

# Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs

A. Hassler, J. E Martin, R. Amiot, T. Tacail, F. Arnaud Arnaud Godet, R.

Allain, V. Balter

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1	Calcium isotopes offer clues on resource partitioning among Cretaceous
2	predatory dinosaurs

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- 4 A. Hassler<sup>1</sup>, J.E. Martin<sup>1\*</sup>, R. Amiot<sup>1</sup>, T. Tacail<sup>1</sup>, F. Arnaud Godet<sup>1</sup>, R. Allain<sup>2</sup>, V. Balter<sup>1</sup>
- <sup>5</sup> <sup>1</sup>Univ. Lyon, ENS de Lyon, Université Claude Bernard Lyon 1, CNRS, UMR 5276 Laboratoire
- 6 de Géologie de Lyon: Terre, Planètes, Environnement, F-69342 46 Allée d'Italie, Lyon, France.
- <sup>7</sup> <sup>2</sup>Sorbonne Universités CR2P MNHN, CNRS, UPMC-Paris 6, Muséum national d'Histoire
- 8 naturelle, 57 rue Cuvier, CP 38, 75231 Paris cedex 05, France.
- 9 \*Correspondence to: jeremy.martin@ens-lyon.fr
- 10

11	Large predators are overabundant in mid-Cretaceous continental dinosaur assemblages of
12	North Africa. Such unbalanced ecosystem structure involves, among predatory dinosaurs,
13	typical abelisaurid or carcharodontosaurid theropods co-occurring with long-snouted
14	spinosaurids of debated ecology. Here, we report calcium isotope values from tooth enamel
15	(expressed as $\delta^{44/42}$ Ca) to investigate resource partitioning in mid-Cretaceous assemblages
16	from Niger (Gadoufaoua) and Morocco (Kem-Kem Beds). In both assemblages,
17	spinosaurids display a distinct isotopic signature, the most negative in our dataset. This
18	distinct taxonomic clustering in calcium isotope values observed between spinosaurids and
19	other predators provides unambiguous evidence for niche partitioning at the top of the
20	trophic chains: spinosaurids foraged on aquatic environments while abelisaurid and
21	carcharodontosaurid theropods relied almost exclusively on terrestrial resources.
22	
23	Keywords: Ecology; Cretaceous terrestrial ecosystems; dinosaurs; calcium isotopes;
24	spinosaurs; palaeodiet
25	

#### 26 **1.INTRODUCTION**

Dietary inference in extinct vertebrates allows addressing the structure of extinct food webs and remains critical for understanding how ecosystems were structured, and how these structures evolved with time and environmental changes. In modern ecosystems, the trophic cascades concept [1] illustrates the complex role of top carnivores in regulating, directly and indirectly, populations from subsequent trophic levels. By modulating the intensity of resource exploitation (top-down), along with productivity feedback loops (bottom-up), top predators can shape the structure of ecosystems. However, reconstructing long extinct ecosystems, such as those of the
 Mesozoic, remains challenging because taxa with unknown ecology and physiology dominated
 the scene.

In contrast to modern mammalian continental ecosystems where herbivores represent 36 most of the biomass of vertebrates, large predatory theropod dinosaurs were overabundant in 37 mid-Cretaceous continental biotas of North Africa. The origin and the significance of this 38 overabundance is debated [2,3] but recent studies have highlighted the peculiar nature of such 39 predator-dominated ecosystems [4,5]. These faunas include very large theropods such as 40 abelisaurids, carcharodontosaurids, and spinosaurids, which are all considered as having high 41 42 food requirements due to their elevated metabolic rates [6,7]. Their high abundance relative to herbivorous dinosaurs thus raises questions about how resources could be partitioned between 43 them. Due to their remarkable anatomy, spinosaurids have attracted attention with previous work 44 inferring a semi-aquatic lifestyle [7,8] associated to a diverse diet [4,5,9–18], although the 45 respective proportions of feeding sources, whether terrestrial or aquatic, remains unknown. 46 Indeed, if for some spinosaurids, trophic links can be assessed using direct evidence like stomach 47 content and feeding marks [10,16], such fossils remain rare and account for a short time window. 48 Morphology can also provide a wealth of data concerning potential trophic links, but 49 50 interpretations remain hypothetical due to the lack of modern analogues for spinosaurids and their ecosystem. The jaw morphology of spinosaurids has been repeatedly, albeit inexactly, 51 considered analogous to that of crocodiles [14,15] and has recently been compared to that of pike 52 53 conger eels [18], reflecting some uncertainty in palaeoecological inference when considering morphological evidence alone [19]. In this context, we investigate diet and resource partitioning 54 among mid-Cretaceous Saharan vertebrates using Ca isotopes ( $\delta^{44/42}$ Ca) of tooth enamel and 55

scale ganoine, a method that has previously proved informative both in modern [20-22] and 56 fossil vertebrate assemblages [22-25]. Because Ca is almost exclusively derived from food 57 among terrestrial vertebrates [20], the systematic change between the isotopic signature of their 58 food relative to their mineralized tissues allows inferring trophic levels and diet. Moreover, Ca is 59 the major constituent of the mineral phase of bone and tooth enamel, i.e. hydroxylapatite 60  $(Ca_{10}(PO_4)_6OH_2)$ , which gives the method two main advantages. First, the diagenetic 61 overprinting of biogenic Ca is unlikely to occur providing that secondary carbonates are absent 62 or have been leached accordingly [23]. Second, minute amounts of bone or tooth enamel sample 63  $(\sim 100 \ \mu g)$  is sufficient for a routine measurement of the Ca isotopic ratios. The technique is thus 64 applicable to precious fossils with minimal damages. 65

Our study is focused on fossils from the Aptian-Albian fluvial deposits of Gadoufaoua 66 (Niger, ~113 Ma ago) [26] and of the Cenomanian Kem Kem beds (Morocco, ~100 Ma ago) 67 [27]. In these vertebrate assemblages, crocodylomorphs, spinosaurids and non-spinosaurid 68 theropods are overabundant relative to herbivorous dinosaurs [11,26,27], making them typical 69 examples of North African mid-Cretaceous ecosystems. Despite age differences, the two 70 deposits share similarities in their environmental context and host a comparable diversity of 71 vertebrates. The analyzed specimens include fish, crocodylomorphs, pterosaurs, herbivorous 72 73 (sauropods, ornithopods) and predatory (theropod) dinosaurs, including spinosaurids. Fossils of the spinosaurids Suchomimus tenerensis and Cristatusaurus lapparenti [11,12] are found in 74 Gadoufaoua, where predators such as the non-spinosaurid theropods Kryptops palaios and 75 76 *Eocarcharia dinops* [28] occur. In the Kem Kem beds, the spinosaurids *Spinosaurus aegyptiacus* 77 and Sigilmassasaurus brevicollis [7,13,29] are associated with fossils of non-spinosaurid theropods such as Carcharodontosaurus saharicus [27]. 78

80 **2. METHODS** 

#### 81 (a) Sample collection

Samples comprising 73 tooth enamel, enameloid and fish scale ganoine from the early to 82 middle Cretaceous of Morocco and Niger have been analyzed for elemental concentration and 83 calcium isotope composition. Niger samples, totaling 7 taxa, come from the locality of 84 Gadoufaoua belonging to the Aptian/Albian Elrhaz Formation [26]. They consist of 8 85 spinosaurid theropod teeth (Suchomimus tenerensis or Cristatusaurus lapparenti), 9 non-86 spinosaurid theropod teeth (cf. Krvptops palaios and cf. Eocarcharia dinops), 2 teeth of the 87 sauropod Nigersaurus taqueti, 9 teeth of the ornithopod Ouranosaurus nigeriensis, 8 teeth of the 88 pholidosaurid crocodylomorph Sarcosuchus imperator, 3 teeth tentatively referred to the 89 notosuchian crocodylomorph cf. Araripesuchus sp., 3 teeth tentatively referred to an 90 indeterminate large pterosaur, 5 teeth referred to an indeterminate pychodont fish, 2 scales of an 91 indeterminate lepisosteiform fish, and 1 scale attributed to the lepisosteiform fish *Pliodetes* sp... 92 Moroccan samples previously analyzed for their apatite oxygen and carbon isotope 93 94 compositions [7] come from three localities (Bou Laâlou, Jebel Al Qabla, and Takemout) from the early Cenomanian Ifezouane Formation of the Kem Kem Beds [27]. They consist of 7 teeth 95 attributed to non-spinosaurid theropods (4 teeth of Carcharodontosaurus saharicus, and 3 teeth 96 97 of an indeterminate large theropod), 8 teeth referred to the spinosaurid theropods Spinosaurus *aegyptiacus* or *Sigilmassasaurus brevicollis*, 3 teeth of an indeterminate crocodylomorph, 3 teeth 98 of an indeterminate large pterosaur, 1 scale of the amiiform fish *Stromerichthys* sp. and 1 tooth 99 plate of the lungfish Neoceratodus africanus. 100

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101 Here we investigate dietary and ecological aspects using the calcium isotope composition of tooth enamel, enameloid and scale ganoine ( $\delta^{44/42}$ Ca) rather than bone or dentine, which are 102 porous and incorporate secondary diagenetic minerals. These biological materials are compact 103 and resistant to diagenetic alteration [24]. Sampling was performed using a handled micro-drill 104 (8200 Dremel with tungsten steel solid carbide bit and diamond burr), a micro-drill station 105 (MicroMill with tungsten steel solid carbide bit and diamond burr), and a scalpel made in 106 stainless steel. Tooth enamel, enameloid and scale ganoine have been carefully separated from 107 dentine and sediment using these tools. 108

109

#### 110 (b) Analytical techniques

Fossil samples were placed in Teflon beakers and dissolved in  $500\mu$ L of ultrapure nitric acid (15 N) at 130°C during 1 hour. Following this attack, samples were dried out, then dissolved in a dilute solution of ultrapure nitric acid (0.5 N).

