

Original article

# Paleoenvironmental reconstruction of the Asbole fauna (Busidima Formation, Afar, Ethiopia) using stable isotopes<sup>☆</sup>

*Reconstruction paléoenvironnementale de la faune d'Asbole  
(Formation de Busidima, Afar, Éthiopie) utilisant les isotopes stables*

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Received 18 June 2009; accepted 28 September 2009

Available online 4 February 2010

## Abstract

The Middle Pleistocene environmental and climatic conditions at Asbole, lower Awash Valley, Ethiopia were reconstructed using stable carbon and oxygen isotopic composition (<sup>13</sup>C, <sup>18</sup>O) of fossil tooth enamel coupled with faunal abundance data. We analyzed the isotopic composition of a total of 80 herbivorous tooth enamel samples from 15 mammalian taxa, which archive the dietary preferences and drinking behavior from the “Asbole faunal zone”. The carbon isotopic data signify a wide range of foraging strategies, across the entire spectrum of pure C4 to C4-dominated diet, mixed C3/C4 diet and C3-dominated diet. The oxygen isotopic enrichment between evaporation sensitive and insensitive taxa ( $\epsilon_{ES-EI}$ ) is 3.7‰ which provides an estimate of the mean annual water deficit of the Middle Pleistocene at Asbole of 1470 mm, a value characteristic of modern arid landscapes in this part of the Awash Valley. The isotopic data coupled with faunal abundance data indicate an arid C4-dominated open-vegetated region, with an abundance of forest-dwelling primates that identify the presence of gallery forests flanking tributary streams to the paleo-Awash River. Thus, with these combined methodologies, it is possible to explicate a more detailed character of the “mosaic” of environments characteristic of Neogene savanna ecosystems. These findings, clearly indicate the importance of avoiding oversimplification of Pleistocene environmental reconstructions, based on single proxies at isolated localities.

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**Keywords:** Asbole; Ethiopia; Carbon and oxygen isotope; Tooth enamel; Paleoenvironment

## Résumé

Les conditions environnementales et climatiques du Pléistocène moyen à Asbole, dans la basse vallée de l'Awash (Éthiopie), ont été reconstituées en utilisant les compositions isotopiques du carbone (<sup>13</sup>C) et de l'oxygène (<sup>18</sup>O) de l'émail dentaire fossile, combinées avec des données de proportions fauniques. Nous avons analysé l'abondance isotopique des 80 prélèvements d'émail dentaire provenant de 15 taxons des mammifères, qui archivent les préférences alimentaires et les comportements de boisson de la « zone faunique d'Asbole ». Les données isotopiques du carbone indiquent des stratégies d'approvisionnement variées, à travers tous les régimes entre C4 pur et C3-dominé. L'enrichissement isotopique en <sup>18</sup>O entre les taxons « sensibles à l'évaporation » et les taxons « insensibles à l'évaporation » ( $\epsilon_{ES-EI}$ ) est de 3,7‰, fournissant une évaluation du déficit annuel de l'eau durant le Pléistocène moyen à Asbole de 1470 mm, une valeur caractéristique des paysages arides modernes dans cette partie de la vallée de l'Awash. Les données isotopiques combinées avec celles d'abondance faunique témoignent d'une région ouverte et aride, dominée par une végétation en C4, avec une abondance de colobes qui montrent la présence des forêts galeries flanquant des fleuves tributaires du paleo-Awash. Ainsi, avec ces approches combinées, il a été possible de préciser les caractéristiques de la « mosaïque »

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d'environnements et d'écosystèmes néogènes de la savane à Asbole. Nos résultats indiquent clairement d'éviter, lors de reconstructions d'environnements pléistocènes, les simplifications excessives basées sur l'utilisation de proxys uniques et de localités isolées.

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*Mots clés* : Asbole ; Éthiopie ; Isotope du carbone et de l'oxygène ; Émail dentaire ; Paléoenvironnement

## 1. Introduction

Measurements of natural variations in stable isotope ratios have become vital tools in fields as diverse as geochemistry, hydrology, ecology, and anthropology. The application of stable isotopes to paleoceanography and marine paleoclimatology has been spectacularly successful, revealing both long-term trends in marine climate and the response of the oceans to short-term orbital forcing and sudden events (Imbrie et al., 1984; Zachos et al., 1993). Isotopic reconstruction of conditions on land is more difficult, however, because terrestrial ecosystems and climates exhibit greater spatial and temporal heterogeneity and the isotope systems applied in these settings are more complex. Even so, over the past decade, there has been a surge in studies of continental paleoclimates and paleoenvironments, spurred by the increased need to understand the response of the more variable land ecosystems to past climate change (e.g., Swart et al., 1993).

Analyses of stable isotopes of carbon and oxygen extracted from fossils have contributed substantially to our understanding and ability to reconstruct paleoenvironmental and paleoclimatic parameters in the Neogene of tropical Africa, which is characterized by mixed C3 and C4 vegetation (Lee-Thorp et al., 1989; Morgan et al., 1994; Bocherens et al., 1996; Kohn et al., 1996; Cerling et al., 1997a, 1997b; Kingston, 1999a, 1999b; Sponheimer and Lee-Thorp, 1999a, 1999b, 1999c; Sponheimer et al., 1999; Zazzo et al., 2000). These approaches have been critical in documenting ecological shifts, elucidating hominin dietary adaptations, constraining vegetation types in past ecosystems, characterizing habitat heterogeneity in space and time, revealing dietary niche partitioning in fossil terrestrial communities, and correlating climatic perturbations and oscillations in terrestrial ecosystems (Kingston and Harrison, 2007). The present study uses stable isotopes of mammalian tooth enamel to assess the paleoclimate conditions and understand the distribution of different types of vegetation between 0.8–0.64 Ma at Asbole in the Awash Valley of Ethiopia, a site which has a direct relevance to the understanding of the paleoenvironmental contexts of Pleistocene hominins in the Horn of Africa (Geraads et al., 2004; Wynn et al., 2008).

## 2. Controls on the isotopic composition of tooth enamel

Stable carbon and oxygen isotopic analysis of tooth enamel has been established as a valuable tool for reconstructing terrestrial paleoenvironments (Bocherens et al., 1996; Koch, 1998; Franz-Odenaal et al., 2002; Kohn and Cerling, 2002; Cerling et al., 2003c; Sponheimer and Lee-Thorp, 2003; Schoeninger et al., 2003; Boisserie et al., 2005; Kingston and

Harrison, 2007). Tooth enamel is an ideal substrate for preserving stable isotopic signatures because it is almost entirely inorganic and has very low porosity (>96% inorganic component by weight and <1% organic material; Wang and Cerling, 1994). The inorganic mineral phase of tooth enamel is hydroxyapatite ( $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$ ), a relatively stable mineral in surface-weathering environments. As such, tooth enamel is less susceptible to diagenesis than bone or dentine because of its lower organic content, higher density, and larger crystalline size (Ayliffe et al., 1994; Bryant et al., 1994). Enamel forms by accretion without remodeling and mineralization is complete prior to tooth eruption. Like enamel, dentin grows by accretion with little remodeling (Lowenstam and Weiner, 1989). However, because of its resistance to diagenetic alteration, enamel is the most suitable fossilized material of vertebrates for paleoenvironmental study using stable isotopes (Wang and Cerling, 1994).

### 2.1. Carbon isotopes

The interpretation of carbon isotopic composition of tooth enamel is based on differences in isotope fractionation between plants that use the two major photosynthetic pathways (C3 and C4), and the consumption of C3 and C4 vegetation by mammalian fauna (Smith and Epstein, 1971). The C3 pathway is most common, occurring in the vast majority of trees and shrubs, as well as those herbs and grasses with a cool and relatively moist (i.e., non-evaporative) growing seasons. C3 plants have  $\delta^{13}\text{C}$  values (mean  $\approx -27\text{‰}$ , range:  $-22$  to  $-35\text{‰}$ ) that are much lower than those of atmospheric  $\text{CO}_2$  ( $\approx -7.7\text{‰}$ ; O'Leary, 1988). C4 photosynthesis is less common and occurs in grasses and some sedges and herbs, but only those that grow under sufficiently dry and/or warm (i.e., evaporative) growing season climates in which this energy-intensive pathway is able to gain a competitive advantage over the C3 pathway. C4 plants have  $\delta^{13}\text{C}$  values (mean  $\approx -13\text{‰}$ , range:  $-19$  to  $-9\text{‰}$ ) that are more similar to those of the atmosphere (O'Leary, 1988). The crassulacean acid metabolism (CAM) pathway is least common, occurring in succulent plants adapted to arid climates. CAM plants fix  $\text{CO}_2$  by both pathways, separating their use of each pathway during high and low light conditions, and thus exhibit a range of  $\delta^{13}\text{C}$  values intermediate between those of C3 and C4 plants (Ehleringer and Monson, 1993).

