Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna

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DATES:
Received: 12 Apr. 2013
Revised: 24 Jul. 2013
Accepted: 22 Aug. 2013

KEYWORDS:
carbon isotopes; oxygen isotopes; Olduvai fossils; moisture sources; vertebrate ecology

HOW TO CITE:
Van der Merwe NJ. Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. S Afr J Sci. 2013;109(11/12), Art. #2013-0105, 14 pages. http://dx.doi.org/10.1590/sajs.2013/20130105

Light stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) of tooth enamel have been widely used to determine the diets and water sources of fossil fauna. The carbon isotope ratios indicate whether the plants at the base of the food web used C_3 or C_4 photosynthetic pathways, while the oxygen isotope ratios indicate the composition of the local rainfall and whether the animals drank water or obtained it from plants. The contrasting diets of two early hominin species – *Homo habilis* and *Paranthropus boisei* – of ca 1.8 Ma (million years ago) in Tanzania were determined by means of stable carbon isotope analysis of their tooth enamel in a previous study. The diets of two specimens of *P. boisei*, from Olduvai and Peninj, proved to be particularly unusual, because 80% of their carbon was derived from C_4 plants. It was suggested that their diet consisted primarily of plants, with particular emphasis on papyrus, a C_4 sedge. The dominance of C_4 plants in the diet of *P. boisei* is a finding supported in another study of 22 specimens from Kenya. The isotopic ecology and diets of fossil fauna that were present at the same time as the two fossil hominin species are described here, in order to provide a fuller understanding of their contrasting diets and of the moisture sources of their water intake. This information was then compared with the isotopic composition of modern fauna from the same region of Tanzania. The carbon isotope ratios for both fossil and modern specimens show that the habitats in which these faunal populations lived were quite similar – grassland or wooded grassland. They had enough bushes and trees to support a few species of browsers, but most of the animals were grazers or mixed feeders. The oxygen isotope ratios of the fossil and modern fauna were, however, very different, suggesting strongly that the source of moisture for the rain in the Olduvai region has changed during the past 1.8 million years.

Introduction

The purpose of this article is to provide isotopic information on the ecology and diets of fossil fauna from Olduvai Gorge Beds I and II at ca 1.8 Ma, in order to provide an ecological context for the diets of two species of early hominins. Recent isotopic analyses of the tooth enamel of *Homo habilis* and *Paranthropus boisei* (formerly *Zinjanthropus boisei*, also *Australopithecus boisei*) showed that the two species had distinctly different diets.[1-3]

Three specimens of *Homo habilis* from Olduvai had, respectively, 23%, 27% and 49% of carbon derived from C_4 plants, much like early hominins from South Africa[4-6]; their diets probably included grass-eating animals and/or insects. However, two specimens of *P. boisei* from Olduvai and Peninj had 77% and 81% of carbon derived from C_4 plants. Because modern humans are limited to about 20–50% protein-rich foods for their energy requirements,[7] it was suggested that the diet of *P. boisei* included a large component of C_4 plants. As grasses, especially edible seeds, are highly seasonal at latitudes applicable to Olduvai, it was also suggested that the C_4 sedge *Cyperus papyrus*, which was presumably available in the freshwater swamps at Lake Olduvai and Lake Natron (Peninj), may have been a major component in the diet of *P. boisei*. The very high contribution of C_4 plants to the diet of this hominin has been confirmed by the isotopic analysis of 22 individuals from sites in Kenya that stretch over 700 km of the Rift Valley.[3] The authors of the latter study suggested that *P. boisei* had a diet that comprised mostly C_4 plants, without specifying whether these were grasses or sedges. An online comment on their article by Lee-Thorp[8] supports the opinion that sedges were predominant in the diet. Recent publications provide further evidence to put these early hominin diets in context.[9,10]

An assessment of the isotopic ecology at Peninj and Olduvai during the presence of *P. boisei* cannot settle the argument about grasses and sedges in *P. boisei*'s diet, but it can illuminate whether the environment was dominated by C_4 plants and their consumers. This assessment is of particular importance at Olduvai around 1.8 Ma, for which the isotope values of the two hominins are available. In East Africa, C_4 plants appeared in the Late Miocene and continued through the Pliocene,[11-15] but did not become dominant until ca 1.8 Ma.[16] At Olduvai, the carbon isotopes in palaeosol carbonates indicate that C_4 plants made up about 40–60% of the biomass during the time of Beds I and II,[17] but a preliminary study of the carbon isotopes in tooth enamel of fossil fauna indicate a much higher C_4 component.[16,18] An assessment of the isotopic ecology at Peninj was undertaken by measuring the carbon and oxygen isotopes in the tooth enamel of 40 specimens of fossil fauna from the Maritinane Type Section.[2] These fossils were all grazers and the carbon isotopes were closely similar to those of modern fauna of related species from the modern Serengeti. The environment was essentially open grassland with very few trees. However, the fossil specimens were some 1.3 million years old, so the results do not provide information about the ecology of Olduvai at ca 1.8 Ma. It was noted that the $\delta^{18}O$ values of the Peninj fossils were distinctly negative, relative to the Vienna Pee Dee Belemnite (VPDB) standard, while those of the modern fauna were all positive. It was suggested that the moisture source of rain in this region had presumably changed during the past 1.3 million years; this suggestion is addressed in detail here.

For this purpose, tooth enamel samples were obtained from 145 specimens of fossil fauna from Olduvai Gorge Middle Bed I (ca 1.785–1.83 Ma) and Lowermost Bed II (ca 1.75–1.83 Ma) and their $\delta^{13}C$ and $\delta^{18}O$ values were measured. These values were then compared with those of 77 modern animals from six wildlife reserves, primarily Serengeti and Maswa, but also Lobo, Lukwati, Ugalla and Selous (Figure 1). Their carbon and oxygen isotope ratios were measured to illuminate their diets and water sources.

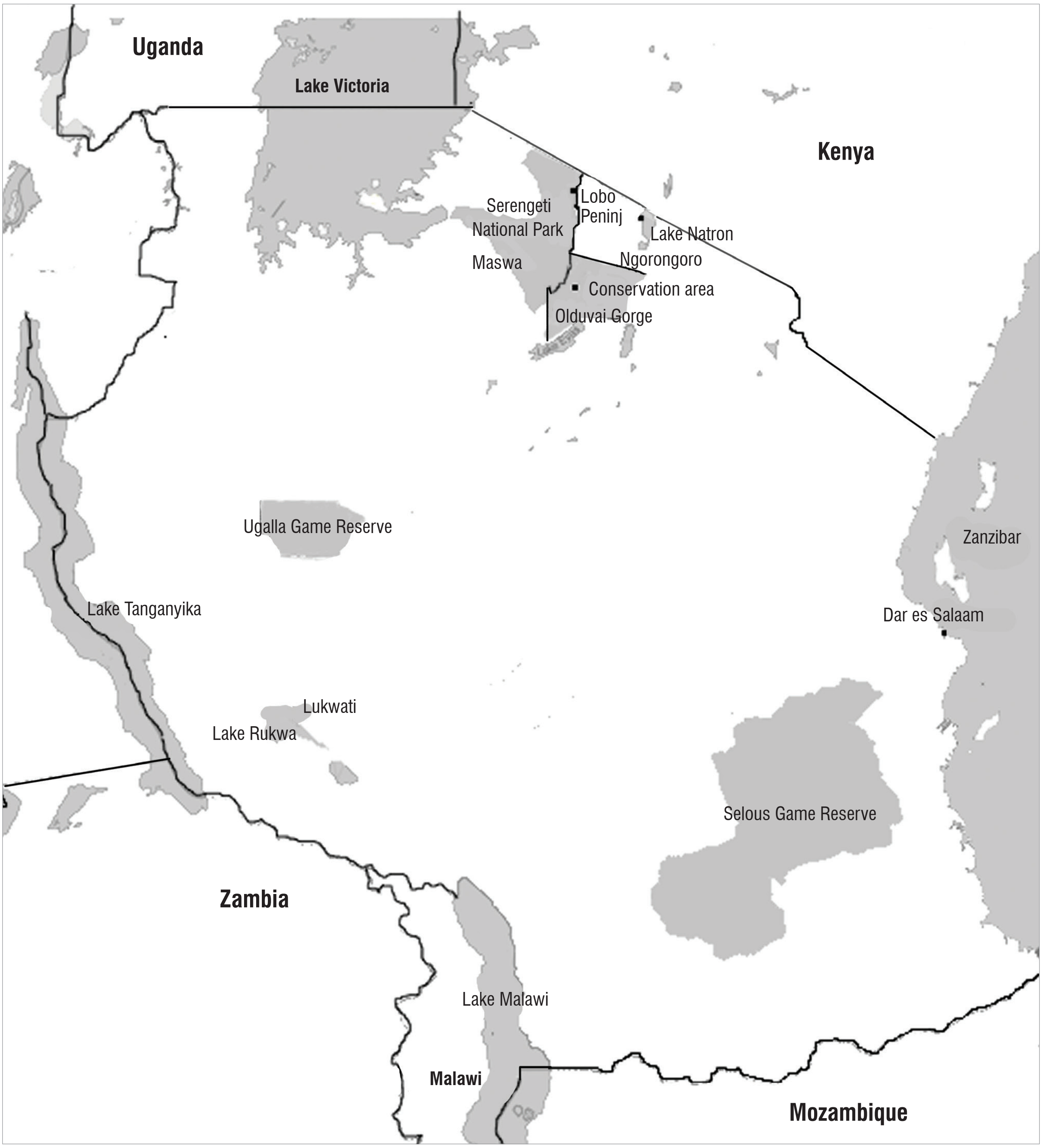

Figure 1: Map of Tanzania showing the six wildlife reserves from which modern faunal specimens were collected, as well as Olduvai and Peninj.

Tooth enamel and stable light isotopes

The assessment of prehistoric diets and environments by means of isotopic analysis of bone has been developed over the past 30 years and is widely used in archaeology[19-21] (for review see Van der Merwe[21]). In the early development of this method, the major interest involved $^{13}C/^{12}C$ ratios ($\delta^{13}C$ values) in bone collagen, which provide a measure of the proportion of C_3 and C_4 plants at the base of the food web. However, collagen in bone has a limited lifetime, especially in hot and humid environments where organic materials deteriorate rapidly. The oldest hominin collagen specimens that have been analysed isotopically were those of Neanderthals from cold, dry caves.[22,23] The fossilised faunal specimens from Olduvai contain no collagen, but carbon and oxygen isotopes can be measured in the mineral phase of their skeletons. The earliest measurements on bone apatite were done on fossil bone,[24,25] but tooth enamel has proved to be the most dependable material for isotopic analysis.[26,27] Tooth enamel is highly crystalline and resists alteration by carbonates in groundwater. Contaminating carbonates may precipitate in cracks in the tooth enamel, but this material is much more soluble than tooth enamel and is readily removed with dilute acetic acid.