A fraction of the solutions was measured for elemental concentrations of trace elements 114 (Rare Earth Elements (REE), strontium (Sr) and barium (Ba)) and major elements (such as 115 calcium (Ca), magnesium (Mg) and phosphorus (P)). These measurements were performed on an 116 inductively coupled plasma mass spectrometer (7500 Series ICP-MS, Agilent Technologies) for 117 118 trace elements, and on an inductively coupled plasma atomic emission spectrometer (ICAP 6000 Series ICP spectrometer, Thermo electron corporation) for major elements. The reliability of 119 measurements has been controlled through a set of blanks and standards (see measures NIST-120 121 SRM1400, USGS-MAPS-4 and USGS-MAPS-5 in supplementary table). Calcium from samples was chemically purified following previously described protocols 122

123 [30]. Briefly, samples were dissolved in double distilled HCl and loaded onto columns filled with

AG 50WX-12, separated from matrix including phosphates. Calcium, collected together with strontium, is then further processed in HNO<sub>3</sub> medium using Eichrom Sr-specific resin, allowing removal of Sr. The reliability of elutions have been controlled by processing and analyzing standard materials (see measures of NIST-SRM1486 in the supplementary table).

Calcium isotope abundance ratios ( ${}^{44}Ca/{}^{42}Ca$ ) were measured using a Neptune Plus MC-ICP-MS (Multi-Collector Inductively Coupled Plasma Mass Spectrometer) following previously described methods [30,31]. After purification, Ca samples were dissolved in ultrapure 0.05N HNO3 and Ca concentration was set at 2 mg.l<sup>-1</sup> for all samples and standards. All Ca isotope compositions are expressed using the "delta" notation defined as follows:

133

134 
$$\delta^{44/42} Ca = (({}^{44}Ca/{}^{42}Ca)_{sample} / ({}^{44}Ca/{}^{42}Ca)_{ICP Ca Lyon}) - 1) \times 1000$$

135

where (<sup>44</sup>Ca/<sup>42</sup>Ca)<sub>sample</sub> and (<sup>44</sup>Ca/<sup>42</sup>Ca)<sub>ICP Ca Lyon</sub> are the Ca isotope abundance ratios measured in sample and ICP Ca Lyon reference standard respectively. The ICP Ca Lyon standard, used as a bracketing standard, is a Specpure calcium plasma standard solution (Alfa Aesar) previously described here: [22,23,30–32]. The SRM1486 cow bone meal standard (NIST) was used as secondary standard, in order to assess accuracy of analytical procedure, including chemical purification.

142

#### 143 (c) Monitoring of the isotopic measurement accuracy

Blanks realized during purification protocols have been analyzed with the MC-ICP-MS. All blanks contained less than 85 ng of Ca, which is 470 times less than the Ca contained in samples. Thus this nano-pollution does not alter the isotopic measurements of our samples, consideringour measurement precision.

The mass dependency curve of the isotopic measures follows the expected relation for Ca (figure 1), with a slope value of  $0.509 \pm 0.016$  (2SE, n=74) [22,23,25,30–32], supporting the accuracy of the measures.

151 Measurements collected for the standard SRM1486 exhibit a  $\delta^{44/42}$ Ca of -1.00 ±0.10‰ (2SD, 152 n=32), which is in the range of previously published data for this standard: -0.96 ±0.14‰ (2SD, 153 n=17) [30], -1.04 ±0.11‰ (2SD, n=25) [22], -1.03 ±0.13‰ (2SD, n=120) [31], -1.03 ±0.12‰

154 (2SD, n=147) [32].

155

#### 156 (d) Diet modelling

In order to perform diet inferences with Ca isotope data, we make use of our data to feed a simple diet mixing model. This model provides estimates of the relative contribution of Ca sources in the diet of predators thanks to  $\delta^{44/42}$ Ca. Two main parameter need to be constrained prior to using it.

First, the isotopic signature of Ca sources needs to be constrained for studied animals. 161 Calcium is more concentrated in mineralized tissues (bone, enamel, scale ganoine) than in soft 162 tissues or in water. Thus, it has been shown that even a few percent of mineralized tissues in diet 163 164 was sufficient to constitute the major source of Ca for organisms [24]. There is fossil evidence of bone and fish scale consumption among numerous taxa of crocodylomorphs, spinosaurid and 165 non-spinosaurid theropods [10,33]. Thus, even if this consumption can be restricted to occasional 166 events such as feeding on juveniles for bones, the high concentration of Ca in mineralized tissues 167 supports that these tissues were most likely the main source of Ca among these taxa. Moreover, 168

169 considering the heterogeneity of modern animal data on soft tissues [20,30,34], and that blood 170 can exhibit  $\delta^{44/42}$ Ca close to bones [30], this supports the use of  $\delta^{44/42}$ Ca values of mineralized 171 tissues as representative of the main source of Ca for predators in our model. We have collected 172 Ca isotope data for herbivorous dinosaurs and fishes from Gadoufaoua, which represent the most 173 likely prey of the analyzed apex predators (crocodylomorphs, spinosaurid and non-spinosaurid 174 theropods). Thus we have constrained the isotopic signature of the potential Ca sources to be 175 entered in the model.

Second, our model needs an estimate of the isotopic shift between Ca from food and teeth 176 177 of the predators. According to data collected on a variety of extant vertebrates (chicken, horse, seal, deer, minipigs, sheep and mouse [20,30,34]), the mean isotopic shift between Ca from diet 178 179 to bones is  $0.57 \pm 0.10\%$  (2SE, n = 21) and is relatively homogenous among these vertebrates. Thus, considering that the studied predators are phylogenetically close (all are archosaurs) and 180 that all of them share comparable Ca-cycles [20], we can reasonably assume that they exhibited a 181 similar diet-bone isotopic offset. Only limited data have been collected on diet and enamel 182 couples in modern faunas. Some studies show differences between these two shifts ( $\pm 0.2\%$ ; [22– 183 24,30,35]) but these studies are often conducted on mammals, whose teeth formed in early life, 184 and thus were not representative of the adult diet for which the comparison is made. However, in 185 human wisdom teeth, which developed along with an adult diet, the isotopic shift between 186 enamel and food is similar to the diet-bone shift of  $-0.57 \pm 0.10\%$  (2SE, n = 21) [32]. Based on 187 these results, we assume a similar diet-enamel shift among studied taxa, and use this shift to 188 estimate the  $\delta^{44/42}$ Ca value of the food of predators. We thus applied this model to *Sarcosuchus* 189 *imperator*, spinosaurid and non-spinosaurid theropods, in order to investigate the proportion of 190 191 fish and herbivorous dinosaurs in the diet of these predators.

192	We estimate the Ca source fractions using the estimation of food $\delta^{44/42}$ Ca between the first
193	and the third quartile of each population of predators, considering that it is more representative of
194	their general diet. Moreover, to take into account the variability of $\delta^{44/42}$ Ca values among
195	sources, these fractions are calculated as if predators with the most depleted $\delta^{44/42}$ Ca values fed
196	on fish and herbivorous dinosaurs with the most enriched $\delta^{44/42}$ Ca values, and vice versa. In this
197	way, we maximized the source fraction scattering, which sets the limit of diet inferences
198	achievable with our model.
199	
200	3. RESULTS
201	(a) Elemental concentrations
202	The full dataset compiling all the elemental concentrations measured in this study are
203	reported in the supplementary table of this article.
204	Among important results, the mean calcium versus phosphorus ratio is of 2.3 $\pm$ 0.1 (1SD).
205	
206	(b) Calcium isotope ratios
207	The full dataset compiling all the calcium isotopic ratios measured in this study are reported in
208	the supplementary table of this article. The $\delta^{44/42}$ Ca values of vertebrates from Gadoufaoua range
209	between -0.35 and -1.51‰ with a mean 2SD of 0.10‰. In this locality, the sauropod
210	<i>Nigersaurus taqueti</i> is the taxon which exhibits the highest $\delta^{44/42}$ Ca with a mean value of -0.43
211	$\pm 0.11\%$ (2SD, n=2), whereas the spinosaurids exhibit the lowest values with $-1.30 \pm 0.15\%$
212	(2SD, n=8). Among the other dinosaurs, the ornithopod <i>Ouranosaurus nigeriensis</i> exhibits
213	values at -0.56 $\pm$ 0.05‰ (2SD, n=9), whereas non-spinosaurid theropods exhibit values at -0.94
214	±0.16‰ (2SD, n=9). The small, supposedly terrestrial crocodylomorph, cf. Araripesuchus sp.,

