope analysis, taxonomic affinity, and ecomorphological analysis are all consistent with *T. sp. aff. T. angasi* being a browser.

Tragelaphus pricei

This small tragelaphine presumably browsed based upon taxonomic uniformitarianism. Functional morphological criteria (Tables 1 and 2; Figure 1) support that conclusion as the DFA assigned *T. pricei* to browsing with 99.9% posterior probability. $\delta^{13}\text{C}$ values ($x = -11.8\text{‰}$, $s.d. = 0.8$, $x = 3$) also suggest that *T. pricei* was a browser.

Aepyceros sp.

The only living relative of this bovid is the impala (*Aepyceros melampus*) which is a mixed feeder with a preference for "edge" habitats between grasslands and denser woodlands (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). The impala tends to eat fresh, young grasses during the rains, but switches to browse when the quality of grasses diminishes during the dry season. Unfortunately, the only index available for this taxon is HI (Table 1), which groups it with mixed feeders and fresh grass grazers. Stable carbon isotope analysis, however, demonstrates a pure C_3 diet ($x = -12.2\text{‰}$, $s.d. = 1.1$, $n = 3$). This can only be interpreted as a pure browsing diet, as will be discussed below.

Gazella vanhoepeni

Extant congeners of this antilopine (e.g., *G. soemmerringi*, *G. granti*, *G. thompsoni*) are mixed feeders (Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991), and DFA assigns this taxon to MF-B with a 73% posterior probability (Tables 1 and 2;

Table 4 Dietary reconstructions of the Makapansgat bovids using taxonomic uniformitarianism, ecomorphology, and stable carbon isotope analysis

Species	Taxonomy	Ecomorphology	Isotopes	Final
<i>Aepyceros</i> sp.	MF-G	MF-G	B	B
<i>Gazella vanhoepeni</i>	MF-?	MF-B	B	B
<i>Makapania broomi</i>	MF-?	MF-G	MF-G	MF-G
<i>Parmularius braini</i>	G	MF-G	G	G
<i>Redunca darti</i>	FG	FG	G	FG
<i>Tragelaphus</i> sp. aff. <i>angasi</i>	B	B	B	B
<i>Tragelaphus pricei</i>	B	B	B	B

The last column (final) contains dietary reconstructions using both morphological and isotopic data. Diets: FG, fresh grass; G, grass; B, browse (leaves); MF-B, mixed feed—preferring leaves; MF-G, mixed feed—preferring grass.

Figure 1). The second most likely feeding type is MF-G with only a 27% posterior probability. $\delta^{13}\text{C}$ values for this bovid ($x = -11.9\text{‰}$, s.d. = 0.9, $n = 4$), however, indicate that it had no significant C_4 grass component to its diet. Some might argue that *G. vanhoepeni* and the aforementioned *Aepyceros* sp. may have been mixed feeders that ate dicots and C_3 grasses. This argument is not tenable, however, as there are abundant grazing taxa at Makapan that have $\delta^{13}\text{C}$ values inconsistent with the consumption of C_3 grasses (Sponheimer & Lee-Thorp, 1999). It would take a remarkable degree of special pleading to suggest that *G. vanhoepeni* and *Aepyceros* sp. were the only taxa that found and consumed C_3 grasses from the area. Other studies have shown that the presence of significant amounts of C_3 grasses results in the depletion of $\delta^{13}\text{C}$ values in all grazing taxa (Lee-Thorp, 1989; Cerling *et al.*, 1997).

Makapania broomi

This ovibovine has no living African relative, although members of this tribe are still found in Asia (*Budorcas*) and Eurasia/North America (*Ovibos*). The takin (*Budorcas*) prefers dense thickets at high elevations while the musk ox (*Ovibos*) is most at home on Arctic tundra. Both of these taxa are mixed feeders, although *Budorcas* has a penchant

for browse while *Ovibos* prefers graze (Nowak & Walker, 1991). The DFA assigns *M. broomi* to the mixed feeder-preferring grass group with a 95.5% posterior probability (Tables 1 and 2; Figure 1), and its carbon isotope composition ($x = -3.4\text{‰}$, s.d. = 1.8, $n = 4$) is consistent with this. Its $\delta^{13}\text{C}$ values are quite variable, however, which suggests that it had a catholic diet.

