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RESEARCH

Isotopic insights into the Early Acheulean (1.95 Ma–1.66 Ma) high-elevation paleoenvironments at Melka Kunture (Upper Awash Valley, Ethiopia)

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Abstract
In this paper, we present stable carbon and oxygen isotope analyses of fauna tooth enamel from Garba IVD (1.95 Ma) and Gombore IB (1.66 Ma), two Early Acheulean sites of Melka Kunture (Upper Awash, Ethiopia), and discuss faunal taxonomy and fossil pollen. Our aim is to infer the diet and habitat of the fossil fauna, as well as the environment of both sites, in order to provide a broader paleoecological reconstruction. During the Pleistocene, the vegetation of the highlands of Ethiopia belonged to the Dry evergreen Afromontane Forest and grassland complex, which is distinct from the savanna of lower elevations in eastern Africa. Our carbon isotopic results indicate that all the analyzed faunal taxa were grazers consuming C_4 plants, whereas oxygen isotopic results discriminate the taxa according to their semiaquatic or terrestrial habitats. These results are consistent with the taxonomic composition of the faunal assemblages and the palynological results, suggesting extended mountain grasslands in the landscape at Garba IVD. In contrast, the carbon isotopic results do not totally agree with the pollen paleoenvironmental reconstruction at Gombore IB, where the open vegetation was interrupted by forests and bushy vegetation. Stable isotope and pollen data provide different outcomes (feeding strategies vs. nearby plants) and have different temporal and spatial resolutions. This is relevant when reconstructing past environments by using independent proxies. Furthermore, isotopic comparisons with other Early Pleistocene paleontological and archaeological sites from eastern Africa indicate that all the analyzed taxa in common fed on C_4 plants and that their dietary strategies were not affected by variations linked to the difference in elevations.

Keywords Melka Kunture · Early Acheulean · Stable isotopes · Paleodiet · Paleoenvironment · Paleoecology

Highlights
• The 1.95–1.66 Ma fossil fauna from Garba IVD and Gombore IB was dominated by grazers and fed on C_4 plants.
• The 1.95–1.66 Ma Early Acheulean at Melka Kunture occurred in both open and closed environments in an Afromontane vegetation complex.
• The variable local vegetation did not impact on the feeding habits of the fossil fauna.

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Introduction

Multiple proxies, such as stable isotopes, dental wear, faunal abundance and taxonomy, fossil pollen and phytolith analysis, geomorphological studies, skeletal morphometrics, and ichnology, provide insights into mammalian diet, behavior, habitat, and environment, which provide a wealth of information for ancient ecological reconstructions.

To date, most environmental and ecological evidence derives from eastern African archaeological and paleontological sites at medium and low altitudes (Harris et al., 2008; van der Merwe, 2013; Ascari et al., 2018; Rivals et al., 2018; Uno et al., 2018; Negash et al., 2020) although few archaeological contexts are known at higher elevations (≥2000 m a.s.l.), such as Melka Kunture, Gadeb, and Melka Wakena in Ethiopia; Kilombe in Kenya; and Isimila in Tanzania. The occupation of the highland of Ethiopia has been interpreted in some case studies (Hovers et al., 2021). Based on the analysis of the lithic tools from Gadeb site, Clark and Kurashina (1979) hypothesized a seasonal movement of humans from the Rift to the highlands over long distances (>100 km) to exploit raw material. Subsequently, Clark (1987) suggested that humans explored the highlands to expand their ecological niche, with implications regarding diet and environmental resources. Recently, Mussi et al. (2016) used a multi-proxy approach to analyze the sequence of Gombore II site (Melka Kunture), suggesting that, at ~800–700 ka, the occupation of the Ethiopian highlands by *Homo erectus* occurred during warm climate phases.

The present study couples and crosschecks faunal taxonomy, fossil pollen, and new stable carbon and oxygen isotope analysis on faunal teeth from Early Acheulean Level D at Garba IV (Garba IVD) and level B at Gombore I (Gombore IB) to investigate the related paleoecology at 1.95 Ma and 1.66 Ma, respectively. The sites are part of the Melka Kunture cluster of prehistoric deposits, located on the highlands of Ethiopia at ~2000–2200 m above sea level. Due to the elevation, the vegetation belonged to the Afromontane complex (Bonnefille et al., 2018), which greatly differs from the savanna vegetation of many Pleistocene African sites at lower altitudes. Pollen analysis documents open vegetation with extended high-elevation grasslands in the paleolandscape of Garba IVD, whereas Gombore IB was marked by a rather forested mountain environment (Bonnefille et al., 2018). The taxonomic composition of the fauna did not significantly differ between the two sites, indicating a preference for open habitats (Geraads et al., 2004, 2022). Given the known faunal assemblages and paleoenvironmental differences between the two layers, our aim is to determine if and how this is reflected in the stable carbon and oxygen isotope composition of the fauna tooth enamel. Accordingly, the objectives of this paper are to (1) provide information on the diet and habitat of the fossil fauna; (2) assess whether the different local vegetation (grassland and forest) influenced the dietary selection of Pleistocene animals; (3) refine the paleoecological characteristics of both Early Acheulean archaeological levels; and (4) evaluate the outcome of different approaches in paleoenvironmental reconstructions.

Archaeological background

The Garba IVD and Gombore IB archaeological layers are part of the multistratified Garba IV and Gombore I sites within the Melka Kunture deposits (8° 42 N, 38° 36 E). They are located approximately 50 km southwest of Addis Ababa, on the western shoulder of the Main Ethiopian Rift, between 2000 and 2200 m a.s.l. (Fig. 1). The Ethiopian plateau is part of a wide region of highly anomalous topography (African Superswell) resulting from strong uplift during the Tertiary period at approximately 30 Ma (Pik et al., 2003; Kieffer et al., 2004; Gani et al., 2007; Corti, 2009). Furthermore, since the Early Pleistocene, the vegetation of Melka Kunture has been of the Afromontane complex, currently developing at 1800–3000 m a.s.l. (Bonnefille et al., 2018). Thus, the altitude of the sites did not change much since their formation compared to the present time.