215	exhibits a mean value of $-1.12 \pm 0.05\%$ (2SD, n=3), whereas for the semi-aquatic
216	crocodylomorph <i>Sarcosuchus imperator</i> this value is of $-1.12 \pm 0.13\%$ (2SD, n=8). For fishes
217	mean values are of -0.74 $\pm$ 0.02‰ (2SD, n=2) for indeterminate Lepisosteiformes, of -0.67‰
218	(n=1) for <i>Pliodetes</i> sp., and of -1.08 $\pm$ 0.04‰ (2SD, n=5) for Pycnodontiformes. Finally,
219	pterosaurs exhibit a mean value of -0.78 $\pm$ 0.05‰ (2SD, n=3). The $\delta^{44/42}$ Ca of spinosaurid
220	theropods is significantly lower than that of non-spinosaurid theropods (Wilcoxon rank sum test:
221	$p \text{ value} = 9.9 \text{ x } 10^{-4}$ ).
222	The $\delta^{44/42}$ Ca values of Kem Kem beds vertebrates range between -0.41 and -1.56 ‰ with a
223	mean 2SD of 0.09‰. In Kem Kem beds, the lungfish Neoceratodus africanus is the taxon which
224	exhibits the highest $\delta^{44/42}$ Ca with a value of -0.41‰ (n=1), whereas the other fish <i>Stromerichthys</i>
225	sp. exhibits a low value of -1.26‰ (n=1). Spinosaurids exhibit the lowest mean value of this
226	fauna, which is $-1.39 \pm 0.27\%$ (2SD, n=8). For large non-spinosaurid theropods
227	( <i>Carcharodontosaurus saharicus</i> and indeterminate theropods) this value is of $-0.64 \pm 0.13\%$
228	(2SD, n=7). Semi-aquatic indeterminate crocodylomorphs exhibit a mean value of $-0.66 \pm 0.09\%$
229	(2SD, n=3), and indeterminate pterosaurs from the family of Anhangueridae exhibit a mean
230	value of -0.67 ±0.17‰ (2SD, n=3). The $\delta^{44/42}$ Ca of spinosaurids is significantly lower than for
231	non-spinosaurid theropods (Wilcoxon rank sum test: p value = $3.1 \times 10^{-4}$ ).
232	

#### (c) Fractions of Ca sources in diet 233

With our diet mixing model we estimate that the maximum Ca fraction from fish in the diet 234 reaches 30%, 58% and 100% for non-spinosaurid theropods, Sarcosuchus imperator and 235 spinosaurids, respectively. On the other hand, the maximum Ca fraction from herbivorous 236 dinosaurs in the diet reaches 100% for all of these predators. The maximum Ca fraction derived 237

from fish reaches 100% for 6 of the 8 studied spinosaurid individuals according to this model,
which is possible for only two individuals of *Sarcosuchus imperator* and one non-spinosaurid
theropod. However, the maximum Ca fraction derived from herbivorous dinosaurs is also 100%
for 4 of the 8 spinosaurid individuals.

242

#### 243 **4. DISCUSSION**

#### 244 (a) Diagenesis

Enamel, ganoine and to a lesser extent enameloid tissues, are highly mineralized and exhibit 245 a lower porosity than dentine or bone. They have a limited exchange surface with surrounding 246 fluids and sediment, and for this reason they are considered resistant to diagenesis [23,24,36]. 247 Moreover, with almost 40% of their mass constituted of Ca, it is very unlikely that the Ca 248 isotopic signature of these tissues can be entirely overprinted during early diagenetic processes. 249 The Ca/P ratios measured for samples (supplementary table) exhibit values of  $2.3 \pm 0.1$  (1SD), 250 which are close to those measured in modern animals [37]. This supports that Ca isotope ratios from 251 these fossils have not been extensively modified during diagenesis. 252

Quantifying elemental concentration of non-essential trace elements such as rare earth 253 elements (REE) and of major elements such as Ca and phosphorus, can provide information on 254 255 both the autochthony and diagenetic alteration [38,39]. Among fossils from Gadoufaoua, REE enrichment profiles (normalized to the Post Archean Australian Shale, PAAS) exhibit a similar 256 shape with different REE enrichment intensity (figure 2A and supplementary table). They can 257 258 thus reasonably be considered as autochthonous [39]. Three teeth exhibit distinct REE profile shapes (figure 2A). They have thus been identified as allochthonous fossils and have not been 259 considered in the palaeoecological discussion. The general REE profile at Gadoufaoua is "hat 260

shaped" according to the definition given by Reynard & Balter 2014 [38]. This shape, associated
with measured La/Yb and La/Sm ratios (supplementary table), differs from the REE profiles and
ratios expected after extensive recrystallization processes during diagenesis [38,40].

Among fossils from the Kem Kem beds REE enrichment profiles (normalized to the Post Archean Australian Shale, PAAS) exhibit a distinct profile between the three studied localities (figure 2B and supplementary table). However, within each locality, fossils exhibit similar REE profiles. They can thus reasonably be considered as autochthonous [39]. As for Gadoufaoua, the general "hat shaped" REE profile of the Kem Kem beds [38] and the measured La/Yb and La/Sm ratios (supplementary table) are different from those expected for diagenetic recrystallization processes [38,40].

Thus, the Ca/P ratios and the REE concentrations jointly support the hypothesis that the Ca 271 isotopic composition of the fossils have not been extensively affected by diagenesis. Moreover, 272 taxa from Gadoufaoua exhibit  $\delta^{44/42}$ Ca values consistent with their putative ecology (figure 3A). 273 Indeed, herbivorous dinosaurs represented by Nigersaurus taqueti and Ouranosaurus nigeriensis 274 exhibit the highest  $\delta^{44/42}$ Ca values of this dataset, with values ranging between -0.35‰ ±0.14 275 (2SD, n=3) and  $-0.66\% \pm 0.05$  (2SD, n=4), respectively. Their potential predators (the 276 pholidosaurid crocodylomorph Sarcosuchus imperator, spinosaurid and non-spinosaurid 277 theropods) exhibit lower  $\delta^{44/42}$ Ca values, below -0.70‰. This isotopic distribution between 278 herbivores and predators follows what has been observed in modern continental faunas [20], and 279 supports, along with the observations presented above, the biogenic nature of  $\delta^{44/42}$ Ca values. 280

281

#### 282 (b) Resource partitioning among predators

283	Compared to non-spinosaurid theropods, spinosaurids exhibit distinctly lower $\delta^{44/42}$ Ca values
284	(Wilcoxon rank sum test: p-value = $9.9 \times 10^{-4}$ ), the lowest ones of the dataset (figure 3A). This
285	distinct pattern is also observed in the Kem Kem beds of Morocco (figure 3B) with spinosaurids
286	possessing significantly lower $\delta^{44/42}$ Ca values compared to non-spinosaurid theropods (Wilcoxon
287	rank sum test: p-value = $3.1 \times 10^{-4}$ ). Physiological homogeneity in Ca isotope fractionation from
288	food to tooth enamel in these theropods is supported both by their phylogenetic proximity, all are
289	archosaurs, and the observed homogeneity in modern vertebrates [20,30,34]. This pattern thus
290	highlights the distinctive ecological niche of spinosaurids relative to the other theropods.
291	The trophic pyramid in these fluvial palaeo-ecosystems could have been supported both
292	by herbivorous dinosaurs and fish [4,5,26,27], which would represent two potential primary
293	sources of Ca for predators. In Gadoufaoua, the Ca source constituted by herbivorous dinosaurs
294	exhibits a higher $\delta^{44/42}$ Ca value than fish, which allows discriminating potential dietary sources
295	among predators. Using the diet model described above (Method (d)) for the vertebrate
296	assemblage of Gadoufaoua, we observed that the estimated fractions of Ca originating from
297	herbivorous dinosaurs and fish in the diet of predators do overlap between predators. The
298	important range of fraction between the maximum and minimum fraction estimated for each
299	predator was expected considering the scattering of the $\delta^{44/42}$ Ca data from fish, herbivorous
300	dinosaurs and predators. However, even with this important scattering in isotopic values, the
301	difference between spinosaurid and non-spinosaurid theropods remains statistically significant,
302	implying distinct resource partitioning between these large predators. Here, $\delta^{44/42}$ Ca data support
303	the idea that a majority of non-spinosaurid theropods mainly fed on herbivorous dinosaurs, with
304	less than 30% of their Ca potentially stemming from fish sources (figure 4A). The giant
305	crocodylomorph Sarcosuchus imperator exhibits an intermediate diet, possibly composed of

306 both fish and herbivorous dinosaurs (figure 4B). Moreover, if the diet of spinosaurid theropods potentially included a mix of fish and herbivorous dinosaurs according to the model, these data 307 also support that a majority of spinosaurids could be exclusively piscivorous (along with one 308 non-spinosaurid theropod and two *Sarcosuchus imperator* individuals), and that half of them 309 were at least partially piscivorous (figure 4C). Nevertheless, if this clearly illustrates that 310 spinosaurids were the predators of Gadoufaoua which had the most piscivorous-oriented diet, 311 this also leads to the conclusion that their diet was potentially a mix between fish and 312 herbivorous dinosaurs. Similarly, Kem Kem spinosaurids are also strongly depleted in heavy Ca, 313 314 confirming a piscivorous diet in another fossil assemblage. In previous studies, several diets have been proposed for these groups of theropods. For spinosaurids, fish consumption inferred on the 315 basis of the ecosystem structure [4,5], morphology [9,11,13–15,17,18], or direct fossil evidences 316 [10] is thus supported by our dataset. The consumption of terrestrial preys, which is also 317 proposed in these papers, as well as the direct evidences related to this behavior [10,16], also 318 remain possible according to our data. In addition, the consumption of herbivorous dinosaurs that 319 is commonly assumed for non-spinosaurid theropods [33], such as abelisaurids and 320 carcharodontosaurids, is also supported by our dataset. The fraction of terrestrial preys in the diet 321 322 of these theropods appears to be significantly higher than that of spinosaurids. However, whether these preys have been acquired through hunting [10,14,16,17], scavenging [10,14,16] or active 323 fishing [9,10,13–15,17,18] cannot be assessed with our dataset. 324