Dietary differences are recorded in developing tissues of animal such as teeth with a relatively constant fractionation factor (Cerling and Harris, 1999). Because most C4 plants are tropical grasses, Koch (1998) suggest stable carbon isotope values can readily distinguish grazing from browsing mammals.

2.2. Oxygen isotopes

The oxygen isotopic composition of mammalian tooth enamel is a function of the isotopic composition of oxygen that enters and exits the body (Kohn, 1996; Kohn et al., 1998). Biogenic phosphate (hydroxyapatite) is precipitated in equilibrium with body water, which is mostly comprised of ingested water (Longinelli, 1984; Luz et al., 1984). Because mammals larger than 1 kg have a constant body temperature near 37 °C, hydroxyapatite is precipitated in these species at a constant temperature, which allows for the oxygen isotopic signature of the ingested material to be recorded without the effects of temperature dependent fractionation. The body’s main oxygen sources are atmospheric O<sub>2</sub>, liquid water and oxygen bound in food, of which only the latter two are likely to cause differences in oxygen isotope values among sympatric taxa. Unlike atmospheric O<sub>2</sub>, the oxygen isotope composition of food and liquid water are highly variable, and thus likely to explain any differences found in the oxygen isotope compositions of animals within a local ecosystem. Liquid water enters the body through drinking and as free water in food. In most cases, liquid water in plant roots and stems is isotopically similar to available

drinking water, but leaf water can be relatively enriched in H<sub>2</sub><sup>18</sup>O due to preferential evapotranspiration of the lighter H<sub>2</sub><sup>16</sup>O molecule (Sternberg, 1989). Thus, animals that derive most of their water from plant leaves (such as *Giraffa* or *Litocranius*) ingest water enriched in <sup>18</sup>O compared to animals that drink regularly (such as *Equus* and *Phacochoerus*).

3. Geological context of the Asbole Fauna

Late Pliocene and early Pleistocene deposits at Asbole belong to the Busidima Formation which is dominated by fluvial sedimentation in an asymmetrical half graben (the Busidima half-graben; Wynn et al., 2006, 2008). The sediments of the Busidima Formation thicken towards the border fault at the western margin (Fig. 1), as is typical of half-graben rift basins throughout the East African and other continental rift systems (Ebinger, 2002). As described in Alemseged and Geraads (2000) and Geraads et al. (2004), the “Asbole fauna” is bracketed between two widespread and mappable stratigraphic markers, i.e., the “top conglomerate” bed (~0.8 Ma) and the Bironita Tuff (0.64 Ma). The Bironita Tuff is correlated to a tuff from Bodo, Dawitoli, and Hargufia areas of the Middle

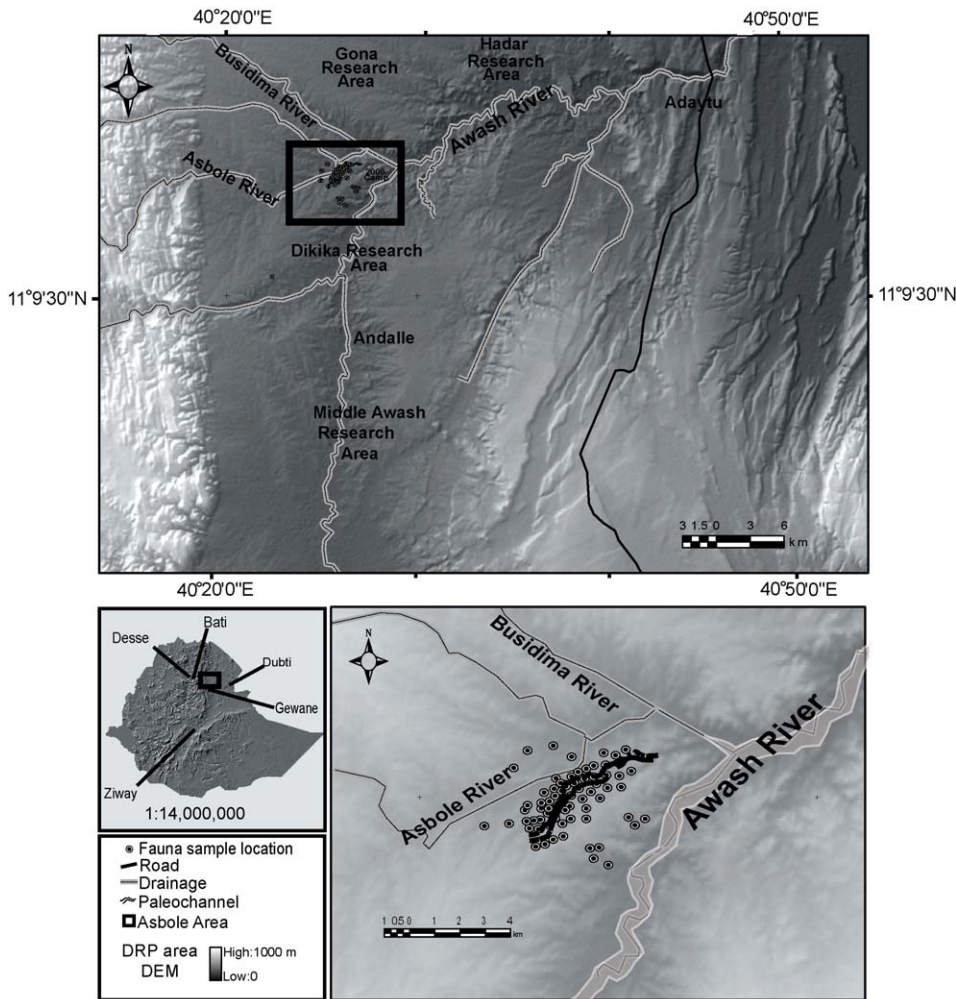


Fig. 1. Location map of the Dikika Research Project (DRP) area showing the main modern drainages, and Asbole Paleochannel, a prominent ephemeral paleochannel mappable through the deposits, and illustrating the fossil tooth enamel sampling locations in relation to the paleochannel outcrop.

Awash which has previously been dated at  $0.64 \pm 0.03$  Ma (Clark et al., 1994). The age boundary of the “top conglomerate” is defined by the uppermost of a series of mappable conglomerates estimated at 0.8 Ma (Geraads et al., 2004). In this study we only analyzed Middle Pleistocene mammalian fossil specimens from the interval between these two markers. The majority of the fossils from Asbole derives from close proximity to a prominent paleochannel that can be mapped throughout the region (Fig. 1).

#### 4. Methods

We analyzed the isotopic composition of a total of 80 samples (Fig. 1) from 15 different mammalian taxa collected in December 2006 and previous field seasons (i.e., museum collections housed in the National Museum of Ethiopia). Bulk enamel samples were taken by drilling down the tooth along the growth axis with a 0.5 mm drill bit, cleaning the drill bit between sampling. Care was taken to avoid dentine, cementum and matrix in the sample powder. About 20 mg of powder enamel was extracted from each tooth.

The powder produced was pretreated with 3% hydrogen peroxide followed by a 1 M acetic acid-calcium acetate buffer to remove organic matter and secondary carbonates, and thoroughly rinsed with distilled water (following standard procedures for the treatment of tooth enamel of Lee-Thorp and van der Merwe, 1987; Quade et al., 1992; Koch, 1998). Approximately 5–7 mg of the treated powder was reacted with 103%  $H_3PO_4$  in He flushed exetainer vials at 25 °C for 24 h to produce the  $CO_2$  analyte gas for analyses of  $\delta^{13}C$  and  $\delta^{18}O$ . Isotope ratios were measured on a Thermo Fisher Scientific (Finnigan) Delta V 3 keV Isotope Ratio Mass Spectrometer and results are reported using the standard per mil notation where:

$$\delta^{13}C \text{ or } \delta^{18}O = \left( \frac{R_{\text{sample}}}{R_{\text{Standard}}} - 1 \right) * 1000$$

$R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}C/^{12}C$  ratios in the sample and standard, respectively, for  $\delta^{13}C$  and the  $^{18}O/^{16}O$  ratios in the sample and standard, respectively, for  $\delta^{18}O$ . The reference standard is the international reference scale VPDB, which was normalized using replicate samples of IAEA reference materials NBS-18 and NBS-19.