Garba IVD and Gombore IB are located on the right bank of the Upper Awash River, at a short geographic and stratigraphic distance from each other (Chavaillon and Piperno, 2004; Piperno et al., 2009; Mussi et al., 2022, 2023). Both levels yielded a high-density assemblage of Early Acheulean lithic artifacts, faunal remains, and unworked pebbles (Gallotti, 2013; Gallotti and Mussi, 2017, 2018; Mussi et al., 2022). ^{40}Ar/^{39}Ar analysis formerly suggested an age of ~1.6 Ma for Garba IVD, which stratigraphically lies on the “Grazia tuff” (<1.719 ± 0.199 Ma). Gombore IB had been estimated to be close in age based on geo-stratigraphic correlations (Raynal and Kieffer, 2004). However, recent magnetostratigraphic analyses established an older chronology, assessing Garba IVD at 1.95 Ma and Gombore IB at 1.66 Ma. Thus, level D of Garba IV contains the earliest Acheulean technocomplex discovered so far (Perini et al., 2021).

Paleontological background

The fauna recovered from Garba IVD is dominated by large hippos (*Hippopotamus* cf. *amphibius*), grazing bovids (mostly Alcelaphini: *Connochaetes gentryi leptoceras*, *Damaliscus strepsiceras*, and Antilopini, with a *Gazella* close to *G. rufifrons*, and *Antidorcas*), and equids (*Hipparion* s.l., and *Equus*). The suids include *Kolpochoerus* and *Metridiochoerus*. The baboon *Theropithecus*, a rare genus at Melka Kunture, is represented by a single specimen (Geraads et al., 2004). The same open country alcelaphins dominate the mammalian collection of both sites; the fauna from Gombore IB includes three species of equids, two species of suids, and two hippos (*H.* cf. *amphibius*, and a dwarf hippo, resembling *H.* cf. *aethiopicus*) (Table 1). Both faunal assemblages point to a preference for open habitats

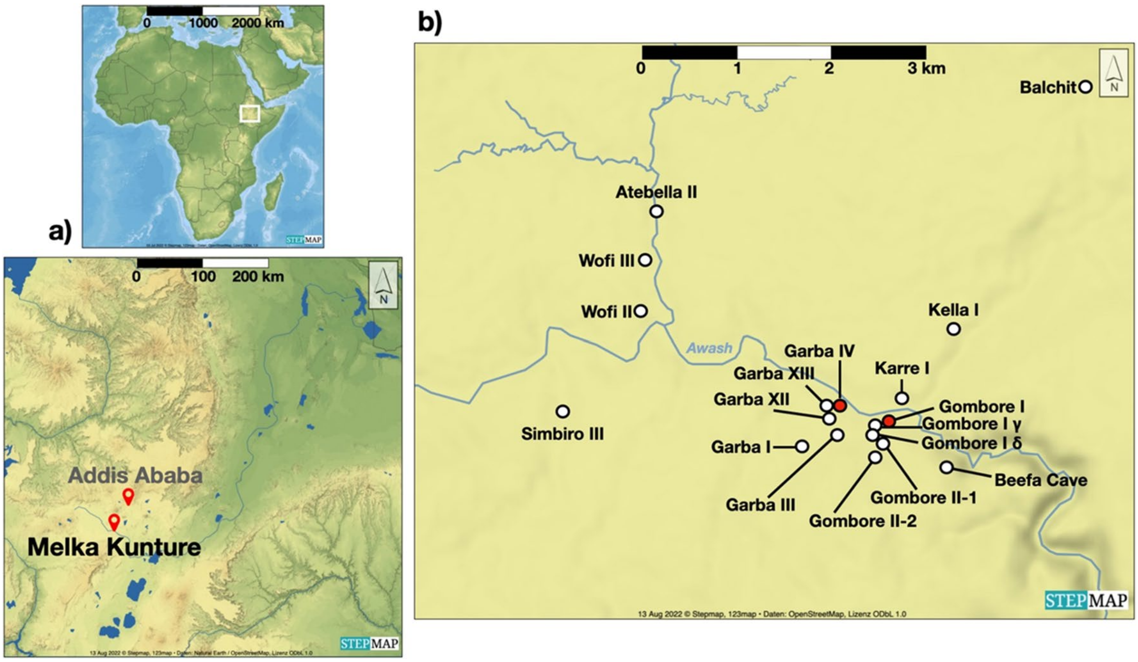

Fig. 1 **a** Location of Melka Kunture in the Upper Awash Valley of Ethiopia; **b** map of the major excavations (red dots indicate the studied sites)

(Geraads et al., 2004, 2022; Mussi et al., in press). A left distal humerus (Gombore IB-7594) attributed to *Homo* cf. *erectus* was found *in situ* at Gombore IB (Di Vincenzo et al., 2015). An *H. erectus* child mandible was also discovered at Garba IV in level E, associated with an Oldowan techno-complex. At ~2 Ma, it predates the overlying level Garba IVD (Le Cabec et al., 2021; Perini et al., 2021).

Palaeobotanical data

The pollen samples collected at Garba IVD (samples G133 and G393 in Bonnefille et al., 2018) record extensive development of high-elevation grasslands, evidenced by a high percentage of grass pollen (*Plantago* and various species of Asteraceae) and the shrub *Myrsine africana*. The assemblages also include some *Podocarpus* and *Dodonaea viscosa* pollen, pointing to limited wooded vegetation either locally or at a distance from the site since these pollen types are known to be easily dispersed. In contrast, the pollen sample from Gombore IB (samples Gomb IB in Bonnefille et al., 2018) records a high amount of *Juniperus* (>20%) and more taxa of present-day mountain forests (such as *Podocarpus*, *Olea*, and *Myrica*). As *Juniperus* disperses pollen not far from the tree, a juniper-dominated forest was developing nearby (a few hundred meters). The finding of a fossilized forest climber (liana) (Chavaillon and Koeniguer, 1970) also confirms this environmental interpretation. However, the large percentage of grass pollen of Poaceae (>63%) attests that grazing land was also available. The open vegetation was interrupted by the forest, probably near the river (Fig. 2) (Bonnefille et al., 2018).

Stable carbon and oxygen isotope analysis of tooth enamel

The analysis of stable carbon and oxygen isotopic abundances in tooth enamel provides direct evidence of the dietary patterns, ecology, and habitat since the isotopic signal is related to the plants consumed and the water ingested during the formation of the analyzed tissue. Tooth enamel is the most suitable fossilized material for preserving stable isotopic signatures since it is almost entirely inorganic (hydroxyapatite) and less susceptible to alteration due to diagenesis (Wang and Cerling, 1994; Schoeninger et al., 2003). The stable isotopic results are typically expressed with the following standard δ-notation: $X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$, where X is referred to as $\delta^{13}C$ and $\delta^{18}O$ values and R represents $^{13}C/^{12}C$ or $^{18}O/^{16}O$, respectively.

