Carbon isotope ratios of Sterkfontein fossils indicate a marked shift to open environments *c.* 1.7 Myr ago

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Sterkfontein straddles a period in the Plio-Pleistocene in which the effects of global-scale climate shifts on continental environments and biota are not yet well understood. Reconstructions based on faunal indicators have suggested incremental shifts from relatively closed, mesic landscapes to open, arid environments at this time. We examined environmental shifts from ~2.5 to 1.7 million years ago (Myr) using a C_3/C_4 index derived from $^{13}C/^{12}C$ data on bovid fossils from Sterkfontein. Data for Member 4 and the Member 5 East infill indicate persistence of a wooded to moderately wooded environment until about 2.0–1.8 Myr. Data indicating a marked shift to open environments are observed only for the younger Member 5 West infill. We conclude that the major shift to open environments occurred near 1.7 Myr rather than at *c.* 2.5 Myr.

Much attention has been paid to questions about the effects of Pliocene and Pleistocene global climate changes, observed from the records of marine sediment cores,[1,2] on African continental environments, and their influence on evolutionary pathways of savanna-dwelling fauna including hominids.[2–7] A climate shift at *c.* 2.8–2.4 million years ago (Myr) related to the onset of northern hemisphere glaciation[1] has been proposed as leading to more open, seasonal, and arid environments in Africa.[5] Detailed correlations between the shifts observed in the marine records and African environments evinced in faunal assemblages, however, have been difficult to establish securely.[3,4,6,7]

Although the South African sites are relatively poorly dated[8] compared to East African sites of comparable age, taken together, the sites of Makapansgat and Sterkfontein Members 4 and 5 straddle a large part of the Plio-Pleistocene period in question. On the evidence mainly of faunal material from these sites, it has been proposed that a major faunal 'turnover' event occurred around 2.8–2.4 Myr.[3,4] This conclusion was based on the well-known 'Alcelaphine + Antelopine' (AA) index derived from modern observations, whereby high percentages of these two tribes indicated open, grassy environments and, conversely, low percentages implied wooded, relatively closed habitats.[9] Application of the AA index to the existing bovid assemblages from the South African sites suggested an incremental opening of the landscape from older to younger deposits, including a fairly marked step centred on Sterkfontein Member 4.[3,4] High abundances of terrestrial versus arboreal fauna largely supported the pattern, with minor revisions.[7] The more recent identification in Sterkfontein Member 4 of fossilized lianas,[10] which are normally found in tropical forest, however, has raised questions about whether the environment was as open as suggested by the faunal studies.

Carbon isotope analysis of the tooth enamel of fossil fauna in these sites provides an alternative means to address questions about the nature of these ancient environments. Tropical grasses following the C_4 photosynthetic pathway are markedly higher in ^{13}C than are trees, shrubs and herbs exemplifying the C_3 pathway.[11] These differences are reflected in the tissue of consumers, including enamel, in which they are particularly well-preserved.[12,13] Where C_4 grasses are present, the proportions of C_3 and C_4 plants in a herbivore's diet can provide a reasonable indication of their habitat requirements, particularly when determined for a large proportion of the fossil faunal assemblage in any one site. As outlined in ref. 14, the indication is based on the principle that in an area with open grasslands and few trees and shrubs there will be little forage suitable for C_3 consumers. Conversely, an area with dense tree cover will offer little grass for grazers. Hence the determination of the relative proportions of browsers, mixed feeders, and grazers — elsewhere called the C_3/C_4 index[14] – from carbon isotope analysis of a fossil faunal assemblage can provide a quantitative indication of the open, grassy or closed, woody nature of the ancient environment.

This approach has the advantage that no prior assumptions need be made about the diets and requirements of the (often extinct) fossil fauna.[14] Although assumptions about diets of extinct fauna based on their modern relatives in taxonomic approaches are generally robust, up to 25% may be in error.[15] Application of the C_3/C_4 carbon isotope-based index to Makapansgat Limeworks Member 3 gave results which emphasized the densely wooded nature of the environment[14] slightly more than earlier analyses.[4,7] The main drawback to this approach relates to the question of representativity of the material sampled for analysis compared to the faunal assemblage, or indeed the representativity of the fossil faunal assemblage compared to the surrounding environment. The latter taphonomic question is, however, an overarching problem not confined to the isotopic method.