In order to calculate the  $\delta^{13}C$  of the total large vertebrate diet in the ecosystem, we calculated a weighted average of the  $\delta^{13}C_{\text{enamel}}$  value, weighted using the relative abundance of each taxon multiplied by an estimate of the daily food intake of respective species:

$$\delta^{13}C_{\text{Ecosystem}} = \frac{\sum (X_{\text{taxa}} Q) \delta^{13}C_{\text{enamel, taxa}}}{\sum (X_{\text{taxa}} Q)} + \Delta_{\text{enamel-diet}}$$

Where  $X_{\text{taxa}}$  is relative faunal abundance expressed as a fraction,  $Q$  is the average daily food intake in kg/day of taxa,  $\delta^{13}C_{\text{enamel, taxa}}$  is the average value for each taxon in per mil (‰), and  $\Delta_{\text{enamel-diet}} = -14‰$  is an offset between diet and

enamel  $\delta^{13}C$  (Kohn and Cerling, 2002). The daily food intake of most of the taxa were estimated based on the calibration of food consumption of African mammals to mean body size (Delaney and Happold, 1979). Dietary intake and body mass data from *Gazella granti*, *Gazella thomsoni*, *Aepyceros melampus*, *Connochaetes taurinus*, *Syncerus caffer*, *Hippopotamus amphibius* and *Loxodonta africana* from Delaney and Happold (1979) were used to calibrate a regression line to estimate dietary intake of all other taxa in this study based on average body mass.

We calculated the percentage of estimated C4 biomass in the animal diet for each taxon based on a linear mixing model between pure C3 and C4 biomass with values of  $-13‰$  and  $+1‰$ , respectively.

For oxygen isotopic composition, we calculated the enrichment factor ( $\epsilon$ ) between two groups of taxa (evaporation sensitive and insensitive) as:

$$\epsilon_{\text{ES-EI}} = \left( \frac{R_{\text{ES}}}{R_{\text{EI}}} - 1 \right) * 1000$$

We used this variable to estimate aridity, which is quantified as water deficit (WD), equal to the difference between Mean Annual Thornthwaite Potential Evapotranspiration (PET) and Mean Annual Precipitation (MAP). For modern comparable climates in Ethiopia, we estimated WD using data from the Ethiopian National Meteorological Agency.

#### 5. Carbon isotope, results and interpretation

$\delta^{13}C_{\text{enamel}}$  values of the Asbole fossils range between  $-11.4$  to  $+3.1‰$  and thus span the entire range of pure C3 and C4 consumers (Table 1).  $\delta^{13}C_{\text{enamel}}$  values of tooth enamel from the Asbole faunal zone indicate that some herbivores, such as *Chlorocebus* and giraffids, consumed dominantly C3 plants, while most bovid tribes of Bovidae (Bovini, Reduncini, Alcelaphini, Hippotragini) consumed C4 grasses, and other tribes, Tragelaphini and Antilopini showed mixed C3/C4 feeding strategies. Other herbivores (hippopotamids, rhinocerotids, equids, suids, Proboscidea and *Theropithecus*) relied heavily on C4 grasses while a few large Rodentia sampled exhibit mixed C3/C4 feeding strategies (Figs. 2 and 3; Table 2). The results from each major taxonomic category are discussed in detail below.

##### 5.1. Rhinocerotidae

The only rhinoceros identified in the “Asbole faunal zone” is *Diceros* cf. *D. bicornis* (Geraads et al., 2004). *Ceratotherium* may also be present, but definite evidence is still lacking, because distinction of the two living African genera is difficult based on fragmentary remains (Geraads et al., 2004).  $\delta^{13}C_{\text{enamel}}$  value of the single *Diceros* from the Asbole fauna zone is  $-5.5‰$  ( $n = 1$ ). The isotopic data suggest that the dietary strategy of this *Diceros* was that of a mixed feeder with both C3 and C4 components, with approximately 54% C4 grass consumed in its diet (Table 2). Previous studies on isotopic analysis of modern rhinocerotid



Table 1

Stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) of fossil tooth enamel collected from Asbole during 2006 and prior field seasons. Samples used in the calculation of  $\epsilon_{\text{ES-EI}}$  shown in Table 3 are indicated here: \* Evaporation Insensitive (EI) species. \*\* Evaporation Sensitive (ES) species.

DRP No	Sample no	ID	Family	Tribe	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
ASB 340	Zk-EN 34	<i>Connochaetes</i>	Bovidae	Alcelaphini **	0.4	-0.5
ASB 283	Zk-EN 27	<i>Damaliscus</i>	Bovidae	Alcelaphini**	0.9	1.2
ASB 262	Zk-EN 19	<i>Megalotragus</i>	Bovidae	Alcelaphini**	2.5	-0.1
ASB 341	Zk-EN 36	<i>Gazella granti</i>	Bovidae	Antilopini**	-5.7	-0.8
ASB 264	Zk-EN 20	<i>Gazella</i> (other)	Bovidae	Antilopini**	-4.7	4.6
ASB 248	Zk-EN 16	<i>Gazella</i> (other)	Bovidae	Antilopini**	-7.7	4.2
ASB 139	Zk-EN 5	<i>Gazella</i> (other)	Bovidae	Antilopini**	-5.5	5.2
ASB 116	Zk-EN 51	<i>Gazella granti</i>	Bovidae	Antilopini**	-3.3	3.2
ASB 220	Zk-EN 52	<i>Gazella</i>	Bovidae	Antilopini**	-8.0	3.1
	Zk-EN 53	<i>Gazella</i>	Bovidae	Antilopini**	-6.4	-2.0
ASB 184	Zk-EN 54	<i>Gazella</i>	Bovidae	Antilopini**	-4.2	2.3
ASB 259	Zk-EN 18	Bovini	Bovidae	Bovini	0.7	0.3
ASB 236	Zk-EN 14	Bovini	Bovidae	Bovini	1.8	-2.2
ASB 226	Zk-EN 13	Bovini	Bovidae	Bovini	-2.3	0.1
ASB 206	Zk-EN 12	Bovini	Bovidae	Bovini	2.5	2.2
ASB 194	Zk-EN 10	Bovini	Bovidae	Bovini	-0.9	0.1
ASB 178	Zk-EN 7	Bovini	Bovidae	Bovini	0.9	1.7
ASB 134	Zk-EN 4	<i>Pelorovis</i>	Bovidae	Bovini	-0.1	5.8
ASB 370	Zk-EN 42	<i>Pelorovis</i>	Bovidae	Bovini	0.8	0.1
	Zk-EN 61	Bovini	Bovidae	Bovini	2.7	3.2
ASB 96	Zk-EN 62	Bovini	Bovidae	Bovini	1.2	1.3
	Zk-EN 63	Bovini	Bovidae	Bovini	3.3	0.4
ASB 26	Zk-EN 64	Bovini	Bovidae	Bovini	0.0	0.3
ASB 305	Zk-EN 31	<i>Chlorocebus</i>	Cercopithecidae	Cercopithecini	-8.9	-0.6
ASB 192	Zk-EN 9	Hippotragini	Bovidae	Hippotragini	1.1	3.8
	Zk-EN 65	Hippotragini	Bovidae	Hippotragini	0.1	0.8
ASB 388	Zk-EN 44	<i>Kobus</i>	Bovidae	Reduncini*	2.3	1.7
ASB 381	Zk-EN 43	<i>Kobus</i>	Bovidae	Reduncini*	1.9	2.1
ASB 360	Zk-EN 41	<i>Kobus</i>	Bovidae	Reduncini*	-3.0	-2.0
ASB 357	Zk-EN 1	<i>Kobus</i>	Bovidae	Reduncini*	1.2	0.6
ASB 331	Zk-EN 33	<i>Kobus</i>	Bovidae	Reduncini*	0.3	0.6
ASB 299	Zk-EN 29	<i>Kobus</i>	Bovidae	Reduncini*	0.2	0.1
ASB 273	Zk-EN 23	<i>Kobus</i>	Bovidae	Reduncini*	1.1	1.8
ASB 186	Zk-EN 8	Reduncini	Bovidae	Reduncini*	0.3	0.3
ASB 124	Zk-EN 2	Reduncini	Bovidae	Reduncini*	-5.7	3.7
ASB 6	Zk-EN 66	<i>Kobus</i>	Bovidae	Reduncini*	1.8	1.2
ASB 132	Zk-EN 67	<i>Kobus</i>	Bovidae	Reduncini*	-2.6	2.5
ASB 182	Zk-EN 68	<i>Kobus</i>	Bovidae	Reduncini*	3.1	1.4
	Zk-EN 69	<i>Kobus</i>	Bovidae	Reduncini*	-0.2	2.0
ASB 390	Zk-EN 45	<i>Theropithecus oswaldi</i>	Cercopithecidae	Papionini	-0.1	-0.4
ASB 130	Zk-EN 3	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-6.5	1.5
ASB 356	Zk-EN 38	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-11.4	4.7
ASB 280	Zk-EN 26	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-3.7	3.7
ASB 414	Zk-EN 47	<i>Elephas</i>	Elephantidae*		-1.4	-1.3
ASB 255	Zk-EN 17	<i>Hippopotamus</i>	Hippopotamidae*		-1.0	-0.5
ASB 155	Zk-EN 70	<i>Hippopotamus</i>	Hippopotamidae*		-1.5	-3.6
ASB 9	Zk-EN 71	<i>Hippopotamus</i>	Hippopotamidae*		-1.4	-6.3
ASB 279	Zk-EN 25	<i>Hystrix</i>	Rodentia		-1.6	-0.2
ASB 269	Zk-EN 22	<i>Hystrix</i>	Rodentia		-8.0	-0.9
ASB 392	Zk-EN 46	<i>Phacochoerus</i>	Suidae*		-0.4	1.2
ASB 322	Zk-EN 32	<i>Kolpochoerus majus</i>	Suidae*		-0.3	-0.5
ASB 268	Zk-EN 21	<i>Kolpochoerus majus</i>	Suidae*		0.2	0.9
ASB 242	Zk-EN 55	<i>Giraffa</i>	Giraffidae**		-8.5	1.3
ASB 224	Zk-EN 56	<i>Giraffa</i>	Giraffidae**		-8.9	8.4
ASB 176	Zk-EN 57	<i>Equus</i>	Equidae*		1.2	1.2
ASB 355	Zk-EN 39	<i>Equus</i>	Equidae*		0.4	2.9
ASB 342	Zk-EN 37	<i>Equus</i>	Equidae*		1.1	3.4
ASB 177	Zk-EN 58	<i>Equus</i>	Equidae*		1.0	0.6
ASB 178	Zk-EN 59	<i>Equus</i>	Equidae*		-0.6	-0.4
ASB 179	Zk-EN 60	<i>Equus</i>	Equidae*		1.0	1.3
ASB 165	Zk-EN 6	<i>Diceros</i>	Rhinocerotidae*		-5.5	-1.0
ASB 110	Zk-EN 72	<i>Elephas</i>	Elephantidae*		-0.4	-0.4

