

Isotopic palaeoecology of Makapansgat Limeworks Perissodactyla

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Relatively little is known about the ecology of South African Pliocene perissodactyls. Researchers usually assume that these taxa were ecologically similar to their modern counterparts, but this assumption is questionable, and can tell us nothing about the ecology of taxa without modern representatives such as chalicotheres. Here we examine the ecology of Makapansgat's Rhinocerotidae, Equidae and Chalicotheridae using stable carbon isotope analysis of tooth enamel. This allows us to test uniformitarianist assumptions, provides insight into the ecology of these taxa, and allows a glimpse into the ecological underpinnings of hominid evolution in South Africa.

The rodents,¹ suids,² bovids,³⁻⁶ cercopithecids,⁷ and hominids^{8,9} from the 3-million-year-old Makapansgat Limeworks have been subjected to intense study. Relatively little attention, however, has been paid to the perissodactyls, which include some of the oldest specimens of the modern white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinos, as well as an extinct equid (*Hipparion lybicum*) and chalicothere (*Ancylotherium hennigi*).¹⁰ To a large extent, our understanding of the ecology of these creatures has been based on taxonomic uniformitarianism and morphology. Specifically, it is assumed that *C. simum* and *H. lybicum* were grazers because their living relatives are, and because they had hypsodont dentition, while it is assumed that *D. bicornis* was a browser because of its low-crowned dentition and dedicated browsing habits of the modern black rhino.^{10,11} As the Chalicotheridae have no living representatives, we can infer their diets from morphology only. *Ancylotherium*'s brachyodont dentition and apparent specialization for rearing up on two hindlegs suggests that it was a browser that gathered material for consumption with its forelimbs.¹² Others have argued that its unique claws were used for extracting food from underground¹³

Neither taxonomic uniformitarianism nor morphology, however, allows us to make unequivocal dietary assignments.^{6,14} For example, a recent isotopic and microwear study examining the diets of North American fossil equids demonstrated that some Pliocene taxa were browsers despite hypsodont dentition and grazing survivors.¹⁵ This necessitates tapping other sources of information to investigate the diets of fossil taxa. Here, we examine the ecology of the Makapansgat perissodactyls in the light of new stable carbon isotope data.

Stable carbon isotope analysis is useful for studying the ecology of fossil taxa because plants that use the C₃ photosynthetic pathway such as trees, bushes, and forbs have depleted ratios of ¹³C/¹²C[†] in their tissues compared to tropical grasses and some

sedges, which use the C₄ pathway.^{16,17} Dietary carbon is incorporated into tooth enamel apatite of herbivores with some further fractionation.^{18,19} In African savanna environments, pure grass consumers (grazers) have δ¹³C values of about +2‰ to -2‰, while animals that eat from trees, bushes, shrubs, and forbs (browsers) have depleted δ¹³C values of between about -10‰ and -16‰. Thus, by determining δ¹³C of a fossil taxon's tooth enamel we can tell if it was a grazer, a browser, or a mixed feeder.

In order to perform stable carbon isotope analysis, enamel was obtained from fossil teeth using a rotary drill equipped with a diamond-tipped burr.²⁰ The powder was pretreated in 1.5% sodium hypochlorite solution to remove organic contaminants and in 0.1 M acetic acid to remove highly soluble diagenetic carbonates, and freeze-dried. One milligram of purified powder was weighed into individual reaction vessels in a Kiel II Autocarbonate device interfaced with a Finnigan MAT 252, for reaction with phosphoric acid at 70°C, cryogenic distillation, and measurement of the resultant CO₂. The raw data were calibrated against several international and laboratory standards before being downloaded for statistical analysis. The results for the Limeworks perissodactyls are presented in Table 1 and Fig. 1. The grazing bovid *Parmularius braini* and browsing bovid *Tragelaphus angasi* from Makapansgat are included for comparison.

Hipparion lybicum was clearly a consumer of C₄ grasses like *Equus* in Africa today. Its δ¹³C values are slightly depleted compared to the alcelaphine bovid *P. braini*, but analysis of variance shows that this difference is not statistically significant. Modern African equids tend to have slightly lower δ¹³C values than coexisting alcelaphines.²¹ While it can be argued that these small differences reflect their differing digestive physiologies, a study of the diet to enamel apatite fractionation in wild and captive animals found no differences between equids and bovids.¹⁹ This, coupled with studies noting that modern equids occasionally browse, suggests that the lower δ¹³C values probably reflect the inclusion of small amounts of (non-grassy) C₃ vegetation.²² An isotopic study of equids from the late Miocene at Lothagam also suggested an early specialization on grasses within this lineage.²³ Thus, it appears likely that Pliocene *Hipparion*, and later *Equus*, filled much the same niche. Future studies of sympatric *Hipparion* and *Equus* (at Swartkrans and Koobi Fora, for example) should improve our understanding of the ecology underpinning the eventual disappearance of the former, and ascendancy of the latter.