Tooth enamel is a biological apatite with about 3% carbonate. With appropriate pretreatment, the carbon and oxygen isotope ratios of the carbonate can be measured with confidence to provide dietary information. The carbon isotope ratio is an average of the plants at the base of the food web, acquired by herbivores from eating the plants and passed along the food chain to omnivores and carnivores, with some digestive differences between different species.[28] The oxygen isotope ratio is a measure of the body water of an animal, acquired from plant water or from drinking water and is altered by the thermophysiology of the animal. The oxygen isotope ratio can contribute to dietary and environmental reconstructions[9,29,30] and is particularly indicative of changes in humidity and aridity.[31-33]

To reach dietary conclusions based on carbon isotope ratios, it is necessary to determine the C_3 and C_4 end members for a given time and place. This determination is most readily achieved by measuring the tooth enamel $\delta^{13}C$ values of dedicated browsers and grazers. Giraffes, for example, rarely eat anything but C_3 leaves of trees and shrubs, while alcelaphine antelope like the wildebeest concentrate on C_4 grasses. At this point in time, dedicated browsing herbivores of the South African interior (whose tooth enamel the Cape Town laboratory has often analysed) have mean $\delta^{13}C$ values of -14.5‰, while dedicated grazers have mean values of -0.5‰. These values can be altered by changes in climate and in the atmosphere. The 'industrial effect' of the past 200 years, for example, substantially increased the CO_2 content of the atmosphere, as a result of fossil fuel burning, resulting in the $\delta^{13}C$ value of the atmosphere (and that of all plants) becoming more negative by 1.5‰. The $\delta^{13}C$ values of all modern specimens must consequently be corrected by adding 1.5‰ to the measured number. Climatic changes that alter $\delta^{13}C$ values of plants include increased humidity, which may make the $\delta^{13}C$ values of C_3 plants (but not C_4) more negative by 2‰.[34] Tropical forests provide an extreme example in this regard – their C_3 plants (they have no C_4 plants) have $\delta^{13}C$ values as much as 10‰ more negative than those of plants growing in the open; this difference results from high humidity, low light and, especially, from recycled CO_2 produced by rotting leaf litter on the forest floor.[35] In contrast, the $\delta^{13}C$ values may become more positive as a result of aridity and bright sunlight,[36,37] while C_4 plants may respond with slightly more negative values, as a result of the increased occurrence of enzymatic C_4 subtypes that are adapted to such conditions.

The approximate ratio of C_3 and C_4 plants in the diet of herbivores can be arrived at by interpolating between the C_3 end member (100% C_3 diet) and C_4 end member (100% C_4 diet) of the ecosystem under study, although there are some slight differences between different species that have the same diets.

Oxygen isotope ratios in tooth enamel can help to understand certain elements of a local habitat. The primary source of oxygen in biological apatite is from water (drinking water or water in food) and from oxygen bound in food. The light ^{16}O isotope evaporates more readily than the heavy ^{18}O isotope, while the latter precipitates more readily. These characteristics have produced such localised effects as the water in modern East African lakes being enriched by 5–10‰ compared to the waters flowing into them.[17] Ultimately, the ^{18}O content of water in an area depends on precipitation – or meteoric water ($\delta^{18}O_{mw}$) – which decreases with distance from the source of moisture (an ocean or lake), increasing latitude, increasing altitude and decreasing temperature.[38-42] An example of the different moisture sources can be seen in East Africa, where $\delta^{18}O$ values of waters in Kenya and Ethiopia differ by about 2–3‰.[43] The $\delta^{18}O$ value of leaf water derived from the same water source also varies with aridity, because of evapotranspiration.

The integrity of $\delta^{13}C$ and $\delta^{18}O$ values in tooth enamel for a given time and place can best be judged by observing the pattern of results for all the animal species in the biome. A considerable database for the Plio-Pleistocene of Africa is available by now and can be used to judge the results of a given study. Browsing animals (C_3 plant feeders) will have distinctly more negative $\delta^{13}C$ values than grazers (C_4 plant feeders), with the most dedicated browsers and grazers differing by about 14‰. There is also a distinct pattern between different species of grazers, depending on the different amounts of C_3 plants like forbs that are included in their diets. Wherever they have been compared, specimens of *Damaliscus* spp. (e.g. the tsessebe and topi) have more positive $\delta^{13}C$ values than *Connochaetes* spp. (wildebeest), which, in turn, have more positive values than *Equus* spp. (zebra). For oxygen isotopes, $\delta^{18}O$ values of hippos are usually more negative than those of equids, because they drink surface water that is closest to meteoric water and feed at night, when humidity increases and plant $\delta^{18}O$ decreases.[44]

Materials and methods

Samples of tooth enamel used for isotopic analysis in this study were removed from the tooth specimens at their location of storage. In the case of Olduvai Beds I and II, this sampling was done at the National Museum of Natural History in Arusha and at the Olduvai field station (Mary Leakey's old field camp, which has been expanded). Most of the teeth from Olduvai Beds I and II had been excavated by the Olduvai Landscape Palaeoanthropology Project (OLAPP) – an international group of researchers who have been working at Olduvai during the mid-year field season since 1989.[45] Specimens from the OLAPP collections can be identified in Tables 1 and 2 on the basis of their catalogue numbers, which are in the format 95/43:156 (excavated 1995, trench 43, number 156). Some specimens from Mary Leakey's collection, which is stored at the Olduvai field station, were also sampled. These are from Bed II (Table 2), excavation sites FLK N and HWKE. In total, 145 faunal specimens were sampled from the collections of Olduvai Middle Bed I (ca 1.785–1.83 Ma) and Lowermost Bed II (ca 1.75–1.78 Ma).

The modern samples from the Serengeti National Park, Maswa Game Reserve (southern Serengeti), Lobo (northeast Serengeti) and Selous Game Reserve (southeast Tanzania) were obtained from collections at Seronera, the headquarters of Serengeti National Park, and from some of the other ranger stations in the park. A few specimens from Lukwati and Ugalla Game Reserves were sampled in Arusha at a taxidermy shop and at the Rock Art Centre. A collection of 77 modern bone specimens, primarily from Serengeti National Park which adjoins Olduvai, was also assembled (120 measurements).

Samples were removed from tooth specimens by using a variable speed drill with a dental diamond drill tip of 0.5-mm diameter. A sample of 3 mg enamel powder is sufficient for at least two isotopic analyses. This amount is the equivalent of about two sugar grains; if it is removed from a broken enamel edge, the sampling scar is usually invisible. By moving the drill tip along an enamel edge, broken along the length of a tooth, seasonal variations (particularly in ^{18}O) are averaged. The enamel powder was gathered on smooth weighing paper and poured into a small centrifuge vial with snap lid, in which all the subsequent chemical pretreatment was carried out at the Stable Light Isotope Facility of the University of Cape Town. The powder was pretreated with 1.5–2.0% sodium hypochlorite (to remove organic materials and humic acids), rinsed with water, and then reacted for 15 min with 0.1 M acetic acid (to remove readily dissolved carbonates).

After washing and drying, 1 mg of the enamel was weighed into an individual reaction vessel of a Kiel II autocarbonate device (Thermo Electron Corporation, Bremen, Germany). The powder sample was reacted at 70°C with 100% phosphoric acid, which produces CO_2 from the carbonate in the enamel. This sample gas was cryogenically distilled and its isotope ratios were measured in a Finnegan MAT 252 ratio mass spectrometer (Thermo Electron Corporation, Bremen, Germany). The $\delta^{13}C$ and $\delta^{18}O$ were calibrated against the international VPDB carbonate standard by using a calibration curve established from National Bureau of Standards standards 18 and 19, as well as by inserting internal laboratory standards of 'Lincoln limestone' and 'Carrara 2 marble' at regular intervals in the autocarbonate device. The precision of replicate analyses was better than 0.1‰.

Results

The $\delta^{13}C$ and $\delta^{18}O$ values for fossil fauna from Olduvai West Middle Bed I (Table 1) and Olduvai East Lowermost Bed II (Table 2) are combined in Figure 2 to illustrate the faunal community in the Olduvai region at ca 1.8 Ma. These values can be compared with the isotope ratios of modern fauna from the adjoining Serengeti National Park, plus some specimens from Maswa, Lobo, Ugalla, Lukwati and Selous wildlife reserves (Table 3, Figure 3). The $\delta^{13}C$ and $\delta^{18}O$ values of the fossil and modern fauna are compared in Figures 4 and 5, respectively.