In the model, for some non-spinosaurid theropod individuals, the inferred  $\delta^{44/42}$ Ca signature of the diet is more positive than the source with the most positive  $\delta^{44/42}$ Ca values. Four nonmutually exclusive hypotheses could be proposed to explain this inconsistency. First of all, it can be due to the absence of a heavier source of Ca in our dataset. One of the possibilities is that this

heavy source indeed corresponds to an unidentified terrestrial taxon at the bottom of the food 329 chain. Alternatively, it can correspond to *Nigersaurus taqueti* mineralized tissues for which only 330 two teeth have been measured, and which exhibit the highest  $\delta^{44/42}$ Ca values of the dataset. 331 Another possibility is that this source of heavy isotopes of Ca comes from the digestion of 332 333 carbonated gastroliths. The ingestion of gastroliths among dinosaurs has been documented thanks to comparisons with modern archosaurs and fossil evidence, notably for spinosaurids 334 [10]. Because of the heavy Ca isotope composition of carbonates [34,41,42], this consumption 335 could buffer the  $\delta^{44/42}$ Ca towards <sup>44</sup>Ca enriched values among studied archosaurs. This could 336 lead to an overestimation of the fraction of herbivorous dinosaurs in diets inferred from our 337 mixing model, which could explain the inconsistency with non-spinosaurid theropods in our 338 model. The third hypothesis is that this inconsistency is the result of an overestimation of the 339 340 diet-enamel shift, due to the lack of data collected on modern archosaurs, which can also lead to an overestimation of the fraction of herbivorous dinosaurs in diets (values potentially shifted 341 toward heavy calcium). However, none of these hypotheses is susceptible to change the 342 conclusions made on the resource partitioning among these predators or to the more piscivorous-343 oriented diet of spinosaurids. Indeed, a validation of these hypotheses will imply a more 344 piscivorous diet for all these predators, even providing more support to the piscivorous-oriented 345 diet of spinosaurids. 346

347

### 348 **5. CONCLUSIONS**

Our data imply that the abundance of apex predators in these peculiar African mid-Cretaceous ecosystems can be sustained simultaneously by at least two main sources: fish and herbivorous dinosaurs, resulting in a general abundance of prey. The present Ca isotope dataset also supports

352	the ecological partitioning of potential predatory competitors [7,8]. Indeed, the different
353	ecological specializations of these predators resulted in different mixtures between carnivorous
354	and piscivorous habits and are likely to have reduced the ecological competition between them.
355	Calcium isotopes support the hypothesis of spinosaurids regarded as semi-aquatic predators [7,8]
356	and adopting a piscivorous diet, with non-spinosaurid theropods having a more terrestrial
357	ecology and diet, feeding mainly on herbivorous dinosaurs. This ecological partitioning,
358	combined with the abundance of prey, is consistent with the observed high abundance of
359	predators in these faunas [4,5].
360	The present study underlines a complex trophic structure relying on the interaction
361	between aquatic and terrestrial environments. One of the key points for the sustainability of these
362	palaeoecosystems was the piscivorous-oriented diet of spinosaurids. Whether this ecological
363	structure is a global feature among other mid-Cretaceous faunas is an open question [7, 10 and
364	reference therein], but beyond this, Ca isotopes offer promising perspectives to study trophic
365	structures in long extinct vertebrate assemblages.
366	
367	Data accessibility.
368	The dataset table compiling all elemental concentrations and isotopic ratio measurements is
369	available as electronic supplementary material.
370	
371	Authors' contributions.

The project was conceived by J.E.M., A.H., R.Am., T.T., R.Al. and V.B. . R.Am. and R.Al.

accessed samples for analysis. A.H. and J.E.M. sampled the specimens and conducted

374	purification in the clean lab. A.H. and F.A.G. performed elemental concentration measurements.
375	A.H., J.E.M. and T.T. performed MC-ICP-MS measurements. All authors discussed the results.
376	The first draft version of the text was written by A.H. then subsequently, J.E.M., R.Am., T.T.,
377	R.Al., F.A.G. and V.B. contributed to it.
378	
379	Competing interests.
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519		
520	Capt	ions
521	<b>Figure 1.</b> Three isotopes plot: $\delta^{43/42}$ Ca as a function of $\delta^{44/42}$ Ca (‰, reference standard ICP Ca)	
522	for all samples and standards analyzed for Ca isotope compositions in this study. Ca isotope	
523	comp	positions fall on a line with a y axis intercept of $0.009 \pm 0.015$ (‰, 2SE), indistinguishable
524	from	theoretical 0% intercept. The slope value of this line is $0.509 \pm 0.016$ (2SE),

- indistinguishable from the 0.507 slope predicted by the exponential mass-dependent
- fractionation law. Error bars at the bottom right are average 2SD for  $\delta^{43/42}$ Ca and  $\delta^{44/42}$ Ca. The
- 527 two most external lines delimit the prediction interval, and the two lines accompanying the
- 528 middle line correspond to the 95% confidence interval of the regression line.

Figure 2. (A) PAAS Shale-normalized REE profiles of fossil bioapatite from the Aptian-Albian
of Gadoufaoua, Niger. Concentrations are plotted on a logarithmic scale. Plain black line: typical
REE profile at Gadoufaoua; yellow line: exotic profile of sample GCA5; purple line: exotic
profile of sample GSA7; red line: exotic profile of sample GSP3. (B) PAAS Shale-normalized
REE profiles of fossil bioapatite from the Cenomanian of Kem Kem beds, Morocco.
Concentrations are plotted on a logarithmic scale. For comparison, the plain black line represents

of Jebel Al Qabla; blue line: typical profile of samples from the locality of Bou Laâlou; red line:

the typical REE profile at Gadoufaoua; yellow line: typical profile of samples from the locality

538 typical profile of samples from the locality of Takemout.

539

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Figure 3.  $\delta^{44/42}$ Ca data reported from Gadoufaoua (A) and Kem Kem beds faunas (B). Groups 540 representing at least 5 specimens are represented through boxplots, for which the middle line 541 represents the median, the box limits correspond to the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, and the whiskers are 542 extended between the maximum and the minimum  $\delta^{44/42}$ Ca. The mean 2SD of each measure is 543 represented at the bottom right of each graph. The degree of significance of the difference 544 545 between the theropod groups are represented with stars (\*), with the three stars indicating a high significance (Wilcoxon rank sum test: p-value < 0.001). Taxonomic groups are identified by 546 their number and represent: 1: Nigersaurus taqueti (n=2), 2: Ouranosaurus nigeriensis (n=9), 3: 547 non-spinosaurid theropods from Gadoufaoua (n=9), 4: Sarcosuchus imperator (n=8), 5: 548 spinosaurids from Gadoufaoua (n=8), 6: Lepisosteiformes (n=3), 7: Pycnodontiformes indet. 549 (n=5), 8: cf. Araripesuchus (n=3), 9: Pterosauria indet. (n=3), 10: non-spinosaurid theropods 550 from Kem Kem beds (n = 7), 11: Crocodylomorpha indet. (n = 3), 12: spinosaurids from Kem 551

Kem (n=8), 13: *Neoceratodus africanus* (n=1), 14: *Stromerichthys* sp. (n=1), 15: Anhangueridae
indet. (n=3).

554

Figure 4. Mixing model of the calcium source for non-spinosaurid theropods (A) Sarcosuchus 555 *imperator* (B) and spinosaurids (C) from the Gadouafaoua fauna.  $\delta^{44/42}$ Ca data collected on 556 herbivorous dinosaurs and fishes are represented respectively in green and blue squares. In each 557 part of the figure the faded lower boxplot represents the enamel  $\delta^{44/42}$ Ca values measured for 558 each apex predators, whereas the dark upper boxplot represents the isotopic signature of their 559 calcium source estimated to be shifted by +0.57% from the signature of their enamel (Methods 560 (d)). Boxplots are yellow for non-spinosaurid theropods (A), violet for Sarcosuchus imperator 561 (B) and red for spinosaurids (C). The line in boxplot is equal to the median, boxes are limited by 562 their 1<sup>st</sup> and 3<sup>rd</sup> quartile, and whiskers represent the maximum and the minimum values. The 563 estimated diet fraction range of Ca derived from the fish source are indicated in bold above the 564 x-axis and expressed in percent. 565







■ Ouranosaurus nigeriensis ■ Spinosauridae

Fish

Deterosauria indet.



