

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

Nikolaas J. van der Merwe^{a*}, Fidelis T. Masao^b and Marion K. Bamford^c

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 then 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 ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values) in the Archaeology 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 CO_3). The stable carbon and oxygen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, relative to the PDB standard) of carbonates in tooth enamel are measured simultaneously in a mass spectrometer. Of these measurements, $\delta^{18}\text{O}$ 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 C_3 and C_4 components of an animal's diet (for review, see ref. 15). In the Tanzanian context at 1.8–1.5 Myr, C_3 plants eaten by herbivores included algae, woody bushes and trees, and some C_3 grasses from shaded environments; C_4 plants included grasses and some forbs and sedges. In the case of carnivores, the C_3 and C_4 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 C_3 and C_4 'end members' of the ecosystem in which they lived. This is done by measuring the $\delta^{13}\text{C}$ values of dedicated browsers (C_3 plant consumers) and grazers (C_4 plant consumers). A database of more than 100 $\delta^{13}\text{C}$ values is available for fossil animals from Olduvai East and West at c.1.8 Myr (van der Merwe, unpublished). The C_4 end member is represented by 19 specimens of the grazing genera *Connochaetes*, *Beatragus* and *Parmularius*, with a mean value $\delta^{13}\text{C}$ value of +2.0‰ (per mil). At the C_3 end of the spectrum, the most negative $\delta^{13}\text{C}$ values are for *Giraffa* sp. at -11.2‰ and *Deinotherium bozasi* (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 C_3 and C_4 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 $\delta^{13}\text{C}$ values for 40 grazing animals¹⁶ provide a C_4 end member of +2‰. In South Africa, estimates for C_3 and C_4 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‰;¹⁵ 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 C_3 and C_4 end members are relatively unimportant in calculating the C_4 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 $\delta^{13}\text{C}$ values, and individual fractionation factors, while the value for the C_4 dietary component may vary slightly with the different digestive strategies of different species.¹⁹

In order to compare the C_4 dietary components of Tanzanian and South African early hominins, it is necessary to use the C_3 and C_4 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

^aDepartment of Archaeology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.

^bUniversity of Dar es Salaam, Tanzania.

^cBernard 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,²⁰ for which C_3 and C_4 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 C_4 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 C_4 dietary component of *A. boisei*. This begs the question: what did *A. boisei* eat?

The foods with C_4 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 C_4 plants. Peters and Vogel,²¹ in considering the possible combinations of C_4 -based foods that could have produced the carbon isotope signatures of early hominins in South Africa, concluded that their access to edible C_4 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 C_4 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.²² 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 C_4 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 C_3 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 *Aeschynomene fluitans*, a floating leguminous plant, of which the leaves taste like lettuce; *Typha 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 C_4 plants, the rhizomes and culms of three other