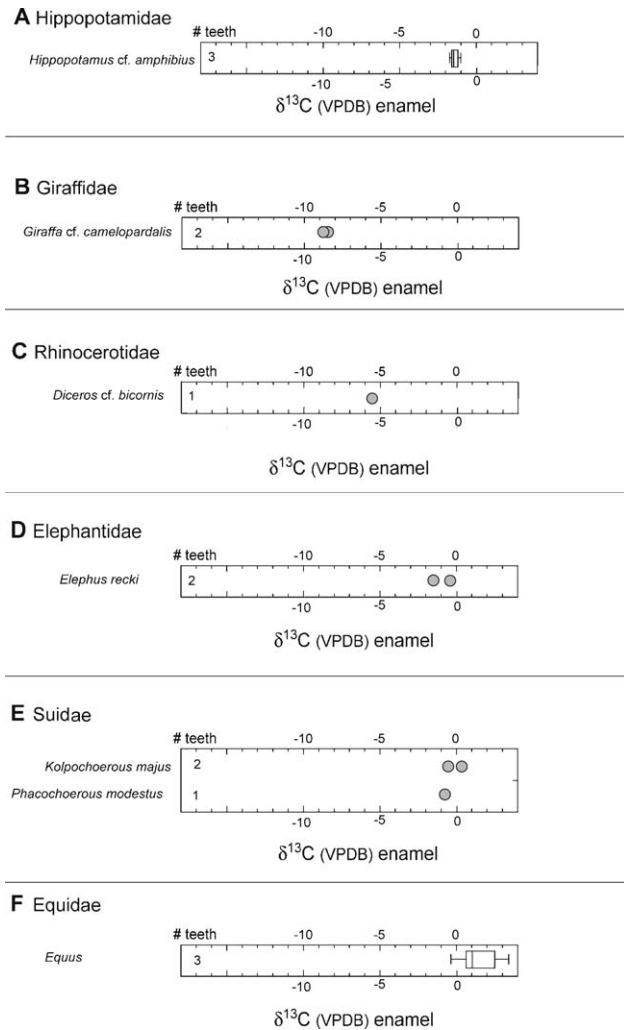


Fig. 2. Box plot of  $\delta^{13}\text{C}_{\text{enamel}}$  values (‰) of large mammal teeth from the Asbole fauna. The edges of the box represent quartile values, the horizontal line indicates the total range and the median values are represented by a vertical line within the box.  $\delta^{13}\text{C}_{\text{enamel}}$  values for taxa represented by one or two samples are plotted as individual circles for each analysis.

teeth clearly reflect dietary partitioning (Lee-Thorp, 1989; Bocherens et al., 1996; Cerling and Harris, 1999; Cerling et al., 2003a; Kingston and Harrison, 2007) with *Ceratotherium simum* yielding  $\delta^{13}\text{C}_{\text{enamel}}$  values consistent with a variable to obligate C4 grazing diet averaging about 0.0‰ and *Diceros bicornis* (black rhino) with a C3 browsing diet with a mean of about  $-10.5\text{‰}$  (Kingston and Harrison, 2007). Our analysis of the rhino tooth enamel from the Asbole faunal zone is consistent with *Diceros cf. D. bicornis*. The  $\delta^{13}\text{C}_{\text{enamel}}$  values of *D. bicornis* from arid habitats such as Amboseli National Park are typically more  $^{13}\text{C}$ -enriched than average (Bocherens et al., 1996), suggesting that Asbole was near the arid end of the habitat preference of *Diceros*, although this is based on a single specimen from Asbole. The fossil rhinocerotids from the late Miocene and early Pliocene western margin deposits at Gona show the same distinction between a browsing and a grazing species as the modern forms (Levin et al., 2008), to which they are probably related (Geraads, 2005). On the other hand, Cerling and Harris (1999) suggested that even the most positive  $\delta^{13}\text{C}_{\text{enamel}}$  values recorded for *D.*

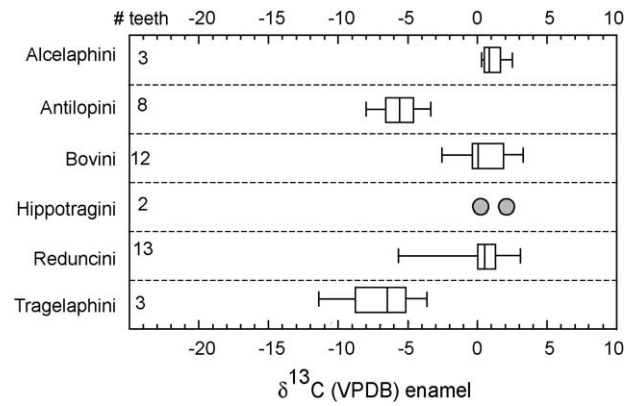


Fig. 3. Box plot of  $\delta^{13}\text{C}_{\text{enamel}}$  values (‰) of bovid teeth from the Asbole (see Fig. 2).

*bicornis* in the Plio-Pleistocene of the Turkana Basin, Koobi Fora is  $10.2\text{‰}$  and by Bocherens et al. (1996) from Amboseli range from  $-10$  to  $-7\text{‰}$ . So, the enriched  $\delta^{13}\text{C}_{\text{enamel}}$  values of the Asbole *Diceros* probably indicate that they ingested a significant fraction of C4 dicots or CAM plants which are abundant in semiarid settings.

### 5.2. Elephantidae

The fossil Elephantidae from Asbole consists only of *Elephas* (Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the only two Elephantidae analyzed averages  $-0.9\text{‰}$  ( $n = 2$ ).  $\delta^{13}\text{C}_{\text{enamel}}$  values of Elephantidae from the Asbole fauna zone indicate that the diets of these large-bodied herbivores were dominated by C4 grass (i.e., 86% of the total diet were C4 grasses; Table 2). These results and others suggesting variable grazing to intermediate foraging isotopic strategies of late Miocene and Pliocene fossil elephantids (Zazzo et al., 2000) contrast with the  $\delta^{13}\text{C}_{\text{enamel}}$  of extant African *Loxodonta*, which indicate a diet generally dominated by C3 biomass (Cerling et al., 1999). Hypotheses to explain this discrepancy include reduction of C4 grasslands at the terminal Pliocene resulting in increased competition from other grazing taxa or incorrect phylogenetic assumptions linking fossil grazing lineages with modern browsing elephants (Cerling et al., 1999).