Table 1: Carbon and oxygen stable isotope ratios in tooth enamel of fossil fauna from Olduvai West Middle Bed I. [Stratigraphy: above Tuff 1B, 1.83 Ma; below 1.785 Ma].[46]

UCT no.	TZ no.	OLAPP no. (year, trench, no.)	Tooth	$\delta^{13}C$	$\delta^{18}O$
ORDER: CARNIVORA					
FAMILY: CANIDAE					
Species: *Canis mesomelas* (black-backed jackal)					
UCT7059	TZ150	96/57:862	LP_4	-7.3	-4.4
ARTIODACTYLA					
SUIDAE					
Phacochoerus modestus (cf. warthog)					
UCT7200			M_3	0.1	-1.4
UCT7186			M^2	-0.3	0.1
	Mean (s.d.), *n*=2			-0.12(0.29)	-0.65(0.01)
BOVIDAE					
Sub-family: Reduncinae					
Kobus sp.					
UCT7056	TZ147	95/57:536	RM_3	-2.0	-1.4
UCT7057	TZ148	95/57:626	$LM^{1/2}$	-5.0	-7.3
UCT7058	TZ149	95/57:621	$RM^{1/2}$	-3.8	-3.8
	Mean (s.d.), *n*=3			-3.6(1.54)	-4.17(2.95)
	[These three specimens could be from one animal]				
Hippotraginae					
Hippotragus gigas					
UCT7055	TZ146	96/65:443	RM_3	-0.3	-3.0
Antelopinae					
Gazella/ Aepyceros (cf. large morph Grant's gazelle/ impala)					
-1.54	TZ144	96/65:121	M_3	0.1	-4.4
UCT7054	TZ145	96/57A:19	$LM^{1/2}$	-2.0	-1.2
		Mean (s.d.), n=2		-1.76(0.30)	-2.79(2.25)
Gazella/ Antidorcas (cf. Thomson's gazelle/ springbok)					
UCT7049	TZ140	96/65:287	$LM^{1/2}$	-3.5	-3.1
UCT7050	TZ141	97/88:204	$RM_{1/2}$	0.7	-3.0
UCT7051	TZ142	96/65:481	RM_3	-4.1	-4.6
UCT7052	TZ143	95/57:863	$RM_{1/2}$	-1.9	-2.2
	Mean (s.d.), *n*=4			-2.22(1.85)	-3.21(0.97)
Alcelaphinae					
Megalotragus sp.					
UCT7037	TZ128	96/65:540	$LM^{1/2}$	-1.6	-3.7
Repeat				-0.9	-3.5
UCT7038	TZ129	96/57A:18	$M^{1/2}$	-0.9	-4.8
UCT7039	TZ130	96/65:42	$LM^{1/2}$	1.7	-4.0
UCT7040	TZ131	96/65:480	M^x	0.2	-5.4
	Mean (s.d.), *n*=4			-0.29(1.31)	-4.28(0.79)
Beatragus/ Connochaetes (cf. wildebeest)					
UCT7045	TZ136	96/65:148	$RM^{1/2}$	0.3	-5.7
UCT7046	TZ137	96/65:438	$M^{1/2}$	-1.1	-3.4
Repeat				-1.1	-4.4
Repeat				-1.1	-3.9
UCT7043	TZ132	96/88:67W	$M^{1/2}$	0.2	-6.9
UCT7044	TZ133	96/88:73W	$RM^{1/2}$	0.2	-4.0
	Mean (s.d.), *n*=4			-0.11(0.66)	-5.01(1.6)
Parmularius sp.					
UCT7041	TZ132	96/65:286	$LM^{1/2}$	1.26	-2.50
UCT7042	TZ133	96/65:349	M^x	1.09	-1.63
	Mean (s.d.), *n*=2			+1.17(0.12)	-2.06(0.61)
	Mean (s.d.), *n*=8 (all alcelaphines)			+0.14(1.06)	-4.21(1.44)
SQUAMATA					
CROCODYLIDAE					
Crocodylus niloticus					
UCT7032	TZ123	96/57A:312		-2.7	-5.1
UCT7033	TZ124	96/57A:313		-3.1	-5.0
UCT7034	TZ125	96/57A187		-2.2	-5.0
UCT7036	TZ127	96/57A:75		-3.3	-6.3
	Mean (s.d.), *n*=4			-2.82(0.48)	-5.36(0.64)
	[These four specimens could be from one animal]				
UCT7035	TZ126	96/57:491-2		-4.4	-7.6
	Mean (s.d.), *n*=5 (all crocodiles)			-3.14(0.82)	-5.81(1.15)
Mean and standard deviation of $\delta^{18}O$ for 27 animals					-4.95(-1.83)

28 measurements from Olduvai West + 2 from Olduvai East are included in the table.

$\delta^{13}C$ and $\delta^{18}O$ values for individual specimens have been rounded off to 0.1 but mean and s.d. are based on original measurements.

In the column headings, the UCT numbers refer to the database of the Stable Light Isotope Facility in the Archaeology Department at the University of Cape Town; TZ numbers are from the author's field collection of specimens from Tanzania; and OLAPP numbers are from the excavations of the Olduvai Landscape Palaeoanthropology Project.

Table 2: Carbon and oxygen stable isotope ratios in tooth enamel of fossil fauna from Olduvai East Lowermost Bed II (plus three hippos from Lower Bed II). [Stratigraphy: overlying Tuff 1F: 1.75–1.78 Ma].

UCT no.	TZ no.	OLAPP no. (year, trench, no.)	Tooth	$\delta^{13}C$	$\delta^{18}O$
ORDER: CARNIVORA					
Family: CANIDAE					
Hyaenid					
UCT7016	TZ107	95/43:157	LP_3	-1.3	-5.7
UCT7017	TZ108	89/3:106	RP_3	-2.5	-5.8
	Mean (s.d.), *n*=2			-1.9(0.85)	-5.73(0.03)
Acinonyx sp. (cf. cheetah)					
UCT7018	TZ109	95/44:158	LI_3	-2.0	-4.8
Lycaon sp. (cf. wild hunting dog)					
UCT7019	TZ110		LP_2	-2.4	-7.88
UCT7020	TZ111		LM_1	-1.9	-6.66
	Mean (s.d.), *n*=5			-2.02(0.48)	-6.168(1.15)
PROBOSCIDEA					
ELEPHANTIDAE					
Elephas recki (grazing elephant)					
UCT9936	TZ179	HWK E/104.4 L1	Juvenile?	2.3	-1.8
		GRID3A			
UCT9937	TZ180	HWK E/104.4L1	Deciduous	1.3	-2.0
UCT9937	TZ180F	HWK E/104.4L1	Fragments of TZ180	0.4	-2.7
	Mean (s.d.), *n*=3			+1.3(1.0)	-2.2(0.5)
Deinotherium bozasi					
UCT9938	TZ181	HWK E/104.4L1	Fist size tooth	-11.1	-4.4
		Grid 3A:35			
UCT9938	TZ181	Repeat measurement		-11.0	-4.3
				-11.1	-4.3
UCT9939	TZ182	HWK E/104.4L1:36	Probably same animal as TZ181	-10.2	-5.8
UCT9939	TZ182	Repeat measurement		-10.4	-5.7
	Mean (s.d.), *n*=4			-10.68(0.42)	-5.04(0.83)
	Mean (s.d.), *n*=2 animals			-10.76(0.4)	-4.9(0.78)
PERISSODACTYLA					
EQUIDAE					
Equus olduwayensis					
UCT7561	TZ59	94/34:474	P_4/M_1	0.5	-2.0
UCT7563	TZ61	94/27:47	M^x	0.2	-2.8
UCT7564	TZ62	94/27:47	M^x	-0.6	-2.3
TZ61 and TZ62 are the same tooth; mean:				-0.4	-2.6
UCT7565	TZ63	94/34:222	M_3	-0.2	-2.5
UCT7566	TZ64	94/34:780	M_1	1.4	-1.9
UCT7568	TZ65	94/53:85		1.0	-1.8
UCT7569	TZ66	95/44:1508	M_3	-0.8	-3.7
UCT7573	TZ70	94/21:229	M^x	0.7	-3.3
UCT7575	TZ72	94/34:230		-1.7	-3.0
	Mean (s.d.), *n*=8			+0.01(0.9)	-2.59(0.6)
Equus olduwayensis?					
UCT9940	TZ184	HWK E/104.2L8	M^x	2.7	-3.1
Equid (no species identification)					
UCT9941	TZ185	HWK E/104.4L1:7		3.0	1.1
Hipparion sp.					
UCT7572	TZ69	94/39:4	M_3	1.0	-5.3
UCT7001	TZ92	89/3:105	LP_4/M_2	-1.8	-4.5
	Mean (s.d.), *n*=2			-0.4(2.0)	-4.9(0.6)
Ambiguous (small morph)					
UCT7559	TZ57	95/43:496	M^x	-1.2	-2.8
UCT7560	TZ58	95/43:644	M^x	0.9	-2.1
UCT7562	TZ60	94/21:302	I	-0.4	-3.8
UCT7570	TZ67	95/43:655	M^3	1.9	-1.7
UCT7571	TZ68	95/43:?		1.2	-4.0
UCT7574	TZ71	95/43:645	M^x	-0.2	-2.8
	Mean (s.d.), *n*=6			+0.37(1.16)	-2.9(0.9)
	All equids, *n*=18			0.36(1.32)	-2.75(1.30)
ARTIODACTYLA					
HIPPOPOTAMIDAE					
Hippopotamus gorgops					
UCT7180	TZ01	94/21:321-26	?	1.8	-6.2
UCT7199	TZ02	95/43:650	$P^{3/4}$	1.4	-6.0
UCT7239	TZ03	94/34:5	?	0.9	-4.3
UCT7185	TZ04	95/45:283	P/M	-0.8	-5.4
UCT7225	TZ05	94/34:18	?	1.7	-3.8
UCT7423	TZ06	94/21:220	?	0.6	-2.4
UCT7181	TZ07	94/34:420	Tusk	-0.8	-4.2

