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Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin of East Africa

J. M. Harris[1], T. E. Cerling[2], M. G. Leakey[3,4] & B. H. Passey[2]

1 Los Angeles County Museum, Los Angeles, CA, USA
2 Department of Geology and Geophysics, University of Utah, Salt Lake City, UT, USA
3 The National Museums of Kenya, Nairobi, Kenya
4 Department of Anthropology, State University of New York at Stony Brook, NY, USA

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Correspondence
T. E. Cerling, Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112, USA
Email: tcerling@comcast.net.

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Abstract

The diet of African hippopotamids can be documented through $\delta^{13}C$ analyses of enamel and other tissues. Analysis of a 10-million-year sequence of hippopotamids in and near the Lake Turkana Basin of northern Kenya shows that hippos have included a substantial fraction of C_3 vegetation in their diets since the late Miocene when C_4 vegetation first appears in hippo diet as a measurable fraction. The C_4 component of vegetation becomes dominant (>50%) by Upper Burgi time (*c*. 2 million years ago) but does not reach 100% for all individuals. It is therefore not unexpected that the $\delta^{13}C$ values of modern hippopotamids show a higher fraction of dietary C_3 biomass than has been estimated from traditional observations. Analysis of $\delta^{18}O$ of hippos from different stratigraphic levels shows no systematic trend over time; the average value for fossil hippos over the last 10 million years is similar to that of modern hippos from the Omo River system.

Introduction

Hippos are non-ruminant artiodactyls whose origin has been debated considerably Different authorities have suggested derivation from anthracotheres (Falconer & Cautley, 1836; Colbert, 1935) or peccaries (Pickford, 1983). More recently, genetic studies have suggested that hippos are closely related to whales. In their recent re-evaluation of hippo relationships and origins, Boisserie, Lihoreau & Brunet (2005*a*) provided convincing evidence that hippos are most closely related to anthracotheres and accepted that the Hippopotamidae and Cetacea were sister groups within the Cetartiodactyla.

The Hippopotamidae is a very diverse family, with at least 30 species named in the literature (Weston, 1997), although few of the African fossil species achieved the widespread distribution enjoyed in historic times by *Hippopotamus amphibius*. Because of their aquatic mode of life, hippos are often the most common mammals in Pliocene and Pleistocene terrestrial assemblages of Africa. Certainly, they are well represented in the vicinity of the Lake Turkana Basin of northern Kenya, an area that provides a history of this group spanning the last 12 million years. Hence, any paleoenvironmental information that representatives of this family could provide has the potential to significantly enhance our understanding of local climatic conditions from the late Miocene onwards.

The earliest-known hippos are from Africa. Pickford (1983) recognized two species of *Kenyapotamus*: *Kenyapotamus ternani* from the middle Miocene of western Kenya and the slightly larger *Kenyapotamus coryndonae* from late Miocene sites in the Gregory (Eastern) Rift Valley and Tunisia. *Kenyapotamus* cheek teeth are smaller, simpler and more bunodont than those of the other two genera (Harrison, 1997), and Pickford (1983) interpreted them to represent a distinct subfamily: the Kenyapotaminae. All other hippos are placed in the subfamily Hippopotaminae.

Boisserie (2005) reviewed the cranial morphology of African and Asian Hippopotaminae and his cladistic analysis provided an innovative view of their relationships. He recognized a primitive clade that included species from Kenya (Lothagam and Rawe) and Abu Dhabi, for which he created the genus *Archaeopotamus*, a West African clade that included the extant *Choeropsis* and the Pliocene *Saotherium* from Chad, an Asian clade that comprised most of the Asian species attributed to *Hexaprotodon* plus *Hexaprotodon bruneti* from the Afar region of Ethiopia and a *Hippopotamus* sensu lato clade that included the Turkana Basin hippos, the extant *H. amphibius* and Ethiopian species from Hadar.

Large samples of fossil hippos from African localities often contain at least two anatomically different but sympatric populations. The Lake Turkana basin has yielded six distinct hippopotamine species plus some unnamed forms,

at least two and sometimes three of which co-occur in any one- time interval. Thus, *Archaeopotamus harvardi*, *Archaeopotamus lothagamensis* and an unnamed larger species have been retrieved from the late Miocene Nawata Formation at Lothagam, whereas in the early Pliocene Nachukui Formation at Lothagam, both *A. harvardi* and aff. *Hippopotamus* cf. *Hippopotamus protamphibius* have been recovered (Weston, 2003). At Kanapoi, two species co-occurred in the early Pliocene: aff. *Hippopotamus* cf. *H. protamphibius* (Weston, 2003) and a smaller species (Harris, Leakey & Cerling, 2003). At least two species, aff. *H. protamphibius* and *Hippopotamus* sp., occurred in the lower (early Pliocene) part of the Koobi Fora Formation, whereas aff. *Hippopotamus aethiopicus*, aff. *Hippopotamus karumensis* and *Hippopotamus gorgops* appear together in the upper (late Pliocene/early Pleistocene) part of the formation (Harris, 1991).