The carbon isotope ratio in tooth enamel is an average of the diet related to the plants eaten by the animals during the period of enamel mineralization. Terrestrial plants are generally divided into C_3 and C_4 plants according to their different photosynthesis pathways, leading to different carbon isotopic fractionation during CO_2 fixation processes (Edwards and Walker, 1983). The C_3 photosynthetic pathway (Calvin-Benson cycle) occurs in almost all tree and bush species, shrubs, and grasses in humid and shady areas in hot environments and temperate/cold or high-altitude herbaceous

Table 1 Distribution of the vertebrate taxa at Garba IVD and Gombore IB

	Garba IVD	Gombore IB
Theropithecus oswaldi	+	
Elephas recki recki	cf.	cf.
Stylohipparion sp.	+	+
Equus cf. *capensis*	+	
Equus cf. *stenonis*	+	+
Equus sp.	+	+
Hippopotamus cf. *amphibius*	+	+
Hippopotamus cf. *aethiopicus*		+
Kolpochoerus majus	+	
Kolpochoerus cf. *olduvaiensis*		+
Metridiochoerus cf. *andrewsi*	+	sp.
Metridiochoerus modestus	cf.	
Giraffa cf. *camelopardalis*	+	
Sivatherium maurusium	+	
Pelorovis turkanensis brachyceras	+	sp.
Kobus sp. (small).	+	
Connochaetes gentryi leptoceras	+	cf.
Damaliscus strepsiceras	+	+
Damaliscus cf. *korrigum*	+	
Parmularius cf. *angusticornis*	+	
Gazella cf. *rufifrons*	+	sp.
Antidorcas cf. *recki*	+	
Arvicanthis sp.	+	
Tachyoryctes konjitae	+	
Hystrix sp.	+	
Cygnus sp.	+	
Crocodylus sp.	+	+
Chelonia indet.	+	
Homo cf. *erectus*		+

monocots (Vogel, 1978; Blondel et al., 2018). The C_3 plants have a modal δ^{13}C value of −27‰ (ranging from −35‰ to −22‰). The C_4 photosynthetic pathway (Hatch-Slack cycle) occurs in grasses, sedges, and non-grassy herbaceous typical of drier and warmer environments and some shrubs in very dry environments (e.g., Amaranthaceae). The C_4 plants have δ^{13}C values ranging from −19‰ to −9‰, showing a modal value of −13‰ (Smith and Epstein, 1971; O'Leary, 1988). The abundance of C_4 plants generally suggests a relatively open grassy environment, whereas C_3 plants point to more woody vegetation under more humid climatic conditions (Farquhar et al., 1989; Cerling and Harris, 1999).

The oxygen isotope composition in mammalian tooth enamel reflects the isotopic composition of the body water, which is determined by the drinking water and ingested food. Mammals are generally classified into two groups: evaporation sensitive (ES) and evaporation insensitive (EI). ES taxa (e.g., giraffids, oryx, dik-dik, Grant's gazelle, and buffalo) are those that ingest evaporated waters, showing a significant increase in δ^{18}O values between tooth enamel and meteoric water as a response to increasing aridity. In contrast, EI taxa (e.g., hippopotamus, bush pig, elephant, rhinoceros, warthog, zebra, impala, and baboon) ingest relatively unevaporated waters and show a strong correlation between enamel and meteoric water δ^{18}O values (Levin et al., 2006).

Due to evaporation, the δ^{18}O values in plant leaves are higher than those in meteoric water. This means that herbivores that get most of their water from consumed leaves have higher oxygen isotopic values than those drinking abundant meteoric water (Kohn, 1996; Kohn et al., 1998), allowing us to distinguish browsers from grazers. Thus, δ^{18}O values will enable us to determine the so-called "obligate drinkers", who obtain water from the rivers or lakes (δ^{18}O of meteoric water), from the other "non-obligate drinkers" that get most of their water from leaves, showing higher δ^{18}O values. The oxygen isotopic composition can also be affected by habitat differences: for semiaquatic mammals such as hippos, the δ^{18}O values are lower compared to those of terrestrial herbivores (Bocherens et al., 1996; Clementz and Koch, 2001; Clementz et al., 2008; Harris et al., 2008). Furthermore, many other aspects can play a relevant role in the variation in oxygen isotope

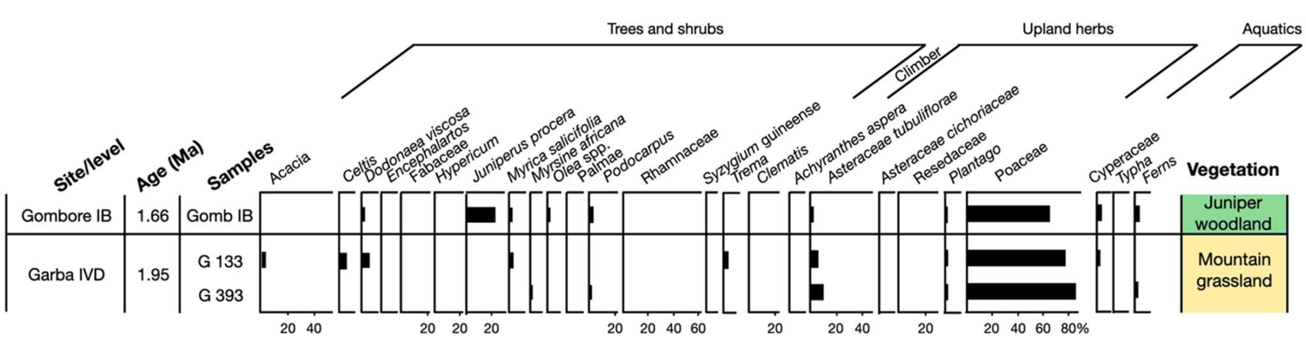

Fig. 2 Distribution (%) of the pollen taxa identified in samples from Garba IVD (samples G133 and G393) and Gombore IB (sample Gomb IB) with the interpretation of the past vegetation (redrawn from Bonnefille et al., 2018)

