Palaeoecological reconstruction of Plio-Pleistocene herbivores from the Ahl al Oughlam site (Casablanca, Morocco): Insights from dental wear and stable isotopes

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Abstract

In this article, we use a multiproxy approach based on stable isotope analyses ($\delta^{18}O$ and $\delta^{13}C$), mesowear, and microwear dental analysis to reconstruct the climate, diet, and habitat of Plio-Pleistocene herbivores at the site of Ahl al Oughlam in western Morocco. This study has been conducted on teeth from several taxa (*Sivatherium maurusium*, *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., Alcelaphini, and *Ancus osiris*), enabling a robust ecological reconstruction. Our isotopic results suggest a predominance of C_3 plant consumption for all analyzed species, while dental wear indicates a varied diet, with evidence for both browsing and grazing behavior being present. The combination of proxies indicates a landscape dominated by open C_3 grasslands in an arid climate, as supported by the Mean Annual Precipitation (MAP) results. These findings contribute to the ongoing debate on the ecological context that facilitated the Plio-Pleistocene dispersal, occupation, and evolution of mammals and hominins in northern Africa, for which limited information is available.

Keywords

North Africa, diet, habitat, stable isotopes, microwear, mesowear.

1. Introduction

The richness and diversity of mammalian fossil remains in the Maghreb during the Late Pliocene and Early Pleistocene (Geraads, 2002; Raynal et al., 2002; Sahnouni and Van der Made, 2009; Sahnouni et al., 2011; Van der Made et al., 2021), provides evidence that the Sahara Desert was not always a natural barrier for mammals in the past. The region experienced multiple green and humid phases, known as Green Sahara periods (GSPs), over millions of years, including the Plio-Pleistocene. During these events, the present desert area consisted of river basins and extensive lakes (Van Zinderen Barker, 1962; Larrasoaña et al., 2003, 2013; Castañeda et al., 2009; Grant et al., 2017, 2022; Larrasoaña, 2021). These environmental conditions would have facilitated episodes of mammalian dispersal from sub-Saharan locations to the north of Africa (Geraads, 2010; Zouhri et al., 2017; Van der Made et al., 2021).

To date, the oldest artifacts and stone tool-cut marked bones in North Africa associated with the presence of hominins have been found at the site of Aïn Boucherit (~1.9 and ~2.4 Ma) in the Beni Fouda intramontane basin in northeast Algeria (Sahnouni et al., 2018; Duval et al., 2021). In the same area, Acheulean technology has been described at the sites of Aïn Hanech and El Kherba (~1.8 Ma) (Sahnouni et al., 2002, 2012, 2017; Parés et al., 2014; Duval et al., 2021, 2023; Van der Made et al., 2021). In the Constantine Basin (Algeria), biochronologically close to Aïn Hanech, is the little-known site of Mansourah, with abundant faunal remains and bifacial artifacts associated with the Oldowan industry (Thomas, 1884, 1886; Chaid-Saoudi et al., 2006; Sahnouni and Van der Made, 2009) and the palaeontological site of Aïn Jourdel (~2.5 Ma) (Thomas, 1884, 1886; Duval et al., 2021). The oldest human remains have been found in western Algeria at Tighennif, also called Ternifine, ~1 Ma (Arambourg and Hoffstetter, 1963; Geraads et al., 1986; Bocherens et al., 1996; Geraads, 2016; Van der Made et al., 2021). In western Morocco, near Casablanca, the earliest archaeological sites date back to the Early and Middle Pleistocene (Raynal et al., 2001, 2002, 2017; Mohib et al., 2019; Gallotti et al., 2022). Up to now, the oldest site with human presence corresponds to unit L of Thomas Quarry I and its abundant ancient Acheulean lithic tools (~1.3 Ma) (Raynal and Texier, 1989; Gallotti et al., 2020, 2021, 2023). (Raynal and Texier, 1989; Gallotti et al., 2020, 2021, 2023). The former Thomas III Quarry, in which *Homo* remains were found (Ennouchi, 1975, Geraads et al., 1980, 2022a and b; Raynal, 2021) was renamed Oulad Hamida 1 Quarry when the *Grotte des Rhinocéros* (~0.7 Ma) was discovered and delivered a single *Homo* remain associated with stone tools and fauna (Raynal et al., 1993, 2022b; Rhodes et al., 2006; Daujeard et al., 2012, 2020; Raynal and Mohib, 2016; Gallotti et al., 2022). In Thomas Quarry I, above level L, Hominid Cave (~0.5/0.7 Ma) is also located, where early *Homo* remains on the Atlantic shore were discovered (Ennouchi, 1975; Geraads et al., 1980, 2022a; Raynal et al., 2010, 2022a; Daujeard et al., 2016, 2020; Raynal, 2021). On the outskirts of Casablanca sits the site of Ahl al Oughlam (AaO), the richest Neogene faunal site in North Africa dated to ~2.5 Ma (Raynal et al., 1990; Geraads, 2006; Geraads et al., 2010, 2022b) and whose ecological context is investigated in this work.

In eastern Morocco, close to the Algerian border in the Aïn Beni Mathar–Guefaït area (Jerada province), several sites have been discovered and excavated since 2006: the Early Pleistocene sites of Aïn Tabouda, Gara Soultana and Charchara 1 with Mode 1 lithic tools, and the Middle Pleistocene site of Oued Rabt with Mode 2 lithic tools (Sala-Ramos et al., 2022). The oldest site, although palaeontological, is Guefaït. This one is biochronologically located at the Plio-Pleistocene boundary (~3–2.5 Ma; Parés et al., 2023), contemporaneous with Ahl al Oughlam, and contains a large diversity of taxa in its fossiliferous levels (Sala-Ramos et al., 2017, 2022; Aouraghe et al., 2019; Piñero et al., 2019; Alba et al., 2021; Madurell-Malapeira et al., 2021; Ramírez-Pedraza et al., 2023).

Work based on palaeoecological reconstructions are underrepresented in North Africa, despite the abundance of archaeopalaeontological sites found from the Late Pliocene to the Early Pleistocene in this territory. In Morocco, the studies published to date are focused on the palaeoecology of the Plio-Pleistocene primates of Ahl al Oughlam (*Theropithecus*; Fannin et al., 2021) and Guefaït-4.2 (*Macaca*; Ramírez-Pedraza et al., 2023). In Algeria, there are more extensive studies available, such as the analysis of carbon and oxygen stable isotopes in herbivores from Tighennif (~1 Ma) (Bocherens et al., 1996; Fannin et al., 2021), and the research based on stable isotopes of pedogenic carbonates from El Kherba (~1.8 Ma) (Sahnouni et al., 2011). However, there still remains a knowledge gap in this area regarding the reconstruction of habitats at the Plio-Pleistocene boundary. This contrasts with the numerous and comprehensive studies carried out in eastern (Kingston and Harrison, 2007; Ségalen et al., 2007; Levin et al., 2008; Bedaso et al., 2013; Cerling et al., 2015; Robinson et al., 2017, 2021; Lüdecke et al., 2018; Mercader et al., 2021), southern (Lee-Thorp and Sponheimer, 2005; Lee-Thorp et al., 2007, 2010; Ségalen et al., 2007; Lehmann et al., 2016) and central Africa (Zazzo et al., 2000; Ségalen et al., 2007; Lee-Thorp et al., 2012) focused on the ecological contexts of Plio-Pleistocene hominins and large herbivores.

One of the commonly used methods for reconstructing past environments has been the analysis of stable carbon isotope ratios ($^{13}C/^{12}C$) in dental enamel bioapatite. This biogenic material is particularly useful due to its resistance to diagenetic processes, preserving the original isotopic signal (Wang and Cerling, 1994). The carbon isotope ratios are primarily influenced by the differential fractionation between the two photosynthetic pathways (C_3 and C_4) used by plants consumed by animals, and it is associated with specific types of landscapes or environmental conditions. The proportion of C_3 or C_4 plants is not distributed homogeneously throughout Africa, varying both geographically and chronologically. Global C_4 ecosystem expansion around 8–10 million years ago, due to the decrease of atmospheric CO_2, higher temperatures and increasing water-stress represents a significant change in the landscape that led to the replacement of C_3 grasses by C_4 grasses in existing open and dry environments in low- to mid-latitude and altitude regions (Ehleringer et al., 1991; Cerling, 1992; Cerling et al., 1997; Edwards et al., 2010; Polissar et al., 2019). During the Plio-Pleistocene, eastern, southern and central Africa was dominated by C_4 grassland (Zazzo et al., 2000; Ségalen et al., 2007; Strömberg, 2011), relegating C_3 grasses to altitudes above 2000 meters and in the forest understory (Tieszen et al., 1979; Young and Young, 1983; Balasse and Ambrose, 2005). The ecological context of these areas, characterized by the high abundance of C_4 grasses, especially in Eastern Africa, has allowed the application of the C_4-grazers and C_3-browsers classification, which is widely used in studies analyzing the diet of mammals based on the analysis of tooth enamel $\delta^{13}C$ values (Vogel, 1978; Zazzo et al., 2000; Sponheimer and Lee-Thorp, 2003; Lee-Thorp and Sponheimer, 2005; Levin et al., 2008; Bedaso et al., 2013; Cerling et al., 2015; Uno et al., 2018).

