Isotopic evidence for contrasting diets of early hominins Homo habilis and Australopithecus boisei of Tanzania

Nikolaa J. van der Merwe*, Fidelis T. Masao* and Marion K. Bamford

Isotopic dietary studies of early hominins have hitherto been confined to specimens from South Africa. We are now able to report isotopic analyses of two species of early hominins from Tanzania: Homo habilis and Australopithecus boisei. The results show that these two species had very different diets. The isotopic analyses of three South African species of early hominins, in contrast, show considerable variation in individual diets, but no marked differences between species.

Three specimens of Homo habilis from Olduvai Gorge, Tanzania, were available for analysis: the type specimen, Olduvai Hominid 7, or OH7;1–3 OH62;4 and OH65.5 Of these, OH7 and OH62 are from Olduvai East (east of palaeolake Olduvai) and OH65 is from Olduvai West. All three are from uppermost Bed 1, dating to about 1.8 million years ago (Myr). Two specimens represent Australopithecus boisei: OH5, the type specimen from Olduvai East (‘Zinjanthropus’), dating to c. 1.8 Myr;6,7 and the ‘Peninj mandible’ from West Lake Natron,8,9 estimated to date to 1.5 Myr.

Initially, the Tanzanian authorities provided a sampling permit for 10 partial hominin specimens from the Olduvai area, which are in the collections of the National Museums of Kenya in Nairobi, but of which Tanzania claims ownership. The Nairobi museum refused sampling access, precipitating an international incident between the two countries. A formal meeting was held in Dar es Salaam, attended by representatives of the Tanzania Commission for Science and Technology, the National Museums of Tanzania, the Department of Antiquities, and archaeologists from the University of Dar es Salaam. After intensive discussion, it was decided that the hominin specimens held in the National Museums should be sampled, including the type specimens OH5 and OH7. The sampling was conducted by van der Merwe and Masao, under the supervision of two representatives of the museum trustees. Samples of 3 mg tooth enamel were removed from each specimen with a diamond-tipped dental drill, allowing for duplicate measurements of stable carbon and oxygen isotope ratios (δ13C and δ18O values) in the Archaeological Department at the University of Cape Town.

A 3 mg sample of tooth enamel provides an average assessment of the diet of an individual over the period when the enamel was laid down. The analyses reported here are for second or third molars, thus representing the adult diets of the five hominins.

An alternative method of sampling, recently developed, is that of laser ablation, which removes sub-millimetre increments along the growth axis and makes it possible to assess seasonal variations in an individual’s diet.10 Laser ablation requires that specimens of whole or broken teeth be taken to the laboratory for analysis. In the case of the Tanzanian hominin fossils, this is not an option.

Isotopic analysis of fossils has been developed over the past 25 years and is a well-established technique for dietary assessment in palaeontology. Tooth enamel has proved to be the most reliable sample material, since it is highly crystalline and resistant to chemical alteration over time.11–13 Tooth enamel is a biological apatite (calcium phosphate) containing carbonate, which makes up about 3% of the enamel weight (as CO2). The stable carbon and oxygen isotope ratios (δ13C and δ18O values, relative to the PDB standard) of carbonates in tooth enamel are measured simultaneously in a mass spectrometer. Of these measurements, δ18O values are related to the water intake (from food and drinking) and water excretion (sweat, urine, breath) of an animal;14 these are not discussed here.

Stable carbon isotope ratios provide a measurement of the C3 and C4 components of an animal’s diet (for review, see ref. 15). In the Tanzanian context at 1.8–1.5 Myr, C3 plants eaten by herbivores included algae, woody bushes and trees, and some C3 grasses from shaded environments; C4 plants included grasses and some forbs and sedges. In the case of carnivores, the C3 and C4 components were provided by herbivores (mammals, fish, insects) that ate the plants; mixed feeders acquired their carbon isotope signatures from plants or herbivores, or both.

To interpret stable carbon isotope results for mixed-feeding hominins, it is necessary to establish the C3 and C4 ‘end members’ of the ecosystem in which they lived. This is done by measuring the δ13C values of dedicated browsers (C3 plant consumers) and grazers (C4 plant consumers). A database of more than 100 δ13C values is available for fossil animals from Olduvai East and West at c.1.8 Myr (van der Merwe, unpublished). The C3 end member is represented by 19 specimens of the grazing genera Connochaetes, Beutragus and Parnamutus, with a mean value δ13C value of +2.0‰ (per mil). At the C4 end of the spectrum, the most negative δ13C values are for Giraffa sp. at ~11.2‰ and Deinotherium bozai (an elephant-like creature with four tusks) at ~11.1‰. Given that Giraffa and Deinotherium were unlikely to be ‘pure browsers’, we can estimate the C3 and C4 end members for Olduvai at c. 1.8 Myr to about ~12‰ and +2‰. The same estimates apply for Peninj at c. 1.5 Myr, where the tooth enamel δ13C values for 40 grazing animals provide a C3 end member of +2‰. In South Africa, estimates for C3 and C4 end members at three hominin sites are available. These are Makapansgat Member 3, c. 3 Myr, at ~12‰ and +2‰;17 Sterkfontein Member 4, c. 2.5–2.0 Myr, at ~13‰ and +1‰;18 and Swartkrans Members 1 and 2, c. 2.0–1.0 Myr, at ~12‰ and +2‰.18

