



Hominin palaeoecology in Late Pliocene Malawi: First insights from isotopes (^{13}C , ^{18}O) in mammal teeth

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Carbon-13 and oxygen-18 abundances were measured in large mammal skeletal remains (tooth enamel, dentine and bone) from the Chiwondo Beds in Malawi, which were dated by biostratigraphic correlation to ca. 2.5 million years ago. The biologic isotopic patterns, in particular the difference in carbon-13 abundances between grazers and browsers and the difference in oxygen-18 abundances between semi-aquatic and terrestrial herbivores, were preserved in enamel, but not in dentine and bone. The isotopic results obtained from the skeletal remains from the Chiwondo Beds indicate a dominance of savannah habitats with some trees and shrubs. This environment was more arid than the contemporaneous Ndolanya Beds in Tanzania. The present study confirms that robust australopithecines were able to live in relatively arid environments and were not confined to more mesic environments elsewhere in southern Africa.

Introduction

Links between the environment and key episodes of hominin evolution in Africa have often been suggested.^{1,2,3,4,5,6} It is therefore of prime importance to have the most accurate knowledge of the environmental conditions at the time and place that hominins were present. Isotopic investigations of mammal remains from Plio-Pleistocene hominin sites have proved highly informative regarding palaeoecosystems in southern and eastern Africa.^{7,8,9,10,11,12,13,14,15,16,17} To date no such investigation has been attempted in Malawi – an area that has yielded hominin fossils important for closing the gap between localities in southern and eastern Africa.^{18,19,20} A recent study of the mammalian fauna indicated a palaeoecological reconstruction that was relatively arid, with a strong affinity to the Somalia-Masai ecozone, and more arid than it is today.²¹ However, the study was made difficult by the taphonomic biases of the localities²² leading to the preferential preservation of large species. To help in refining this palaeoecological reconstruction, we present here preliminary isotopic results on mammal remains from unit 3A of the Chiwondo Beds that yielded *Homo rudolfensis* and *Paranthropus boisei*.^{18,23} The fauna from both hominin sites are biostratigraphically correlated to the Plio-Pleistocene boundary, around 2.5 million years ago (MYA), a period for which an aridification event has been tentatively linked to a turnover and a radiation of hominin species, with the first appearance of the genera *Paranthropus* and *Homo*.^{24,25} For almost 50 years, the conventional opinion on this dichotomy of the hominin clade has favoured the hypothesis that the major adaptive differences between the *Homo* and *Paranthropus* lineages developed because of the increasing dietary specialisation of *Paranthropus* as a result of climate change, while *Homo* adopted a generalist strategy.²⁶ Wood and Strait²⁷ tested the diet/climate hypothesis by analysing a set of criteria and suggested that both genera probably were eurytrope and that derived morphology does not always mirror specialised adaptation towards a particular diet or habitat preference. Therefore it is striking to see how many of the habitat reconstructions for early *Homo* and *Paranthropus* draw a mosaic picture, interpreting that both hominin groups existed in variable environments. The goal of this study is to evaluate the state of preservation of the fossil mammal material for carbonate isotopic investigations and to draw some first conclusions on the palaeoenvironment inhabited by these early hominins in south-east Africa in order to improve our knowledge about their environmental distribution and constraints.

Significance of isotopic (palaeo-)ecology

The relative abundance of carbon-13 (^{13}C) in mammalian tissues is directly linked to their average diet. In African tropical environments, two types of vegetation are clearly distinguished by their carbon isotopic signatures: plants using the C3 photosynthetic pathway (trees and shrubs) and plants using the C4 photosynthetic pathway (grasses). As herbivores record the carbon isotopic signature of their plant food, analysing their fossil remains allows the reconstruction of some aspects of the vegetation in their preferred habitat, as long as the isotopic signatures have not been significantly modified post-mortem. Some species exhibit a restricted dietary spectrum and can be used as tracers of possible diagenetic alteration.²⁸ For example, giraffes and the proboscidean