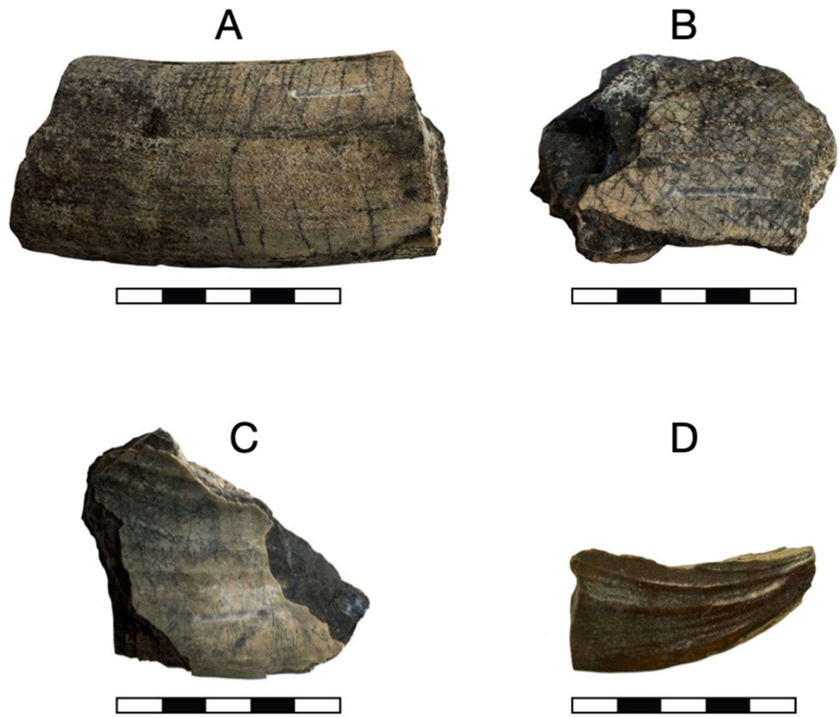

Fig. 3 Examples of teeth from Garba IVD sampled for the isotopic analyses: **A** *Hippopotamus* cf. *amphibius* upper canine fragment (MK 74 GAR IVD 6394); **B**, **C** *Hippopotamus* cf. *amphibius* lower canine fragment (MK 74 GAR IVD 1230; MK 75 GAR IVD 6750); **D** Suidae (cf. *Metridiochoerus* sp.) upper canine fragment (MK 74 GAR IVD 6958); scale bar = 5 cm

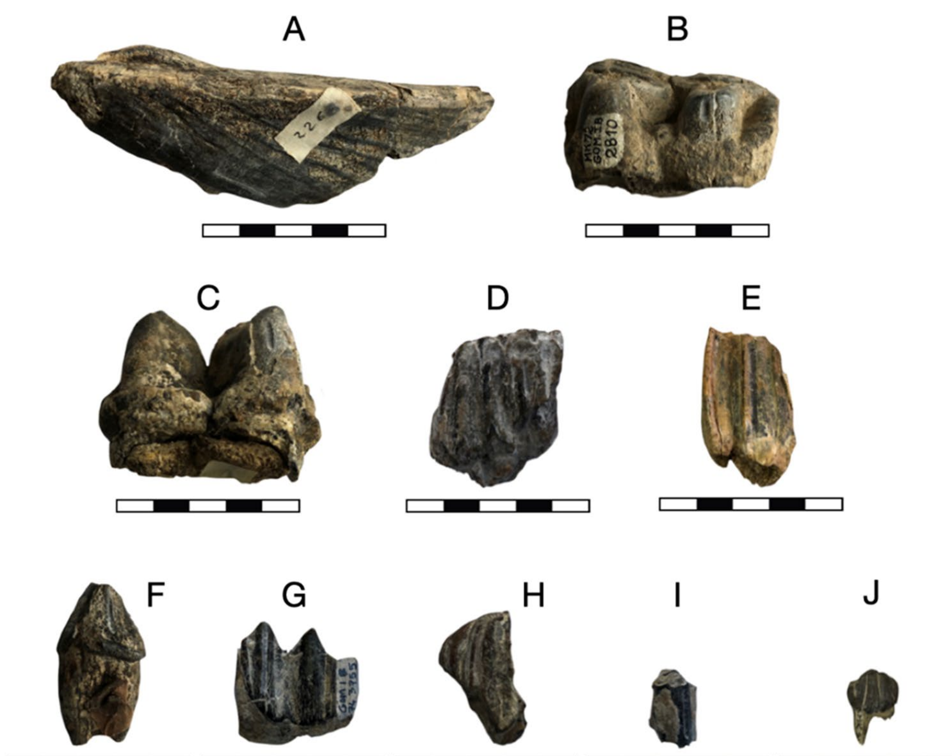

Fig. 4 Examples of teeth from Gombore IB sampled for the isotopic analyses: **A** *Hippopotamus* cf. *amphibius* upper canine fragment (MK 69 GOM IB 2268); **B**, **C** *Hippopotamus* cf. *amphibius* upper molar (MK 72 GOM IB 2810; MK 74 GOM IB 5056); **D** *Metridiochoerus* molar fragment (MK 73 GOM IB 1487); **E** Alcelaphini upper molar (MK 73 GOM IB 4804); **F** *Hippopotamus* cf. *amphibius* premolar (MK 74 GOM IB 90); **G** Bovidae (cf. Bovini) molar (MK 74 GOM IB 3755); **H** *Metridiochoerus* molar fragment (MK 74 GOM IB 3637); **I** Alcelaphini lower molar fragment (MK 70 GOM IB 1005); **J** *Kolpochoerus* upper premolar (MK 81 GOM IB 9400); scale bar = 5 cm

Table 2 Distribution of the analyzed enamel samples from Garba IVD and Gombore IB

	Garba IVD	Gombore IB	Total
Hippopotamidae	8	6	15
Bovidae	1	5	6
Equidae	1	1	2
Suidae	1	4	4
Total	11	16	27

composition, such as precipitation, continentality, seasonality, latitude, and altitude (Pederzani and Britton, 2019).

Materials and methods

We analyzed the stable carbon and oxygen isotopic compositions of 18 fossil teeth (5 enamel samples from Garba IVD (Fig. 3) and 13 enamel samples from Gombore IB) (Fig. 4). We further added 9 samples published by Bocherens et al. (1996) (6 samples from Garba IVD and 3 samples from Gombore IB). Overall, we discuss 27 enamel samples (Table 2) from fossil teeth taxonomically identified by one of us (Geraads et al., 2004, 2022). The specimens include Artiodactyla (Hippopotamidae, Bovidae, Suidae) and Perissodactyla (Equidae) (Table S1). The enamel samples were collected in November 2019 at the National Museum of Ethiopia (Addis Ababa), where the paleontological collection is stored. Each specimen is labeled with the acronym of the archaeological area (MLK = Melka Kunture), followed by a progressive number (i.e., MLK 15, MLK 16, etc.). Briefly, 12–15 mg of enamel was pretreated with NaOCl followed by buffer acetic acid-calcium acetate; then, 2.5–3 mg of powdered enamel was analyzed at the Biogeology Research Group (Department of Geosciences, University of Tübingen) using a MultiFlow-Geo interface with the Elementar IsoPrime 100 IRMS (Supplementary Text A and B).