The diversity of fossil hippopotamids is in stark contrast to their modern representation. *Hippopotamus amphibius*, the common extant hippo, was formerly widespread in the lakes and rivers of sub-Saharan Africa and is frequently interpreted as a grazer. *Choeropsis liberiensis*, the endangered extant pygmy hippo, is restricted to West Africa, where it is said to be more terrestrial and to exploit a mixture of browse and graze. Differences in tooth height and postcranial anatomy between African fossil hippo species have been interpreted to suggest that *Hippopotamus* species were aquatic grazers whereas the African species formerly assigned to *Hexaprotodon* were thought to be more terrestrial and more inclined to browsing. However, Boisserie's recent re-interpretation of hippopotamid relationships indicates that Turkana Basin hippos formerly attributed to *Hexaprotodon* are instead much more closely related to the extant common hippo.

Stable isotopes record different temporal aspects of mammalian dietary behavior in different tissues. Stable carbon isotopes are particularly powerful for distinguishing browsing and grazing behavior in East Africa where virtually all grasses utilize the C_4 photosynthetic pathway, browse plants (e.g. trees, shrubs, forbs) utilize the C_3 pathway and these two pathways have very different chemical ($^{13}C/^{12}C$) compositions. These different foodstuffs are absorbed into mammalian tissues with a predictable and a relatively constant isotopic fractionation. Different tissues provide different time-averaged glimpses of diet. As reported elsewhere (Cerling *et al*., in press), hair provides a relatively high-resolution record, averaging diet over a few days to a few weeks. Tooth enamel provides a record that is time averaged over a longer time period, several months to several years, but models have been developed that allow time-averaged intra-tooth sequences (such as sequential analyses along the lengths of hippo tusks) to be transformed into instantaneous dietary inputs (Passey & Cerling, 2002; Kohn, 2004; Passey *et al*., 2005*a*,*b*).

Stable oxygen isotopes, on the other hand, record information about the water balance and thermoregulatory strategies of mammals, which derive water from drinking (e.g. from springs, rivers, lakes, water holes), from plant water (e.g. stems and leaves) and from metabolic water (by reaction with carbohydrates). Meteoric water in the form of rainfall is least enriched in^{18}O but evaporation from open water sources (such as lakes) augments the $\delta^{18}O$ of water by 5–15‰. Plant food in the form of cellulose and carbohydrates is enriched in ^{18}O compared with the source water but, again, evaporation from leaf surfaces further enriches the ^{18}O component by 5–15‰. Metabolic water is derived by the oxidation of carbohydrates and is related both to the enriched $\delta^{18}O$ of the carbohydrates and to atmospheric oxygen (*c.* +22‰, but see discussion in Kohn, 1996). Thus, water sources for large mammals can be a combination of an ^{18}O-depleted source (meteoric water) and several ^{18}O-enriched sources (leaf water and metabolic water; Bryant & Froelich, 1995; Kohn, 1996). For aquatic and water-dependent mammals such as hippos, stable oxygen isotopes provide information about the habitat as well as the diet.

The diversity of hippo species encountered in the African fossil record seems to imply that anatomically distinct but synchronous species interacted differently with the prevailing habitats. The questions then follow: does the stable isotopic composition of fossil hippo teeth provide a mechanism for determining how the different fossil species partitioned the available food resources, and was such partitioning independent of their phylogenetic relationships? Boisserie *et al*. (2005*b*) established a baseline for such an investigation by determining from stable carbon isotopes that extant common hippos sampled throughout sub-Saharan Africa were opportunistic rather than obligate grazers. They also interpreted, on the basis of dental microwear (a procedure not followed here), that scratches on extant hippo teeth were consistent with fresh, short C_4 grasses with a low silicon content. Boisserie *et al*. (2005*b*) further established, on the basis of stable isotope analysis, that late Miocene hippos from Toros-Ménalla, Chad (~6 MA), had a mixed C_3/C_4 diet whereas the early to middle Pliocene hippos from Chad had a more exclusive C_4 diet (Zazzo *et al*., 2000). In contrast, the diet of early Pliocene hippoptamids from Langebaanweg was clearly dominated by C_3 plants (Franz-Odendaal, Lee-Thorp & Chinsamy, 2002), although this is not unexpected, given the persistent Mediterranean climate of the southern tip of Africa. In this paper, we examine the long-term dietary history of hippos from the Lake Turkana Basin, which has an excellent record of hippopotamids from the late Miocene to the present, to investigate overall dietary trends and dietary differences between species.

Methods

We sampled 122 fossil hippopotamid specimens from East Africa (Table 1), mostly from fossiliferous deposits near Lake Turkana in northern Kenya, plus 75 *H. amphibius* specimens (reported elsewhere, Cerling *et al*., in Press). We analyzed enamel because it is the material least susceptible to diagenesis (Ayliffe, Chivas & Leakey, 1994; Wang & Cerling, 1994). We sampled modern vegetation in Kenya and Uganda between 1999 and 2003, and modern waters between 1977 and 2003. We interpreted these results in light of those from other East African mammals, fossil and extant, that have been analyzed in our laboratory.