### 5.3. Equidae

The fossil Equidae from Asbole are represented by the genus *Equus* and because of limited fossil finds, further specific identification is not possible (Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the *Equus* from the Asbole Fauna averages  $0.7 \pm 0.7\text{‰}$  ( $n = 6$ ). The isotopic data suggest that the dietary strategies of the Equids grazed primarily on C4 grass (i.e., 98% of the total diet, Table 2). These results are consistent with isotopic data of equid enamel younger than about 7 Ma in tropical and sub-tropical Africa, including all modern samples, which yield  $\delta^{13}\text{C}_{\text{enamel}}$  values in the range of  $-2\text{‰}$  to  $+3\text{‰}$ , indicating C4 dominated to exclusive C4 grass diets (Morgan et al., 1994; Bocherens et al., 1996; Cerling et al., 1997b, 2003a, 2003b; Kingston and Harrison, 2007).

Table 2

The values of Faunal abundance, average  $\delta^{13}\text{C}_{\text{ecosystem}}$  and average food consumption (kg/day) is rounded up to one significant digit after the decimal and C4 proportion in the diet to zero significant digits after the decimal. Daily food consumption and C4 proportion in the diet of Asbole Fauna used in the calculation of  $\delta^{13}\text{C}_{\text{ecosystem}}$ . Average weight of animals (kg) and average food consumption (kg/day) of Elephantidae: *Hippopotamus amphibius*, *Syncerus caffer*, *Gazella granti*, *Gazella thomsoni*, *Aepyceros melampus* and *Connochaetes taurinus* are from Delany and Happold (1979). These data are used to calibrate the relationship between body mass and average food consumption used for the rest of the taxa.

Fauna	Fauna abundance (%)	Average $\delta^{13}\text{C}_{\text{enamel}}$ (‰)	C4 proportion in the diet (%)	Weight of animal (kg)	Average food (consumption (kg/day))
Elephantidae	1.2	−0.9	86	3500–6500	41.6
Rhinocerotidae	4.2	−5.5	54	800–1400	3.3
Equidae	2.0	0.7	98	270–400	1.3
Suidae	17.1	−0.2	92.5	45–100	0.4
Hippopotamidae	3.1	−1.3	83	510–3200	18.0
Giraffidae	0.3	−8.7	31	1180–1930	4.3
Theropithecus	4.0	−0.9	86	13–21	0.5
Colubus	12.5	−9.6	24	5.0–14.0	0.6
Papio	1.7	−7.6	39	13–21	0.7
Chlorocebus	1.7	−8.9	29	4.0–8.0	0.01
Alcelaphini	2.6	1.3	102	140–260	4.0
Tragelaphini	3.6	−7.2	41	30–80	0.4
Reduncini	28.6	0.1	93	43–65	0.3
Hippotragini	1.0	0.6	97	400–500	1.7
Bovini	10.9	0.9	99	250–850	8.0
Antilopini	5.2	−5.7	52	38–67	1.1

#### 5.4. Suidae

In addition to their key role in biochronology, pigs are frequently utilized as paleoecological indicators. The fossil Suidae from Asbole are represented by *Metridiochoerus modestus* and *Kolpochoerus majus* (the most common species in Asbole; Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the Suidae average  $-0.2 \pm 0.9\text{‰}$  ( $n = 3$ ). The suid specimens analyzed consist of two upper molars of *Kolpochoerus majus* and one lower third molar of *Metridiochoerus* sp.  $\delta^{13}\text{C}_{\text{enamel}}$  values from both species indicate exclusively C4 grazers (i.e., 92% C4 grasses, Table 2). By contrast, extant suids from eastern Africa display the full spectrum of herbivore  $\delta^{13}\text{C}_{\text{enamel}}$  values. *M. modestus* had a diet based on grasses, as its close relative the warthog, but it is surprising to find similar dietary signals in *K. majus* that had much lower crowned teeth (although higher than in *Potamochoerus* or *Sus*) and M3s that are not more elongated than those of the early members of *K. limnetes*, suggesting that increase in molar height and length are not required for grazing (Harris and Cerling, 2002).

#### 5.5. Giraffidae

The fossil Giraffidae from Asbole are represented by *Giraffa* cf. *G. camelopardalis* (Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the Giraffidae averages  $-8.7 \pm 0.3\text{‰}$  ( $n = 2$ ). The isotopic data from both *Giraffa* specimens, indicate diets dominated by C3 plants with 31% C4 component, consistent with isotopic data from all modern and fossil *Giraffa* (Cerling and Harris, 1999; Kingston and Harrison, 2007; Cerling et al., 2008), showing that the specialized selective feeding strategy of the giraffe was already established in the Pliocene. Harris and Cerling (1998) report that late Miocene and early Pliocene sivatheres from East Africa have exclusive browsing isotopic

signatures, but they become grazers in the late Pliocene. Similarly, a carbon isotopic signature of  $-1.2\text{‰}$  was reported for an enamel fragment attributed to cf. *Sivatherium* recovered from the Pliocene GWM-5 block ( $\sim 4.3\text{--}3.7$  Ma) at Gona (Semaw et al., 2005), indicating a foraging strategy dominated by C4 grazing in the early to middle Pliocene.

#### 5.6. Hippopotamidae

Hippos are quite rare in Asbole, and are represented by *Hippopotamus* cf. *H. amphibius* L. which is indistinguishable from the living *H. amphibius*, but no diagnostic feature allows a specific identification (Geraads et al., 2004). The average  $\delta^{13}\text{C}_{\text{enamel}}$  value of the Asbole hippos is  $-1.3 \pm 0.6\text{‰}$  ( $n = 3$ ). The isotopic data indicate diets dominated by C4 plants (i.e., 83% C4 grasses). Reconstruction of fossil hippo diets has often been based on observations of cranio-dental morphology (Boisserie et al., 2005). Grazing or browsing diets have been assessed by using the degree of hypsodonty of the cheek teeth, the morphology of the anterior dentition (Coryndon, 1977), and general morphological comparisons with modern species (Coryndon, 1967). However, the degree of hypsodonty is a weak variable in hippos and cannot be used to distinguish dietary adaptations (Solounias and Dawson-Saunders, 1988; MacFadden et al., 1999). Stable carbon isotope analyses of tooth enamel, on the other hand, provide a more reliable information on fossil hippo diet. So far, provided data (Morgan et al., 1994; Bocherens et al., 1996; Kingston, 1999a; Zazzo et al., 2000; Franz-Odenaal et al., 2002; Cerling et al., 2003a; Schoeninger et al., 2003; Boisserie et al., 2005) conclude that the  $\delta^{13}\text{C}_{\text{enamel}}$  is rather variable in the modern form ( $-10.9$  to  $+1\text{‰}$ ) and that this range of value was almost the same since the Late Miocene (Boisserie et al., 2005). Our isotopic data suggest that the dietary strategies of the Hippopotamidae at

Asbole were grazing and fed primarily on C4 grass (i.e., here all the three data points indicate grazing on C4 grasses), likely reflecting the aridity of Asbole and the resulting predominance of C4 vegetation. On the other hand, both C4 dominated (Levin et al., 2008) and mixed C3-C4 diets have also been reported in different parts of Africa (e.g., Toros-Menalla, Chad; Boissier et al., 2005).

### 5.7. Bovidae

African bovids are a diverse group of mammals that live in habitats ranging from tropical rainforest to deserts (Cerling et al., 2003c). Evolutionary pattern of this family has been linked specially to environmental change and faunal turnover during the Miocene and Plio-Pleistocene (Vrba, 1980, 1985, 1995; Bobe and Eck, 2001; Alemseged, 2003; Kingston and Harrison, 2007). As in most African paleontological sites, bovids are the most abundant mammalian taxa in the Asbole faunal assemblage, comprising 52% of the analyzed sample. The samples from Asbole include representatives of the tribes Tragelaphini, Bovini, Hippotragini, Alcelaphini, Reduncini, and Antilopini (Fig. 3).