This clear distinction between C_4-grazers and C_3-browsers is not valid at high latitudes, as the contribution of C_4 plants is non-existent or marginal. This pattern has been observed in multiple studies conducted during the Pliocene and Early Pleistocene in Europe (Edwards et al., 2010; Domingo et al., 2013; Szabó et al., 2022). The same observation applies to studies conducted in North Africa on Pleistocene and Pliocene archaeological and palaeontological sites mentioned above (Bocherens et al., 1996; Sahnouni et al., 2011; Fannin et al., 2021). All of them, based on carbon isotope evidence, reveal a vegetation consisting of C_3 plants including all available resources such as trees, woody shrubs, bushes and grasses. This makes it challenging to discern different diets and habitats for mammals and therefore to draw a consistent ecological reconstruction with this single method.

To address this challenge, we combine three high-resolution approaches that cover different moments in the animal's life: the $\delta^{18}O$ and $\delta^{13}C$ values of tooth enamel bioapatite (which reflect the first years of life related to the crown formation times), tooth mesowear (which reflects the last months/years before death) and tooth occlusal microwear (which reflects the last days/weeks before death). By combining these approaches, this work aims at providing a robust ecological reconstruction of the Ahl al Oughlam (AaO) mammal communities, which will shed light on their diets, habitats, and seasonality. Understanding the role of this territory is crucial in contributing to the debate about the first hominin dispersions and occupations, as well as highlighting the importance of Africa in the adaptation and development of mammal behavior during the Late Pliocene and Early Pleistocene.

2. Site: Ahl al Oughlam

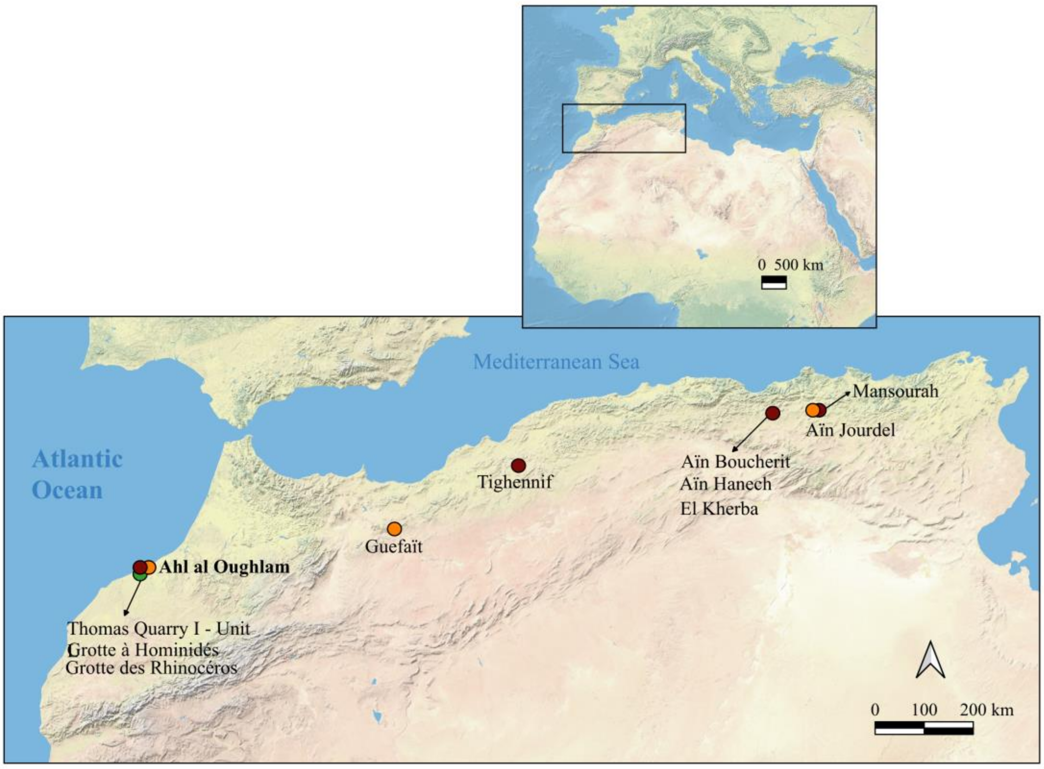

Fig.1. Location map of North African sites mentioned in the text. Plio-Pleistocene boundary sites = orange circle (Ahl al Oughlam (this study), Guefaït and Aïn Jourdel); Early Pleistocene sites = brown circle

(Thomas Quarry I-Unit L, Tighennif, Aïn Boucherit, Aïn Hanech, El Kherba and Mansourah); Middle Pleistocene sites = green circle (Grotte des Rhinocéros and Grotte à Hominidés).

The fossiliferous locality of Ahl al Oughlam (33°34'11"N, 07°30'44"W) is an abandoned sandstone quarry located at the southeast boundary of the city of Casablanca (Morocco), 6.5 km from the present-day Atlantic shore (**Fig. 1;** Raynal et al., 1990; Geraads et al., 2022b). Stratigraphically, the quarry cuts through calcarenitic intertidal, supratidal and aeolian deposits correlative to sea-level highstands associated with a platform developed about 105 m a.s.l. which belong to the *Ahl al Oughlam Morphostratigrafic Unit* (Lefèvre and Raynal, 2002; Lefèvre et al., 2021; Geraads et al., 2022b), formerly included in the *Messaoudian* stage of Biberson's Moroccan Quaternary Chronostratigraphy (Biberson, 1961a; Stearns, 1978). The site was investigated in 1953 by Biberson (Biberson, 1961a, 1961b), under the name of *Carrière Déprez*, who reported the occurrence of some broken pebbles that he considered as representing reworked artifacts of the "archaic pebble culture" representing an initial stage of North African technological evolution. Raynal and Texier (1989) demonstrated that they are actually "geofacts" of natural origin found in marine deposits. In 1985, J.-P. Raynal and J.-P. Texier discovered abundant fossil faunal remains in karst formations and in a network of fissures and interconnected galleries between calcarenite blocks, at the foot of what was once a palaeoshoreline.

A biostratigraphic analysis of the mammal assemblage dates this locality to the Plio-Pleistocene boundary, indicating an approximate age of 2.5 Ma (Geraads, 1997; Geraads et al., 2022b). The genus *Equus* is absent, suggesting that the site is older than 2.3 Ma (Geraads, 2006). The mammalian fauna includes at least fifty-five species of both small and large mammals. A new species of *Hipparion*, *H. pomeli*, has been described subsequently from the site (Eisenmann and Geraads, 2007). The vertebrate fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards and snakes) and fishes. The most unexpected element of the mammalian fauna is a walrus, a pinniped marine mammal. No living or fossil walrus was previously known in the Eastern Atlantic, south of Belgium (Geraads, 2006). The site was formed along the oceanic seashore which explains why both marine and terrestrial forms are found among birds. A list of the identified faunal taxa is given in several publications (Raynal et al., 1990; Geraads, 1993, 1995, 1996, 1997, 2002, 2004, 2006; Alemseged and Geraads, 1998; Geraads and Amani, 1998; Geraads and Metz-Muller, 1999; Eisenmann and Geraads, 2007; Mourer-Chauviré and Geraads, 2008; Geraads et al., 2010; Mourer-Chauviré and Geraads, 2010; Gunnell et al., 2011; Sen and Geraads, 2023).

3. Material & methods

The material sampled and analyzed is currently stored at the *Institut national des Sciences de l'Archéologie et du Patrimoine* (INSAP) in Rabat (Morocco). The species included in this research are the following: *Sivatherium maurusium*, *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., Alcelaphini and *Anancus osiris*.

3.1 Stable isotopes (^{13}C and ^{18}O)

In this study, we performed stable carbon (^{13}C) and oxygen (^{18}O) isotope analysis of 82 fossil fauna specimens recovered from AaO (**Supplementary Table 1**). Sampling has been conducted on the buccal surface of molars and premolars from adult individuals. The tooth surfaces were cleaned with a tungsten abrasive drill bit to remove any adhering external material. Enamel powder for bulk analysis was obtained using gentle abrasion with a diamond-tipped drill.

Powdered enamel samples were chemically treated at the biomolecular laboratory at the *Institut Català de Paleoecologia Humana i Evolució Social* (IPHES - CERCA). Samples weighed from 3.5 to 9.5 mg. Chemical treatment of samples was based on protocols originally proposed by Koch et al. (1997) and later modified in Tornero et al. (2013). Samples were treated for 4 h in 0.1 M acetic acid [CH3COOH] (0.1 ml solution/0.1 mg of sample), neutralized with distilled water and freeze-dried.

The ^{18}O and ^{13}C of carbonates were measured using an automated carbonate preparation device (KIEL-III) coupled with a gas-ratio mass spectrometer (Finnigan MAT 252) at the environmental isotope laboratory at the University of Arizona, US. Powdered samples were allowed to react with dehydrated phosphoric acid under a vacuum at 70°C. Accuracy and precision of the measurements were checked and calibrated using calcium carbonate international standards (NBS-19 and NBS-18). Replicate measurements of the standards during analysis had errors of ±0.1‰ for $\delta^{18}O$ and ±0.08‰ for $\delta^{13}C$ (1 sigma). Carbon isotope composition is reported in δ notation, where $\delta^{13}C = [(Rsample/Rstandard) – 1]$, $R = {}^{13}C/{}^{12}C$ and δ is expressed in per mil, ‰. Carbon and oxygen values are reported relative to PDB (Vienna Pee Dee Belemnite).