We followed a similar but slightly altered approach to assess the nature of the environments during deposition of the Member 4 and 5 deposits at Sterkfontein, and hence to establish the pattern of environmental change over a timespan of approximately 2.4 to 1.7 Myr. The use of isotopic data from individual bovid specimens to calculate proportions of C_3 and C_4 bovids was a deviation from the species- and tribe-level calculations of the original C_3/C_4 index application to Makapansgat,[14] necessitated by the problem that many Sterkfontein specimens were not identified to species level or only tentatively assigned. Carbon isotope analyses were performed on enamel of all available bovid tooth specimens from Sterkfontein Members 4 (sample size 38) and 5 (n = 46), sampled from the existing older collection in the Transvaal Museum, Pretoria, and from more recent excavations. The latter were usually identified only to genus. Between one and seven individuals were sampled in each case from specimens within the Tragelaphini, Hippotragini, Reduncini, Alcelaphini, and Antilopini subfamilies. Specimens were prepared for analysis using methods refined for small samples in order to minimize damage to fossil teeth,[16,17] and isotope ratio measurements performed on a Finnigan Mat 252 mass spectrometer interfaced with a Kiel autocarbonate device. Carbon isotope ratios were calibrated using international and laboratory standards, and are reported by convention in the δ notation

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Table 1. Mean $\delta^{13}C$ values for enamel apatite, standard deviations and number of samples (*n*) of bovids from Sterkfontein Member 4, Member 5 East and Member 5 West, from which diet was assigned according to the estimated proportions of C_3 and C_4 vegetation consumed.

Species	Mean $\delta^{13}C$ (‰)	s.d. (‰)	*n*	Diet*		
Member 4						
Antilopini (III)	–12.7	0.9	2			B
Antidorcas bondi	–1.5	0.5	2	G		
Antidorcas recki	–11.2	4.0	5			B
Connochaetes cf. *taurinus*	–2.5	2.2	3	G		
Damaliscus/or *Parmularis*	–6.4	0.8	3		MF	
Damaliscus sp.	0.5	1.9	6	G		
Hippotragus cf. *gigas* (?)	–10.2	0.4	2			B
Hippotragus cf. *gigas*	–5.4	1.1	2		MF	
Hippotragus equinus	–1.1	1.6	2	G		
Makapania broomi	–7.4	2.8	5		MF	
Redunca arundinum	–1.3		1	G		
Tragelaphus sp. aff. *angasi*	–4.7	0.0	2		MF	
Tragelaphus strepsiceros	–9.0	0.8	3			B
	n			14	12	12
	Calculation by species			37%	32%	32%
	n (grouped by individual)			14	11	13
	Calculation (by individual)			34%	32%	34%
Member 5 East (Oldowan)						
Tragelaphini cf. *taurotragus*	–9.4	0.0	2			B
Large Alcelaphini	–4.8	3.4	4	G		
Antelopini cf. *antidorcas*	–9.4	0.2	2			B
Small Alcelaphini cf. *damaliscus*	–2.7	2.2	5		MF	
Equid	–3.8	0.9	2		MF	
	n			4	7	4
	Calculation by species			27%	47%	27%
	n (grouped by individual)			6	5	4
	Calculation (by individual)			20%	53%	27%
Member 5 West (Acheulian)						
Large Alcelaphini	–0.5	3.0	5	G		
Antelopini	0.7		1	G		
Antelopini	–7.4		1		MF	
Small Alcelaphini cf. *damaliscus*	–1.0	1.1	3	G		
Damaliscus	–0.4	1.4	4	G		
Equid	–0.9	1.1	5	G		
Antidorcas recki	–11.7	1.3	2			B
Hippotragus. sp. af. *gigas*	–5.3		1		MF	
	n			18	7	4
	Calculation by species			82%	9%	9%
	n (grouped by individual)			17	3	2
	Calculation (by individual)			68%	23%	9%