Deinotherium are exclusively browsers and therefore exhibit C3-consumer isotopic signatures, while the Alcelaphini antelopes exclusively consume C4 grasses.^{10,29,30,31,32} In contrast, other species are more opportunistic and their carbon isotopic signatures can be used to evaluate the relative importance of C3 and C4 plants available to them. For instance, hippopotamuses consume different amounts of C3 plants depending on their availability.^{8,33,34,35}

Oxygen-18 (¹⁸O) abundances in skeletal tissues are linked to those of drinking water and water contained in the food, and they vary according to temperature and aridity. They typically increase with increasing temperature and decreasing precipitation.^{36,37} Different habitats and water conservation strategies between herbivores lead to coherent patterns in the oxygen isotopic signatures of African herbivores, with giraffes systematically ¹⁸O-enriched compared to other terrestrial herbivores^{11,38} and hippopotamuses systematically ¹⁸O-depleted compared to terrestrial herbivores.^{8,34,39} These biogenic patterns can also be used to track possible diagenetic alteration in fossil material. The variations of $\delta^{18}\text{O}$ values of a given herbivorous species through space and time can be tentatively related to changes in climatic conditions, but

caution is necessary in the interpretation of small datasets as terrestrial mammals typically exhibit significant variation of their $\delta^{18}\text{O}$ values within a living population.³⁹

Materials and methods

All specimens studied were derived from unit 3A-2 in the Chiwondo Beds (Malawi), either from Malema RC11 (12 specimens) or from Uraha (2 specimens). Biozone 2 in unit 3A is relatively dated by the correlation of suid remains with other radiometric dated sites in eastern and South Africa to between 2.5 MYA and 2.3 MYA. Most of the material comes from the Malema excavation site RC11 from the same level that yielded the *Paranthropus* maxilla fragment HCRP-RC-911.^{20,21} Tooth or jawbone fragments with teeth have been selected from the following taxa: proboscidians (*Deinotherium* sp., *Elephas recki*), giraffids (*Giraffa* sp., *Sivatherium* sp.), bovids (one undetermined specimen, *Megalotragus* sp.), camel (*Camelus* sp.), *Hippopotamus* sp. and equids (*Hipparion* sp.). Small enamel fragments were retrieved, as well as fragments of dentine and bone for some specimens (Table 1). Whenever possible, the calcareous matrix was also sampled.

TABLE 1: List of isotopic results obtained on fossil material from the Chiwondo Beds, Malawi.

Sample no.	Site	Taxon	Specimen	Sample	$\delta^{13}\text{C}$	$\delta^{18}\text{O}_{\text{SMOW}}$
MW100	Malema RC11 (unit 3a)	Bovini indet (young)	mandible	enamel	-2.6	29.7
MW110	-	-	-	jaw bone	-4.0	29.6
MW120	-	-	-	limestone matrix	-9.0	24.0
MW200	Malema RC11 (unit 3a)	indet	bone	bone	-2.7	28.3
MW210	-	-	-	matrix from MW200	-8.1	24.6
MW220	-	-	-	limestone concretion	-7.6	24.5
MW230	-	-	-	bone	-2.8	29.0
MW240	-	-	-	matrix from MW230	-8.9	24.5
MW300	Malema RC11	<i>aff Giraffa pygmaeus</i>	upper molar	enamel	-11.3	34.4
MW310	-	-	-	dentine	-7.0	31.7
MW400	Malema RC11	<i>Megalotragus</i>	bone + molar	bone	-2.8	31.2
MW410	-	-	-	matrix from MW400	-9.2	24.6
MW420	-	-	-	enamel	1.6	31.6
MW430	-	-	-	dentine	-3.6	31.3
MW440	-	-	-	limestone matrix	-9.0	24.1
MW500	Malema RC11	<i>Elephas recki</i>	molar fragment	enamel	-3.6	29.1
MW800	Malema RC11	<i>Hippopotamus</i> sp.	-	enamel	1.1	30.1
MW810	-	-	-	dentine	-3.1	30.5
MW820	-	-	-	limestone concretion	-9.4	24.3
MW900	Malema RC11	<i>Hippopotamus</i> sp.	tooth	enamel	0.9	29.1
MW1100	Malema RC11	<i>Giraffa stillei</i>	tooth	enamel	-12.8	35.7
MW1200	Malema RC11	<i>Hipparion</i>	tooth	enamel	0.9	28.0
MW1210	-	-	-	dentine	-1.5	29.8
MW1300	Malema RC11	<i>Hipparion</i>	tooth	enamel	-1.9	32.2
MW1310	-	-	-	dentine	-4.6	30.8
MW1500	Malema RC11	<i>Megalotragus</i>	tooth	enamel	1.3	33.5
MW1510	-	-	-	dentine	-3.0	31.6
MW1600	Malema RC11	<i>Sivatherium</i>	tooth	enamel	-7.9	34.0
MW1610	-	-	-	dentine	-7.9	31.7
MW1700	Malema RC11	<i>Notochoerus scotti</i>	tooth	enamel	-1.1	n.d.
MW2100	Malema RC1	<i>Deinotherium bozasi</i>	tooth	enamel	-12.6	30.1
MW600	Uraha U9 (unit 3a)	<i>Deinotherium</i>	tooth	enamel	-12.9	29.5
MW610	-	-	-	concretion from MW600	-7.4	26.1
MW1400	Uraha U16 (unit 3a)	<i>Camelus</i> sp.	tooth	enamel	-11.0	30.4
MW1410	-	-	-	dentine	-7.9	31.5