The modern plants using a C_3 photosynthetic pathway (including most trees, woody shrubs, bushes, herbs and grasses) have an average isotopic $\delta^{13}C$ value of -28.5‰ (global range -20 to -37‰), with -23‰ as the maximum value for typical C_3 plants and a cut-off of -31.5‰ for closed-canopy forests (Kohn, 2010). In this work, we use the average $\delta^{13}C$ value of -27‰ for modern C_3 plants, excluding analyses from the understory of closed-canopy forests below -31.5‰ (Kohn, 2010). Modern plants that employ the C_4

photosynthetic pathway (primarily tropical grasses and sedges) have an average isotopic composition of -12‰ (global range -10 to -14‰) (Cerling et al., 1997; Cerling and Harris, 1999; Kohn and Cerling, 2002). The bivariate graphs were made with the Past 4.02 software (Hammer et al., 2001).

3.1.2 Estimation of enrichment factor, %C_4, $\delta^{13}C_{diet\text{-}meq}$ and MAP

Abundance of atmospheric CO_2 has been changing over time (Tipple et al., 2010) with a consequent influence on the carbon values of plants during its fixation in the photosynthesis process (Farquhar et al., 1989). To make a comparison between the carbon values of present-day plants with those consumed by animals in the past, it is crucial to perform corrections. In our work, we have corrected the $\delta^{13}C$ values of modern plants by +1.5‰, due to the difference between the pre-Industrial $\delta^{13}C_{CO2}$ value of ~ -6.5‰ established for the Plio-Pleistocene (Tipple et al., 2010), and the $\delta^{13}C_{CO2}$ value of ~ -8‰ at the time the reference collection of modern plants was collected (Kohn, 2010). When plants are consumed, a fixation occurs in the tooth enamel of the animals, a process of isotopic fractionation (Krueger and Sullivan, 1984; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005). In this study, we use formula (1) in Tejada et al. 2018 which determines that there is a positive correlation between body mass and enamel-diet enrichment fractionation (expressed as $\varepsilon^*_{enamel\text{-}diet}$). The $\varepsilon^*_{enamel\text{-}diet}$ has been calculated from the estimation of the body mass of the species analyzed: *S. maurusium* (Basu et al., 2016), *H. pomeli* (Bernor et al., 2021), *Gazella* sp. and Alcelaphini (Bibi and Kiessling, 2015), *M. phacochoeroides* (Rannikko, 2019) and *A. osiris* (Larramendi, 2016).

(1) $\varepsilon^* = 2.4 + 0.034\ (\text{Body Mass})$

The $\delta^{13}C$ values in plants and animals have also been proposed to estimate mean annual precipitation (MAP) in the fossil record. We use the formulae (2 and 3) developed in Kohn (2010) and Kohn et al. (2015) to estimate the MAP, which applies corrections for altitude, latitude, and $\delta^{13}C$ of atmospheric CO_2 from the average modern equivalent of diet composition ($\delta^{13}C_{diet\text{-}meq} = \delta^{13}C_{enamel} - \varepsilon^*_{enamel\text{-}diet}$ - Plio-Pleistocene atmospheric CO_2):

(2) $$MAP = 10 \wedge [\Delta^{13}C - 2.01 + 0.000198 \times elev - 0.0129 \times |lat| / 5.88] - 300$$

where *elev* is elevation in meters, *lat* is latitude in degrees, and

(3) $$\Delta^{13}C = (\delta^{13}C_{atm} - \delta^{13}C_{diet\text{-}meq})/(1 + \delta^{13}C_{diet\text{-}meq}/1000)$$

where $\delta^{13}C_{atm}$ is the carbon isotope of atmospheric CO_2 (-6.5‰ in the Plio-Pleistocene; Tipple et al., 2010) and $\delta^{13}C_{diet\text{-}meq}$ is the modern equivalent of diet composition ($\delta^{13}C_{diet\text{-}meq}$) estimated from $\delta^{13}C_{enamel}$ after $\varepsilon^*_{enamel\text{-}diet}$ correction (see formula (1)).

We estimated (4) the fraction of C_4 vegetation consumed by AaO herbivores using $\delta^{13}C$modern plant values, -24‰ for C_3 vegetation ecosystems (Kohn, 2010) and -12‰ for C_4 vegetation (Cerling et al., 1997). The fossil $\delta^{13}C_{enamel}$ values have been corrected for $\delta^{13}C$ of Plio-Pleistocene atmospheric CO_2 and $\varepsilon^*_{enamel\text{-}diet}$ to obtain the $\delta^{13}C_{diet\text{-}meq.}$

(4) $$\%_{C_4} = 100 \times (\delta^{13}C_{diet\text{-}meq} - \delta^{13}C_{C_3})/(\delta^{13}C_{C_4} - \delta^{13}C_{C_3})$$

3.2 Dental wear analysis

3.2.1 Dental mesowear analysis

A total of 74 molars were studied using mesowear analysis, excluding 28 teeth that were unworn, extremely worn, or had broken or damaged cusp apices (**Supplementary Table 2**). The sensitivity of cusp sharpness to ontogenetic age has been documented for both young and old individuals. Conversely, mesowear displays a weaker correlation with age in intermediate age groups, and demonstrates a stronger relationship with dietary factors (Rivals et al., 2007). The mesowear analysis method assesses the relief and sharpness of worn cusp apices, which are related to attritive and abrasive wear on dental enamel. These analyses were performed on the buccal side of upper molars and the lingual side of lower molars, with a preference for the paracone of the upper M2. To evaluate wear on teeth from P3 to M3, we used the extended mesowear method proposed by Kaiser and Solounias (2003). In this study, we applied the method introduced by Mihlbachler et al. (2011), which uses seven cusp categories ranging from high and sharp (stage 0) to completely blunt with no relief (stage 6). A low-abrasion diet such as browsing, which induces high attrition, preserves sharpened apices on buccal cusps as teeth wear down, while a high-abrasion diet results in more rounded and blunted buccal cusp apices. The bivariate graph was performed with the Past 4.02 software (Hammer et al., 2001).

3.2.2 Dental microwear analysis

For the microwear analysis, a total of 109 molars and premolars were selected and molded. After examination of the molds under a stereomicroscope, 49 specimens were discarded due to poor preservation or taphonomic defects (**Supplementary Table 2**) (El-Zaatari, 2010; King et al., 1999). Examination of enamel microwear features was conducted through standard light microscopy, using a Zeiss Stemi 2000C stereomicroscope at a magnification of 35x on high-resolution epoxy casts of the teeth. The cleaning, molding, casting, and examination protocols, as well as feature classification criteria, were consistent with those established by Semprebon and Solounias (2002) and Semprebon et al. (2004). Upper and lower teeth, spanning from P4 to M3, were included in the analysis following Xafis et al. (2017). The occlusal surface of each specimen was first cleaned with acetone and 96% ethanol before being molded with high-resolution silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set) and transparent casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). Scoring of microwear features, including small and large pits (round scars), scratches (elongated scars with parallel sides), gouges (irregular edges and much larger and deeper than the large pits), puncture pits (deepest at their centers, symmetrical, craterlike features with regular margins), and cross scratches (oriented perpendicularly to the majority of scratches), was performed using a standard 0.16 mm^2 ocular reticle. In order to achieve a more precise categorization of grazers, browsers, and mixed feeders, we used the percentage of individuals in a sample possessing scratch numbers that fall between 0 and 17 (Semprebon and Rivals, 2007). The scratch width score (SWS) was calculated based on the ratio of fine to coarse scratches (“0” predominantly fine scratches per tooth surface, “1” to those with a mixture of fine and coarse scratches, and “2” to those with predominantly coarse scratches). The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002; Rivals and Semprebon, 2011). To reduce inter-observer error, dental microwear analysis was conducted by a single experienced researcher (IRP).

4. Results

4.1 Stable isotopes (δ^{13}C and δ^{18}O)

The δ^{13}C values of all taxa measured in AaO ranged from -14.1 to -8‰ with a mean of -11.4 ± 1.2‰ (*n* = 82) (**Fig. 2**). The data for each species are described below: *H. pomeli* (*n* = 16; range = -13.5 to -10.6‰; mean = -11.7 ± 0.9‰), Alcelaphini (*n* = 18; range = -13 to -8‰; mean = -10.3 ± 1.3‰), *Gazella* sp. (*n* = 18; range = -12.8 to -10.6‰; mean = -11.6 ± 0.6‰), *S. maurusium* (*n* = 6; range = -14.1 to -10.8‰; mean = -12.4 ± 1.4‰), *M. phacochoeroides* (*n* = 23; range = -13.2 to -8.4‰; mean = -11.7 ± 1.2‰) and *A. osiris* (*n* = 1; -13.3‰). The two taxa with the highest variability and the most positive values are Alcelaphini and *M. phacochoeroides*. *Gazella* sp. and *H. pomeli* are the species with the lowest variability and *S. maurusium* is the species with the most negative values.