*Diet was assigned as follows: G = grazer ($\delta^{13}C$ = > –2.6 ‰ or >80% C_4), B = browser ($\delta^{13}C$ < –9 ‰), and MF = mixed feeder (intermediate $\delta^{13}C$ values). Specimens are grouped by species where possible; in other cases where identification to species was tentative or not possible, we used an assignment to genus. The proportions (as %) and number (*n*) of grazers, mixed feeders and browsers calculated from these groupings are shown for each member. In addition, proportions (as %) and number (*n*) of individual grazers, mixed feeders and browsers, based in $\delta^{13}C$ of *individual* specimens, is shown in the row immediately below. As can be seen, the different calculations make little difference to the overall trend. The original data can be found in ref. 17.

relative to the international PDB standard*. The results are summarized in Table 1.

The relative frequencies of grazers, browsers and mixed feeders for each member was at first calculated by counting the number of individual specimens showing relatively enriched values > –2.6‰ (or ~>80% C_4, as described elsewhere[14]), the number with values <N>–9‰ (or ~> 80% C_3), and those in between. In the interests of brevity, Table 1 shows summarized data in the form of mean $\delta^{13}C$ values and standard deviations, together with assigned diets, for groupings according to species, tentative species designation, *or* genus. Calculations of percentages of grazers, mixed feeders and browsers, based on these groupings, are close to calculations based in individual specimens (also shown in Table 1). The minor deviations are in the Member 5 East infill, where the proportion of grazers is lower, and mixed feeders higher, and for the West infill, where a similar effect is observed, using the individual-method calculation. However, both calculation methods are close enough to follow the same overall trends.

*$\delta^{3}C_{PDB}$ (‰) = (R_{sample}/R_{ref} – 1) × 1000.

Using the calculations based on individuals, which we consider to be more precise, the percentages of grazers (34%), browsers (34%) and mixed feeders (32%) in Sterkfontein Member 4 are roughly equal. This indicates a modest proportion of grazing animals in the assemblage, slightly higher than the proportion observed for Makapansgat Member 3.[14] The main difference is observed in the higher percentage of mixed feeders in Sterkfontein Member 4. Overall, these results suggest a slightly more open, grassier and possibly bushier environment than Makapansgat. The proportion of grazers rises sharply, and that of the browsers falls, to 48% and 13%, respectively, in Sterkfontein Member 5 considered as a whole unit (not shown in Table 1), suggesting a more open environment. This pattern echoes the results obtained earlier by Vrba.[3,4]

More recent excavations since the earlier phases of excavation on which Vrba's analyses were based, have suggested that Member 5 is best considered as consisting of two infills, separable spatially and on the basis of sediments and distinct stone tool compositions.[18] Since Olduwan stone tools have been found in the East infill, and some Acheulian (handaxe) tools in the West infill,[18] the former must predate the latter as Olduwan tools are older and Acheulian tools more recent. The East infill is now believed to date to around 2.0–1.8 Myr, while the West infill may be younger than 1.7 Myr.[18] When the calculations for grazers, browsers and mixed feeders are performed separately for the two infills (Table 1), the results show that the percentage of browsers in Member 5 (East) drops slightly compared to Member 4, while proportions of grazers and mixed feeders are reduced and increased, respectively. In Member 5 (West), however, the proportion of grazers rises steeply, while percentages of browsers and mixed feeders are markedly reduced. Admittedly, while the division of the data has provided new insights, an unwelcome effect is a reduction in data points for each time period.

These results suggest a time transgressive trend from medium density woodland with small or modest amounts of grass during Member 4 times to a markedly more open environment by about 1.7 Myr. According to the results for the Member 5 East Oldowan infill, a medium density woodland persisted until after 1.8–2.0 Myr. The most significant shift occurred between the time that the East and West infills were deposited. This observation, suggesting that the single largest step towards an open environment occurred near 1.7 Myr, rather than earlier, accords with East African evidence that both soil carbonate isotopic data,[5] and faunal ecomorphological indicators[7] show a major shift to open environments after ~1.8 Myr. Since a number of South African sites fall into this time period, further application of isotope-based methods should allow us to confirm whether the pattern observed for Sterkfontein holds for other South African sites.