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Table 1 δ^{13}C and δ^{18}O data from tooth enamel from fossils in and near the Turkana Basin. Isolated teeth are identified only to genus

Sample	Formation or member	Species	δ^{13}C	δ^{18}O
MS 4892	Galana Boi Fm	*Hippopotamus amphibius*	−2.9	−3.7
MS 4901	Galana Boi Fm	*H. amphibius*	−5.8	−1.7
KNM-ER 2045	Okote Mb	aff. *Hippopotamus aethiopicus*	−3.6	−5.7
KNM-ER 5502	Okote Mb	aff. *H. aethiopicus*	−2.7	1.2
KNM-ER 5512	Okote Mb	aff. *H. aethiopicus*	−1.3	−4.7
KNM-ER 5573	Okote Mb	aff. *H. aethiopicus*	−1.0	−2.1
ER 5501	Okote Mb	aff. *Hippopotamus karumensis*	−0.6	−5.0
KNM ER 5500	Okote Mb	aff. *H. karumensis*	−2.1	−3.5
KNM ER 5577	Okote Mb	aff. *H. karumensis*	−0.6	−2.6
ER 1427	Okote Mb	*Hippopotamus gorgops*	−0.7	−2.7
KNM ER 1396	Okote Mb	*H. gorgops*	0.1	−5.7
KNM ER 1409	Okote Mb	*H. gorgops*	−1.6	−3.9
KNM ER 5543	Okote Mb	*H. gorgops*	−1.4	−4.8
ER 1412	KBS Mb	aff. *H. aethiopicus*	−2.9	−0.2
KNM-ER 5576	KBS Mb	aff. *H. aethiopicus*	−1.5	−3.0
KNM-ER 638	KBS Mb	aff. *H. aethiopicus*	−0.3	−2.6
KNM-ER 671	KBS Mb	aff. *H. aethiopicus*	−1.9	−2.3
ER 5648	KBS Mb	aff. *H. karumensis*	−2.7	−5.7
KNM ER 1422	KBS Mb	aff. *H. karumensis*	0.0	−2.7
KNM ER 2186	KBS Mb	aff. *H. karumensis*	−1.8	−4.1
KNM ER 5464	KBS Mb	aff. *H. karumensis*	−0.5	−3.8
ER 5513	KBS Mb	*H. gorgops*	−0.1	−1.8
KNM ER 5509	KBS Mb	*H. gorgops*	−3.0	−0.7
KNM ER 5510	KBS Mb	*H. gorgops*	−0.2	−3.0
KNM ER 637	KBS Mb	*H. gorgops*	−1.1	−0.5
DF 623	Upper Burgi Mb	aff. *H. aethiopicus*	−0.8	−2.9
ER 2184	Upper Burgi Mb	aff. *H. karumensis*	−1.8	−3.5
KNM ER 1426	Upper Burgi Mb	aff. *H. karumensis*	−2.4	−3.3
KNM-ER 4887	Upper Burgi Mb	aff. *H. karumensis*	−0.1	−4.5
KNM-ER 943	Upper Burgi Mb	aff. *H. karumensis*	−1.2	−3.6
ER 1394	Upper Burgi Mb	*H. gorgops*	0.1	−4.8
KNM ER 1514	Upper Burgi Mb	*H. gorgops*	−0.4	−3.9
KNM ER 2279	Upper Burgi Mb	*H. gorgops*	0.0	−1.9
KNM ER 785	Upper Burgi Mb	*H. gorgops*	−3.1	0.6
KNM ER 2803	Tulu Bor Mb	aff. *Hippopotamus protamphibius*	−5.1	−1.1
KNM ER 2804	Tulu Bor Mb	aff. *H. protamphibius*	−2.4	−5.1
KNM-ER 2802	Tulu Bor Mb	aff. *H. protamphibius*	−2.7	−5.8
ER 2801	Lokochot Mb	aff. *H. protamphibius*	−2.6	−2.7
ER 4119	Lokochot Mb	aff. *H. protamphibius*	−6.1	−3.1
KNM ER 4120	Lokochot Mb	aff. *H. protamphibius*	−2.6	−2.8
KNM ER 5231	Lokochot Mb	aff. *H. protamphibius*	−9.9	−0.8
261-1G	Lokochot Mb	aff. *Hippopotamus* sp. indet	−3.9	−0.6
ER 3631	Lokochot Mb	aff. *Hippopotamus* sp. indet	−5.4	−3.8
ER 3638	Lokochot Mb	aff. *Hippopotamus* sp. indet	−5.6	−4.0
ER 3645	Lokochot Mb	aff. *Hippopotamus* sp. indet	−0.9	−2.2
ER 3645	Lokochot Mb	aff. *Hippopotamus* sp. indet	−0.8	−1.7
MS 4891a	Lokochot Mb	aff. *Hippopotamus* sp. indet	−8.9	−3.6
KNM ER 6171	Moiti Mb	aff. *H. protamphibius*	−5.4	−2.5
LOTH-102	Apak Mb	aff. *H. protamphibius*	−3.6	−3.2
LOTH-102	Apak Mb	aff. *H. protamphibius*	−3.4	−2.9
LOTH-102	Apak Mb	aff. *H. protamphibius*	−3.3	−4.5
LOTH-104	Apak Mb	aff. *H. protamphibius*	−4.6	−1.4
LOTH-109	Apak Mb	aff. *H. protamphibius*	−0.9	−5.2
LOTH-112	Apak Mb	aff. *H. protamphibius*	−8.2	−4.0
LOTH-62	Apak Mb	aff. *H. protamphibius*	−4.4	−3.8
LOTH-63	Apak Mb	aff. *H. protamphibius*	−3.3	−3.7
LOTH-99	Apak Mb	aff. *H. protamphibius*	−7.0	0.2
LT 23856	Upper Nawata Mb	*Archaeopotamus harvardi*	−2.4	−4.8