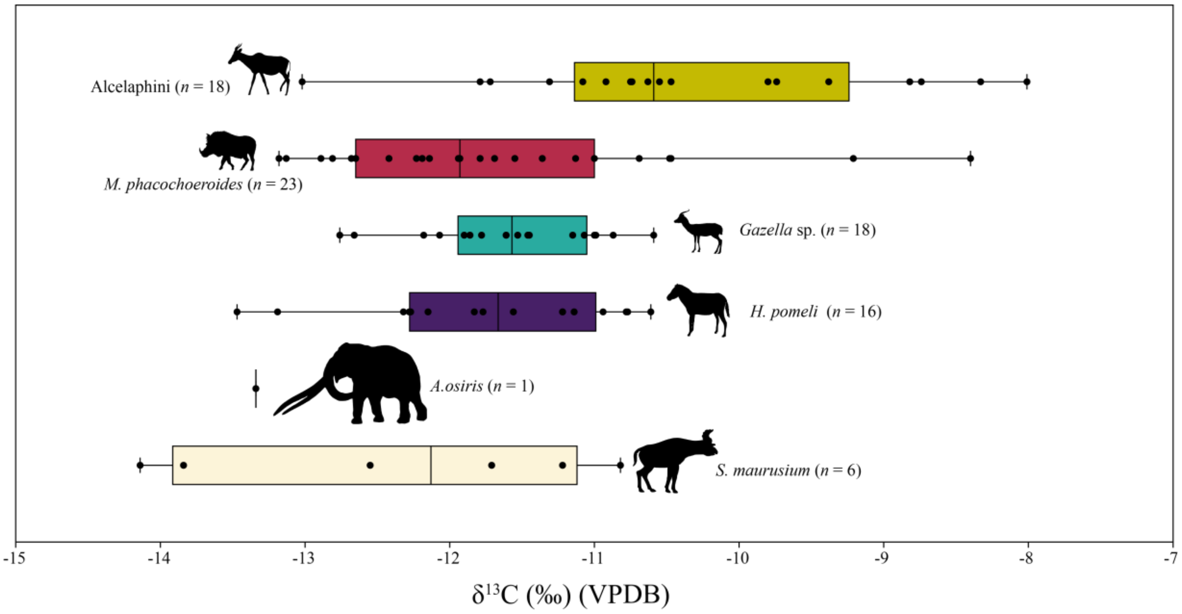

Fig. 2. Jitter boxplots for $\delta^{13}C$ values of the ungulates from the Plio-Pleistocene site of AaO. Boxes = first and third quartile for each taxon, whiskers = full range for each taxon and hashes within boxes = median value.

The $\delta^{18}O$ values ranged from -3 to 2.9‰ with a mean of -0.6 ± 1.2‰ (*n* = 82) (**Fig. 3**). The data for each species are described below: *H. pomeli* (*n* = 16; range = -3 to 0.2‰; mean = -1.8 ± 0.9‰), Alcelaphini (*n* = 18; range = -2.2 to 0.6‰; mean = -0.8 ± 0.7‰), *Gazella* sp. (*n* = 18; range = -2.3 to 2.1‰; mean = -0.2 ± 1.3‰), *S. maurusium* (*n* = 6; range = -0.9 to 2.9‰; mean = 1.2 ± 1.3‰), *M. phacochoeroides* (*n* = 23; range = -1.8 to 2‰; mean = -0.4 ± 0.9‰) and *A. osiris* (*n* = 1; -1.4‰). The whole isotopic dataset is provided in **Supplementary Table 1**.

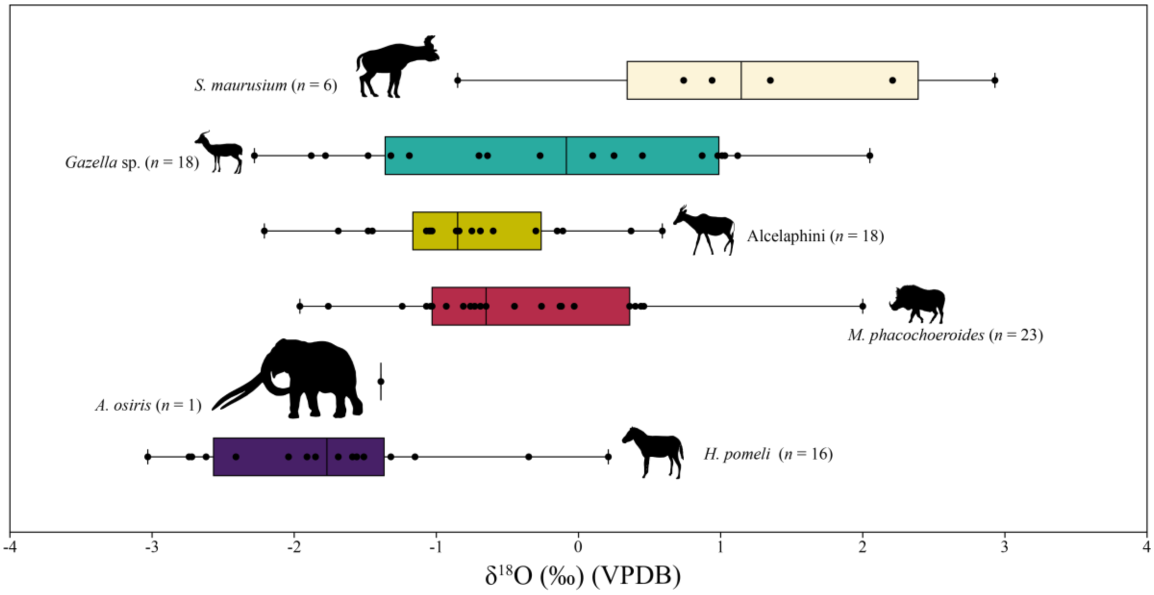

Fig. 3. Jitter boxplots for $\delta^{18}O$ values of the ungulates from the Plio-Pleistocene site of AaO. Boxes = first and third quartile for each taxon, whiskers = full range for each taxon and hashes within boxes = median value.

4.1.2 Estimation of enrichment factor, %C_4, $\delta^{13}C_{diet-meq}$ and MAP

The $\varepsilon^*_{enamel\text{-}diet}$ of the AaO species ranges from 12.4 to 14.7‰, depending on the body mass. C_4 plants are virtually absent in the diet of AaO species. They are only present, in low percentages, in four individuals of Alcelaphini (%C_4 = 4, 5, 8 and 11%) and in one individual of *M. phacochoeroides* (%C_4 = 6%) (**Supplementary Table 1**). The MAP results are estimated in **Table 1**. In order to calculate it, the five individuals with C_4 presence have been excluded based on the criteria established by Kohn (2010). The average $\delta^{13}C_{diet\text{-}meq}$ value (-26.1‰) and MAP (385 mm/yr) suggest a relatively arid environment for AaO, defined by Kohn (2010) as ecosystems with a MAP ≤ 500 mm/yr and $\delta^{13}C_{diet\text{-}meq}$ values between -26 and -24‰ (**Table 1**; **Supplementary Table 1**).

Table 1. Summary of $\delta^{13}C$ (‰), Body Mass (Kg), $\varepsilon^*_{enamel\text{-}diet}$ (‰), $\delta^{13}C_{diet\text{-}meq}$ (‰), %C_4 and Mean Annual Precipitation (MAP - mm/yr).

Species	***n***	**$\delta^{13}C$ (‰)**	**Body Mass (Kg)**	**$\varepsilon^*_{enamel\text{-}diet}$ (‰)**	**$\delta^{13}C_{diet\text{-}meq}$ (‰)**	**%C_4**	**MAP (mm/yr)**
S. maurusium	6	-12.4 ± 1.4	1236	+14	-27.9 ± 1.4	0	1041 ± 760
Alcelaphini	18	-10.3 ± 1.3	200	+13.2	-23.9 ± 1.3	1.5 ± 3.2	177 ± 210
Gazella sp.	18	-11.6 ± 0.6	30	+12.4	-24.1 ± 0.6	0	139 ± 112
H. pomeli	16	-11.7 ± 0.9	250	+13.3	-26.5 ± 0.9	0	400 ± 269
M. phacochoeroides	23	-11.7 ± 1.2	297	+13.4	-26.5 ± 1.2	0.3 ± 1.3	455 ± 274
A. osiris	1	-13.3	5000	+14.7	-29.6	0	1996
All species	82	-11.4 ± 1.2	-	+13.2	-26.1 ± 1.4	0.4 ± 1.7	385 ± 419

4.2 Dental wear analysis

Table 2. Summary of mesowear and microwear data of the fossil assemblages from AaO. Abbreviations: *n*, number of specimens; MWS, mesowear score; NS, average number of scratches; NP, average number of pits; SD, standard deviation; SWS, scratch width score; %PP, percentage of specimens with puncture pits; %HC, percentage of specimens with hyper-coarse scratches; %LP, percentage of specimens with large pits; %G, percentage of specimens with gouges; %XS, percentage of specimens with cross scratches; %0–17, percentage of specimens with number of scratches ranging between 0 and 17.