Discussion and conclusion

These data demonstrate that dietary reconstructions based upon taxonomic uniformitarianism are incorrect for two (*Aepyceros* sp. and *G. vanhoepeni*) of the seven fossil species analyzed. Carbon isotope and morphological analyses also allow us to refine the mixed feeding dietary reconstruction for *M. broomi* to mixed feeder-preferring grass. Thus, the combined morphological and isotopic dietary reconstructions differ from those based upon taxonomic affinity for nearly half of the taxa analyzed. This strongly suggests that dietary reconstructions should include morphological and isotopic data. However, both ecomorphological and carbon isotope analyses have limitations. Morphology may not always reconstruct diets accurately since it is the product of both behavioral adaptations and phylogeny. For instance, although

incisor size has long been known to be related to feeding behavior (Hylander, 1975; Fleagle, 1999), platyrrhines have relatively smaller incisors than catarrhines when controlling for diet (Rosenberger, 1992). This seems to be the problem we experienced here with *G. vanhoepeni*, which groups morphologically with its congeners, and not with more distantly related taxa that share the same browsing diet. Thus, morphology may belie behavior when not examined within the appropriate phylogenetic context.

On the other hand, stable carbon isotope analysis is limited in the types of information it can provide. While it is particularly useful for determining whether an animal ate browse, graze, or both, the method is unable to address more subtle questions such as does a grazer prefer fresh grass? This, however, is a task to which morphological analysis is eminently suited. In addition, stable carbon isotope analysis cannot differentiate between the consumption of C₃ grasses and C₃ dicots. Thus, if we can fruitfully wed these techniques we should be able to overcome the limitations of each and improve our understanding of the feeding ecology of fossil taxa.

The fact that *G. vanhoepeni* is reconstructed as a browser is particularly salient as high percentages of antilopines (with alcelaphines) in fossil localities have been used on a taxonomic uniformitarian basis to indicate more open, arid habitats (Vrba, 1980, 1985). Several extant antilopines prefer C₃ plants when they are available. For instance, *G. granti* prefers dicots at the end of the rainy season and during the dry season, but eats grasses early in the wet season when they are sprouting (Hofmann & Stewart, 1972; Kingdon, 1982, 1997; Spinage, 1986; Estes, 1991). Thus, the browsing diet of *G. vanhoepeni* did not differ too much from that of today's *G. granti*, although it was markedly different from that of extant grass-living gazelles such as *G. thomsoni*. Moreover, its HI value (3.16) is

lower than that of extant *Gazella* spp. (Table 1), which may hint at its adaptation to C₃ plants. In any case, having mixed feeding morphology allows effective utilization of both graze and browse; it does not necessarily reflect dietary preference. Perhaps mixed feeding morphology in a browsing bovid serves as a buffer against the periodic loss of preferred habitat. Regardless, these data make it clear that we must be careful in assuming that diets, and thus habitat preferences have remained unchanged within a lineage. Such dietary disparities may simply mean that the ancestral taxon utilized the same environment in different ways, but may also indicate very real differences in habitat preferences.

It has not been our purpose here to proffer an environmental reconstruction of the 3 Ma Makapansgat Valley. Rather, we hoped to test taxonomic uniformitarian assumptions using morphological and isotopic data. Nonetheless, these new dietary reconstructions do have modest implications for habitat reconstructions of Makapansgat Member 3. The percentage of alcelaphines and antilopines in Member 3 is low (27%) and indicates woodland whether or not *G. vanhoepeni* is included in the analysis (and this study intimates that it may be best excluded) (Vrba, 1980, 1985). In addition, these dietary reconstructions demonstrate that Member 3 has more browsers (21%) and fewer mixed feeders (5.7%) than was previously supposed, which is in keeping with a bush and woodland habitat (Reed, 1997, 1998). The presence of the fresh grass grazer *R. darti* also betokens wetlands.

Although this is a preliminary analysis of morphology and isotopes, we expect to examine the remaining Makapan fauna isotopically and compare it to the morphological reconstructions already completed (Reed, 1997, 1998). Ultimately, this should help refine our knowledge of the environment of the 3 Ma Makapansgat Valley.

Furthermore, once accurate feeding reconstructions are made for various species across time, dietary change and stasis can be compared within and between lineages to provide insight into the mechanisms driving evolution. That is, we should be able to place fossil hominin species into “evolving communities”, giving us a glimpse of the ecological patterns and processes that influenced hominin evolution.