SMOW, standard mean ocean water.

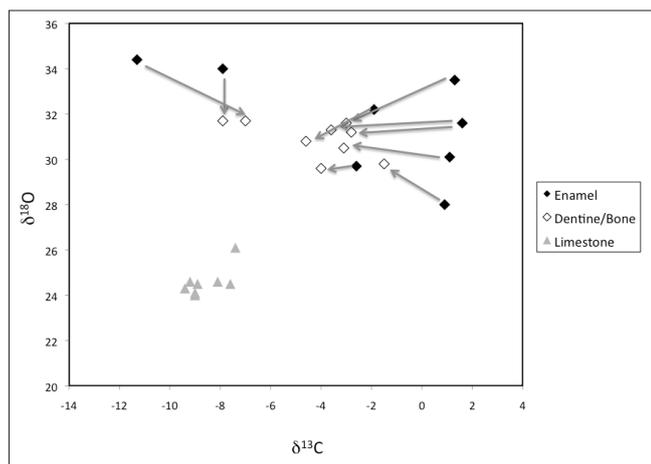


FIGURE 1: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of enamel, dentine, bone and limestone matrix from samples from the Chiwondo Beds. Arrows connect the enamel and dentine values from the same tooth.

Comparing enamel, dentine, bone and limestone isotopic signatures allows evaluation of possible diagenetic alteration of the isotopic signatures.^{40,41,42}

A chemical pre-treatment aimed at the removal of exogenous contaminants, such as organic residues and carbonates, was applied to the enamel, dentine and bone samples.⁸ Powdered samples were soaked in 2–3% NaOCl for 20 h at 20 °C to oxidise organic residues, rinsed with distilled water, then treated with 1 M acetic acid-Ca acetate buffer (pH = 4.75) for 20 h at 20 °C to remove exogenous carbonate. Carbon dioxide was produced from the treated powders (± 15 mg) by dissolution in 100% H_3PO_4 at 50 °C for 5 h. Carbon dioxide was collected and purified by cryogenic distillation in a vacuum line, and carbon isotope compositions were measured on a VG Optima gas source mass spectrometer (Manchester, UK). The isotopic ratios are expressed as $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values with an analytical precision better than 0.1‰ and 0.2‰, respectively; the international standards are Pee Dee belemnite (PDB) and standard mean ocean water (SMOW) for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, respectively.⁸

Results

The carbon and oxygen isotopic signatures of enamel exhibited a much larger variation than those of dentine, bone and embedding limestone (Table 1, Figure 1). The $\delta^{13}\text{C}$ values ranged from -12.9‰ to +1.6‰ in enamel, from -7.9‰ to -1.5‰ in dentine, from -4.0‰ to -2.7‰ in bone and from -9.4‰ to -7.4‰ in embedding limestone. A similar pattern was observed for $\delta^{18}\text{O}$ values: they ranged from 28.0‰ to 35.7‰ in enamel, from 29.8‰ to 31.7‰ in dentine, from 28.3‰ to 31.2‰ in bone and from 24.0‰ to 26.1‰ in embedding limestone.

