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

4
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22
23 **Abstract**

24 In this article, we use a multiproxy approach based on stable isotope analyses ($\delta^{18}\text{O}$ and
25 $\delta^{13}\text{C}$), mesowear, and microwear dental analysis to reconstruct the climate, diet, and

26 habitat of Plio-Pleistocene herbivores at the site of Ahl al Oughlam in western Morocco.
27 This study has been conducted on teeth from several taxa (*Sivatherium maurusium*,
28 *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., Alcelaphini, and
29 *Anancus osiris*), enabling a robust ecological reconstruction. Our isotopic results
30 suggest a predominance of C₃ plant consumption for all analyzed species, while dental
31 wear indicates a varied diet, with evidence for both browsing and grazing behavior
32 being present. The combination of proxies indicates a landscape dominated by open C₃
33 grasslands in an arid climate, as supported by the Mean Annual Precipitation (MAP)
34 results. These findings contribute to the ongoing debate on the ecological context that
35 facilitated the Plio-Pleistocene dispersal, occupation, and evolution of mammals and
36 hominins in northern Africa, for which limited information is available.

37

38 **Keywords**

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

40

41 **1. Introduction**

42 **1.2 The archaeopaleontological context during the Plio-Pleistocene in North Africa**

43 The richness and diversity of mammalian fossil remains in the Maghreb during the Late
44 Pliocene and Early Pleistocene (Geraads, 2002; Raynal et al., 2002; Sahnouni and Van
45 der Made, 2009; Sahnouni et al., 2011; Van der Made et al., 2021) provides evidence
46 that the Sahara Desert was not always a natural barrier for mammals in the past. The
47 region experienced multiple green and humid phases, known as Green Sahara periods
48 (GSPs), over millions of years, including the Plio-Pleistocene. During these events, the
49 present desert area consisted of river basins and extensive lakes (Van Zinderen Barker,
50 1962; Larrasoña et al., 2003, 2013; Castañeda et al., 2009; Grant et al., 2017, 2022;

51 Larrasoña, 2021). These environmental conditions would have facilitated episodes of
52 mammalian dispersal from sub-Saharan locations to the north of Africa (Geraads, 2010;
53 Zouhri et al., 2017; Van der Made et al., 2021).

54

55 To date, the oldest artifacts and stone tool-cut marked bones in North Africa associated
56 with the presence of hominins have been found at the site of Aïn Boucherit (~1.9 and
57 ~2.4 Ma) in the Beni Fouda intramontane basin in northeast Algeria (Sahnouni et al.,
58 2018; Duval et al., 2021). In the same area, Acheulean technology has been described at
59 the sites of Aïn Hanech and El Kherba (~1.8 Ma) (Sahnouni et al., 2002, 2012, 2017;
60 Parés et al., 2014; Duval et al., 2021, 2023; Van der Made et al., 2021). In the
61 Constantine Basin (Algeria), biochronologically close to Aïn Hanech, is the little-
62 known site of Mansourah, with abundant faunal remains and bifacial artifacts associated
63 with the Oldowan industry (Thomas, 1884, 1886; Chaid-Saoudi et al., 2006; Sahnouni
64 and Van der Made, 2009) and the palaeontological site of Aïn Jourdel (~2.5 Ma)
65 (Thomas, 1884; 1886; Duval et al., 2021). The oldest human remains have been found
66 in western Algeria at Tighennif, also called Ternifine, ~1 Ma (Arambourg and
67 Hoffstetter, 1963; Geraads et al., 1986; Bocherens et al., 1996; Geraads, 2016; Van der
68 Made et al., 2021). In western Morocco, near Casablanca, the earliest archaeological
69 sites date back to the Early and Middle Pleistocene (Raynal et al., 2001, 2002, 2017;
70 Mohib et al., 2019; Gallotti et al., 2022). Up to now, the oldest site with human
71 presence corresponds to unit L of Thomas Quarry I and its abundant ancient Acheulean
72 lithic tools (~1.3 Ma) (Raynal and Texier, 1989; Gallotti et al., 2020, 2021, 2023). The
73 former Thomas III Quarry, in which *Homo* remains were found (Ennouchi, 1975,
74 Geraads et al., 1980, 2022a and b; Raynal, 2021) was renamed Oulad Hamida 1 Quarry
75 when the *Grotte des Rhinocéros* (~0.7 Ma) was discovered and delivered a single *Homo*

76 remain associated with stone tools and fauna (Raynal et al., 1993, 2022b; Rhodes et al.,
77 2006; Daujeard et al., 2012, 2020; Raynal and Mohib, 2016; Gallotti et al., 2022). In
78 Thomas Quarry I, above level L, Hominid Cave (~0.5/0.7 Ma) is also located, where
79 early *Homo* remains on the Atlantic shore were discovered (Ennouchi, 1975; Geraads et
80 al., 1980, 2022a; Raynal et al., 2010, 2022a; Daujeard et al., 2016, 2020; Raynal, 2021).
81 On the outskirts of Casablanca sits the site of Ahl al Oughlam (AaO), the richest
82 Neogene faunal site in North Africa dated to ~2.5 Ma (Raynal et al., 1990; Geraads,
83 2006; Geraads et al., 2010, 2022b) and whose ecological context is investigated in this
84 work.

85

86 In eastern Morocco, close to the Algerian border in the Aïn Beni Mathar–Guefaït area
87 (Jerada province), several sites have been discovered and excavated since 2006: the
88 Early Pleistocene sites of Aïn Tabouda, Gara Soultana and Charchara 1 with Mode 1
89 lithic tools, and the Middle Pleistocene site of Oued Rabt with Mode 2 lithic tools (Sala-
90 Ramos et al., 2022). The oldest site, although palaeontological, is Guefaït. This one is
91 biochronologically located at the Plio-Pleistocene boundary (~3–2.5 Ma; Parés et al.,
92 2023), contemporaneous with Ahl al Oughlam, and contains a large diversity of taxa in
93 its fossiliferous levels (Sala-Ramos et al., 2017, 2022; Aouraghe et al., 2019; Piñero et
94 al., 2019; Alba et al., 2021; Madurell-Malapeira et al., 2021; Ramírez-Pedraza et al.,
95 2023).

96

97 Work based on palaeoecological reconstructions are underrepresented in North Africa,
98 despite the abundance of archaeopalaeontological sites found from the Late Pliocene to
99 the Early Pleistocene in this territory. In Morocco, the studies published to date are
100 focused on the palaeoecology of the Plio-Pleistocene primates of Ahl al Oughlam

101 (*Theropithecus*; Fannin et al., 2021) and Guefaït-4.2 (*Macaca*; Ramírez-Pedraza et al.,
102 2023). In Algeria, there are more extensive studies available, such as the analysis of
103 carbon and oxygen stable isotopes in herbivores from Tighennif (~1 Ma) (Bocherens et
104 al., 1996; Fannin et al., 2021), and the research based on stable isotopes of pedogenic
105 carbonates from El Kherba (~1.8 Ma) (Sahnouni et al., 2011). However, there still
106 remains a knowledge gap in this area regarding the reconstruction of habitats at the Plio-
107 Pleistocene boundary. This contrasts with the numerous and comprehensive studies
108 carried out in eastern (Kingston and Harrison, 2007; Ségalen et al., 2007; Levin et al.,
109 2008; Bedaso et al., 2013; Cerling et al., 2015; Robinson et al., 2017, 2021; Lüdecke et
110 al., 2018; Mercader et al., 2021), southern (Lee-Thorp and Sponheimer, 2005; Lee-
111 Thorp et al., 2007, 2010; Ségalen et al., 2007; Lehmann et al., 2016) and central Africa
112 (Zazzo et al., 2000; Ségalen et al., 2007; Lee-Thorp et al., 2012) focused on the
113 ecological contexts of Plio-Pleistocene hominins and large herbivores.

114

115 **1.3 The distribution of C₃-C₄ plants in North Africa**

116 One of the commonly used methods for reconstructing past environments has been the
117 analysis of stable carbon isotope ratios (¹³C/¹²C) in dental enamel bioapatite. This
118 biogenic material is particularly useful due to its resistance to diagenetic processes,
119 preserving the original isotopic signal (Wang and Cerling, 1994). The carbon isotope
120 ratios are primarily influenced by the differential fractionation between the two
121 photosynthetic pathways (C₃ and C₄) used by plants consumed by animals, and it is
122 associated with specific types of landscapes or environmental conditions. The
123 proportion of C₃ or C₄ plants is not distributed homogeneously throughout Africa,
124 varying both geographically and chronologically. Global C₄ ecosystem expansion
125 around 8–10 million years ago, due to the decrease of atmospheric CO₂, higher

126 temperatures and increasing water-stress represents a significant change in the
127 landscape that led to the replacement of C₃ grasses by C₄ grasses in existing open and
128 dry environments in low- to mid-latitude and altitude regions (Ehleringer et al., 1991;
129 Cerling, 1992; Cerling et al., 1997; Edwards et al., 2010; Polissar et al., 2019). During
130 the Plio-Pleistocene, eastern, southern and central Africa were dominated by C₄
131 grassland (Zazzo et al., 2000; Ségalen et al., 2007; Strömberg, 2011), relegating C₃
132 grasses to altitudes above 2000 meters and in the forest understory (Tieszen et al., 1979;
133 Young and Young, 1983; Balasse and Ambrose, 2005). The ecological context of these
134 areas, characterized by the high abundance of C₄ grasses, especially in Eastern Africa,
135 has allowed the application of the C₄-grazers and C₃-browsers classification, which is
136 widely used in studies analyzing the diet of mammals based on the analysis of tooth
137 enamel $\delta^{13}\text{C}$ values (Vogel, 1978; Zazzo et al., 2000; Sponheimer and Lee-Thorp, 2003;
138 Lee-Thorp and Sponheimer, 2005; Levin et al., 2008; Bedaso et al., 2013; Cerling et al.,
139 2015; Uno et al., 2018).

140

141 This clear distinction between C₄-grazers and C₃-browsers is not valid at high latitudes,
142 as the contribution of C₄ plants is non-existent or marginal. This pattern has been
143 observed in multiple studies conducted during the Pliocene and Early Pleistocene in
144 Europe (Edwards et al., 2010; Domingo et al., 2013; Szabó et al., 2022). The same
145 observation applies to studies conducted in North Africa on Pleistocene and Pliocene
146 archaeological and palaeontological sites mentioned above (Bocherens et al., 1996;
147 Sahnouni et al., 2011; Fannin et al., 2021). All of them, based on carbon isotope
148 evidence, reveal a vegetation consisting of C₃ plants including all available resources
149 such as trees, woody shrubs, bushes and grasses. This makes it challenging to discern

150 different diets and habitats for mammals and therefore to draw a consistent ecological
151 reconstruction with this single method.

152

153 To address this challenge, we combine three high-resolution approaches that cover
154 different moments in the animal's life: the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of tooth enamel
155 bioapatite (which reflect the first years of life related to the crown formation times),
156 tooth mesowear (which reflects the last months/years before death) and tooth occlusal
157 microwear (which reflects the last days/weeks before death). By combining these
158 approaches, this work aims at providing a robust ecological reconstruction of the Ahl al
159 Oughlam (AaO) mammal communities, which will shed light on their diets, habitats,
160 and seasonality.

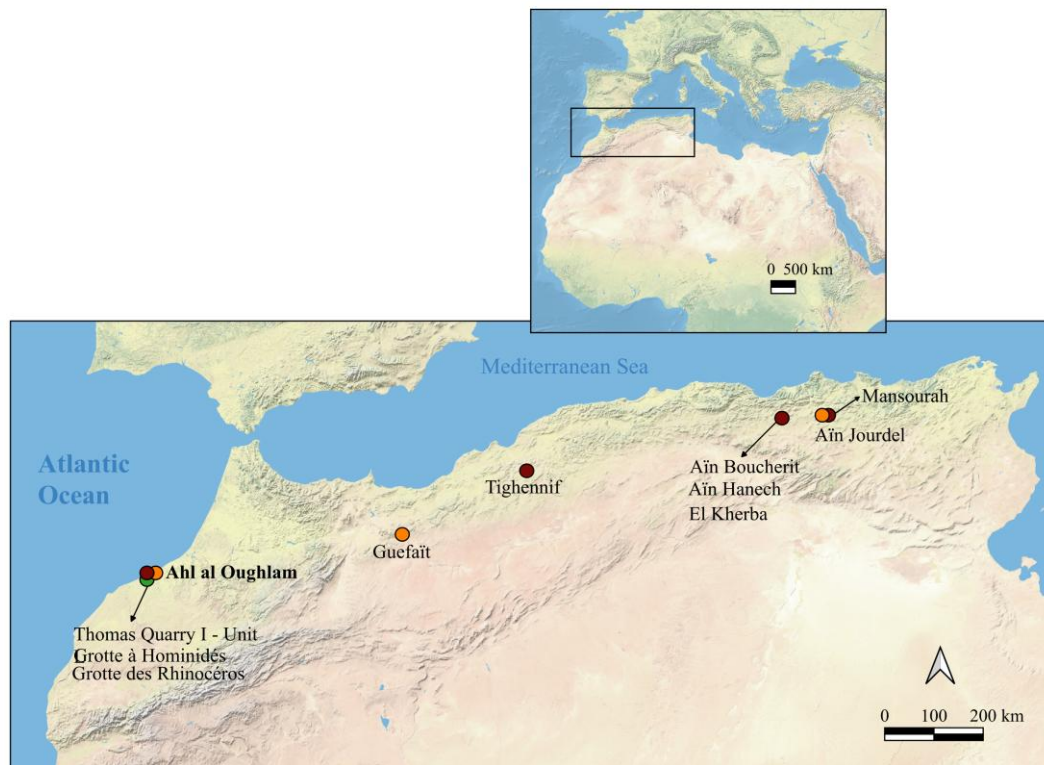
161 Up to the present, there is no evidence of hominins at AaO. The earliest known
162 occupation on the Atlantic coast, in western Morocco, corresponds to level TH-L at 1.3
163 Ma (Gallotti et al., 2023). However, 2.5 Ma ago, hominins were widespread in East and
164 South Africa (Hammond and Mongle, 2023), in Chad, at the Koro Toro site (3.5 Ma;
165 Brunet et al., 1995), and in Northern Africa with the oldest occupation at Ain Boucherit
166 at 2.4 Ma (Sahnouni et al., 2018). The absence of hominins in AaO does not necessarily
167 imply their absence during the Plio-Pleistocene in the area, as it is possible that they
168 have simply not been discovered in the fossil record. Another possibility could be that
169 the environmental conditions did not facilitate the occupation of this area. In this study,
170 we have also compared the ecology of the taxa from AaO with the same taxa from other
171 sites in North, South, East, and Central Africa.

172 Understanding the role of this territory is crucial in contributing to the debate about the
173 first hominin dispersions and occupations, as well as highlighting the importance of

174 North Africa in the adaptation and development of mammal behavior during the Late
175 Pliocene and Early Pleistocene.

176

177 2. Site: Ahl al Oughlam



178

179 **Fig.1.** Location map of North African sites mentioned in the text. Plio-Pleistocene boundary sites =
180 orange circle (Ahl al Oughlam (this study), Guefaït and Aïn Jourdel); Early Pleistocene sites = brown
181 circle (Thomas Quarry I-Unit L, Tighennif, Aïn Boucherit, Aïn Hanech, El Kherba and Mansourah);
182 Middle Pleistocene sites = green circle (Grotte des Rhinocéros and Grotte à Hominidés).

183

184 The fossiliferous locality of Ahl al Oughlam (33°34'11"N, 07°30'44"W) is an
185 abandoned sandstone quarry located at the southeast boundary of the city of Casablanca
186 (Morocco), 6.5 km from the present-day Atlantic shore (**Fig. 1**; Raynal et al., 1990;
187 Geraads et al., 2022b). Stratigraphically, the quarry cuts through calcarenitic intertidal,

188 supratidal and aeolian deposits correlative to sea-level highstands associated with a
189 platform developed about 105 m a.s.l. which belong to the *Ahl al Oughlam*
190 *Morphostratigraphic Unit* (Lefèvre and Raynal, 2002; Lefèvre et al., 2021; Geraads et al.,
191 2022b), formerly included in the *Messaoudian* stage of Biberson's Moroccan
192 Quaternary Chronostratigraphy (Biberson, 1961a; Stearns, 1978). The site was
193 investigated in 1953 by Biberson (Biberson, 1961a, 1961b), under the name of *Carrière*
194 *Déprez*, who reported the occurrence of some broken pebbles that he considered as
195 representing reworked artifacts of the "archaic pebble culture" representing an initial
196 stage of North African technological evolution. Raynal and Texier (1989) demonstrated
197 that they are actually "geofacts" of natural origin found in marine deposits. In 1985, J.-
198 P. Raynal and J.-P. Texier discovered abundant fossil faunal remains in karst formations
199 and in a network of fissures and interconnected galleries between calcarenite blocks, at
200 the foot of what was once a palaeoshoreline.