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References

- Ambrose, S. H. & Norr, L. (1993). Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In (J. B. Lambert & G. Grupe, Eds) *Prehistoric Human Bone: Archaeology at the Molecular Level*, pp. 1–37. Berlin: Springer-Verlag.
- Brain, C. K. (1981). *The Hunters or the Hunted?* Chicago: University of Chicago Press.
- Brock, A., McFadden, P.L. & Partridge, T. C. (1977). Preliminary palaeomagnetic results from Makapansgat and Swartkrans. *Nature* **266**, 249–250.
- Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V. & Ehleringer, J. R. (1997). Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158.
- Coppens, Y. (1975). Evolution des hominides et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l’Omo en Ethiopie. *C. R. Acad. Sci. Paris* **281**, 1693–1696.
- Dart, R. A. (1925). *Australopithecus africanus*: the man-ape of South Africa. *Nature* **115**, 195–199.
- Darwin, C. (1871). *The Descent of Man*. New York: Modern Library.
- Deines, P. (1980). The isotopic composition of reduced organic carbon. In (P. Fritz & J. C. Fontes, Eds) *Handbook of Environmental Isotope Geochemistry*, pp. 329–406. Amsterdam: Elsevier.
- Delson, E. (1984). Cercopithecoid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Cour. Forsch. Inst. Seckenberg* **69**, 199–218.
- DeNiro, M. J. & Epstein, S. (1978). Carbon isotopic evidence for different feeding patterns in two hyrax species occupying the same habitat. *Science* **201**, 906–908.
- Estes, R. D. (1991). *The Behavior Guide to African Mammals*. Berkeley: University of California Press.
- Fleagle, J. G. (1999). *Primate Adaptation and Evolution*. 2nd Edition. New York: Academic Press.
- Gentry, A. W. (1970). The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In (L. S. B. Leakey & R. J. G. Savage, Eds) *Fossil Vertebrates of Africa, Vol. 2*, pp. 243–323. London: Academic Press.
- Harris, J. M. & White, T. D. (1979). Evolution of the Plio-Pleistocene African Suidae. *Trans Am. phil. Soc.* **69**, 1–128.
- Harris, J. M. (1991). *Koobi Fora Research Project, Vol. 3. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments*. Oxford: Clarendon Press.
- Hofmann, R. R. & Stewart, D. R. M. (1972). A classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* **36**, 226–240.
- Howell, F. C. (1978). Hominidae. In (V. J. Maglio & H. B. S. Cooke, Eds) *Evolution of African Mammals*, pp. 154–248. Cambridge: Harvard University Press.
- Hylander, W. L. (1975). Incisor size and diet in anthropoids with special reference to Cercopithecoidea. *Science* **189**, 1095–1098.
- 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 (D. E. Russell, J. Santoro & D. Sigogneau-Russell, Eds) *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology, Paris, 1986*. Mem. Mus. Nat. Hist. Nat. **53**, 367–387.