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Using carbon isotope data of fossil bovid communities for palaeoenvironmental reconstruction

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Reconstructing palaeoenvironments is a major focus of palaeoanthropological research. While many techniques are now available for exploring past environments, fossil bovids remain amongst the most widely utilized sources of environmental information. Most studies of fossil bovids, however, assume implicitly that bovid ecology is the same now as it was in the distant past. Because such uniformitarianist assumptions are not always valid, we have developed a method to provide palaeoenvironmental information from fossil bovids that requires no ecological assumptions. Here, we show that the percentages of C_3 and C_4 vegetation-consuming bovids in modern environments generally vary according to the amount of woody vegetation present. Application of this C_3/C_4 index to the fossil bovid assemblage at Makapansgat shows that, based on carbon isotope data, the percentage of C_3-consuming bovids is high, suggesting a great deal of woody vegetation in this vicinity about 3 million years ago.

Introduction

Stable carbon isotope analysis of tooth enamel has been used for palaeoenvironmental reconstruction,[1–3] but it has been more or less limited to establishing the consumption, and thus presence, of C_3 plants (such as trees, bushes and forbs) and C_4 vegetation (for example tropical grasses and sedges). While this information is useful, it does little to elucidate vegetational structure, which is a primary concern of palaeoanthropologists.[4–6] For instance, the presence of C_4 grasses in the ancient Makapansgat Valley was demonstrated,[7] but these grasses may have existed in environments as different as open grassland or closed woodland.

Fossil bovids remain one of the most widely utilized sources of palaeoenvironmental information.[5,8–13] A widely employed method for using bovids in palaeoenvironmental reconstruction was developed by Vrba[8,9] and subsequently adopted and refined by others.[10–12] Vrba's seminal work was based on a literature review of modern bovid population statistics in 16 game parks and reserves.[9] She observed that the percentage of alcelaphini plus antilopini never exceeded 30% of the total bovid population in areas with considerable tree and bush cover (hereafter 'closed' areas). In contrast, these tribes always exceeded 60% of the total bovid population in areas with few trees and bushes (hereafter 'open' areas) (Table 1). She applied this principle to fossil sites in order to reconstruct palaeoenvironments. For example, it was observed that since Makapansgat (at 3 million years ago) had a low percentage of alcelaphini and antilopini (28%), it reflected a relatively closed environment. In contrast, the high percentages of alcelaphini and antilopini (~80%) at the 1.8-Myr sites of Kromdraai and Swartkrans suggested far more open environments.[5]

Vrba's method is based upon the assumption that antilopini and alcelaphini were open landscape- and arid-adapted several million years ago, as they generally are today, using the principle of taxonomic uniformitarianism. While most evidence suggests that fossil alcelaphini shared the same habitat tolerances as their modern counterparts,[6,7,13] the same cannot be said for fossil antilopini. For instance, recent research shows that *G. vanhoepeni* and *Antidorcas recki* were predominantly browsers and not mixed feeders like most modern antilopini, which forces us to question whether they really preferred open, arid environments.[1,7] Such dietary disparities likely indicate differences in habitat preference or tolerance as well. Thus, while variations of Vrba's method have been instructive, it would be helpful to find ways to derive environmental signals from bovids that make no assumptions about the ecology of fossil taxa.

Method

To this end, we modified Vrba's method to test habitat reconstruction based on bovid carbon isotope compositions. The modification is based on a simple ecological principle. In relatively open areas such as grasslands, there will be relatively little C_3 vegetation and thus limited ecospace for C_3 consumers. As the percentage of woody vegetation increases, however, there will be an increasing amount of C_3 vegetation available for consumption, and concomitantly, more C_3-consuming bovids.

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