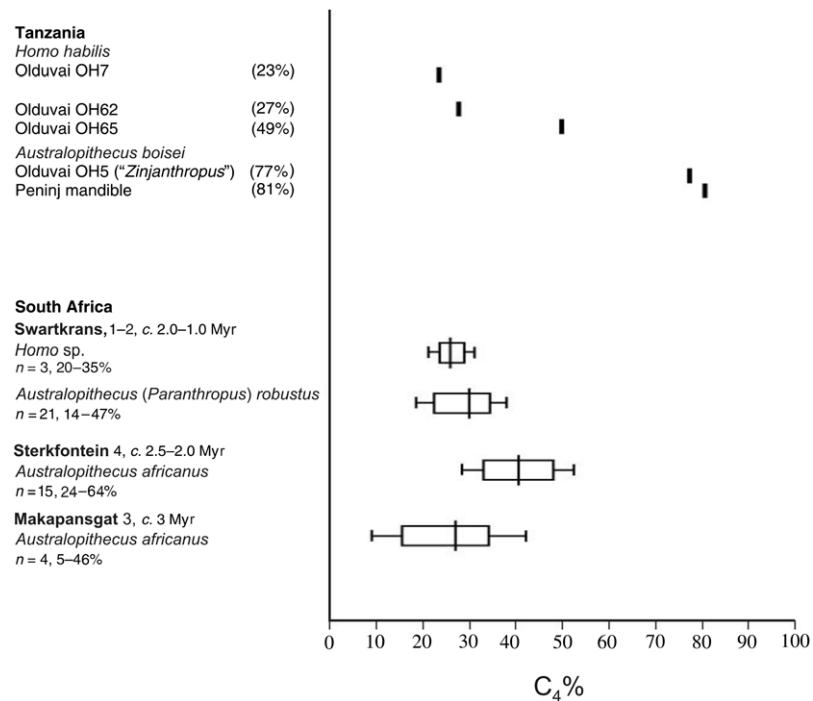


Fig. 1. The C_4 dietary components (C_4 %) of early hominins of Tanzania and South Africa. The results for individual specimens from Tanzania have been calculated from the $\delta^{13}\text{C}$ values reported in Table 1 and are given in the left-hand column for each specimen. For South African hominins, 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 C_4 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 C_4 dietary components for South African hominins, all the published carbon isotope values for Makapansgat,¹⁷ Sterkfontein,^{15,20} and Swartkrans^{10,13,20,26} have been used. Myr, million years ago.

Table 1. Stable carbon isotope ratios ($\delta^{13}\text{C}$ values) for tooth enamel of Tanzanian hominins, relative to PDB. Precision of repeated measurements was better than 0.1‰.

Lab. no.	Taxon and specimen	Tooth	Origin	$\delta^{13}\text{C}$ (‰)	C_4 % in diet
<i>Homo habilis</i>					
UCT7483	<i>Homo habilis</i> OH7 (type specimen)	LM ₂	Olduvai East	-8.8	23
UCT7481	OH62	LM ²	Olduvai East	-8.3	27
UCT7484	OH65	LM ³	Olduvai West	-5.2	49
<i>Australopithecus boisei</i>					
UCT7081	<i>Australopithecus boisei</i> OH5 (type specimen)	LM ²	Olduvai East	-1.2	77
UCT7483	Peninj mandible	LM ₂	Peninj	-0.7	81
C_3 end member (<i>Giraffa</i> sp., <i>Deinotherium bozasi</i>)					-12
C_4 end member (<i>Connochaetes</i> , <i>Beatragus</i> , <i>Parmularius</i>)					+2
					0
					100

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 C_4 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 2. Nutritional analysis* of raw rhizome and culm (base of stem) of papyrus (*Cyperus papyrus*) and raw potato tuber (*Solanum tuberosum*).

	Papyrus		Potato tuber
	Rhizome	Culm	
Volume (ml)	150	300	89
Wet weight (g)	100	100	100
Carbohydrates (calculated) (g)	25	17	18
Fat (acid hydrolysis) (g)	0.4	0.2	0.1
Protein (g)	1.0	0.5	2.1
Energy content [†] : (kJ)	438	282	332
(kcal)	104	67	79

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

[†]Analysis by Biofoodtek, CSIR, Cape Town.

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 C₄-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.²³ *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.²⁴ 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

tourist lodges at Jao and Kwetsani 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 Sponnheimer 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.

Received 29 February. Accepted 18 April 2008.