Table 1. Continued.

Sample	Formation or member	Species	$\delta^{13}C$	$\delta^{18}O$
LT 409	Upper Nawata Mb	*A. harvardi*	−1.0	−4.5
LT 23871	Upper Nawata Mb	*Archaeopotamus lothagamensis*	−5.2	−4.4
LOTH 157	Upper Nawata Mb	*Archaeopotamus* sp. indet	−0.3	0.7
LOTH-150	Upper Nawata Mb	*Archaeopotamus* sp. indet	−3.1	−4.6
LOTH-151	Upper Nawata Mb	*Archaeopotamus* sp. indet	−3.7	−0.5
LOTH-153	Upper Nawata Mb	*Archaeopotamus* sp. indet	0.8	1.6
LOTH-156	Upper Nawata Mb	*Archaeopotamus* sp. indet	−0.4	−3.5
LOTH-160	Upper Nawata Mb	*Archaeopotamus* sp. indet	−2.9	−4.4
LOTH-165	Upper Nawata Mb	*Archaeopotamus* sp. indet	0.9	−1.2
LOTH-168	Upper Nawata Mb	*Archaeopotamus* sp. indet	−1.6	−4.6
LOTH-172	Upper Nawata Mb	*Archaeopotamus* sp. indet	−5.1	−6.2
LOTH-173	Upper Nawata Mb	*Archaeopotamus* sp. indet	−3.2	−2.8
LOTH-174	Upper Nawata Mb	*Archaeopotamus* sp. indet	−1.0	−6.8
LOTH-175	Upper Nawata Mb	*Archaeopotamus* sp. indet	−1.0	−3.4
LOTH-42	Upper Nawata Mb	*Archaeopotamus* sp. indet	−7.6	−4.5
LOTH-43	Upper Nawata Mb	*Archaeopotamus* sp. indet	−2.5	−4.1
LOTH-44	Upper Nawata Mb	*Archaeopotamus* sp. indet	−4.3	−3.9
LOTH-46	Upper Nawata Mb	*Archaeopotamus* sp. indet	0.6	−4.6
LOTH-49	Upper Nawata Mb	*Archaeopotamus* sp. indet	−4.7	−2.4
LOTH-49	Upper Nawata Mb	*Archaeopotamus* sp. indet	−2.6	−2.5
LOTH-51	Upper Nawata Mb	*Archaeopotamus* sp. indet	−3.1	−4.1
LOTH-55	Upper Nawata Mb	*Archaeopotamus* sp. indet	−2.8	−5.0
LOTH-56	Upper Nawata Mb	*Archaeopotamus* sp. indet	−5.2	−4.2
LOTH-65	Upper Nawata Mb	*Archaeopotamus* sp. indet	−3.2	−2.9
LOTH-68	Upper Nawata Mb	*Archaeopotamus* sp. indet	−2.6	−4.3
LT 23269	Lower Nawata Mb	*A. harvardi*	−2.2	−3.7
LT 23270	Lower Nawata Mb	*A. harvardi*	−3.4	−2.4
LT 23831	Lower Nawata Mb	*A. harvardi*	−0.7	−4.2
LT 23872	Lower Nawata Mb	*A. harvardi*	−2.6	−4.6
LT 22864	Lower Nawata Mb	*A. lothagamensis*	−2.1	−4.5
LT 23839	Lower Nawata Mb	*A. lothagamensis*	−3.3	−3.6
LT 23879	Lower Nawata Mb	*A. lothagamensis*	−7.8	−4.0
LT 8585	Lower Nawata Mb	*Archaeopotamus* sp. indet	−4.1	−2.8
LT 23874	Lower Nawata Mb	*Archaeopotamus* sp. indet	−2.2	−3.6
LOTH-122	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.0	−5.9
LOTH-126	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.4	−4.8
LOTH-135	Lower Nawata Mb	*Archaeopotamus* sp. indet	−7.9	−4.5
LOTH-138	Lower Nawata Mb	*Archaeopotamus* sp. indet	−4.2	−4.7
LOTH-69	Lower Nawata Mb	*Archaeopotamus* sp. indet	−3.4	−6.8
LOTH-69	Lower Nawata Mb	*Archaeopotamus* sp. indet	−2.1	−4.7
LOTH-71	Lower Nawata Mb	*Archaeopotamus* sp. indet	−2.8	−4.6
LOTH-73	Lower Nawata Mb	*Archaeopotamus* sp. indet	−0.7	−4.1
LOTH-74	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.5	−4.8
LOTH-78	Lower Nawata Mb	*Archaeopotamus* sp. indet	−7.2	−3.7
LOTH-81	Lower Nawata Mb	*Archaeopotamus* sp. indet	−4.0	−6.1
LOTH-85	Lower Nawata Mb	*Archaeopotamus* sp. indet	−3.8	−4.3
LOTH-86	Lower Nawata Mb	*Archaeopotamus* sp. indet	−3.2	−4.3
LOTH-86	Lower Nawata Mb	*Archaeopotamus* sp. indet	−3.0	−4.3
LOTH-87	Lower Nawata Mb	*Archaeopotamus* sp. indet	−1.7	−4.6
LOTH-89	Lower Nawata Mb	*Archaeopotamus* sp. indet	−3.1	−2.8
LOTH-92	Lower Nawata Mb	*Archaeopotamus* sp. indet	−9.2	−2.8
LOTH-93	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.8	−4.2
LOTH-93	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.7	−4.0
LOTH-93	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.4	−7.2
LOTH-95	Lower Nawata Mb	*Archaeopotamus* sp. indet	−5.1	−5.0
861009-1-Hippo	Namurungule Fm	*Kenyapotamus* sp. indet	−9.1	−3.3
KNM-SH 14792	Namurungule Fm	*Kenyapotamus* sp. indet	−6.2	−4.3
KNM-SH 18001	Namurungule Fm	*Kenyapotamus* sp. indet	−6.8	−7.1
KNM-NA 246	Nakali Fm	*Kenyapotamus coryndoni*	−10.0	−1.8