Results

The $\delta^{13}C$ and $\delta^{18}O$ values from Garba IVD

The $\delta^{13}C$ values of tooth enamel samples from Garba IVD range from −4.7 ‰ to + 2.7 ‰, covering the range of mixed C_3-C_4 and C_4 plant consumers (Table S1) (Fig. 5). Notably, the $\delta^{13}C$ values of hippopotamids ($n = 8$) varied from −4.7 ‰ to + 2.6 ‰ (median = +0.4 ‰), indicating a C_4 diet. Only a single $\delta^{13}C$ value (−4.7 ‰) was lower compared with the other values, indicating a mixed C_3-C_4 diet for this hippo. A bovid ($n = 1$), equid ($n = 1$), and suid ($n = 1$) with $\delta^{13}C$ values of + 1.9 ‰, + 2.7 ‰, and + 0.6 ‰, respectively, consumed C_4 plants. The $\delta^{18}O$ values ranged from + 21.2 ‰ to + 31.7 ‰. The $\delta^{18}O$ values were lower for the hippos ($n = 8$; median = + 24.9 ‰) than for the fully terrestrial animals such as a suid ($n = 1$; + 25.9 ‰), equid ($n = 1$; + 30.9 ‰), and bovid ($n = 1$; + 31.7 ‰), reflecting distinct physiologies, behaviors, and habitats (Mann-Whitney U-test, $p = 0.0294$).

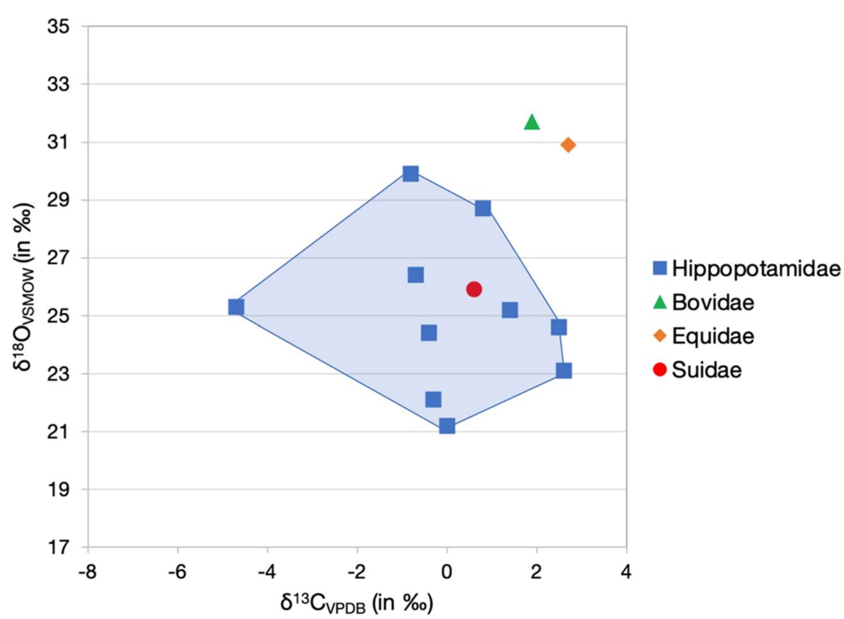

Fig. 5 The $\delta^{13}C$ and $\delta^{18}O$ (enamel) values of mammal teeth from Garba IVD

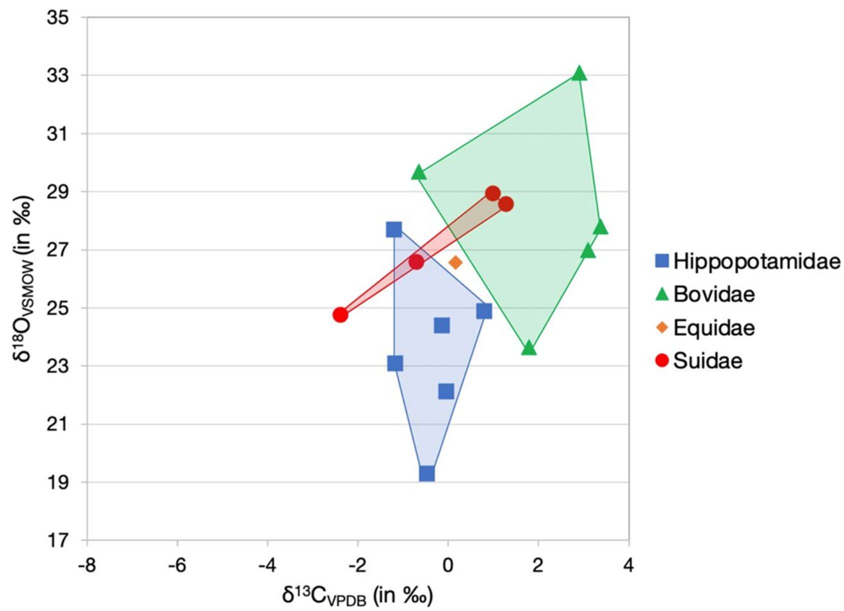

Fig. 6 The δ^{13}C and δ^{18}O (enamel) values of mammal teeth from Gombore IB

The δ^{13}C and δ^{18}O values from Gombore IB

At Gombore IB, the δ^{13}C values of tooth enamel ranged from −2.4 ‰ to + 3.4 ‰, suggesting a pure C_4 diet for herbivores (Table S1) (Fig. 6). The hippopotamid ($n = 6$) δ^{13}C values ranged from −1.2 ‰ to + 0.8 ‰ (median = −0.3 ‰), and the bovids ($n = 5$) had a δ^{13}C median of +2.9 ‰, with δ^{13}C values ranging from −0.6 ‰ to + 3.4 ‰. The δ^{13}C values of suids ($n = 4$) varied from −2.4 ‰ to + 1.3 ‰ (median = + 0.3 ‰), whereas the δ^{13}C value of the single equid sample (*Hipparion*) was + 0.1 ‰. The δ^{18}O values for all analyzed mammals ranged from + 19.2 ‰ to + 33.1 ‰. As for the Garba IVD, the hippopotamids had lower δ^{18}O values ($n = 6$; median = + 23.6 ‰), whereas those of bovids ($n = 5$; median = + 27.7 ‰), equid ($n = 1$; + 26.5 ‰), and suids ($n = 4$; median = + 27.5 ‰) were higher, consistent with the expected difference between aquatic and terrestrial habitats (Mann-Whitney *U*-test, $p = 0.0169$).