Tragelaphini from Asbole are represented by the genus *Taurotragus* and *Tragelaphus scriptus* (Geraads et al., 2004), but all specimens analyzed here are probably from *Taurotragus*. Their  $\delta^{13}\text{C}_{\text{enamel}}$  values average  $-7.2 \pm 3.9\text{‰}$  ( $n = 3$ ). These isotopic data suggest that *Taurotragus* at Asbole was adapted to a wide range of diets with a suggested preference for browsing, but at least with significant C4 component in the diet (41% C4 grasses). Modern tragelaphines (i.e., nyala, kudu, eland, and bushbuck) are generally browsers with low-crowned teeth and digestive tracts adapted for nutritious vegetation and fruit (Kingdon, 1982, 1997). Isotopic analyses of enamel and horn keratin of extant tragelaphines from South and East Africa indicate diets dominated by browsing (i.e., *Tragelaphus imberbis* and *Tragelaphus strepsiseros*), although there is evidence for mixed C3/C4 in *Taurotragus oryx* (Lee-Thorp, 1989; Cerling et al., 2003b; Sponheimer et al., 2003), and this is in agreement with our results of the Asbole Tragelaphini.

Bovini are represented at Asbole by an incomplete skull of the genus *Bos* (Geraads et al., 2004), but it is likely that some, if not most, of the teeth sampled here are from a buffalo, either *Syncerus caffer* or a long-horned form close to *Pelorovis*.  $\delta^{13}\text{C}_{\text{enamel}}$  values of the samples analyzed have an average  $\delta^{13}\text{C}_{\text{enamel}}$  value of  $0.9 \pm 1.8\text{‰}$  ( $n = 12$ ). The isotopic data suggest that the dietary strategies of Bovini were generally grazing and fed primarily on C4 grass (i.e., 99% C4 grass).

Alcelaphini from Asbole are represented by cf. *Connochaetes* sp. and *Damaliscus niro* (Geraads et al., 2004) although they are not common. The tribe Alcelaphini today includes wildebeest, topi, hirola and kongoni; all are variable to obligate grazers (Gagnon and Chew, 2000), inhabiting open woodland or edaphic and secondary grasslands (Estes, 1991).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the three samples from Asbole average  $1.3 \pm 1.1\text{‰}$  ( $n = 3$ ). Our isotopic data suggest that the dietary strategies of the Alcelaphini were grazing and fed exclusively on C4 grass (i.e., 100% C4 grass), like their modern relatives (Cerling et al.,

2003c; Sponheimer et al., 2003) although Kingston and Harrison (2007) indicate that early lineages or individual taxa of small-sized alcelaphines may not have been as committed to specialized grazing niches as their modern-day counterparts.

The fossil Reduncini from Asbole are represented by *Kobus kob* (the most common species in Asbole) and *Redunca* sp. (Geraads et al., 2004) but molars of these species are almost of the same size and could not be identified below tribal level.  $\delta^{13}\text{C}_{\text{enamel}}$  values of the samples analyzed have an average of  $0.1 \pm 2.5\text{‰}$  ( $n = 13$ ). These isotopic data suggest that the dietary strategies of the Reduncini were generally C4 grazers, (i.e., 93% C4 grasses) as do most modern reduncines (Levin et al., 2008). One of our samples has a  $\delta^{13}\text{C}_{\text{enamel}}$  value of  $-5.7\text{‰}$ , suggesting the presence of C3 plants in its diet, but we note that one species of *Redunca redunca* (Bohor reedbuck) sampled from the Bale Mountains in Ethiopia had a  $\delta^{13}\text{C}_{\text{enamel}}$  value of  $-7.1\text{‰}$ , suggesting that some reduncines in less arid environments may consume C3 vegetation (Levin et al., 2008).

Hippotragini are represented in Asbole solely by the genus *Oryx* (Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the samples analyzed have an average of  $0.6 \pm 0.7\text{‰}$  ( $n = 2$ ). These isotopic data suggest that the dietary strategies of Hippotragini were generally grazing and fed primarily on C4 grass, like modern representatives of this tribe (Kingston and Harrison, 2007).

Antilopini from Asbole are represented by *Gazella* cf. *G. thomsoni* and *Gazella* aff. *granti* (Geraads et al., 2004).  $\delta^{13}\text{C}_{\text{enamel}}$  values of the samples analyzed here have an average of  $-5.7 \pm 1.7\text{‰}$  ( $n = 8$ ), but individual specimens could not be identified to the species level. The isotopic data suggest that Antilopines were adapted to a wide range of diets more preferably browsing with significant arid-adapted C4 vegetation and/or some C4 biomass (i.e., 52% C4 grasses). Modern gazelles, dibatag, and gerenuk inhabit desert, grassland, savanna and open woodland biomes (Gentry, 1992), and have diets ranging from variable grazers dominated by C4 grass for Thomson's gazelle (*G. thomsoni*) to greater emphasis on browsing (*G. granti*), while the gerenuk (*Litocranius walleri*) is an essentially pure C3 browser. Studies of fossils from Eastern and Southern Africa (Lee-Thorp, 1989; Sponheimer et al., 1999; Gagnon and Chew, 2000; Cerling et al., 2003c) have indicated a similar range of some of the Antilopine diets. Some had mixed feeding strategies with emphasis on browsing (i.e., Grant's gazelle), others had a variable isotopic signature, but one dominated by C4 grass (i.e., Thomson's gazelle) while others had  $\delta^{13}\text{C}_{\text{enamel}}$  values corresponding to a diet of essentially pure C3 browse (i.e., gerenuk).

## 6. Paleoenvironmental interpretations based on faunal abundance

The faunal composition of the Asbole fauna, in and of itself allows drawing some paleoecological inferences. Fig. 4 shows the relative abundances of the various mammalian families, based upon all identifiable specimens, collected and uncollected ( $n = 642$ ). Although comparable quantitative data are badly lacking in Eastern Africa, two significant points stand out about the Asbole fauna: the scarcity of hippos and the high



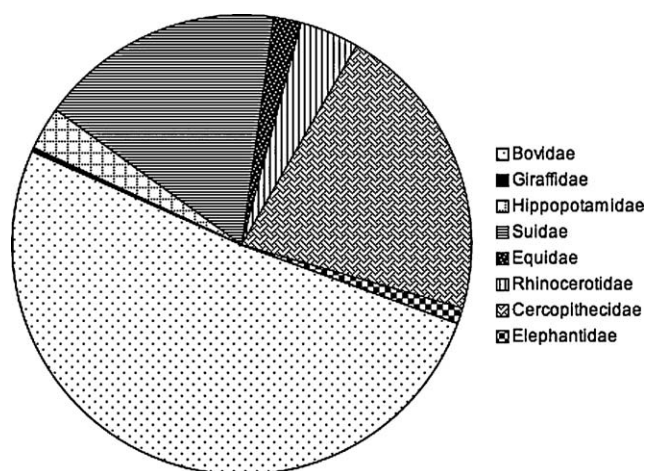


Fig. 4. Relative abundance of the mammalian families from the Asbole fauna, excluding rodents and carnivores.

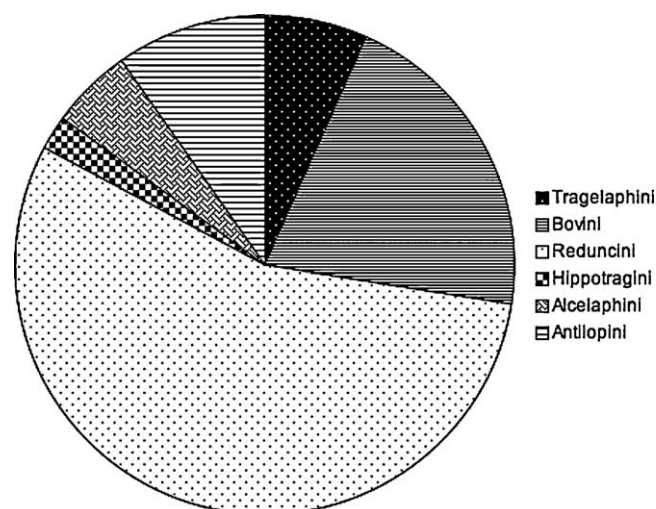


Fig. 5. Relative abundance of the bovid tribes from the Asbole fauna.

proportion of cercopithecids represented by five species, with colobines as the dominant primate group. The abundance of arboreal primates is an indicator of high tree cover (Reed, 1997), and this is especially true at Asbole where the primates mostly consist of colobines, an arboreal group specialized in leaf eating (almost 2/3 of the total primates are colobines; Frost and Alemseged, 2007). The low frequency of hippos contrasts with their abundance in most other eastern African vertebrate fossil sites; it can perhaps be explained by the absence of perennial streams or lakes large enough for these animals.