Continued on next page

UCT no.	TZ no.	OLAPP no. (year, trench, no.)	Tooth	δ13C	δ18O
UCT6982	TZ73	97/98:36	?	0.5	-5.1
	Mean (s.d.), *n*=8			+0.66(1.0)	-4.7(1.2)
LOWER BED II					
Hippopotamus gorgops					
UCT9952	TZ196	HWK E/104.4	Canine	2.2	-7.2
		GRID 1C, L1:25			
UCT9953	TZ197	HWK E/104.4	M_3	0.6	-5.7
		GRID 1A, L1:37			
UCT9954	TZ198	HWK E/104.4	M_2?	-0.9	-3.6
		GRID 1B, L1:11			
UCT9954	Repeat			-0.8	-3.8
Average UCT9954				-0.85	-3.7
	Mean (s.d.), *n*=3			1.64(1.5)	-5.53(1.7)
SUIDAE					
Phacochoerus modestus					
UCT7196	TZ14	94/27:321	P_4	-1.5	-3.7
UCT6987	TZ78	94/35:16	?	-2.0	-2.9
UCT6988	TZ79	95/44:331-2	?	-1.1	-4.7
UCT7548	TZ47	94/27:48	RC	-1.1	-2.4
UCT7547	TZ46	94/27:48	LC	-1.5	-3.1
UCT7549	TZ48	94/27:48		0.0	-1.8
[TZ46–48 are from the same animal; means -0.9, -2.4]					
	Mean (s.d.), *n*=4			-1.4(0.5)	-3.4(1.0)
Kolpochoerus limnetes					
UCT7191	TZ08	95/45:327	?	-1.4	-2.3
UCT7428	TZ12	95/45:328	?	-0.9	-2.8
UCT6990	TZ81	95/45:202	M_3	-0.6	-3.1
	Mean (s.d.), *n*=3			-1.0(0.4)	-2.7(0.4)
[These three teeth from trench 45 could be from the same animal]					
Kolpochoerus afarensis					
UCT7230	TZ10	95/44:1509	?	-0.5	-3.0
UCT7240	TZ11	95/43:824	M^1	-1.9	-3.2
UCT6992	TZ83	95/44:659	P^4	-2.5	-7.0
UCT6993	TZ84	95/44:1516	LM^1	-3.1	-6.5
UCT6994	TZ85	97/44:670	RP^4	-3.1	-6.0
UCT6995	TZ86	97/44:1511	RM^1	-2.2	-7.0
UCT6996	TZ87	97/44:1510	?	-0.5	-5.4
UCT6997	TZ88	97/100:169	P^4	-2.2	-5.3
	Mean (s.d.), *n*=8			-2.0(1.0)	-5.4(1.6)
[Teeth from Trench 44 could be from the same animal]					
BOVIDAE					
Reduncinae					
Kobus sp. (cf. waterbuck)					
UCT7015	TZ106	95/43:662	$LM^{1/2}$	-0.6	-4.4
Tragelaphinae					
Tragelaphus strepsiceros (greater kudu)					
UCT6983	TZ74	89/11:45	RM^3	-2.4	-0.3
UCT6984	TZ75	89/11:41-46	LM_2	-5.7	-0.1
Tragelaphus scriptus (bushbuck)					
UCT6985	TZ76	94/43:196	LM_1	-5.7	0.6
Tragelaphus oryx (eland)					
UCT7237	TZ21	94/24:12	M^x	-4.2	-2.2
Tragelaphus sp. (no species identification)					
UCT7201	TZ20	94/21:104 ID?	M?	-2.9	-3.8
UCT76986	TZ77	94/23:73	M_x	-9.2	0.3
	Mean (s.d.), *n*=6			-5.0(2.5)	-1.0(1.7)
Alcelaphinae					
Connochaetes / *Beatragus* (cf. wildebeest)					
UCT7193	TZ30	95/43:330	$M^{1/2}$	3.3	-2.1
UCT7223	TZ31	94/34:284	M^x	2.3	-2.5
UCT7188	TZ35	95/50:2	M^x	2.1	-1.2
UCT7426	TZ39	95/44:332	P_4	1.2	-3.4
UCT7224	TZ41	95/43:940	P4	2.4	-1.4
UCT7234	TZ42	95/43:331	M_3?	4.0	-3.8
UCT7422	TZ43	95/45:198	M_3	3.5	-0.1
UCT7043	TZ134	96/88:67W	$M^{1/2}$	0.2	-6.9
UCT7044	TZ135	96/88:73W	$RM^{1/2}$	0.2	-4.0
	Mean (s.d.), *n*=9			+2.13(1.38)	-2.82(2.0)
Parmularius sp.					
UCT6981	TZ33	94/34:79	$LM_{1/2}$	2.0	-2.3
UCT7198	TZ36	95/50:11	M_3	2.1	-1.3
UCT7228	TZ37	95/44:325	$M_{1/2}$	2.5	-4.2
UCT7238	TZ38	95/44:334	$P_{3/4}$	3.8	-1.1

Continued on next page

UCT no.	TZ no.	OLAPP no. (year, trench, no.)	Tooth	δ¹³C	δ¹⁸O
UCT7184	TZ40	95/21:101-102	$M_{1/2}$	0.9	-1.6
UCT7545	TZ44	95/50:10	$M_{1/2}$	1.3	-1.3
UCT6999	TZ90	95/44:21	$RM_{1/2}$	1.1	-1.1
UCT7000	TZ91	95/43:142	$RM_{1/2}$	1.7	-4.5
	Mean (s.d.), *n*=8			+1.9(1.0)	-2.2(1.4)
Megalotragus?					
UCT9942	TZ186	Tr104.2L8C	$M^{1/2}$	2.7	-3.1
Hippotraginae					
Hippotragus gigas (cf. roan, sable antelope)					
UCT7002	TZ93	95/43:487	RM_3	0.7	-3.9
UCT7003	TZ94	95/43:141	M^x	-0.7	-2.5
UCT9943	TZ187	Tr104.2L8	P_4	0.5	0.2
UCT9944	TZ188	Tr104.2L8	M_2	1.3	1.0
UCT9946	TZ190	Tr104.2L8	P_x	0.2	-0.1
UCT9946	Repeat			0.2	-0.1
UCT9946	Average			0.2	-0.1
UCT9947	TZ191	Tr104.2L8	M_3	0.5	-0.1
UCT9948	TZ192	Tr104.2L8C	P_3	1.1	1.0
UCT9949	TZ193	Tr104.2L8C	P_4	1.2	0.1
UCT9950	TZ194	Tr104.2L8C	P_x	0.8	0.8
	Mean (s.d.), *n*=9			+0.54(0.58)	-0.33(1.51)
Antelopinae					
Gazella sp. [large morph, cf. Grant's gazelle/ *Aepyceros* (impala)]					
UCT7007	TZ98	95/44:1278	$M^{1/2}$	0.2	-6.2
UCT7008	TZ99	95/44:904	$LM_{1/2}$	-7.7	-1.9
UCT7006	TZ97	95/44:1325	$M_{1/2}$	-9.0	-7.5
	Mean (s.d.), *n*=3			-5.5(5.0)	-5.2(2.9)
[Compare modern impala from Maswa, δ¹³C =1.8]					
Gazella sp. [small morph, cf. Thomson's gazelle/ *Antidorcas* (springbok)]					
UCT7009	TZ100	95/43:156	$M_{1/2}$	1.2	-1.6
UCT7012	TZ103	95/3:107	$RM^{1/2}$	0.3	-4.7
UCT7014	TZ105	95/43:35	$RM^{1/2}$	0.0	-2.9
UCT7010	TZ101	95/43:147	LM_3	-5.2	-3.4
UCT7011	TZ102	95/43:163	LM_3	-5.6	1.1
UCT7013	TZ103	95/44:1314	$RM_{1/2}$	-9.1	-5.6
	Mean (s.d.), *n*=6			-3.1(4.2)	-2.85(2.4)
[Compare modern Thomson's gazelle from Maswa, δ¹³C = -5.7, -6.7; springbok species have been grazers (*A. bondi*) and browsers (*A. marsupialis*)]					
GIRAFFIDAE					
Giraffa sp.					
UCT7187	TZ24	95/57:797	Juvenile	-8.1	-1.2
UCT7197	TZ25	94/34:940	jumae?	-8.1	-3.7
UCT7227	TZ26	94/34:951		-11.2	-1.6
	Mean (s.d.), *n*=3			-9.1(1.8)	-2.2(1.3)
Sivatherium sp. (giant grazing giraffe)					
UCT7429	TZ23	96/57:797	M_3	-1.3	0.2
UCT7546	TZ45	94/34:940	M_x	-3.7	2.2
UCT6998	TZ89	94/34:951	M_2	0.5	-2.7
	Mean (s.d.), *n*=3			-1.5(2.1)	-0.1(2.5)
SQUAMATA					
CROCODYLIDAE					
Crocodylus niloticus					
UCT7226	TZ15	94/21:103	N/A	-0.7	-5.1
UCT7236	TZ16	95/44:1257	N/A	-3.3	-4.2
UCT7424	TZ17	95/44:1258	N/A	-2.3	-5.1
UCT7182	TZ18	94/23:72	N/A	0.2	-3.8
UCT7192	TZ19	94/21:109	N/A	-2.5	-5.7
UCT9955	TZ201	FLK N Tr112B:2	N/A	-0.5	-4.3
UCT9956	TZ202	FLK N Tr112B:1	N/A	-2.2	-5.3
UCT9957	TZ203	HWKE Tr104.2L8B:9		-2.4	-6.3
UCT9957	Repeat			-2.2	-5.5
UCT9957	Average			-2.3	-5.8
UCT9958	TZ204	HWKE Tr104.4:25		2.5	-3.4
UCT9958	TZ204F		Fragments of TZ204	1.7	-2.8
UCT9958	Average			2.1	-3.1
UCT9959	TZ205	VEKIII:26	N/A	1.04	-3.73
	Mean (s.d.), *n*=10			-1.05(1.76)	-4.62(0.92)
Mean(s.d.) δ¹⁸O for 112 animals = -3.19 (2.18)					

120 measurements are included in the table.

δ¹³C and δ¹⁸O values for individual specimens have been rounded off to 0.1 but mean and s.d. are based on original measurements.

In the column headings, the UCT numbers refer to the database of the Stable Light Isotope Facility in the Archaeology Department at the University of Cape Town; TZ numbers are from the author's field collection of specimens from Tanzania; and OLAPP numbers are from the excavations of the Olduvai Landscape Palaeoanthropology Project.

Table 3: Carbon and oxygen stable isotope ratios in tooth enamel of modern fauna from Serengeti National Park and Maswa Game Reserve (southwest Serengeti), Lobo (northeast Serengeti), Selous Game Reserve (southeast Tanzania), Ugalla and Lukwati (southwest Tanzania)

