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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 palaeo-anthropological 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  $\text{C}_3$  and  $\text{C}_4$  vegetation-consuming bovids in modern environments generally vary according to the amount of woody vegetation present. Application of this  $\text{C}_3/\text{C}_4$  index to the fossil bovid assemblage at Makapansgat shows that, based on carbon isotope data, the percentage of  $\text{C}_3$ -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,<sup>1–3</sup> but it has been more or less limited to establishing the consumption, and thus presence, of  $\text{C}_3$  plants (such as trees, bushes and forbs) and  $\text{C}_4$  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.<sup>4–6</sup> For instance, the presence of  $\text{C}_4$  grasses in the ancient Makapansgat Valley was demonstrated,<sup>7</sup> 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.<sup>5,8–13</sup> A widely employed method for using bovids in palaeoenvironmental reconstruction was developed by Vrba<sup>8,9</sup> and subsequently adopted and refined by others.<sup>10–12</sup> Vrba's seminal work was based on a literature review of modern bovid population statistics in 16 game parks and reserves.<sup>9</sup> 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.<sup>5</sup>

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,<sup>6,7,13</sup> 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.<sup>17</sup> 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  $\text{C}_3$  vegetation and thus limited ecospace for  $\text{C}_3$  consumers. As the percentage of woody vegetation increases, however, there will be an increasing amount of  $\text{C}_3$  vegetation available for consumption, and concomitantly, more  $\text{C}_3$ -consuming bovids.

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**Table 1.** Vrba's original alcelaphine plus antilopine criterion for 16 modern reserves and for Makapansgat Member 3.<sup>9</sup> The last three columns show the percentages of C<sub>3</sub> consumers, C<sub>4</sub> consumers, and mixed feeders (MF) as determined by stable carbon isotope analysis.

Area	Habitat	%Alcelaphines + antelopines	%C <sub>3</sub>	%C <sub>4</sub>	%MF
Kruger	Closed	5	9	19	72
Manyara	Closed	0	1	68	31
Quicama	Closed	0	46	54	0
Bicuar	Closed	18	48	46	0
Luando	Closed	0	29	71	0
Cuelei	Closed	6	52	48	0
Mkuzi	Closed	12	5	13	82
Hluhluwe	Closed	24	21	46	33
Kafue	Closed	28	23	76	1
Wankie	Closed	7	29	50	21
Kalahari	Open	65	12	53	35
Nairobi	Open	73	3	48	49
Lake Turkana	Open	70	0	76	24
Serengeti	Open	82	1	67	32
Ngorongoro	Open	97	2	72	26
Etosha	Open	67	14	38	48
Makapansgat M3	?	28	51	31	18

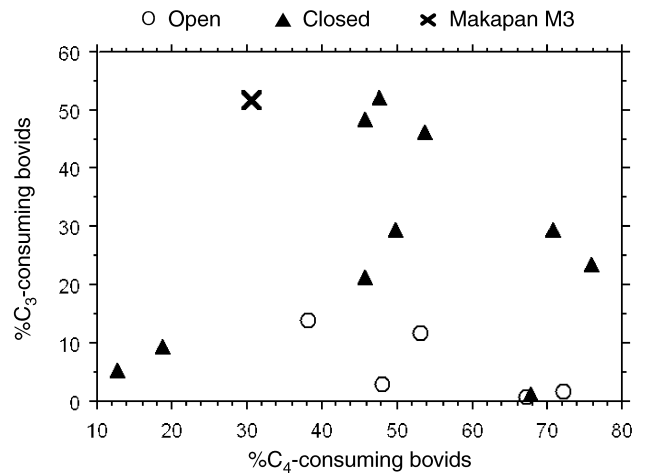
Thus, in biomes where the grasses are C<sub>4</sub>, the percentages of C<sub>3</sub>- and C<sub>4</sub>-consuming bovids should provide information about the local environment. More specifically, the percentages of C<sub>4</sub> consumers and mixed feeders should provide information similar to the percentage of alcelaphini (which consume C<sub>4</sub> vegetation) and antilopini (which eat C<sub>3</sub> and C<sub>4</sub> vegetation). When applied to the fossil record, however, this isotopic method has the distinct advantage of being derived empirically — we do not need to assume anything about behaviour, it is made manifest from the analytical data.

We determined the percentages of C<sub>3</sub> and C<sub>4</sub> consumers in modern habitats using stable carbon isotope analyses of 312 individual bovids,<sup>14</sup> and gleaned isotope data for another 408 individuals from the literature<sup>15</sup> (Table 2). Based on these results, we then determined the percentages of bovids that eat more than 80% C<sub>3</sub> vegetation (hereafter C<sub>3</sub> consumers), eat more than 80% C<sub>4</sub> vegetation (hereafter C<sub>4</sub> consumers), and all others (hereafter mixed feeders) from each park in Vrba's original study (Table 1). The carbon isotope data show that the vast majority of all African bovids are C<sub>3</sub> or C<sub>4</sub> specialists that change their diets very little anywhere within their range.<sup>14,15</sup> A few taxa, however, such as impala (*Aepyceros melampus*), are mixed feeders whose diets can vary markedly from place to place.<sup>14,16</sup> In order to test our isotope-based classifications we divided the bovids from these parks into the same three groups using a literature review

**Table 2.** Stable isotope compositions, standard deviations, sample sizes, percentage C<sub>4</sub> grass consumed, and dietary classifications [C<sub>3</sub>, C<sub>4</sub>, or MF (mixed feeder)] for 720 individual bovid specimens divided into nine tribes, as tribes form the basis of most palaeoenvironmental reconstructions.