The isotopic signatures of fossil enamel were clearly related to the specific origin of the samples. The browsing taxa, such as *Giraffa* and *Deinotherium*, clearly exhibited $\delta^{13}\text{C}$ values indicating exclusive consumption of C3 plants (-12.9‰ to

-11.3‰), while *Megalotragus*, a specialised grazer, exhibited $\delta^{13}\text{C}$ values typical of exclusive C4-plant consumption (1.3‰ to 1.6‰). The variations of the $\delta^{18}\text{O}$ values were also related to taxonomic affinity of the samples: the *Giraffa* samples exhibited the most positive $\delta^{18}\text{O}$ values (34.4‰ and 35.7‰) while *Hippopotamus* specimens exhibited slightly less positive $\delta^{18}\text{O}$ values (29.1‰ and 30.1‰).

Discussion

Effects of diagenetic alteration and preservation of enamel isotopic signals

The predicted biogenic patterns in $\delta^{13}\text{C}$ values were found for the enamel isotopic patterns in exclusive browsers such as *Giraffa* and *Deinotherium*, in comparison to grazers such as *Megalotragus*. Giraffids exhibited more positive $\delta^{18}\text{O}$ values than other herbivores and *Hippopotamus* exhibited lower $\delta^{18}\text{O}$ values than the average of terrestrial herbivores. In contrast, the isotopic signatures of dentine and bone from the same specimens did not display such a clear trend. For instance the $\delta^{13}\text{C}$ values tended to gather around intermediate values ranging from -8‰ to -1‰, instead of clustering according to the predicted dietary preferences (Figure 1). Interestingly, the $\delta^{13}\text{C}$ values of carbonate from the surrounding matrix and concretions showed $\delta^{13}\text{C}$ values between -10‰ and -7‰, which suggests that the $\delta^{13}\text{C}$ values of dentine were influenced by this background carbon, especially for grazers that tended to shift towards these values. A similar pattern was visible for the $\delta^{18}\text{O}$ values, in which the differences related to taxonomic affiliation exhibited in enamel were not reflected in bone and dentine (Figure 1). This pattern suggests that the $\delta^{18}\text{O}$ values of bone and dentine were also affected by diagenetic alteration, in contrast with those of enamel. These results are similar to those published by Lee-Thorp²⁸ on South African material. In this study, there was no evidence that the enamel isotopic ratios were significantly altered by diagenesis.

Palaeoenvironmental reconstruction of the Chiwondo Beds

Although the small number of individuals analysed per species does not allow statistically based inferences, the isotopic patterns seen in various taxa will be used to draw preliminary palaeoenvironmental conclusions. An interesting pattern is observed in the giraffid *Sivatherium*, which exhibited less negative $\delta^{13}\text{C}$ values than the purely browsing *Giraffa*, -7.9‰ compared to -11.3‰ to -12.8‰ (Table 1 and Figure 2). This fossil genus has been interpreted as a mixed feeder based on hypsodonty and tooth wear,⁴³ and it seems that the studied individual from Malema incorporated some C4 grass in its diet. This was, however, not the case for *Sivatherium marusium* from Makapansgat member 3 dated to 3 MYA, that exhibited $\delta^{13}\text{C}$ values similar to those of *Giraffa* in the same site.¹⁵ This difference could indicate that Malema is a more open environment than the South African site, Makapansgat.