Table 2 Summary data for stable isotope profiles from a fossil hippopotamus canine (*Archaeopotamus* sp.) from Lothagam

Sample	*n*	δ^{13}C ave $\pm 1\sigma$	δ^{18}O ave $\pm 1\sigma$
LOTH-87	56	-1.2 ± 0.8	-4.1 ± 0.5
(two segments)	(−2.7, 0.3)	(−5.3, −3.1)	

Tooth enamel was separated from dentine, ground to a fine powder, washed in dilute H_2O_2, 0.1 M acetic acid and rinsed with distilled water following the standard procedures for the treatment of tooth enamel (Lee-Thorp & van der Merwe, 1987; Quade *et al.*, 1992; Koch, Tuross & Fogel, 1997). One stable isotope profile was undertaken on an *Archaeopotamus* canine (Table 2), sampling at 10-mm intervals along its length. Approximately 0.5 mg of the treated powder was reacted with 100% H_3PO_4 under helium at 90 °C using the Finnigan Carboflo device. Isotope ratios were measured on a mass spectrometer and results are reported using the standard ‰ notation where

$$\delta^{13}\mathrm{C}(\mathrm{or}\ \delta^{18}\mathrm{O}) = (R_{sample}/R_{standard} - 1) \times 1000$$

and R_{sample} and R_{standard} are the $^{13}C/^{12}C$ (or $^{18}O/^{16}O$) ratios in the sample and standard, respectively, for δ^{13}C (or δ^{18}O); the standard is the isotope reference standard V-PDB for both carbon and oxygen. δ^{18}O values for biogenic apatite are often assumed to have the same fractionation–temperature relationship as does calcite for the CO3–H3PO4 reaction; we corrected modern and fossil enamel samples to internal modern and fossil enamel laboratory standards, respectively, that were reacted at 25 °C *in vacuo* with 100% H_3PO_4.

Results

Extant *H. amphibius*: δ^{13}C and δ^{18}O

The average δ^{13}C for 83 different hippopotamus teeth from 68 different individuals was -3.6 ± 2.5‰ and that of δ^{18}O was -1.8 ± 1.8‰ (Cerling *et al.*, in press). Stable isotope profiles on six different individuals included profiles where δ^{13}C and δ^{18}O were relatively constant along the length of the profiles and some with large ranges in δ^{13}C or δ^{18}O (Cerling *et al.*, in press). A single 75-mm-long hippo hair from the Lake Edward region (DR Congo) had an average δ^{13}C value of −14.2‰, with a range from −10.9 to −18.7‰.