Species	**Mesowear**		**Microwear**											
	n	**MWS**	***n***	**NS**	**SD**	**NP**	**SD**	**SWS**	**%PP**	**%HC**	**%LP**	**%G**	**%XC**	**%0–17**
S. maurusium	4	1	4	12.8	1.9	24.75	2.7	1	0	0	50	100	25	100
Alcelaphini	22	2.2	17	20.0	2.6	20.1	3.4	1.1	11.8	0	82.4	29.4	11.8	17.6
Gazella sp.	17	1.2	8	9.5	1.6	23.4	4.6	1	0.0	0	100	50	12.5	100
H. pomeli	6	4.3	13	20.6	3	19.1	4	1	15.4	0	84.6	7.7	0	0
M. phacochoeroides	-	-	18	19.7	4.6	23	3.6	0.9	5.6	0	83.3	22	100	33.3
A. osiris	-	-	1	26	-	25.5	-	1	0	100	100	0	100	0

4.2.1 Dental mesowear analysis

The mesowear pattern of AaO specimens is characterized by occlusal surfaces ranging from sharp cusps and high relief (low abrasion) to low relief with rounded cusps (high abrasion). It corresponds to mesowear scores with values from 0 to 5 (**Table 2; Fig. 4**). All three Bovidae have sharp cusps, which means that attrition predominates strongly over abrasion. The *S. maurusium* has the lowest level of abrasion with a MWS of 1, falling in the MWS average of extant leaf browsers. The *Gazella* sp. has also a low average MWS (1.2), being in the range of MWS of extant mixed feeders but with a tendency towards a browsing diet. The Alcelaphini, with variability in abrasion levels, has an average MWS of 2.2 and is categorized as a grass-dominated mixed feeder. In the case of the Equidae *H. pomeli*, the MWS indicates high levels of abrasion, with a MWS average of 4.3. This pattern places *H. pomeli* among extant grazers.

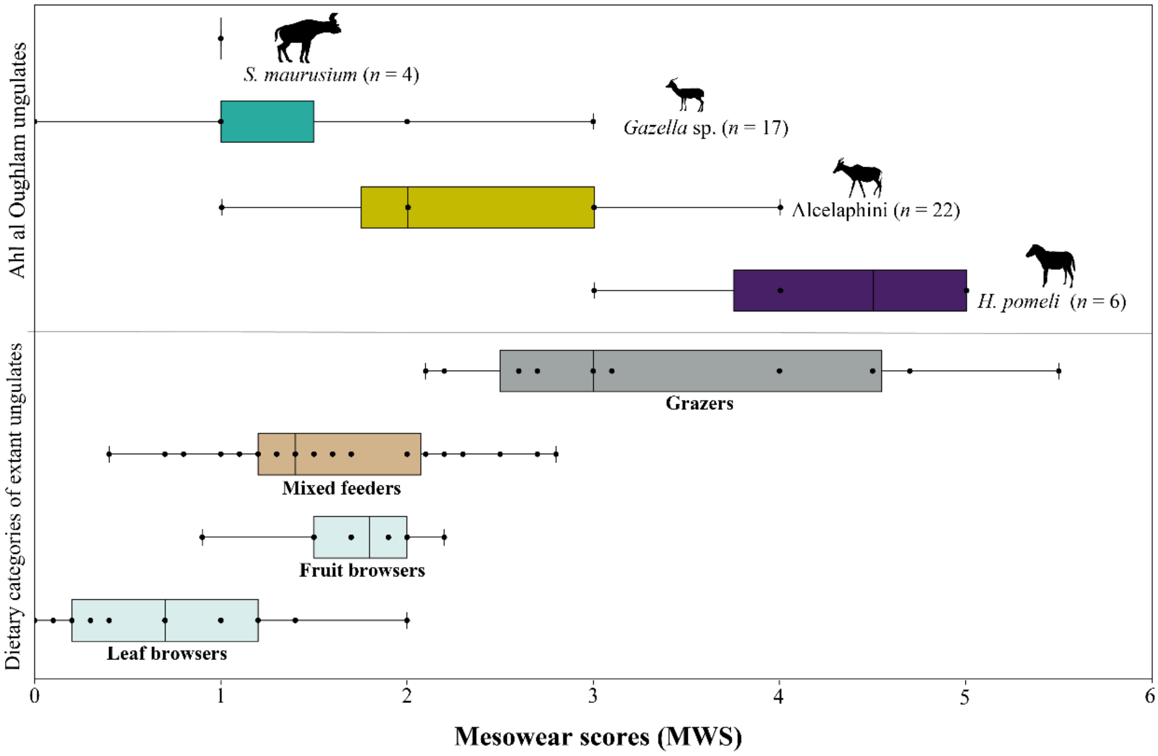

Fig. 4. Jitter boxplot with mesowear scores (MWS) of the ungulates from AaO. Boxes = first and third quartile for each taxon; whiskers = full range for each taxon and hashes within boxes = median value. Extant ungulates database (Fortelius and Solounias, 2000).

4.2.2 Dental microwear analysis

At AaO, all herbivores display browsing or mixed feeding dietary traits (**Fig. 5**). The species analyzed are classified into two groups. The first group includes the *S. maurusium* and *Gazella* sp. and plot among extant browser ungulates. The second group, which includes Alcelaphini, *H. pomeli*, *M. phacochoeroides* and *A. osiris*, plot among extant mixed feeders. The first group has microwear patterns characterized by a high number of pits (NP = 24.1) and a small number of scratches (NS = 11.2) and the second group has a microwear pattern defined by a similar number of pits (NP = 21.9) and scratches (NS = 21.6). *Gazella* sp. (NS = 9.5) and *S. maurusium* (NS = 12.8) are the species with a lower number of scratches, and *H. pomeli* (NS = 20.6) and *A. osiris* (NS = 26) have a higher number of scratches. All species have a similar and a relatively high number of pits. The *A. osiris* (NP = 25.5) and *S. maurisium* (NP = 9.5) have the highest abundance of pits. Although the Alcelaphini, *H. pomeli*, *M. phacochoeroides* and *A. osiris* in **Figure 5** are classified among extant mixed feeders, the high number of scratches (see **Table 2**, NS and 0–17%) indicates a high proportion of grasses in their diet.

The SWS, being between 0.9 and 1.1, indicates a mixture of both fine and coarse scratches for all species. Hyper-coarse scratches have been found only in *A. osiris*. Cross scratches are absent in *H. pomeli* and present in a low percentage in Alcelaphini, *Gazella* sp. and *S. maurusium*. *A. osiris* and *M. phacochoeroides* have them in 100% of the individuals. This trait is characteristic of animals with a bunodont dental morphology as in the case of the latter two species. Gouges have been observed in all species except in *A. osiris* and their presence is remarkable in the four individuals of *S. maurusium*. Puncture pits are present in a low percentage in Alcelaphini, *H. pomeli* and *M. phacochoeroides*, and large pits are present in all species in proportions varying from 50% to 100% of the individuals.

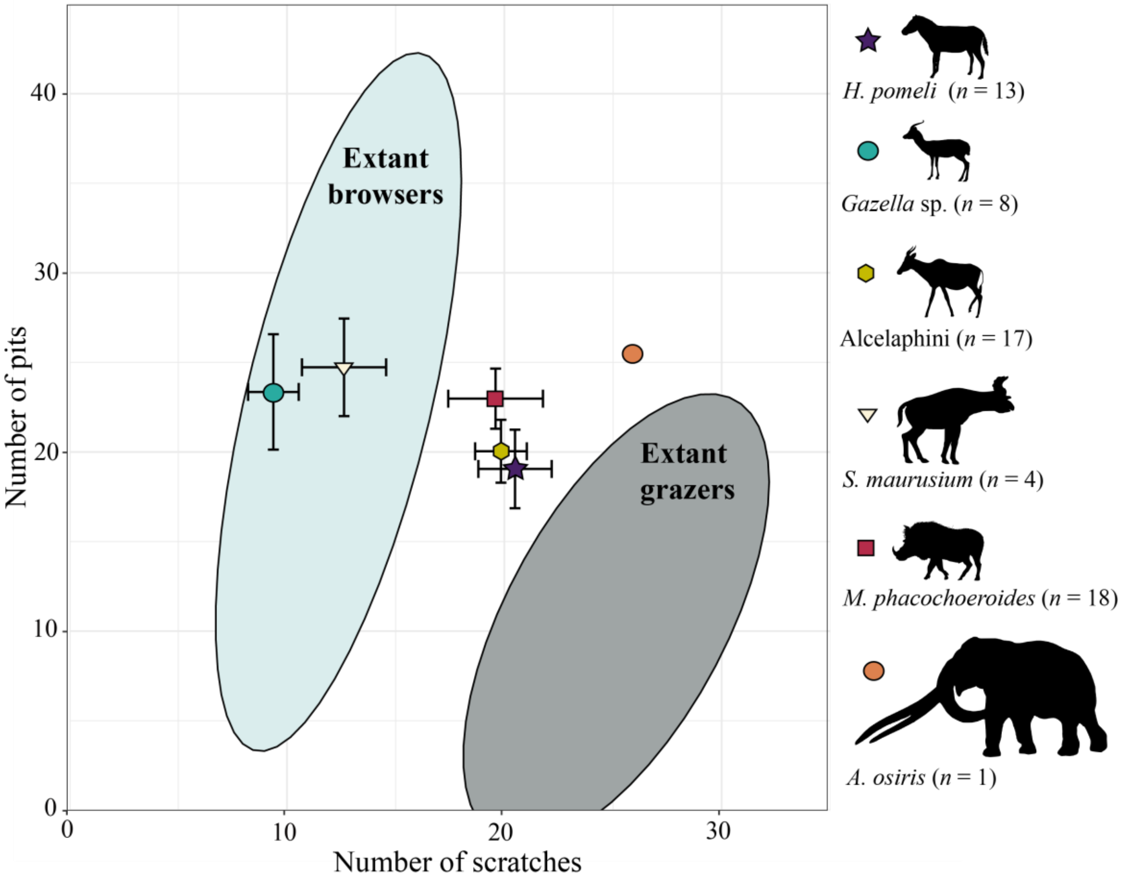

Fig. 5. Bivariate plot of the average numbers of pits and scratches for the species from AaO. Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant browsers and grazers based on the database from Solounias and Semprebon (2002).