Discussion

Dietary and paleoenvironmental reconstruction

The carbon and oxygen isotopic results reflect ecological conditions based on faunal lifestyles and preferred habitats. This is evidenced by the δ^{18}O values from Garba IVD (1.95 Ma) and Gombore IB (1.66 Ma), which discriminate the taxa according to their semiaquatic or terrestrial habitats. The δ^{13}C values from both sites/levels suggest that all the analyzed faunal taxa fed mostly on C_4 plants. Only a hippo δ^{13}C value from Garba IVD indicates a mixed C_3-C_4 isotopic signal that could be interpreted as consuming C_3 cool-season grass, C_3 browse, including fruits, or a mix of C_3 grass and C_3 browse. Indeed, Melka Kunture is located at the elevation where grasslands would include mostly C_4 grasses but also some C_3 grasses that become dominant above 2000 m of elevation (Tieszen et al., 1979).

The isotopic results are consistent with the faunal taxonomy that suggests environments characterized by open grasslands (Geraads et al., 2022). Our carbon isotopic data also agree with the palynological results at Garba IVD, where extended mountain grasslands are documented. In contrast, isotopic results do not totally agree with the paleoenvironmental reconstruction by fossil pollen at Gombore IB, where the open landscape was interrupted by forests and bushy woodland of which the fossil fauna and isotopic analyses provide no evidence. The possibility that the C_4 isotopic signal could indicate the movement of fossil fauna from lower to higher elevation grasslands and woodlands is in contrast with the development of endemic animal species and subspecies, such as *Damaliscus strepsiceras* and *Connochaetes gentryi leptoceras*, pointing to some degree of isolation of the Ethiopian highlands (Mussi et al., in press). Another possibility is that the sample does not depict the whole faunal signal or that taxa relying more on C_3 resources were not sampled.

A distinct environment at Garba IVD and Gombore IB is not surprising, given the different ages. The wet-dry climate variability on the timescale of 20,000 years of processional monsoon cycles could easily cause a significant change in vegetation cover (Bonnefille and Riollet, 1988). We emphasize that at Melka Kunture, even in the relatively open landscape of Garba IVD, grassland and wooded areas were always available in various percentages at a short distance.

The animals were likely to be selective when feeding. Their diet was likely based on preferred plants rather than immediately available vegetation. Modern hippos are notably known to regularly travel some kilometers to forage at night on preferred grass spots whenever they are not available close to the body of water where they spend the daytime (Eltringham, 1999). At Melka Kunture, there is direct evidence of a hippo trail produced by *H*. cf. *amphibius*, which predates 0.7 Ma (Altamura et al., 2017).

When reconstructing the paleoenvironment, stable isotope and pollen analyses are better understood as complementary proxies. The stable isotope composition of the tooth enamel does not record diet at the time of death of the individuals but over a long period (several months to years) or a shorter period, depending on the sampling strategies. They are also related to each individual's feeding strategies and behavior, including the selection of the preferred vegetation. Fossil pollen analysis registers local plants and wind-pollinated plants located at some distance from the deposit. Thus, isotopes and pollen record different temporal and spatial aspects.

The $\delta^{13}C$ and $\delta^{18}O$ comparison from tooth enamel in eastern Africa

We selected 284 isotopic results ($\delta^{13}C$ and $\delta^{18}O$ values) from the fauna tooth enamel of eastern African archaeological and paleontological areas of the Early Pleistocene age (Olduvai Gorge, and several sites of the Lake Turkana Basin) to compare our results and interpretations from a broader regional perspective. Overall, we discuss 308 isotopic results, including data from Melka Kunture. The selected archaeological sites are located at medium and low elevations, between ~1400 and 336 m a.s.l., whereas Melka Kunture is the only site at ~2000 m a.s.l. The isotopic dataset includes four faunal family groups: Hippopotamidae, Bovidae, Equidae, and Suidae. Only isotopic values from specimens dated between ~2.0–1.95 Ma and ~1.6 Ma were selected (Table S3).

Hippopotamidae The fossil hippopotamids (n = 59) from Melka Kunture, Lake Turkana Basin, and Olduvai Gorge belong to *Hippopotamus* cf. *amphibius*, *Hippopotamus gorgops*, aff. *Hippopotamus aethiopicus*, aff. *Hippopotamus karumensis*, and other hippopotamids (Fig. 7). The median $\delta^{13}C$ value is −0.3 ‰ with minimum and maximum values of −7.2 ‰ and + 2.6 ‰, respectively. The carbon isotopic data suggest that the hippopotamids had a C_4-dominated diet. However, some $\delta^{13}C$ values from Shungura Formation, within the Lake Turkana Basin, and Melka Kunture point to a mixed C_3-C_4 diet. This is consistent with other isotopic studies (Morgan et al., 1994; Bocherens et al., 1996; Zazzo et al., 2000; Cerling et al., 2003; Boisserie et al., 2005; Levin et al., 2008; Souron et al., 2012), showing opportunistic feeding strategies for hippos, which sampled the available vegetation within long and short distances from their aquatic shelter. The $\delta^{18}O$ values show a median of + 26.5 ‰ with a range from + 19.2 ‰ to + 31 ‰ (Bocherens et al., 1996; Harris et al., 2008; van der Merwe, 2013; Ascari et al., 2018; Rivals et al., 2018; Uno et al., 2018; Negash et al., 2020).

We note that the hippopotamids from Melka Kunture show lower $\delta^{18}O$ values (median = + 24.5 ‰) than those of mid- and low-altitude sites (median = + 27 ‰) (t-test, p = 0.0168). However, the $\delta^{18}O$ median of hippos from Shungura Formation (Lake Turkana Basin) is + 23.9 ‰ which is lower than the $\delta^{18}O$ median of the same specimens from Upper Burgi Member (+ 27 ‰) (Lake Turkana Basin) and those from Olduvai Gorge (+ 27.1 ‰). This could be explained by

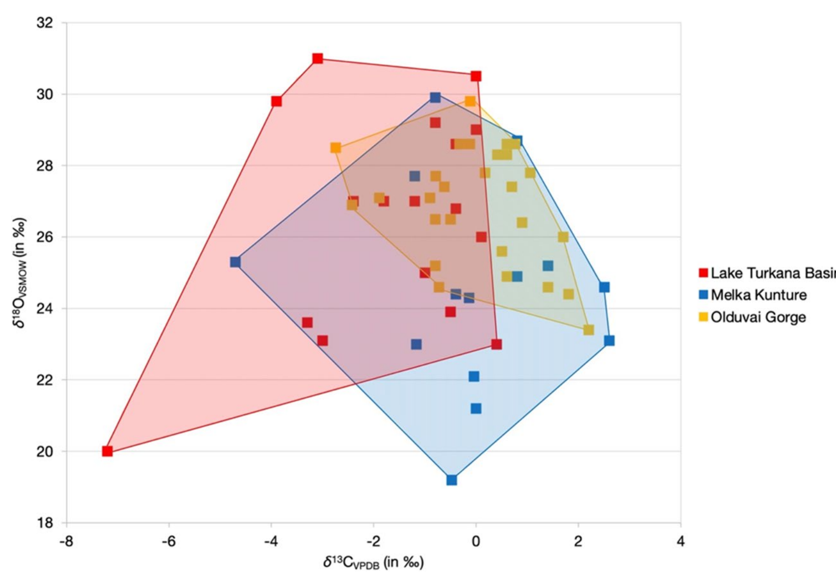

Fig. 7 Scatter plots of $\delta^{13}C$ and $\delta^{18}O$ values (tooth enamel) of hippopotamids from Lake Turkana Basin (n = 17), Melka Kunture (n = 15), and Olduvai Gorge (n = 27)

the different states of evaporation of the water in which the animals shelter. In contrast, we explain the lower δ^{18}O values from Melka Kunture with the altitude effect. The water condensation that continues throughout a storm, along a mountain slope, or across a continent, select heavier isotopes, and the remaining vapor becomes depleted in heavy isotopes. Consequently, δ^{18}O values are lower in high-altitude precipitation and higher in low-altitude precipitation (Dansgaard, 1964; Gat, 2000; Pederzani and Britton, 2019). This could also have implications for the past temperature, indicating colder climatic conditions in the mountain environment at Melka Kunture. Currently, in Ethiopia, the "big rains" (June–September) are sourced by moist south-westerlies and westerlies from the Atlantic Ocean, whereas the shorter rainy season (March–May) is associated with the southeastern monsoon from the Indian Ocean (Griffiths, 1972; Gamachu, 1977; Vizy and Cook, 2003; Bedaso and Wu, 2021). This is confirmed by isotopic data and model simulations indicating that δ^{18}O in eastern African rainfall is closely related to the Indian Ocean Zonal Mode (Vuille et al., 2005). The maximum rainfall at Melka Kunture is recorded during the long rainy season, although some variability exists. The Boneja meteorological station (20 km north of Melka Kunture) recorded a mean annual rainfall of 860 mm. During 1974–2012, a wide rainfall variability was recorded, with a minimum value of 388 mm and a maximum of 1419 mm (Bonnefille et al., 2018). The mean maximum temperature is 17.2 °C, and the mean minimum is 8 °C (meteorological station from Addis Ababa) (Fekadu, 2012). Therefore, lower δ^{18}O values provided in this study confirm the high-elevation environment attested by the pollen study (Bonnefille et al., 2018).

Bovidae This group comprises several bovids (n = 158) of Alcelaphini, Antilopini, Bovini, Hippotragini, Reduncini, Tragelaphini, and other bovids from Melka Kunture, Lake Turkana Basin, and Olduvai (Fig. 8). Overall, the δ^{13}C values (median = + 0.5 ‰) suggest that the diverse tribes of bovids had a wide range of feeding strategies, including a significant C_4 component in their diet but also feeding on mixed C_3-C_4 resources. Some bovids from Shungura Formation (Lake Turkana Basin) and Olduvai Gorge show lower δ^{13}C values, indicating a mixed C_3-C_4 diet (Bocherens et al., 1996; van der Merwe, 2013; Ascari et al., 2018; Rivals et al., 2018; Uno et al., 2018; Negash et al., 2020). The δ^{18}O values record a wide range, reflecting the different drinking habits of these bovid tribes.

Equidae The fossil equids (n = 33) from Melka Kunture and Olduvai Gorge are *Equus oldowayensis*, *Hipparion*, and other equids (Fig. 9). The δ^{13}C values range from −1.8 ‰ to + 3 ‰ (median = + 0.9 ‰), indicating a dominant C_4 diet. The δ^{18}O values are homogeneous with a median value of + 30.4 ‰ and values ranging from + 25.3 ‰ to + 31.9 ‰ (Bocherens et al., 1996; van der Merwe, 2013; Rivals et al., 2018; Uno et al., 2018).

Suidae The suid group (n = 61) consists of *Kolpochoerus*, *Kolpochoerus limnetes*, *Kolpochoerus majus*, *Kolpochoerus* cf. *olduvaiensis*, *Kolpochoerus paiceae*, *Metridiochoerus*, *Metridiochoerus compactus*, *Notochoerus*, *Phacochoerus modestus*, and other suids from Melka Kunture, Lake Turkana Basin, and Olduvai Gorge (Fig. 10). The δ^{13}C values indicate diets dominated by C_4 plants for all genera, ranging from −3.1 ‰ to + 1.5 ‰ (median = −0.3 ‰). In contrast, only some lower δ^{13}C values indicate a mixed C_3-C_4 feeding strategy. The δ^{18}O values have a median of + 29.4 ‰, ranging from + 23.6 ‰ to + 37.1 ‰ (van der Merwe, 2013; Ascari et al.,

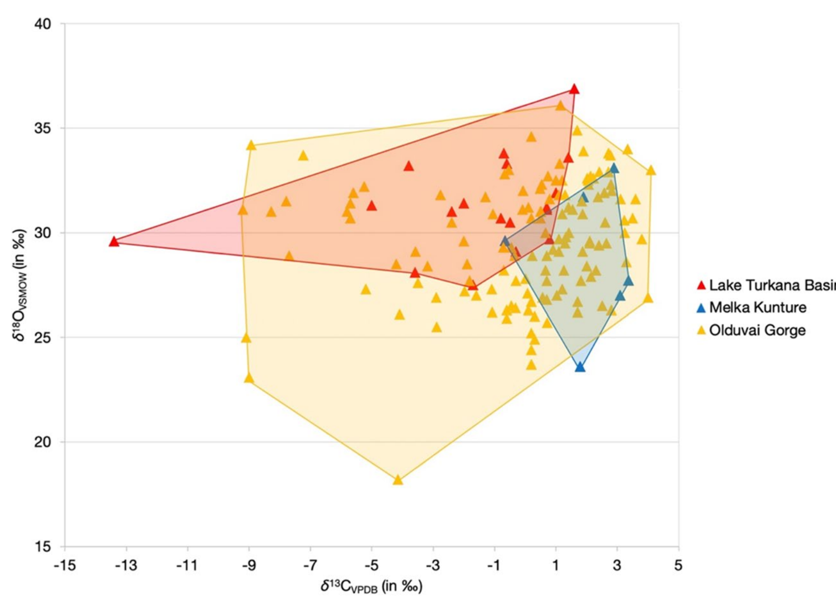

Fig. 8 Scatter plots of δ^{13}C and δ^{18}O values (tooth enamel) of bovids from Lake Turkana Basin (n = 18), Melka Kunture (n = 6), and Olduvai Gorge (n = 134)