UCT no.	TZ no.	Collection locus	Tooth	$\delta^{13}C$	$\delta^{18}O$
Order: CARNIVORA					
Family: FELIDAE					
Panthera pardus (leopard)					
UCT7076	TZ167 (1)	Lukwati	RM^1	-11.2	2.5
UCT7077	TZ167 (2)	Lukwati	LM^1	-10.7	1.7
	Mean (s.d.), $n=2$			-10.95(0.40)	+2.1(0.59)
[TZ167 (1) and (2) are from the same animal]					
Panthera leo					
UCT9974	TZ220	Serengeti		-4.0	-0.2
UCT9993	TZ239	Serengeti		-5.0	0.1
UCT10015	TZ261	Serengeti		-3.1	-2.2
	Mean (s.d.), $n=3$			-4.04(0.98)	-0.73(1.24)
HYAENIDAE					
Crocuta crocuta (spotted hyaena)					
UCT9994	TZ240	Serengeti	?	N/A	only organic
UCT10002	TZ248	Serengeti	?	-5.2	-0.7
UCT10018	TZ264	Serengeti	?	-3.1	-2.8
	Mean (s.d.), $n=3$			-4.18(1.5)	-1.76(1.5)
Lycaon pictus (wild hunting dog)					
UCT10019	TZ265	Serengeti		-4.2	0.3
PROBOSCIDEA					
ELEPHANTIDAE					
Loxodonta africana					
UCT10014	TZ260	Serengeti	?	-11.9	-1.6
PERISSODACTYLA					
EQUIDAE					
Equus burchelli					
UCT9983	TZ229	Serengeti	?	0.6	2.8
UCT9984	TZ230	Serengeti	?	0.5	1.7
UCT9985	TZ231	Serengeti	?	0.6	3.4
UCT9986	TZ232	Serengeti	?	1.2	2.3
UCT9987	TZ233	Serengeti	?	1.1	3.3
UCT9988	TZ234	Serengeti	?	0.8	1.5
	Mean (s.d.), $n=6$			0.77(0.3)	2.49(0.81)
UCT7079	TZ169 (1)	Lukwati	RM^3	-0.7	-1.2
REPEAT	TZ169 (1)	Lukwati	RM^3	-1.4	-2.6
UCT7079	TZ169 (2)	Lukwati	LM^3	-3.1	-3.7
REPEAT	TZ169 (2)	Lukwati	LM^3	-2.7	-3.0
	Mean (s.d.), $n=4$			-1.97(1.13)	-2.5(0.87)
RHINOCEROTIDAE					
Diceros bicornis (black rhino)					
UCT10025	TZ271	Serengeti	?	-15.9	-0.1
UCT10026	TZ272	Serengeti	?	-11.8	-2.9
	Mean (s.d.), $n=2$			-13.856(2.9)	-1.5(1.5)
ARTIODACTYLA					
HIPPOPOTAMIDAE					
Hippopotamus amphibius					
UCT9964	TZ210	Serengeti	?	-6.1	-0.2
GIRAFFIDAE					
Giraffa camelopardalis					
UCT9973	TZ219	Serengeti		-12.8	4.4
UCT9995	TZ241	Serengeti		-12.8	3.2

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UCT no.	TZ no.	Collection locus	Tooth	$\delta^{13}C$	$\delta^{18}O$
UCT10060	TZ306	Serengeti		-12.6	3.3
	Mean (s.d.), $n=3$			-12.71(0.14)	3.59(0.66)
BOVIDAE					
Syncerus caffer (buffalo)					
UCT7071	TZ162	Maswa	RM^3	0.7	-0.8
UCT9967	TZ213	Serengeti		2.0	3.3
UCT9968	TZ214	Serengeti		1.9	2.6
UCT9969	TZ215	Serengeti		2.3	3.6
UCT9970	TZ216	Serengeti		-0.4	4.5
UCT9971	TZ217	Serengeti		-0.2	3.2
UCT9975	TZ221	Serengeti		0.2	2.1
UCT10000	TZ246	Serengeti		1.4	3.3
UCT10001	TZ247	Serengeti		0.5	2.3
	Mean (s.d.), $n=9$			0.93(1.0)	2.69(1.48)
Tragelaphus strepsiceros (greater kudu)					
UCT7062	TZ153	Maswa	LM^3	-14.1	2.0
UCT7063	TZ154	Maswa	RM^3	-16.6	-3.5
	Mean (s.d.), $n=2$			-15.35(1.7)	-0.78(3.9)
Tragelaphus imberbes (lesser kudu)					
UCT7061	TZ152	Maswa	RM^2	-12.6	0.5
Tragelaphus scriptus (bushbuck)					
UCT7069	TZ160	Maswa	RM^3	-14.8	1.5
UCT7070	TZ161	Maswa	RM^3	-15.4	-1.8
	Mean (s.d.), $n=2$			-15.11(0.4)	-0.13(2.3)
Redunca redunca (Bohor reedbuck)					
UCT1067	TZ158	Maswa	RM^3	-1.0	0.4
Kobus ellipsiprymnus (common waterbuck)					
UCT7068	TZ159	Maswa	LM^3	0.5	-0.7
Hippotragus niger (sable)					
UCT 7060	TZ151	Maswa	RM^3	0.2	-0.1
Hippotragus equinus (roan)					
UCT7078	TZ168 (1)	Ugalla		1.6	-0.2
UCT7078	TZ168 (2)	Ugalla		2.1	0.5
	Mean (s.d.), $n=1$ (same animal)			1.87(0.33)	0.67(0.45)
Connochaetes taurinus (blue wildebeest)					
UCT7065	TZ156	Selous	RM^3	2.1	-1.2
Connochaetes gnu (black wildebeest)					
UCT9965	TZ211	Serengeti		2.5	2.5
UCT9966	TZ212	Serengeti		1.2	3.9
UCT9976	TZ222	Serengeti		1.4	3.1
UCT9977	TZ223	Serengeti		0.6	3.0
UCT9978	TZ224	Serengeti		1.3	4.8
UCT9978	TZ225	Serengeti		2.66	-1.24
	Repeat			2.69	-0.71
	Average			2.68	-0.98
UCT9980	TZ226	Serengeti		1.5	2.8
UCT9981	TZ227	Serengeti		2.7	2.9
UCT9982	TZ228	Serengeti		1.6	4.9
UCT9996	TZ242	Serengeti		1.9	5.6
	Mean (s.d.), $n=10$			1.74(0.71)	2.54(2.3)
Alcelaphus buselaphus (Kongoni, Coke's hartebeest)					
UCT7064	TZ155	Maswa	LM^3	0.5	-0.7
UCT10023	TZ269	Serengeti		-1.0	1.7
UCT10024	TZ270	Serengeti		2.2	1.4
	Mean (s.d.), $n=3$			0.55(1.63)	0.78(1.31)

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UCT no.	TZ no.	Collection locus	Tooth	$\delta^{13}C$	$\delta^{18}O$
Alcelaphus lichtensteini (Lichtenstein's hartebeest)					
UCT7075	TZ166	Lobo	LM^3	2.1	0.4
Repeat				2.4	-0.6
Average				*2.25*	*-0.27*
UCT7076	TZ166 (1)			1.6	3.7
UCT7076	TZ166X			1.9	3.6
Repeat	TZ166X			1.9	1.1
	Mean (s.d.), n=1			+1.79(0.21)	2.80(1.51)
	Mean (s.d.), n=2			2.08(0.22)	0.39(0.9)
Damaliscus lunatus (topi)					
UCT10005	TZ251	Serengeti		-1.2	1.0
UCT10005	TZ251	Repeat		-0.9	2.1
Average	TZ251			-1.05	1.55
UCT9990	TZ236	Serengeti		2.1	4.6
UCT7066	TZ157	Maswa	RM^2	-2.3	-4.1
	Mean (s.d.), n=3			-0.38(2.28)	0.71(4.4)
Aepyceros melampus (impala)					
UCT7074	TZ165	Maswa	RM^3	1.8	1.0
UCT9992	TZ238	Serengeti		-2.6	0.5
UCT9999	TZ245	Serengeti		-2.3	3.0
	Mean (s.d.), n=3			-1.04(2.45)	1.50(1.3)
Gazella thomsonii (Thompson's gazelle)					
UCT10016	TZ262	Serengeti		-1.3	4.8
UCT10016	Repeat			-1.2	5.1
UCT10016	Average	n=1		-1.2	4.9
UCT10006	TZ252	Serengeti		-0.9	5.2
UCT10007	TZ253	Serengeti		-2.4	5.0
UCT10008	TZ254	Serengeti		-2.8	4.8
UCT10013	TZ259	Serengeti		-3.0	4.9
UCT7072	TZ163	Maswa	RM^3	-6.7	-0.9
UCT7073	TZ164	Maswa	RM^3	-5.7	-0.8
	Mean (s.d.), n=7			-3.26(2.19)	3.29(2.85)
Gazella granti					
UCT10020	TZ266	Serengeti		-7.7	5.0
UCT10020	Repeat			-7.8	5.1
UCT10020	Average			-7.7	5.8
UCT10021	TZ267	Serengeti		-11.7	3.5
UCT10021	Repeat			-11.6	3.7
UCT10021	Average			-11.7	3.6
UCT10022	TZ268	Serengeti		-8.4	2.9
UCT10022	Repeat			-8.3	3.1
UCT10022	Average			-8.4	3.0
	Mean (s.d.), n=3			-9.25(2.11)	+4.14(1.47)
Ostrich eggshell					
UCT10003	TZ249	Serengeti		-10.2	6.7
Repeat				-10.0	6.7
Repeat				-9.8	6.8
	Mean (s.d.), n=3			-9.99(0.19)	6.71(0.06)
$\delta^{18}O$ mean for Serengeti animals (tooth enamel) only, n=50: +1.78 (2.56)					

78 tooth enamel samples (72 animals) and 1 ostrich eggshell are included in the table. Most of these specimens were sampled from the collections in Serengeti National Park; the specimens from Ugalla and Lukwati were sampled at a taxidermist in Arusha.

$\delta^{13}C$ and $\delta^{18}O$ values for individual specimens have been rounded off to 0.1 but mean and s.d. are based on original measurements. To compare modern $\delta^{13}C$ values with those of fossil specimens, 1.5% should be added to correct for the industrial effect of the past 200 years.

In the column headings, the UCT numbers refer to the database of the Stable Light Isotope Facility in the Archaeology Department at the University of Cape Town; TZ numbers are from the author's field collection of specimens from Tanzania.

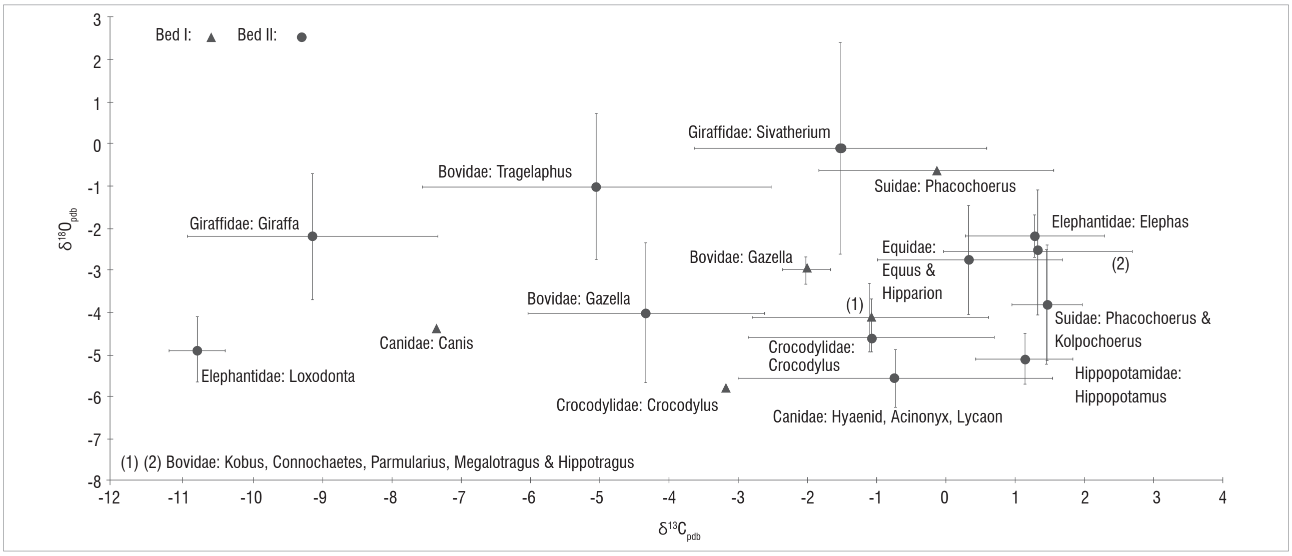


Figure 2: $\delta^{13}C$ and $\delta^{18}O$ values obtained from tooth enamel of fossil fauna from Olduvai Beds I and II.