5. Discussion

5.1 Palaeodiet

The combination of the three approaches allows us to characterize the dietary preferences of the different taxa, as well as to reconstruct the general ecological context (**Table 3**). In

AaO, all species have a predominantly plant-based C_3 diet with values ranging from -14 to -8‰, with a small consumption of C_4 plants in Alcelaphini and *M. phacochoeroides* (**Table 1**). In some contexts, interpreting the carbon isotopic signal can be complex, especially when there are no extreme values that can indicate high consumption of C_4 plants linked to grass consumption (ca. $\delta^{13}C > 0$‰; Cerling and Harris, 1999) or the presence of C_3 closed canopy forests (ca. $\delta^{13}C < -16$‰; Kohn, 2010), types of environments in which the signal is obvious. In AaO, there is both inter- and intra-species variability in carbon values. Recent isotopic studies on extant species in sub-Saharan Africa have shown a weak relationship between intra-taxon variation in $\delta^{13}C_{enamel}$ (C_3 and C_4) and corresponding changes in herbivore diet and vegetation structure (woody cover). Therefore, adopting a community-level approach when making inferences about vegetation using isotopic data, focusing on the relationships between different taxa is recommended. This approach allows for a more accurate understanding of the vegetation dynamics and ecological context (Robinson et al., 2021). In AaO, the interspecific difference between Alcelaphini and *S. maurusium* is striking and could represent different ecological niches and diets (**Fig. 2**). Dental wear analysis (micro- and mesowear) shows variable feeding traits that range from browser to mixed-feeder to grazer behavior, including Alcelaphini with a grass-dominated, mixed-feeding diet or *S. maurusium* as the most browsing taxon (**Table 3**). Oxygen isotope data are consistent with the dental wear feeding pattern, with browser species having more positive values (*S. maurusium* and *Gazella* sp.) than the rest, and grass-dominated mixed feeders having more negative values. The correlation in oxygen is higher between the most grazing species, according to dental wear pattern, such as *H. pomeli*, and the most browsing ones such as *S. maurusium*, showing very distant values between them. This could suggest the consumption of different resources, such as the preference for grasses by the former and leaves by the latter.

Table 3. Summary of dietary interpretations based on tooth wear and stable carbon isotope data. Abbreviations: B = browser, MF-B = browsing-dominated mixed feeder, MF = mixed feeder, MF-G = grass-dominated mixed feeder, and G = grazer. The parentheses indicate the consumption of C_4 plants (in very low percentage) in some species.

Species	**Stable isotopes**	**Mesowear**	**Microwear**
S. maurusium	C_3	B	B
Alcelaphini	C_3 (C_4)	MF-G	MF-G
Gazella sp.	C_3	MF-B	B
H. pomeli	C_3	G	MF-G
M. phacochoeroides	C_3 (C_4)	-	MF-G
A. osiris	C_3	-	MF-G

5.1.1 Comparison of AaO with other African sites

The ***Sivatherium maurusium*** from AaO has the most negative C_3 carbon values ($\delta^{13}C$ mean = -12.4 ± 1.4‰) and the most positive oxygen values (**Fig. 2 and 3**) compared to other AaO species. These oxygen and carbon values could be attributed to the preferential consumption of leaves from the upper parts of trees or shrubs which is consistent with dental wear patterns suggesting a browsing diet for AaO *S. maurusium*. The same isotopic pattern in $\delta^{13}C$ and $\delta^{18}O$ values has also been observed in *Sivatherium* from Hadar and

Aramis (Ethiopia; ~4–3 Ma) (Wynn et al., 2016) and Makapansgat (South Africa; ~3 Ma (Lee-Thorp et al., 2010). Although this species is known from various North African sites such as Aïn Boucherit, Aïn Hanech and El-Kherba (Early Pleistocene; Algeria), Aïn Jourdel (Late Pliocene; Algeria), and Ichkeul and Aïn Brimba (Late Pliocene; Tunisia), this is the first time that data on its diet has been obtained from this area.

In East Africa, the Giraffidae were represented by two genera: *Giraffa* and *Sivatherium*, from the early Pliocene onwards. *Sivatherium* became extinct during the Middle Pleistocene. Overall, its diet underwent changes in the Turkana Basin (Kenya), being a browser (C_3 plants) at ~4 Ma and switching to grazing (C_4 plants) between ~2.5 and 1 Ma (Cerling et al., 2015). In the Chiwondo beds (Malawi; ~2.5 Ma), *Sivatherium* exhibited less negative $\delta^{13}C$ values (n = 1; $\delta^{13}C$= -7.9‰) than the purely browsing fossil *Giraffa* (n = 2; $\delta^{13}C$ mean = -12.1 ± 1.1‰), indicating that it incorporated some C_4 grass in its diet (Bocherens et al., 2011). In Olduvai (Tanzania; ~1.8 Ma), a multiproxy approach suggested a mixed diet for *S. maurusium*, C_4-dominated or mixed diets, a mesowear characteristic of grazers, but with microwear indicating a browsing-dominated mixed diet, likely due to seasonal changes in its diet (Uno et al., 2018).

In South Africa, *Sivatherium* maintained its preference for C_3 plants from ~5 to 3 Ma. In the Langebaanweg site (~5 Ma), the $\delta^{13}C$ mean value (n = 26) is -11.5 ± 1.1‰ (Franz-Odendaal et al., 2002). However, hypsodonty indices, dental mesowear, and dental microwear suggested mixed feeding dietary traits with a browsing tendency for this species (Franz-Odendaal and Solounias, 2004). In the Makapansgat Limeworks Member 3 (~3 Ma), *Sivatherium* exhibited carbon values (n = 2; $\delta^{13}C$ mean = -11.4 ± 0.1‰) similar to those of *Giraffa* (n = 8; $\delta^{13}C$ mean = -11 ± 0.9‰) at the same site (Sponheimer and

Lee-Thorp, 2009).The diet of AaO *Sivatherium* follows the same C_3-browser pattern as that of the rest of Africa during the ~3 to 2.5 Ma period, but further multiproxy studies are needed in more recent North African sites such as Aïn Hanech or El-Kherba (~1.8 Ma) to determine whether this dietary pattern remains the same or changes, as in the case of East Africa.

The **Alcelaphini** from AaO is the taxon with the least negative carbon values, with a predominance of C_3 plant consumption values (mean $\delta^{13}C$ = -10.3 ± 1.3‰), indicating even some C_4 consumption (**Table 2**). The results of micro- and mesowear tooth analysis indicate a mixed diet, but with a high content of grasses in its feeding ecology. In general, this taxon is indicative of open dry environments, both during the African Pliocene and Pleistocene and in extant populations. Regardless of the consumption of C_3 or C_4 plants, their feeding behavior is predominantly grazing (Vrba, 1984; Sponheimer et al., 1999; 2003; Bobe and Behrensmeyer, 2004; Cerling et al., 2015).

Different species of Alcelaphini were present in North Africa from the Late Pliocene (Arambourg, 1979; Geraads & Amani, 1998) until they were declared extinct in this area in 1994 (Mallon and Kingswood, 2001), but the only fossil record of their diet has been carried out at the site of Tighennif (1 Ma; Algeria). At this site, the Alcelaphini tribe is represented by the species *Connochaetes taurinus prognu*. The pattern of $\delta^{13}C$ values (*n* = 6; mean $\delta^{13}C$ = -10.5 ± 1.4‰) is similar to that observed in the Alcelaphini from AaO (Bocherens et al., 1996; Fannin et al., 2021). Compared to the carbon values of different ungulates analyzed in Tighennif, this species has the most positive carbon values, indicating, as in the case of AaO, a small consumption of C_4 plants in some individuals.

In central Africa, 2500 km west of the Rift Valley, at the Koro Toro site (Chad; ~3.5–3 Ma), Alcelaphini have a grazing diet based on C_4 plants with an average $\delta^{13}C$ value (n = 6) of 1.4 ± 0.8‰ (Zazzo et al., 2000).