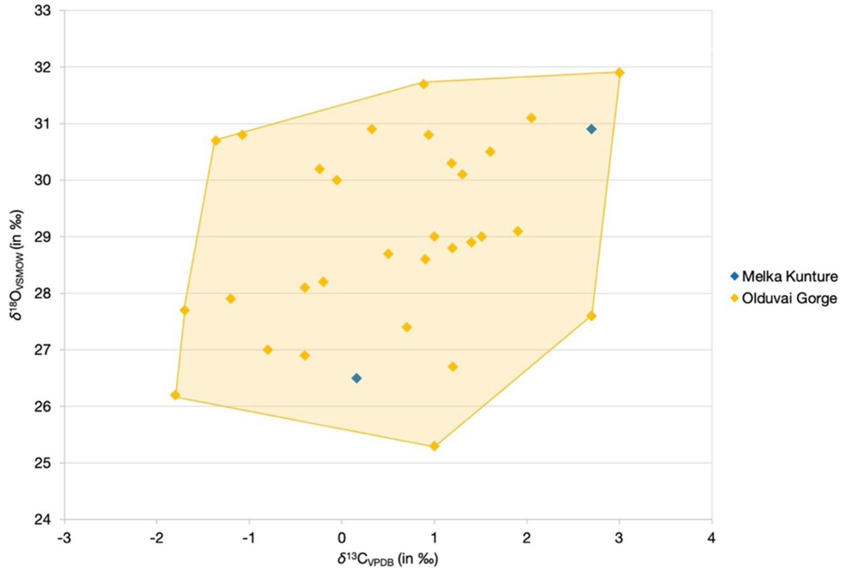

Fig. 9 Scatter plots of $\delta^{13}C$ and $\delta^{18}O$ values (tooth enamel) of equids from Melka Kunture (n = 2), and Olduvai Gorge (n = 31)

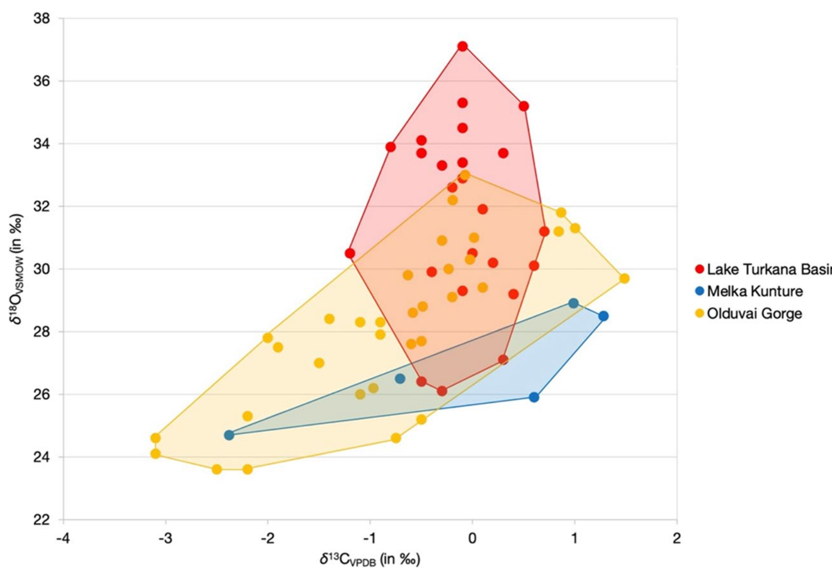

Fig. 10 Scatter plots of $\delta^{13}C$ and $\delta^{18}O$ values (tooth enamel) of suids from Lake Turkana Basin (n = 24), Melka Kunture (n = 5), and Olduvai Gorge (n = 33)

2018; Rivals et al., 2018; Uno et al., 2018; Negash et al., 2020).

Overall, the isotopic comparisons indicate that Hippopotamidae, Bovidae, Equidae, and Suidae were grazing and fed primarily on C_4 plants, including a mix of C_3-C_4 resources. Accordingly, C_4 plants were an important part of the mammalian diet, and the ungulate's feeding strategies were overall not affected by variations linked to differences at low, medium, and high altitudes. Moreover, the oxygen isotopic data of Melka Kunture's hippos point to a cooler temperature than elsewhere at lower elevations.

Conclusions

The analysis of stable isotopes on faunal tooth enamel from the Early Acheulean layers of Garba IVD (1.95 Ma) and Gombore IB (1.66 Ma) was used to reconstruct the diet and habitat of the Pleistocene fauna. The carbon isotopic data indicate a C_4-dominated diet for all the analyzed taxa. The oxygen isotopic data show a clear distinction between semiaquatic and terrestrial habitats. Our isotopic results are consistent with the faunal analysis, indicating an extended C_4 landscape in the vegetation. However, at Garba IVD, pollen documents a mountain grassland, whereas a relatively forested environment is also recorded at Gombore IB. This complementary information helps track the feeding strategies of mammals and the paleoenvironment. The paleovegetation changed over time, whereas isotopic studies of the fossil fauna showed more or less constant feeding habits on C_4 plants.

Comparisons with isotopic results from eastern African sites do not allow to identify variations in feeding strategies at high, medium, and low altitudes, even though at Melka Kunture is recorded the Dry evergreen Afromontane Forest and grassland complex, a distinct mountain vegetation that does not include any of the species of the lowland savannas. The vegetation changed over approximately 300,000 years, between 1.95 Ma (Garba IVD) and 1.66 Ma (Gombore IB), whereas the dietary strategies of the fauna were scarcely modified. This has implications for environmental reconstructions based exclusively on fauna isotopic studies.

Reconstructing the environment using more than a single method of analysis produces sounder results, which is especially important if the development of grasslands and open landscapes is used as a proxy for aridification. At Melka Kunture, *H. erectus* definitely made Early Acheulean technocomplexes in mixed upland habitats that were quite different from the lowland savanna ones.

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Author contribution GB conceived the ideas and designed the paper with the supervision of MM. GB collected, performed, and elaborated the isotopic data. GB led the writing of the manuscript with the support of MM and the contribution of all the authors (HB, RB, DG). All authors read and approved the manuscript and agree with its submission to the journal.

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Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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