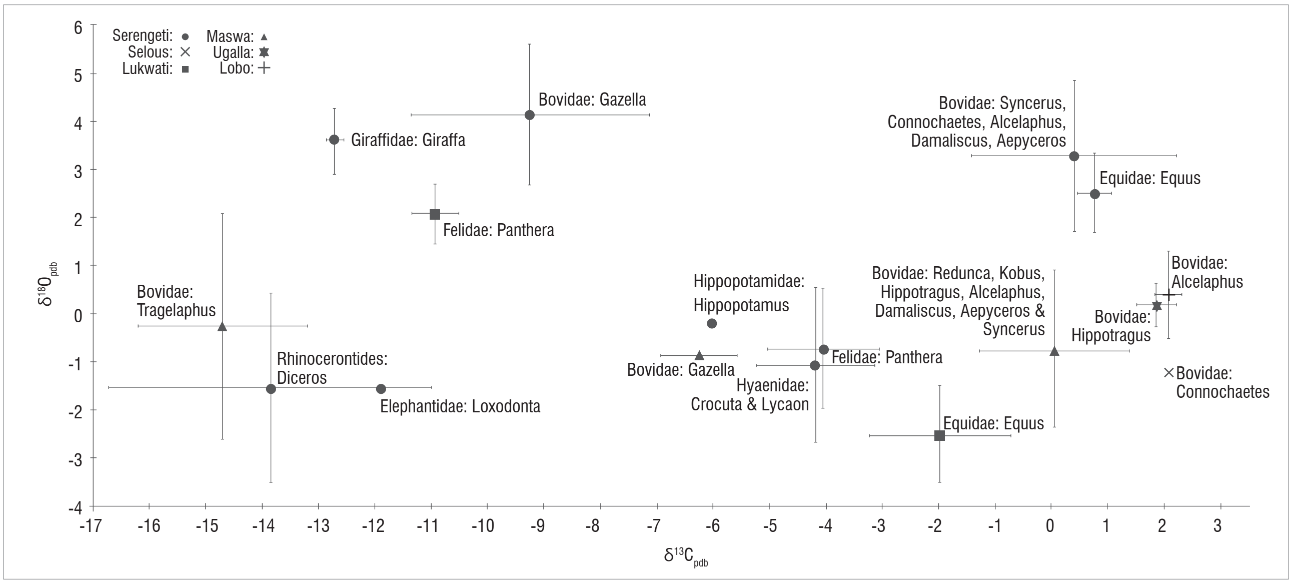
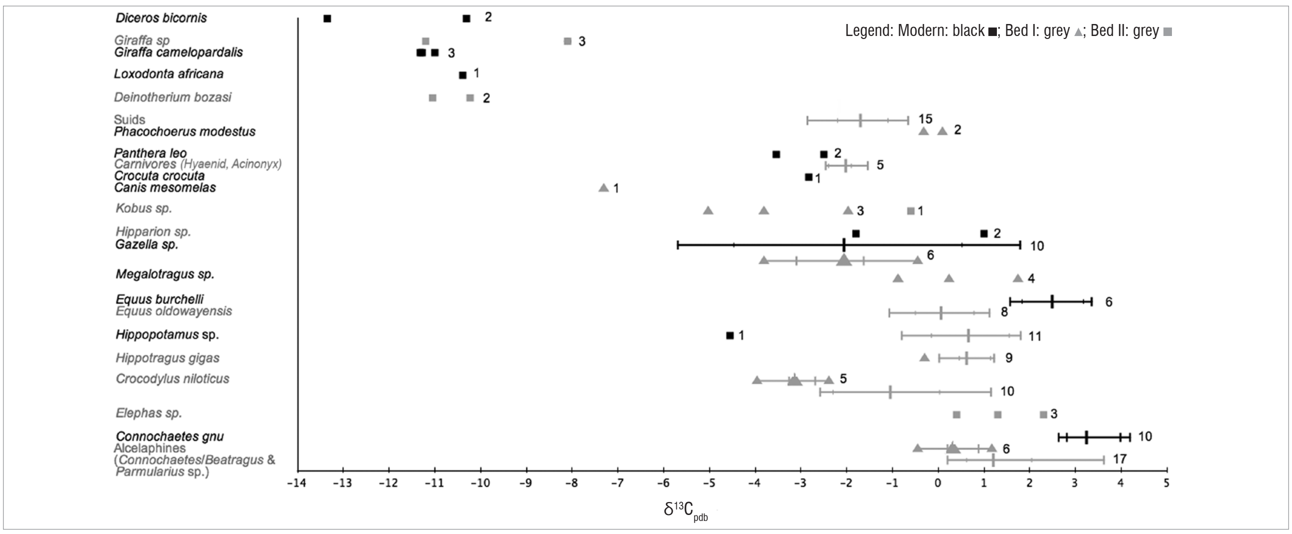


Figure 3: $\delta^{13}C$ and $\delta^{18}O$ values obtained from tooth enamel of modern fauna from Serengeti, Maswa, Lobo, Ugalla, Lukwati and Selous wildlife reserves.



+1.5‰ has been added to the modern values to correct for the industrial effect.

Figure 4: $\delta^{13}C$ from tooth enamel of modern fauna from the Serengeti (in black) and from fossil fauna from Olduvai Beds I and II at ca 1.8 Ma (in grey).

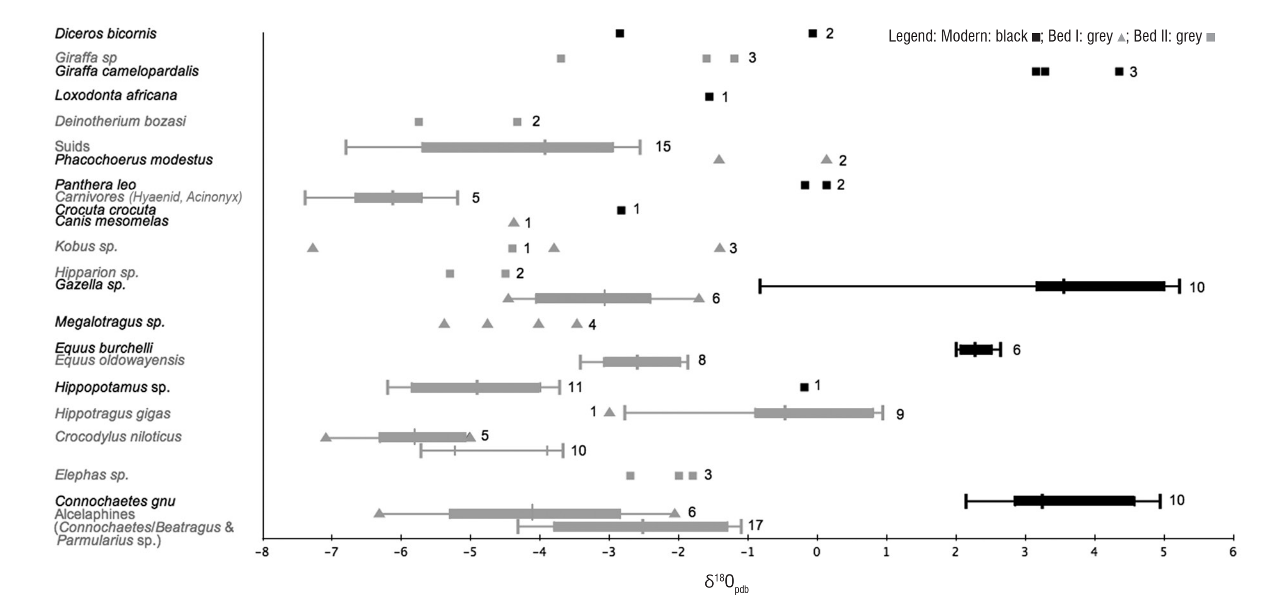


Figure 5: $\delta^{18}O$ from tooth enamel of modern fauna from the Serengeti (in black) and from fossil fauna from Olduvai Beds I and II at ca 1.8 Ma (in grey).

In general, the carbon isotope ratios of the same or related species have stayed remarkably similar over 1.8 million years. The available plant foods have obviously stayed much the same. The oxygen isotope ratios, in contrast, have become enriched by some 6‰. One obvious difference can be found in the case of hippos: the 11 specimens of *Hippopotamus gorgops* from Beds I and II were dedicated grazers, while the single modern specimen of *Hippopotamus amphibious* from the Serengeti was a mixed feeder. Hippos are generally regarded as dedicated grazers, but this assumption is not correct[44] – they will eat C_3 plants if grasses are not available nearby.

Carbon isotopes

The collection from Olduvai West Bed I is somewhat limited: the 27 specimens comprise 1 black-backed jackal, 6 crocodiles and 20 grazing animals (suids and bovids). No browsers are included, which makes it impossible to determine the C_3 end member of this faunal community. At the C_4 end of the collection, the most positive $\delta^{13}C$ value is that of +1.1‰ for two specimens of *Parmularius* (an alcelaphine). The $\delta^{13}C$ values from the Bed I specimens are very similar to those from the larger collection of 118 specimens from Bed II, which includes canids, suids, hippotragines, antelopines, alcelophines and crocodylids. The values for Beds I and II have been added together in the figures to represent the fossil fauna.