The relative abundance of the various bovid tribes (Fig. 5) is often used as a paleoecological indicator (Vrba, 1980), as it is very informative. Here, the very high proportion of reduncines (mostly *Kobus*) very likely points towards the dominance of a seasonally inundated open environment, such as a floodplain or even swamp that would also suit the bovines which are also quite common. In contrast, indicators of drier grasslands in uplands, such as alcelaphines and antilopines, are rare. We may also note the low frequency of tragelaphines and the absence of the impala; this might suggest poor representation of a suitable ecotone between forest and grassland, but is consistent with the interpretation of narrow gallery forest or wooded environment with a sharp boundary to a widespread open environment.

The other mammals provide less clear ecological indications, but support the previous ones. Among rhinos, the browser or mixed-feeder *Diceros* is more common than the grazer *Ceratotherium*. Although there was certainly a size bias in the collection of rodents, the common *Thryonomys* is a mesic-adapted genus found in swamps and other moist habitats, and similar conditions may suit the other taxa, namely *Tachyoryctes*, *Otomys*, and *Arvicanthis*. Although they are rare and not very good ecological indicators, the carnivores at Asbole do not contradict these interpretations.

## 7. Faunal-abundance-weighted $\delta^{13}\text{C}_{\text{ecosystem}}$ value

In general, our carbon isotopic results shows that C4 grasses were significant components of the total diet of the Asbole

fauna, but to better account for the average carbon isotopic value of the ecosystem, we calculate a weighted average  $\delta^{13}\text{C}_{\text{ecosystem}}$  value using the average  $\delta^{13}\text{C}_{\text{enamel}}$  of each taxon weighted by faunal abundance and the estimated daily food intake of each large vertebrate (>50 kg) taxon (Table 2). This value approximates the  $\delta^{13}\text{C}$  value of the total vegetation present in an ecosystem, or at least that consumed by large vertebrates. Using the data in Table 2, the  $\delta^{13}\text{C}_{\text{ecosystem}}$  value for the Asbole faunal zone was  $-14.9\text{‰}$ , which underscores the near-absolute dominance of C4 vegetation in the region sampled by the total large vertebrate fauna (C4 vegetation ranges from  $-19$  to  $-9\text{‰}$  with a mean of  $-13\text{‰}$ ). Using these endmember isotopic compositions of vegetation, the proportion of C3 vegetation at Asbole is estimated as 14%. Sensitivity tests were done to check the effect on the calculated  $\delta^{13}\text{C}_{\text{ecosystem}}$  value by categorically including/excluding primates, which are comparatively abundant but consume little biomass in comparison to large vertebrates. Including primates in this analysis shows little effect (i.e.,  $-0.3\text{‰}$  change in  $\delta^{13}\text{C}_{\text{ecosystem}}$ ), which contributes an additional 2% to the estimated C3 vegetation cover. The faunal abundance weighted average  $\delta^{13}\text{C}_{\text{ecosystem}}$  values in this study remains to be calibrated with modern analogs using robust data sets of natural faunal abundance and isotopic composition. To better calibrate the data and obtain a representation of all the species, a large range of environments should be considered.

## 8. Oxygen isotopic composition

### 8.1. Observed $\delta^{18}\text{O}$ values

The wide range of  $\delta^{18}\text{O}$  values of tooth enamel from the Asbole fauna ( $-6.3$  to  $+8.4\text{‰}$ ; Fig. 6) indicates significant variation in the oxygen isotope composition of animal water sources, food, and thermophysiological adaptations (e.g., Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999b). Given the theoretical constraints on  $\delta^{18}\text{O}_{\text{enamel}}$ , we can distinguish “obligate drinkers” that get water from river or lakes, and

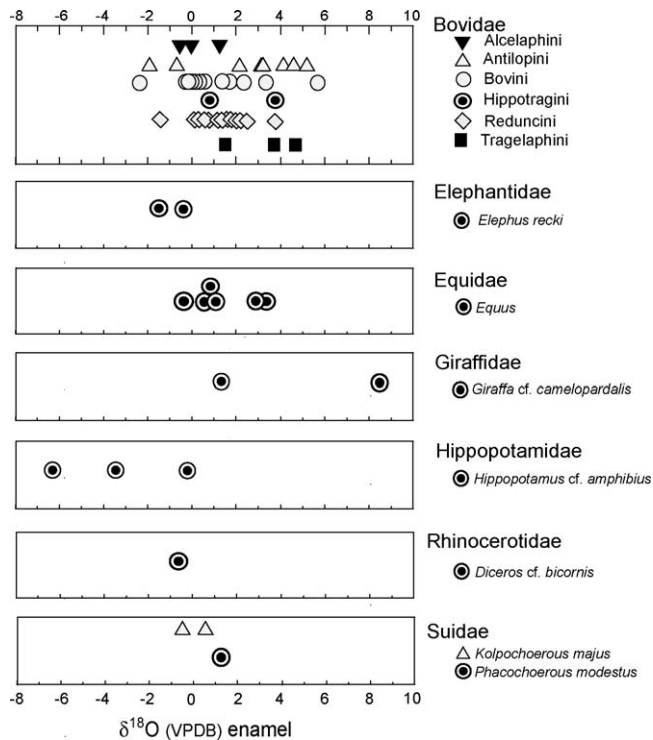


Fig. 6.  $\delta^{18}\text{O}_{\text{enamel}}$  of herbivores teeth from the Asbole fauna (see Fig. 2).

thus track  $\delta^{18}\text{O}$  of meteoric water most faithfully (e.g., Reduncini, *Equus* and suids) from other “non-obligate drinkers” that obtain most of their water from leaves in which  $^{18}\text{O}$  is enriched compared to the local meteoric water (e.g., *Giraffa*). Still others are aquatic, in which  $^{18}\text{O}$  is significantly depleted in relation to other herbivores (e.g., *Hippopotamus*; Levin et al., 2006).  $\delta^{18}\text{O}_{\text{enamel}}$  values of the Asbole fossils range between  $-6.3$  and  $+8.4\%$ , reflecting all drinking habits of animals from non-obligate drinkers (i.e., *Giraffa*, Antilopini and Tragelaphini) through intermediates (i.e., Hippotragini and Bovini) to obligate drinkers (i.e., Reduncini, Alcelaphini, hippopotamids, rhinocerotids, elephantids and to less extent equids and suids). The range of  $\delta^{18}\text{O}_{\text{enamel}}$  values also differs between taxa, which may be explained by the degree of adaptation of the animal, specialization of different taxa in different ecotone or differences in seasonal migrations. The largest range of  $\delta^{18}\text{O}_{\text{enamel}}$  within individual taxon occurs in Bovini, Antilopini and *Giraffa* ( $8.0$  [ $n = 12$ ],  $7.2$  [ $n = 8$ ] and  $7.2\%$  [ $n = 2$ ], respectively), while the rest of the fauna shows lower ranges of  $\delta^{18}\text{O}_{\text{enamel}}$  values between  $0.7$ – $5.8\%$  ( $n$  between 1 and 13). *Hystrix*, *Elephas*, *Chlorocebus*, *Theropithecus* and *Diceros* are represented by a single value. The narrow range of the  $\delta^{18}\text{O}$  of the Asbole rodentia would indicate its potential to provide localized paleoenvironmental signals at a finer scale than other lines of evidence (Reed, 2007).