In eastern Africa (Turkana Basin), the remarkable predominance and similarity in the C_4 isotopic signature of Alcelaphini from approximately ~4.4 Ma to present-day specimens is particularly notable (White et al., 2009; Cerling et al., 2015). In Olduvai (Tanzania; ~1.8 Ma), the carbon isotope data indicate C_4-dominated diets, while dental wear classifies this species as a grass-dominated mixed feeder (Uno et al., 2018).

In southern Africa, Wonderwerk Cave has a longer temporally stratified sequence from the Early Pleistocene to the Holocene, with the presence of Alcelaphini in all layers. They show a progressive increase in C_4 consumption from 50% in the Early Pleistocene to 100% in the Holocene (Ecker et al., 2018). In the Makapansgat Limeworks Member 3 (~3 Ma), Alcelaphini (*Parmularius*, *Damaliscus* and *Connochaetes*) have C_4 values, in contrast to the Tragelaphini from the same level, which have a clear C_3 values. Ecomorphological and microwear data confirm a grazing diet for the former and a browsing for the latter (Sponheimer et al., 1999; Schubert et al., 2006). In Haasgat cave (~2.6–1.9 Ma), as in Makapansgat, Alcelaphini have a C_4 consumption while Tragelaphini have C_3 plant consumption values (Adams et al., 2013). In Swartkrans cave (~1.9–1.8 Ma), the Alcelaphini *Connochaetes* sp. also has a C_4-based diet (Lee-Thorp et al., 1989). However, in other South African sites, the Alcelaphini carbon values are clearly C_3, although attributed to grass consumption. This is the case of Hoedjiespunt (~0.35–0.25 Ma) with a mean $\delta^{13}C$ (n = 16) of -9.8 ± 1.3‰, Elandsfontein (~1.0–0.6 Ma) with a mean $\delta^{13}C$ (n = 19) of -10.3 ± 1.2‰, and Langebaanweg (~5 Ma) with a mean $\delta^{13}C$ (n = 7) of -10.8 ± 1‰ (Lehmann et al., 2016).

The ***Hipparion pomeli*** from AaO has a diet based on C_3 plants (δ^{13}C mean = -11.7 ± 0.9‰). It is the species with the highest mesowear, indicative of a grazing diet. Microwear classifies it as a mixed feeder, but the high number of scratches is related to a high consumption of grasses. The presence of *Hipparion* between ~3.5 and 1.7 Ma is well documented in North Africa in sites such as Aïn Brimba and Lake Ichkeul in Tunisia, Aïn el Bey, Aïn el Hadj Baba, Aïn Jourdel, Mansourah, Aïn Boucherit, Aïn Hanech, Puits Carouby, Carrière Brunie, Carrières Quartier St-Pierre in Algeria, and Fouarat, Oued Akrech, and Guefaït in Morocco. The dating of the youngest North African hipparion record occurs at Aïn Hanech (~1.7 Ma) (Van der Made et al., 2022). Regarding studies on the feeding habits of this species in North Africa, there are only preliminary results for the *Hipparion* sp. from the Guefaït site (~3–2.5 Ma; Morocco), which show a predominance of C_3 plant consumption (n = 4; δ^{13}C mean = -9.5 ± 1‰), although with less negative carbon values than those of the *H. pomeli* from AaO (Ramírez-Pedraza et al., 2023).

In Central Africa, diachronic (~6–3 Ma) isotopic studies carried out on the species *Hipparion* cf. *hasumense* in Chad show a clear predominance of C_4 plant consumption. In Kossom Bougoudi (~6–5 Ma), the average δ^{13}C (n = 6) is -1.3 ± 0.8‰, and in the Koro Toro site (~3.5–3 Ma) the average δ^{13}C value (n = 2) is 0.9 ± 1.1‰ (Zazzo et al., 2000).

In East Africa, as was the case with the Alcelaphini, the hipparion equid *Eurygnathohippus* has continuity in C_4-grazer plant consumption from ~4 to 1.5 Ma (Bocherens et al., 2011; Cerling et al., 2015; Manthi et al., 2020). Other methods such as microwear and mesowear also indicate a grazing diet for the *Eurygnathohippus* from Olduvai (Tanzania; ~1.8 Ma) (Uno et al., 2018).

In southern Africa, the *Hipparion* from Langebaanweg (~5 Ma) has a $\delta^{13}C$ mean value (*n* = 6) of -11.3 ± 0.9‰, implying a consumption of C_3 plants (Franz-Odendaal et al., 2002). Other lines of evidence, such as mesowear analysis, in this species are consistent with grazing behavior (Franz-Odendaal et al., 2003). Therefore, it would have a diet based on C_3 grasses, like the *H. pomeli* from AaO. In contrast, at the Makapansgat site (~3 Ma), the *Hipparion* indicates C_4 plant consumption (Sponheimer and Lee-Thorp, 2009; Lee-Thorp et al., 2010). In general, during the African Plio-Pleistocene, *Hipparion* had a diet mainly based on the consumption of C_4 grasses. Grass consumption has also been observed in AaO, although with the intake of C_3 plants. Despite the low presence of C_4 plants in North Africa during the study period, some species in AaO show a consumption of C_4 plants, but this is not the case for *H. pomeli*, which may indicate slightly different dietary preferences compared to its relatives in other parts of Africa.

The ***Metridiochoerus phacochoeroides*** from AaO shows a predominance of C_3 plant carbon values (mean $\delta^{13}C$ = -11.7 ± 1.2‰), but with significant variability, including a small percentage of C_4 consumption in one individual as observed in Alcelaphini. Microwear analysis shows a mixed diet, although with significant consumption of grasses, like other species classified as mixed feeders. The combination of both proxies indicates a preferential diet based on C_3 grass consumption.

The genus *Metridiochoerus* first appeared in Africa ~3.5 Ma. *Metridiochoerus phacochoeroides* is endemic to northern Africa and is distinct from the east and South

African representatives of the genus. Besides AaO, *Metridiochoerus* is rare in North Africa, but is also known from its type-locality Aïn Jourdel (Thomas, 1884).

In East Africa, *Metridiochoerus* between ~4 and 1 Ma were predominantly grazers with high C_4-grazer proportions (Harris and Cerling, 2002; Cerling et al., 2015; Uno et al., 2018). Dental microwear analysis conducted on *Metridiochoerus* from Olduvai (~1.8 Ma, Tanzania) points to mixed feeding and grazing behavior (Uno et al., 2018). In the Chiwondo Beds in Malawi (~2.5–1.5 Ma), *M. andrewsi* and *M. compactus* exhibit a predominant consumption of C_3 plants (Lüdecke et al., 2016).

Little is known about the diet of *Metridiochoerus* in South Africa. Some populations of *M. andrewsi* from Elandsfontein (~1.0–0.6 Ma) were consuming mostly C_3 plants (Luyt et al., 2000), but due to the overall predominance of C_3 plants in this area, as in the Chiwondo Beds in the Malawi Rift, could have been including grasses in their diet as well.

The ***Gazella* sp.** from AaO has carbon values that correspond to a C_3 plant-based diet (mean $\delta^{13}C = -11.6 \pm 0.6‰$). Microwear analysis shows a browser pattern; however, mesowear analysis indicates a mixed diet with a browsing tendency. This could imply a more purely browsing diet over a relatively brief period and a more varied consumption of plants, including grasses in their diet, for most of the year. As with Alcelaphini, *Gazella* has been present in North Africa since the Pliocene (Sahnouni et al., 2011; Van der Made et al., 2021) until the present day in Morocco, Algeria, and Tunisia (Schmid et al., 2005).

In North Africa, isotopic studies have been carried out on this species in both Tighennif (~1 Ma; Algeria) with a mean $\delta^{13}C$ value ($n = 5$) of -11.9 ± 0.9‰ and Guefaït (~3–2.5 Ma; Morocco) with a mean $\delta^{13}C$ value ($n = 4$) of -10.9 ± 1.1‰. At both sites, there is a clear predominance of C_3 plant consumption by *Gazella* (Fannin et al., 2021; Ramírez-Pedraza et al., 2023).

In East Africa, *Gazella janenschi* from the Laetolil Beds (∼4.3–3.5 Ma) has carbon values ranging from -1.9 to -9.8‰, implying a variable diet from C_4-grazing to C_3-browsing (Kingston and Harrison, 2007). This dietary flexibility has also been observed in different Antilopini analyzed in the Turkana Basin (Kenya), with extracted proportions of the isotopic signal of 17% C_4-grazing, 75% mixed C_3–C_4, and 8% C_3-browsing for the period of ~4.3 to 2.3 Ma, and 54% C_4-grazing, 46% mixed C_3–C_4, and 0% C_3-browsing for the period ~2.3 to 1.0 Ma (Cerling et al., 2015). The multiproxy study (isotopes, microwear, and mesowear) of Antilopini from Olduvai (1.8 Ma) also indicates a mixed feeder diet (Uno et al., 2018). The *Gazella* sp. from AaO, as well as those from the Pleistocene and Pliocene in Africa in general, seem to have the plasticity to consume distinct types of plants, adapting to seasonal availability. Even in East Africa before ~2.3 Ma, with a predominance of C_4 grassland in the area, they maintain a percentage of contribution from C_3 plant consumption.