Olduvai Bed II is represented by 118 specimens, which provide a comprehensive view of the community at ca 1.8 Ma. The browsing end of the spectrum is represented by two specimens of *Deinotherium bozasi* (-11.05; -10.32), a giant browsing elephant with tusks growing from its lower jaw and bent downwards towards the ground. A specimen of giraffe, *Giraffa* sp. (probably *gracilis*), has a less negative $\delta^{13}C$ value of -9.1‰. It is of interest that *Elephas recki*, an elephant species that occurred widely from East to southern Africa at this time, was clearly a grazer ($\delta^{13}C$ = +1.3), while *Sivatherium* sp. (also *Libytherium* sp.), a short-necked grazing giraffe ($\delta^{13}C$ = -1.5), was also present during Bed II times. These species of elephant and giraffe were later replaced by the modern dedicated browsing elephant, *Loxodonta africana,* and giraffe, *Giraffa camelopardis*. The grazing end of the spectrum at Olduvai in Bed II times was represented by alcelaphines of the genera *Beatragus/ Connochaetes* ($\delta^{13}C$ = +2.1), *Parmularius* (+1.9) and *Megalotragus* (+2.7). Based on these values and that of *Deinotherium bozasi*, one can estimate the $\delta^{13}C$ values for the C_3 and C_4 end members for Bed II at about -11.5‰ and +2.5‰, respectively.

It should be noted that the Bed II specimens are clustered toward the grazing end of the spectrum with few browser representatives. This pattern is especially evident when the Bed II assemblage is compared with that of the modern Serengeti, which has a similar scarcity of browsers. It is noteworthy that the tragelaphines (kudu, bushbuck and eland) from Bed II have a mean $\delta^{13}C$ value of -5.0‰. They were evidently mixed feeders, in contrast to the modern kudu and bushbuck from Maswa, which are dedicated browsers with a mean $\delta^{13}C$ value of -14.7‰.

The $\delta^{13}C$ values for modern fauna (Table 3) have not been corrected for the industrial effect. In order to compare them with the $\delta^{13}C$ values for Olduvai Beds I and II, it is necessary to add 1.5‰. Figure 4 shows the corrected values.

The $\delta^{13}C$ values of modern animals (Table 3) represent several different biomes in Tanzania. This multi-representation is immediately obvious when one compares the $\delta^{13}C$ values for *Equus burchelli* (plains zebra) from Serengeti National Park (+0.8) with those from Lukwati (-2.0). Lukwati is located near Lake Rukwa, between Lakes Tanganyika and Nyasa, and its grazers clearly have more C_3 plants in their diet. Similarly, the browsers from the Serengeti include the modern giraffe (*Giraffa camelopardis*, $\delta^{13}C$ = -12.7), elephant (*Loxodonta africana,* $\delta^{13}C$ = -11.9) and black rhino (*Diceros bicornis*, $\delta^{13}C$ = -13.9). Maswa Game Reserve, which borders Serengeti on the southwest side but is much more wooded, is represented among the browsers by three tragelaphines: the greater kudu (*Tragelaphus strepsiceros,* $\delta^{13}C$ = -15.4), lesser kudu (*T. imberbes*, $\delta^{13}C$ = -12.6) and bushbuck (*T. scriptus*, $\delta^{13}C$ = -15.1). The grazing end of the Serengeti spectrum is represented by *Hippotragus equinus* (roan antelope, $\delta^{13}C$ = +1.9), *Connochaetes gnu* (black wildebeest, $\delta^{13}C$ = +1.7) and *Alcelaphus lichtensteini* (Lichtenstein's hartebeest, $\delta^{13}C$ = +2.0). In calculating the C_3 and C_4 end members, the Serengeti specimens have been emphasised, yielding approximately -12.5 and +1.5. When corrected for the industrial effect, the end members are about -11.0 and +3.0. This result is similar to that from Olduvai Bed II; however, similarity does not mean that the plant communities of the two biomes were the same, only that the availability of C_3 and C_4 plants for browsers and grazers were similar.

In Figure 1, a selection of tooth enamel $\delta^{13}C$ values from Olduvai Bed II and the modern Serengeti are compared; the modern values have been corrected for the industrial effect. The results are extraordinarily similar, suggesting two similar landscapes of wooded grassland. The exception is a single $\delta^{13}C$ value for a modern hippo from the Serengeti, which is evidently a mixed feeder.

Oxygen isotopes

From the $\delta^{18}O$ values reported in Tables 1, 2 and 3, it is clear that oxygen isotope ratios vary substantially with time and place. Among 27 measurements for Olduvai West Bed I (27 animals, Table 1) there is only a single positive value for $\delta^{18}O$. Among 124 measurements for Olduvai East Bed II (111 animals, Table 2) there are only 10 positive $\delta^{18}O$ values. Among 77 measurements for $\delta^{18}O$ in the tooth enamel of modern animals (74 animals, Table 3), 56 values are positive. This contrast is well illustrated in Figure 5, which shows that modern animals have $\delta^{18}O$ values that are more positive than those of the fossil specimens by about 6‰. To be precise, the 50 animals from the Serengeti are 6.24‰ more positive than 27 animals from Bed I and 5.56 more positive than those from Bed II (112 animals). Of the 21 negative $\delta^{18}O$ values for modern animals, 9 are for animals from the Serengeti (out of 53 animals, exact location unknown), 8 are for animals from Maswa (out of 13 animals) and 2 are for animals from Lukwati (out of 4 animals).

As the body water of animals is largely controlled by the rain in the area, it is suggested that the source(s) of rain in the Serengeti, Maswa and Lukwati are different. This hypothesis is under investigation, with the aim of establishing when the change in the rain source in the Olduvai/ Serengeti area occurred.

Conclusions

The stable carbon and oxygen isotope ratios of faunal tooth enamel at Olduvai and in the adjoining Serengeti National Park in Tanzania provide valuable information about the environment in that region at ca 1.8 Ma and in modern times. In general, the carbon isotope ratios indicate that the environment of Olduvai Bed I and II was very similar to that of the modern Serengeti – that is, 'savannah grassland with scrub and bush' (Gentry and Gentry, quoted by Cerling and Hay[17]). In terms of the UNESCO definition,[46] it was a wooded grassland with 10–40% woody plant cover or a grassland with less than 10% woody plants. When the carbon isotope ratios of modern fauna have been corrected for the industrial effect in the modern atmosphere, the values of the fossil fauna are essentially the same as those of their modern counterparts. There is, however, a contrast between the fossil and modern tragelaphines. The woody plants growing at Olduvai at ca 1.8 Ma were evidently insufficient for these animals to be dedicated browsers.

A major change in the environment at Olduvai obviously occurred when Lake Olduvai dried up when the Gorge was formed (later than Bed II). This change removed a number of water-related plant species and freshwater fauna from the environment, but did not result in major changes in the diets of browsing and grazing animals, or in their relative prevalence in the landscape. However, if the major component of the diet of *P. boisei* was papyrus, then their staple food disappeared.

In contrast to the lack of difference in carbon isotope signatures in the fauna at Olduvai between fossil and modern specimens, their oxygen isotope signatures are distinctly different. The $\delta^{18}O$ ratios of the modern faunal community are about 6‰ more positive than those of the fossil fauna from Beds 1 and II. A change of this magnitude has been observed in palaeosol carbonates in Olduvai Gorge by Cerling and Hay[17], with the major change taking place at about 0.5 Ma.

A ready explanation for such a change in $\delta^{18}O$ ratios is that there was a major change in temperature and humidity at some point during the past 1.8 Ma. This environmental change would have caused a major change in the rate of leaf water evaporation and would have increased the difference in enamel $\delta^{18}O$ ratios between water-independent (evaporation-sensitive) Giraffidae and water-dependent (evaporation-insensitive) Hippopotimidae. Such an increase is not observable in this case. The $\delta^{18}O$ ratios of *Giraffa* sp. (-2.2) and *Hippopotamus gorgops* (-5.5) from Lower Bed II differ by 3.3. Among the modern fauna, the $\delta^{18}O$ ratios of *Giraffa camelopardis* (-3.6) and *Hippopotamus amphibious* (-0.2) differ by 3.4. Therefore the difference did not change, indicating that the humidity and temperature did not change. The relatively small difference between the $\delta^{18}O$ ratios of water-dependent and water-independent animals also indicates that the environment in each case was not very dry and that water was permanently available.

An alternative explanation for the change in enamel $\delta^{18}O$ ratios is that the primary source of meteoric water changed at some point during the past 1.8 Ma. It is suggested that this change took place with the introduction of the Indian Ocean monsoon to this part of East Africa. Currently, the major source of rain is the Indian Ocean monsoon which brings the 'long rains' at mid-year, while the Atlantic Ocean provides the 'short rains' at the end of the year. Given the long distance from the Atlantic Ocean, across Angola and Tanzania, the heavy isotopes of hydrogen and oxygen are substantially rained out along the way. This phenomenon has been documented for the rainfall at the research station at Seronera in the Serengeti National Park. A research project, as yet unfinished, has been launched by the author in collaboration with Cassian Mumbi of TAWIRI (Tanzania Wildlife Research Institute) and staff members at Seronera, to measure the oxygen isotopes in samples from the rain gauge over nearly 2 years. The oxygen isotope values of rain from the two oceanic moisture sources differ by as much as 10‰. It is also possible that nearby Lake Victoria, which was only formed around 50 ka, could be adding ^{18}O to the local rainfall.

It is noteworthy that the same isotopic phenomenon (no change in $\delta^{13}C$, but substantial enrichment in $\delta^{18}O$) can be observed at Lake Natron between ca 1.5 Ma and modern times.[2] As more isotopic analyses are done on fossil tooth enamel from northwest Tanzania, it is likely that the timing of this change will be established.

Acknowledgements

The fossil specimens from Olduvai were obtained from the collections of the Olduvai Landscape Archaeology and Palaeoanthropology Project (OLAPP), curated at the National History Museum in Arusha and at the Olduvai Field Camp. Rutgers graduate student Amy Cushing identified the fossil specimens and helped with sampling. The modern specimens from Serengeti National Park were obtained from the Research Station at Seronera. Emily Kisamo, the acting chief warden of Serengeti National Park at the time, was instrumental in providing sampling access. The isotopic ratios of all the specimens were measured at the Stable Light Isotope Facility of the Archaeology Department at the University of Cape Town by Ian Newton and John Lanham. Cape Town graduate students helped with the production of the manuscript: Mariagrazia Galimberti produced the figures, while Kerryn Warren typed the manuscript and checked the statistical calculations. I thank all of these individuals most heartily. Funds for the research were provided by the National Research Foundation of South Africa, the University of Cape Town, and the Landon T. Clay Fund of Harvard University.