Fossil hippopotamids of the Turkana Basin region

The modern Turkana Basin includes the Omo, Turkwell and Kerio rivers in its drainage basin. The southern end of the basin is truncated by the Barrier, a recent volcanic chain. Before construction of the Barrier, the Suguta Valley was part of the Turkana drainage basin. We include several formations (Nakali and Namarungule) from the Suguta Valley in our discussion of the long-term history of the Turkana Basin. Hippopotamids in the Turkana Basin range in age from late Miocene to the present. Late Miocene samples were obtained from the Namurungule Formation in the Samburu Hills, and from the Lower Nawata, Upper Nawata and Apak Formations in the Lothagam region. Pliocene samples were derived from the Moiti, Tulu Bor and Lokochot Members of the Koobi Fora Formation. Pleistocene samples came from the Upper Burgi, KBS and Okote Members of the Koobi Fora Formation. Two Holocene hippos were also analyzed. For δ^{13}C, all samples from the Lokochot and from older strata are statistically different from those that are of Upper Burgi age or younger (ANOVA; Bonferroni's test, $P < 0.05$). Figure 1 shows the long-term trend in δ^{13}C for hippos from the Turkana Basin. For δ^{18}O, there was only one difference in any population compared with another (ANOVA; Bonferroni's test, $P < 0.05$); the KBS and Lower Nawata did show a slight difference in δ^{18}O ($P = 0.026$). Figure 2 shows a box-and-whisker plot for the hippos from the Turkana basin grouped by a major stratigraphic interval.

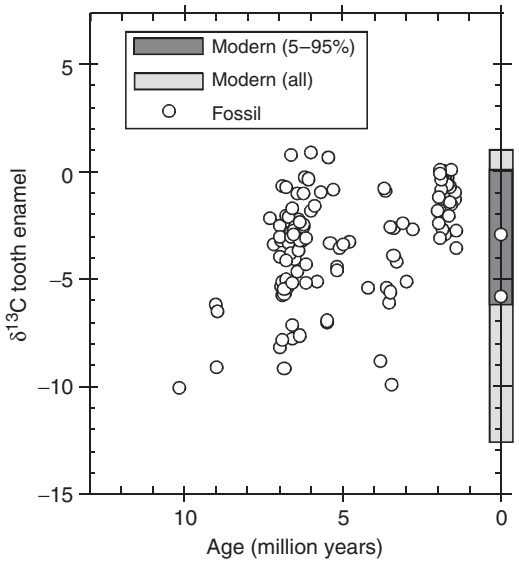

Figure 1 Time series of δ^{13}C values from hippopotamus tooth enamel from the Turkana Basin in northern Kenya and southern Ethiopia. Total range of δ^{13}C values for modern East African hippos and 5–95‰ range are shown for comparison.

Regional comparison of δ^{18}O of hippos in East Africa

Hippos from the Lake Turkana–Omo River system exemplify the importance of the drinking water source. Today, Lake Turkana is a closed basin and its water has an average δ^{18}O value between +5 and +6‰ (>30 measurements at Koobi Fora between 1977 and 1986). It is thus enriched in ^{18}O compared with local meteoric water (*c.* −3‰) or the inflowing Omo River (*c.* −1‰). The principal food source for both lower Omo River hippos and Lake Turkana hippos should have similar δ^{18}O values because local meteoric waters are the principal sources of water for non-aquatic plants. However, four extant hippos from Lake Turkana

have $\delta^{18}O$ values that average +2.8‰ compared with −2.3‰ for a single hippo from the Omo River. These results reflect the state of evaporation of the water in which the animals shelter rather than the food that they ate. Thus, hippos from freshwater closed basin lakes are likely to be enriched in $\delta^{18}O$ compared with hippos dwelling in nearby rivers (Table 3), and our data show that the isotope enrichment for the Lake Turkana hippos is 28.7‰ whereas the Omo River hippos have an enrichment typical for river-dwelling hippos (31‰).

Discussion

Record of fossil hippos from the Turkana Basin

The $\delta^{13}C$ content observed in samples from Turkana basin hippo teeth (Table 1) ranges from −9.9‰ (100% C_3) to 0.9‰ (~100% C_4). Specimens from the late Miocene and early Pliocene display the greatest range and include individuals that were wholly C_4 grazers and those who fed only from C_3 vegetation (Fig. 1). The range of variation is much smaller in the Plio-Pleistocene samples, even when the results from different species are pooled together. Preliminary results are consistent with hippos being opportunistic feeders, sampling available vegetation within a relatively short distance from their source of aquatic shelter. Changes in $\delta^{18}O$ reflect climatic and environmental changes.

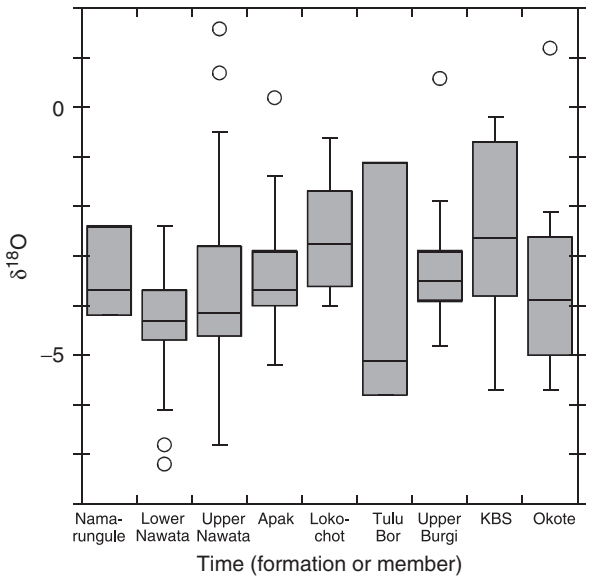

Figure 2 Box-and-whisker plot of $\delta^{18}O$ of hippo tooth enamel grouped by major stratigraphic interval. Only the KBS and Lower Nawata show significant differences ($P = 0.03$).