								-		-			-			-		_				-						-	-	
Taxonomy	Locality	Lab name	Material	Ca	P	Mg	Mn	Fe	Sr	Ba (rom)	CalP La	Ce Iromi-	Pr (nom).	Nd [mm]	Sm (rom).	Eu	Gd	Tb Inneri	Dy	Ho form)	Er (nom)-	Tm (nom)-	Yb (nom)-	Lu (mm)	La/Yb	La/Sm	Y	Pb [nnm]	Th	U [nom]
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA1	tooth ename!	37	16	687.2	1185	2965.8	1682	948	2.3 10.0	10.2	12.3	12.7	12.7	17.7	19.2	19.1	18.0	16.2	12.4	8.2	5.2	4.0	1.9	0.8	559.7	15.6	2.2	11.9
Non-spinosaurid theropod Non-spinosaurid theropod	Gadoufaoua, Niger Gadoufaoua, Niger	GCA2 GCA3	tooth ename!	36 34	15	858.7 792.3	1461	652.2 985.9	2163	1054	2.3 11.2 2.3 10.0	20.2	23.8	26.6	49.9	61.4 35.8	34.5	32.6	41.7 27.4	32.1 22.4	21.7	12.7	6.3	5.8	1.5	0.2	978.0 711.6	15.0	18.9	16.2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA4	tooth ename!	34	15	980.0	1460	1520.0	1140	800	2.3 10.1	15.7	16.2	16.9	20.2	22.5	21.9	21.3	17.5	14.7	10.7	6.8	4.2	3.1	2.4	0.5	448.5	15.6	1.6	13.1
Non-spinosaurid theropod	Gadoufaoua, Niger	GCAB	tooth ename!	41	18	895.8	542	177.1	1635	875	2.3 10.3	21.1	26.3	29.9	34.5	42.8	37.2	35.3	29.9	23.8	15.8	10.4	6.5	4.7	1.6	0.3	723.9	16.1	7.7	17.7
Non-spinosaurid theropod Non-spinosaurid theropod	Gadoufaoua, Niger Gadoufaoua, Niger	GCA7 GCA8	tooth ename!	37	16	748.5 813.4	1407	1272.5	1737	1198 861	2.3 11.5 2.3 9.4	22.1 20.4	25.8	31.1	39.9	49.0 45.6	46.8 43.4	42.8	35.6	28.6	19.5	12.4	7.7	5.6	15	0.3	978.9 894.2	14.9	8.3	20.2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA9	tooth ename!	41	18	1378.3	1774	88.0	1877	1261	2.3 9.6	14.3	15.1	15.7	16.4	18.5	21.8	20.4	18.3	15.9	12.0	8.2	52	3.8	1.9	0.6	638.9	15.1	12.5	15.8
cf. Anaripeauchus ap	Gadoufaoua, Niger	GAR1	tooth ename!	38	17	784.1	1199	507.4	1799	1061	2.3 8.6	10.8	10.3	10.4	10.6	14.0	14.8	14.2	13.3	11.8	9.1	6.4	4.1	3.2	2.1	0.8	422.5	18.0	1.2	11.3
cf. Anaripeauchus ap. cf. Anaripeauchus ap.	Gadoufaoua, Niger Gadoufaoua, Niger	GARS GAR4	tooth ename! tooth ename!	37 42	16	109.2	2966	1279.9	2331	939 847	2.3 10.0 2.3 11.8	16.7 21.1	18.0	20.6	25.5	29.1	28.5	27.6 43.8	22.7	19.6	13.4	8.3	63	4.0	2.0	0.4	632.2 832.1	12.9	4.3	19.2
cf. Anaripeauchus ap.	Gadoufaoua, Niger	GAR5	tooth enamel	37	16	1449.3	1691	603.9	1932	986	23 92	12.8	12.1	12.5	12.5	14.9	17.1	16.4	15.3	13.6	10.6	7.1	45	3.5	2.0	0.7	481.5	16.1	5.7	10.8
Lepisostelformes indet.	Gadoufaoua, Niger	GLE2	scale ganoine	41	17	991.2	938	354.0	2044	858	2.4 7.1	15.8	17.9	19.2	17.7	23.3	21.5	20.9	18.3	15.7	10.4	6.0	3.3	2.2	2.2	0.4	617.8	10.2	0.0	6.0
Lepisosteformes indet. Mewsonia	Gadoufaoua, Niger Gadoufaoua, Niger	GLE3 GMA1	dermic bone	39	16	449.4	1400	191.0	786	2573	2.6 17.9	21.4 41.0	47.4 53.3	53.3	58.0	85.0 74.2	63.5	56.8	43.6	36.3	23.1	13.4	7.9	5.7	23	0.3	1238.0	2.4	5.3	131.9
Nigersaurus taqueti	Gadoufaoua, Niger	GAU1	tooth ename!	35	15	500.0	978	456.5	2239	630	2.5 7.8	14.8	17.0	19.5	23.6	27.5	24.5	24.0	19.8	16.1	11.1	6.8	4.4	3.4	1.8	0.3	483.7	10.6	18.0	17.1
Ouranosaurus rigeriensis	Gadoufaoua, Niger	GON2	tooth ename!	34	15	1314.2	921	1563.1	5844	1021	2.2 9.3	16.7	19.1	22.6	28.3	36.7	31.0	29.3	25.3	18.4	13.0	7.6	4.7	3.6	2.0	0.3	576.9	19.4	1.6	9.6
Ouranosaurus nipariensis Ouranosaurus nipariensis	Gadoufaoua, Niger Gadoufaoua, Niger	GONS GON4	tooth ename! tooth ename!	34	15	1451.2	1262	1052.3 846.0	2708	628 996	2.2 9.5 2.2 10.5	15.5	25.7	29.5	31.6 12.3	39.5	35.4	32.3	27.9	21.4	9.6	9.0 6.3	5.8	4.3	2.7	0.3	688.0	14.1	2.7	16.1
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GONS	tooth ename!	36	16	1193.9	1069	1068.7	4939	1107	2.2 10.9	15.2	14.1	12.6	13.0	15.8	16.1	15.8	14.6	12.4	9.7	6.5	42	3.3	2.6	0.8	419.8	23.9	3.2	7.0
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON8	tooth ename!	38	17	1244.7	1899	2068.6	3376	928	2.2 9.6	18.1	20.0	22.0	25.1	33.3	29.2	27.3	23.7	19.6	13.5	8.4	5.1	3.8	1.9	0.4	639.6	16.6	1.0	15.4
Ouranosaurus nigeriensis Ouranosaurus nigeriensis	Gadoufaoua, Niger Gadoufaoua, Niger	GON9 GON10	tooth ename!	38	17	1102.2	2473	940.9 882.6	4677	1102	22 88	11.7	10.7	10.4	10.3	12.9	14.8	14.7	14.0	13.1	9.5 7.3	6.6	42	3.2	2.1	0.9	454.3	12.7	0.4	8.9
Plodetez sp.	Gadoufaoua, Niger	GPL1 total	ganoine + dentin scale	35	14	793.7	937	365.1	1111	206	2.4 17.7	29.8	43.2	47.6	44.7	57.6	54.1	50.3	42.9	35.8	23.3	13.6	7.9	5.8	22	0.4	1373.5	9.3	2.6	117.7
Pterosauria indet.	Gadoufaoua, Niger	GAU2	tooth enamel	36	15	866.5	1504	6838.3	1843	1223	2.4 26.7	45.2	71.9	93.8	116.9	154.0	127.4	121.9	87.8	62.2	42.6	23.6	15.0	12.6	1.8	0.2	1870.0	21.4	82.0	70.2
Pterceauria indet. Pterceauria indet	Gadoufaoua, Niger Gadoufaoua, Niger	GAUS	tooth ename!	47	18	1041.7	4190	2430.6	2589	1551	2.6 25.5	45.8	57.9	68.4 82.2	65.9	88.3	77.1	69.3	58.0	49.3	33.2	20.1	12.6	9.8 10.9	2.0	0.4	1789.8	10.5	62.2 32.1	140.5
Pterosauria indet.	Gadoufaoua, Niger	GAUS	tooth ename!	37	14	642.9	3310	1142.9	1500	881	2.5 21.3	37.1	45.2	56.1	59.2	86.7	73.7	69.1	57.3	48.9	31.4	19.0	12.6	10.0	1.7	0.4	1533.7	14.3	49.2	105.8
Pterosauria indet.	Gadoufaoua, Niger	GAU7	tooth ename!	30	15	720.4	2330	2465.7	1695	1157	2.4 26.2	35.4	65.6	87.8	117.4	160.2	127.4	114.7	89.0	67.8	43.5	25.6	15.5	12.9	1.7	0.2	1895.7	13.8	27.5	71.7
Pterosauria indet. Pterosauria indet	Gadoufaoua, Niger Gadoufaoua, Niger	GAU8 GAU9	tooth ename!	33	13	614.8	658 2885	2459.3	1466	1140	2.5 17.8	27.9	50.1	64.5	86.9	115.9	95.8 153.6	86.8	68.3	52.7	33.9	20.7	12.7	10.5	1.4	0.2	1498.5	13.4	35.8	60.8
Pterosauria indet.	Gadoufaoua, Niger	GAU13	tooth enamel	32	13	450.5	1291	2524.4	918	826	2.5 22.6	41.8	53.6	64.1	77.1	105.1	79.0	69.1	53.6	41.9	27.2	16.4	10.3	8.4	22	0.3	1139.4	17.0	226.8	21.0
Pserosauria indet. Pycnodontiformes indet.	Gadoufaoua, Niger	GPY1	tooth enameloid	35	17	620.7	552	730.5	1000	840	2.1 7.8	11.0	10.4	10.5	9.6	12.2	13.2	13.3	12.7	11.0	34.5	5.6	3.5	2.6	22	0.2	368.0	13.2	0.4	6.0
Pycnodontiformes indet	Gadoufaoua, Niger	GPY2 CBY2	tooth enameloid	35	15	594.1	1287	528.1	1155	677	2.4 8.3	12.7	11.7	11.8	12.7	14.9	14.1	14.0	12.6	10.8	7.7	5.1	33	2.4	2.6	0.7	330.0	10.9	0.1	5.0
Pychodontiformes indet	Gadoufaoua, Niger	GPY4	tooth enameloid	35	16	539.4	1133	2276.2	1305	734	2.2 10.2	15.4	16.9	16.0	18.1	20.5	20.1	19.4	17.1	13.5	10.0	6.5	42	3.3	2.4	0.6	398.6	11.8	1.5	6.3
Pychodontiformes indet. Pychodontiformes indet.	Gadoufaoua, Niger Gadoufaoua, Niger	GPY5 GPY5	tooth enameloid tooth enameloid	36	16	486.6	1074	435.2 416.7	956 1122	386 545	2.3 5.5 2.1 4.1	6.4	62	7.3	8.1 6.8	9.8	8.9	9.3 8.9	8.3	7.1	5.1	3.5	22	1.6	2.5	0.6	213.9	10.5	0.1	2.3
Pycnodontiformes indet.	Gadoufaoua, Niger	GPY7	tooth enameloid	41	19	492.1	1516	1102.4	1161	650	2.2 5.5	83	7.8	8.2	8.6	11.7	11.2	10.5	9.9	8.3	6.0	4.1	2.6	1.9	2.1	0.6	273.3	11.7	0.8	4.4
Pychodontiformes indet	Gadoufaoua, Niger	GPYS	tooth enameloid	27	13	260.9	783	173.9	565	304	2.1 2.6	3.9	3.9	3.9	4.3	5.6	5.1	5.7	4.5	3.8	3.9	1.9	1.0	0.8	22	0.6	124.3	5.2	0.1	1.5
Pychodontiformes indet. Seconductive imperator	Gadoufaoua, Niger Gadoufaoua, Niger	GPY10 GSA1	tooth enameloid	37	18	334.5 1054.3	775	140.8	1021	440	2.1 3.1	45	43	4.4	4.3	8.2	5.9	6.2 22.5	5.6	5.0	3.8	25	1.6	1.2	1.9	0.7	166.8	58.7	1.3	1.6
Sarcosuchus imperator	Gadoufaoua, Niger	GSA2	tooth ename!	38	15	1072.7	2400	1309.1	1891	582	2.4 10.3	17.0	16.7	18.1	21.3	27.3	23.9	24.0	20.8	17.5	12.1	7.7	4.8	3.5	22	0.5	604.8	16.0	2.5	8.7
Sercosuchus imperator	Gadoufaoua, Niger	GSA4	tooth ename!	39	17	794.1	436	613.5	2183	881	2.2 7.0	12.1	14.3	15.4	15.9	22.1	20.7	20.0	18.5	14.8	10.9	6.5	3.8	2.8	1.8	0.4	523.2	13.7	0.8	5.3
Sercosuchus imperator Sercosuchus imperator	Gadoufaoua, Niger Gadoufaoua, Niger	GSA5 GSA8	tooth ename!	40	18	705.2	401	469.3	2118	923 755	22 81	10.0	10.3	10.0	9.0 26.9	10.5	11.1	11.3	10.7	9.4 19.2	7.6	5.3	3.4	27	2.4	0.9	340.4	14.5	2.7	5.0
Sarcosuchus imperator	Gadoufaoua, Niger	GSA7	tooth ename!	34	15	709.6	1139	709.6	1667	776	2.2 5.2	5.6	5.3	5.0	4.2	7.2	9.3	9.1	10.8	11.5	9.5	6.4	4.0	2.8	1.3	1.2	541.4	11.3	0.4	5.7
Sarcosuchus imperator	Gadoufaoua, Niger	GSAG	tooth ename!	37	16	724.1	310	275.9	1759	914	2.2 8.0	13.5	17.1	18.6	20.6	23.8	23.5	22.8	19.3	16.0	11.5	7.0	42	3.1	1.9	0.4	539.0	11.7	2.3	6.7
Sarcosuchus imperator Suchomimus teneransis	Gadoufaoua, Niger Gadoufaoua, Niger	GSA10 GSP1	tooth ename!	33	15	736.8	253	63.2	1453	737	22 56 25 84	10.5	11.7	12.6	14.7	19.9	17.2	17.4	14.9	12.6	9.3	5.7	3.4	2.4	1.7	0.4	461.0	12.3	1.5	4.1
Suchomimus tenerenais	Gadoufaoua, Niger	GSP2	tooth ename!	36	16	1027.5	1646	2594.9	1620	932	2.3 8.9	19.3	23.0	26.0	28.0	38.2	34.2	31.8	28.3	22.6	16.5	2.9	6.2	4.7	1.4	0.3	731.7	16.8	2.3	11.7
Suchomimus tenerenais Suchomimus tenerenais	Gadoufaoua, Niger Gadoufaoua, Niger	GSP3 GSP4	tooth ename!	38	15	1087.0 880.5	708	1159.4 756.1	1830 2345	1051	25 65 23 23	6.6 11.9	4.1 13.7	3.8	3.0	4.8	6.8 17.8	6.9 17.1	7.9	9.3 12.6	7.9 9.6	5.8	3.9	2.9	2.4	0.7	590.5 429.6	18.2	1.2	4.7
Suchomimus tenerenais Suchomimus tenerenais	Gadoufaoua, Niger Gadoufaoua, Niger	GSP5 GSP5	tooth ename!	39	16	932.4 507.6	1649	2851.4	1419	649	2.4 10.3	20.8	24.3	28.4	26.4	31.8	27.5	26.6	22.6	18.9	12.8	7.9	4.8	3.6	2.1	0.4	685.8	17.8	2.3	12.2
Suchomimus tenerenais	Gadoufaoua, Niger	GSP7	tooth ename!	36	16	531.1	1142	1833.7	1904	631	2.2 7.4	10.6	10.6	10.9	12.4	14.1	15.1	14.8	13.1	11.6	8.7	5.5	3.4	2.5	2.2	0.6	421.8	13.2	16.2	4.8
Suchomimus tenerenais Suchomimus tenerenais	Gadoufaoua, Niger Gadoufaoua, Niger	GSP8 GSP9	tooth ename!	37 34	16	490.9	2029	479.5	1558	776	2.3 9.6 2.3 6.8	8.7	9.5	9.5 8.1	9.1 8.4	10.9	12.3	12.1	11.3	10.8	8.4 7.2	4.8	3.0	2.9	2.4	0.8	421.5 337.8	15.0	3.0	9.7
Suchomimus tenerenais Astronominidas indet	Gadoufaoua, Niger	GSP10	tooth ename!	35	16	627.6	690	1004.2	2029	900	2.2 6.7	11.3	12.0	13.3	17.0	23.8	19.7	20.4	17.1	13.3	9.5	5.7	3.5	2.5	1.9	0.4	435.3	22.4	4.6	3.8
Carcharodontosaurus saharicus	Bou Lallou, Morocco	MBL-024	tooth ename!	28	12	871.0	468	1935.5	1113	97	2.4 16.9	21.1	29.0	38.1	44.3	68.0	55.5	49.5	41.5	38.4	28.3	19.4	14.0	11.6	12	0.4	1223.9	345.5	1.6	35.6
Carcharodontosaurus saharicus Archosauria indet.	Bou Lallou, Morocco Bou Lallou, Morocco	MBL-025 MBL-041	tooth ename! tooth ename!	29	13	1397.3	445 721	-198.6	1753	178	2.3 15.7 2.3 3.7	15.7	28.6	55.2 6.3	41.7	62.8 10.3	54.2	48.5	40.4	54.8	26.4	18.9	13.4	2.3	12	0.4	248.1	550.0	3.7	88.2
Spinoseurus eegypticus Spinoseurus eegypticus	Bou Laliou, Morocco Bou Laliou, Morocco	MBL-042 MBL-043	tooth ename!	29	13	811.6	232	3478.3	754	261	23 37	5.8	55	6.6	8.7	12.5	10.8	10.4	8.7	7.1	5.4	3.6	2.8	2.0	13	0.4	232.9	2069.1	1.4	4.4
Spinoseurus eegypticus	Bou Laálou, Morocco	MBL-044	tooth ename!	29	13	709.7	312	1473.1	973	194	2.2 4.4	6.4	6.6	7.8	8.8	12.6	12.2	11.3	9.9	8.7	6.9	5.2	3.8	3.2	12	0.5	319.0	440.8	1.7	13.2
Anhangueridae indet.	Chaeft, Morocco	MCH-045	tooth ename!	34	14	617.2	1199	5910.2	1039	477	2.3 5.0 2.4 38.4	8.5	65.6	81.9	96.5	129.1	105.4	93.3	72.8	57.5	42.5	29.3	19.8	16.3	1.3	0.4	1510.3	3.3	5.6	26.7
Titanosauridae Shinosaurus aerunticus	Chaeft, Morocco Cheeft Morocco	MCH-005 MCH-011	tooth ename!	28	12	680.0	920 298	4900.0	1480	160	2.4 31.1	7.1	63.8	76.8	96.4 91.1	131.8	118.2	111.6	95.7 81.4	81.7	63.6 46.7	47.2	29.5	25.4	1.1	0.3	2300.1	50.2	9.4 14.0	155.6
Carcharodontosaurus saharicus	Chaeft, Morocco	MCH-012	tooth enamel	33	14	841.6	426	6227.7	1099	257	2.3 19.4	6.4	31.4	36.6	43.9	57.3	51.2	47.5	40.6	33.6	26.1	20.4	13.4	12.0	1.5	0.4	945.1	3.4	7.6	38.6
Archosauria indet.	Chaeft, Morocco	MCH-025	tooth enamel	21	2	698.1	547	1584.9	792	189	2.4 13.4	3.9	27.1	34.6	44.9	61.0	46.3	41.0	32.5	26.0	19.4	34.5 14.6	2.9	8.7	1.5	0.3	708.3	1.0	3.5	11.7
Spinoseurus eegypticus Spinoseurus eegypticus	Chaeft, Morocco Cheeft Morocco	MCH-035 MCH-037	tooth ename!	28 28	11	648.9 585.7	588	1732.8	656	198	23 87	2.8	16.1	20.3	26.8	39.1	30.7 30.1	27.4	22.2	17.9	13.4	10.0	6.4	5.5	13	0.3	498.8	1.2	0.9	8.4
Anhangueridae indet.	Jebel Al Qabla, Morocco	MJQ-001	tooth enamel	22	9	714.3	2143	14809.5	762	381	2.3 16.6	17.6	24.6	30.9	44.3	65.4	69.3	74.0	70.3	64.0	49.6	35.7	22.2	17.9	0.7	0.4	1880.1	5.4	11.5	18.5
Theropoda indet.	Jebel Al Qabla, Morocco	MJQ-009	tooth ename!	27	12	704.1	2418	15336.7	918	305	2.3 14.5	16.0	20.4	25.8	37.1	53.1	59.6	64.5	63.9	61.9	51.1	40.4	25.8	22.2	0.6	0.4	1957.0	9.1	2.3	26.4
Theropoda indet. Testudioes	Jebel Al Qabla, Morocco Jebel Al Qabla, Morocco	MJQ-010 MIO-017	tooth enamel	16	7	384.6	1415	4276.9	554 924	354	2.4 8.7	10.9	13.4	17.3	25.1	37.5	39.4	42.1	40.4	38.2	30.5	23.2	15.0	12.6	0.6	0.3	1172.5	5.7	1.3	33.3
Testudines	Jebel Al Qabla, Morocco	MJQ-018	osteoscute	12	5	338.7	561	3112.2	510	143	2.4 28.1	27.6	44.9	59.1	88.2	136.5	128.0	132.3	121.4	106.5	81.4	54.7	38.1	27.8	0.7	0.3	3002.3	7.0	4.2	48.1
Neoceratodus africanus	Jebel Al Qabla, Monocco Jebel Al Qabla, Monocco	MJQ-019 MJQ-020	tooth enameloid	29	13	1000.0	479	5791.7	771	313	2.3 7.6	9.5	15.2	19.5	21.7	31.8	32.1	34.2	32.0	29.9	23.4	18.0	12.3	10.5	0.6	0.4	913.8	6.6	3.1	17.1
Stromerichthys sp. Stromerichthys sn	Jebel Al Qabla, Morocco Jebel Al Cobla, Morocco	MJQ-036	scale ganoine	20	2	490.9	491	4381.8	618	218	23 31	3.8	45	5.7	8.4	12.1	12.5	12.8	12.9	12.3	10.1	8.0	5.6	47	0.6	0.4	388.6	4.4	2.1	5.0
Stromerichthyz sp.	Jebel Al Qabla, Morocco	MJQ-038C	scale ganoine	46	20	1202.9	2362	24159.4	1899	638	2.3 16.5	19.1	25.8	34.3	50.2	73.8	74.3	78.6	76.0	70.9	57.0	42.3	26.6	21.9	0.6	0.3	2187.4	11.4	1.4	24.3
Spinoseurus eegypticus Crocodylomorphe indet.	Jebel Al Qabla, Morocco Jebel Al Qabla, Morocco	MJQ-039 MJQ-040	tooth ename!	16 10	74	466.0 266.7	155 283	3534.0 5616.7	505 283	252 683	2.2 3.7 2.3 3.6	42 43	4.6	5.7	8.1 9.4	12.1 14.5	12.6 14.8	13.0	12.8 14.7	12.6	11.0 11.5	8.8	6.3 7.2	5.1 6.4	0.6	0.5	446.8 461.8	11.1 10.0	1.1 2.4	6.7 14.5
Crocodylomorpha indet.	Jebel Al Qabla, Morocco	MJQ-040A	tooth ename!	40	17	1312.5	1500	23937.5	1438	469	2.3 17.7	23.8	26.1	33.3	48.8	76.2	79.5	85.4	82.8	75.9	60.2	44.6	27.5	22.8	0.6	0.4	2283.1	11.4	1.8	47.2
Crocodylomorpha indet.	Jebel Al Qabla, Morocco	MJQ-040C	tooth enamel	14	6	330.2	321	3971.7	406	94	2.4 12.3	18.3	23.4	30.3	43.3	65.6	60.9	61.8	56.3	49.8	37.5	25.3	15.1	12.1	0.8	0.3	1458.3	2.8	2.6	12.3
Crocodylomorpha indet. Testudines	Takemout, Morocco Takemout, Morocco	MTA-004 MTA-009	cranial bone osteoscute	27	11	1690.9	1855	2400.0 8387.8	909 1163	527 11714	2.5 12.2 2.4 17.0	9.6 28.8	13.8 45.8	17.3	23.3 80.3	34.6	35.0 82.0	34.0 78.6	31.3 64.7	29.0 52.2	23.8 38.8	19.0	13.4 17.5	12.2	0.9	0.5	954.2 1318.0	19.0 10.4	4.0 31.1	36.5
Testudines	Takemout, Morocco	MTA-011	osteoscute	18	7	514.6	796	1126.2	602	408	2.5 15.3	10.8	23.4	29.6	40.1	55.9	49.5	46.5	39.3	33.7	25.4	19.5	12.8	12.1	12	0.4	986.5	8.9	6.1	22.4
Carcharodontosaurus saharicus Carcharodontosaurus saharicus	Takemout, Morocco Takemout, Morocco	MTA-017 MTA-019	tooth enamel tooth enamel	32 35	13	755.1 1102.0	2469 551	1030.6 3367.3	1122 1122	520 327	2.4 28.5 2.3 14.2	19.9 13.5	35.2 21.3	49.1 27.3	68.8 38.8	103.6	98.5 49.6	94.8 47.9	82.7 39.2	70.9 33.7	55.2 26.5	41.7 20.6	26.8 13.5	24.5 12.4	1.1	0.4	2110.9 982.0	34.3 27.7	8.4 5.0	54.4 18.9
Anhangueridae indet. Anhangueridae indet.	Takemout, Morocco Takemout, Morocco	MTA-020 MTA-021	tooth ename!	37	15	920.0 1245.9	1960	3893.3	1653	267	2.4 33.0	52.7 19.6	56.6 32.8	72.3	101.5	141.7	119.5	110.3	90.7 79.3	74.4	55.3 52.4	38.3	23.5 25.8	20.3	1.4	0.3	2004.5	34.0	3.2	29.8
Spinosaurus aegypticus	Takemout, Morocco	MTA-025	tooth enamel	22	10	688.5	180	836.1	672	295	23 33	43	4.9	6.1	8.5	11.9	11.2	10.0	8.7	8.0	6.5	5.8	4.4	4.5	0.7	0.4	318.5	17.0	0.8	15.5
opnoseurus eegypticus Spinoseurus eegypticus	Takemout, Morocco Takemout, Morocco	MTA-027 MTA-028	tooth enamel tooth enamel	27 33	12	1041.7 1086.2	271 382	916.7 1137.9	813	458	23 4.1 24 92	3.9 10.1	4.2	5.3 15.2	7.0 20.2	10.6	10.9 28.6	10.5	10.0 23.3	8.9 20.5	7.7	5.9 12.5	4.5	3.8	0.9	0.5	324.8 707.7	21.9 23.4	0.8 3.8	15.7
Crocodylomorpha indet.	Takemout, Morocco Takemout, Morocco	MTA-030 MTA-031	tooth ename!	24.5	10.2	714.3	571.4	1935.1	1207.8	285.7	2.4 19.7	21.3	34.8	46.7	70.0	102.1	88.3 95.1	87.0	73.3	60.8 72.3	45.3	33.5	20.2	18.4	1.0	0.3	1583.5	13.7	0.4	19.6
Melenosuchus niger	Pierrelatte, France	Croc. Act.	tooth enamel	34.6	15.1	3362.6	14.6	102.3	350.9	43.9	2.3 0.2	0.9	0.1	0.5	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0			0.3	0.3	0.1	0.0
MAPS-4			bone ash synthetic Ca phosphate	38.7	18.3	718.8	14.9 853.8	633.1 1502.0	246.7 2948.3	248.6 2752.0	20.8	29.5	27.6	0.0 49.8	0.0 52.3	22.2	0.0 44.7	0.0 43.8	35.4	28.5	0.0 35.8	22.2	18.9	20.5						
MAPS-5			synthetic Ca phosphate	36.1	17.8	242.0	44.9	219.9	205.1	47.6	0.4	0.4	1.0	1.4	2.2	2.9	2.4	3.5	3.5	4.3	4.6	5.0	3.1	5.1						