References

1. Van der Merwe NJ, Masao FT, Bamford MK. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. S Afr J Sci. 2008;104:153–156.
2. Van der Merwe NJ. Isotopic ecology and diets of fossil fauna from the T-1 (Type Section, Maritanane) paleosurface. In: Dominguez-Rodrigo M, Alcala L, Luque L, editors. Peninj, a research project on human origins (1995–2005). Oxford: Oxbow Books; 2009. p. 109–114.
3. Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, et al. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. Proc Natl Acad Sci USA. 2011;108:9337–9341. http://dx.doi.org/10.1073/pnas.1104627108
4. Lee-Thorp JA, Thackeray JF, Van der Merwe NJ. The hunters and the hunted revisited. J Hum Evol. 2000;39:565–576. http://dx.doi.org/10.1002/oa.659
5. Lee-Thorp JA, Sponheimer M, Van der Merwe NJ. What do stable isotopes tell us about the hominid dietary and ecological niches in the Pliocene? Int J Osteoarchaeol. 2003;13:104–113. http://dx.doi.org/10.1002/oa.659
6. Van der Merwe NJ, Thackeray JF, Lee-Thorp JA, Luyt J. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. J Hum Evol. 2003;44:581–597. http://dx.doi.org/10.1016/S0047-2484(03)00050-2
7. Noli D, Avery G. Protein poisoning and coastal subsistence. J Archaeol Sci. 1988;15:395–401. http://dx.doi.org/10.1016/0305-4403(88)90037-4
8. Lee-Thorp JA. The demise of 'Nutcracker Man'. Proc Natl Acad Sci USA. 2011;108:9319–9320. http://dx.doi.org/10.1073/pnas.1105808108

9. Cerling TE, Manthi FK, Mbua EN, Leakey LN, Leakey MG, Leakey RE, et al. Stable isotope-based diet reconstructions of Turkana Basin hominids. Proc Natl Acad Sci USA. 2013;110(26):10501–10506. http://dx.doi.org/10.1073/pnas.1222568110

10. Sponnheimer M, Alamseged Z, Cerling TE, Grine FE, Kimbel WH, Leakey MG, et al. Isotopic evidence of early hominin diets. Proc Natl Acad Sci USA. 2013;110:10513–10518. http://dx.doi.org/10.1073/pnas.1222579110

11. Cerling TE, Bowman JC, O'Neill JR. An isotopic study of a fluvial-lacustrine sequence: The Plio-Pleistocene Koobi for a sequence, East Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 1988;63:335–356. http://dx.doi.org/10.1016/0031-0182(88)90104-6

12. Cerling TE. Development of grasslands and savannas in East Africa during the Neogene. Palaeogeogr Palaeoclimatol Palaeoecol. 1992;97:241–247. http://dx.doi.org/10.1016/0031-0182(92)90211-M

13. Kingston JD, Marina BD, Hill A. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science. 1994;264:955–959. http://dx.doi.org/10.1126/science.264.5161.955

14. Wolde-Gabriel G, Haile-Selassie Y, Rennie PR, Hart WK, Ambrose SH, Asfaw B, et al. Geology and palaeontology of the Late Miocene Middle Awash Valley, Afar Rift, Ethiopia. Nature. 2001;412:175–178. http://dx.doi.org/10.1038/35084058

15. Wynn JG. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. Am J Phys Anthropol. 2004;123:106–118. http://dx.doi.org/10.1002/ajpa.10317

16. Lee-Thorp JA, Sponnheimer M. Contribution of stable light isotopes to paleoenvironmental reconstruction. In: Henke W, Tattersall TH, editors. Handbook of paleoanthropology. vol.1. Bremen: Springer Verlag; 2007. p. 289–310. http://dx.doi.org/10.1007/978-3-540-33761-4_9

17. Cerling TE, Hay RL. An isotopic study of paleosol carbonates from Olduvai Gorge. Quarternary Res. 1986;25:63–78. http://dx.doi.org/10.1016/0033-5894(86)90044-X

18. Van der Merwe NJ, Cushing AE, Blumenschine RJ. Stable isotope ratios of fauna and the environment of palaeolake Olduvai. J Hum Evol. 1999;34:A24–A25. http://dx.doi.org/10.1038/276815a0

19. Vogel JC, Van der Merwe NJ. Isotopic evidence for early maize cultivation in New York State. Am Antiq. 1977;42:238–242. http://dx.doi.org/10.2307/278984

20. Van der Merwe NJ, Vogel JC. ^{13}C content of human collagen as a measure of prehistoric diet in woodland North America. Nature. 1978;276:815–816.

21. Van der Merwe NJ. Carbon isotopes, photosynthesis, and archaeology. Am Sci. 1982;70:596–606.

22. Bocherens H, Billiou D, Mariotti A, Pathou-Mathi M, Otte M, Bojean D, et al. Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of last interglacial Neanderthal and mammal bones in Scladina Cave (Belgium). J Archaeol Sci. 1999;26:599–607. http://dx.doi.org/10.1006/jasc.1998.0377

23. Richards MP, Pettitt PB, Trinkhaus E, Smith FH, Paunovic M, Karavanic I. Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. Proc Natl Acad Sci. 2000;97:7663–7666. http://dx.doi.org/10.1073/pnas.120178997

24. Sullivan CH, Krueger HW. Carbon isotope analysis of separate phases in modern and fossil bone. Nature. 1981;292:333–335. http://dx.doi.org/10.1038/292333a0

25. Sullivan CH, Krueger HW. Carbon isotope ratios of bone apatite and animal diet reconstruction. Nature. 1983;301:177. http://dx.doi.org/10.1038/301177a0

26. Lee-Thorp JA, Van der Merwe NJ. Carbon isotope analysis of fossil bone apatite. S Afr J Sci. 1987;83:712–715.

27. Lee-Thorp JA, Van der Merwe NJ. Aspects of the chemistry of fossil and modern biological apatites. J Archaeol Sci. 1991;18:343–354. http://dx.doi.org/10.1016/0305-4403(91)90070-6

28. Passey BH, Robinson TF, Ayliffe LK, Cerling TE, Sponnheimer M, Dearing MD, et al. Carbon isotope fractionation between diet, breath, and bioapatite in different mammals. J Archaeol Sci. 2005;32:1459–1470. http://dx.doi.org/10.1016/j.jas.2005.03.015

29. Quade J, Cerling TE, Barry JC, Morgan ME, Pilbeam D, Chivas AR, et al. A 16- Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. Chem Geol (Isotope Geosc). 1992;94:183–192. http://dx.doi.org/10.1016/0168-9622(92)90011-X

30. Sponnheimer M, Lee-Thorp JA. Oxygen isotope ratios in enamel carbonate and their ecological significance. J Archaeol Sci. 1999;26:723–728. http://dx.doi.org/10.1006/jasc.1998.0388

31. Helliker BR, Ehleringer JR. Differential ^{18}O enrichment of leaf cellulose in C_3 versus C_4 grasses. Functional Plant Biol. 2002;29:435–442. http://dx.doi.org/10.1071/PP01122

32. Levin NE, Cerling TE, Passey BH, Harris JM, Ehleringer JR. A stable isotope aridity index for terrestrial environments. Proc Natl Acad Sci. 2006;103:11201–11205. http://dx.doi.org/10.1073/pnas.0604719103

33. White TD, Ambrose SH, Suwa G, Su DF, DeGusta D, Bernot RL, et.al. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. Science. 2009;326:67–93. http://dx.doi.org/10.1126/science.1175822

34. Tieszen LL. Natural variation in the carbon isotope values of plants: Implications for archaeology, ecology and palaeoecology. J Archaeol Sci. 1991;18:227–248. http://dx.doi.org/10.1016/0305-4403(91)90063-U

35. Van der Merwe NJ, Medina E. Photosynthesis and the ^{13}C/^{12}C ratios in Amazonian rain forests. Geochim Cosmochim Acta. 1989;53:1091–1094. http://dx.doi.org/10.1016/0016-7037(89)90213-5

36. Ehleringer JR, Field CB, Lin ZF, Kuo CY. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. Oecologia. 1986;70:520–526. http://dx.doi.org/10.1007/BF00379898

37. Ehleringer JR, Cooper TA. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia. 1988;76:562–566.

38. Bowen GJ, Wilkinson B. Spatial distribution of δ^{18}O in meteoric precipitation. Geology. 2002;30:315–318. http://dx.doi.org/10.1130/0091-7613(2002)030<0315:SDOOIM>2.0.CO;2

39. Dansgaard W. Stable isotopes in precipitation. Tellus. 1964;16:436–438. http://dx.doi.org/10.1111/j.2153-3490.1964.tb00181.x

40. Epstein S, Mayeda T. Variation of ^{18}O content of waters from natural sources. Geochim Cosmochim Acta. 1953;4:213–224. http://dx.doi.org/10.1016/0016-7037(53)90051-9

41. Gat JR. Oxygen and hydrogen isotopes in the hydrologic cycle. Annu Rev Earth Pl Sci. 1996;24:225–262. http://dx.doi.org/10.1146/annurev.earth.24.1.225

42. Koch PL. Isotopic reconstruction of past continental environments. Annu Rev Earth Pl Sci. 1998;26:573–613. http://dx.doi.org/10.1146/annurev.earth.26.1.573

43. Levin N, Zipser E, Cerling TE. Isotopic composition of waters from Ethiopia and Kenya: Insights into moisture sources from Eastern Africa. J Geophys Res. 2009;114:D23306. http://dx.doi.org/10.1029/2009JD012166

44. Cerling TE, Harris JM, Hart JA, Kaleme P, Klingel H, Leakey MG, et.al. Stable isotope ecology of the common hippopotamus. J Zool. 2008;276:204–212. http://dx.doi.org/10.1111/j.1469-7998.2008.00450.x

45. Blumenschine RJ, Peters CR, Masao FT, Clarke RJ, Deino AL, Hay RL, et al. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. Science. 2003;299:1217–1221. http://dx.doi.org/10.1126/science.1075374

46. White F. The vegetation of Africa. Natural Resources Research. Vol. 20. Paris: UNESCO; 1983.