Four specimens of *Kenyapotamus* were sampled from Gregory Rift Valley localities immediately south of the Lake Turkana basin. The sole specimen of *Kenyapotamus* from Nakali indicates a diet of C_3 vegetation but predates the widespread radiation of C_4 grasses. The isotopic evidence does not indicate whether the C_3 vegetation consumed by the Nakali hippo included grasses. Somewhat younger specimens of *Kenyapotamus* from the Namurungule Formation of the Samburu Hills evidently exploited a mixture of C_3 vegetation and C_4 grasses.

Three hippo species have been recorded from the late Miocene Nawata Formation at Lothagam. Although each displays substantial variation, the common species *A. harvardi* seems to have a largely C_4 diet, as did the much larger unnamed species. In contrast, the diet of the smaller *A. lothagamensis* included a significant fraction of C_3 browse. Grazing mammals generally have wider mandibular symphyses than browsing mammals and so it is interesting that Weston (2003) documents the mandible of *A. lothagamensis* as being much narrower than that of *A. harvardi*. Many of the sampled Nawata Formation specimens were isolated teeth that could not be identified to species; these teeth displayed dietary preferences that ranged from pure C_3 to pure C_4. Those from the upper Nawata are, in general, more positive in both $\delta^{13}C$ and $\delta^{18}O$ than those from the lower Nawata.

When all Lothagam results are pooled regardless of taxon, hippos from the Nawata Formation had a slightly higher proportion of C_4 vegetation in their diet than those from the superjacent Apak Member of the Nachukui Formation, although this is not statistically significant. This is also interesting because Weston (2003) documents aff.

Table 3 Estimates of stable isotopic composition of local meteoric waters and lake waters from samples discussed in text

Region	Waters $\delta^{18}O \pm 1\sigma$ (n) SMOW	Hippo $\delta^{18}O \pm 1\sigma$ (n) PDB	SMOW	ε^*
Meteoric sources (*rivers, streams, waterholes*)				
Laikipia – Mpala	−3.3 ± 0.9 (4)	−1.6 ± 0.7 (5)	29.3	32.7
Nairobi – Athi Plains	−4.0 ± 1.1 (15)	−2.6 ± 0.6 (3)	28.2	32.4
Turkana/Omo River	−3.0 ± 1.2 (11)	−2.3 (1)	28.5	31.6
Tsavo	−4.0 ± 1.1 (12)	−2.5 ± 0.6 (8)	28.3	32.5
Coast	−2.3 (1)	−2.7 ± 1.0 (8)	28.1	30.5
Lakes				
Lake Turkana	5.6 ± 0.6 (25)	2.8 ± 1.0 (4)	33.8	28.0

Meteoric waters include springs, rivers and groundwater; waters were collected between 1977 and 2003. The isotope enrichment is calculated having converted $\delta^{18}O$ on the PDB scale to the SMOW scale.

Hippopotamus cf. *H. protamphibius* from the Apak Member, and the same species from the Koobi Fora Formation has a substantial fraction of C_3 vegetation in its diet. This and the greater prevalence of *A. harvardi* in the Nawata Formation seem to confirm that that the late Miocene hippo species exploiting the Lothagam region may have had slightly different dietary preferences from those elsewhere in the basin. The $\delta^{18}O$ results appear to become slightly more positive through the sequence from Lower Nawata to Apak, although this is not statistically significant.

The common hippo from Kanapoi and from the lower part of the Koobi Fora Formation (Moiti, Lokochot, Tulu Bor Members) is aff. *Hippopotamus* cf. *H. protamphibius* but a smaller unnamed species is also documented from Kanapoi and a larger *Hippopotamus* species from sites in the Allia Bay region. Samples from this time interval again indicate a dietary range from pure C_3 to pure C_4, samples from the Tulu Bor Member being more positive in terms of $\delta^{13}C$ but more negative in terms of $\delta^{18}O$ than samples from the earlier part of the Koobi Fora Formation.

The common hippo from the upper (Plio-Pleistocene) portion of the Koobi Fora Formation is aff. *H. karumensis* but aff. *H. aethiopicus* and *H. gorgops* also occur throughout this interval. There is no apparent dietary difference between aff. *H. karumensis* and *H. gorgops* although these two large species were formerly attributed to different genera. All three species seem to have a virtually pure C_4 diet; the slightly larger fraction of browse in the diet of aff. *H. aethiopicus*, together with a greater range of $\delta^{18}O$ (Table 1), may indicate that this species had a more terrestrial mode of life than the other two species.

Two hippo specimens were sampled from FwJj5, a late Holocene pastoral Neolithic site. One yielded $\delta^{13}C$ and $\delta^{18}O$ results that would not seem out of place for an early Pleistocene hippo from this region. In the other sample, however, the $\delta^{13}C$ is much more negative than any specimen from the lower Pleistocene biota (being very similar to that of extant Omo River hippos) but the $\delta^{18}O$ is much more positive.