1. Leakey L.S.B. (1961). New finds at Olduvai Gorge. *Nature* **189**, 649.
2. Leakey L.S.B., Tobias P.V. and Napier J.R. (1964). A new species of genus *Homo* from Olduvai Gorge. *Nature* **202**, 7–9.
3. Tobias P.V. (1991). *Olduvai Gorge*. Vol. 4a and 4b: *The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge University Press, Cambridge.
4. Johansson D.C., Masao F.T., Eck G.G., White T.D., Walter R.C., Kimbel W.H., Asfaw B., Manega P., Ndessokia P. and Suwa G. (1987). A new partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* **327**, 205–209.
5. Blumenschein R.J., Peters C.R., Masao F.T., Clarke R.J., Deino A.L., Hay R.L., Swisher C.C., Stanisstreet I.G., Ashley G.M., McHenry L.J., Sikes N.E., van der Merwe N.J., Tactikos J.C., Cushing A.E., Deocampo D.M., Njau J.K. and Ebert J.I. (2003). Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. *Science* **299**, 1217–1221.
6. Leakey L.S.B. (1959). A new fossil skull from Olduvai Gorge. *Nature* **184**, 491–493.
7. Tobias P.V. (1967). *Olduvai Gorge*. Vol. 2: The cranium and maxillary dentition of *Australopithecus (Zinjanthropus) boisei*. Cambridge University Press, Cambridge.
8. Leakey L.S.B. and Leakey M.D. (1965). Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. *Nature* **202**, 5–7.
9. Isaac G.L. (1965). The stratigraphy of the Peninj Beds and provenience of the Natron australopithecine mandible. *Quaternaria* **7**, 101–130.
10. Sponnheimer M., Passey B.H., de Ruiter D.J., Gautelli-Steinberg D., Cerling T.E. and Lee-Thorp J.A. (2006). Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science* **314**, 980–982.
11. Lee-Thorp J.A. and van der Merwe N.J. (1987). Carbon isotope analysis of fossil bone apatite. *S. Afr. J. Sci.* **83**, 712–715.
12. Lee-Thorp J.A. and van der Merwe N.J. (1991). Aspects of the chemistry of fossil and modern biological apatites. *J. Archaeol. Sci.* **18**, 343–354.
13. Lee-Thorp J.A., Thackeray J.F. and van der Merwe N.J. (2000). The hunters and the hunted revisited. *J. Hum. Evol.* **39**, 565–576.
14. Sponnheimer M. and Lee-Thorp J.A. (1999). Oxygen isotope ratios in enamel carbonate and their ecological significance. *J. Archaeol. Sci.* **26**, 723–728.
15. van der Merwe N.J., Thackeray J.F., Lee-Thorp J.A. and Luyt J. (2003). The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *J. Hum. Evol.* **44**, 581–597.
16. van der Merwe N.J. (in press). Isotopic ecology and diets of fossil fauna from Maritanane, Peninj, West Lake Natron. In *The Archaeology of Early Humans at Peninj (Tanzania), Hominid Adaptation to an Early Pleistocene Open Savanna*, eds L. Alcalá, L. Luque and M. Dominguez-Rodrigo. Brill, Boston.
17. Sponnheimer M. and Lee-Thorp J.A. (1999). Isotopic evidence for the diet of an early hominin, *Australopithecus africanus*. *Science* **283**, 368–370.
18. Lee-Thorp J.A. and van der Merwe N.J. (1993). Stable carbon isotope studies of Swartkrans fossils. In *Swartkrans, a Cave's Chronicle of Early Man*, ed. C.K. Brain, pp. 251–256. *Transvaal Museum Monographs*, Pretoria.
19. Passey B.H., Robinson T.F., Ayliffe L.K., Cerling T.E., Sponnheimer M., Dearing M.D., Roeder B.L. and Ehleringer J.R. (2005). Carbon isotopic fractionation between diet, breath, and bioapatite in different mammals. *J. Archaeol. Sci.* **32**, 1459–1470.
20. Sponnheimer M., Lee-Thorp J.A., de Ruiter D., Codron D., Codron J., Baugh A.T. and Thackeray F. (2005). Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *J. Hum. Evol.* **48**, 301–312.
21. Peters C.R. and Vogel J.C. (2005). Africa's wild C₄ plant foods and possible early hominin diets. *J. Hum. Evol.* **48**, 219–236.
22. Hay R.L. (1976). *The Geology of Olduvai Gorge*. University of California Press, Berkeley.
23. Noli D. and Avery G. (1988). Protein poisoning and coastal subsistence. *J. Archaeol. Sci.* **15**, 395–401.
24. Jones M.B. and Muthuri F.M. (1997). Standing biomass and carbon distribution in a papyrus (*Cyperus papyrus* L.) swamp on Lake Naivasha, Kenya. *J. Trop. Ecol.* **13**, 347–356.
25. Ungar P. (2004). Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J. Hum. Evol.* **46**, 605–622.
26. Lee-Thorp J.A., van der Merwe N.J. and Brain C.K. (1994). Diet of *Australopithecus robustus* and associated fauna from Swartkrans. *J. Hum. Evol.* **27**, 361–372.