201 The fillings lack stratification. Given that the populations of the diverse rodent species
202 within the interconnected fissures exhibit no significant distinctions in tooth
203 measurements, they can be regarded as synchronous on a geological scale. Since
204 absolute dating and paleomagnetic analysis are unattainable, the age of the fossiliferous
205 fillings hinges on the identification and evolutionary stages of various taxa (Geraads,
206 2002, 2010). A biostratigraphic analysis of the mammal assemblage dates this locality
207 to the Plio-Pleistocene boundary, indicating an approximate age of 2.5 Ma (Geraads,
208 1997; Geraads et al., 2022b). The genus *Equus* is absent, suggesting that the site is older
209 than 2.3 Ma (Geraads, 2006). The mammalian fauna includes at least fifty-five species
210 of both small and large mammals. A new species of *Hipparion*, *H. pomeli*, has been
211 described subsequently from the site (Eisenmann and Geraads, 2007). The vertebrate
212 fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards

213 and snakes) and fishes. The most unexpected element of the mammalian fauna is a
214 walrus, a pinniped marine mammal. No living or fossil walrus was previously known in
215 the Eastern Atlantic, south of Belgium (Geraads, 2006). The site was formed along the
216 oceanic seashore which explains why both marine and terrestrial forms are found among
217 birds. A list of the identified faunal taxa is given in several publications (Raynal et al.,
218 1990; Geraads, 1993, 1995, 1996, 1997, 2002, 2004, 2006; Alemseged and Geraads,
219 1998; Geraads and Amani, 1998; Geraads and Metz-Muller, 1999; Eisenmann and
220 Geraads, 2007; Mourer-Chauviré and Geraads, 2008; Geraads et al., 2010; Mourer-
221 Chauviré and Geraads, 2010; Gunnell et al., 2011; Sen and Geraads, 2023).

222 **3. Material & methods**

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

227

228 **3.1 Stable isotopes (¹³C and ¹⁸O)**

229

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

236

237 Powdered enamel samples were chemically treated at the biomolecular laboratory at the
238 *Institut Català de Paleoecologia Humana i Evolució Social* (IPHES - CERCA).
239 Samples weighed from 3.5 to 9.5 mg. Chemical treatment of samples was based on
240 protocols originally proposed by Koch et al. (1997) and later modified in Tornero et al.
241 (2013). Samples were treated for 4 h in 0.1 M acetic acid [CH₃COOH] (0.1 ml
242 solution/0.1 mg of sample), neutralized with distilled water and freeze-dried.

243

244 The ¹⁸O and ¹³C of carbonates were measured using an automated carbonate preparation
245 device (KIEL-III) coupled with a gas-ratio mass spectrometer (Finnigan MAT 252) at
246 the environmental isotope laboratory at the University of Arizona, US. Powdered
247 samples were allowed to react with dehydrated phosphoric acid under a vacuum at
248 70°C. Accuracy and precision of the measurements were checked and calibrated using
249 calcium carbonate international standards (NBS-19 and NBS-18). Replicate
250 measurements of the standards during analysis had errors of ±0.1‰ for δ¹⁸O and
251 ±0.08‰ for δ¹³C (1 sigma). Carbon isotope composition is reported in δ notation, where
252 $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ and δ is expressed in per mil, ‰. Carbon
253 and oxygen values are reported relative to PDB (Vienna Pee Dee Belemnite).

254

255 The modern plants using a C₃ photosynthetic pathway (including most trees, woody
256 shrubs, bushes, herbs and grasses) have an average isotopic δ¹³C value of -28.5‰
257 (global range -20 to -37‰), with -23‰ as the maximum value for typical C₃ plants and
258 a cut-off of -31.5‰ for closed-canopy forests (Kohn, 2010). In this work, we use the
259 average δ¹³C value of -27‰ for modern C₃ plants, excluding analyses from the
260 understory of closed-canopy forests below -31.5‰ (Kohn, 2010). Modern plants that
261 employ the C₄ photosynthetic pathway (primarily tropical grasses and sedges) have an

262 average isotopic composition of -12‰ (global range -10 to -14‰) (Cerling et al., 1997;
263 Cerling and Harris, 1999; Kohn and Cerling, 2002). The bivariate graphs were made
264 with the Past 4.02 software (Hammer et al., 2001). All mean values in the text are
265 followed by their standard deviation.

266

267

268 3.1.2 Estimation of enrichment factor, $\%C_4$, $\delta^{13}C_{\text{diet-meq}}$ and MAP

269

270 Abundance of atmospheric CO₂ has been changing over time (Tippie et al., 2010) with a
271 consequent influence on the carbon values of plants during its fixation in the
272 photosynthesis process (Farquhar et al., 1989). To make a comparison between the
273 carbon values of present-day plants with those consumed by animals in the past, it is
274 crucial to perform corrections. In our work, we have corrected the $\delta^{13}C$ values of
275 modern plants by +1.5‰, due to the difference between the pre-Industrial $\delta^{13}C_{\text{CO}_2}$ value
276 of ~ -6.5‰ established for the Plio-Pleistocene (Tippie et al., 2010), and the $\delta^{13}C_{\text{CO}_2}$
277 value of ~ -8‰ at the time the reference collection of modern plants was collected
278 (Kohn, 2010). When plants are consumed, a fixation occurs in the tooth enamel of the
279 animals, a process of isotopic fractionation (Krueger and Sullivan, 1984; Koch, 1998;
280 Cerling and Harris, 1999; Passey et al., 2005). In this study, we use formula (1) in
281 Tejada et al. 2018 which determines that there is a positive correlation between body
282 mass and enamel-diet enrichment fractionation (expressed as $\epsilon^*_{\text{enamel-diet}}$). The $\epsilon^*_{\text{enamel-diet}}$
283 has been calculated from the estimation of the body mass of the species analyzed: *S.*
284 *maurusium* (Basu et al., 2016), *H. pomeli* (Bernor et al., 2021), *Gazella* sp. and
285 Alcelaphini (Bibi and Kiessling, 2015), *M. phacochoeroides* (Rannikko, 2019) and *A.*
286 *osiris* (Larramendi, 2016).

287

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

289

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

296

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

298

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

300

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

302

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

306

307 We estimated (4) the fraction of C_4 vegetation consumed by AaO herbivores using $\delta^{13}\text{C}$
308 modern plant values, -24‰ for C_3 vegetation ecosystems (Kohn, 2010) and -12‰ for C_4
309 vegetation (Cerling et al., 1997). The fossil $\delta^{13}\text{C}_{\text{enamel}}$ values have been corrected for
310 $\delta^{13}\text{C}$ of Plio-Pleistocene atmospheric CO_2 and $\epsilon^*_{\text{enamel-diet}}$ to obtain the $\delta^{13}\text{C}_{\text{diet-meq}}$.

311

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

313

314 3.1.3 Obligate drinkers vs. non-obligate drinkers taxa

315

316 To calculate relative aridity in AaO, we relied on the fundamental principle of different
317 drinking behaviors exhibited by mammals (Nicholson, 1985; Kohn, 1996; Levin et al.,
318 2006; Blumenthal et al., 2017). In arid environments, both open water sources and plant
319 water and tissues experience evaporation of ^{16}O and enrichment of ^{18}O (Gonfiantini et
320 al., 1965). However, this evaporative effect is more pronounced in plants. As a result, it
321 is anticipated that animals primarily obtaining water through plant consumption (non-
322 obligate drinkers) will display higher $\delta^{18}O_{\text{enamel}}$ values compared to obligate drinkers
323 relying on direct access to surface water (Bocherens et al., 1996; Kohn, 1996). The
324 greater the difference in $\delta^{18}O$ values between these two groups, the higher the aridity
325 (Lehmann et al., 2016; Roberts et al., 2018; Lüdecke et al., 2022). For this comparison,
326 we selected the most reliable species from AaO to classify the mentioned categories.
327 Specifically, we chose *S. maurusium* and *Gazella* sp. as non-obligate drinkers, and *H.*
328 *pomeli* and *A. osiris* as obligate drinkers. Generally, grazers among ungulates have a
329 higher dependence on surface water than browsers (Western, 1975; Faith, 2018). This
330 pattern is supported by the dental wear results from AaO, which classified *S. maurusium*
331 and *Gazella* sp. as browsers and *H. pomeli* and *A. osiris* as grazers.

332

333 3.2 Dental wear analysis

334

335 3.2.1 Dental mesowear analysis

336

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

354

355 3.2.2 Dental microwear analysis

356

357 The investigation of dental microwear has a rich history in elucidating the dietary
358 preferences and ecological niches of fossil species. Starting with early studies in the late
359 1970s, which employed scanning electron microscopy (SEM) at high magnifications
360 (~100–500x) (Rensberger, 1978; Walker et al., 1978), to subsequent research
361 employing low-magnification light microscopy (MacFadden et al., 1999; Solounias and

362 Semprebon, 2002), and more recently, dental microwear texture analysis (DMTA)
363 utilizing three-dimensional surface measurements acquired through white-light confocal
364 microscopy and scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2006).
365 Despite all methods being valid and complementary, for this study, we opted for at low-
366 magnification microwear approach due to the accessibility of an extensive microwear
367 reference collection of extant species, particularly those of African origin (Solounias
368 and Semprebon, 2002).

369 In this work, a total of 109 molars and premolars were selected and molded. After
370 examination of the molds under a stereomicroscope, 49 specimens were discarded due
371 to poor preservation or taphonomic defects (**Supplementary Table 2**) (El-Zaatari,
372 2010; King et al., 1999). Examination of enamel microwear features was conducted
373 through standard light microscopy, using a Zeiss Stemi 2000C stereomicroscope at a
374 magnification of 35x on high-resolution epoxy casts of the teeth. The cleaning, molding,
375 casting, and examination protocols, as well as feature classification criteria, were
376 consistent with those established by Semprebon and Solounias (2002) and Semprebon et
377 al. (2004). Upper and lower teeth, spanning from P4 to M3, were included in the
378 analysis following Xafis et al. (2017). The occlusal surface of each specimen was first
379 cleaned with acetone and 96% ethanol before being molded with high-resolution
380 silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set)
381 and transparent casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 +
382 K151). Scoring of microwear features, including small and large pits (round scars),
383 scratches (elongated scars with parallel sides), gouges (irregular edges and much larger
384 and deeper than the large pits), puncture pits (deepest at their centers, symmetrical,
385 craterlike features with regular margins), and cross scratches (oriented perpendicularly
386 to the majority of scratches), was performed using a standard 0.16 mm² ocular reticle. In

387 order to achieve a more precise categorization of grazers, browsers, and mixed feeders,
388 we used the percentage of individuals in a sample possessing scratch numbers that fall
389 between 0 and 17 (Semprebon and Rivals, 2007). The scratch width score (SWS) was
390 calculated based on the ratio of fine to coarse scratches (“0” predominantly fine
391 scratches per tooth surface, “1” to those with a mixture of fine and coarse scratches, and
392 “2” to those with predominantly coarse scratches). The results were compared with a
393 database constructed from extant ungulate taxa (Solounias and Semprebon, 2002; Rivals
394 and Semprebon, 2011). To reduce inter-observer error, dental microwear analysis was
395 conducted by a single experienced researcher (IRP).

396

397 **4. Results**

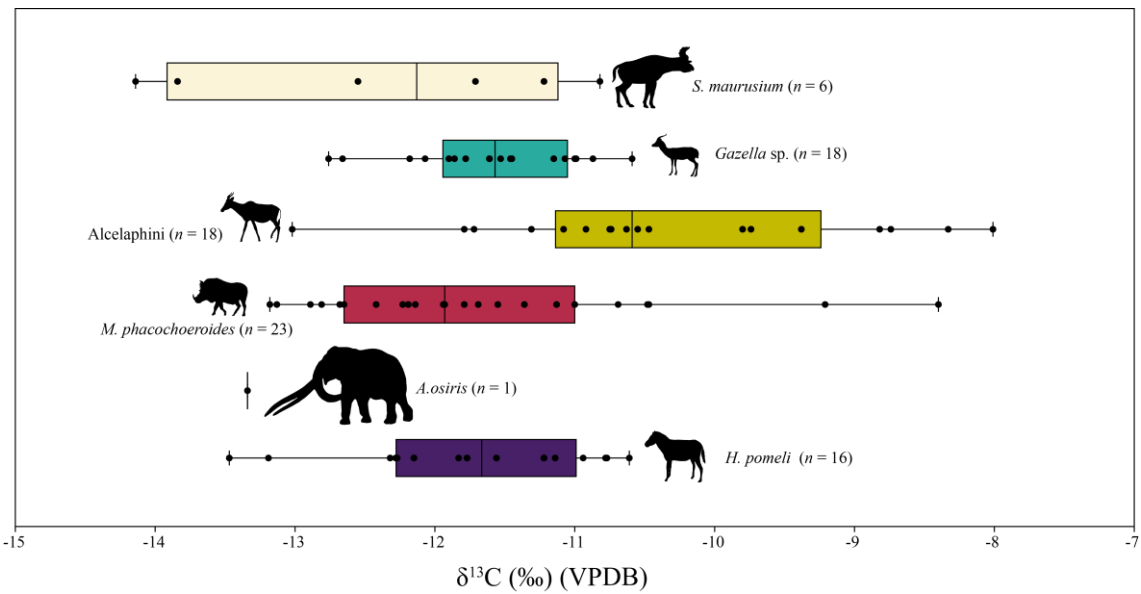
398

399 **4.1 Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$)**

400

401 The $\delta^{13}\text{C}$ values of all taxa measured in AaO ranged from -14.1 to -8‰ with a mean and
402 standard deviation of $-11.4 \pm 1.2\text{‰}$ ($n = 82$) (**Fig. 2**). The data for each species are
403 described below: *H. pomeli* ($n = 16$; range = -13.5 to -10.6‰; mean = $-11.7 \pm 0.9\text{‰}$),
404 Alcelaphini ($n = 18$; range = -13 to -8‰; mean = $-10.3 \pm 1.3\text{‰}$), *Gazella* sp. ($n = 18$;
405 range = -12.8 to -10.6‰; mean = $-11.6 \pm 0.6\text{‰}$), *S. maurusium* ($n = 6$; range = -14.1 to
406 -10.8‰; mean = $-12.4 \pm 1.4\text{‰}$), *M. phacochoeroides* ($n = 23$; range = -13.2 to -8.4‰;
407 mean = $-11.7 \pm 1.2\text{‰}$) and *A. osiris* ($n = 1$; -13.3‰). The two taxa with the highest
408 variability and the most positive values are Alcelaphini and *M. phacochoeroides*.
409 *Gazella* sp. and *H. pomeli* are the species with the lowest variability and *S. maurusium*
410 is the species with the most negative values.

411



412

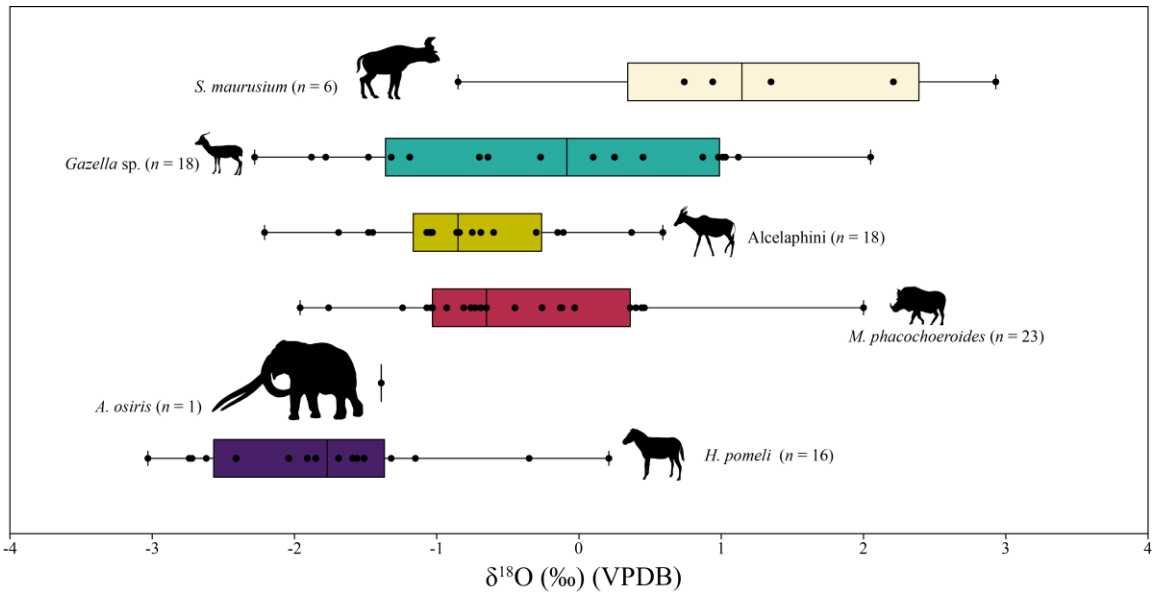
413

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

417

418 The $\delta^{18}\text{O}$ values ranged from -3 to 2.9‰ with a mean and standard deviation of $-0.6 \pm$
 419 1.2% (n = 82) (**Fig. 3**). The data for each species are described below: *H. pomeli* (n =
 420 16; range = -3 to 0.2‰; mean = $-1.8 \pm 0.9\%$), Alcelaphini (n = 18; range = -2.2 to
 421 0.6‰; mean = $-0.8 \pm 0.7\%$), *Gazella* sp. (n = 18; range = -2.3 to 2.1‰; mean = $-0.2 \pm$
 422 1.3%), *S. maurusium* (n = 6; range = -0.9 to 2.9‰; mean = $1.2 \pm 1.3\%$), *M.*
 423 *phacochoeroides* (n = 23; range = -1.8 to 2‰; mean = $-0.4 \pm 0.9\%$) and *A. osiris* (n =
 424 1; -1.4‰). The whole isotopic dataset is provided in **Supplementary Table 1**.

425



426

427

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

431

432 4.1.2 Estimation of enrichment factor, $\%C_4$, $\delta^{13}C_{\text{diet-meq}}$ and MAP

433

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

443

444 **Table 1.** Summary of $\delta^{13}\text{C}$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}\text{C}_{\text{diet-meq}}$ (‰), %C₄ and Mean
 445 Annual Precipitation (MAP - mm/yr).

446

Species	<i>n</i>	$\delta^{13}\text{C}$ (‰)	Body Mass (Kg)	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}\text{C}_{\text{diet-meq}}$ (‰)	%C ₄	MAP (mm/yr)
<i>S. maurusium</i>	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
<i>Gazella</i> sp.	18	-11.6 ± 0.6	30	+12.4	-24.1 ± 0.6	0	139 ± 112
<i>H. pomeli</i>	16	-11.7 ± 0.9	250	+13.3	-26.5 ± 0.9	0	400 ± 269
<i>M. phacochoeroides</i>	23	-11.7 ± 1.2	297	+13.4	-26.5 ± 1.2	0.3 ± 1.3	455 ± 274
<i>A. osiris</i>	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

447

448 4.1.3 Obligate drinkers vs. non-Obligate drinkers taxa

449

450 The ANOVA statistical test and Tukey's pairwise comparison show significant
 451 differences in the $\delta^{18}\text{O}_{\text{enamel}}$ values among the obligate drinkers ($n = 17$; *A. osiris* and *H.*
 452 *pomeli*) and non-obligate drinkers ($n = 24$; *S. maurusium* and *Gazella* sp.) with a *p*-
 453 value of 1.819. The non-obligate drinkers mean is 0.15‰ and the obligate drinker mean
 454 is -1.77‰, implying a difference between the two groups of 1.9‰.

455

456 4.2 Dental wear analysis

457

458 **Table 2.** Summary of mesowear and microwear data of the fossil assemblages from AaO. Abbreviations:
 459 *n*, number of specimens; MWS, mesowear score; NS, average number of scratches; NP, average number
 460 of pits; SD, standard deviation; SWS, scratch width score; %PP, percentage of specimens with puncture
 461 pits; %HC, percentage of specimens with hyper-coarse scratches; %LP, percentage of specimens with

462 large pits; %G, percentage of specimens with gouges; %XS, percentage of specimens with cross
 463 scratches; %0–17, percentage of specimens with number of scratches ranging between 0 and 17.
 464
 465
 466
 467
 468
 469

Species	Mesowear			Microwear											
	<i>n</i>	MWS	<i>n</i>	NS	SD	NP	SD	SWS	%PP	%HC	%LP	%G	%XC	%0–17	
<i>S. maurusium</i>	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	
<i>Gazella</i> sp.	17	1.2	8	9.5	1.6	23.4	4.6	1	0.0	0	100	50	12.5	100	
<i>H. pomeli</i>	6	4.3	13	20.6	3	19.1	4	1	15.4	0	84.6	7.7	0	0	
<i>M. phacochoeroides</i>	-	-	18	19.7	4.6	23	3.6	0.9	5.6	0	83.3	22	100	33.3	
<i>A. osiris</i>	-	-	1	26	-	25.5	-	1	0	100	100	0	100	0	

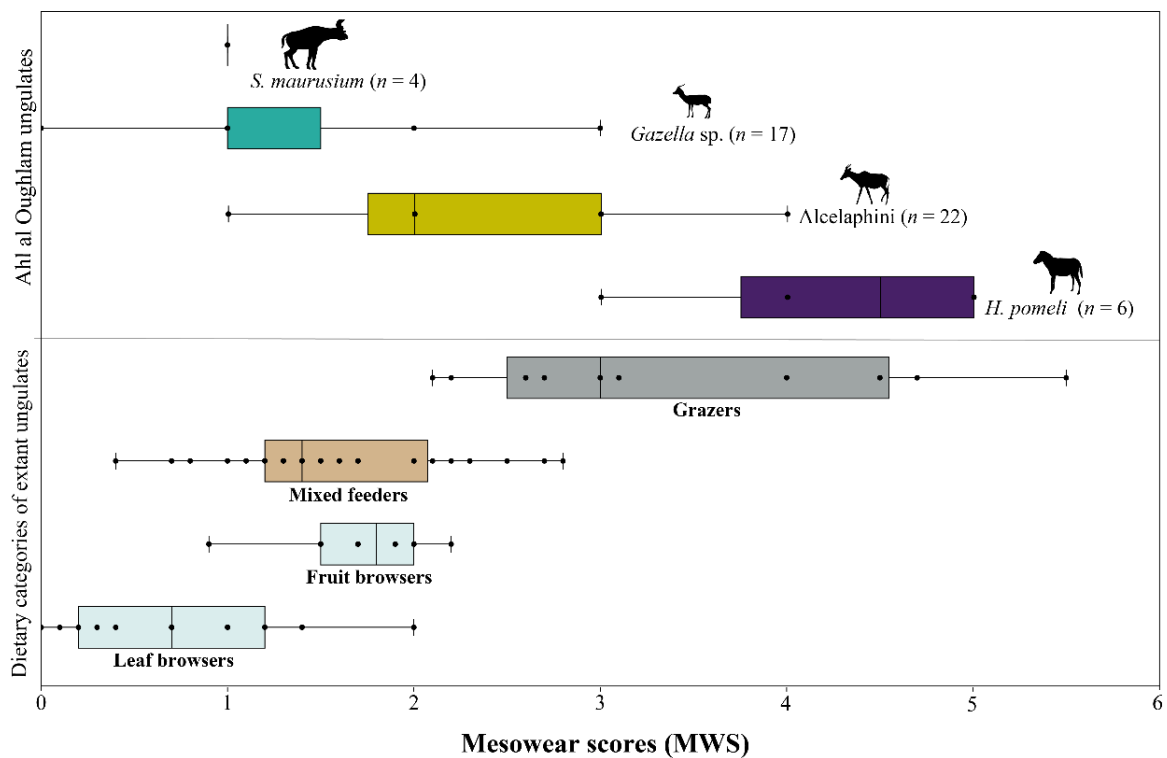
470

471 4.2.1 Dental mesowear analysis

472 Some authors have observed differences in the mesowear score between the upper and
 473 lower molars of the same individuals (Kaiser and Fortelius, 2003). Since the *Gazella* sp.
 474 and Alcelaphini teeth analysed include both upper and lower molars, we conducted an
 475 ANOVA statistical test and Tukey's pairwise comparison to enhance the analysis
 476 conducted. The statistical results did not reveal significant differences in the mesowear
 477 score values between lower molars ($n = 5$) and upper molars ($n = 12$) of *Gazella* sp.,
 478 with a p -value of 0.9694, nor between lower molars ($n = 13$) and upper molars ($n = 9$)
 479 of Alcelaphini, with a p -value of 0.9826.

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

491



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

497

498 4.2.2 Dental microwear analysis

499

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

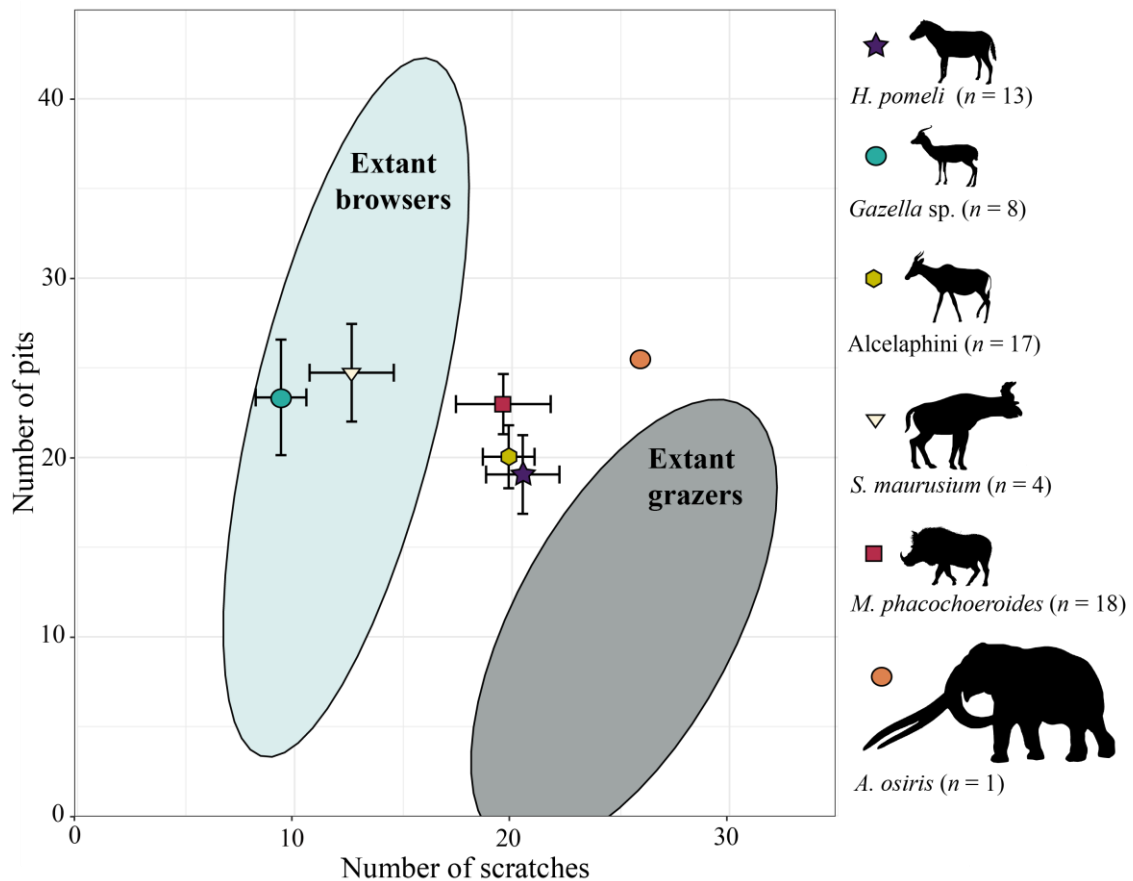
515

516 The SWS, being between 0.9 and 1.1, indicates a mixture of both fine and coarse
517 scratches for all species. Hyper-coarse scratches have been found only in *A. osiris*.
518 Cross scratches are absent in *H. pomeli* and present in a low percentage in Alcelaphini,
519 *Gazella* sp. and *S. maurisium*. *A. osiris* and *M. phacochoeroides* have them in 100% of

520 the individuals. This trait is characteristic of animals with a bunodont dental
 521 morphology as in the case of the latter two species. Gouges have been observed in all
 522 species except in *A. osiris* and their presence is remarkable in the four individuals of *S.*
 523 *maurusium*. Puncture pits are present in a low percentage in Alcelaphini, *H. pomeli* and
 524 *M. phacochoeroides*, and large pits are present in all species in proportions varying
 525 from 50% to 100% of the individuals.

526

527



528

529

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

534

535 **5. Discussion**

536

537 **5.1 Palaeodiet**

538

539 The combination of the three approaches allows us to characterize the dietary
540 preferences of the different taxa, as well as to reconstruct the general ecological context
541 (**Table 3**). In AaO, all species have a predominantly plant-based C₃ diet with values
542 ranging from -14 to -8‰, with a small consumption of C₄ plants in Alcelaphini and *M.*
543 *phacochoeroides* (**Table 1**). In some contexts, interpreting the carbon isotopic signal
544 can be complex, especially when there are no extreme values that can indicate high
545 consumption of C₄ plants linked to grass consumption (ca. $\delta^{13}\text{C} > 0\text{‰}$; Cerling and
546 Harris, 1999) or the presence of C₃ closed canopy forests (ca. $\delta^{13}\text{C} < -16\text{‰}$; Kohn,
547 2010), types of environments in which the signal is obvious. In AaO, there is both inter-
548 and intra-species variability in carbon values. Recent isotopic studies on extant species
549 in sub-Saharan Africa have shown a weak relationship between intra-taxon variation in
550 $\delta^{13}\text{C}_{\text{enamel}}$ (C₃ and C₄) and corresponding changes in herbivore diet and vegetation
551 structure (woody cover). Therefore, adopting a community-level approach when making
552 inferences about vegetation using isotopic data, focusing on the relationships between
553 different taxa is recommended. This approach allows for a more accurate understanding
554 of the vegetation dynamics and ecological context (Robinson et al., 2021). In AaO, the
555 interspecific difference between Alcelaphini and *S. maurusium* is striking and could
556 represent different ecological niches and diets (**Fig. 2**). Dental wear analysis (micro- and
557 mesowear) shows variable feeding traits that range from browser to mixed-feeder to
558 grazer behavior, including Alcelaphini with a grass-dominated, mixed-feeding diet or *S.*

559 *maurusium* as the most browsing taxon (**Table 3**). Oxygen isotope data are consistent
 560 with the dental wear feeding pattern, with browser species having more positive values
 561 (*S. maurusium* and *Gazella* sp.) than the rest, and grass-dominated mixed feeders having
 562 more negative values. The correlation in oxygen is higher between the most grazing
 563 species, according to dental wear pattern, such as *H. pomeli*, and the most browsing
 564 ones such as *S. maurusium*, showing very distant values between them. This could
 565 suggest the consumption of different resources, such as the preference for grasses by the
 566 former and leaves by the latter.

567

568 **Table 3.** Summary of dietary interpretations based on tooth wear and stable carbon isotope data.
 569 Abbreviations: B = browser, MF-B = browsing-dominated mixed feeder, MF = mixed feeder, MF-G =
 570 grass-dominated mixed feeder, and G = grazer. The parentheses indicate the consumption of C₄ plants (in
 571 very low percentage) in some species.

572

Species	Stable		
	isotopes	Mesowear	Microwear
<i>S. maurusium</i>	C ₃	B	B
Alcelaphini	C ₃ (C ₄)	MF-G	MF-G
<i>Gazella</i> sp.	C ₃	MF-B	B
<i>H. pomeli</i>	C ₃	G	MF-G
<i>M. phacochoeroides</i>	C ₃ (C ₄)	-	MF-G
<i>A. osiris</i>	C ₃	-	MF-G

573

574 5.1.1 Comparison of AaO with other African sites

575

576 The *Sivatherium maurusium* from AaO has the most negative C₃ carbon values ($\delta^{13}\text{C}$
577 mean = $-12.4 \pm 1.4\text{‰}$) and the most positive oxygen values (**Fig. 2 and 3**) compared to
578 other AaO species. These oxygen and carbon values could be attributed to the
579 preferential consumption of leaves from the upper parts of trees or shrubs which is
580 consistent with dental wear patterns suggesting a browsing diet for AaO *S. maurusium*.
581 The same isotopic pattern in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values has also been observed in
582 *Sivatherium* from Hadar and Aramis (Ethiopia; ~4–3 Ma) (Wynn et al., 2016) and
583 Makapansgat (South Africa; ~3 Ma (Lee-Thorp et al., 2010). Although this species is
584 known from various North African sites such as Aïn Boucherit, Aïn Hanech and El-
585 Kherba (Early Pleistocene; Algeria), Aïn Jourdel (Late Pliocene; Algeria), and Ichkeul
586 and Aïn Brimba (Late Pliocene; Tunisia), this is the first time that data on its diet has
587 been obtained from this area.

588

589 In East Africa, the Giraffidae were represented by two genera: *Giraffa* and *Sivatherium*,
590 from the early Pliocene onwards. *Sivatherium* became extinct during the Middle
591 Pleistocene. Overall, its diet underwent changes in the Turkana Basin (Kenya), being a
592 browser (C₃ plants) at ~4 Ma and switching to grazing (C₄ plants) between ~2.5 and 1
593 Ma (Cerling et al., 2015). In the Chiwondo beds (Malawi; ~2.5 Ma), *Sivatherium*
594 exhibited less negative $\delta^{13}\text{C}$ values ($n = 1$; $\delta^{13}\text{C} = -7.9\text{‰}$) than the purely browsing fossil
595 *Giraffa* ($n = 2$; $\delta^{13}\text{C}$ mean = $-12.1 \pm 1.1\text{‰}$), indicating that it incorporated some C₄ grass
596 in its diet (Bocherens et al., 2011). In Olduvai (Tanzania; ~1.8 Ma), a multiproxy
597 approach suggested a mixed diet for *S. maurusium*, C₄-dominated or mixed diets, a
598 mesowear characteristic of grazers, but with microwear indicating a browsing-
599 dominated mixed diet, likely due to seasonal changes in its diet (Uno et al., 2018).

600

601 In South Africa, *Sivatherium* maintained its preference for C₃ plants from ~5 to 3 Ma. In
602 the Langebaanweg site (~5 Ma), the $\delta^{13}\text{C}$ mean value ($n = 26$) is $-11.5 \pm 1.1\text{‰}$ (Franz-
603 Odendaal et al., 2002). However, hypsodonty indices, dental mesowear, and dental
604 microwear suggested mixed feeding dietary traits with a browsing tendency for this
605 species (Franz-Odendaal and Solounias, 2004). In the Makapansgat Limeworks
606 Member 3 (~3 Ma), *Sivatherium* exhibited carbon values ($n = 2$; $\delta^{13}\text{C}$ mean = $-11.4 \pm$
607 0.1‰) similar to those of *Giraffa* ($n = 8$; $\delta^{13}\text{C}$ mean = $-11 \pm 0.9\text{‰}$) at the same site
608 (Sponheimer and Lee-Thorp, 2009). The diet of AaO *Sivatherium* follows the same C₃-
609 browser pattern as that of the rest of Africa during the ~3 to 2.5 Ma period, but further
610 multiproxy studies are needed in more recent North African sites such as Ain Hanech or
611 El-Kherba (~1.8 Ma) to determine whether this dietary pattern remains the same or
612 changes, as in the case of East Africa.

613

614 The **Alcelaphini** from AaO is the taxon with the least negative carbon values, with a
615 predominance of C₃ plant consumption values (mean $\delta^{13}\text{C} = -10.3 \pm 1.3\text{‰}$), indicating
616 even some C₄ consumption (**Table 2**). The results of micro- and mesowear tooth
617 analysis indicate a mixed diet, but with a high content of grasses in its feeding ecology.
618 In general, this taxon is indicative of open dry environments, both during the African
619 Pliocene and Pleistocene and in extant populations. Regardless of the consumption of
620 C₃ or C₄ plants, their feeding behavior is predominantly grazing (Vrba, 1984;
621 Sponheimer et al., 1999; 2003; Bobe and Behrensmeyer, 2004; Cerling et al., 2015).

622

623 Different species of Alcelaphini were present in North Africa from the Late Pliocene
624 (Arambourg, 1979; Geraads & Amani, 1998) until they were declared extinct in this
625 area in 1994 (Mallon and Kingswood, 2001), but the only fossil record of their diet has

626 been carried out at the site of Tighennif (1 Ma; Algeria). At this site, the Alcelaphini
627 tribe is represented by the species *Connochaetes taurinus prognu*. The pattern of $\delta^{13}\text{C}$
628 values ($n = 6$; mean $\delta^{13}\text{C} = -10.5 \pm 1.4\text{‰}$) is similar to that observed in the Alcelaphini
629 from AaO (Bocherens et al., 1996; Fannin et al., 2021). Compared to the carbon values
630 of different ungulates analyzed in Tighennif, this species has the most positive carbon
631 values, indicating, as in the case of AaO, a small consumption of C_4 plants in some
632 individuals.

633

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

637

638 In eastern Africa (Turkana Basin), the remarkable predominance and similarity in the C_4
639 isotopic signature of Alcelaphini from approximately ~4.4 Ma to present-day specimens
640 is particularly notable (White et al., 2009; Cerling et al., 2015). In Olduvai (Tanzania;
641 ~1.8 Ma), the carbon isotope data indicate C_4 -dominated diets, while dental wear
642 classifies this species as a grass-dominated mixed feeder (Uno et al., 2018).

643 In southern Africa, Wonderwerk Cave has a longer temporally stratified sequence from
644 the Early Pleistocene to the Holocene, with the presence of Alcelaphini in all layers.
645 They show a progressive increase in C_4 consumption from 50% in the Early Pleistocene
646 to 100% in the Holocene (Ecker et al., 2018). In the Makapansgat Limeworks Member
647 3 (~3 Ma), Alcelaphini (*Parmularius*, *Damaliscus* and *Connochaetes*) have C_4 values, in
648 contrast to the Tragelaphini from the same level, which have a clear C_3 values.
649 Ecomorphological and microwear data confirm a grazing diet for the former and a
650 browsing for the latter (Sponheimer et al., 1999; Schubert et al., 2006). In Haasgat cave

651 (~2.6–1.9 Ma), as in Makapansgat, Alcelaphini have a C₄ consumption while
652 Tragelaphini have C₃ plant consumption values (Adams et al., 2013). In Swartkrans
653 cave (~1.9–1.8 Ma), the Alcelaphini *Connochaetes* sp. also has a C₄-based diet (Lee-
654 Thorp et al., 1989). However, in other South African sites, the Alcelaphini carbon
655 values are clearly C₃, although attributed to grass consumption. This is the case of
656 Hoedjiespunt (~0.35–0.25 Ma) with a mean $\delta^{13}\text{C}$ ($n = 16$) of $-9.8 \pm 1.3\%$, Elandsfontein
657 (~1.0–0.6 Ma) with a mean $\delta^{13}\text{C}$ ($n = 19$) of $-10.3 \pm 1.2\%$, and Langebaanweg (~5 Ma)
658 with a mean $\delta^{13}\text{C}$ ($n = 7$) of $-10.8 \pm 1\%$ (Lehmann et al., 2016).

659

660 The *Hipparion pomeli* from AaO has a diet based on C₃ plants ($\delta^{13}\text{C}$ mean = $-11.7 \pm$
661 0.9%). It is the species with the highest mesowear, indicative of a grazing diet.
662 Microwear classifies it as a mixed feeder, but the high number of scratches is related to
663 a high consumption of grasses. The presence of *Hipparion* between ~3.5 and 1.7 Ma is
664 well documented in North Africa in sites such as Aïn Brimba and Lake Ichkeul in
665 Tunisia, Aïn el Bey, Aïn el Hadj Baba, Aïn Jourdel, Mansourah, Aïn Boucherit, Aïn
666 Hanech, Puits Carouby, Carrière Brunie, Carrières Quartier St-Pierre in Algeria, and
667 Fouarat, Oued Akrech, and Guefaït in Morocco. The dating of the youngest North
668 African hipparion record occurs at Aïn Hanech (~1.7 Ma) (Van der Made et al., 2022).
669 Regarding studies on the feeding habits of this species in North Africa, there are only
670 preliminary results for the *Hipparion* sp. from the Guefaït site (~3–2.5 Ma; Morocco),
671 which show a predominance of C₃ plant consumption ($n = 4$; $\delta^{13}\text{C}$ mean = $-9.5 \pm 1\%$),
672 although with less negative carbon values than those of the *H. pomeli* from AaO
673 (Ramírez-Pedraza et al., 2023).

674

675 In Central Africa, diachronic (~6–3 Ma) isotopic studies carried out on the species
676 *Hipparion cf. hasumense* in Chad show a clear predominance of C₄ plant consumption.
677 In Kossom Bougoudi (~6–5 Ma), the average $\delta^{13}\text{C}$ ($n = 6$) is $-1.3 \pm 0.8\text{‰}$, and in the
678 Koro Toro site (~3.5–3 Ma) the average $\delta^{13}\text{C}$ value ($n = 2$) is $0.9 \pm 1.1\text{‰}$ (Zazzo et al.,
679 2000).

680

681 In East Africa, as was the case with the Alcelaphini, the hipparion equid
682 *Eurygnathohippus* has continuity in C₄-grazer plant consumption from ~4 to 1.5 Ma
683 (Bocherens et al., 2011; Cerling et al., 2015; Manthi et al., 2020). Other methods such
684 as microwear and mesowear also indicate a grazing diet for the *Eurygnathohippus* from
685 Olduvai (Tanzania; ~1.8 Ma) (Uno et al., 2018).

686

687 In southern Africa, the *Hipparion* from Langebaanweg (~5 Ma) has a $\delta^{13}\text{C}$ mean value
688 ($n = 6$) of $-11.3 \pm 0.9\text{‰}$, implying a consumption of C₃ plants (Franz-Odendaal et al.,
689 2002). Other lines of evidence, such as mesowear analysis, in this species are consistent
690 with grazing behavior (Franz-Odendaal et al., 2003). Therefore, it would have a diet
691 based on C₃ grasses, like the *H. pomeli* from AaO. In contrast, at the Makapansgat site
692 (~3 Ma), the *Hipparion* indicates C₄ plant consumption (Sponheimer and Lee-Thorp,
693 2009; Lee-Thorp et al., 2010). In general, during the African Plio-Pleistocene,
694 *Hipparion* had a diet mainly based on the consumption of C₄ grasses. Grass
695 consumption has also been observed in AaO, although with the intake of C₃ plants.
696 Despite the low presence of C₄ plants in North Africa during the study period, some
697 species in AaO show a consumption of C₄ plants, but this is not the case for *H. pomeli*,
698 which may indicate slightly different dietary preferences compared to its relatives in
699 other parts of Africa.

700

701 The *Metridiochoerus phacochoeroides* from AaO shows a predominance of C₃ plant
702 carbon values (mean $\delta^{13}\text{C} = -11.7 \pm 1.2\text{‰}$), but with significant variability, including a
703 small percentage of C₄ consumption in one individual as observed in Alcelaphini.
704 Microwear analysis shows a mixed diet, although with significant consumption of
705 grasses, like other species classified as mixed feeders. The combination of both proxies
706 indicates a preferential diet based on C₃ grass consumption.

707

708 The genus *Metridiochoerus* first appeared in Africa ~3.5 Ma. *Metridiochoerus*
709 *phacochoeroides* is endemic to northern Africa and is distinct from the east and South
710 African representatives of the genus. Besides AaO, *Metridiochoerus* is rare in North
711 Africa, but is also known from its type-locality Aïn Jourdel (Thomas, 1884).

712

713 In East Africa, *Metridiochoerus* between ~4 and 1 Ma were predominantly grazers with
714 high C₄-grazer proportions (Harris and Cerling, 2002; Cerling et al., 2015; Uno et al.,
715 2018). Dental microwear analysis conducted on *Metridiochoerus* from Olduvai (~1.8
716 Ma, Tanzania) points to mixed feeding and grazing behavior (Uno et al., 2018). In the
717 Chiwondo Beds in Malawi (~2.5–1.5 Ma), *M. andrewsi* and *M. compactus* exhibit a
718 predominant consumption of C₃ plants (Lüdecke et al., 2016).

719

720 Little is known about the diet of *Metridiochoerus* in South Africa. Some populations of
721 *M. andrewsi* from Elandsfontein (~1.0–0.6 Ma) were consuming mostly C₃ plants (Luyt
722 et al., 2000), but due to the overall predominance of C₃ plants in this area, as in the
723 Chiwondo Beds in the Malawi Rift, could have been including grasses in their diet as
724 well.

725

726 The *Gazella* sp. from AaO has carbon values that correspond to a C₃ plant-based diet
727 (mean $\delta^{13}\text{C} = -11.6 \pm 0.6\text{‰}$). Microwear analysis shows a browser pattern; however,
728 mesowear analysis indicates a mixed diet with a browsing tendency. This could imply a
729 more purely browsing diet over a relatively brief period and a more varied consumption
730 of plants, including grasses in their diet, for most of the year. As with Alcelaphini,
731 *Gazella* has been present in North Africa since the Pliocene (Sahnouni et al., 2011; Van
732 der Made et al., 2021) until the present day in Morocco, Algeria, and Tunisia (Schmid et
733 al., 2005).

734

735 In North Africa, isotopic studies have been carried out on this species in both Tighennif
736 (~1 Ma; Algeria) with a mean $\delta^{13}\text{C}$ value ($n = 5$) of $-11.9 \pm 0.9\text{‰}$ and Guefaït (~3–2.5
737 Ma; Morocco) with a mean $\delta^{13}\text{C}$ value ($n = 4$) of $-10.9 \pm 1.1\text{‰}$. At both sites, there is a
738 clear predominance of C₃ plant consumption by *Gazella* (Fannin et al., 2021; Ramírez-
739 Pedraza et al., 2023).

740

741 In East Africa, *Gazella janenschi* from the Laetolil Beds (~4.3–3.5 Ma) has carbon
742 values ranging from -1.9 to -9.8‰, implying a variable diet from C₄-grazing to C₃-
743 browsing (Kingston and Harrison, 2007). This dietary flexibility has also been observed
744 in different Antilopini analyzed in the Turkana Basin (Kenya), with extracted
745 proportions of the isotopic signal of 17% C₄-grazing, 75% mixed C₃–C₄, and 8% C₃-
746 browsing for the period of ~4.3 to 2.3 Ma, and 54% C₄-grazing, 46% mixed C₃–C₄, and
747 0% C₃-browsing for the period ~2.3 to 1.0 Ma (Cerling et al., 2015). The multiproxy
748 study (isotopes, microwear, and mesowear) of Antilopini from Olduvai (1.8 Ma) also
749 indicates a mixed feeder diet (Uno et al., 2018). The *Gazella* sp. from AaO, as well as

750 those from the Pleistocene and Pliocene in Africa in general, seem to have the plasticity
751 to consume distinct types of plants, adapting to seasonal availability. Even in East
752 Africa before ~2.3 Ma, with a predominance of C₄ grassland in the area, they maintain a
753 percentage of contribution from C₃ plant consumption.

754

755 In South Africa, *Gazella vanhoepeni* from Makapansgat (~3 Ma) is considered either a
756 browser or a mixed-feeder preferring browsing based on isotopic, ecomorphological,
757 microwear, and mesowear dental studies (Schubert et al., 2006). The diachronic and
758 multiproxy study (isotopes, dental microwear texture, and mesowear analysis) of
759 Antilopini (*Antidorcas*) from Sterkfontein Member 4 (~2.8–2 Ma) and Swartkrans
760 Members (~2–0.8 Ma) also indicates a mixed diet with a certain browsing tendency for
761 this genus (Sewell et al., 2019).

762

763 **5.2 Palaeohabitat and palaeoclimate**

764

765 The results of the combination of proxies suggest for AaO a landscape with a
766 predominance of open and dry habitat, composed of C₃ woody plants and grasses and a
767 low presence of C₄ plants. The closed canopy forest is absent in the surroundings of
768 AaO, since no species has $\delta^{13}\text{C}_{\text{diet-meq}}$ values below -31.5‰, which is established as a
769 limit for this habitat.

770

771 **5.2.1 Dry environment and seasonality**

772 The Mean Annual Precipitation (MAP) in AaO measured 385 mm/year, indicating a dry
773 climate. The aridity of the region is supported by the fact that environments dominated
774 by C₃ plants with a MAP of 500 mm/year or less are typically associated with arid

775 conditions. This aridity pattern is also evident in the Tighenif site (1 Ma; Algeria),
776 recording a MAP of 297 mm/year (**Supplementary Table 3**). This reinforces the
777 enduring prevalence of dry climates even with established hominin presence in North
778 Africa. Kohn (2010) argues that the indicator's reliability depends on the mean MAP of
779 all analyzed taxa. Thus, the average MAP remains the critical factor for assessing the
780 robustness of this indicator. However, the variability in $\delta^{13}\text{C}_{\text{enamel}}$, MAP, and $\delta^{13}\text{C}_{\text{diet-meq}}$
781 values, both inter- and intra-species (**Table 1**), suggests the presence of microhabitats
782 (Patalano et al., 2021). In arid regions like those surrounding AaO and Tighenif, there
783 can be localized areas of higher humidity, particularly in close proximity to water
784 sources. Vegetation in these zones may exhibit lower $\delta^{13}\text{C}$ values than expected for the
785 surrounding dry environment, especially in a particularly wet year or season (Kohn,
786 2010). This variability in the values could also be explained by the dynamics of the
787 assemblage accumulation. Although the formation data of the site suggest a rapid
788 accumulation over time (Geraads et al., 2022), we cannot precisely determine how long
789 it took to form, potentially encompassing many years with diverse climates and
790 resources for consumption.

791

792 In dry environments, C_4 plants exhibit greater efficiency than C_3 plants under conditions
793 of low atmospheric CO_2 concentration, high temperatures, and moisture stress
794 (Ehleringer et al., 1991; Cerling et al., 1993). Therefore, the presence of C_4 plants in the
795 diet of Alcelaphini and *M. phacochoeroides*, even in small proportions, aligns with arid
796 environments. The variability in $\delta^{13}\text{C}_{\text{enamel}}$ values within species, especially in the
797 aforementioned species, may suggest the existence of pronounced seasonal fluctuations.
798 Relative to aridity, the difference observed in the $\delta^{18}\text{O}$ values of obligate and non-
799 obligate drinkers in AaO (1.9‰) is slightly higher than the difference found in

800 herbivores from the Tsavo (1.7‰) region (Kenya), which has been defined as a dry
801 savannah with vegetation characterized by semi-desert bushland with riparian woodland
802 and a MAP of 500 mm/yr (Cerling et al., 2003; 2015). The species *S. maurusium*
803 exhibits the highest $\delta^{18}\text{O}$ values, even in comparison to *Gazella* sp. Given that dental
804 wear patterns indicate a browsing diet for both species, the elevated $\delta^{18}\text{O}$ values in *S.*
805 *maurusium* may be attributed to its consumption of leaves from tall plants that it has
806 access to due to its large size. Sun-exposed leaves, particularly in arid conditions, are
807 highly sensitive to evaporative fractionation, resulting in an enrichment of ^{18}O
808 (Gonfiantini et al., 1965; Barbour, 2007).

809 In this line, the combination of tooth microwear (short-term) and tooth mesowear (long-
810 term) proxies has been used as a tool to identify seasonality (Sánchez-Hernández et al.,
811 2016). Considering that microwear reflects the signal of a short-term diet, such as a
812 single season, while mesowear reflects a longer period including probably all seasons,
813 discrepancies in the results between both proxies would be indicative of dietary changes
814 due to seasonal availability of resources. In AaO, *S. maurusium* exhibits a browsing
815 pattern with the two proxies, indicating that its diet does not change throughout the
816 year. For *Gazella* sp., tooth mesowear indicates browse-dominated mixed feeding,
817 while microwear suggests browsing. This species is likely to have a more diverse diet,
818 characterized by a higher consumption of grasses throughout the year, along with a
819 significant increase in browsing during a particular season. In the case of Alcelaphini
820 and *H. pomeli*, tooth mesowear indicates grass-dominated mixed feeding and grazing,
821 respectively, while microwear suggests mixed feeding. It indicates a predominant
822 consumption of grasses throughout the year with the introduction of other food items
823 during specific periods of the year.

824

825 5.2.2 C₃ grassland and open habitat

826

827 In all species from AaO, the most discriminant microwear feature is the number of
828 scratches, which is different in browsers and mixed feeders (**Fig. 5**). The high number
829 of scratches in mixed feeders indicates significant consumption of grasses (see %0–17
830 in **Table 2**). However, the number of pits is very similar between browsers and mixed
831 feeders with grazing tendencies. The relatively high number of pits and the presence of
832 large pits in all species could be caused by incidental ingestion of abrasive grit resulting
833 from feeding close to the ground in open and arid habitats (Semprebon and Rivals,
834 2007; Hoffman et al., 2015). This enables us to emphasize two environmental aspects:
835 (1) The prevalence of taxa with a C₃ plant-based diet, many of which consume a
836 significant amount of grasses, indicating the significant presence of C₃ grasslands in the
837 study area. This assertion is corroborated by previous research on the feeding habits of
838 *Theropithecus atlanticus* in AaO. In that study, they employed time- and graminivore-
839 calibrated carbon stable isotope values to illustrate a progressive transition towards an
840 increased dependence on high-throughput bulk-feeding graminivory and proposed a
841 consumption of grasses exhibiting a distinct C₃ isotopic signature (Fannin et al., 2021).
842 (2) The presence of C₃ grassland, feeding close to the ground, and the presence of *T.*
843 *atlanticus* (Alemseged and Geraads, 1998; Fannin et al., 2021) are indicators of open
844 habitats. It is noteworthy that no other cercopithecine species have been discovered at
845 the AaO site in Morocco. Additionally, while no fossil remains of *Theropithecus* have
846 been found at the contemporaneous site of Guefaït in Morocco, the presence of *M. cf.*
847 *sylvanus* has been noted (Alba et al., 2021). Previous ecological studies suggest that this
848 macaque inhabited a woodland ecosystem, where it had a folivorous-frugivorous diet
849 with hard item consumption which was primarily based on C₃ plants (Ramirez-Pedraza

850 et al., 2023). This indicates a low wood cover in the landscape of western Morocco
851 during the Plio-Pleistocene boundary. In the same line, the relative frequency of two
852 species of bovids found in Guefaït and AaO may provide insight into the predominant
853 environmental conditions. Specifically, Tragelaphini are associated with wooded and
854 humid habitats, while Alcelaphini are linked to more open environments (Bobé et al.,
855 2007). Notably, the abundance of Alcelaphini and the scarcity of Tragelaphini in AaO is
856 significant (Geraads and Amani, 1998; Geraads et al., 2022a), while the opposite trend
857 is observed in Guefaït (Sala-Ramos et al., 2022; Ramírez-Pedraza et al., 2023). Previous
858 works on AaO have used a method for predicting palaeohabitats using measurements
859 (height/width proportions) of bovid astragali (DeGusta and Vrba, 2003). The
860 proportions of this bone in the bovids from AaO confirm the absence of heavy wood
861 cover and the predominance of open habitat (Geraads et al., 2022a).

862

863 **6. Conclusion**

864

865 This research highlights the importance of integrating different proxies for
866 palaeoecological reconstructions, being particularly useful in areas where there is a
867 predominance of C₃ plants such as in North Africa, where it is more challenging to
868 define the diet and habitat of mammals from stable isotope analysis alone. In this work,
869 the complementarity of dental wear analysis has allowed us to determine diets that
870 range from grazing to browsing behavior. Our multiproxy analysis indicates that during
871 the Plio-Pleistocene boundary in the western coastal region of Morocco, open C₃
872 grasslands and shrubland predominated in an arid climate.

873 The most notable distinction between taxa from East, South, and Central Africa in
874 comparison to those from the North is their extensive reliance on C₄ plants, which are

875 associated with tropical grasses from open arid habitats. In the AaO area, although there
876 was a consumption of C₃ plants, the environment was similarly arid and characterized
877 by open grasslands. This aridity was also evident in Tighenif, even with the presence of
878 hominins in the region. Therefore, the dry environment should not have been a
879 limitation to hominins occupation in North Africa. Despite AaO being one of the most
880 abundant fossil fauna sites in North Africa during the Plio-Pleistocene, taxon diversity
881 remains relatively low compared to contemporary sites in the East and South. This
882 could be attributed to the limited diversity of habitats in AaO, such as the absence of
883 woody vegetation or, for instance, the possible lack of permanent water sources, as
884 indicated by the absence of taxa like Hippopotamidae, crocodiles, or freshwater birds
885 (Geraads et al., 2022).

886 However, further research in different archaeological and palaeontological sites from
887 the Early Pleistocene and Late Pliocene in the Maghreb is necessary to gain a holistic
888 understanding of the ecological and climatic dynamics that contributed to the dispersal,
889 occupation, and evolution of mammals and early hominins.

890

891 **CRedit author statement**

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926

927 **Appendix A. Supplementary data**

928

929 **References**

930

931 Adams, J.W., Kegley, A.D.T., Krigbaum, J., 2013. New faunal stable carbon isotope
932 data from the Haasgat HGD assemblage, South Africa, including the first reported
933 values for *Papio angusticeps* and *Cercopithecoides haasgati*. *J. Hum. Evol.* 64,
934 693–698. <https://doi.org/10.1016/j.jhevol.2013.02.009>

935 Alba, D.M., Rodríguez-Hidalgo, A., Aouraghe, H., Van der Made, J., Oujaa, A.,
936 Haddoumi, H., Saladié, P., Mahdi, A., Marín, J., Farkouch, M., Lorenzo, C.,
937 Bengamra, S., Delson, E., Chacón, M., Sala-Ramos, R., 2021. New macaque fossil
938 remains from Morocco. *J. Hum. Evol.* 153, 1–8.
939 <https://doi.org/10.1016/j.jhevol.2021.102951>

940 Alemseged, Z., Geraads, D., 1998. *Theropithecus atlanticus* (Thomas, 1884) (Primates:
941 Cercopithecidae) from the late Pliocene of Ahl al Oughlam, Casablanca, Morocco.
942 *J. Hum. Evol.* 34, 609–621. <https://doi.org/10.1006/jhev.1998.9999>

943 Aouraghe, H., Haddoumi, H., Rodríguez-Hidalgo, A., Van der Made, J., Piñero, P.,
944 Agustí, J., Álvarez-Posada, C., Benito-Calvo, A., Blain, H.-A., Duval, M., El
945 Hammouti, K., Expósito, I., Marín, J., Mejías, D., Oujaa, A., Parés, J., Pla, S.,
946 Ramírez-Pedraza, I., Rivals, F., Saladié, P., Tornero, C., Chacón, M.G, Sala-
947 Ramos, R., 2019. Nouvelles données sur le site du Pliocène Final/Pléistocène
948 Inférieur de Guefaït 4: Mission 2019, in: 10^{ème} Rencontre Des Quaternaristes

- 949 Marocains, Kénitra. Recueil Des Résumés. pp. 47–48.
- 950 Arambourg, C., 1979. Vertébrés villafranchiens d’Afrique du Nord (Artiodactyles,
951 Carnivores, Primates, Reptiles, Oiseaux), Fondation Singer-Polignac. Paris.
952 <https://doi.org/10.2113/gssgfbull.s5-xix.1-3.195>
- 953 Arambourg, C., Hoffstetter, R., 1963. Le Gisement de Ternifine. Masson et Cie
954 Editeurs, Paris.
- 955 Balasse, M., Ambrose, S.H., 2005. Distinguishing sheep and goats using dental
956 morphology and stable carbon isotopes in C₄ grassland environments. J. Archaeol.
957 Sci. 32, 691–702. <https://doi.org/10.1016/j.jas.2004.11.013>
- 958 Barbour, M.M., 2007. Stable oxygen isotope composition of plant tissue: A review.
959 Funct. Plant Biol. 34, 83–94. <https://doi.org/10.1071/FP06228>
- 960 Basu, C., Falkingham, P.L., Hutchinson, J.R., 2016. The extinct, giant giraffid
961 *Sivatherium giganteum*: Skeletal reconstruction and body mass estimation. Biol.
962 Lett. 12, 0–3. <https://doi.org/10.1098/rsbl.2015.0940>
- 963 Bedaso, Z.K., Wynn, J.G., Alemseged, Z., Geraads, D., 2013. Dietary and
964 paleoenvironmental reconstruction using stable isotopes of herbivore tooth enamel
965 from middle Pliocene Dikika, Ethiopia: Implication for *Australopithecus afarensis*
966 habitat and food resources. J. Hum. Evol. 64, 21–38.
967 <https://doi.org/10.1016/j.jhevol.2012.05.015>
- 968 Bernor, R.L., Kaya, F., Kaakinen, A., Saarinen, J., Fortelius, M., 2021. Old world
969 hipparion evolution, biogeography, climatology and ecology. Earth-Science Rev.
970 221, 103784. <https://doi.org/10.1016/j.earscirev.2021.103784>
- 971 Biberson, P., 1961a. Le Paleolithique inferieur du Maroc atlantique, fascicule. ed.
972 Publications du Service des Antiquités du Maroc, fascicule 17, Rabat.
- 973 Biberson, P., 1961b. Le cadre palaeogéographique de la Préhistoire du Maroc

974 atlantique, fascicule. ed. Publications du Service des Antiquités du Maroc,
975 fascicule 16, Rabat.

976 Bibi, F., Kiessling, W., 2015. Continuous evolutionary change in Plio-Pleistocene
977 mammals of eastern Africa. Proc. Natl. Acad. Sci. U. S. A. 112, 10623–10628.
978 <https://doi.org/10.1073/pnas.1504538112>

979 Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.P., Chritz, K.L., Harris, J.M.,
980 Jehle, G.E., Cerling, T.E., O’Connell, J., 2017. Aridity and hominin environments.
981 Proc. Natl. Acad. Sci. U. S. A. 114, 7331–7336.
982 <https://doi.org/10.1073/pnas.1700597114>

983 Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa
984 in relation to mammalian evolution and the origin of the genus *Homo*.
985 Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 399–420.
986 <https://doi.org/10.1016/j.palaeo.2003.09.033>

987 Bobe, R., Behrensmeyer, A.K., Eck, G.G., Harris, J.M., 2007. Patterns of abundance
988 and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya
989 and Ethiopia, in: Bobe, R., Alemseged, Z., Behrensmeyer, K. (Eds.), Hominin
990 Environments in the East African Pliocene: An Assessment of the Faunal
991 Evidence. Springer, pp. 129–157. https://doi.org/10.1007/978-1-4020-3098-7_6

992 Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.J., 1996. Isotopic
993 biogeochemistry (^{13}C , ^{18}O) of mammalian enamel from african pleistocene
994 hominid sites. Palaios 11, 306–318. <https://doi.org/10.2307/3515241>

995 Bocherens, H., Sandrock, O., Kullmer, O., Schrenk, F., 2011. Hominin palaeoecology
996 in Late Pliocene Malawi: First insights from isotopes (^{13}C , ^{18}O) in mammal teeth.
997 S. Afr. J. Sci. 107, 13–18. <https://doi.org/10.4102/sajs.v107i3/4.331>

998 Castañeda, I.S., Mulitza, S., Schefuß, E., Dos Santos, R.A.L., Damsté, J.S.S., Schouten,

999 S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in
1000 North Africa. *Proc. Natl. Acad. Sci. U. S. A.* 106, 20159–20163.
1001 <https://doi.org/10.1073/pnas.0905771106>

1002 Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the
1003 Neogene. *Glob. Planet. Change* 5, 241–247. [https://doi.org/10.1016/0921-](https://doi.org/10.1016/0921-8181(92)90013-Z)
1004 [8181\(92\)90013-Z](https://doi.org/10.1016/0921-8181(92)90013-Z)

1005 Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M.,
1006 Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E.,
1007 Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores
1008 in the Turkana Basin, Kenya from 4 to 1 Ma. *Proc. Natl. Acad. Sci. U. S. A.* 112,
1009 11467–11472. <https://doi.org/10.1073/pnas.1513075112>

1010 Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and
1011 bioapatite in ungulate mammals and implications for ecological and
1012 paleoecological studies. *Oecologia* 120, 347–363.
1013 <https://doi.org/10.1007/s004420050868>

1014 Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V.,
1015 Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene
1016 boundary. *Nature* 389, 153–158. <https://doi.org/10.1038/38229>

1017 Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African Bovidae based on
1018 stable isotope analysis. *J. Mammal.* 84, 456–470. [https://doi.org/10.1644/1545-](https://doi.org/10.1644/1545-1542(2003)084<0456:DOEABB>2.0.CO;2)
1019 [1542\(2003\)084<0456:DOEABB>2.0.CO;2](https://doi.org/10.1644/1542(2003)084<0456:DOEABB>2.0.CO;2)

1020 Cerling, T.E., Wang, Y., Quade, J., 1993. Expansion of C₄ ecosystems as an indicator of
1021 global ecological change in the late Miocene. *Nature* 361, 344–345.
1022 <https://doi.org/10.1038/361344a0>

1023 Chaid-Saoudi, Y., Geraads, D., Raynal, J.P., 2006. The fauna and associated artefacts

1024 from the Lower Pleistocene site of Mansourah (Constantine, Algeria). *Comptes*
1025 *Rendus - Palevol* 5, 963–971. <https://doi.org/10.1016/j.crpv.2006.08.001>

1026 Daujeard, C., Falguères, C., Shao, Q., Geraads, D., Hublin, J.J., Lefèvre, D., Graoui, M.,
1027 El, Rué, M., Gallotti, R., Delvigne, V., Queffelec, A., Ben Arous, E., Tombret, O.,
1028 Mohib, A., Raynal, J.-P., 2020. Earliest African evidence of carcass processing and
1029 consumption in cave at 700 ka, Casablanca, Morocco. *Sci. Rep.* 10, 1–15.
1030 <https://doi.org/10.1038/s41598-020-61580-4>

1031 Daujeard, C., Geraads, D., Gallotti, R., Lefèvre, D., Mohib, A., Raynal, J.-P., Hublin,
1032 J.J., 2016. Pleistocene hominins as a resource for carnivores: A c. 500,000-year-old
1033 human femur bearing tooth-marks in North Africa (Thomas Quarry I, Morocco).
1034 *PLoS One* 11, 1–22. <https://doi.org/10.1371/journal.pone.0152284>

1035 Daujeard, C., Geraads, D., Gallotti, R., Mohib, A., Raynal, J.-P., 2012. Carcass
1036 acquisition and consumption by carnivores and hominins in Middle Pleistocene
1037 sites of Casablanca (Morocco). *J. Taphon.* 10, 349–372.

1038 DeGusta, D., Vrba, E., 2003. A method for inferring paleohabitats from the functional
1039 morphology of bovid astragali. *J. Archaeol. Sci.* 30, 1009–1022.
1040 [https://doi.org/10.1016/S0305-4403\(02\)00286-8](https://doi.org/10.1016/S0305-4403(02)00286-8)

1041 Domingo, L., Koch, P.L., Hernández Fernández, M., Fox, D.L., Domingo, M.S.,
1042 Alberdi, M.T., 2013. Late Neogene and Early Quaternary paleoenvironmental and
1043 paleoclimatic conditions in Southwestern Europe: Isotopic analyses on mammalian
1044 taxa. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0063739>

1045 Duval, M., Sahnouni, M., Parés, J.M., Van der Made, J., Abdessadok, S., Harichane, Z.,
1046 Cheheb, R.C., Boulaghrif, K., Pérez-González, A., 2021. The Plio-Pleistocene
1047 sequence of Oued Boucherit (Algeria): A unique chronologically-constrained
1048 archaeological and palaeontological record in North Africa. *Quat. Sci. Rev.* 271,

1049 107116. <https://doi.org/10.1016/j.quascirev.2021.107116>

1050 Duval, M., Sahnouni, M., Parés, J.M., Zhao, J. xin, Grün, R., Abdessadok, S., Pérez-

1051 González, A., Derradji, A., Harichane, Z., Mazouni, N., Boulaghraief, K., Cheheb,

1052 R.C., Van der Made, J., 2023. On the age of Aïn Hanech Oldowan locality

1053 (Algeria): First numerical dating results. *J. Hum. Evol.* 180.

1054 <https://doi.org/10.1016/j.jhevol.2023.103371>

1055 Ecker, M., Brink, J.S., Rossouw, L., Chazan, M., Horwitz, L.K., Lee-Thorp, J.A., 2018.

1056 The palaeoecological context of the Oldowan-Acheulean in southern Africa. *Nat.*

1057 *Ecol. Evol.* 2, 1080–1086. <https://doi.org/10.1038/s41559-018-0560-0>

1058 Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., Bond, W.J., Christin,

1059 P.A., Cousins, A.B., Duvall, M.R., Fox, D.L., Freckleton, R.P., Ghannoum, O.,

1060 Hartwell, J., Huang, Y., Janis, C.M., Keeley, J.E., Kellogg, E.A., Knapp, A.K.,

1061 Leakey, A.D.B., Nelson, D.M., Saarela, J.M., Sage, R.F., Sala, O.E., Salamin, N.,

1062 Still, C.J., Tipple, B., 2010. The origins of C₄ grasslands: Integrating evolutionary

1063 and ecosystem science. *Science* (80-.). 328, 587–591.

1064 <https://doi.org/10.1126/science.1177216>

1065 Ehleringer, J.R., Sage, R.F., Flanagan, L.B., Pearcy, R.W., 1991. Climate change and

1066 the evolution of C₄ photosynthesis. *Trends Ecol. Evol.* 6, 95–99.

1067 Eisenmann, V., Geraads, D., 2007. *Hipparion pomeli* sp. nov from the late Pliocene of

1068 Ahl al Oughlam, Morocco, and a revision of the relationships of Pliocene and

1069 Pleistocene African hipparions. *Palaeontol. Africana* 42, 51–98.

1070 El-Zaatari, S., 2010. Occlusal microwear texture analysis and the diets of

1071 historical/prehistoric hunter-gatherers. *Int. J. Osteoarchaeol.* 20, 67–87.

1072 <https://doi.org/10.1002/oa.1027>

1073 Ennouchi, E., 1975., New discovery of an Archanthropian in Morocco. *J. Hum. Evol.* 4,

1074 441–443. [https://doi.org/10.1016/0047-2484\(75\)90141-4](https://doi.org/10.1016/0047-2484(75)90141-4)

1075 Fannin, L.D., Yeakel, J.D., Venkataraman, V. V., Seyoum, C., Geraads, D., Fashing,
1076 P.J., Nguyen, N., Fox-Dobbs, K., Dominy, N.J., 2021. Carbon and strontium
1077 isotope ratios shed new light on the paleobiology and collapse of *Theropithecus*, a
1078 primate experiment in graminivory. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 572,
1079 110393. <https://doi.org/10.1016/j.palaeo.2021.110393>

1080 Fortelius, M., Solounias, N., 2000. Functional Characterization of Ungulate Molars
1081 Using the Abrasion-Attrition Wear Gradient: A New Method for Reconstructing
1082 Paleodiets. *Am. Museum Novit.* 3301, 1–36. [https://doi.org/10.1206/0003-](https://doi.org/10.1206/0003-0082(2000)301<0001:FCOUMU>2.0.CO;2)
1083 [0082\(2000\)301<0001:FCOUMU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2000)301<0001:FCOUMU>2.0.CO;2)

1084 Franz-Odenaal, T.A., Kaiser, T.M., Bernor, R.L., 2003. Systematics and dietary
1085 evaluation of a fossil equid from South Africa. *S. Afr. J. Sci.* 99, 453–459.

1086 Franz-Odenaal, T.A., Lee-Thorp, J.A., Chinsamy, A., 2002. New evidence for the lack
1087 of C₄ grassland expansions during the early Pliocene at Langebaanweg, South
1088 Africa. *Paleobiology* 28, 378–388. [https://doi.org/10.1666/0094-](https://doi.org/10.1666/0094-8373(2002)028<0378:neftlo>2.0.co;2)
1089 [8373\(2002\)028<0378:neftlo>2.0.co;2](https://doi.org/10.1666/0094-8373(2002)028<0378:neftlo>2.0.co;2)

1090 Franz-Odenaal, T.A., Solounias, N., 2004. Comparative dietary evaluations of an
1091 extinct giraffid (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) from
1092 Langebaanweg, South Africa (early Pliocene). *Geodiversitas* 26, 675–685.

1093 Gallotti, R., Mohib, A., Fernandes, P., El Graoui, M., Lefèvre, D., Raynal, J.-P., 2020.
1094 Dedicated core-on-anvil production of bladelet-like flakes in the Acheulean at
1095 Thomas Quarry I - L1 (Casablanca, Morocco). *Sci. Rep.* 10, 1–16.
1096 <https://doi.org/10.1038/s41598-020-65903-3>

1097 Gallotti, R., Mohib, A., Lefevre, D., Raynal, J.-P., 2022. The African Acheulean: a
1098 view from the western Maghreb. L'Acheuléen africain vu de l'extrême Maghreb.
1099 Bull. d'Archéologie Marocaine 27, 7-26.

1100 Gallotti, R., Muttoni, G., Lefèvre, D., Degeai, J.P., Geraads, D., Zerboni, A., Ponei,
1101 V.A., Maron, M., Perini, S., Graoui, M. El, Laliberté, S.S., Daujeard, C.,
1102 Fernandes, P., Mathieu, R., Magoga, L., Mohib, A., Raynal, J.-P., 2021. First high
1103 resolution chronostratigraphy for the early North African Acheulean at Casablanca
1104 (Morocco). Sci. Rep. 11, 1–14. <https://doi.org/10.1038/s41598-021-94695-3>

1105 Gallotti, R., Raynal, J.-P., Mohib, A., Fernandes, P., Magoga, L., El Graoui, M., Rué,
1106 M., Muttoni, G., Lefèvre, D., 2023. Early North African Acheulean techno-
1107 economic systems at Thomas Quarry I - L1 (Casablanca, Morocco). J. Anthropol.
1108 Sci. 101. <https://doi.org/10.4436/JASS.10015>

1109 Geraads, D., 2016. Pleistocene Carnivora (Mammalia) from Tighennif (Ternifine),
1110 Algeria. Geobios 49, 445–458. <https://doi.org/10.1016/j.geobios.2016.09.001>

1111 Geraads, D., 2010. Biogeographic relationships of Pliocene and Pleistocene North-
1112 western African mammals. Quat. Int. 212, 159–168.
1113 <https://doi.org/10.1016/j.quaint.2009.06.002>

1114 Geraads, D., 2006. The late Pliocene locality of Ahl al Oughlam, Morocco: Vertebrate
1115 fauna and interpretation. Trans. R. Soc. South Africa 61, 97–101.
1116 <https://doi.org/10.1080/00359190609519958>

1117 Geraads, D., 2004. New skulls of *Kolpochoerus phacochoeroides* (Suidae: Mammalia)
1118 from the late Pliocene of Ahl al Oughlam, Morocco. Palaeontol. Africana 69–83.

1119 Geraads, D., 2002. Plio-Pleistocene mammalian biostratigraphy of Atlantic Morocco.
1120 Quaternaire 13, 43–53. <https://doi.org/10.3406/quate.2002.1702>

1121 Geraads, D., 1997. Carnivores du Pliocene terminal de Ahl al Oughlam (Casablanca,

- 1122 Maroc). *Geobios* 127–164.
- 1123 Geraads, D., 1996. Le *Sivatherium* (Giraffidae, Mammalia) du Pliocène final d’Ahl al
1124 Oughlam (Casablanca, Maroc), et l’évolution du genre en Afrique.
1125 *Paläontologische Zeitschrift* 70, 623–629. <https://doi.org/10.1007/BF02988097>
- 1126 Geraads, D., 1995. Rodents and insectivores (Mammalia) from the Late Pliocene of Ahl
1127 al Oughlam (Casablanca, Morocco). *Geobios* 28, 99–115.
- 1128 Geraads, D., 1993. *Kolpochoerus phacochoeroides* (Thomas, 1884)(Suidae,
1129 Mammalia), du Pliocène supérieur de Ahl al Oughlam (Casablanca, Maroc).
1130 *Geobios* 26, 731–743. [https://doi.org/10.1016/S0016-6995\(93\)80056-W](https://doi.org/10.1016/S0016-6995(93)80056-W)
- 1131 Geraads, D., Amani, F., 1998. Bovidae (Mammalia) du Pliocène final d’Ahl al
1132 Oughlam, Casablanca, Maroc. *Paläontologische Zeitschrift* 72, 191–205.
1133 <https://doi.org/10.1007/bf02987826>
- 1134 Geraads, D., Beriro, P., Roche, H., 1980. La faune et l’industrie des sites à *Homo*
1135 *erectus* des carrières Thomas (Maroc). Précisions sur l’âge de ces Hominidés.
1136 *Comptes Rendu Acad. Sci. Pari* 291, 195–197.
- 1137 Geraads, D., Daujeard, C., Lefèvre, D., Gallotti, R., Mohib, A., Raynal, J.-P., 2022a.
1138 Early *Homo* on the Atlantic shore: the Thomas I and Oulad Hamida 1 Quarries,
1139 Morocco, in: Reynolds, S., Bobe, R. (Eds.), *African Paleoecology and Human*
1140 *Evolution*. Cambridge University Press, Cambridge, pp. 481–491.
- 1141 Geraads, D., Hublin, J.J., Jaeger, J.J., Tong, H., Sen, S., Toubeau, P., 1986. The
1142 Pleistocene hominid site of Ternifine, Algeria: New results on the environment,
1143 age, and human industries. *Quat. Res.* 25, 380–386. [https://doi.org/10.1016/0033-](https://doi.org/10.1016/0033-5894(86)90008-6)
1144 [5894\(86\)90008-6](https://doi.org/10.1016/0033-5894(86)90008-6)
- 1145 Geraads, D., Lefèvre, D., Raynal, J.-P., 2022b. Ahl al Oughlam, Morocco: The Richest
1146 Fossil Site in North Africa at the Pliocene/Pleistocene Boundary, in: Reynolds,

- 1147 S.C., Bobe, R. (Eds.), African Paleocology and Human Evolution. Cambridge
1148 University Press, Cambridge, pp. 468–475.
- 1149 Geraads, D., Metz-Muller, F., 1999. Proboscidea (Mammalia) du Pliocène final d’Ahl al
1150 Oughlam (Casablanca, Maroc). Neues Jahrb. fur Geol. und Palaontologie -
1151 Abhandlungen 1, 52–64.
- 1152 Geraads, D., Raynal, J.P., Sbihi-Alaoui, F.Z., 2010. Mammalian faunas from the
1153 Pliocene and Pleistocene of Casablanca (Morocco). Hist. Biol. 22, 275–285.
1154 <https://doi.org/10.1080/08912960903458011>
- 1155 Gonfiantini, R., Gratziu, S., Tongiorgi, E., 1965. Oxygen isotopic composition of water
1156 in leaves, in: Isotopes and Radiation in Soil Plant Nutrition Studies. International
1157 atomic energy agency, Vienna, pp. 405–410.
- 1158 Grant, K.M., Amarathunga, U., Amies, J.D., Hu, P., Qian, Y., Penny, T., Rodriguez-
1159 sanz, L., Zhao, X., Heslop, D., Liebrand, D., Hennekam, R., Westerhold, T.,
1160 Gilmore, S., Lourens, L.J., Roberts, A.P., Rohling, E.J., 2022. Organic carbon
1161 burial in Mediterranean sapropels intensified during Green Sahara Periods since
1162 3.2 Myr ago. Commun. earth Environ. 3, 1–9. [https://doi.org/10.1038/s43247-021-](https://doi.org/10.1038/s43247-021-00339-9)
1163 [00339-9](https://doi.org/10.1038/s43247-021-00339-9)
- 1164 Grant, K.M., Rohling, E.J., Westerhold, T., Zabel, M., Heslop, D., Konijnendijk, T.,
1165 Lourens, L., 2017. A 3 million year index for North African humidity/aridity and
1166 the implication of potential pan-African Humid periods. Quat. Sci. Rev. 171, 100–
1167 118. <https://doi.org/10.1016/j.quascirev.2017.07.005>
- 1168 Gunnell, G.F., Eiting, T.P., Geraads, D., 2011. New late pliocene bats (Chiroptera) from
1169 Ahl al Oughlam, Morocco. Neues Jahrb. fur Geol. und Palaontologie -
1170 Abhandlungen 260, 55–71. <https://doi.org/10.1127/0077-7749/2011/0128>

- 1171 Hammer, Ø., Harper, D.A., Ryan, P.D., 2001. Past: Paleontological Statistics Software
1172 Package for Education and Data Analysis. *Palaeontol. Electron.* 4, 5–7.
1173 <https://doi.org/10.1016/j.bcp.2008.05.025>
- 1174 Hammond, A.S., Mongle, C., 2023. Pleistocene Hominin Fossil Record of Africa, in:
1175 Beyin, A., Wright, D.K., Wilkins, J., Olszewski, D.I. (Eds.), *Handbook of*
1176 *Pleistocene Archaeology of Africa*. Springer, Cham, pp. 1807–1820.
1177 https://doi.org/https://doi.org/10.1007/978-3-031-20290-2_119
- 1178 Harris, J.M., Cerling, T.E., 2002. Dietary adaptations of extant and Neogene African
1179 suids. *J. Zool.* 256, 45–54. <https://doi.org/10.1017/s0952836902000067>
- 1180 Hoffman, J.M., Fraser, D., Clementz, M.T., 2015. Controlled feeding trials with
1181 ungulates: a new application of in vivo dental molding to assess the abrasive factors
1182 of microwear. *J. Exp. Biol.* 218, 1538–1547. <https://doi.org/10.1242/jeb.118406>
- 1183 Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and
1184 extant equids. *Geodiversitas* 25, 321–345.
- 1185 Kaiser, T.M., Fortelius, M., 2003. Differential Mesowear in Occluding Upper and
1186 Lower Molars: Opening Mesowear Analysis for Lower Molars and Premolars in
1187 Hypsodont Horses. *J. Morphol.* 258, 67–83. <https://doi.org/10.1002/jmor.10125>
- 1188 King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental
1189 microwear. *Am. J. Phys. Anthropol.* 108, 359–373.
1190 [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:3<359::AID-](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.CO;2-9)
1191 [AJPA10>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.CO;2-9)
- 1192 Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene
1193 herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeogr.*
1194 *Palaeoclimatol. Palaeoecol.* 243, 272–306.
1195 <https://doi.org/10.1016/j.palaeo.2006.08.002>

1196 Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annu. Rev.*
1197 *Earth Planet. Sci.* 26, 573–613. <https://doi.org/10.1146/annurev.earth.26.1.573>

1198 Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and
1199 diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *J.*
1200 *Archaeol. Sci.* 24, 417–429.

1201 Kohn, M.J., 1996. Predicting animal $\delta^{18}\text{O}$: Accounting for diet and physiological
1202 adaptation. *Geochim. Cosmochim. Acta* 60, 4811–4829.
1203 [https://doi.org/10.1016/S0016-7037\(96\)00240-2](https://doi.org/10.1016/S0016-7037(96)00240-2)Kohn, M.J., 2010. Carbon isotope
1204 compositions of terrestrial C_3 plants as indicators of (paleo)ecology and
1205 (paleo)climate. *Proc. Natl. Acad. Sci. U. S. A.* 107, 19691–19695.
1206 <https://doi.org/10.1073/pnas.1004933107>

1207 Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite.
1208 *Phosphates Geochemical, Geobiol. Mater. Importance* 48, 455–488.
1209 <https://doi.org/10.2138/rmg.2002.48.12>

1210 Krueger, H.W., Sullivan, C.H., 1984. Models for carbon isotope fractionation between
1211 diet and bone, in: Turnlund, J., Al, E. (Eds.), *Stable Isotopes in Nutrition*. ACS
1212 *Symposium Series*, Washington, pp. 205–220. [https://doi.org/10.1021/bk-1984-](https://doi.org/10.1021/bk-1984-0258.ch014)
1213 [0258.ch014](https://doi.org/10.1021/bk-1984-0258.ch014)

1214 Larramendi, A., 2016. Shoulder height, body mass, and shape of proboscideans. *Acta*
1215 *Palaeontol. Pol.* 61, 537–574. <https://doi.org/10.4202/app.00136.2014>

1216 Larrasoana, J.C., 2021. A review of West African monsoon penetration during Green
1217 Sahara Periods; implications for human evolution and dispersals over the last three
1218 million years. *Oxford Open Clim. Chang.* 1, 1–19.
1219 <https://doi.org/10.1093/oxfclm/kgab011>

1220 Larrasoana, J.C., Roberts, A.P., Rohling, E.J., 2013. Dynamics of Green Sahara Periods

1221 and their role in hominin evolution. PLoS One 8.
1222 <https://doi.org/10.1371/journal.pone.0076514>

1223 Larrasoana, J.C., Roberts, A.P., Rohling, E.J., Winklhofer, M., Wehausen, R., 2003.
1224 Three million years of monsoon variability over the northern Sahara. *Clim. Dyn.*
1225 21, 689–698. <https://doi.org/10.1007/s00382-003-0355-z>

1226 Lee-Thorp, J.A., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M.,
1227 2012. Isotopic evidence for an early shift to C₄ resources by Pliocene hominins in
1228 Chad. *Proc. Natl. Acad. Sci. U. S. A.* 109, 20369–20372.
1229 <https://doi.org/10.1073/pnas.1204209109>

1230 Lee-Thorp, J.A., Sponheimer, M., 2005. Opportunities and constraints for
1231 reconstructing palaeoenvironments from stable light isotope ratios in fossils. *Geol.*
1232 *Q.* 49, 195–203.

1233 Lee-Thorp, J.A., Sponheimer, M., Luyt, J., 2007. Tracking changing environments
1234 using stable carbon isotopes in fossil tooth enamel: an example from the South
1235 African hominin sites. *J. Hum. Evol.* 53, 595–601.
1236 <https://doi.org/10.1016/j.jhevol.2006.11.020>

1237 Lee-Thorp, J.A., Sponheimer, M., Passey, B.H., De Ruiter, D.J., Cerling, T.E., 2010.
1238 Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift
1239 in the Pliocene. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3389–3396.
1240 <https://doi.org/10.1098/rstb.2010.0059>

1241 Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1989. Isotopic evidence for dietary
1242 differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.*
1243 18, 183–189. [https://doi.org/10.1016/0047-2484\(89\)90048-1](https://doi.org/10.1016/0047-2484(89)90048-1)

1244 Lefèvre, D., El Graoui, M., Geraads, D., Rué, M., Mohib, A., Raynal, J.-P., 2021. Casablanca
1245 plio-pleistocene palaeoshorelines, chronostratigraphic and palaeogeographic framework

1246 for the ancient prehistory of the Atlantic Morocco. Les paléolittoraux plio-pléistocènes
1247 de Casablanca, cadre chronostratigraphique et paléogéographique de la Préhistoire
1248 ancienne du Maroc atlantique. Bull. d'Archéologie Marocaine, 26, 39-70.

1249 Lefèvre, D., Raynal, J.P., 2002. The plio-pleistocene formations of Casablanca and the
1250 marine quaternary chronostratigraphy of Morocco revisited. Quaternaire 13, 9–21.
1251 <https://doi.org/10.3406/quate.2002.1700>

1252 Lehmann, S.B., Braun, D.R., Dennis, K.J., Patterson, D.B., Stynder, D.D., Bishop, L.C.,
1253 Forrest, F., Levin, N.E., 2016. Stable isotopic composition of fossil mammal teeth
1254 and environmental change in southwestern South Africa during the Pliocene and
1255 Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 457, 396–408.
1256 <https://doi.org/10.1016/j.palaeo.2016.04.042>

1257 Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable
1258 isotope aridity index for terrestrial environments. Proc. Natl. Acad. Sci. 103,
1259 11201–11205. <https://doi.org/10.1073/pnas.0604719103>

1260 Levin, N.E., Simpson, S.W., Quade, J., Cerling, T.E., Frost, S.R., 2008. Herbivore
1261 enamel carbon isotopic composition and the environmental context of *Ardipithecus*
1262 at Gona, Ethiopia. Spec. Pap. Geol. Soc. Am. 446, 215–235.
1263 [https://doi.org/10.1130/2008.2446\(10\)](https://doi.org/10.1130/2008.2446(10))

1264 Lüdecke, T., Leichliter, J.N., Aldeias, V., Bamford, M.K., Biro, D., Braun, D.R.,
1265 Capelli, C., Cybulski, J.D., Duprey, N.N., Silva, M.J.F. da, Foreman, A.D.,
1266 Habermann, J.M., Haug, G.H., Martínez, F.I., Mathe, J., Mulch, A., Sigman, D.M.,
1267 Vonhof, H., Bobe, R., Carvalho, S., Martínez-García, A., 2022. Carbon, nitrogen,
1268 and oxygen stable isotopes in modern tooth enamel: A case study from Gorongosa
1269 National Park, central Mozambique. Front. Ecol. Evol. 1–26. Lüdecke, T., Kullmer,
1270 O., Wacker, U., Sandrock, O., Fiebig, J., Schrenk, F., Mulch, A., 2018. Dietary

1271 versatility of Early Pleistocene hominins. Proc. Natl. Acad. Sci. U. S. A. 115,
1272 13330–13335. <https://doi.org/10.1073/pnas.1809439115>

1273 Lüdecke, T., Schrenk, F., Thiemeyer, H., Kullmer, O., Bromage, T.G., Sandrock, O.,
1274 Fiebig, J., Mulch, A., 2016. Persistent C₃ vegetation accompanied Plio-Pleistocene
1275 hominin evolution in the Malawi Rift (Chiwondo Beds, Malawi). J. Hum. Evol. 90,
1276 163–175. <https://doi.org/10.1016/j.jhevol.2015.10.014>

1277 Luyt, J., Lee-Thorp, J.A., Avery, G., 2000. New light on Middle Pleistocene west coast
1278 environments from Elandsfontein, Western Cape Province, South Africa. S. Afr. J.
1279 Sci. 96, 399–402.

1280 MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient Diets, Ecology, and
1281 Extinction of 5-Million-Year-Old Horses from Florida. Science (80-.). 283, 834.
1282 [https://doi.org/10.1016/s0016-0032\(26\)90726-6](https://doi.org/10.1016/s0016-0032(26)90726-6)

1283 Madurell-Malapeira, J., Rodríguez-Hidalgo, A., Aouraghe, H., Haddoumi, H., Lucenti,
1284 S.B., Oujaa, A., Saladié, P., Bengamra, S., Marín, J., Souhir, M., Farkouch, M.,
1285 Mhamdi, H., Aissa, A.M., Werdelin, L., Chacón, M.G., Sala-Ramos, R., 2021.
1286 First small-sized *Dinofelis*: Evidence from the Plio-Pleistocene of North Africa.
1287 Quat. Sci. Rev. 265. <https://doi.org/10.1016/j.quascirev.2021.107028>

1288 Mallon, D.P., Kingswood, S.C., 2001. Antelopes: North Africa, the Middle East, and
1289 Asia. International Union for the Conservation of Nature and Natural Resources
1290 (IUCN), Gland.

1291 Manthi, F.K., Cerling, T.E., Chritz, K.L., Blumenthal, S.A., 2020. Diets of mammalian
1292 fossil fauna from Kanapoi, northwestern Kenya. J. Hum. Evol. 140, 1–8.
1293 <https://doi.org/10.1016/j.jhevol.2017.05.005>

1294 Mercader, J., Akuku, P., Boivin, N., Bugumba, R., Bushozi, P., Camacho, A., Carter,
1295 T., Clarke, S., Cueva-Temprana, A., Durkin, P., Favreau, J., Fella, K., Haberle, S.,

1296 Hubbard, S., Inwood, J., Itambu, M., Koromo, S., Lee, P., Mohammed, A.,
1297 Mwambwiga, A., Olesilau, L., Patalano, R., Roberts, P., Rule, S., Saladié, P.,
1298 Siljedal, G., Soto, M., Umbsaar, J., Petraglia, M., 2021. Earliest Olduvai hominins
1299 exploited unstable environments ~ 2 million years ago. *Nat. Commun.* 1–15.
1300 <https://doi.org/10.1038/s41467-020-20176-2>

1301 Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary change
1302 and evolution of horses in North America. *Science* (80-.). 331, 1178–1181.
1303 <https://doi.org/10.1126/science.1196166>

1304 Mohib, A., Raynal, J.-P, Gallotti, R., Daujeard, C., Graoui, M. El, Fernandes, P.,
1305 Geraads, D., Magoga, L., Rué, M., Sbihi-Alaoui, F.Z., Lefèvre, D., 2019. Forty
1306 years of research at Casablanca (Morocco): New insights in the Early/Middle
1307 Pleistocene archaeology and geology. *Hespéris-Tamuda LIV*, 25–56.

1308 Mourer-Chauviré, C., Geraads, D., 2010. The upper Pliocene avifauna of Ahl al
1309 Oughlam, Morocco. *Systematics and biogeography. Rec. Aust. Museum* 62, 157–
1310 184. <https://doi.org/10.3853/j.0067-1975.62.2010.1538>

1311 Mourer-Chauviré, C., Geraads, D., 2008. The Struthionidae and Pelagornithidae (Aves:
1312 Struthioniformes, Odontopterygiformes) from the late Pliocene of Ahl al Oughlam,
1313 Morocco. *Oryctos* 7, 169–194.

1314 Nicholson, M.J., 1985. The water requirements of livestock in Africa. *Outlook Agric.*
1315 14, 156–164. <https://doi.org/10.1177/003072708501400401>

1316 Parés, J.M, Haddoumi,
1317 H., Duval, M., Aouraghe, H., Álvarez-Posada, C., Pla-Pueyo, S., Benito-Calvo, A.,
1318 Rodríguez-Hidalgo, A., Van der Made, J., Piñero, P., Agustí, J., Oujaa, A., Grün,
1319 R., Chacón, M.G, Sala-Ramos, R., 2023. First magnetostratigraphic results in the
1320 Aïn Beni Mathar-Guefaït Basin, Northern High Plateaus (Morocco): the Pliocene-
Pleistocene Dhar Iroumyane composite section. *Geobios* 76, 17–36.

1321 <https://doi.org/10.1016/j.geobios.2023.01.004>

1322 Parés, J.M., Sahnouni, M., Van der Made, J., Pérez-González, A., Harichane, Z.,
1323 Derradji, A., Medig, M., 2014. Early human settlements in Northern Africa:
1324 paleomagnetic evidence from the Aïn Hanech Formation (northeastern Algeria).
1325 Quat. Sci. Rev. 99, 203–209. <https://doi.org/10.1016/j.quascirev.2014.06.020>

1326 Passey, B.H., Cerling, T.E., Schuster, G.T., Robinson, T.F., Roeder, B.L., Krueger,
1327 S.K., 2005. Inverse methods for estimating primary input signals from time-
1328 averaged isotope profiles. Geochim. Cosmochim. Acta 69, 4101–4116.
1329 <https://doi.org/10.1016/j.gca.2004.12.002>

1330 Piñero, P., Agustí, J., Haddoumi, H., El Hammouti, K., Chacón, M.G., Sala-Ramos, R.,
1331 2019. *Golunda aouraghei*, sp. nov., the last representative of the genus *Golunda* in
1332 Africa. J. Vertebr. Paleontol. 39, 1–6.
1333 <https://doi.org/https://doi.org/10.1080/02724634.2020.1742726>

1334 Polissar, P.J., Rose, C., Uno, K.T., Phelps, S.R., DeMenocal, P., 2019. Synchronous rise
1335 of African C₄ ecosystems 10 million years ago in the absence of aridification. Nat.
1336 Geosci. 12, 657–660. <https://doi.org/10.1038/s41561-019-0399-2>

1337 Ramírez-Pedraza, I., Martínez, L.M., Aouraghe, H., Rivals, F., Tornero, C., Haddoumi,
1338 H., Estebanz-Sánchez, F., Rodríguez-Hidalgo, A., Van der Made, J., Oujaa, A.,
1339 Ibáñez, J.J., Mhamdi, H., Souhir, M., Aissa, A.M., Chacón, M.G., Sala-Ramos, R.,
1340 2023. Multiproxy approach to reconstruct fossil primate feeding behavior: Case
1341 study for macaque from the Plio-Pleistocene site Guefaït-4.2 (eastern Morocco).
1342 Front. Ecol. Evol. 2. <https://doi.org/10.3389/fevo.2023.1011208>

1343 Rannikko, J., 2019. Adaptations of the Turkana Basin pigs (Suidae) to changing
1344 environments in the Plio-Pleistocene: tooth wear, diets and habitats, Thesis.
1345 Helsinki.

- 1346 Raynal J.-P., 2021. Lettre de Casablanca où fut trouvé *Homo darelbeidae*. A letter from
1347 Casablanca where *Homo darelbeidae* was found. Bull. d'Archéologie Marocaine 26,
1348 9-38.
- 1349 Raynal, J.-P., Gallotti, R., Mohib, A., Fernandes, P., Lefèvre, D., 2017. The western
1350 quest, First and Second Regional Acheuleans at Thomas-Oulad Hamida Quarries
1351 (Casablanca, Morocco), in: Wojtczak, D., Al Najjar, M., Jagher, R., Elsuede, H.,
1352 Wegmüller, F., Otte, M., (Eds.), Vocation préhistoire, Hommage à Jean-Marie Le
1353 Tensorer. ERAUL 148, Liège, pp. 309–322.
- 1354 Raynal, J.-P., Geraads, D., Magoga, L., Hajraoui, A. El, Teixer, J.P., Lefèvre, D., Sbihi-
1355 Alaoui, F.Z., 1993. La grotte des Rhinocéros (Carrière Oulad Hamida 1,
1356 anciennement Thomas III, Casablanca), nouveau site acheuléen du Maroc
1357 atlantique. Comptes Rendus de l'Académie des Sci. 316, 1477–1483.
- 1358 Raynal, J.-P., Lefèvre, D., Gallotti, R., Geraads, D., Daujeard, C., Hublin, J.-J., Graoui,
1359 M. El, Fernandes, P., Rué, M., Magoga, L., Queffelec, A., Degeai, J.-P., Muttoni,
1360 G., Perini, S., Sbihi-Alaoui, F.Z., Mohib, A., 2022a. Thomas Quarry I, Morocco,
1361 in: Beyin, E.A., Wright, D.K., Wilkins, J., Olszewski, D.I. (Eds.), Handbook of
1362 Pleistocene Archaeology of Africa. Springer Nature, Cham, Switzerland, pp.
- 1363 Raynal, J.-P., Mohib, A., Gallotti, R., El Graoui, M., Rué, M., Geraads, D., Daujeard,
1364 C., Falguères, C., Hublin, J.-J., Magoga, L., Fernandes, P., Queffelec, A.,
1365 Delvigne, V., Sbihi-Alaoui, F.Z., Lefèvre, D., 2022b. Grotte des Rhinocéros at
1366 Oulad Hamida Quarry 1, Morocco, in: Beyin, A., Wright, D.K., Wilkins, J.,
1367 Olszewski, D. (Eds.), Handbook of Pleistocene Archaeology of Africa. Springer
1368 Nature, Cham, Switzerland, pp.
- 1369 Raynal J.-P., Mohib A., 2016. Préhistoire de Casablanca. 1 – La Grotte des Rhinocéros
1370 (fouilles 1991 et 1996). Villes et Sites archéologiques du Maroc, volume 6, Ministère

- 1371 de la Culture, INSAP, Rabat.
- 1372 Raynal, J.-P., Teixer, J.P., 1989. Découverte d' Acheuléen ancien dans la carrière
1373 Thomas I à Casablanca et problème de l' ancienneté de la présence humaine au
1374 Maroc. Comptes Rendus de l'Académie des Sci. 308, 1743–1749.
- 1375 Raynal, J.-P., Texier J.-P., Geraads D. & Sbihi-Alaoui F.-Z., 1990. Un nouveau gisement
1376 paléontologique plio-pléistocène en Afrique du Nord: Ahl Al Oughlam (ancienne
1377 carrière Deprez) à Casablanca (Maroc). Comptes Rendus de l'Académie des Sci.
1378 310, 315-320.
- 1379 Raynal, J.-P., Sbihi-Alaoui, F.Z., Mohib, A., El Graoui, M., Lefèvre, D., Texier, J.P.,
1380 Geraads, D., Hublin, J.J., Smith, T., Tafforeau, P., Zouak, M., Grün, R., Rhodes,
1381 E.J., Eggins, S., Daujeard, C., Fernandes, P., Gallotti, R., Hossini, S., Queffelec,
1382 A., 2010. Hominid Cave at Thomas Quarry I (Casablanca, Morocco): Recent
1383 findings and their context. *Quat. Int.* 223–224, 369–382.
1384 <https://doi.org/10.1016/j.quaint.2010.03.011>
- 1385 Raynal, J.-P., Sbihi-Alaoui, F.Z., Geraads, D., Magoga, L., Mohib, A., 2001. The
1386 earliest occupation of North-Africa: the Moroccan perspective, *Quat. Int.* 75, 65-75.
- 1387 Raynal, J.-P., Sbihi Alaoui, F.Z., Magoga, L., Mohib, A., Zouak, M., 2002. Casablanca
1388 and the earliest occupation of North Atlantic Morocco. *Quaternaire* 13, 65–77.
1389 <https://doi.org/10.3406/quate.2002.1704>
- 1390 Raynal, J.-P., Teixer, J.P., Geraads, D., Sbihi-Alaoui, F.Z., 1990. Un nouveau gisement
1391 paléontologique plio-pléistocène en Afrique du Nord: Ahl al Oughlam (ancienne
1392 carrière Deprez) à Casablanca (Maroc). Comptes Rendus l'Académie des Sci. 310,
1393 315–320.
- 1394 Rensberger, J.M., 1978. Scanning electron microscopy of wear and occlusal events in
1395 some small herbivores, in: Butler, P.M., Joysey, K.A., (Eds.), *Development,*

1396 Function and Evolution of Teeth. Academic, New York, pp. 415–438

1397 Rhodes, E.J., Singarayer, J.S., Raynal, J.-P., Westaway, K.E., Sbihi-Alaoui, F.Z., 2006.

1398 New age estimates for the Palaeolithic assemblages and Pleistocene succession of

1399 Casablanca, Morocco. *Quat. Sci. Rev.* 25, 2569–2585.

1400 <https://doi.org/10.1016/j.quascirev.2005.09.010>

1401 Rivals, F., Mithlacher, M.C., Solounias, N., 2007. Effect of ontogenetic-age

1402 distribution in fossil and modern samples on the interpretation of ungulate

1403 paleodiets using the mesowear method. *J. Vertebr. Paleontol.* 27, 763–767.

1404 [https://doi.org/10.1671/0272-4634\(2007\)27](https://doi.org/10.1671/0272-4634(2007)27)

1405 Rivals, F., Semprebon, G.M., 2011. Dietary plasticity in ungulates: Insight from tooth

1406 microwear analysis. *Quat. Int.* 245, 279–284.

1407 <https://doi.org/10.1016/j.quaint.2010.08.001>

1408 Robinson, J.R., Rowan, J., Barr, W.A., Sponheimer, M., 2021. Intrataxonomic trends in

1409 herbivore enamel $\delta^{13}\text{C}$ are decoupled from ecosystem woody cover. *Nat. Ecol.*

1410 *Evol.* <https://doi.org/10.1038/s41559-021-01455-7>

1411 Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late

1412 Pliocene environmental change during the transition from *Australopithecus* to

1413 *Homo*. *Nat. Ecol. Evol.* 1, 1–7. <https://doi.org/10.1038/s41559-017-0159>

1414 Roberts, P., Stewart, M., Alagaili, A.N., Breeze, P., Candy, I., Drake, N., Groucutt,

1415 H.S., Scerri, E.M.L., Lee-Thorp, J., Louys, J., Zalmout, I.S., Al-Mufarreah, Y.S.A.,

1416 Zech, J., Alsharekh, A.M., al Omari, A., Boivin, N., Petraglia, M., 2018. Fossil

1417 herbivore stable isotopes reveal middle Pleistocene hominin palaeoenvironment in

1418 ‘Green Arabia.’ *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-018-0698-9>

1419 Sahnouni, M., Everet, M., Van der Made, J., Harichane, Z., 2017. Mise en évidence

1420 d’un changement climatique dans le site pléistocène inférieur d’El Kherba

1421 (Algérie), et son possible impact sur les activités des hominidés, il y a 1,7 Ma. L'

1422 Anthropol. 121, 146–162. <https://doi.org/10.1016/j.anthro.2017.03.015>

1423 Sahnouni, M., Hadjouis, D., Van der Made, J., Derradji, A. el K., Canals, A., Medig,
1424 M., Belahrech, H., Harichane, Z., Rabhi, M., 2002. Further research at the
1425 Oldowan site of Aïn Hanech, North-eastern Algeria. J. Hum. Evol. 43, 925–937.
1426 <https://doi.org/10.1006/jhev.2002.0608>

1427 Sahnouni, M., Parés, J.M., Duval, M., Cáceres, I., Harichane, Z., Made, Van der Made,
1428 J., Pérez-González, A., Abdessadok, S., Kandi, N., Derradji, A. el K, Medig, M.,
1429 Boulaghraif, K., Semaw, S., 2018. 1.9-million- and 2.4-million-year-old artifacts
1430 and stone tool–cutmarked bones from Aïn Boucherit, Algeria. Science (80-.).
1431 0008, 1–10.

1432 Sahnouni, M., Rosell, J., Van der Made, J., Vergès, J.M., Ollé, A., Kandi, N.,
1433 Harichane, Z., Derradji, A., Medig, M., 2012. The first evidence of cut marks and
1434 usewear traces from the Plio-Pleistocene locality of El-Kherba (Aïn Hanech),
1435 Algeria: Implications for early hominin subsistence activities circa 1.8 Ma. J. Hum.
1436 Evol. 64, 137–150. <https://doi.org/10.1016/j.jhevol.2012.10.007>

1437 Sahnouni, M., Van der Made, J., 2009. The Oldowan in North Africa within a
1438 biochronological framework, in: Schick, K., Toth, N. (Eds.), The Cutting Edge:
1439 New Approaches to the Archaeology of Human Origins. Stone Age Institute Press,
1440 Gosport, pp. 180–210.

1441 Sahnouni, M., Van der Made, J., Everett, M., 2011. Ecological background to Plio-
1442 Pleistocene hominin occupation in North Africa: The vertebrate faunas from Aïn
1443 Boucherit, Aïn Hanech and El-Kherba, and paleosol stable-carbon-isotope studies
1444 from El-Kherba, Algeria. Quat. Sci. Rev. 30, 1303–1317.
1445 <https://doi.org/10.1016/j.quascirev.2010.01.002>

1446 Sala-Ramos, R., Aouraghe, H., Chacón, M.G., Agustí, J., Álvarez-Posada, C., Arnold,
1447 L., 2017. Guéfait 4: un nouveau site paléontologique dans un environnement
1448 humide et ouvert au Maroc Oriental, in: 9ème Rencontre Des Quaternaristes
1449 Marocains (RQM9), Faculté Polydisciplinaire de Safi, Morocco. 15th-17th
1450 November 2017. Book of Abstracts. Safi, p. 48.

1451 Sala-Ramos, R., Aouraghe, H., Haddoumi, H., Morales, J., Rodríguez-Hidalgo, A.,
1452 Tornero, C., Oujaa, A., Soto, M., Farkouch, M., Aissa, E.M., Atmani, A. El, Duval,
1453 M., Lee, A., Demuro, M., Blain, H.-A., Piñero, P., Rivals, F., Burjachs, F., Tarrío,
1454 A., Álvarez-Posada, C., Souhir, M., Saladié, P., Pla-Pueyo, S., Larrasoña, J.C.,
1455 Mischke, S., Marín, J., Moreno-Ribas, E., Hermida, A.D.L., Bartrolí, R., Lombao,
1456 D., García-Argudo, G., Ramírez-Pedraza, I., Díez-Canseco, C., Tomasso, S.,
1457 Expósito, I., Allué, E., Hajji, N., Mhamdi, H., Rhosne, H., Carrancho, Á., Villalaín,
1458 J.J., Van der Made, J., Canals, A., Benito-Calvo, A., Agustí, J., Parés, J.M.,
1459 Chacón, M.G., 2022. Pleistocene and Holocene peopling of Jerada province,
1460 eastern Morocco: introducing a research project. Le peuplement humain pendant le
1461 Pléistocène et l'Holocène dans la province de Jerada, Maroc oriental: introduction
1462 d'un projet de recherche. Bull. d'Archéologie Marocaine 27, 27–40.

1463 Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2016. Tale of two timescales:
1464 Combining tooth wear methods with different temporal resolutions to detect
1465 seasonality of Palaeolithic hominin occupational patterns. J. Archaeol. Sci. Reports
1466 6, 790–797. <https://doi.org/10.1016/j.jasrep.2015.09.011>

1467 Schmid, R., Wilson, D.E., Reeder, D.M., 2005. Mammal species of the world: A
1468 taxonomic and geographic reference (3rd ed.). Johns Hopkins University Press,
1469 Baltimore. <https://doi.org/10.2307/1223169>

1470 Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence

1471 for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa.
1472 Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 301–319.
1473 <https://doi.org/10.1016/j.palaeo.2006.04.004>
1474 Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F.,
1475 Walker, A., 2006. Dental microwear texture analysis: technical considerations. J.
1476 Hum. Evol. 51, 339–349. <https://doi.org/10.1016/j.jhevol.2006.04.006>
1477 Ségalen, L., Lee-Thorp, J.A., Cerling, T., 2007. Timing of C₄ grass expansion across
1478 sub-Saharan Africa. J. Hum. Evol. 53, 549–559.
1479 <https://doi.org/10.1016/j.jhevol.2006.12.010>
1480 Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L.,
1481 2004. Can low-magnification stereomicroscopy reveal diet? J. Hum. Evol. 47,
1482 115–144. <https://doi.org/10.1016/j.jhevol.2004.06.004>
1483 Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past?
1484 An assessment of the dietary adaptations of Miocene to Recent Antilocapridae
1485 (Mammalia: Artiodactyla). Palaeogeogr. Palaeoclimatol. Palaeoecol. 253, 332–
1486 347. <https://doi.org/10.1016/j.palaeo.2007.06.006>
1487 Sen, S., Geraads, D., 2023. Lagomorpha (Mammalia) from the Pliocene- Pleistocene
1488 locality of Ahl al Oughlam, Morocco. Palaeobiodiversity and Palaeoenvironments.
1489 <https://doi.org/10.1007/s12549-022-00569-5>
1490 Sewell, L., Merceron, G., Hopley, P.J., Zipfel, B., Reynolds, S.C., 2019. Using
1491 springbok (*Antidorcas*) dietary proxies to reconstruct inferred palaeovegetational
1492 changes over 2 million years in Southern Africa. J. Archaeol. Sci. Reports 23,
1493 1014–1028. <https://doi.org/10.1016/j.jasrep.2018.02.009>
1494 Solounias, N., Semprebon, G.M., 2002. Advances in the Reconstruction of Ungulate
1495 Ecomorphology with Application to Early Fossil Equids. Am. Museum Novit.

1496 3366, 1–49. <https://doi.org/10.1206/0003->
1497 0082(2002)366<0001:AITROU>2.0.CO;2

1498 Souron, A., 2017. Diet and ecology of extant and fossil wild pigs, in: Melletti, M.,
1499 Meijaard, E. (Eds.), *Ecology, Conservation and Management of Wild Pigs and*
1500 *Peccaries*. Cambridge University Press, pp. 29–38.
1501 <https://doi.org/10.1017/9781316941232.005>

1502 Sponheimer, M., Lee-Thorp, J.A., 2009. Biogeochemical Evidence for the
1503 Environments of Early Homo in South Africa, in: Grine, F.E., Fleagle, J.G.,
1504 Leakey, R.E. (Eds.), *The First Humans: A Summary Perspective on the Origin and*
1505 *Early Evolution of the Genus Homo*. *Vertebrate Paleobiology and*
1506 *Paleoanthropology*. Springer, pp. 197–207. <https://doi.org/10.1007/978-1-4020->
1507 9980-9_17

1508 Sponheimer, M., Lee-Thorp, J.A., 2003. Using carbon isotope data of fossil bovid
1509 communities for palaeoenvironmental reconstruction. *S. Afr. J. Sci.* 99, 273–275.

1510 Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., Van Der Merwe, N.J.,
1511 Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C., Marcus,
1512 W., 2003. Diets of southern African Bovidae: Stable isotope evidence. *J. Mammal.*
1513 84, 471–479. <https://doi.org/10.1644/1545->
1514 1542(2003)084<0471:DOSABS>2.0.CO;2

1515 Sponheimer, M., Reed, K.E., Lee-Thorp, J.A., 1999. Combining isotopic and
1516 ecomorphological data to refine bovid paleodietary reconstruction: A case study
1517 from the Makapansgat Limeworks hominin locality. *J. Hum. Evol.* 36, 705–718.
1518 <https://doi.org/10.1006/jhev.1999.0300>

1519 Stearns, C.E., 1978. Pliocene-Pleistocene emergence of the Moroccan Meseta. *Geol.*
1520 *Soc. Am. Bull.*, 89, 1630-1644.

1521 Strömberg, C.A.E., 2011. Evolution of grasses and grassland ecosystems. *Annu. Rev.*
1522 *Earth Planet. Sci.* 39, 517–544. <https://doi.org/10.1146/annurev-earth-040809->
1523 152402

1524 Szabó, P., Kovács, J., Kocsis, L., Vennemann, T., Domingo, L., Újvári, G., Halmai, Á.,
1525 Pirkhoffer, E., Codrea, V., 2022. Pliocene - Early Pleistocene continental climate
1526 and vegetation in Europe based on stable isotope compositions of mammal tooth
1527 enamel. *Quat. Sci. Rev.* 288, 107572.
1528 <https://doi.org/10.1016/j.quascirev.2022.107572>

1529 Thomas, P., 1886. Notes additionnelles sur les vertébrés fossiles de la province de
1530 Constantine. *Bull. Soc. géol. Fr* 15, 139–143.

1531 Thomas, P., 1884. Recherches stratigraphiques et paléontologiques sur quelques
1532 formations d'eau douce de l'Algérie. *Mém. Soc. géol. Fr., Paléontol* 3,1–57.

1533 Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., Troughton, J.H., 1979. The distribution
1534 of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and
1535 moisture gradient in Kenya. *Oecologia* 37, 337–350.

1536 Tipple, B.J., Meyers, S.R., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO₂: A
1537 comparative evaluation of available geochemical proxies. *Paleoceanography* 25, 1–
1538 11. <https://doi.org/10.1029/2009pa001851>

1539 Tornero, C., Bălăşescu, A., Ughetto-Monfrin, J., Voinea, V., Balasse, M., 2013.
1540 Seasonality and season of birth in early Eneolithic sheep from Cheia (Romania):
1541 Methodological advances and implications for animal economy. *J. Archaeol. Sci.*
1542 40, 4039–4055. <https://doi.org/10.1016/j.jas.2013.05.013>

1543 Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A., 2003. Quantification of dental
1544 microwear by tandem scanning confocal microscopy and scale-sensitive fractal
1545 analyses. *Scanning* 25, 185–193. <https://doi.org/10.1002/sca.4950250405>

1546 Uno, K.T., Rivals, F., Bibi, F., Pante, M., Njau, J., de la Torre, I., 2018. Large mammal
1547 diets and paleoecology across the Oldowan–Acheulean transition at Olduvai
1548 Gorge, Tanzania from stable isotope and tooth wear analyses. *J. Hum. Evol.* 120,
1549 76–91. <https://doi.org/10.1016/j.jhevol.2018.01.002>

1550 Van der Made, J., Boulaghraief, K., Chelli-Cheheb, R., Cáceres, I., Harichane, Z.,
1551 Sahnouni, M., 2022. The last North African hipparions – hipparion decline and
1552 extinction follows a common pattern. *Neues Jahrb. für Geol. und Paläontologie -*
1553 *Abhandlungen* 303, 39–88. <https://doi.org/10.1127/njgpa/2022/1037>

1554 Van der Made, J., Boulaghraief, K., Chelli Cheheb, R., Parés, J.M., Cáceres, I., Semaw,
1555 S., Sahnouni, M., 2021. The North African earliest Pleistocene faunal sequence:
1556 from biostratigraphy to biochronology. *Mémoire du Serv. Géologique l'Algérie* 9,
1557 73–90.

1558 Van Zinderen Barker, E., 1962. A Late-Glacial and Post-Glacial Climatic Correlation
1559 between East Africa and Europe. *Nature* 194, 201–203.

1560 Vrba, E.S., 1984. Evolutionary Pattern and Process in the Sister-Group Alcelaphini-
1561 Aepycerotini (Mammalia: Bovidae), in: Eldredge, N., Stanley, S.M. (Eds.), *Living*
1562 *Fossils*. Springer, New York, pp. 62–79. [https://doi.org/10.1007/978-1-4613-8271-](https://doi.org/10.1007/978-1-4613-8271-3_7)
1563 [3_7](https://doi.org/10.1007/978-1-4613-8271-3_7)

1564 Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an
1565 indicator of diet. *Science* (80-.). 201, 908–910.
1566 <https://doi.org/10.1126/science.684415>

1567 Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis:
1568 implications for paleodiet reconstruction from stable isotopes. *Palaeogeogr.*
1569 *Palaeoclimatol. Palaeoecol.* 107, 281–289. [https://doi.org/10.1016/0031-](https://doi.org/10.1016/0031-0182(94)90100-7)
1570 [0182\(94\)90100-7](https://doi.org/10.1016/0031-0182(94)90100-7)

1571 White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., Degusta, D., Bernor, R.L., Boisserie,
1572 J.R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, L.X., Haile-
1573 Selassie, Y., Clark Howell, F., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H.,
1574 Semprebon, G., Teaford, M., Vrba, E., 2009. Macrovertebrate paleontology and
1575 the Pliocene habitat of *Ardipithecus ramidus*. *Science* (80-.). 326, 87–93.
1576 <https://doi.org/10.1126/science.1175822>

1577 Wynn, J.G., Reed, K.E., Sponheimer, M., Kimbel, W.H., Alemseged, Z., Bedaso, Z.K.,
1578 Campisano, C.J., 2016. Dietary flexibility of *Australopithecus afarensis* in the face
1579 of paleoecological change during the middle Pliocene: Faunal evidence from
1580 Hadar, Ethiopia. *J. Hum. Evol.* 99, 93–106.
1581 <https://doi.org/10.1016/j.jhevol.2016.08.002>

1582 Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study
1583 of the utility of premolar/non-carnassial teeth in the microwear analysis of
1584 mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
1585 <https://doi.org/10.1016/j.palaeo.2017.09.003>

1586 Young, H.J., Young, T.P., 1983. Local distribution of C₃ and C₄ grasses in sites of
1587 overlap on Mount Kenya. *Oecologia* 58, 373–377.

1588 Zazzo, A., Bocherens, H., Brunet, M., Beauvilain, A., Billiou, D., Mackaye, H.T.,
1589 Vignaud, P., Mariotti, A., 2000. Herbivore paleodiet and paleoenvironmental
1590 changes in Chad during the Pliocene using stable isotope ratios of tooth enamel
1591 carbonate. *Paleobiology* 26, 294–309. [https://doi.org/10.1666/0094-](https://doi.org/10.1666/0094-8373(2000)026<0294:hpapci>2.0.co;2)
1592 [8373\(2000\)026<0294:hpapci>2.0.co;2](https://doi.org/10.1666/0094-8373(2000)026<0294:hpapci>2.0.co;2)

1593 Zouhri, S., Benammi, M., Geraads, D., El Boughabi, S., 2017. Mammifères du Néogène
1594 continental du Maroc: Faunes, biochronologie et paléobiogéographie. *Mém. Soc.*
1595 *géol. Fr., Paléontol*180, 527–588.

1596

1597