Of the extant hippos sampled from the Lake Turkana basin, those from the lower reaches of the Omo River evidently include a significant sample of C_3 browse in their diet whereas those from the lake margins are pure C_4 grazers. This reflects the nature of the vegetation adjacent to the water in which the hippos shelter. The $\delta^{18}O$ results were much more positive than those of the late Pleistocene fossils but, as might be predicted, the hippos from the Omo River were slightly less positive than those from the lake. The difference between the two geographically adjacent populations is interesting because it seems to indicate that they do not invade each other's territory.

We analyzed a single isotope profile from an *Archaeopotamus* sp. canine from Lothagam (Table 2). Figure 3 shows that the long-term diet consisted of about 75% C_4 biomass, similar to that of modern hippos. Inversion of the $\delta^{13}C$ data shows that this individual ranged from a diet of *c.* 100% C_4 to *c.* 50% C_4 biomass. The C_4 biomass 'peaks' were about 25 mm apart – indicating a regular, presumably seasonal,

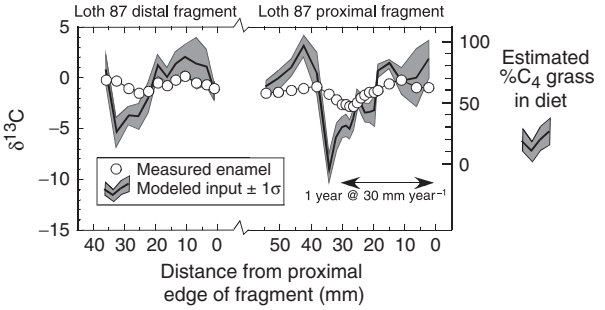

Figure 3 Detailed profile of a single fossil hippo canine, with circles showing the $\delta^{13}C$ data. Inversion (solid thick line) of the $\delta^{13}C$ data shows a range from about 100% C_4 biomass to *c.* 50% C_4 biomass on a length scale of 30 mm, which may correspond to 1 year of growth. The shaded area represents $\pm 1\sigma$ for the diet estimate; this represents 100 simulations using random combinations of maturation length (50–70 mm) and sampling uncertainties (as discussed in Passey *et al.*, 2005*a*,*b*).

change in diet. Hippo canine growth rates between 15 and 30 mm year^{-1} were determined for modern hippos (Passey *et al.*, 2005*a*). We anticipate that further detailed stable isotope profiles of hippopotamus canines, both modern and fossil, may increase our understanding of hippo feeding ecology.

An important conclusion from the fossil hippos seems to be that, because of their specialized mode of life, spending much of their time in water but feeding opportunistically on vegetation adjacent to their source of shelter, they provide a better proxy for the water chemistry and local vegetation than any other medium- or large-sized terrestrial mammal from the same fossil assemblage. The late Miocene and early Pliocene hippos appear catholic in their choice of vegetation whereas the early Pleistocene forms from the Turkana Basin were largely restricted to a grazing diet. This may reflect the transition from an open to a closed basin that took place in the Turkana Basin during the late Pliocene and its consequent effect on the vegetation adjacent to the lake. Given the isotopic differences evident between the hippos found today in Lake Turkana and those from the lower Omo River that feeds the lake, it would be interesting to learn how the Omo Shungura hippos (Géze, 1985) contrast isotopically with those from the Kenyan portion of the basin. The transition in hippos from a C_4 grazing diet in the early Pleistocene to an opportunistic grazing/browsing diet in extant forms provides an intriguing parallel to the preferred feeding adaptations of Pleistocene versus extant elephants documented by Cerling, Harris & Leakey (1999), Cerling *et al.* (2004).

There is no long-term trend in the $\delta^{18}O$ of hippos in the Turkana Basin from the late Miocene to the present. Most of these samples were from fluvial environments. Because riverine hippos occupy an environment that is relatively insensitive to evaporation, this could serve as a useful baseline for other mammals that are more sensitive to environmental parameters such as aridity (Levin *et al.*, 2006).

Summary

The earliest hippos appeared during the late Miocene, which is about the time that C_4 plants became an important fraction of biomass in East African ecosystems. Isotopic analyses of fossil hippopotamids from the Turkana Basin in Kenya and Ethiopia show that the proportions of C_3 and C_4 vegetation in the diets of hippo species have always varied throughout their known history but with an overall trend towards a C_4 diet. Because of their dependence on water for shelter, and propensity to harvest available vegetation close to their shelter, hippos provide a more reliable proxy for the water chemistry and local vegetation than other large mammals from the same fossil assemblage. However, evaporative effects in closed basin lakes are large so that the distinction between river and lake hippos has an important role in interpreting $\delta^{18}O$ measurements on hippos. The Turkana Basin hippo results contrast with those from a Mediterranean climate setting in South Africa (Franz-Odendaal *et al*., 2002) but are supported by those from the late Miocene of North Africa (Boisserie *et al*., 2005*a*,*b*). All three studies confirm that hippos are and were opportunistic in their diet rather than obligate grazers.

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