Tribe	δ <sup>13</sup> C	s.d.	n	%C <sub>4</sub>	Diet
Aepycerotini	-5.9	2.9	63	52	MF
Alcelaphini	1.2	1.1	119	97	C <sub>4</sub>
Antilopini	-9.2	1.5	78	29	MF
Bovini	-1.9	0.6	120	80	C <sub>4</sub>
Cephalophini	-14.6	1.7	46	1	C <sub>3</sub>
Hippotragini	0.8	1.1	62	92	C <sub>4</sub>
Neotragini	-13.1	1.6	37	19	C <sub>3</sub>
Reduncini	0.6	1.7	82	93	C <sub>4</sub>
Tragelaphini	-12.5	2.2	113	9	C <sub>3</sub>

The percentages of C<sub>4</sub> consumption (%C<sub>4</sub>) represent an average calculated directly from southern and East Africa datasets.<sup>15,16</sup> References 15 and 16 also contain carbon isotope data for individual species.



**Fig. 1.** Plot of the percentage of bovids that consume more than 80% C<sub>3</sub> vegetation against those that eat more than 80% C<sub>4</sub> vegetation from modern 'closed' and 'open' environments.

of their diets.<sup>17</sup> The two methods provided identical results, demonstrating remarkable agreement between the stable isotope and traditional ecological data. Thus, we are confident that our isotopically derived results are robust.

## Results and discussion

Using the percentages of C<sub>3</sub> specialists (rather like an inverse of the alcelaphini plus antilopini criterion), the areas Vrba termed 'closed' and 'open' were successfully separated in 13 of 16 cases (ANOVA;  $P < 0.02$ ). In every case, the 'open' areas contained less than 15% C<sub>3</sub>-consuming bovids. In 7 of the 10 'closed' areas, C<sub>3</sub> consumers accounted for more than 20% of the bovids present. In the three cases in which 'closed' areas had less than 15% C<sub>3</sub> eaters, the bovids were dominated by grass-eating yet woodland-loving buffalo (*Syncerus caffer*) or impala. When the percentages of C<sub>3</sub> consumers are plotted against the percentages of C<sub>4</sub> consumers, however, the distinction between 'open' and 'closed' environments is improved, as 'open' areas are isolated in the bottom right corner of Fig. 1. The only 'closed' area that clusters with 'open' habitats is Lake Manyara in Tanzania, for which buffaloes comprise 66% of the total bovid population. It is highly unlikely, however, that bovines would be so preponderant had the local ecosystem suffered less from human incursion.

These data indicate that the presence of more than 20% C<sub>3</sub>-consuming bovids indicates a relatively 'closed' environment. Equally important, however, this C<sub>3</sub>/C<sub>4</sub> index eliminates a host of assumptions and supplants them with an ecological imperative: an animal can only eat food that is available. When applied to the fossil site of Makapansgat, the carbon isotope data show that 51% of its bovids were C<sub>3</sub> consumers (Table 1; Fig. 1), which is a higher percentage of C<sub>3</sub> consumers than all but one of Vrba's modern 'closed' areas (Culei, Angola, at 52% contains woodland, thicket, and riverine forest). Hence, these results strengthen previous environmental reconstructions that suggest that significant amounts of woody vegetation were present in the 3-Myr Makapansgat Valley.

Several caveats should be considered. For one, further such analyses should be undertaken in more modern environments to determine the universality of these patterns. Ideally, one should analyse the entire macrofauna, as bovids alone may not be peerless environmental indicators. For instance, a relatively high percentage of C<sub>3</sub> consumers within the larger faunal community might leave limited ecospace for C<sub>3</sub>-consuming bovids, leading to a disproportionately high percentage of C<sub>4</sub>

consumers among the bovid fauna. If this were the case, the percentage of  $C_3$  vegetation would be under-represented in the bovid sample. Analyses of entire modern and fossil communities will go a long way towards eliminating such potential biases. Another problem is the unknown length of time in which a fossil assemblage accumulated. The Makapansgat Member 3 fauna, for instance, may have accumulated in a few thousand or even 100 000 years.<sup>20,21</sup> Thus, the fauna do not represent a 'snapshot' in time, but rather a series of snapshots laid atop each other. Therefore, the composite assemblage may or may not fairly represent the fauna found in the vicinity of the cave at any given time. This is further exacerbated by the fact that the percentages of animals found at Makapan may not accurately reflect the living community during Member 3 times due to collection biases.<sup>22-24</sup> However, these last two difficulties plague *all* faunal and palynological analyses.

Notwithstanding these constraints, in the case of Makapansgat it seems unlikely that the very large percentage of  $C_3$  consumers could be due to predator selection alone, since the most abundant bovid species is the fresh-grass grazing *R. darti* (16% of all bovinds)<sup>17</sup> — hence  $C_4$  consumers were also abundant and preyed upon. Moreover, even if we were to halve the number of  $C_3$  consumers at Makapan, it would still cluster with the modern 'closed' environments. The great excess of  $C_3$ -consuming bovinds from Makapan is consistent with earlier studies that suggested 'closed' environments with riparian forest and edaphic grasslands.<sup>7,18,21</sup> Importantly, the carbon isotope-based  $C_3/C_4$  index requires no assumptions about the behaviour of fossil taxa, as the only data used are those established empirically by carbon isotope analysis. Further research on the percentages of  $C_3$  and  $C_4$  consumers in modern habitats among all taxa will greatly improve the utility of this tool.

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