Predictably, the δ¹³C values of *C. simum* and *D. bicornis* are significantly different ($P < 0.0001$). The ¹³C-depleted *D. bicornis* was clearly a browser as generally assumed, as its δ¹³C values are nearly identical to those of the browsing bovid *T. angasi*. But although *C. simum* certainly consumed C₃ grasses, its δ¹³C values are significantly different from those of the aforementioned grazers *P. braini* and *H. lybicum* ($P < 0.01$). Therefore, unlike the modern white rhino, the Makapansgat *Ceratotherium* was not a pure grazer. Indeed, these data indicate that browse comprised over 30% of its diet, much like the greater Indian rhinoceros today (*Rhinoceros unicornis*).²⁴ A hypsodonty index of 2.9 for the single unworn M₃ of Makapansgat's *Ceratotherium* falls closer to the mean hypsodonty index of modern browsing *Diceros* (HI = 2.2) than it does to modern *Ceratotherium* (HI = 3.9). This, coupled with the isotopic evidence, strongly suggests that *Ceratotherium* had neither the morphological equipment nor the behavioural propensities of the extant white rhino. The result is perplexing given that many African bovid and equid taxa had already become specialized grazers by this time.^{6,14} Apparently

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[†]¹³C/¹²C is expressed as δ¹³C values in parts per thousand (per mil) relative to the PDB standard.

Table 1. Mean $\delta^{13}\text{C}$ values, standard deviations, and specimens sampled for the Makapansgat Limeworks perissodactyls and grazing and browsing bovid outgroups.

Species	$\delta^{13}\text{C}$ (‰)	s.d.	n
<i>Ancylotherium hennigi</i>	-10.3	0.3	3
<i>Ceratotherium simum</i>	-3.5	0.7	4
<i>Diceros bicornis</i>	-11.6	1.3	3
<i>Hipparion lybicum</i>	-0.8	0.9	5
<i>Parmularius braini</i>	0.7	0.7	4
<i>Tragelaphus angasi</i>	-11.7	1.5	4

the rhinoceros *Ceratotherium* lineage remained less-specialized until well into the middle to late Pliocene faunal turnover. Given this evidence, it is unlikely that the Makapansgat *Ceratotherium*, and the extant white rhino, are conspecific. More likely, it is a late representative of *C. praecox*, or a new South African endemic species.

The $\delta^{13}\text{C}$ values for *A. hennigi* are consistent with its being a C_3 feeder. It is slightly enriched in ^{13}C compared to the browsers *D. bicornis* and *T. angasi*, but the difference is not significant (given the small sample numbers). *Ancylotherium* was clearly a browsing herbivore, but the results allow that approximately 10% of its diet could have consisted of C_4 plants. We cannot, therefore, exclude the possibility that *Ancylotherium* dug for underground parts of C_4 plants occasionally. Moreover, $\delta^{13}\text{C}$ analysis alone does not allow us to address the possibility of their digging for the tubers of C_3 plants. We suggest that microwear studies could be used to examine this possibility.

Although the results presented here are in accord with previous thinking for three of the four taxa analysed, the $\delta^{13}\text{C}$ values for *Ceratotherium* are unanticipated and important. Recent carbon isotope studies have shown that 25% or more Pliocene taxa had diets different from those reported (or assumed) in the literature.^{6,14,25} Since many palaeoenvironmental reconstructions are founded on our reputed knowledge of the diets and habitat tolerances fossil taxa,^{5,26,27} this discrepancy is highly significant. Stable carbon isotope studies can clearly improve our understanding of the ecology of these fossil species, and in turn, better our palaeoenvironmental reconstructions. Studies that combine isotopic, morphological, microwear and elemental components will improve our understanding of the processes that shaped today's biotic community.

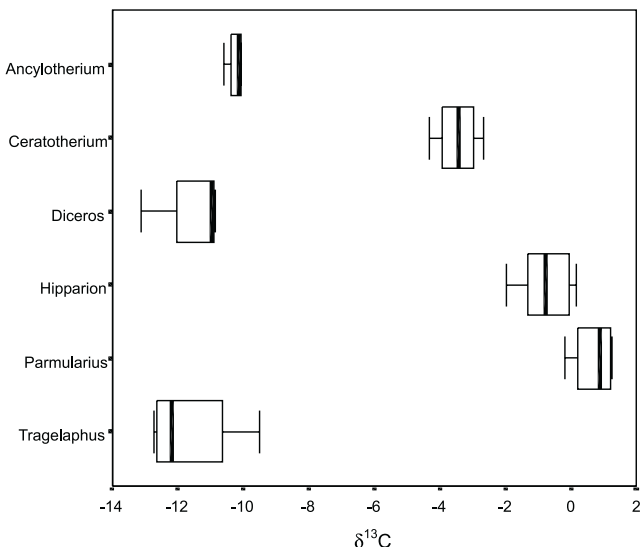


Fig. 1. Box plot showing the interquartile range (25–75%, indicated by boxes), the means (thick vertical bars) and the range (thin horizontal bars) of the $\delta^{13}\text{C}$ values of the taxa analysed for this study.

While fauna abundance-based environmental reconstructions are best made within the broad context of community ecology, these data do allow us to make some general statements about the ancient Makapansgat Valley. Some researchers believe that the ancient valley was relatively arid,^{2,28–30} although recent research suggests that it contained riverine forest, bushland and edaphic grassland.^{5,6,10,31} Since three of the six taxa shown in Fig. 1 were C_4 plant consumers (and grazers, fresh-grass grazers, and mixed feeders make up nearly 50% of the large-bodied herbivores),¹⁴ it is likely that extensive grasslands or woodlands were to be found in the vicinity. Thus, while subtropical forest may have existed in patches (as it does, probably to a lesser extent, today), it would not have been the dominant habitat. On the other hand, the high percentage of browsing taxa in Fig. 1 (and about 50% of the large-bodied herbivores)¹⁴ does suggest an abundance of woody vegetation. Thus, these results are consistent with reconstructions suggesting that the area contained riverine forest, edaphic grassland and perhaps bushland. More precise reconstructions will be possible when further analyses provide us with more information about the ecology of the entire Makapansgat fauna.

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