- Kappelman, J. (1984). Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **48**, 171–196.
- Kappelman, J., Plummer, T., Bishop, L., Duncan, A. & Appleton, S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in east Africa. *J. hum. Evol.* **32**, 229–256.
- Kingdon, J. (1982). *East African Mammals*, Vols. IIIC & IIID. Chicago: University of Chicago Press.
- Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals*. New York: Academic Press.
- Lee-Thorp, J. A. (1989). Stable carbon isotopes in deep time: the diets of fossil fauna and hominids. Ph.D. Dissertation, University of Cape Town.
- Lee-Thorp, J. A. & van der Merwe, N. J. (1991). Aspects of the chemistry of modern and fossil biological apatites. *J. Archaeol. Sci.* **18**, 343–354.
- Lee-Thorp, J. A., Sealy, J. C. & van der Merwe, N. J. (1989). Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *J. Archaeol. Sci.* **16**, 585–599.
- Lee-Thorp, J. A., Manning, L. & Sponheimer, M. (1997). Exploring problems and opportunities offered by down-scaling sample sizes for carbon isotope analyses of fossils. *Bull. Soc. geol. France* **168**, 767–773.
- Lewis, M. E. (1997). Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. *J. hum. Evol.* **32**, 257–288.
- MacFadden, B. J. & Shockey, B. J. (1997). Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiol.* **23**, 77–100.
- McFadden, P. L., Brock, A. & Partridge, T. C. (1979). Paleomagnetism and the age of the Makapansgat hominid site. *Earth Planet. Sci. Lett.* **44**, 373–382.
- Nowak, R. M. & Walker, E. P. (1991). *Mammals of the World*. Baltimore: Johns Hopkins University Press.
- Plummer, T. W. & Bishop, L. C. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J. hum. Evol.* **27**, 47–75.
- Potts, R. (1996). Evolution and climate variability. *Science* **273**, 922–923.
- Quade, J., Cerling, T. E., Barry, J. C., Morgan, M. E., Pilbeam, D. R., Chivas, A. R., Lee-Thorp, J. A. & van der Merwe, N. J. (1992). A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chemical Geology (Isotope Geoscience Section)* **94**, 183–192.
- Reed, K. E. (1996). The Paleocology of Makapansgat and other African Plio-Pleistocene hominid localities. Ph.D. Dissertation, State University of New York at Stony Brook.
- Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. hum. Evol.* **32**, 289–322.
- Reed, K. E. (1998). Using large mammal communities to examine ecological and taxonomic organization and predict vegetation in extant and extinct assemblages. *Paleobiol.* **32**, 384–408.
- Robinson, J. T. (1963). Adaptive radiation in the australopithecines and the origin of man. In (F. C. Howell & F. Bourliere, Eds) *African Ecology and Human Evolution*, pp. 385–416. Chicago: Aldine.
- Rosenberger, A. (1992). Evolution of feeding niches in New World monkeys. *Am. J. phys. Anthrop.* **88**, 525–562.
- Shipman, P. & Harris, J. M. (1988). Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In (F. E. Grine, Ed.) *The Evolutionary History of the "Robust" Australopithecines*, pp. 343–381. New York: Aldine de Gruyter.
- Smith, B. N. & Epstein, S. (1971). Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant Physiol.* **47**, 380–384.
- Solounias, N. & Dawson-Saunders, B. (1988). Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **65**, 149–172.
- Spencer, L. M. (1995a). Antelopes and Grasslands: Reconstructing African Hominid Environments. Ph.D. Dissertation, State University of New York at Stony Brook.
- Spencer, L. M. (1995b). Morphological correlates of dietary resource partitioning in the African Bovidae. *J. Mammal.* **76**, 448–471.
- Spencer, L. M. (1997). Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. *J. hum. Evol.* **32**, 201–228.
- Spinage, C. A. (1986). *The Natural History of Antelopes*. Beckenham: Croom Helm.
- Sponheimer, M. & Lee-Thorp, J. A. (1999). Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* **283**, 368–370.
- Sponheimer, M. & Lee-Thorp, J. A. (1999). The alteration of enamel carbonate environments during fossilisation. *J. Archaeol. Sci.* (in press).
- Stanley, S. M. (1992). An ecological theory for the origin of *Homo*. *Paleobiol.* **18**, 237–257.
- Tobias, P. V. (1991). The environmental background of hominid emergence and the appearance of the genus *Homo*. *Hum. Evol.* **6**, 129–142.
- Van Valkenburgh, B. (1987). Skeletal indicators of locomotor behavior in living and extinct carnivores. *J. Vert. Paleontol.* **7**, 162–182.
- Vogel, J. C., Fuls, A. & Ellis, R. P. (1978). The geographical distribution of kranz grasses in South Africa. *S. Afr. J. Sci.* **74**, 209–215.
- Vrba, E. S. (1980). The significance of bovid remains as indicators of environment and predation patterns. In (A. K. Behrensmeier & A. P. Hill, Eds) *Fossils in the Making*, pp. 247–272. Chicago: University of Chicago Press.
- Vrba, E. S. (1982). Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; and also Elandsfontein (Saldanha), Broken Hill (not Kabwe) and Cave of Hearths. *Proc. of 1st Inter. Congr. Hum. Palaeont.* **2**, 707–752.

- Vrba, E. S. (1985). Ecological and adaptive changes associated with early hominid evolution. In (E. Delson, Ed.) *Ancestors: The Hard Evidence*, pp. 63–71. New York: Alan R. Liss.
- Vrba, E. S. (1987). A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeontol. Afr.* **26**, 33–46.
- Wang, Y. & Cerling, T. (1994). A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **107**, 281–289.
- Wells, L. H. & Cooke, H. B. S. (1956). Fossil Bovidae from the Limeworks quarry, Makapansgat, Potgietersrust. *Palaeontol. Afr.* **4**, 1–55.
- WoldeGabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W. K. & Helken, G. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* **371**, 330–333.