It should be noted that the exact values for C3 and C4 end members are relatively unimportant in calculating the C3 dietary component; a variation of 1‰ or 2‰ at either end do not make a substantial difference to the result. The end members may vary slightly with plant δ13C values, and individual fractionation factors, while the value for the C4 dietary component may vary slightly with the different digestive strategies of different species.19

In order to compare the C3 dietary components of Tanzanian and South African early hominins, it is necessary to use the C3 and C4 end members for the time and place of each specimen. The results are illustrated in Fig. 1. This figure is based on the carbon isotope values for Tanzanian early hominins reported

*Department of Archaeology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.
*University of Dar es Salaam, Tanzania.
*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa.
*Author for correspondence. E-mail: nikolaas.vandermerwe@uct.ac.za
here and all the published values for South African early hominins, excepting a single measurement from Kromdraai, for which C4 and C3 end members are not available. In compiling the results for the early hominins from Tanzania and South Africa, arguments about their taxonomic designations have been avoided. Some authors use the generic name Paranthropus for the two robust australopithecines, A. boisei and A. robustus, whereas Homo sp. from Swartkrans has been referred to as H. ergaster. This is not the appropriate place to discuss these taxonomic arguments.

Figure 1 clearly illustrates that the two specimens of A. boisei from Tanzania had C4 dietary components (77% and 81%) that far exceeded those of all the other early hominins for which carbon isotope values are available. The two australopithecines from South Africa, as well as the two species of Homo from South Africa and Tanzania, show considerable variation between individuals in all cases, but do not approach the extreme C4 dietary component of A. boisei. This begs the question: what did A. boisei eat?

The foods with C4 carbon isotope signatures that were available to all these early hominins included grasses, some sedges and forbs, and a variety of animals (invertebrates, reptiles, birds and mammals) that consumed C4 plants. Peters and Vogel, in considering the possible combinations of C4-based foods that could have produced the carbon isotope signatures of early hominins in South Africa, concluded that their access to edible C4 plants were somewhat restricted in a dryland environment, but that the presence of large wetlands elsewhere in southern and eastern Africa would have offered early hominins greater opportunities for a C4 plant diet. This opportunity was clearly present in Tanzania. At 1.8 Myr, there were extensive wetlands on the eastern side of palaeolake Olduvai, where a river entered the lake from the Ngorongoro mountain range.21 At 1.5 Myr, the Peninj River flowed into Lake Natron from the west, as it does today, and also produced wetlands.

One of the authors (M.K.B.) has identified fossilized plant remains from Olduvai East. Most of the specimens were of woody plants, but about 5% were sedges. These are identifiable from their triangular cross sections, but it is not possible to determine whether they were of the C4 photosynthetic type. They were relatively small sedges (stem diameters less than 1 cm), probably of the type that grows in the seasonally inundated grasslands on the edges of a wetland.

Bamford and van der Merwe investigated (and ate) the edible plants of the Okavango Delta in Botswana during the dry season (July 2003), assisted by Ezaya Karesaza, a tourist guide who grew up in this extensive wetland. Among the C4 plants that are traditionally eaten raw in this region are a variety of fruits and seeds, as well as plants of which the leaves and rhizomes are eaten. The latter include Aschnynomone fluitans, a floating leguminous plant, of which the leaves taste like lettuce; Tynpha capensis, which grows in thick stands along the water’s edge, of which the rhizomes have a pleasant taste; and Schoenoplectus corymbosus, a big water sedge, of which the stem is succulent at the bottom end. Among C3 plants, the rhizomes and culms of three other species of sedges are edible. These include Cyperus denudatus and C. dives, which grow in the grasslands of the floodplains. Unlike the grasses, they are green year-round, although not particularly prolific. The most common C3 sedge, by far, is Cyperus papyrus, which grows in dense thickets along the water edge. This species has culms as high as 4 m, of which the lowermost 0.5 m is frequently chewed by local people. It has a soft, white rind about 0.5 cm thick; the interior, about 2 to 3 cm in diameter, is more fibrous. It is chewy and pleasant tasting. The thick rhizome of papyrus is more fibrous and starchy than the culm, somewhat astringent, and requires considerable chewing effort. It produces a bolus in the mouth that has to be spat out at intervals.