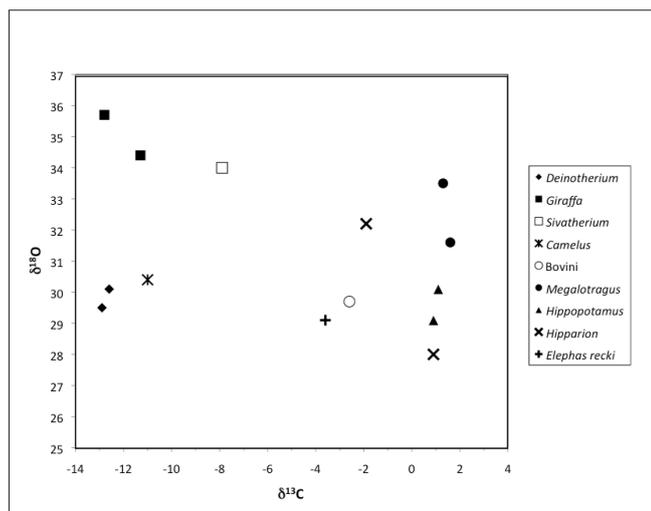


FIGURE 2: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of enamel from different large mammal species from the Chiwondo Beds.

Both *Hippopotamus* analysed in this study exhibited high $\delta^{13}\text{C}$ values, indicating a purely C4 diet. Such values are reached in modern *Hippopotamus* living in open surroundings without closed forests.³³ These isotopic values suggest a predominance of open environments dominated by C4 plants.

In conclusion, the environmental reconstruction that can be tentatively drawn from the available isotopic data suggests a dominance of savannah habitats, based on the $\delta^{13}\text{C}$ values of *Hippopotamus* and possibly *Sivatherium*, with some trees and shrubs yielding C3 biomass present, as indicated by the low $\delta^{13}\text{C}$ values of *Deinotherium*, *Camelus* and *Giraffa*.

Regional comparison

A preliminary comparison is possible with contemporaneous sites in eastern and southern Africa; specifically the Ndolanya Beds at Laetoli (Tanzania) and Swartkrans 1 (South Africa), for which the carbon and oxygen isotopic signatures of fossil material have been published.^{11,44} Comparison of the isotopic data with Swartkrans is made difficult by the fact that $\delta^{18}\text{O}$ values are not published and the taxa are different from those in the Chiwondo Beds. Nevertheless, the bovid assemblage in general indicates more arid conditions at Swartkrans than at Sterkfontein,^{45,46} suggesting a less woodland and more open habitat at Swartkrans – a conclusion also supported by a comparison of the micromammal fauna⁴⁷ and the stable carbon isotopes of fossil mammals⁴⁸ from these cave sites. In contrast, there are common taxa in the Chiwondo Beds and Ndolanya Beds, such as *Sivatherium*, Alcelaphini, *Hipparion* (= *Eurygnathohippus*), elephantids (*Loxodonta* cf. *exoptata* and *Elephas recki*, respectively) providing $\delta^{13}\text{C}$ values that can be compared between both sites (Figure 3). Elephantids and *Hipparion* do not exhibit a clear pattern for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, but for Alcelaphini and *Sivatherium*, the $\delta^{13}\text{C}$ values appear slightly more positive in the Chiwondo Beds and the $\delta^{18}\text{O}$ clearly more positive. This could reflect more arid conditions for the Chiwondo Beds than for the Ndolanya Beds. The latter has been interpreted as semi-arid bushland,⁴⁹ comprising a faunal mixture of 75% from bushland and

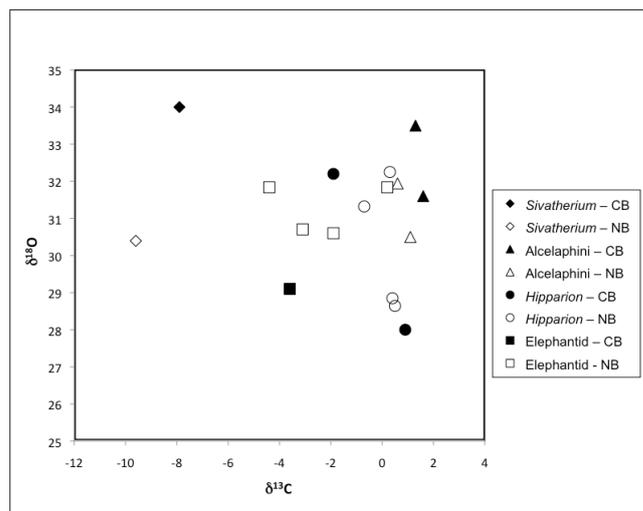


FIGURE 3: Comparison of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of enamel in selected species from the Chiwondo Beds (CB) and the Ndolanya Beds (NB).