In South Africa, *Gazella vanhoepeni* from Makapansgat (~3 Ma) is considered either a browser or a mixed-feeder preferring browsing based on isotopic, ecomorphological, microwear, and mesowear dental studies (Schubert et al., 2006). The diachronic and multiproxy study (isotopes, dental microwear texture, and mesowear analysis) of Antilopini (*Antidorcas*) from Sterkfontein Member 4 (~2.8–2 Ma) and Swartkrans

Members (~2–0.8 Ma) also indicates a mixed diet with a certain browsing tendency for this genus (Sewell et al., 2019).

5.2 Palaeohabitat and palaeoclimate

The results of the combination of proxies suggest for AaO a landscape with a predominance of open and dry habitat, composed of C_3 woody plants and grasses and a low presence of C_4 plants. The closed canopy forest is absent in the surroundings of AaO, since no species has $\delta^{13}C_{diet-meq}$ values below -31.5‰, which is established as a limit for this habitat.

5.2.1 Dry environment and seasonality

The mean annual precipitation (MAP) in AaO was 385 mm/year, indicating a dry climate. The aridity of the region is supported by the fact that environments dominated by C_3 plants with a MAP of 500 mm/year or less are typically associated with arid conditions. Kohn (2010) argues that the indicator's reliability depends on the mean MAP of all analyzed taxa. Thus, the average MAP remains the critical factor for assessing the robustness of this indicator. However, the variability in $\delta^{13}C_{enamel}$, MAP, and $\delta^{13}C_{diet-meq}$ values, both inter- and intra-species (**Table 1**), suggests the presence of microhabitats (Patalano et al., 2021). Arid regions such as AaO can present small areas with higher humidity, such as those found near water sources. Plants growing in these areas may display lower $\delta^{13}C$ values than expected for the surrounding dry environment, especially in a particularly wet year or season (Kohn, 2010).

In dry environments, C_4 plants exhibit greater efficiency than C_3 plants under conditions of low atmospheric CO_2 concentration, high temperatures, and moisture stress (Ehleringer et al., 1991; Cerling et al., 1993). Therefore, the presence of C_4 plants in the diet of Alcelaphini and *M. phacochoeroides*, even in small proportions, aligns with arid environments. The variability in $\delta^{13}C_{enamel}$ values within species, especially in the aforementioned species, may suggest the existence of pronounced seasonal fluctuations. Another approach to determine the relative aridity in the environment is to measure the differences in $\delta^{18}O$ values in tooth enamel between obligate and non-obligate drinking animals, the larger the difference the higher the estimated aridity (Levin et al., 2006; Blumenthal et al., 2017). In arid environments, evaporation of ^{16}O and enrichment of ^{18}O occurs both in open water sources and in plant water and tissues (Gonfiantini et al., 1965). However, this evaporative effect is much more pronounced in plants. Consequently, it is expected that animals that primarily obtain water through plant consumption (non-obligate drinkers) will exhibit higher $\delta^{18}O_{enamel}$ values compared to obligate drinkers that rely on direct access to surface water. For this comparison, we selected the most reliable species in AaO for classifying the mentioned categories. Specifically, we chose *S. maurusium* and *Gazella* sp. as non-obligate drinkers, and *H. pomeli* as an obligate drinker. Generally, grazers among ungulates have a higher dependence on surface water than browsers (Western, 1975; Faith, 2018). This pattern is supported by the dental wear results in AaO, that classified the *S. maurusium* and *Gazella* sp. as browsers and *H. pomeli* as a grazer. The ANOVA statistical test and Tukey’s pairwise comparison show significant differences in the $\delta^{18}O_{enamel}$ values among the obligate drinkers (n = 16) and non-obligate drinkers (n = 24) with a p-value of 1.819. The non-obligate drinkers mean is 0.15‰ and the obligate drinker mean is-1.77‰, implying a difference between the two groups of 1.9‰. The 1.9‰ difference observed in the $\delta^{18}O$ values of obligate and non-obligate drinkers in AaO is slightly higher than the 1.7‰ difference found in herbivores from the Tsavo region (Kenya), which has been defined as a dry savannah with vegetation characterized by semi-desert bushland with riparian woodland and a MAP of 500mm/yr (Cerling et al., 2003; 2015). The species *S. maurusium* exhibits the highest $\delta^{18}O$ values, even in comparison to *Gazella* sp. Given that dental wear patterns indicate a browsing diet for both species, the elevated $\delta^{18}O$ values in *S. maurusium* may be attributed to its consumption of leaves from tall plants that it has access to due to its large size. Sun-exposed leaves, particularly in arid conditions, are highly sensitive to evaporative fractionation, resulting in an enrichment of ^{18}O (Gonfiantini et al., 1965; Barbour, 2007). In this line, the combination of tooth microwear (short-term) and tooth mesowear (long-term) proxies has been used as a tool to identify seasonality (Sánchez-Hernández et al., 2016). Considering that microwear reflects the signal of a short-term diet, such as a single season, while mesowear reflects a longer period including probably all seasons, discrepancies in the results between both proxies would be indicative of dietary changes due to seasonal availability of resources. In AaO, *S. maurusium* exhibits a browsing pattern with the two proxies, indicating that its diet does not change throughout the year. For *Gazella* sp., tooth mesowear indicates browse-dominated mixed feeding, while microwear suggests browsing. This species is likely to have a more diverse diet, characterized by a higher consumption of grasses throughout the year, along with a significant increase in browsing during a particular season. In the case of Alcelaphini and *H. pomeli*, tooth mesowear indicates grass-dominated mixed feeding and grazing, respectively, while microwear suggests mixed feeding. It indicates a predominant consumption of grasses throughout the year with the introduction of other food items during specific periods of the year.

5.2.2 C_3 grassland and open habitat

In all species from AaO, the most discriminant microwear feature is the number of scratches, which is different in browsers and mixed feeders (**Fig. 5**). The high number of scratches in mixed feeders indicates significant consumption of grasses (see %0–17 in **Table 2**). However, the number of pits is very similar between browsers and mixed feeders with grazing tendencies. The relatively high number of pits and the presence of large pits in all species could be caused by incidental ingestion of abrasive grit resulting from feeding close to the ground in open and arid habitats (Semprebon and Rivals, 2007; Hoffman et al., 2015). This enables us to emphasize two environmental aspects: (1) The prevalence of taxa with a C_3 plant-based diet, many of which consume a significant amount of grasses, indicating the significant presence of C_3 grasslands in the study area. This assertion is corroborated by previous research on the feeding habits of *Theropithecus atlanticus* in AaO. In that study, they employed time- and graminivore-calibrated carbon stable isotope values to illustrate a progressive transition towards an increased dependence on high-throughput bulk-feeding graminivory and proposed a consumption of grasses exhibiting a distinct C_3 isotopic signature (Fannin et al., 2021). (2) The presence of C_3 grassland, feeding close to the ground, and the presence of *T. atlanticus* (Alemseged and Geraads, 1998; Fannin et al., 2021) are indicators of open habitats. It is noteworthy that no other cercopithecine species have been discovered at the AaO site in Morocco. Additionally, while no fossil remains of *Theropithecus* have been found at the contemporaneous site of Guefaït in Morocco, the presence of *M.* cf. *sylvanus* has been noted (Alba et al., 2021). Previous ecological studies suggest that this macaque inhabited a woodland ecosystem, where it had a folivorous-frugivorous diet with hard item consumption which was primarily based on C_3 plants (Ramirez-Pedraza et al., 2023). This indicates a low wood cover in the landscape of western Morocco during the Plio-Pleistocene boundary. In the same line, the relative frequency of two species of bovids found in Guefaït and AaO may provide insight into the predominant environmental conditions. Specifically, Tragelaphini are associated with wooded and humid habitats, while Alcelaphini are linked to more open environments (Bobe et al., 2007). Notably, the abundance of Alcelaphini and the scarcity of Tragelaphini in AaO is significant (Geraads and Amani, 1998; Geraads et al., 2022a), while the opposite trend is observed in Guefaït (Sala-Ramos et al., 2022; Ramírez-Pedraza et al., 2023). Previous works on AaO have used a method for predicting palaeohabitats using measurements (height/width proportions) of bovid astragali (DeGusta and Vrba, 2003). The proportions of this bone in the bovids from AaO confirm the absence of heavy wood cover and the predominance of open habitat (Geraads et al., 2022a).

6. Conclusion

This research highlights the importance of integrating different proxies for palaeoecological reconstructions, being particularly useful in areas where there is a predominance of C_3 plants such as in North Africa, where it is more challenging to define the diet and habitat of mammals from stable isotope analysis alone. In this work, the complementarity of dental wear analysis has allowed us to determine diets that range from grazing to browsing behavior. Our multiproxy analysis indicates that during the Plio-Pleistocene boundary in the western coastal region of Morocco, open C_3 grasslands and shrubland predominated in an arid climate. Further research in different archaeological and palaeontological sites from the Early Pleistocene and Late Pliocene in the Maghreb is necessary to gain a holistic understanding of the ecological and climatic dynamics that contributed to the dispersal, occupation, and evolution of mammals and early hominins.

CRediT author statement

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Appendix A. Supplementary data

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: