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1       **Geochemical investigation of the taphonomy, stratigraphy, and palaeoecology of the**  
2       **mammals from the Ouled Abdoun Basin (Paleocene-Eocene of Morocco)**

3  
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19  
20      **ABSTRACT**

21      We performed different geochemical analyses of Paleogene terrestrial mammal remains  
22      to establish their taphonomy, stratigraphic provenance, and palaeoenvironmental  
23      conditions. Rare earth element (REE) results indicate a similar diagenetic history to that of  
24      previously investigated marine taxa from these beds. Therefore, the mammal remains were  
25      initially deposited in a marine setting, and probably not long after the death of the animals  
26      their bodies were washed into the sea. The Ce/Ce\* and Pr/Pr\* ratios for the mammal fossils  
27      were compared with the background dataset from the phosphate mines, which varies with  
28      time. This allowed us to characterize the stratigraphic levels bearing the fossils. The  
29      provenances of fossils with known origins were confirmed, while remains with unknown  
30      origins could be assigned to certain stratigraphic horizons that are compatible with  
31      previously proposed phylogenetic relationships.

32 Marine diagenesis affected the various skeletal tissues differently, with the largest  
33 alteration in the bone and the least or none in the enamel. This is mostly demonstrated by  
34 the high F concentration, high Ca/P, and seawater related  $^{87}\text{Sr}/^{86}\text{Sr}$  in the bone/dentine  
35 samples. Enamel shows the opposite, and retained the most pristine terrestrial values. The  
36  $\delta^{18}\text{O}_{\text{PO}_4}$  and  $\delta^{13}\text{C}$  results from mammal enamel revealed warm ( $>20^\circ\text{C}$  mean annual  
37 temperature-MAT) and dry ( $<500\text{mm}$  mean annual precipitation) conditions for Paleocene-  
38 Eocene period in the region. From the early to mid-Ypresian about  $+5^\circ\text{C}$   $\Delta\text{MAT}$  is recorded  
39 that might be linked to the Early Eocene Climatic Optimum.

40 Furthermore, the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios derived from shark tooth enameloid fit the global open  
41 ocean Sr-isotope record during the latest Paleocene and early Eocene providing further  
42 evidence for the age of these phosphate beds in the Ouled Abdoun Basin. However, older  
43 marine fossils yielded higher ratios than the global Sr-isotope curve, reflecting an alteration  
44 and/or somewhat restricted conditions in the Moroccan coastal basins, possibly triggered by  
45 global sea-level changes.

46

47 **Keywords:** bioapatite, rare earth elements, stable isotopes, strontium isotopes,  
48 phosphorite.

49

## 50 **1. Introduction**

51 The phosphate series of the Ouled Abdoun Basin in Morocco, which is exploited in large  
52 industrial quarries, is renowned for its Upper Cretaceous-Lower Eocene vertebrate  
53 assemblages (e.g., [Arambourg, 1952](#); [Bardet et al., 2017](#)). The fauna predominantly  
54 comprises sub-autochthonous marine aquatic organisms such as cartilaginous and bony  
55 fishes, mosasaurs, and turtles, but occasionally terrestrial remains have also been described,  
56 such as non-avian dinosaurs, birds, and mammals (e.g., [Gheerbrant et al., 2003](#); [Pereda  
57 Suberbiola et al., 2004](#); [Bourdon et al., 2005](#)). The mammals are rare and most of the time  
58 scientists come to know about them from private collectors living near the phosphate  
59 quarries, and often cannot determine their precise stratigraphic origin. Knowing the  
60 stratigraphic origins of the Ouled Abdoun fossils is crucial to elucidating the early Cenozoic  
61 evolution of African mammals (e.g., [Gheerbrant et al., 2018](#)). Accurate dating of the Ouled  
62 Abdoun mammals is also important for knowledge and characterization of the early  
63 Cenozoic successive African faunal assemblages.

64 To tackle the stratigraphic origins of vertebrate remains, geochemical taphonomy is a  
65 widely used method (e.g., [Staron et al., 2001](#); [Trueman et al., 2003](#); [Metzger et al., 2004](#);  
66 [MacFadden et al., 2007](#); [Suarez et al., 2010](#); [Herwartz et al., 2013](#); [Botfalvai et al., 2021](#)).  
67 This is based on trace element contents that are absent or occur only in very low  
68 concentrations (sub-ppm) in modern bones and teeth, however, after the death of the  
69 animals their concentrations increase through the influence of the sedimentary  
70 environment (e.g., [Elderfield and Pagett, 1986](#)). The most widely used elements are the rare  
71 earths (REE) and uranium, which can reach 4-5 orders of magnitude enrichment in fossil  
72 material compared to modern concentrations (e.g., [Trueman and Tuross, 2003](#)). These  
73 elements therefore could reflect the chemistry of the pore fluid in which the vertebrate  
74 remains were fossilized. There are several studies using REE chemistry of fossil bioapatite to  
75 reconstruct palaeoenvironmental conditions in terrestrial and marine depositional settings  
76 (e.g., [Trueman et al., 2003](#); [Lécuyer et al. 2004](#); [Shield and Webb, 2004](#); [Kocsis et al., 2009](#);  
77 [Žigaitė et al., 2016](#); [2020](#)), which are all based on the assumption that REEs are  
78 quantitatively taken up from the burial environment (e.g., [Reynard et al., 1999](#)). During their  
79 incorporation into the bioapatite structure, however, fractionation could occur between the  
80 light and heavy REEs due to size differences along the REE series and related diffusion (e.g.,  
81 [Trueman et al., 2011](#); [Herwartz et al., 2013](#)). In addition, protracted late diagenetic  
82 modification ([Kocsis et al., 2010](#); [Herwartz et al., 2011](#)) may further complicate  
83 environmental interpretations, especially for older samples ([Kowal-Linka et al., 2014](#)). To  
84 address these issues, a large number of samples, including different types of materials (e.g.,  
85 bones, teeth, enamel, and dentine), and multiple *in-situ* analyses, are needed to evaluate  
86 further the origin of the REEs within the bioapatite.

87 In relation to the Moroccan phosphate series in the Ouled Abdoun and Ganntour basins,  
88 the trace element chemistry of nearly 200 marine samples (fish teeth, bones, coprolites)  
89 was published in [Kocsis et al. \(2016\)](#). Fractionation and late diagenetic overprint were  
90 completely ruled out. All the samples yielded similar, typical oxic seawater REE distributions  
91 with heavy REE enrichment and a negative Ce-anomaly. Importantly, however, the Ce-  
92 anomalies show a distinct change with stratigraphic level ([Kocsis et al., 2016](#)), a trend that is  
93 used in this work to assign a stratigraphic age for unprovenanced fossils. Such an approach  
94 was successful for the Embrithopoda mammal taxa of *Stylolophus minor* and *S. major* in the  
95 Ouled Abdoun Basin ([Gheerbrant et al., 2018](#)).

96 The main aim of this study is to further investigate the validity of the trace element  
97 provenancing method for the rare mammal fossils with known and unknown origins in the  
98 Ouled Abdoun Basin. To help better assess the taphonomy of these remains, major and  
99 other trace elements, and strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) of selected mammal fossils,  
100 were compared with marine end-members such as data from shark teeth. Enameloid  
101  $^{87}\text{Sr}/^{86}\text{Sr}$  data derived from the latter also provide a proxy for the age of the phosphate  
102 beds, through comparing their ratios with the global  $^{87}\text{Sr}/^{86}\text{Sr}$  record. In addition, some  
103 mammal fossils were measured for their stable oxygen and carbon isotopic compositions to  
104 get an insight into the ecological conditions of some of these early African placental  
105 mammals.

106

## 107 **2. Geological and stratigraphical settings**

108 The Ouled Abdoun Basin is one of the ancient epicontinental marine basins along the  
109 Atlantic coast of Africa, where large amounts of phosphorite accumulated during the late  
110 Cretaceous - early Eocene period. The basement rocks are covered by Cenomanian-Turonian  
111 carbonates followed by yellow marls with possible age within the Coniacian-Campanian  
112 interval ([El Assel et al., 2013](#)), which were eventually succeeded by the phosphorite series.  
113 The top of the succession is either covered by Lutetian dolomitic limestone or by Neogene  
114 continental beds ([OCP, 1989](#)). In the phosphorite series, three sequences (A-C) of 2<sup>nd</sup> order  
115 transgressive-regressive (T-R) cycles ([Vail et al., 1991](#)) are recognized, with ages of  
116 Maastrichtian (latest Cretaceous) (A), Danian-Thantetian (Paleocene) (B), and Ypresian (early  
117 Eocene) (C). These T-R cycles are further divided into 3<sup>rd</sup> order cycles that begin with P-rich  
118 phosphate (often granular in appearance), and end with clayey, carbonate, or siliceous  
119 deposits. The phosphorite series is often followed by a fourth sequence (D) but without  
120 phosphate occurrences ([EL Haddi, 2014](#)), marking the reduction of phosphogenesis and the  
121 installation of silicified limestone with lumachellic texture and the occurrence of Thersitea-  
122 type gastropods ([Mouflih, 2015](#)).

123 Regional correlation and biostratigraphy of these sediments are achieved by examining  
124 selachian remains (i.e., shark and ray teeth), which are extremely abundant (e.g.,  
125 [Arambourg, 1952](#); [Noubhani and Cappetta, 1997](#); [Cappetta et al., 2014](#)), while other, non-  
126 phosphatic fossils are either very poorly preserved or do not have significant stratigraphic  
127 value (e.g., [Ollivier-Pierre, 1982](#); [Rauscher, 1985](#); [Soncini, 1990](#)). Chemostratigraphy based

128 on the  $\delta^{13}\text{C}$  of residual organic matter (Yans et al., 2014) and the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  of marine  
129 vertebrate fossils (Kocsis et al., 2014a), however, revealed some details about the timing of  
130 the Paleogene beds such as (1) sedimentation occurred during the middle Paleocene  
131 (Selandian, 61.5-59.2 Ma); (2) a possible lack of sedimentation during the latest Paleocene  
132 (late Thanetian, ~57-56 Ma), probably including the Paleocene-Eocene Thermal Maximum  
133 (PETM); and (3) the third sequence (C) was deposited during the early Eocene (early - ?late  
134 Ypresian, ~56-51 Ma) including the Early Eocene Climatic Optimum (EECO).

135 Traditionally, the phosphate succession in the Ouled Abdoun Basin is further subdivided  
136 into several phosphate-rich beds of industrial value (from base to top, beds III, II, I, 0) with  
137 the non-exploited horizons of calcareous phosphate, chert, or thin clay between them called  
138 intercalary beds (Figure 1). Bed III refers to the Late Cretaceous layers, Bed IIa and Bed IIb to  
139 the Paleocene beds, while Bed I, Bed 0', Bed 0, and the top layers called "sillons" are early  
140 Eocene, as determined from the associated selachian faunas (Arambourg, 1952; Noubhani  
141 and Cappetta, 1997) (Figure 1). Upsection the proportions of phosphate decrease and chert-  
142 rich sediments occur more often. The successive phosphate beds recurrently enclose "bone  
143 beds" where vertebrate remains are concentrated, probably as a result of hydrodynamic  
144 accumulations and/or during a period of condensation of bioclastic material with a low  
145 sedimentation rate (Gheerbrant et al., 2003). Three of them also yielded unique mammal  
146 remains: (1) the *Eritherium* bone bed at the base of Bed IIa, dated Selandian (61.6 - 59.2  
147 Ma); (2) the big coprolite bone bed in the upper part of Bed IIa, dated Thanetian (59.2-56  
148 Ma); and (3) the earliest Ypresian (~56-55 Ma) *Otodus obliquus* bone bed within intercalary  
149 bed II/I (Figure 1). Mammals also derived from two younger levels (Figure 1) such as (4) the  
150 base of Bed I, dated lower Ypresian (~55-54 Ma); and (5) the upper phosphate horizons, Bed  
151 0 and the "sillons", dated middle Ypresian (~53-51 Ma) (Yans et al., 2014; Kocsis et al.,  
152 2014a).

153 The mammals recovered from these Paleocene and lower Eocene phosphate beds are  
154 the earliest known placentals in Africa, together with those from the Ouarzazate Basin  
155 (Gheerbrant et al., 2017). Despite their rarity, they document an unexpected taxonomic  
156 diversity, especially for paenungulates (Afrotheria), which comprise 7 genera and 10 species  
157 (*Abounodus*, *Ocepeia daouiensis*, *O. grandis*, *Eritherium*, *Phosphatherium*, *Daouitherium*,  
158 *Seggeurius*, Paenungulata indet., *Stylolophus minor*, *S. major*; see Gheerbrant et al., 1998,  
159 2001, 2003, 2009, 2014, 2018; Bardet et al., 2017).

160

### 161 **3. Material and Methods**

#### 162 *3.1. Investigated materials*

163 Several mammal species and/or other fossils from the mammal-related sediment matrix  
164 were involved in our research. Some of the fossils have known stratigraphic positions, while  
165 the origins of the others are questionable or completely unknown (Table 1). We focused  
166 primarily on the trace element compositions of the fossils (Table 1). However, some  
167 specimens were also analyzed for the presence of major elements (Ca, P, F), stable oxygen  
168 and carbon isotopes, and radiogenic strontium isotopes. The latter taxa are *Daouitherium*  
169 *rebouli* (Bed 0), *Phosphatherium escuilliei* (intercalary Bed II/Bed I, and Bed I), Hyracoidea  
170 indet (unknown bed; Gheerbrant et al., 2003), *Ocepeia grandis* (Bed IIa; Gheerbrant et al.,  
171 2014), and *Eritherium azzouzorom* (base of Bed IIa, i.e., *Eritherium* bone bed). These  
172 mammals are mostly known by fragments of jaws and, in the best cases, by a few skulls, and  
173 all of them are early representatives of the African endemic placental ungulates  
174 (Paenungulata). In particular *Eritherium* (Gheerbrant, 2009, Gheerbrant et al., 2012),  
175 *Phosphatherium* (Gheerbrant et al., 2005), and *Daouitherium* (Gheerbrant et al., 2002) are  
176 the earliest and most basal proboscideans. They document the very early emergence in  
177 Africa of one of the most remarkable lineage of extant placentals, the elephant order  
178 (Gheerbrant, 2009).

179 Often different parts have been analyzed and compared in parallel, such as mammal  
180 tooth enamel and dentine, bone, and – from the sediment matrix – shark tooth enameloid,  
181 dentine, and coprolites. More details about the analyses of these are presented in the  
182 Methods section.

183 In addition, the background trace element dataset (Kocsis et al., 2016) is extended here  
184 by samples analyzed from the big coprolite bone bed (upper part of Bed IIa) from quarries of  
185 Sidi Chennane (N32°38'25", W6°43'22") and Sidi Daoui (Meraa El Arech Nord - N32°46'47",  
186 W6°45'4"), while a few specimens from the *Eritherium* and *Otodus obliquus* bone beds were  
187 also added from Sidi Daoui near Meraa El Arech Nord and Boujniba (N32°52'16",  
188 W6°47'13"), respectively (Supplementary Material Table-1).

189

#### 190 *3.2. Major and trace element compositions*

191 All the analyses were carried out at the Institute of Earth Sciences, University of  
192 Lausanne, Switzerland. The mammal remains (teeth and bones) and fossils from the  
193 associated matrix (fish teeth, coprolites) were cut with a micro-saw, then small pieces were  
194 embedded in epoxy resin and flat-polished. The major-element contents of selected fossils  
195 were determined by using wavelength-dispersive analysis with a JEOL 8200 microprobe. The  
196 concentrations of rare earth and other trace elements were measured by Laser Ablation-  
197 Inductively Coupled Plasma-Mass Spectrometry (LA-ICP-MS), using a GeoLas 200M ArF  
198 excimer laser (193nm) coupled to a Perkin-Elmer ELAN 6100 DRC quadrupole spectrometer  
199 or via Element XR ICP-MS with a linked RESOLUTION ablation system. The ablation was carried  
200 out in a He atmosphere using spot sizes of 60-80  $\mu\text{m}$  in diameter. Standard reference  
201 materials 612 from NIST, representing silica-lime-alumina glasses doped with trace  
202 elements, were used for external standardization (Pearce et al., 1997).  $^{42}\text{Ca}$  was analyzed as  
203 an internal standard; CaO values of 54, 51 and 50 wt.% were used respectively for shark  
204 tooth enameloid, mammal enamel, and for more porous material such as dentine, bone and  
205 coprolites. These values are the overall average CaO content of the different remains  
206 derived from the microprobe data presented here (Supplementary Material Table-2) and  
207 provided in Kocsis et al. (2014a). The analytical reproducibility was generally better than  
208  $\pm 5\%$  SE.

209

### 210 3.3. Strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ )

211 The chemical separation of Sr and mass spectrometry were performed at the  
212 Department of Earth Sciences, University of Geneva (Switzerland). Selected fossils were  
213 cleaned in an ultrasonic bath to reduce any sedimentary contamination, then the external  
214 0.5-1 mm surface was removed that might have been altered in the depositional  
215 environment. From the cleaned surface about 2-5 mg of mammal enamel(oid) / dentine /  
216 bone powder was obtained using a micro-drill, and was dissolved in Teflon beakers at 80°C  
217 in 2M HCl. Sr separation was performed by extraction chromatography using Eichrom's Sr-  
218 Spec resin according to a protocol modified from Pin et al. (1994). Strontium was analysed in  
219 2%  $\text{HNO}_3$  solution on a Neptune Plus Multi Collector ICP-MS. Interferences at masses  $^{84}\text{Sr}$   
220 ( $^{84}\text{Kr}$ ),  $^{86}\text{Sr}$  ( $^{86}\text{Kr}$ ) and  $^{87}\text{Sr}$  ( $^{87}\text{Rb}$ ) were corrected by monitoring  $^{83}\text{Kr}$  and  $^{85}\text{Rb}$ . Mass  
221 fractionation was internally corrected assuming a  $^{88}\text{Sr}/^{86}\text{Sr}$  ratio of 8.375209. The values  
222 were internally corrected further for external fractionation based on repeat analyses of the



223 strontium NBS 987 standard (nominal value of 0.710248), which yielded an average  $^{87}\text{Sr}/^{86}\text{Sr}$   
224 value of 0.710270 (10 ppm long-term reproducibility,  $1\sigma$ ).

225

### 226 3.4. Stable isotope analyses ( $\delta^{18}\text{O}_{\text{PO}_4}$ , $\delta^{13}\text{C}$ , $\delta^{18}\text{O}_{\text{CO}_3}$ )

227 The sample preparation and analyses were performed in the Stable Isotope Laboratory  
228 of the Institute of Earth Surface Dynamics at the University of Lausanne, Switzerland.  
229 Sample preparation and some of the analytical backgrounds are summarized in [Kocsis et al.](#)  
230 [\(2014a\)](#). The oxygen isotope composition of  $\text{PO}_4^{3-}$  ion was analysed with a high-temperature  
231 conversion elemental analyser (TC/EA) coupled to a Finnigan MAT Delta Plus XL mass  
232 spectrometer. The results were corrected to in-house  $\text{Ag}_3\text{PO}_4$  phosphate standards (LK-2 L:  
233 12.1‰ and LK-3 L: 17.9‰) with better than  $\pm 0.3\%$  ( $1\sigma$ ) standard deviations during the runs.  
234 NBS-120c phosphorite reference material was prepared in parallel with the samples and an  
235 average value of  $21.6 \pm 0.3\%$  ( $n = 10$ ) was obtained. The carbon and oxygen isotope  
236 compositions of the structural carbonate in the apatite were analysed with a Gasbench II  
237 coupled to a Finnigan MAT Delta Plus XL mass spectrometer. The measured isotopic ratios  
238 were normalized to an in-house Carrara marble calcite standard that is calibrated against  
239 NBS-19. The analytical precision for this method is better than  $\pm 0.1\%$  for O and C isotopes.  
240 The data are expressed in delta notation, in the case of  $\delta^{18}\text{O}_{\text{PO}_4}$  relative to VSMOW (Vienna  
241 Standard Mean Ocean Water), while the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}_{\text{CO}_3}$  results from the structural  
242 carbonate analyses are shown relative to VPDB (Vienna Pee Dee Belemnite).

243

## 244 4. Results

### 245 4.1. Major element compositions

246 The remains of four mammal taxa, *Daouitherium rebouli* (PM65), *Phosphatherium*  
247 *escuilliei* (MNHN.F PM25), Hyracoidea indet (MNHN.F PM52), and *Ocepeia grandis* (PM66)  
248 were analyzed for CaO,  $\text{P}_2\text{O}_5$  and F content ([Table 2](#), [Figure 2](#)). The Ca/P ratio ranges from  
249 1.70 to 2.02, with the values increasing from enamel to dentine to bone. The F content  
250 varies between 0.73 and 3.95 wt% and a similar trend to the Ca/P ratio can be seen, as the  
251 lower values come from the enamel, and the highest ones from the bone samples ([Figure 2](#)).

252

### 253 4.2. Trace element compositions

254 Nineteen mammal specimens, sometimes represented by several different parts (tooth  
255 enamel, dentine, and bone fragments) and/or related sediment matrix elements (coprolites,  
256 fish teeth), were involved in the trace element study. Often multiple fragments of the same  
257 individual together with dentine-enamel pairs were analyzed and considered separately.  
258 The stratigraphic origin of each mammal specimen (i.e., the layer it comes from), therefore  
259 is represented by between one and eight sub-samples (see [Table 1](#)). Each of these  
260 represents the average of 1 to 4 spot analyses ([Table 2](#)). Altogether, 67 sub-samples were  
261 analyzed, of which 32 are directly from mammal remains, while the rests are from sediment  
262 matrix elements related to the mammals. Prior study indicates that samples from the same  
263 layers yielded a similar REE distribution ([Kocsis et al., 2016](#)), and hence unique mammal  
264 fossils (e.g., types specimens) not available for sampling can be represented by geochemical  
265 data analyzed from the matrix elements in the sediments attached to these rare fossils.

266 The trace element concentration data and ratios are listed in Supplementary Material  
267 Table-3, and selected ones are plotted in [Figures 3-5](#). A range of elements, such as Sr, Zn, Ba,  
268 totREE and U, are compared in the boxplots ([Figure 3](#)). Sr is especially enriched in the shark  
269 tooth enameloid (average > 2035 ppm), while other types of remains hardly reach 1000  
270 ppm. On average, the zinc concentration is somewhat higher in the enamel and enameloid,  
271 while barium is more enriched in the terrestrial remains. Variations of the early diagenetic  
272 rare earth elements (REE) and U concentrations within the samples are similar to data  
273 already reported from the Ouled Abdoun Basin ([Kocsis et al., 2016](#)). For example, the denser  
274 enamel/enameloid generally yielded lower concentrations compared to dentine, bones or  
275 coprolites. Importantly, all the investigated specimens, the mammals and the marine matrix  
276 elements, show very similar REE patterns with a negative Ce-anomaly and heavy REE  
277 enrichment. The Ce-anomaly and the Pr-anomaly can be quantified as  $Ce/Ce^* = 2Ce_N /$   
278  $(La_N + Pr_N)$  and  $Pr/Pr^* = 2 Pr_N / (Ce_N + Nd_N)$ , where N denotes the Post-Archean Australian  
279 Shale (PAAS) normalized value ([McLennan, 1989](#)). These parameters, however reveal subtle  
280 variations among the samples, as they link to stratigraphic origin rather than taxon  
281 affiliation ([Figures 4-6](#)).

282

### 283 4.3. Strontium isotope ratios ( $^{87}Sr/^{86}Sr$ )

284 Four mammal specimens from different ages were chosen and altogether nine separated  
285 analyses were carried out: four enamel, three dentine and two bones ([Table 2, Figure 7](#)).

286 The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios vary between 0.707856 and 0.708182, and a clear decreasing trend from  
287 enamel through dentine to bones is observed. In addition, twenty-four shark tooth  
288 enameloids - 16 from the Ouled Abdoun Basin and 8 from the nearby Ganntour Basin - were  
289 measured for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios, and yielded a range from 0.707714 to 0.707920  
290 (Supplementary Material Table-5). The data are shown in [Figure 7](#), together with a  
291 comparison to the global strontium evolution curve for the open ocean (see [McArthur et al.,](#)  
292 [2020](#)).

293

#### 294 4.4. Stable isotope analyses ( $\delta^{18}\text{O}_{\text{PO}_4}$ , $\delta^{13}\text{C}$ , $\delta^{18}\text{O}_{\text{CO}_3}$ )

295 Ten mammal specimens from five taxa (*D. rebouli*, Hyracoidea indet., *P. escuilliei*, *O.*  
296 *grandis*, *E. azzouzorom*; [Table 2](#)) were analysed for phosphate oxygen isotopic composition,  
297 chiefly in the tooth enamel, but a few dentine and bone samples were analysed as well. No  
298 systematic variation was observed among these materials. The  $\delta^{18}\text{O}_{\text{PO}_4}$  data vary between  
299 18.0 and 22.6 ‰ and the overall average value is  $19.8 \pm 1.1$  ‰ (n = 19). Individual mean  
300 values and taxon averages are shown in [Table 2](#), while the taxon-related variation is plotted  
301 in [Figure 8](#). One of the *Daouitherium rebouli* specimens (MNHN.F PM3) yielded the highest  
302  $\delta^{18}\text{O}_{\text{PO}_4}$  value ( $22.3 \pm 0.4$  ‰, n = 2), while the other specimens (PM65, ML 20269987) of this  
303 species vary between 18.6 and 21.2 ‰. Only eight samples were analyzed for isotopic  
304 composition in the structural carbonate in the bioapatite ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}_{\text{CO}_3}$ ), belonging to four  
305 taxa. The  $\delta^{13}\text{C}$  derived enamel (n = 5) ranged between -7.1 and -8.6 ‰, while a dentine and  
306 two bone samples yielded higher values of -6.3, -4.6, and -3.9 ‰, respectively ([Table 2](#),  
307 [Figure 8](#)). The values of  $\delta^{18}\text{O}_{\text{CO}_3}$  ranged between -3.7 and -5.1 ‰ for the enamel, whereas  
308 the dentine and the two bones yielded somewhat lower values of -5.6, -5.6, and -5.1 ‰,  
309 respectively ([Table 2](#)).

310

## 311 5. Discussion

### 312 5.1. Terrestrial, marine, and diagenetic signals

313 Hard tissues (i.e., bones, teeth) of terrestrial and marine animals record the chemical and  
314 isotopic signatures of their respective environments, hence when these remains are  
315 fossilized the ancient ecological conditions can be traced in the case of no alteration (e.g.,  
316 [Tütken et al., 2006](#); [Kocsis et al., 2007](#); [Domingo et al., 2009](#); [Reynard and Balter, 2014](#);

317 Akhtar et al., 2020). Generally, freshwater (e.g., terrestrial drinking sources) has a lower F  
318 and Sr content than seawater, while Ba is instead expected to be higher in rivers and lakes  
319 (White 1998; Bruland and Lohan 2003; Gaillardet et al. 2003). Therefore, these elements can  
320 help tracing *in-vivo* preserved environmental signals, and can give information on alteration  
321 during fossilization. Moreover, the taphonomic relations of mixed assemblages, such as the  
322 one studied here, can be further investigated (e.g., Trueman et al., 2003; Tütken et al.,  
323 2008).

324 In this study, the low F and high Ba content, but also the low Ca/P and high  $^{87}\text{Sr}/^{86}\text{Sr}$   
325 ratios in the mammal tooth enamel, indicate at least partially preserved *in-vivo* values  
326 reflecting a continental source and origin. The higher F and lower Ba concentrations, and Sr-  
327 isotope ratios in the mammal dentine and bone that are closer to marine values, are best  
328 explained by diagenesis in a seawater-dominated pore fluid (Figures 2-3). The burial  
329 condition is also reflected by the chemistry of the marine coprolites (Figure 2), which  
330 phosphatized within the sediments (Cosmidis et al., 2013), and yielded similar compositions  
331 to those of the mammal bones and dentine. Therefore, the Ca/P ratio and F of these  
332 mammal remains were altered in a marine depositional setting. The latter materials have a  
333 higher susceptibility to interaction and exchange with the depositional fluid due to their  
334 lower crystallinity and density, and originally higher porosity and organic content when  
335 compared to the enamel. The higher concentrations of REE and U, and possibly the higher  
336  $\delta^{13}\text{C}$  and lower  $\delta^{18}\text{O}_{\text{CO}_3}$  values, in the dentine and bone are also the result of the postulated  
337 structural differences and related diagenesis in a marine pore-fluid (Figure 3 & 8, Table 2).

338 As an *in-vivo* marine environmental end-member, shark tooth enameloid is the best  
339 suited material, as it is indicated by the following geochemical data: (1) a high F content, (2)  
340 low Ca/P ratios, (3) a high Sr concentration, and (4) very similar  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios to the open  
341 seawater of the time (McArthur et al., 2020; see chapter 5.3), and partly also (5) oxic-  
342 seawater related REE patterns (Figure 4; Kocsis et al., 2016) (Figure 2).

343 Based on the above observations, enamel/enameloid geochemical values should be used  
344 in any ecological and *in-vivo* interpretations. In this sense, the somewhat higher  
345 concentrations of Zn in both the mammal enamel and shark tooth enameloid call for further  
346 explanation, as these values may link to a common *in-vivo* origin. Zn has been connected to  
347 enzymes (e.g., kallikrein - KLK4) that play an important role in mammal tooth enamel  
348 formation (amelogenesis). In fact, KLK4 helps in removing organic matter at a later stage, so

349 as to make the enamel harder (e.g., [Simmer et al., 2009](#); [Goettig et al., 2010](#)). A high Zn  
350 concentration has been detected in modern shark enameloid and a similar enzymatic  
351 process has been proposed ([Kocsis et al., 2015](#)). Therefore, the observed relatively higher Zn  
352 concentration in our enamel/enameloid may partly relate to the process of enamel  
353 mineralization during amelogenesis. For other *in-vivo* interpretations based on the stable  
354 isotope and strontium isotope ratios, see Sections 5.3 and 5.4.

355

## 356 5.2. REE element taphonomy and stratigraphy

357 The rare earth element content of fossil bioapatite is predominantly of early diagenetic  
358 origin and can reflect the burial fluid's REE composition (e.g., [Elderfield and Pagett, 1986](#);  
359 [Trueman and Tuross, 2002](#)). This signature of fluid composition is frequently used to address  
360 taphonomic questions related to fossil vertebrates (e.g., [Staron et al., 2001](#); [Trueman et al.,](#)  
361 [2003](#); [MacFadden et al., 2007](#); [Tütken et al., 2008](#); [Botfalvai et al., 2021](#)) or to assess  
362 palaeoenvironmental conditions (e.g., [Picard et al., 2002](#); [Shield and Webb, 2004](#); [Kocsis et](#)  
363 [al., 2007, 2009](#); [Žigaitė et al., 2016, 2020](#)). From the Ouled Abdoun and Ganntour basins in  
364 Morocco, [Kocsis et al. \(2016\)](#) tested over 200 bioapatite specimens, and this database has  
365 been extended here (Supplementary Material Table-1). Based on the REE concentrations,  
366 their variations along the phosphate series, and their variations within the specimens, any  
367 late diagenetic overprint or fractionation along the REE series is ruled out (e.g., [Kocsis et al.,](#)  
368 [2016](#)). Therefore, the REE patterns we have obtained, and the related elemental ratios, can  
369 confidently be linked to the depositional environment.

370 As was the case in the prior study, the REE content of the fossils analyzed here increases  
371 from enamel/enameloid to coprolite, dentine, and bone, which, as mentioned earlier,  
372 reflects original structural and compositional (i.e., organic content) differences among these  
373 materials. However, a very important fact is that all the samples (in this study and in [Kocsis](#)  
374 [et al. 2016](#)), yielded similar REE distributions, which mimic oxalic seawater patterns (i.e., a  
375 negative Ce-anomaly and HREE enrichment) regardless of the material and taxa involved  
376 ([Figure 4](#)). This further supports the conjecture that the terrestrial mammal remains were  
377 fossilized within a marine depositional setting together with the marine fossils, and that  
378 they gained their REE content from seawater dominated pore fluids. An additional  
379 implication is that the mammal carcasses were most likely directly transported into the  
380 marine realm, without any previous terrestrial depositional site in the hinterland. This is

381 compatible with the hypothesis that the terrestrial mammals were drained as floated bodies  
382 from the nearby hinterland by local rivers in the Ouled Abdoun phosphate basin, shortly  
383 after their deaths (Gheerbrant et al., 2003).

384 Despite the very similar REE patterns, the samples do vary in their Ce/Ce\* and Pr/Pr\*  
385 ratios, which together express the degree of Ce-anomaly (Figure 4) (Bau and Dulski, 1996).  
386 The variations in the ratios are time related, meaning that samples from the same bed  
387 cluster around similar values. Therefore the REE distribution of any remains from the  
388 sediment matrix, such as coprolites, pellets or small teeth, attached or embedded with the  
389 mammal fossils, represents these rare fossils with no bias (see Table 1).

390 The few mammal samples and/or their sediment matrix whose stratigraphic origins were  
391 previously known perfectly match the reference Ce/Ce\* curve established by Kocsis et al.  
392 (2016) (Figure 5). Moreover, taxa with presumably Paleocene (e.g., Ocepeiidae spp.,  
393 *Abdounodus*, *Eritherium*) or Eocene (e.g., *Phosphatherium*, *Daouitherium*, *Stylolophus* spp.)  
394 ages fit in the corresponding data cluster (Figure 4).

395 The background Ce/Ce\* dataset for the Ouled Abdoun Basin allows for comparison of the  
396 mammal-derived data with their possible stratigraphic positions (Figures 4-6). The  
397 sedimentary section was divided into ten chemostratigraphic horizons based on the Ce/Ce\*  
398 variation and major sedimentological units including the three bone-beds (Horizons 3, 5,  
399 and 7), where mammal remains presumably were found. The variance and mean of the  
400 Ce/Ce\* values for the consecutive layers were compared using the F and Student's-t tests  
401 respectively (Supplementary Material Table-6), and these yielded significant differences  
402 (Student's t-test  $p < 0.05$ ) with the exceptions of the top of Bed-IIb (Horizon 8) and the  
403 *Eritherium* bone bed (Horizon 7) ( $p = 0.604$ ). Then, in order to trace the possible  
404 stratigraphic origin of the mammals, each mammal data-group ( $n > 2$ ) was compared to the  
405 respective horizons using one-way ANOVA (i.e., Eocene mammals to Horizons 1 - 5;  
406 Paleocene mammals to Horizons 5 - 10), and the underlying differences in the mean Ce/Ce\*  
407 values were checked using Tukey's pairwise tests (Table 3).

408

#### 409 5.2.1 Paleocene taxa

410 The three specimens of *Eritherium azzouzorum* (PM40; MNHN.F.PM42; PM100a see  
411 Table 1) found in the *Eritherium* bone bed fit the background Ce/Ce\* data from this horizon  
412 (Horizon 7). However, they are also statistically similar to the horizons below and above. The

413 Ce/Ce\* data of the taxa with unknown provenance revealed that their origin is restricted to  
414 the interval between the very top of Bed IIb and the base of Bed IIa, including the *Eritherium*  
415 bone bed (chemostratigraphic Horizons 6-8 i.e., early Thanetian–Selandian–?latest Danian  
416 age)(Figure 6, Table 3). This suggests that these mammal specimens do not come from  
417 younger Paleocene bone beds such as the big coprolite bone bed (base of Horizon 5), which  
418 was the suspected provenance of one of the *O. grandis* specimens (PM66) based on  
419 information from local collectors. Fossil collectors usually target higher accumulations of  
420 bones (i.e., the bone beds) to find unique specimens, hence the *Eritherium* bone bed  
421 (Horizon 7) could be the most important source of these fossils. However, our results  
422 support the hypothesis that some mammal specimens such as MNHN.F PM39 of *O. grandis*,  
423 – and solely based on its Ce/Ce\* ratio – maybe even the MNHN.F PM42 of *E. azzouorum*,  
424 might be derived from layers overlying the base of Bed IIa (Horizon 6) (Figure 6). Among the  
425 Ocepeiidae, the overlapping probabilities of their stratigraphic provenance indicate that the  
426 smaller *O. daouiensis* and the larger *O. grandis* were co-existing, therefore refuting the  
427 possibility that they were successive chronospecies (Table 3-4, Figure 5). For the specimens  
428 where only one Ce/Ce\* data point is available (Ocepeiidae? – MHNM.KHG.224 and  
429 *Abdounodus hamdii* - PM67), the result agree with the suggested origin in Horizons 6-8.

430

### 431 5.2.2 Eocene taxa

432 The Eocene taxa reveal a wider range of possible provenance beds, based on the  
433 statistical analysis (Table 3). This relates partly to the fact that the Ce/Ce\* values are  
434 increasing in the youngest beds, and so they overlap with some of the older levels, while the  
435 latest Paleocene beds (top Bed IIa – Horizon 5) show very similar values to those of the early  
436 Ypresian beds (Figure 5). An exception is Horizon 4, with few specimens (the very base of  
437 intercalary II/I), which clearly does not match any of the taxa due to its high Ce/Ce\* values,  
438 and which are similar to the older Paleocene data series. This small spike in the Ce/Ce\*  
439 values may reflect reworked older specimens from Bed IIa, as has been recognized also by  
440 Gheerbrant et al. (2003), and/or a very brief episode of less oxic, somewhat confined  
441 conditions (probably after the PETM event) (Kocsis et al., 2016).

442 On the other hand, most of the taxa show significant undifferentiated similarities to the  
443 whole range of chemostratigraphic Horizons 1, 3, and 5, i.e. upper Thanetian-Ypresian  
444 (Figure 6). Unfortunately, the Ce/Ce\* chemostratigraphic approach alone could not help to

445 define the exact provenance of the mammal taxa in these three horizons, so additional  
446 information from the sediment matrix and related selachian fauna (i.e., shark and ray) are  
447 needed for further stratigraphic assignment.

448 The origin of the few *Phosphatherium escuilliei* specimens (MNHN.F PM14 and MNHN.F  
449 PM17) is known for certain to be the *Otodus obliquus* bone bed in the intercalary phosphate  
450 Beds II/I (i.e., base Horizon 3) (Table-1, Gheerbrant et al., 2005), but no trace element  
451 analyses were carried out on these specimens. However, the specimens of this species with  
452 unknown provenance (MNHN.F PM25, OCP DEK/GE336) yielded Ce/Ce\* data fitting an  
453 origin in Horizon 3, which includes the *Otodus obliquus* bone bed (Figure 6).

454 The sediment matrix and the related selachian remains assigned the *Stylolophus minor*  
455 (OCP DEK/GE 668) specimen to the *Otodus obliquus* bone bed, a conclusion which is further  
456 confirmed by its Ce/Ce\* values (Figure 5). Selachian taxa found in the matrix of the other  
457 specimen of *S. minor* (MNHN.F PM30) are also compatible with Horizon 3 (see  
458 Supplementary Material Table-7). The Ce/Ce\* data for the other specimens analyzed  
459 (MNHN.F PM30 & OCP DEK/GE 667) would also match an origin in Horizon 3 (early Ypresian)  
460 (Figure 6).

461 For these two species (*P. escuilliei* and *S. minor*), however, the general similarity in the  
462 Ce/Ce\* values to the latest Paleocene beds (Horizon 5: top Bed IIa including the big  
463 coprolite bone bed) raise the possibility that some of these specimens may have belonged  
464 to the older Horizon 5. Thus, we cannot exclude that these species have crossed the PETM  
465 boundary. It must be mentioned that the provenance of *P. escuilliei* and *S. minor* from  
466 Horizon 1 (Table 3) is completely rejected here, due to the lack of strong similarities with the  
467 thick succession of Horizon 2, which stratigraphically follows Horizon 3 (Figure 5).

468 *Stylolophus major* (MNHN.F PM53) has the highest probability of occurrence in the  
469 youngest Horizon 1 (the sillons beds – Table 3, Figure 6). If it is correct, it would be the  
470 stratigraphically youngest mammal recovered in the Ouled Abdoun phosphate series. A  
471 stratigraphic origin of *S. major* from the sillons beds is further supported by its larger size  
472 and its more derived morphology with respect to *S. minor*, and also by the chert content  
473 and the selachian assemblage found in its matrix (Gheerbrant et al., 2018, 2020). In fact, this  
474 species yielded very different Ce/Ce\* and Pr/Pr\* ratios from the rest of the mammals (see  
475 Figure 4d), and when Tukey's pairwise comparison is applied to all these younger taxa it  
476 reveals that *S. major* is significantly different from the rest of the remains ( $p < 0.05$ , Table 4),



477 which further supports its younger origin in the phosphate series (i.e., Horizon 1 – late  
478 Middle Ypresian).

479 For *Daouitherium rebouli*, the matrix data and related fauna suggest an origin in Bed 0 or  
480 Bed 0' (Horizon 2) (see Supplementary Material Table-7). Generally, our Ce/Ce\* data  
481 support this scenario, although Horizons 1 and 3 yielded a higher probability match.  
482 Moreover, these specimens do not differ in their Ce/Ce\* values from those of *P. escuilliei*  
483 and *S. minor* (Table 4). The Ce/Ce\* data match Horizon 5 (Paleocene), but the attached  
484 matrix-type and related selachian fauna preclude this scenario (see Table 3). *Daouitherium*  
485 is the largest proboscidean from the Ouled Abdoun Basin and most probably evolved  
486 somewhat later than *Phosphatherium*, so the younger age might be possible too  
487 (Gheerbrant et al., 2002). Here we propose an origin in the interval from the top Horizon 3  
488 to Horizon 2 (middle Ypresian) (see the grey shaded area in Figure 5).

489 The difficulties in pinpointing more precise stratigraphic provenances based on only the  
490 Ce/Ce\* data is clear from the above example, and the limitations of the method are further  
491 highlighted by the Hyracoidea specimen (MNHN.F PM52), for which no additional matrix  
492 related information is available. The similar probability pattern to the *D. rebouli* specimens  
493 (Table 3) may suggest a similar origin; while significant differences from the holotype of *S.*  
494 *major* (Table 4) would argue against a provenance in Horizon 1. Therefore, we propose here  
495 a possible origin for the Hyracoidea from the top of Horizon 3 to Horizon 2 (middle  
496 Ypresian).

497

498 To sum up, in general the chemostratigraphic approach supports the previous  
499 assumptions made about the provenances of the mammal taxa investigated here, but it has  
500 also shed light on certain peculiarities such as (1) the Ocepeiidae species, in particular *O.*  
501 *daouiensis* and *O. grandis*, coexisted in the Ouled Abdoun phosphate series for an  
502 undetermined period from the latest Danian to the early Thanetian; (2) the Ypresian species  
503 *P. escuilliei* and *S. minor* might have already evolved in the latest Paleocene; (3) *Stylolophus*  
504 *major* is the youngest and only known mammal taxon derived from the highest phosphorite  
505 sillon beds (late Middle Ypresian). Based on the Ce/Ce\* data and additional matrix and  
506 biostratigraphic (i.e., selachian fauna) information, the most probable stratigraphic origin of  
507 the mammal specimens are marked by the grey areas in Figure 6.

508

### 509 5.3. Strontium isotope ratios in terrestrial and marine fossils

510 The Sr that is biologically available in a terrestrial environment is affected by the local  
511 geology, and it is incorporated into the skeletal tissues via ingestion without fractionation  
512 along the food chain (e.g., [Blum et al., 2000](#)). Therefore, the strontium isotope ratios  
513 ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) of fossil terrestrial mammals are often used to trace migration patterns (e.g.,  
514 [Hoppe et al., 1999](#); [Tütken et al., 2006](#); [Arppe et al., 2009](#)). On the other hand, in the open  
515 marine realm the seawater has a constant  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio due to the long residence time of  
516 Sr. However, on longer timescale the ratio does vary, and this variation is the basis of  
517 strontium isotope stratigraphy (e.g., [McArthur et al. 2020](#)). Dating marine rocks with well-  
518 preserved fish remains is one widely used approach (e.g., [Ingram 1995](#); [Kocsis et al., 2013](#);  
519 [Harrell et al., 2016](#)), while in the case of mixed terrestrial and marine assemblages,  
520 taphonomy of the remains can give further information.

521 Our  $^{87}\text{Sr}/^{86}\text{Sr}$  analyses from the Ouled Abdoun basin yielded differences between the  
522 continental and marine taxa, with the mammal fossils in general having higher ratios ([Figure](#)  
523 [7a](#)). The highest ratios come from mammal enamel that represents possibly unaltered  
524 terrestrially-derived and ingested Sr (i.e., *in-vivo*), which reflects the hinterland geology of  
525 the time. The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios decrease through dentine to the bone samples, which  
526 approaches the values of the open ocean ([Figure 7a](#)). This decreasing trend within the  
527 different types of mammal remains clearly indicates diagenesis in a marine depositional  
528 environment, and as mentioned earlier this has an important taphonomic message. The  
529 remains were originally deposited in a marine setting and they are not reworked from  
530 previous deposits.

531 On the other hand, the data derived from the shark tooth enameloid more or less follow  
532 the global open ocean Sr-evolution curve. This is most noticeable for the latest Paleocene  
533 and Eocene where the Sr-isotope ages agree with other chemostratigraphic data ([Yans et](#)  
534 [al., 2014](#); [Kocsis et al., 2014a](#)). However, the rest of the Paleocene and part of the  
535 Cretaceous samples yielded  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios that cannot fit the global Sr-isotope curve  
536 because their values are too high ([Figure 7](#)). The most plausible interpretation is that these  
537 samples were altered during early diagenesis. A high  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio could have derived from  
538 a terrestrial source, as attested by the mammal enamel's high  $^{87}\text{Sr}/^{86}\text{Sr}$  values. However,  
539 there is no evidence of strong continental input in the sedimentary record of the  
540 phosphates series, which corresponds mostly to non-clastic deposits of biogenic origin (i.e.,

541 marine bioproductite see [Lucas and Prevôt-Lucas, 1995](#)). The continental influence is  
542 marked there only by occasional rare terrestrial fossils in the phosphate levels. The  
543 terrestrial sediment input in the Moroccan phosphate basins was low, due maybe to the flat  
544 topography in the hinterland (low hydrodynamism and erosion) and perhaps also to the  
545 filtering role of coastal mangroves (e.g., [Fechner, 1988](#)). However, the river water and/or  
546 sub-terrain water draining from the hinterland towards the basin may have had some  
547 effects, at least in the transportation of the floating bodies/carcasses of the Ouled Abdoun  
548 mammals ([Gheerbrant et al., 2003](#)).

549 The REE element patterns, however, were still compatible with oxic seawater ([Figure 4](#)).  
550 Though the Ce/Ce\* ratios are somewhat higher here than in the younger samples ([Figure 5](#)),  
551 the stratigraphic changes in these values were interpreted as a reflection of the enhanced  
552 opening of the Atlantic Ocean and hence a better connection with the global oceanic  
553 circulation ([Kocsis et al., 2016](#)). In this sense the  $^{87}\text{Sr}/^{86}\text{Sr}$  data of the Cretaceous and older  
554 Paleocene samples could indicate somewhat more restricted conditions in which seawater  
555 was slightly locally controlled. First-order sea-level changes during the late Cretaceous and  
556 early Paleogene indicate global regression (e.g., [Hardenbol et al., 1998](#); [Snedden and Liu,](#)  
557 [2010](#); [van der Meer et al., 2017](#)), which could support the semi-confined situation in the  
558 Moroccan phosphate basins. Interestingly, the  $^{87}\text{Sr}/^{86}\text{Sr}$  data reported from foraminifera  
559 from the South Atlantic (Walvis Ridge) also yielded rather higher ratios than the global  
560 ocean Sr-isotope curve during this part of the Paleocene ([Hodell et al., 2007](#)). Even if some  
561 samples were clearly affected by diagenesis the lowest Sr-isotopic ratios have a perfect fit  
562 with McArthur's curve between 52 and 58 Ma ([Figure 7b](#)), but the older samples are above  
563 the curve at the Walvis Ridge as well. This might hint at a common cause altering the Sr-  
564 budget and its mixing in the Central and South Atlantic, which may have been related to the  
565 formation of wider scales of global oceanic circulation. Nevertheless, better suited samples  
566 covering larger regions are needed to seriously assess this scenario.

567

#### 568 *5.4. Mammal ecology based on stable isotope chemistry*

569 The oxygen and carbon isotopic compositions of fossil mammal teeth are often used for  
570 palaeoecological and palaeoenvironmental reconstructions (e.g., [Ayliffe et al., 1994](#); [Kohn](#)  
571 [and Cerling, 2002](#); [Amiot et al., 2004](#)), even for extinct taxa of the Paleocene and Eocene for  
572 which the physiology of the animals is more difficult to assess (e.g., [Liu et al., 2008](#); [Secord](#)

573 et al., 2008; Kocsis et al., 2014b; Mahboubi et al., 2014; Tütken, 2014). Nevertheless, based  
574 on the tooth morphology the mammals from the Ouled Abdoun Basin investigated here  
575 were all herbivores (Ypresian proboscideans are especially folivorous specialists). Their body  
576 fluid  $\delta^{18}\text{O}$  depends on the ingested water, which mainly came from drinking sources and/or  
577 dietary plant water, while their  $\delta^{13}\text{C}$  was entirely driven by their diet and can be related to  
578 the palaeoflora (e.g., Kohn and Cerling, 2002). The growth of teeth and bones record these  
579 ecological parameters, and can be used to gain information about the past environment.  
580 The teeth and bones are composed of bioapatite with a simplified formula of  $\text{Ca}_5(\text{PO}_4,$   
581  $\text{CO}_3)_3(\text{OH}, \text{CO}_3)$ . From the oxygen bearing ions, the phosphate ion dominates the apatite  
582 structure and is considered to be the most resistant to diagenesis due to the strong P-O  
583 bond. Therefore, the phosphate oxygen isotopic composition ( $\delta^{18}\text{O}_{\text{PO}_4}$ ) can provide the most  
584 reliable ecological information. To further evaluate possible alterations, enamel, dentin and  
585 bone can be analyzed separately and compared, with the enamel considered to be less  
586 prone to diagenetic alteration (e.g., Zazzo et al., 2004). The  $\delta^{18}\text{O}_{\text{PO}_4}$  data from the Moroccan  
587 mammals do not show consistent variations across these materials, but the  $\delta^{13}\text{C}$  of *O.*  
588 *grandis* and *P. escuilliei* clearly point towards higher values in the less dense material of  
589 bone and dentine (Figure 8). This can be interpreted as meaning that the  $\delta^{18}\text{O}_{\text{PO}_4}$  data are  
590 more robust across the various materials; however the isotope values from the structural  
591 carbonate underwent partial interaction and exchange with the marine pore fluid in the  
592 depositional environment. For this reason, only the enamel data are taken into account  
593 when the ecology of these ancient mammals is discussed, even for the  $\delta^{18}\text{O}_{\text{PO}_4}$  results.

594 The overall average  $\delta^{18}\text{O}_{\text{PO}_4}$  value for the enamel is  $20.0 \pm 1.3 \text{‰}$  ( $n = 12$ ), and no obvious  
595 species-specific variations occur. The largest variation is between two specimens of  
596 *Daouitherium rebouli* (MNHN.F PM3 and PM65), with a nearly 3 ‰ difference in their  
597 enamel values (Figure 8). The relationship between mammal  $\delta^{18}\text{O}_{\text{PO}_4}$  and the local meteoric  
598 water (i.e., consumed water) can be taxon specific and dependent also on the relative  
599 humidity (e.g., Kohn, 1996; Ayliffe et al., 1994; Kohn and Cerling, 2002). This can be  
600 complicated further by the migration of animals, seasonal variations, and/or locally available  
601 water sources that are different from the local meteoric water. Moreover, the physiology of  
602 the investigated taxa is hard to assess, and for these reasons Amiot et al. (2004)'s globally  
603 compiled mammal database and latitude adjusted  $\delta^{18}\text{O}_{\text{PO}_4}$  versus meteoric water correlation

604 is used here, with the assumption that the ancient mammals' body fluids were affected by  
605 the local meteoric fluid (i.e., drinking water or plant water). This would yield an average of -  
606  $4.2 \pm 1.3$  ‰ (n = 12) local meteoric water isotopic composition, which in turn can be linked  
607 to a mean annual temperature of  $20.4 \pm 3.0$  °C (n = 12) (see [Amiot et al., 2004](#)) for the late  
608 Paleocene and early Eocene ([Figure 8](#)). This is about 2-3 °C degrees higher than today's MAT  
609 for the coastal area of Morocco (e.g., Agadir-Casablanca, see [climate-data.org](#)). Considering  
610 the palaeolatitudinal temperature gradient for a greenhouse climate regime ([Amiot et al.,](#)  
611 [2004](#)) and the fact that the studied sites were not much further south (~22°-24°N, see [van](#)  
612 [Hinsbergen et al., 2015](#)) than today, the absolute MAT result we obtained seems  
613 reasonable. Nevertheless, the higher isotopic composition in the bioapatite indicates a  
614 higher isotopic composition in the ingested water, which in turn reflects a higher MAT  
615 ([Figure 8](#)). The high  $\delta^{18}\text{O}_{\text{PO}_4}$  values for one of the *D. rebouli* (MNHN.F PM3) and Hyracoidea  
616 (MNHN.F PM52) teeth may reflect the effects of the Early Eocene Climatic Optimum (EECO),  
617 with a related global temperature rise and/or enhanced dryer periods (i.e., more  
618 evaporation of the drinking sources). However, only a few samples were analyzed and the  
619 high  $\delta^{18}\text{O}_{\text{PO}_4}$  values and related temperature calculations might be biased by the migration  
620 of the animals or strong evaporation of the local drinking source. Geochemical analysis of  
621 the sediments and the marine fossils had also detected the EECO event in the phosphorite  
622 series ([Yans et al., 2014](#); [Kocsis et al., 2014](#)). Moreover, the stratigraphic average MATs  
623 reveals a rise of about 5 °C degree from the early Ypresian to mid-Ypresian ([Figure 8](#)), which  
624 agrees well with the peak of the EECO and related  $\Delta\text{MAT}$  estimates (e.g., [Hyland et al.](#)  
625 [2016](#)). If these analyses indeed reflect the EECO, then the proposed stratigraphic origin of  
626 these taxa (*D. rebouli* & Hyracoidea) in Horizons 3 (upper part) and 2 is further confirmed  
627 (see section 4.2 and [Figure 6](#)).

628 The average enamel  $\delta^{13}\text{C}$  value is  $-7.9 \pm 0.8$  ‰ (n = 5), which can be translated to a  
629 consumed plant isotopic composition of  $-22 \pm 0.8$  ‰ (e.g., [Kohn and Cerling, 2002](#); [Figure 8](#)).  
630 This mean value is at the very high end of a C3 palaeoflora, and because the C4  
631 photosynthetic pathway was not yet widespread (i.e., high  $\delta^{13}\text{C}_{\text{plant}}$ ), this suggests a very dry  
632 Thanetian-middle Ypresian local continental palaeoecosystem with mean annual  
633 precipitation well below 500 mm ([Kohn, 2010](#)). A dry arid early Eocene climate was also  
634 suggested by palynology and palaeobotanic finds in the Moroccan south Atlas, which

635 indicated mangrove and marsh vegetation along the palaeo-coast, together with a fairly dry  
636 and scarcely vegetated hinterland (Mohr, 1986; Mohr and Fehner, 1986; Fehner, 1988).  
637 Mangrove vegetation along the coast line is also predicted by models (Descombes et al.,  
638 2018; Couvreur et al., 2021). The presence of early diagenetic dolomite and gypsum in some  
639 of these deposits were also interpreted as a consequence of an arid climate during the  
640 Ypresian, and only a low amount of seasonal precipitation was proposed (e.g., Mohr, 1986;  
641 Fehner, 1988). In addition, the rarity of detritic (clastic) material in the phosphate basins  
642 (Lucas and Prevôt-Lucas, 1995), and the high quantity of palygorskite clay mineral in the  
643 Paleogene deposits in the Atlas (Daoudi, 2004; Knidiri et al., 2014) and offshore Morocco  
644 (e.g., Chamley et al., 1980), would further suggest a dry semi-arid late Paleocene - Ypresian  
645 climate in the region. By contrast, Herbig and Gregor (1990) have advocated a tropical  
646 humid climate based on the discovery of mangrove macro-plant remains of *Nypa* palms  
647 from Thanetian-Ypresian levels in the Ouarzazate Basin, based on a re-evaluation of early  
648 available data.

649 In the view of the mammal enamel  $\delta^{13}\text{C}$  values from the Ouled Abdoun Basin, the  
650 ingested plants must have lived in water-stressed, and maybe also salinity-stressed (i.e.,  
651 mangrove vegetation, e.g., Wei et al., 2008) environment, supporting the hypothesis of arid  
652 late Paleocene - Ypresian climatic conditions in the region. The minimal variation in the  $\delta^{13}\text{C}$   
653 values through time could reflect a steady dry ecosystem along the Moroccan coastline  
654 during the Paleocene-Eocene. Still, the EECO warm period may have stressed the  
655 palaeoflora further, and even somewhat higher values of  $\delta^{13}\text{C}$  may be expected (e.g., even  
656 more water stress, Farquhar et al., 1989). However, this may have been compensated by a  
657 higher relative humidity and / or higher atmospheric  $\text{pCO}_2$  during the EECO (Pearson and  
658 Palmer, 2000; Schubert and Jahren, 2002). The EECO warming is likely also to have driven an  
659 evolution to increased size the Ouled Abdoun mammals (e.g., Yans et al., 2014). The  
660 embrithopods lineage *S. minor*- *S. major* (Gheerbrant et al., 2020) records a significant  
661 increase in size during the early-middle Ypresian. Similar size changes are observed between  
662 *Phosphatherium* and *Daouitherium*, however with much less stratigraphic difference  
663 between these taxa as inferred here (Figure 6).

664

## 665 6. Conclusions

666 The rare but diverse terrestrial mammal fossils from the Ouled Abdoun phosphorite are  
667 proven to have a similar diagenetic history to that of the marine fossils. This is reflected by a  
668 similar REE distribution and stratigraphy matched Ce/Ce\* and Pr/Pr\* ratios. The Ce/Ce\*  
669 variation along the phosphate series either confirmed previous known origins or helped to  
670 estimate the stratigraphic provenance of the Ouled Abdoun mammal specimens whose  
671 origin was unknown. Exchanges with marine pore fluid affected the enamel, dentine, and  
672 bone differently, with the enamel being the most robust to alteration, and hence the best to  
673 use for investigation of the palaeoenvironment of the African Paleogene mammals from the  
674 Ouled Abdoun sites.

675 This study has identified ten chemostratigraphic horizons in the Maastrichtian-Ypresian  
676 phosphates series of the Ouled Abdoun Basin. It confirms most of the previously proposed  
677 age determinations for the mammals found in the Ouled Abdoun Basin, but with some  
678 corrections and additions. One new conclusion is that all the Paleocene mammal material  
679 studied here ranges from the Selandian to the lower Thanetian (uppermost Bed IIb to the  
680 base of Bed IIa). In particular, *O. grandis* does not come from the upper part of Bed IIa (late  
681 Thanetian) but is actually a coexisting lineage with *O. daouiensis*, which highlights the little-  
682 known radiation of the stem paenungulates. The study suggests that some mammal species  
683 might have a wider stratigraphical extension than previously known, including across the  
684 PETM. However, as the Ouled Abdoun mammal material remains scarce, it is unknown if  
685 this relates to the presence of undetermined chronospecies or to the succession of  
686 intraspecific diachronic populations. Chemostratigraphic results indicate that the  
687 embrithopod *S. major* likely comes from the uppermost phosphates levels (late Middle  
688 Ypresian) of the Ouled Abdoun series, and is the youngest Paleogene mammal known in the  
689 Ouled Abdoun Basin.

690 While the mammal enamel yielded the highest  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios, indicating the composition  
691 of the hinterland rocks (a terrestrial Sr-source), the ratios for the shark tooth enameloid  
692 from the latest Paleocene to early Eocene are compatible with the open ocean Sr isotope  
693 ratios of the time. Older marine fossils deviate from the global Sr-isotope curve, which most  
694 probably reflects alteration or may link to somewhat restricted conditions and a variable Sr-  
695 budget in the African coastal basins of the Atlantic Ocean. The enamel derived oxygen and  
696 carbon isotopic compositions of the Ouled Abdoun mammal teeth point to warm and arid  
697 climatic conditions along the Atlantic palaeocoast of North Western Africa. In addition, an

698 increase about 5 °C degrees in MAT was recorded by the mid-Ypresian, which is linked to  
699 the EECO. Our geochemical study of the Ouled Abdoun fossils provides support for the  
700 evolution of endemic African lineages of placental mammals, such as the early embriothopod  
701 *Stylolophus*, during the EECO event.

702

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### 719 **References**

- 720 Akhtar, A.A., Santi, M.L., Griffiths, L.M., Becker, M., Eagle, A.R., Kim, S., Kocsis, L., Rosenthal, Y., Higgins, J.A.,  
721 2020. A record of the  $\delta^{44}/^{40}\text{Ca}$  and [Sr] of seawater over the last 100 million years from fossil  
722 elasmobranch tooth enamel. *Earth and Planetary Science Letters* 543,  
723 doi.org/10.1016/j.epsl.2020.116354.
- 724 Amiot, R., Lecuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., Martineau, F., 2004. Latitudinal temperature  
725 gradient during the Cretaceous Upper Campanian Middle Maastrichtian:  $\delta^{18}\text{O}$  record of continental  
726 vertebrates. *Earth Planet. Sci. Lett.* 226, 255–272. <http://dx.doi.org/10.1016/j.epsl.2004.07.015>.
- 727 Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes*  
728 *Mémoires du Service géologique du Maroc* 92, pp. 1–372.
- 729 Arppe L., Karhu J.A., Vartanyan S.L., 2009. Bioapatite  $^{87}\text{Sr}/^{86}\text{Sr}$  of the last woolly mammoths – implications for  
730 the isolation of Wrangel Island. *Geology* 37, 347–350.
- 731 Ayliffe, L.K., Chivas, A.R., Leakey, M.G., 1994. The retention of primary oxygen isotope compositions of fossil  
732 elephant skeletal phosphate. *Geochim. Cosmochim. Acta* 58, 5291–5298.  
733 [http://dx.doi.org/10.1016/0016-7037\(94\)90312-3](http://dx.doi.org/10.1016/0016-7037(94)90312-3).
- 734 Bardet, N., Gheerbrant, E., Noubhani, A., Cappetta, H., Jouve, S., Bourdon, E., Pereda Suberbiola, X., Jalil, N.-E.,  
735 Vincent, P., Houssaye, A., Solé, F., El Houssaini, Kh., Adnet, S., Rage, J.-C., Lapparent de Broin, F., Sudre,  
736 J., Bouya, B., Amaghazaz, M., Meslouh, S., 2017. Les vertébrés fossiles des phosphates crétacés-



737 paléogènes (72,1-47,8 Ma) du Maroc, in Zouhri, S. ed., Paléontologie des Vertébrés du Maroc: état des  
738 connaissances. Mémoire de la Société Géologique de France, v. 180, p. 351–452.

739 Bau, M., Dulski, P., 1996. Distribution of yttrium and rare-earth elements in the Penge and Kuruman iron-  
740 formations, Transvaal Supergroup, South Africa. *Precambrian Res.* 79, 37–55.

741 Blum, J.D., Talianferro, E.H., Weisse, M.T., Holmes, R.T., 2000. Changes in Sr/Ca, Ba/Ca and 87Sr/86Sr ratios  
742 between two forest ecosystems in the northeastern USA. *Biogeochemistry* 49, 87–101.

743 Botfalvai, G., Csiki-Sava, Z., Kocsis, L., Gáspár, A., Magyar, J., Bodor, R.E., Ţabără, D., Ulyanov, A., Makádi, L.,  
744 2021. X' marks the spot! Sedimentological, geochemical and palaeontological investigations of Late  
745 Cretaceous (Maastrichtian) vertebrate fossil localities from Vălioara Valley (Densus-Ciula Formation,  
746 Hateg Basin, Romania). *Cretaceous Research*, 123.

747 Bourdon, E., Bouya, B., Iarochene, M. 2005. Earliest African neornithine bird: A new species of  
748 Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of Vertebrate Paleontology*, 25 (1),  
749 157–170.

750 Bruland, K.W., Lohan, M.C., 2003. Controls of Trace Metals in Seawater. In: Holland, H.D., Turekian, K.K. (eds)  
751 *Treatise on Geochemistry*, vol. 6. pp 23–47.

752 Cappetta, H., Bardet, N., Pereda-Suberbiola, X., Adnet, S., Akkrim, D., Amalik, M., Benabdallah, A., 2014.  
753 Marine vertebrate faunas from the Maastrichtian phosphate deposits of the Benguérir area (Ganntour  
754 Basin, Morocco): biostratigraphy, palaeobiogeography and palaeoecology. *Palaeogeogr. Palaeoclimatol.*  
755 *Palaeoecol.* 409, 217–238.

756 [climate-data.org](https://climate-data.org)

757 Chamley H., Giroud d'Argoud G., Robert C., 1980. Clay mineralogy of Cretaceous and Cenozoic sediments off  
758 the Moroccan margin, Deep Sea Drilling Project sites 415, 416. Initial Rep. Deep Sea Drilling Proj., 50,  
759 715–721.

760 Cosmidis, J., Benzerara, K., Menguy, N., Arning, E., 2013. Microscopy evidence of bacterial microfossils in  
761 phosphorite crusts of the Peruvian shelf: Implications for phosphogenesis mechanisms. *Chemical*  
762 *Geology*, 359, 10–22.

763 Couvreur, T.L.P., Dauby, G., Blach-Overgaard, A., Deblauwe, V., Dessein, S., Droissart, V., Hardy, O.J., Harris,  
764 D.J., Janssens, S.B., Ley, A.C., Mackinder, B.A., Sonké, B., Sosef, M.S.M., Stévant, T., Svenning, J.-C.,  
765 Wieringa, J.J., Faye, A., Missoup, A.D., Tolley, K.A., Nicolas, V., Ntie, S., Fluteau, F., Robin, C.,  
766 Guillocheau, F., Barboni, D., Sepulchre, P., 2021. Tectonics, climate and the diversification of the  
767 tropical African terrestrial flora and fauna. *Biol. Rev.* 96, 16–51.

768 Daoudi L., 2004. Palygorskite in the uppermost Cretaceous-Eocene Rocks from Marrakech High Atlas, Morocco.  
769 *Journal of African Earth Sciences*, 39, 353–358.

770 Descombes, P., Gaboriau, T., Albouy, C., Heine, C., Leprieur, F., Pellissier, L., 2018. Linking species  
771 diversification to palaeo-environmental changes: a processbased modelling approach. *Global Ecology*  
772 *and Biogeography* 27, 233–244.

773 Domingo, L., Cuevas-González, J., Grimes, S.T., Hernández Fernández, M., López-Martínez, N., 2009. Multiproxy  
774 reconstruction of the paleoclimate and paleoenvironment of the Middle Miocene Somosaguas site  
775 (Madrid, Spain) using herbivore tooth enamel. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 272, 53–68.

776 El Assel, N., Kchikach, A., Durllet, C., AlFedy, N., El Hariri, K., Charroud, M., Jaffal, M., Jourani, E., Amaghaz, M.,  
777 2013. Mise en évidence d'un Sénonien gypseux sous la série phosphatée du bassin des Ouled Abdoun:  
778 Un nouveau point de départ pour l'origine des zones dérangées dans les mines à ciel ouvert de  
779 Khouribga, Maroc. *Estudios Geológicos*, 69(1), 47–70. <https://doi.org/10.3989/egeol.40781.168>

780 Elderfield, H., Pagett, R., 1986. Rare earth elements in ichthyoliths: variations with redox conditions and  
781 depositional environment. *Sci. Total Environ.* 49, 175–197.

782 El Haddi, H., 2014. Les silicifications de la série phosphatée des Ouled Abdoun (Maastrichtien-Lutétien Maroc):  
783 Sédimentologie, Minéralogie, Géochimie et Contexte Génétique, [PhD Thesis]: Université Hassan II de  
784 Casablanca, Faculté des Sciences Ben M'Sik, 135 p.

785 Farquhar G.D., Ehleringer J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. *Ann. Rev.*  
786 *Plant Physiol. Plant Mol. Biol.* 40, 503–537.

787 Fechner, G.G., 1988. Selected palynomorphs from the Lower to Middle Eocene of the south Atlas Border Zone  
788 (Morocco) and their environmental significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 65, 73–79.

789 Gaillardet, J., Viers, J., Dupré, B., 2003. Trace Elements in River Waters. In: Holland, H.D., Turekian, K.K. (eds)  
790 *Treatise on Geochemistry*, vol. 5. Pp. 225–272.

791 Gheerbrant, E., 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates.  
792 *Proceedings of the National Academy of Sciences* 106, 10717–10721.

793 Gheerbrant, E., Sudre, J., Cappetta, H., Bignot, G., 1998. *Phosphatherium escuilliei* du Thanétien du bassin des  
794 Ouled Abdoun (Maroc), plus ancien proboscidiien (Mammalia) d'Afrique. *Geobios* 30, 247–269.

795 Gheerbrant, E., Sudre, J., Iarochene, M., Moumni, A., 2001. First ascertained African "condylarth" mammals  
796 (primitive ungulates : cf. *Bulbulodontata* & cf. *Phenacodonta*) from the Earliest Ypresian of the Ouled  
797 Abdoun Basin, Morocco. *Journal of Vertebrate Paleontology* 21, 107–118.

798 Gheerbrant, E., Sudre, J., Cappetta, H., Iarochène, M., Amaghaz, M., Bouya, B., 2002. A new large mammal  
799 from the Ypresian of Morocco: Evidence of surprising diversity of early proboscideans. *Acta*  
800 *Palaeontologica Polonica*. 47 (3), 493–506.

801 Gheerbrant, E., Sudre, J., Cappetta, H., Mourer-Chauvire, C., Bourdon, E., Iarochene, M., Amaghaz, M., Bouya,  
802 B., 2003. Les localités à mammifères des carrières de Grand Daoui, Bassin des Ouled Abdoun, Maroc,  
803 Yprésien : premier état des lieux. *Bulletin de la Société Géologique de France* 174, 279–293.

804 Gheerbrant, E., Sudre, J., Tassy, P., Amaghaz, M., Bouya, B., Iarochène, M., 2005. "Nouvelles données sur  
805 *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Eocene inférieur du Maroc, apports à la  
806 phylogeny of the Proboscidea et the ongulés lophodontes". *Geodiversitas*. 27 (2), 239–333.

807 Gheerbrant, E., Bouya, B., Amaghaz, M., 2012. Dental and cranial anatomy of *Eritherium azzouzorom* from the  
808 Paleocene of Morocco, earliest known proboscidean mammal. *Palaeontographica, A* 297, 151–183.

809 Gheerbrant, E., Amaghaz, M., Bouya, B., Goussard, F., Letenneur, C., 2014. *Ocepeia* (middle Paleocene of  
810 Morocco): the oldest skull of an afrotherian mammal. *PLOS One* 9, 1–30 (DOI:  
811 10.1371/journal.pone.0089739).

812 Gheerbrant, E., Cappetta, H., Lapparent de Broin, F. de, Rage, J.-C., and Tabuce, R., 2017. Les faunes de  
813 vertébrés marins et terrestres du Paléogène du Bassin d'Ouarzazate, Maroc, in Zouhri, S. ed.,  
814 Paléontologie des Vertébrés du Maroc: état des connaissances. Mémoire de la Société Géologique de  
815 France, v. 180, p. 485–525.

816 Gheerbrant, E., Schmitt, A., Kocsis, L., 2018. Early African fossils elucidate the origin of embrithopod mammals.  
817 – *Current Biology* 28, 1–7. – <https://doi.org/10.1016/j.cub.2018.05.032>

818 Gheerbrant, E., Khaldoune, F., Schmitt, A., Tabuce, R., 2020. Earliest embrithopod mammals (Afrotheria,  
819 Tethytheria) from the Early Eocene of Morocco: anatomy, systematics and phylogenetic significance.  
820 *Journal of Mammal Evolution*. <https://doi.org/10.1007/s10914-020-09509-6>

821 Goettig, P., Magdolen, V., Brandstetter, H., 2010. Natural and synthetic inhibitors of kallikrein-related  
822 peptidases (KLKs). *Biochimie* 92, 1546–1567.

823 Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., de Graciansky, P.-C., Vail, P.R., 1998. Mesozoic and Cenozoic  
824 sequence stratigraphy of European basins. *SEPM Spec. Publ.* 60, 3–13.

825 Harrell, T.L., Pérez-Huerta, A., Phillips, G., 2016. Strontium isotope age-dating of fossil shark tooth enameloid  
826 from the Upper Cretaceous Strata of Alabama and Mississippi, USA. *Cretac. Res.* 62, 1–12.

827 Herbig, H.G., Gregor H.J., 1990. The mangrove-forming palm *Nypa* from the early Paleogene of southern  
828 Morocco. *Paleoenvironment and paleoclimate*. In: *Géologie Méditerranéenne*. Tome 17, numéro 2,  
829 1990. pp. 123–137.

830 Herwartz, D., Tütken, T., Münker, C., Jochum, K.P., Stoll, B., Sander, P.M., 2011. Timescales and mechanisms of  
831 REE and Hf uptake in fossil bones. *Geochim. Cosmochim. Acta* 75, 82–105.

832 Herwartz, D., Tütken, T., Jochum, K.P., Sander, P.M., 2013. Rare earth element systematics of fossil bone  
833 revealed by LA-ICPMS analysis. *Geochim. Cosmochim. Acta* 103, 161–183.

834 Hodell, D.A., Kamenov, G.D., Hathorne, E.C., Zachos, J.C., Röhl, U., Westerhold, T., 2007. Variations in the  
835 strontium isotope composition of seawater during the Paleocene and early Eocene from ODP Leg 208  
836 (Walvis Ridge). *Geochem Geophys Geosyst* 8:Q09001. doi:10.1029/2007GC001607

837 Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Tracking mammoths and mastodons: reconstruction  
838 of migratory behavior using strontium isotope ratios. *Geology* 27, 439–442.

839 Hyland, G.E., Sheldon, D.N., Cotton, M.J. 2017. Constraining the early Eocene climatic optimum: A terrestrial  
840 interhemispheric comparison. *GSA Bulletin*, 129 (1-2), 244–252.

841 Ingram, B.L., 1995. High-resolution dating of deep-sea clays using Sr isotopes in fossil fish teeth. *Earth and*  
842 *Planetary Science Letters* 134, 545–555.

843 Knidiri, A., Daoudi, L., El Ouahabi, M., Rhouta, B., Rocha, F., Fagel, N., 2014. Palaeogeographic controls on  
844 palygorskite occurrence in Maastrichtian-Palaeogene sediments of the western High Atlas and Meseta  
845 Basins (Morocco). *Clay Minerals* 49, 595–608.

846 Kocsis, L., Vennemann, T.W., Fontignie, D., 2007. Migration of sharks into freshwater systems during the  
847 Miocene and implications for Alpine paleoelevation. *Geology*, 35, 451–454.

848 Kocsis, L., Osi, A., Vennemann, T.W., Trueman, N.C., Palmer, R.M., 2009. Geochemical study of vertebrate  
849 fossils from the Upper Cretaceous (Santonian) Csehbánya formation (Hungary): evidence for a

850 freshwater habitat of mosasaurs and pycnodont fish. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280,  
851 532–542.

852 Kocsis, L., Trueman, C.N., Palmer, M., 2010. Protracted diagenetic alteration of REE contents in fossil  
853 bioapatites: direct evidence from Lu–Hf isotope systematics. *Geochim. Cosmochim. Acta* 74, 6077–  
854 6092.

855 Kocsis, L., Ounis, A., Chaabani F., Salah, N.M., 2013. Paleoenvironmental conditions and strontium isotope  
856 stratigraphy in the Paleogene Gafsa Basin (Tunisia) deduced from geochemical analyses of phosphatic  
857 fossils. *International Journal of Earth Sciences* 102, 1111–1129.

858 Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., Amaghaz, M., 2014a. Comprehensive stable  
859 isotope investigation of marine biogenic apatite from the late Cretaceous-early Eocene phosphate beds  
860 of Morocco. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 394, 74–88.

861 Kocsis, L., Ozsvart, P., Becker, D., Ziegler, R., Scherler, L., Codrea, V., 2014b. Orogeny forced terrestrial climate  
862 variation during the late Eocene-early Oligocene in Europe. *Geology* 42, 727–730.  
863 <http://dx.doi.org/10.1130/g35673.1>.

864 Kocsis, L., Vennemann, T., Ulianov, A., Brunnschweiler, J.M., 2015. Tracing bull shark (*Carcharhinus leucas*)  
865 freshwater habitats in Fiji by chemical and isotopic compositions of their teeth. *Environ. Biol. Fish* 98  
866 (6), 1609–1622.

867 Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Ulianov, A., Chiaradia, M., Bardet, N., 2016. Gradual  
868 changes in upwelled seawater conditions (redox, pH) from the late Cretaceous through early Paleogene  
869 at the northwest coast of Africa: Negative Ce anomaly trend recorded in fossil bio-apatite. *Chemical  
870 Geology* 421, 44–54.

871 Kohn, M.J., 1996. Predicting animal  $\delta O-18$ : Accounting for diet and physiological adaptation. *Geochim.  
872 Cosmochim. Acta* 60, 4811–4829. [http://dx.doi.org/10.1016/s0016-7037\(96\)00240-2](http://dx.doi.org/10.1016/s0016-7037(96)00240-2).

873 Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and  
874 (paleo)climate. *National Academy of Sciences Proceedings*, v. 107, p. 19691–19695,  
875 doi:10.1073/pnas.1004933107.

876 Kohn, M.J., Cerling, T.E., 2002, Stable isotopes of biological apatite, in Kohn, M.L., et al., eds., *Phosphates:  
877 Geochemical, geobiological and materials importance: Mineralogical Society of America Reviews in  
878 Mineralogy Volume 48*, p. 455–488.

879 Kowal-Linka, M., Jochum, K.P., Surmik, D., 2014. LA-ICP-MS analysis of rare earth elements in marine reptile  
880 bones from the Middle Triassic bonebed (Upper Silesia, S Poland): impact of long-lasting diagenesis, and  
881 factors controlling the uptake. *Chem. Geol.* 363, 213–228.

882 Lécuyer, C., Reynard, B., Grandjean, P., 2004. Rare earth element evolution of Phanerozoic seawater recorded  
883 in biogenic apatites. *Chem. Geol.* 204, 63–102.

884 Liu, A.G.S.C., Seiffert, E.R., Simons, E.L., 2008. Stable isotope evidence for an amphibious phase in early  
885 proboscidean evolution. *Proceedings of the National Academy of Sciences* 105, 5786–5791.  
886 <https://doi.org/10.1073/pnas.0800884105>

887 Lucas, J., Prevôt-Lucas, L., 1995. Tethyan phosphates and bioproductites. In: Nairn, A.E. (Ed.), *The Ocean Basins  
888 and Margins. The Tethys Ocean*, vol. 8. Plenum Press, pp. 367–391.

889 Mahboubi, S., Bocherens, H., Scheffler, M., Benammi, M., Jaeger, J.-J., 2014. Was the Early Eocene  
890 proboscidean *Numidotherium koholense* semi-aquatic or terrestrial? Evidence from stable isotopes and  
891 bone histology. *Comptes Rendus Palevol* 13, 501–509. <https://doi.org/10.1016/j.crpv.2014.01.002>

892 McArthur, J.M., Howarth, R.J., Shields, G.A., Zhou, Y. 2020. Strontium isotope stratigraphy, Chapter 7. In:  
893 Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *A Geologic Time Scale*, Elsevier B.V., Vol 1 of  
894 2, pp. 211–238.

895 MacFadden, B.J., Labs-Hochstein, J., Hulbert Jr., R.C., Baskin, J.A., 2007. Revised age of the late Neogene terror  
896 bird (*Titanis*) in North America during the Great American interchange. *Geology* 35, 123–126.

897 McLennan, S.M. 1989. Rare earth elements in sedimentary rocks: Influence of provenance and sedimentary  
898 processes. In: Lipin RB, McKay AG (Eds.), *Geochemistry and Mineralogy of Rare Earth Elements. Review  
899 in Mineralogy and Geochemistry* vol. 21, pp. 169–200.

900 Metzger, C.A., Terry, D.O., Grandstaff, D.E., 2004. Effect of paleosol formation on rare earth element  
901 signatures in fossil bone. *Geology* 32, 467–500.

902 Mohr, B., 1986. Palynologischer Nachweis eines Mangrovenbiotops in der Südatlas-Randzone (Marokko) und  
903 seine paläoökologische Bedeutung. *Documenta naturae* 33, 20–28.

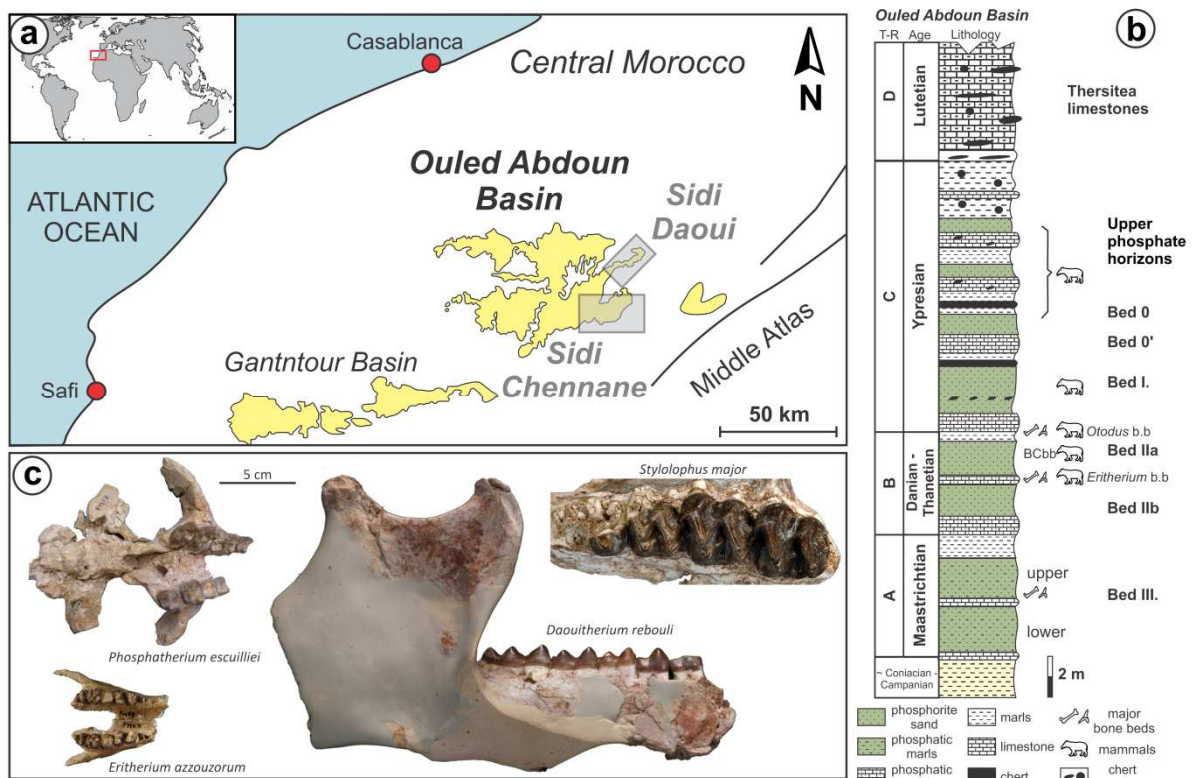
904 Mohr, B., Fechner, G., 1986. Eine eozäne Mikroflora (Sporomorphae und Dinoflagellaten-Zysten) aus der  
905 Südatlas-Randzone westlich Boumalne du Dadès (Marokko). *Berl. Geowiss. Abh. A.* 66, 414–481.

- 906 Mouflih, M., 2015. Les phosphates du Maroc central et du Moyen Atlas (Maastrichtien-Lutétien, Maroc):  
907 Sédimentologie, stratigraphie séquentielle, contexte génétique et valorisation. Doctorat d'Etat Es-  
908 sciences. Université Cadi Ayyad de Marrakech, Maroc 246 p.
- 909 Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes  
910 (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc (Maastrichtien-Lutétien basal).  
911 Systématique, biostratigraphie, évolution et dynamique des faunes. *Palaeo-Ichthyologica* 8, 1–327.
- 912 Office Chérifien des Phosphates, 1989. The phosphates basins of Morocco. In: Notholt, A.J.G., Sheldon, R.P.,  
913 Davidson, D.F. (Eds.), *Phosphates Deposits of the World, Phosphate Rock Resources*. Cambridge  
914 University Press, Cambridge, pp. 301–311.
- 915 Ollivier-Pierre, M.F., 1982. La microflore du Paléocène et de l'Eocène des séries phosphatées des gantour  
916 (Maroc). *Sci. Géol. Bull.* 35 (3), 117–127.
- 917 Pearce, N.J.G., Perkins, W.T., Westgate, J.A., Gorton, M.P., Jackson, S.E., Neal, C.R., Chenery, S.P., 1997. A  
918 compilation of new and published major and trace element data for NIST SRM 610 and NIST SRM 612  
919 glass reference materials. *Geostand. Geoanal. Res.* 21, 115–144.
- 920 Pearson, P.N., Palmer, M.R., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years.  
921 *Nature* 406, 695–699.
- 922 Pereda Suberbiola, X., Bardet, N., Iarochène, M., Bouya, B., Amaghaz, M., 2004. The first record of a sauropod  
923 dinosaur from the Late Cretaceous phosphates of Morocco. *Journal of African Earth Sciences* 40, 81–88.
- 924 Picard, P., Lécuyer, C., Barrat, J.-A., Garcia, J.-P., Dromart, G., Sheppard, S.M.F., 2002. Rare earth element  
925 contents of Jurassic fish and reptile teeth and their potential relation to seawater composition (Anglo-  
926 Paris Basin, France and England). *Chem. Geol.* 186, 1–16.
- 927 Pin, C., Briot, D., Bassin, C., Poitrasson, F., 1994. Concomitant separation of strontium and samarium–  
928 neodymium for isotopic analysis in silicate samples, based on specific extraction chromatography. *Anal.*  
929 *Chim. Acta* 298, 209–217.
- 930 Rauscher, R., 1985. Les dinokystes, des outils stratigraphiques pour les séries phosphatées. Application aux  
931 phosphorides du Maroc. *Sci. Géol. Bull.* 77, 69–74.
- 932 Reynard, B., Balter, V., 2014. Trace elements and their isotopes in bones and teeth: Diet, environments,  
933 diagenesis, and dating of archeological and paleontological samples. *Palaeogeogr. Palaeoclimatol.*  
934 *Palaeoecol.* 416, 4–16
- 935 Reynard, B., Lécuyer, C., Grandjean, P., 1999. Crystal–chemical controls on rare earth element concentrations  
936 in fossil biogenic apatites and implications for paleoenvironmental reconstructions. *Chem. Geol.* 155,  
937 233–241.
- 938 Schubert, A.B., Jahren, A.H., 2012. The effect of atmospheric CO<sub>2</sub> concentration on carbon isotope  
939 fractionation in C<sub>3</sub> land plants. *Geochimica et Cosmochimica Acta* 96, 29–43.
- 940 Secord, R., Wing, L.S., Chew, A., 2008. Stable Isotopes in Early Eocene Mammals as Indicators of Forest Canopy  
941 Structure and Resource Partitioning. *Paleobiology*, 34(2), 282–300.
- 942 Shields, G.A., Webb, G.E., 2004. Has the REE composition of seawater changed over geologic time. *Chem. Geol.*  
943 204, 103–107.
- 944 Simmer, J.P., Hu, Y., Lertlam, R., Yamakoshi, Y., Hu, J.C.C., 2009. Hypomaturation enamel defects in *Klk4*  
945 knockout/*LacZ* knockin mice. *J Biol Chem* 284, 19110–19121.
- 946 Snedden, J.W., Liu, C., 2010. A compilation of Phanerozoic sea level change, coastal onlaps, and recommended  
947 sequence designations: AAPG Search and Discovery article 40594,  
948 [http://www.searchanddiscovery.net/documents/2010/40594snedden/ndx\\_snedden.pdf](http://www.searchanddiscovery.net/documents/2010/40594snedden/ndx_snedden.pdf) (accessed  
949 October 2020)
- 950 Soncini, M.-J., 1990. Palynologie des phosphates des Oulad Abdoun (Maroc). Biostratigraphie et  
951 environnements de lab phosphatogénèse dans le cadre de la crise Crétacé/Tertiaire. Université Louis  
952 Pasteur, Strasbourg, p. 243. Ph.D. thesis.
- 953 Staron, R.M., Grandstaff, B.S., Gallagher, W.B., Grandstaff, D.E., 2001. REE signatures in vertebrate fossils from  
954 Sewell, NJ: implications for location of the K–T boundary. *Palaios* 16, 255–265.
- 955 Suarez, C.A., Macpherson, G.L., González, L.A., Grandstaff, D.E., 2010. Heterogeneous rare earth element (REE)  
956 patterns and concentrations in a fossil bone: implications for the use of REE in vertebrate taphonomy  
957 and fossilisation history. *Geochim. Cosmochim. Acta* 74, 2970–2988.
- 958 Trueman, C.N., Tuross, N., 2002. Trace elements in recent and fossil bone apatite. In: Kohn, M.J., Rakovan, J.,  
959 Hughes, J.M. (Eds.), *Phosphates: Geochemical, Geobiological, and Materials Importance*. Review in  
960 *Mineralogy and Geochemistry* vol. 48, pp. 489–521.
- 961 Trueman, C.N., Benton, M.J., Palmer, M.R., 2003. Geochemical taphonomy of shallow marine vertebrate  
962 assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 197, 151–169.

963 Trueman, C.N., Kocsis, L., Palmer, M.R., Dewdney, C., 2011. Fractionation of rare earth elements within bone  
964 mineral: a natural cation exchange system. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 124–132.  
965 Tütken, T., Vennemann, W.T., Janz, H., Heizmann, E.P.J. 2006. Palaeoenvironment and palaeoclimate of the  
966 Middle Miocene lake in the Steinheim basin, SW Germany: A reconstruction from C, O, and Sr isotopes  
967 of fossil remains. *Palaeogeography, Palaeoclimatology, Palaeoecology* 241, 457–491.  
968 Tütken, T., Vennemann, T.W., Pfretzschner, H.-U., 2008. Early diagenesis of bone and tooth apatite in fluvial  
969 and marine settings: constraints from combined oxygen isotope, nitrogen and REE analysis.  
970 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 254–268.  
971 Tütken, T., 2014. Isotope compositions (C, O, Sr, Nd) of vertebrate fossils from the Middle Eocene oil shale of  
972 Messel, Germany: Implications for their taphonomy and palaeoenvironment. *Palaeogeography,*  
973 *Palaeoclimatology, Palaeoecology* 416, 92–109  
974 Vail, P.R., Audemard, E., Bowman, S.A., Eisner, P.N., Perez-Crus, C., 1991. The stratigraphic signatures of  
975 tectonics, eustasy and sedimentology—an overview, in Einsele, G., Ricken, W., and Seilacher, A., eds.,  
976 *Cycles and events in stratigraphy: Springer-Verlag, Berlin*, p. 617–659.  
977 van der Meer, D.G., van den Berg van Saparoea, A.P., van Hinsbergen, D., van de Weg, R., Godderis, Y., Le Hir,  
978 G., Donnadiou, Y., 2017. Reconstructing first-order changes in sea level during the Phanerozoic and  
979 Neoproterozoic using strontium isotopes: *Gondwana Research* 44, 22–34.  
980 van Hinsbergen, D.J.J., de Groot, L.V., van Schaik, S.J., Spakman, W., Bijl, P.K., Sluijs, A., Langereis, C.G.,  
981 Brinkhuis, H., 2015. A paleolatitude calculator for paleoclimate studies. *PLoS ONE* 10, e0126946–21.  
982 <http://dx.doi.org/10.1371/journal.pone.0126946>  
983 Wei, L., Yan, C., Ye, B., Guo, X., 2008. Effects of Salinity on Leaf  $\delta^{13}\text{C}$  in Three Dominant Mangrove Species  
984 along Salinity Gradients in an Estuarine Wetland, Southeast China. *J. of Coastal Research*, 241, 267–272.  
985 White, W.M., 1998. The Ocean as a Chemical system. *Geochemistry, an on-line textbook*, vol. 15. pp 645–701.  
986 Yans, J., Amaghazaz, M., Bouya, B., Cappetta, H., Iacumin, P., Kocsis, L., Mouflih, M., Selloum, O., Sen, S.,  
987 Storme, J.-Y., Gheerbrant, E., 2014. First carbon isotope chemostratigraphy of the Ouled Abdoun  
988 phosphate Basin, Morocco; implications for dating and evolution of earliest African placental mammals.  
989 *Gondwana Research* 25, 257–269.  
990 Zazzo, A., Lécuyer, C., Mariotti, A., 2004. Experimentally-controlled carbon and oxygen isotope exchange  
991 between bioapatites and water under inorganic and microbially-mediated conditions: *Geochimica et*  
992 *Cosmochimica Acta* 68, 1–12, doi:10.1016/S0016-7037(03)00278-3.  
993 Žigaitė, Ž., Fadel, A., Blom, H., Pérez-Huerta, A., Jeffries, T., Märss, T., Ahlberg, P.E., 2016. Palaeoenvironments  
994 revealed from rare earth element systematics in vertebrate bioapatite from the Lower Devonian of  
995 Svalbard. In: Melchin, M., Jisou, J. (Eds.), *Canadian Journal of Earth Sciences*, vol. 53. pp. 788–794 8.  
996 Žigaitė, Ž., Qvarnström, M., Bancroft, A., Pérez-Huerta, A., Blom, H., Ahlberg, P.E., 2020. Trace and rare earth  
997 element compositions of Silurian conodonts from the Vesiku Bone Bed: Histological and  
998 palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 549 109449.  
999

1001 **Figure captions**

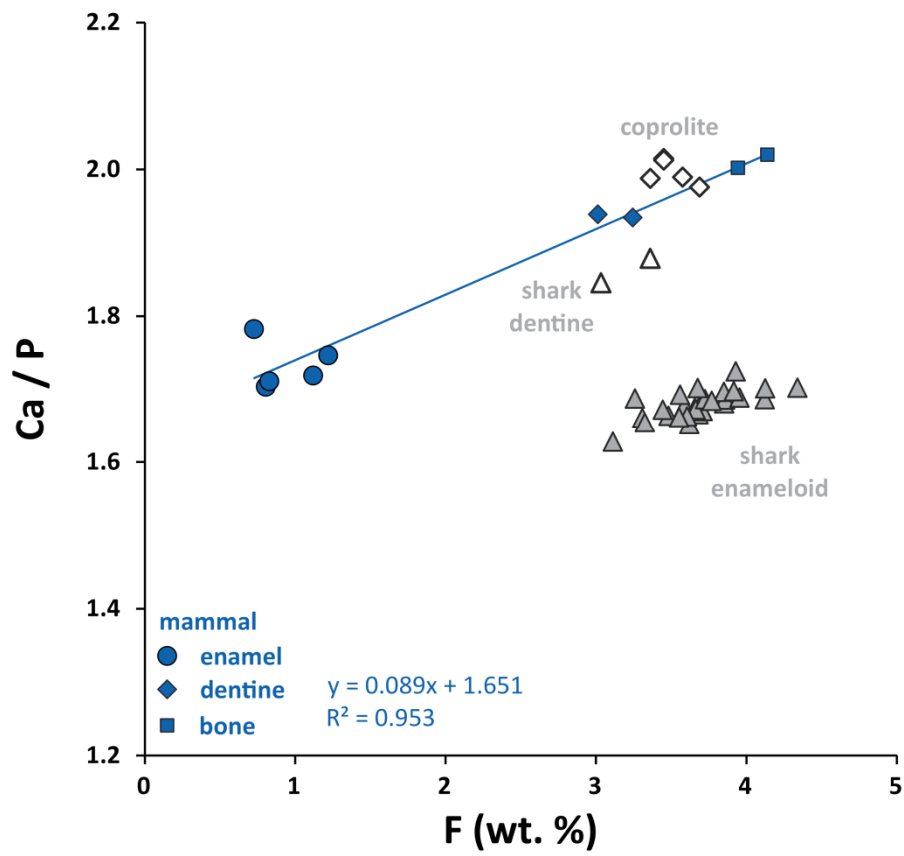
1002 **Figure 1 (a)** The origins of the fossils from the Ouled Abdoun Basin in Morocco studied here.  
 1003 Quarries in the Sidi Daoui and Sidi Chennane (grey boxes) are the regions from which most  
 1004 of the remains were reported. The background geochemical data are also derived here (see  
 1005 **Figure 5**). **(b)** Generalized stratigraphic log of the Ouled Abdoun Basin. Note the major bone  
 1006 beds and the mammal-bearing layers, however, many specimens were obtained without an  
 1007 exact stratigraphic position. Abbreviation: BCbb – big coprolite bone bed. **(c)** Examples of  
 1008 some of the mammals found in the Ouled Abdoun phosphate series, successively from  
 1009 lowermost to uppermost levels: *Eritherium azzouzorom* (skull rostrum with teeth in ventral  
 1010 view; [Gheerbrant, 2009](#)), the earliest known proboscidean, lower bone bed of bed IIa,  
 1011 Selandian; *Phosphatherium escuilliei* (skull in ventral view; [Gheerbrant et al., 2005](#)), early  
 1012 proboscidean, intercalary beds II/I, early Ypresian; *Daouitherium rebouli* (lower jaw ML  
 1013 20269987 in lateral view), the first large proboscidean ([Gheerbrant et al., 2002](#)), upper  
 1014 phosphates levels (bed 0?), middle Ypresian; *Stylolophus major* (maxillary with teeth;  
 1015 [Gheerbrant et al., 2018, 2020](#)), earliest known embrithopod with *S. minor*, uppermost  
 1016 phosphates levels, bed 0 or sillons, middle Ypresian.



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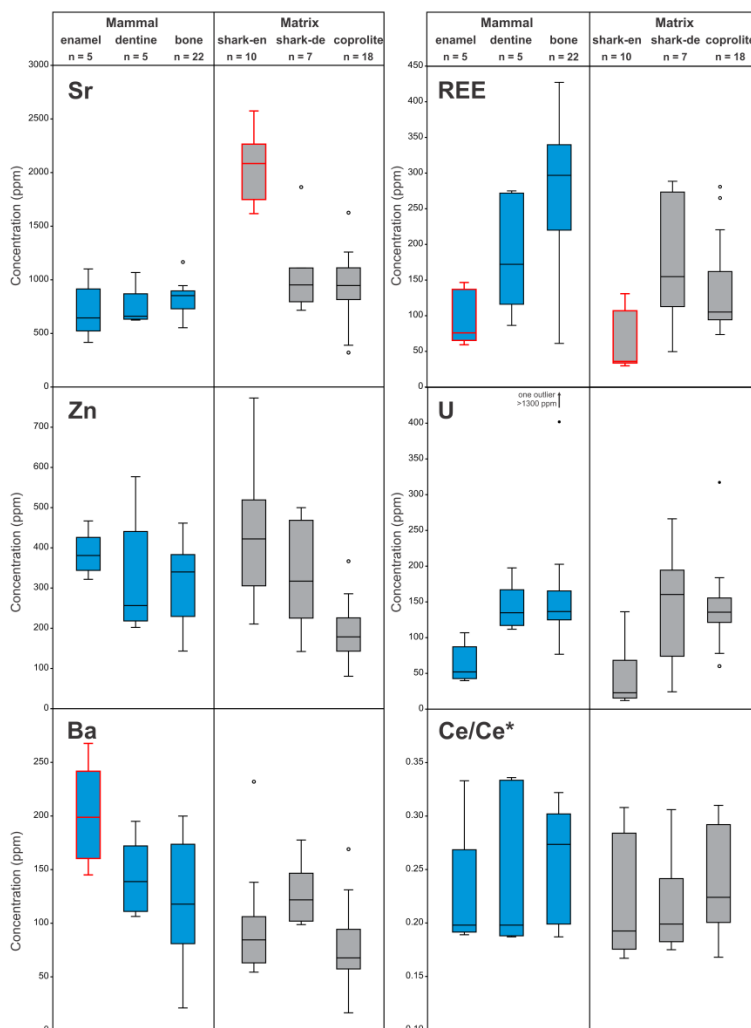
1019 **Figure 2** Major element compositions of selected mammals, shark teeth and coprolites from  
1020 the Ouled Abdoun Basin.



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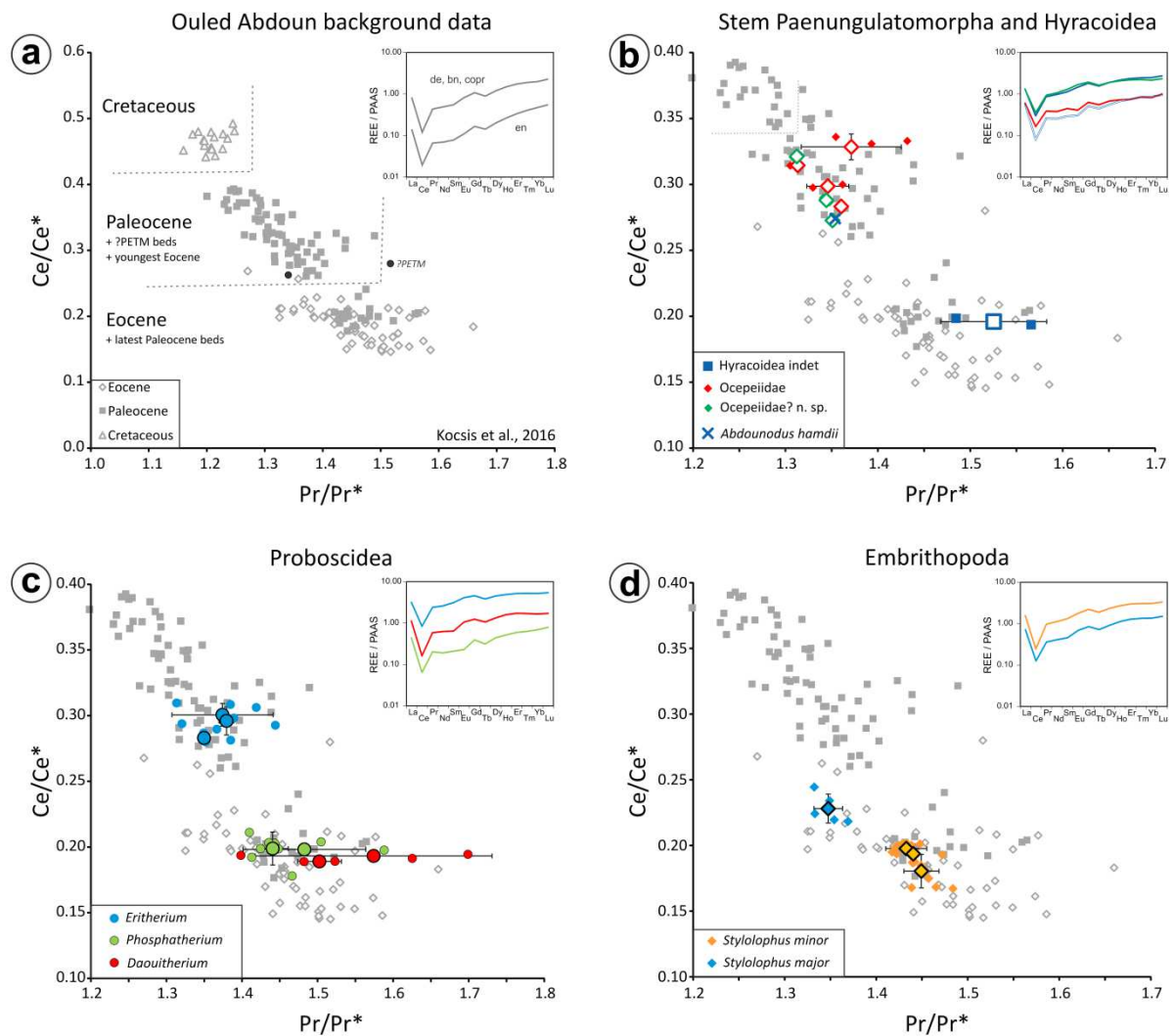
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1023 **Figure 3** Boxplots of selected trace elements. The label “Mammal” reflects data directly  
 1024 analyzed from the mammal remains (tooth enamel, dentine, and bone), while the label  
 1025 “Matrix” refers to data from fossils derived from the sediment matrix (shark tooth  
 1026 enameloid, dentine, and coprolite) related to the mammals. Student’s t-tests were  
 1027 performed to check for statistical differences among these groups (Supplementary Material  
 1028 Table-4). Note that, Sr content in shark tooth enameloid and Ba content in mammal enamel  
 1029 are significantly higher than in the rest of the materials (marked red). Zinc concentration is  
 1030 the highest in enamel and enameloid, and both differ significantly from the coprolite data,  
 1031 whereas shark tooth enameloid is also statistically dissimilar from the dentine and bone  
 1032 data. The REE concentration is the lowest in the enamel/enameloid with significant  
 1033 differences from the other materials (marked red). Distribution of U content among the  
 1034 materials mimics more or less that of the REEs, however with various significances among  
 1035 the different groups (see Supplementary Material Table-4). The Ce/Ce\* data yielded no  
 1036 statistical differences among the groups.





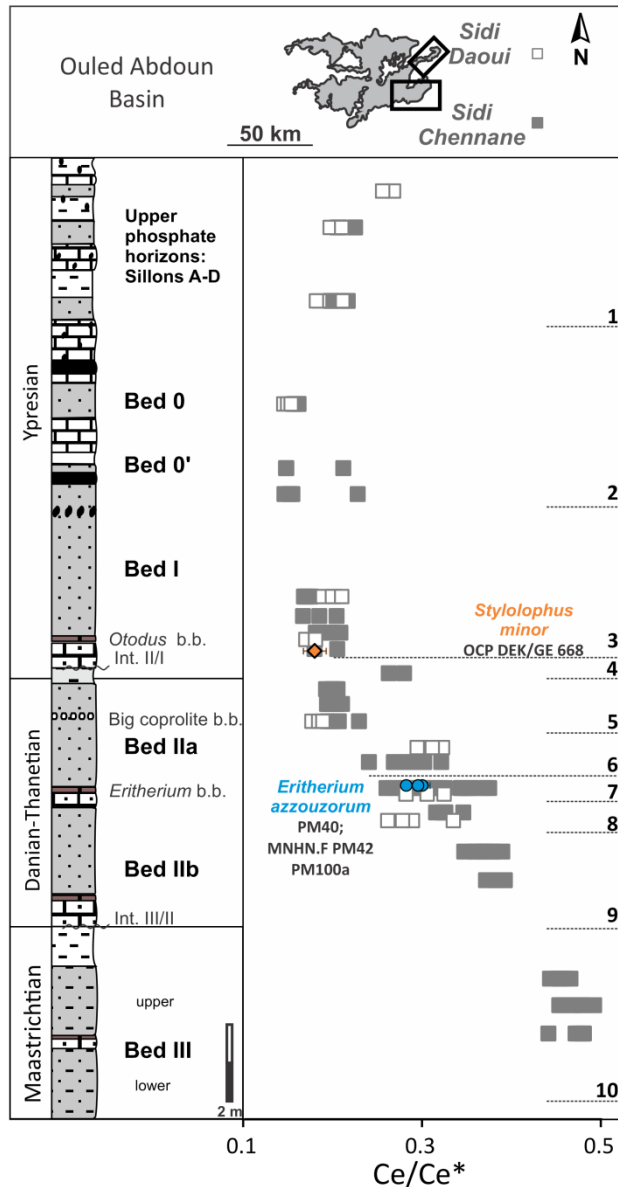
1038 **Figure 4** Ce/Ce\* and Pr/Pr\* variations among the samples. **(a)** Background data from the  
 1039 Ouled Abdoun Basin derived from fish teeth, bones and coprolites (Kocsis et al., 2016). Note  
 1040 the time-wise trending of the samples in the basin. The few overlapping samples show  
 1041 meaningful stratigraphic separation, see Figure 5. **(b-d)** Comparisons of the Paleocene and  
 1042 Eocene background data with the various mammal groups being investigated. Note that the  
 1043 samples are better separated by Ce/Ce\* than by Pr/Pr\*. Inset figures display examples of  
 1044 PAAS normalized REE patterns. Note the similarities in the REE distributions among the  
 1045 various materials (a) and taxa (b-d).



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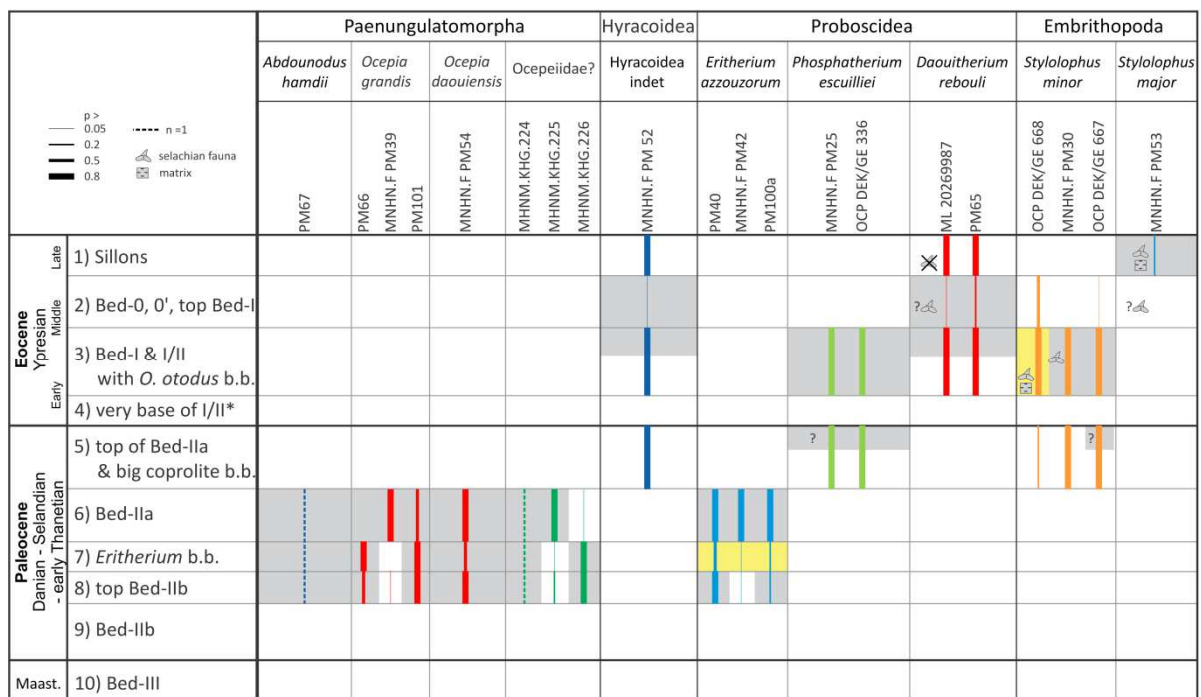
1048 **Figure 5** Stratigraphic variation of Ce/Ce\* in the Ouled Abdoun Basin based on [Kocsis et al.](#)  
 1049 [\(2016\)](#) and new data provided in Supplementary Material Table-1. Note that the data are  
 1050 derived from two quarrying areas: Sidi Daoui and Sidi Chennane. Based on the variation of  
 1051 the Ce/Ce\* values the section is divided into 10 horizons (see text and Table 3). Int. III/II and  
 1052 Int. II/I refer to intercalary beds respectively between Bed III and II, and, Bed II and I. Note  
 1053 that the Ce/Ce\* data for the few mammal remains (*S. minor* and *E. azzouzorum*) with known  
 1054 stratigraphic origins fit well with the background dataset.



1055

1056

1057 **Figure 6** Stratigraphic origins of the mammal remains from the Ouled Abdoun Basin studied  
 1058 here, inferred from comparisons of their mean Ce/Ce\* ratios with the average stratigraphic  
 1059 values of the 10 chemostratigraphic horizons (see also **Table 3**). Note that the thickness of  
 1060 the lines reflects different probabilities. Where only one specimen was analyzed a dashed  
 1061 line is used. In some cases, the composition of the sediment matrix and the selachian fauna  
 1062 (i.e., sharks and rays) give further clue about the possible provenance. The vertical  
 1063 extension of the bar across several levels for some species does not necessarily indicate a  
 1064 wide stratigraphic range, but the best probability of their stratigraphic origin following the  
 1065 Ce/Ce\* chemostratigraphy. However, when other factors (e.g., the sedimentary matrix and  
 1066 related fauna) are considered, their provenance can be reduced further, as indicated by the  
 1067 grey background. The yellow background is used for those fossils whose stratigraphic origin  
 1068 was known previously (see **Figure 5**).

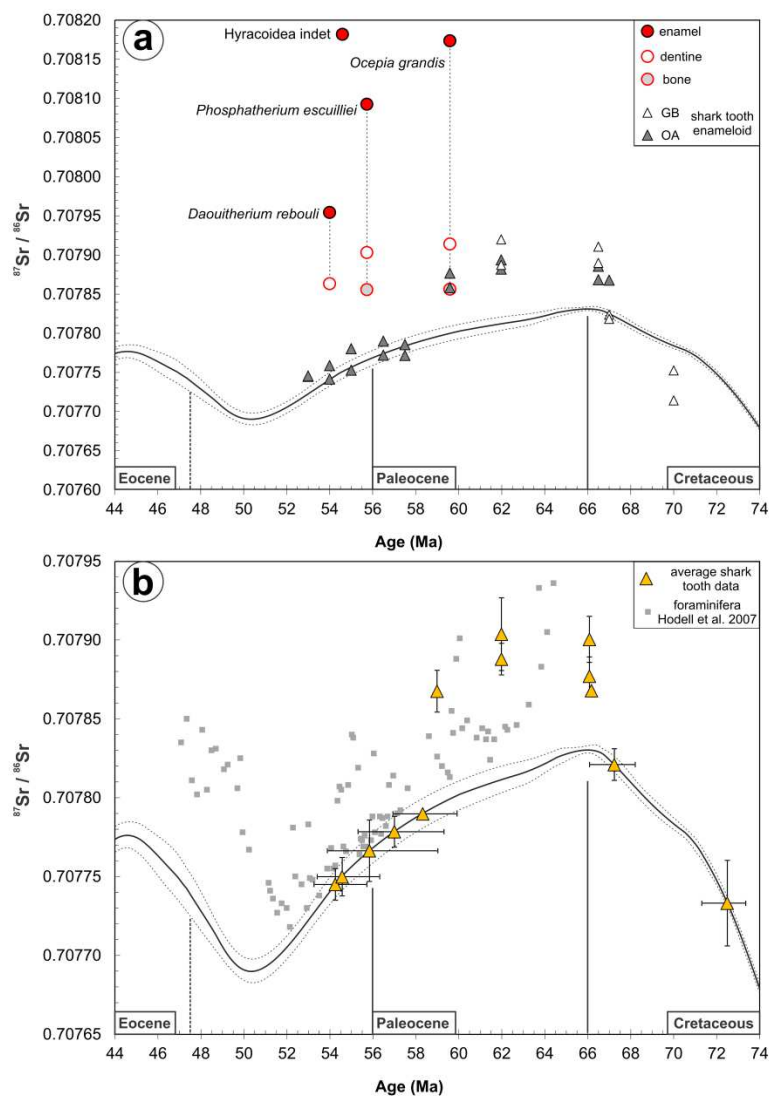


\*possibly reflect reworked element from older Paleocene

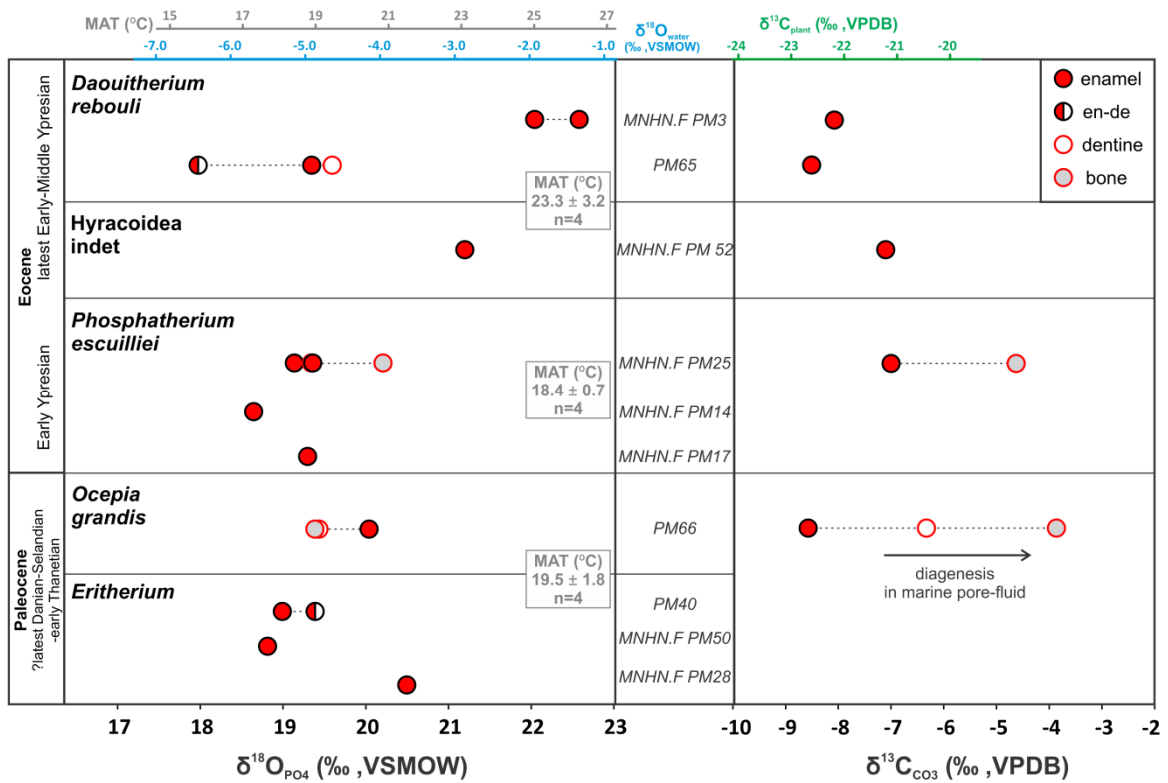
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1071 **Figure 7** Strontium isotope variation and its comparison with the global Sr-evolution curve  
 1072 (McArthur et al., 2020). Dashed lines represent the 95% confidence limits. **(a)** Mammal  
 1073 samples with circles. Note that these data are well above the open ocean Sr-evolution curve  
 1074 and the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios decrease from enamel to bone. The enamel end-members could  
 1075 reflect *in-vivo* Sr ratios, while the dentine and bone show various interactions with  
 1076 seawater. Triangles are individual shark tooth enameloid analyses from the Ouled Abdoun  
 1077 (OA) and Ganntour (GB) basins. The data are plotted according to stratigraphic occurrence  
 1078 and predicted ages (see Supplementary material Table-5). **(b)** Layer averaged  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios  
 1079 of shark tooth enameloid from the previous graph for the phosphate series (triangles) and  
 1080 foraminifera Sr-isotope data from Hodell et al. (2007). The average data are plotted  
 1081 according to ages derived from McArthur et al. (2020). Note that the latest Cretaceous and  
 1082 most of the Paleocene are above the Sr-evolution curve.



1084 **Figure 8** Stable isotope compositions of selected mammal taxa and related ecological and  
 1085 environmental parameters. **(a)** Oxygen isotopic composition of phosphate. The derived  
 1086 isotopic composition of the ingested water and the mean annual temperature (MAT) are  
 1087 calculated based on [Amiot et al. \(2004\)](#). **(b)** Carbon isotopic composition of the structural  
 1088 carbonate and the calculated plant diet isotopic composition after [Kohn and Cerling \(2002\)](#).  
 1089 Note the increasing trend from enamel to bone, indicating an alteration in the presence of  
 1090 seawater.



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1107 **Table 3** Tukey's pairwise tests comparing the samples separately with designated horizons.

1108 In the case of Eocene mammals Horizons 1-5, while for the Paleocene taxa Horizons 5-10

1109 were used. Note that only the probability values are listed. Layers with highlighted values

1110 could be considered as a possible provenance for the given mammal fossils, while the

1111 strikethrough numbers indicate invalid scenarios. See also text and **Figure 6**.

Eocene mammals												
Tukey's pairwise test		MNHN.F PM53	OCF DEK/GE 668	MNHN.F PM30	OCF DEK/GE 667	MNHN.F PM25	OCF DEK/GE 336	ML 20269987	PM65	MNHN.F PM 52		
p (same) relative to the horizons (1-5)		<i>S. major</i>	<i>S. minor</i>	<i>S. minor</i>	<i>S. minor</i>	<i>P. escuillei</i>	<i>P. escuillei</i>	<i>D. rebouli</i>	<i>D. rebouli</i>	Hyracoidea indet		
H. Age	Beds	n	5	8	5	5	4	5	3	2		
1	late Ypresian	Sillons	22	0.30	0.19	0.98	0.90	0.99	0.99	0.92	0.81	0.98
2	latest Early - Middle Ypresian	Bed 0-0' & Top Bed I	14	< 0.05	0.56	< 0.05	0.07	< 0.05	< 0.05	0.12	0.34	0.12
3	early Ypresian	Bed-I & I/II	23	< 0.05	0.99	0.93	0.99	0.92	0.90	1.00	1.00	0.98
4	?PETM	base I/II	2	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
5	late Thanetian	Top Bed III & Big Copr Bed	18	0.10	0.47	1.00	1.00	1.00	1.00	1.00	0.97	1.00

Paleocene mammals											
Tukey's pairwise test		PM40	MNHN.F PM42	PM100a	PM66	MNHN.F PM39	PM101	MNHN.F PM54	MHNM.KHG.225	MHNM.KHG.226	
p (same) relative to the horizons (5-10)		<i>E. azzouorum</i>	<i>E. azzouorum</i>	<i>E. azzouorum</i>	<i>O. grandis</i>	<i>O. grandis</i>	<i>O. grandis</i>	<i>O. daouiensis</i>	<i>O. daouiensis</i>	<i>O. daouiensis</i>	
H. age	Beds	n	4	3	5	4	2	2	2	2	
5	late Thanetian	Top Bed-IIa & Big Copr Bed	18	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
6	Selandian-early Thanetian	Bed-IIa	10	0.99	0.96	1.00	< 0.05	0.98	0.53	1.00	1.00
7	Selandian-early Thanetian	Eritherium bone bed	30	0.49	< 0.05	0.17	0.96	< 0.05	1.00	0.59	0.11
8	Early Selandian-latest Danian	top Bed-IIb	11	0.85	0.06	0.49	0.73	0.14	1.00	0.87	0.30
9	earliest Selandian-late Danian	Bed-IIb	15	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
10	latest Maastrichtian	Bed-III	18	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

1112

1113 **Table 4** Tukey's pairwise tests among the Eocene and Paleocene mammal samples. Note

1114 that *S. major* is completely different from the rest of the Eocene fossils, while among the

1115 Paleocene samples some of the Ocepeiidae spp. (e.g., PM66 & MHNM.KHG.226) are

1116 somewhat different from the rest.

Eocene mammals										
Tukey's pairwise test	MNHN.F PM53	OCF DEK/GE 668	MNHN.F PM30	OCF DEK/GE 667	MNHN.F PM25	OCF DEK/GE 336	ML 20269987	PM65	MNHN.F PM 52	
Q / p (same)	<i>S. major</i>	<i>S. minor</i>	<i>S. minor</i>	<i>S. minor</i>	<i>P. escuillei</i>	<i>P. escuillei</i>	<i>D. rebouli</i>	<i>D. rebouli</i>	Hyracoidea indet	
<i>S. major</i>		< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	
<i>S. minor</i>	9.68		0.27	0.61	0.25	0.21	0.65	0.94	0.41	
<i>S. minor</i>	6.16	3.53		1.00	1.00	1.00	1.00	0.93	1.00	
<i>S. minor</i>	6.97	2.71	0.82		1.00	1.00	1.00	1.00	1.00	
<i>P. escuillei</i>	6.07	3.62	0.09	0.91		1.00	1.00	0.92	1.00	
<i>P. escuillei</i>	5.95	3.73	0.20	1.02	0.11		1.00	0.89	1.00	
<i>D. rebouli</i>	7.07	2.62	0.91	0.10	1.00	1.11		1.00	1.00	
<i>D. rebouli</i>	7.94	1.74	1.78	0.97	1.88	1.99	0.87		0.98	
Hyracoidea indet	6.52	3.16	0.37	0.45	0.46	0.57	0.54	1.42		

Paleocene mammals										
Tukey's pairwise test	PM40	MNHN.F PM42	PM100a	PM66	MNHN.F PM39	PM101	MNHN.F PM54	MHNM.KHG.225	MHNM.KHG.226	
Q / p (same)	<i>E. azzouorum</i>	<i>E. azzouorum</i>	<i>E. azzouorum</i>	<i>O. grandis</i>	<i>O. grandis</i>	<i>O. grandis</i>	<i>O. daouiensis</i>	<i>O. daouiensis</i>	<i>O. daouiensis</i>	
<i>E. azzouorum</i>		0.25	1.00	< 0.05	0.28	0.55	1.00	0.64	0.12	
<i>E. azzouorum</i>	3.70		0.63	< 0.05	1.00	< 0.05	0.36	1.00	< 0.05	
<i>Eritherium</i>	1.03	2.67		< 0.05	0.68	0.20	1.00	0.96	< 0.05	
<i>O. grandis</i>	5.78	9.48	6.81		< 0.05	0.53	< 0.05	< 0.05	0.98	
<i>O. grandis</i>	3.59	0.10	2.56	9.37		< 0.05	0.40	1.00	< 0.05	
<i>O. grandis</i>	2.86	6.56	3.90	2.92	6.46		0.40	< 0.05	0.98	
<i>O. daouiensis</i>	0.36	3.33	0.67	6.15	3.23	3.23		0.78	0.08	
<i>Ocepeiidae?</i>	2.66	1.04	1.63	8.44	0.94	5.52	2.29		0.00	
<i>Ocepeiidae?</i>	4.32	8.02	5.35	1.46	7.92	1.46	4.69	6.98		

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1118

1119 **Supplementary Data Tables**

1120 **SM Table 1** Supplementary trace element concentration and ratio data from Sidi Chennane  
1121 and Sidi Daoui areas, focusing on some of the bone beds: the *Eritherium* bone bed (base Bed  
1122 IIa), big coprolite bone bed (top Bed IIa), and *Otodus* bone bed (intercalary II/I). The Ce/Ce\*  
1123 and Pr/Pr\*ratios are plotted in [Figures 4 and 5](#) as a part of the background dataset.

1124

1125 **SM Table 2** Major element compositions of marine remains (shark teeth, coprolites) from  
1126 the Sidi Chennane quarry of the Ouled Abdoun Basin (see [Figure 2](#) in the paper).

1127

1128 **SM Table 3** Trace element concentrations, Ce/Ce\* and Pr/Pr\*ratios of the mammal  
1129 specimens and related matrix from the Ouled Abdoun Basin investigated here (see [Figures](#)  
1130 [3-5](#) in the paper).

1131

1132 **SM Table 4** Student's t-tests on selected geochemical data displayed as boxplots in [Figure 3](#).  
1133 The six different types of materials studied are mammal enamel, dentine, bones, and shark  
1134 tooth enameloid, dentine, and coprolites. Significant differences ( $p < 0.05$ ) are marked red,  
1135 whereas underlined data indicate unequal variances between the compared groups.

1136

1137 **SM Table 5** Strontium isotope ratios of shark tooth enameloid from the Ouled Abdoun Basin  
1138 (see [Figure 7](#) in the paper). Individual analyses are plotted in [Figure 7a](#), while the average  
1139 data and derived Sr-isotope ages based on [McArthur et al. \(2020\)](#) are in [Figure 7b](#).

1140

1141 **SM Table 6** Ten defined chemostratigraphic horizons and their average Ce/Ce\* values and  
1142 the related F and Student's t-test statistics. df- degree of freedom; p- probability.

1143 Underlined p-values for the F-test indicate significantly different variances. In this case, the  
1144 Student's t-tests were performed for unequal variance. The grey p-values for the Student's  
1145 t-test highlights horizon pairs for which the means of the Ce/Ce\* values do not differ  
1146 significantly.

1147

1148 **SM Table 7** Recovered selachian fauna and matrix data from a few mammal specimens  
1149 belonging to the species *S. minor*, *S. major*, and *D. rebouli*.