## 8.2. Estimating paleo-aridity using $\delta^{18}\text{O}_{\text{enamel}}$

We applied the novel method of Levin et al. (2006) to estimate the paleo-aridity at Asbole based on interpretation of the  $\delta^{18}\text{O}_{\text{enamel}}$  values of evaporation sensitive (ES) and

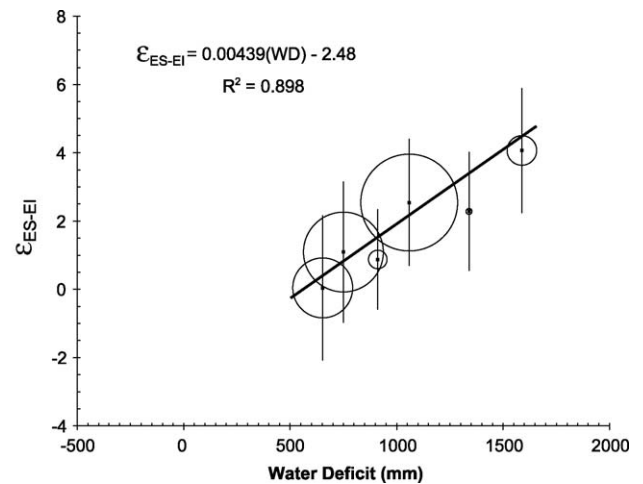


Fig. 7. Relationship between aridity (measured as water deficit, WD) and the oxygen isotopic enrichment between evaporation sensitive (ES) and evaporation insensitive (EI) taxa ( $\epsilon_{\text{ES-EI}}$ ), based on the calibration data in Levin et al. (2006). From the Asbole data set, we chose only the clearly identified taxa for the ES (*Syncerus caffer*, *Oryx beisa*, *Giraffa camelopardalis*, *Madoqua kirkii*, *Gazella granti*) and EI (*Loxodonta africana*, *Hippopotamus amphibius*, *Equus burchelli*, *Aepyceros melampus*, *Potamochoerus larvatus*, *Diceros bicornis*, *Phacochoerus africanus*, *Papio anubis*) categories. Each point represents a location, with climate determined from East African Meteorological Department data. Based on the suggestion of minimum sample size required, only locations from this calibration data set with  $>10$  combined ES and EI samples are used in the regression, which is weighted to the total number of ES and EI samples from each location. The size of the circle surrounding each point is proportional to the total number of samples from that location, while the error bars represent the average of the standard deviations for ES and EI samples from each location. The regression slope ( $0.00439/\text{mm}$ ) corresponds well to the suggested value based on the pooled or common slope of individual regressions from Levin et al. (2006;  $0.00501/\text{mm}$ ).

evaporation insensitive (EI) taxa. EI taxa are those that are obligate drinkers, and thus track the  $\delta^{18}\text{O}$  value of local meteoric water as their main source of oxygen in body water. Meanwhile ES taxa are the non-obligate drinkers whose main source of oxygen is from the evaporatively  $^{18}\text{O}$ -enriched water in leaves. Because the  $\delta^{18}\text{O}$  value of leaf water increases by evaporation and this increase is proportional to aridity, the oxygen isotopic enrichment between ES and EI taxa ( $\epsilon_{\text{ES-EI}}$ ) also increases with aridity, and is independent of the isotopic composition of local meteoric water, making it an ideal paleoaridity index in terrestrial environments. Water deficit (WD) values are used to characterize environmental aridity, which is the difference between potential evapotranspiration (PET) and the mean annual precipitation (MAP). Fig. 7 shows the calibration data set from Levin et al. (2006) of  $\epsilon_{\text{ES-EI}}$  to water deficit from a range of climates in East Africa. Based on this calibration, and our estimate of the  $\epsilon_{\text{ES-EI}}$  determined from the Asbole fauna, the mean annual water deficit of the Middle Pleistocene at Asbole is calculated to be  $1470$  mm. Thus, the paleoclimatic condition of Asbole is similar to that near the most arid end members of the modern calibration data set: Ologesaile (Magadi station;  $1341$  mm) and the Turkana Basin (Lodwar station;  $1588$  mm). We also calculated WD for climate stations near Asbole in Ethiopia for comparative modern analogs (Table 3). WD values from Gewane, Bati, Dubti, Ziway

Table 3

Calculated Water Deficit (WD) from the highlands and lowlands of the Rift Valley of Ethiopia, compared to the estimated value for the Middle Pleistocene at Asbole based on  $\epsilon_{ES-EI}$ . MAP: mean annual precipitation; PET: potential evapotranspiration; WD: water deficit (where  $WD = PET - MAP$ ). Meteorological data of Gewane, Bati, Dubti, Ziway and Desse are adopted from the Ethiopian National Meteorological Agency.

Location	MAP	PET	WD	Elevation (m)
Based on modern climate data				
Desse	1230	721	−509	2510
Bati	916	960	44	1502
Ziway	740	930	191	1643
Gewane	417	1906	1435	618
Dubti	195	3143	2948	503
Fossil locality based on $\epsilon_{ES-EI}$				
Asbole			1470	

and Desse indicate a wide variation environmental aridity between Ethiopian Rift Valley highland and the lowlands. Of these data, the paleo-water deficit for Asbole is most similar to the nearby Gewane station, indicating little change in aridity in this part of the Ethiopian Rift since the Middle Pleistocene. This interpretation is also supported by the dominance of arid-adapted C4 vegetation evident from the  $\delta^{13}C_{ecosystem}$  value discussed above.

## 9. Conclusions

Isotopic analyses of mammalian herbivore taxa from the “Asbole faunal zone” (0.8–0.64 Ma), including multiple samples of 15 taxa representing 9 different families, were sampled to analyze dietary adaptations and reconstruct the range of paleoenvironmental conditions in which the fauna lived. The Asbole carbon isotopic data indicate a wide range of foraging strategies, across the entire spectrum of pure C4 to C4 – dominated diet, mixed C3/C4 diet and C3 – dominated diet.

The stable oxygen isotope data signifies that most of the species are evaporation insensitive which track the meteoric water faithfully, while a few species, such as *Giraffa*, Antilopini and Tragelaphini are evaporation sensitive and track the isotopic composition of vegetation consumed. Our estimate of the oxygen isotopic enrichment between these two groups ( $\epsilon_{ES-EI}$ ) determined from representative samples of the Asbole fauna is 3.7‰. This value provides an estimate of the mean annual water deficit of the Middle Pleistocene at Asbole to be 1470 mm, which is similar to the present day water deficit at the climate station of Gewane, in an arid climate.

Although no hominin remains have been found at Asbole thus far, the presence of abundant MSA archeological remains at Asbole (Alemseged and Geraads, 2000) shows that hominins were present in the area between 0.6 and 0.8 Ma. The very diverse nature of mammalian species at the site is rather unique and not common for the Middle Pleistocene: five primate species are encountered and overall primates are very abundant, while hippos are much less abundant than at many similarly-aged sites. Based on previous study, Alemseged and Geraads

(2000) suggested that overall, the ecological implications of the bovid assemblage recalls more some Pliocene sites than Pleistocene ones.

Based on carbon isotopic analysis of the large vertebrate fauna, combined with faunal abundance and dietary intake data, we interpret the overall environment at Asbole between 0.64 and 0.8 Ma to be an arid, C4 dominated open vegetation region, with an abundance of forest dwelling primates indicating the presence of isolated gallery forests flanking tributary streams (~14% C3 biomass). So, with these combined methodologies, we can elucidate a more detailed character of the “mosaic” of environments. By combining the stable isotopes, which emphasize the widespread open and xeric condition, with faunal abundance data, which indicated the presence of wooded environment as gallery forests along the main river (Geraads et al., 2004), we are able to obtain a more detailed picture than with a single proxy alone. More stable isotopic studies, specifically of the diverse primate fauna from Asbole, will be the next platform to better quantify the abundance and specific nature of the gallery forest environments.

It is generally accepted that environmental conditions in East Africa became more open and xeric through time in the Plio-Pleistocene, with cooler and drier conditions in the late Early Pleistocene (Coppens, 1975; Vrba, 1985, 1988, 1995). The stable carbon and oxygen isotope data presented here, in the context of similarly analyzed African Plio-Pleistocene sites, lends support to this hypothesis. Previous work at Asbole based on faunal abundance combined with the current study demonstrate that though major trends in environmental changes could be true, regional and local environmental variations were equally important. A good example is the abundant remains of water loving (reduncini) and forest dwelling (colobines) species at the Middle Pleistocene site of Asbole, compared to Andale in the Middle Awash Region, located not far from Asbole and with the same geological age, and documenting a similar fauna, but with very different proportions (Kalb et al., 1982). For example, among the bovids at this site, Reduncini is not the most common as this tribe is over taken by Tragelaphini, probably showing some local environmental distinction among the two proximal sites. These findings caution against oversimplification of Pleistocene environmental reconstructions based on single proxies at isolated localities.

## Acknowledgements

We thank the members of the Dikika Research Project for support in the field, and with the collection of vertebrate fossils. At the Authority for Research and Conservation of Cultural Heritage (ARCCCH) of the Ministry of Culture and Tourism, we thank Ato Jarra H/Mariam, Dr. Yonas Beyene and Mamitu Yilma for their cooperation and permission to sub-sample tooth enamel from the samples archived at the National Museum of Ethiopia. We also thank Zachary Atlas and Hanna Weldeselasse who helped with isotopic analyses in the Department of Geology at University of South Florida. We thank John M. Harris and an anonymous reviewer, who provided useful reviews of this paper.

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