The nutritional qualities of papyrus compare quite well with those of the domesticated potato Solanum tuberosum, as reported in Table 2. The analyses were conducted by Biofoodtek, a CSIR

<table>
<thead>
<tr>
<th>Lab. no.</th>
<th>Taxon and specimen</th>
<th>Tooth</th>
<th>Origin</th>
<th>δ13C (%)</th>
<th>C4% in diet</th>
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<tr>
<td>UCT7483</td>
<td>Homo habilis</td>
<td>LM1</td>
<td>Olduvai East</td>
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<td>UCT7481</td>
<td>OH7 (type specimen)</td>
<td>LM3</td>
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<td>OH62</td>
<td>LM4</td>
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<td>Olduvai West</td>
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<td>Austraolopithecus boisei</td>
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<td>Peninj mandible</td>
<td>LM6</td>
<td>Peninj</td>
<td>+2</td>
<td>100</td>
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**Table 1. Stable carbon isotope ratios (δ13C values) for tooth enamel of early hominins, relative to PDB. Precision of repeated measurements was better than 0.1‰.**

**Fig. 1.** The C4 dietary components (C4 %) of early hominins of Tanzania and South Africa. The results for individual specimens from Tanzania have been calculated from the δ13C values reported in Table 1 and are given in the left-hand column for each specimen. For South African hominins, the left-hand column lists the site and stratigraphic unit (e.g. Sterkfontein 4 for Member 4), the approximate age of the unit(s), the number of specimens of each species for which isotopic values are available, and the full range of C4 dietary components represented by these specimens. In the box-and-whisker plots for South African hominins, the vertical line is the mean, the box covers 25–75% of the range, and the whiskers cover 10–90% of the range. For calculation of the C4 dietary components for South African hominins, all the published carbon isotope values for Makapansgat, Sterkfontein, and Swartkrans have been used. Myr, million years ago.
laboratory in Cape Town, using raw samples of potato, papyrus rhizome and papyrus culm. The results show that papyrus rhizome and culm have more carbohydrates and fat than potato, but somewhat less protein. About 2 kg of raw papyrus rhizome could supply the daily energy requirements of a human adult. This would only be possible, however, if humans had the intestinal enzymes and bacteria to digest raw cellulose, as apes do. Humans do not have this capacity, of course, but it is not beyond the realm of possibility that an early hominin such as A. boisei did have it.

It is not our intention to suggest that A. boisei had a staple diet of papyrus, but to offer this plant from the permanent freshwater swamps as a strong candidate for a major role in its diet, along with other C₄ species of Cyperaceae that are tolerant of brackish water. In the first place, such a major role could not have been played by C₃-consuming animals. Modern humans are limited to about 20–50% protein- rich foods for their energy requirements. Excess protein consumption leads to protein poisoning with potentially fatal consequences. A. boisei clearly had a substantial dietary intake of C₄ plants. While grasses could have supplied part of this diet, particularly in the form of seeds, this dietary item is highly seasonal. Cyperaceae are perennials, available in all seasons in the vicinity of water.

Papyrus is a particularly good candidate for a C₄ plant diet, since it is such a prolific producer. As measured at Lake Naivasha in Kenya, it produces 6.3 kg (dry weight) per square metre per year, among the highest productivity recorded for natural ecosystems. It grows in shallow water and the whole plant can be pulled from the mud with some muscle power. While papyrus has not been identified among the fossil plants of Olduvai East, this is probably the result of a lack of preservation, not an absence of the species. Fossilized papyrus has not been identified at Peninj either, but there are dense stands of papyrus today, where the Peninj River flows into Lake Natron.

Two areas of investigation may be able to add substantially to a further understanding of the contrasting diets of H. habilis and A. boisei of Tanzania. The first is dental topographic analysis (e.g. ref. 25), to illuminate the dental wear and chewing behaviour of the two species. Such a study is already under way (P. Ungar, pers. comm.). The second is the stable carbon isotope analysis of early hominin specimens from Kenya and Ethiopia, which has not been attempted yet.

In Tanzania, the Department of Antiquities, the National Museums, and the Commission for Science and Technology granted permission to sample the five specimens of early hominins for isotopic analysis. The directors and personnel of the museums in Dar es Salaam and Arusha provided assistance during the sampling. In Botswana, David and Cathy Kays hosted the week-long stay of two of us in their touristic lodges at Jao and Kvetsnani in the Okavango Delta. In the Stable Light Isotope Facility in the Archaeology Department, University of Cape Town, technical assistance and advice were provided by John Lanham, Ian Newton, Matt Spötl and Julia Lee-Thorp. The field work and laboratory analyses were financially supported by Landon T. Clay of Boston, the National Research Foundation of South Africa, and the University of Cape Town. An anonymous reviewer provided useful editorial comment. We thank them all most heartily.

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### Table 2. Nutritional analysis$^*$ of raw rhizome and culm (base of stem) of papyrus (Cyperus papyrus) and raw potato tuber (Solanum tuberosum).

<table>
<thead>
<tr>
<th></th>
<th>Rhizome</th>
<th>Culm</th>
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<tr>
<td>Volume (ml)</td>
<td>150</td>
<td>300</td>
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<tr>
<td>Weight (g)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Carbohydrates (calculated) (g)</td>
<td>25</td>
<td>17</td>
</tr>
<tr>
<td>Fat (acid hydrolysis) (g)</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>Protein (g)</td>
<td>1.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Energy content$^†$ (kJ)</td>
<td>438</td>
<td>282</td>
</tr>
<tr>
<td>(kcal)</td>
<td>104</td>
<td>67</td>
</tr>
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</table>

$^*$Daily requirement (human adult): 2000 kcal/ 8400 kJ.

$^†$Analysis by Biofoodtek, CSIR, Cape Town.