Taxonomy	Locality	Lab name	Material	δ44/42Ca (‰)	2SD	δ43/42Ca (‰)	2SD	n
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA1	tooth enamel	-0.92	0.34	-0.45	0.22	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA2	tooth enamel	-0.74	0.00	-0.37	0.11	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA3	tooth enamel	-1.03	0.03	-0.52	0.02	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA4	tooth enamel	-0.87	0.24	-0.43	0.13	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA7	tooth enamel	-0.88	0.12	-0.44	0.00	3
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA8	tooth enamel	-1.09	0.18	-0.56	0.03	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA9	tooth enamel	-0.92	0.05	-0.46	0.06	2
Non-spinosaurid theropod	Gadoufaoua, Niger	GCA10	tooth enamel	-1.27	0.12	-0.64	0.10	3
cf. Araripesuchus sp.	Gadoufaoua, Niger	GAR1	tooth enamel	-1.12	0.07	-0.54	0.02	2
ct. Araripesuchus sp.	Gadoufaoua, Niger	GAR3	tooth enamel	-1.15	0.15	-0.57	0.09	5
L'enisosteiformes indet	Gadoufaoua, Niger	GAR5 GLE1	scale ganoine	-1.06	0.00	-0.52	0.01	2
Lepisosteiformes indet.	Gadoufaoua, Niger	GLE2	scale ganoine	-0.72	0.00	-0.35	0.06	2
Nigersaurus taqueti	Gadoufaoua, Niger	GAU1	tooth enamel	-0.35	0.14	-0.17	0.09	3
Nigersaurus taqueti	Gadoufaoua, Niger	GAU12	tooth enamel	-0.50	0.05	-0.24	0.00	2
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON1	tooth enamel	-0.60	0.07	-0.29	0.00	2
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON2	tooth enamel	-0.59	0.12	-0.25	0.08	2
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON3	tooth enamel	-0.53	0.01	-0.27	0.07	2
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON4 GON5	tooth enamel	-0.57	0.05	-0.28	0.02	2
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON7	tooth enamel	-0.57	0.00	-0.28	0.02	3
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON8	tooth enamel	-0.50	0.09	-0.24	0.08	3
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON9	tooth enamel	-0.66	0.05	-0.33	0.07	4
Ouranosaurus nigeriensis	Gadoufaoua, Niger	GON10	tooth enamel	-0.53	0.14	-0.29	0.10	3
Pliodetes sp.	Gadoufaoua, Niger	GPL2	scale ganoine	-0.67	0.19	-0.33	0.17	2
Pterosauria indet.	Gadoufaoua, Niger	GAU3	tooth enamel	-0.83	0.06	-0.38	0.05	2
Pterosauria indet.	Gadoufaoua, Niger	GAU5	tooth enamel	-0.73	0.09	-0.40	0.07	2
Pychodontiformes indet	Gadoufaoua, Niger	GPY1	tooth enameloid	-0.79	0.10	-0.37	0.04	2
Pycnodontiformes indet.	Gadoufaoua, Niger	GPY2	tooth enameloid	-1.13	0.10	-0.56	0.10	3
Pycnodontiformes indet.	Gadoufaoua, Niger	GPY3	tooth enameloid	-1.09	0.15	-0.54	0.19	3
Pycnodontiformes indet.	Gadoufaoua, Niger	GPY4	tooth enameloid	-1.05	0.11	-0.53	0.13	3
Pycnodontiformes indet.	Gadoufaoua, Niger	GPY5	tooth enameloid	-1.05	0.08	-0.52	0.04	3
Sarcosuchus imperator	Gadoufaoua, Niger	GSA1	tooth enamel	-0.98	0.08	-0.48	0.09	2
Sarcosuchus imperator	Gadoufaoua, Niger	GSA2	tooth enamel	-1.09	0.03	-0.51	0.00	2
Sarcosuchus imperator	Gadoulaoua, Niger	GSA3 GSA4	tooth enamel	-1.22	0.20	-0.62	0.13	ა ვ
Sarcosuchus imperator	Gadoufaoua, Niger	GSA5	tooth enamel	-1.00	0.10	-0.49	0.04	5
Sarcosuchus imperator	Gadoufaoua, Niger	GSA6	tooth enamel	-1.11	0.10	-0.54	0.10	4
Sarcosuchus imperator	Gadoufaoua, Niger	GSA9	tooth enamel	-1.10	0.04	-0.54	0.01	2
Sarcosuchus imperator	Gadoufaoua, Niger	GSA10	tooth enamel	-1.34	0.01	-0.75	0.08	2
Suchomimus tenerensis	Gadoufaoua, Niger	GSP1	tooth enamel	-1.43	0.01	-0.72	0.09	2
Suchomimus tenerensis	Gadoufaoua, Niger	GSP2	tooth enamel	-1.37	0.17	-0.66	0.02	2
Suchomimus tenerensis	Gadoulaoua, Niger	GSP4 GSP5	tooth enamel	-1.23	0.03	-0.01	0.02	2
Suchomimus tenerensis	Gadoufaoua, Niger	GSP6	tooth enamel	-1.30	0.01	-0.66	0.03	2
Suchomimus tenerensis	Gadoufaoua, Niger	GSP7	tooth enamel	-1.04	0.09	-0.55	0.04	3
Suchomimus tenerensis	Gadoufaoua, Niger	GSP8	tooth enamel	-1.51	0.09	-0.76	0.06	2
Suchomimus tenerensis	Gadoufaoua, Niger	GSP9	tooth enamel	-1.15	0.20	-0.60	0.10	2
Anhangueridae indet.	Bou Laâlou, Morocco	MBL-003	tooth enamel	-0.59	0.09	-0.31	0.09	2
Carcharodontosaurus saharicus	Bou Laalou, Morocco	MBL-024	tooth enamel	-0.59	0.08	-0.26	0.08	3
Spinosaurus aegypticus	Bou Laalou, Morocco	MBL-025	tooth enamel	-0.00	0.02	-0.31	0.02	2
Spinosaurus aegypticus	Bou Laalou, Morocco	MBL-042	tooth enamel	-1 48	0.07	-0.75	0.07	2
Spinosaurus aegypticus	Bou Laâlou, Morocco	MBL-044	tooth enamel	-1.35	0.02	-0.66	0.02	2
Spinosaurus aegypticus	Bou Laâlou, Morocco	MBL-045	tooth enamel	-1.38	0.02	-0.70	0.02	2
Anhangueridae indet.	Jebel Al Qabla, Morocco	MJQ-001	tooth enamel	-0.76	0.06	-0.39	0.06	2
Theropoda indet.	Jebel Al Qabla, Morocco	MJQ-008	tooth enamel	-0.66	0.03	-0.35	0.03	2
I neropoda Indet.	Jebel Al Qabla, Morocco	MJQ-009	tooth enamel	-0.66	0.05	-0.32	0.05	2
Neoceratodus africanus	Jebel Al Qabla, Morocco	MJQ-010	tooth enameloid	-0.09	0.10	-0.35	0.10	2
Stromerichthys sp.	Jebel Al Qabla, Morocco	MJQ-036	scale ganoine	-1.26	0.07	-0.65	0.07	3
Spinosaurus aegypticus	Jebel Al Qabla, Morocco	MJQ-039	tooth enamel	-1.44	0.23	-0.72	0.23	2
Crocodylomorpha indet.	Jebel Al Qabla, Morocco	MJQ-040A	tooth enamel	-0.66	0.14	-0.33	0.14	2
Carcharodontosaurus saharicus	Takemout, Morocco	MTA-017	tooth enamel	-0.53	0.02	-0.29	0.02	2
Carcharodontosaurus saharicus	Takemout, Morocco	MTA-019	tooth enamel	-0.72	0.16	-0.34	0.16	2
Annangueridae indet.	Takemout, Morocco	MTA-020	tooth enamel	-0.68	0.06	-0.34	0.06	2
Spinosaurus aegypticus	Takemout Morocco	MTA-020	tooth enamel	-1.13	0.11	-0.55	0.08	2
Spinosaurus aeavoticus	Takemout, Morocco	MTA-028	tooth enamel	-1.28	0.06	-0.65	0.06	2
Crocodylomorpha indet.	Takemout, Morocco	MTA-030	tooth enamel	-0.62	0.10	-0.35	0.10	2
Crocodylomorpha indet.	Takemout, Morocco	MTA-031	tooth enamel	-0.71	0.10	-0.39	0.10	2
SRM1486 (NIST)	-	standard	bone meal	-1.00	0.10	-0.51	0.09	32