25% from grassland habitats⁵⁰ and corresponding to an area dominated by wooded grassland, ranging from limited areas of closed woodland to much more extensive areas of open bushland and grassland.⁵¹ At present, the preliminary results on *Sivatherium*, present in both sites, suggest more arid conditions in south-eastern than in eastern Africa.

Implications for hominin palaeoecology

The discoveries of *Paranthropus aethiopicus* in the Ndolanya Beds,⁵² and of *P. boisei* in the Chiwondo Beds¹⁹ imply that the eastern African robust australopithecines could adapt to open bushland and grassland conditions. This finding is quite striking because the Laetoli area has never been adjacent to a lake, while the Chiwondo Beds' fauna was associated with a lake throughout most of its succession. Wood and Constantino⁵³ summarised the combined evidence of locality reconstructions and indicated that *P. boisei* favours grassland and/or open woodland habitats. Although Shipman and Harris⁵⁴ placed *P. boisei* towards the closed habitat spectrum, Wood and Constantino⁵³ and Wood and Strait²⁷ argue that *P. boisei* possibly had a broad ecological tolerance. According to Reed⁵⁵, *P. robustus* appears to be slightly more arid adapted than eastern African *P. boisei*. In any case, the appearance of *P. boisei* in the Chiwondo Beds about 2.5 MYA suggests ecological conditions that may be comparable to the ones of *A. robustus* in South Africa after 2 MYA.

Interestingly, carbon isotopic data have been recently published for *P. boisei* from Tanzania, at Olduvai East and Peninj.¹³ In contrast with the robust australopithecines from South Africa that present $\delta^{13}\text{C}$ values indicative of limited amounts of C4 biomass in their diet, those from eastern Africa exhibit $\delta^{13}\text{C}$ values of about -1.0‰ , indicating a C4 biomass in their diet of up to 80%. It remains unclear if this very high C4 component was acquired directly through C4 grasses, especially their seeds (though these are highly seasonal resources), or indirectly through the consumption of the flesh of herbivores that consumed C4 plants, other small mammals or invertebrates, such as termites.^{55,56} Another possibility is



the consumption of sedges such as papyrus, a semi-aquatic plant that bears perennial underground storage organs available to hominins all year round.^{13,57}

The geographic position of the Malawi Rift in south-eastern Africa is of special interest when comparing the dietary adaptations of east and South African robust australopithecines. Ungar et al.⁵⁸ showed that the diet of *P. boisei* included similar amounts of tough (or fibrous) foods to that of *A. africanus*. In contrast, the food of *P. robustus* was much harder (including seeds, nuts and hard fruits) but less tough (i.e. there were fewer fibrous foods such as leaves) than that of *P. boisei*. Additional isotopic data may prove whether this distinction is as a result of different diets or different feeding strategies.

Conclusion

The isotopic preservation of tooth enamel carbonate fraction in the fossil mammals of the Chiwondo Beds was sufficient to allow preliminary palaeoenvironmental reconstruction. This reconstruction, based on the analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of large herbivorous mammal tooth enamel, was consistent with that based on the analysis of the faunal community.^{20,21,59} The environment was dominated by a savannah ecosystem with some trees, and was probably drier than the modern ecosystem in this region. The environment in the Chiwondo Beds was possibly drier than in Tanzanian sites at the same period, about 2.5 MYA, but additional isotopic data are necessary to confirm this trend.

The present study supports the view that *P. boisei* was able to live in arid environments and underlines the broad ecological spectrum of this hominin.

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