

# 1 Taphonomic evidence supports an aquatic 2 lifestyle for *Spinosaurus*

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## 12 ABSTRACT

13 A new locality near Tarda on the northern margin of the Tafilalt, south eastern Morocco exposes  
14 extensive sequences of the Ifezouane and Aoufous formations of the fluvial Kem Kem Group  
15 (Cretaceous, ?Albian-Cenomanian) on the south western flank of Ikfh n'Oufza escarpment of the  
16 Hamada du Meski. The stratigraphic sequence here differs significantly from better known  
17 exposures of the Kem Kem Group in the southern Tafilalt, and includes a heterolithic sequence of  
18 alternating grey mudstones and fine sandstones and a thin (~1.5 m) marine limestone. The locality is  
19 noteworthy for three vertebrate-bearing horizons within the upper part of the Ifezouane Formation.  
20 The upper two (Sites 1 and 2 in ascending order) are dominated by dental remains of the sawfish  
21 *Onchopristis* and the aquatic theropod dinosaur *Spinosaurus*. Significantly, the remains of terrestrial  
22 dinosaurs constitute less than 1 % of the total dental assemblage at Site 1 and 5.6% at Site 2. At Site  
23 2 teeth of *Spinosaurus* outnumber the rostral "teeth" of *Onchopristis*. The remarkably high  
24 abundance of spinosaur teeth compared to remains of terrestrial dinosaurs, and even some aquatic  
25 animals strongly supports *Spinosaurus* being an aquatic animal spending much of its life in water  
26 where its teeth were shed and preserved.

27  
28 *Key words:* Cretaceous; Dinosauria; *Spinosaurus*; Taphonomy; Palaeoecology; Morocco

## 30 1. Introduction

31 The enigmatic theropod dinosaur *Spinosaurus aegyptiacus* Stromer, 1915 has been interpreted as a  
32 piscivorous and semi-aquatic animal (Stromer, 1936, Taquet, 1984; Ibrahim et al., 2014; Arden et al.,  
33 2019), and more recently shown to have possessed a highly modified tail suited for propelling the  
34 animal through water (Ibrahim et al., 2020a). The hypothesis that this spectacular dinosaur was  
35 semi-aquatic - or even perhaps fully aquatic – has met with some opposition (e.g. Henderson, 2018;  
36 Hone and Holtz, 2019), not least because it challenges decade-old ideas on dinosaur ecology and  
37 evolution. Evidence for an aquatic lifestyle hinges mainly on skeletal data, which provides compelling  
38 evidence, including a rearward position of the external nares, flattened pedal unguals and  
39 considerable divergence of pedal digits, a series of elongate neural spines on the caudal vertebrae  
40 giving the tail a fin-like morphology, a reduced pelvic girdle and hindlimb, with a disproportionately  
41 short femur and osteoclerosis/pachyostosis of the skeleton (Ibrahim et al., 2020a), as well as  
42 circumstantial evidence for specialized sensory structures to detect prey in water (Ibrahim et al.,  
43 2014). Possession of a narrow, somewhat crocodile-like overall skull morphology and a dentition of  
44 simple conical teeth, often with pronounced apicobasal ridges, has also been interpreted as  
45 indicating a piscivorous diet (Stromer 1936, Taquet 1984, Ibrahim et al., 2014; McCurry et al., 2019).  
46 Comparisons with more distantly related forms – large piscivorous fish – have also been used to  
47 support piscivory in *Spinosaurus* (Vullo et al., 2016). Additional evidence from phylogenetic analysis  
48 suggest a very close relationship to the European *Baryonyx walkeri*, a spinosaurid in which possibly  
49 acid-etched lepidotid fish scales were discovered in the ribcage, providing potential evidence for a  
50 degree of piscivory in these animals (Charig and Milner, 1986, 1997). Isotopic evidence was also used  
51 to suggest an aquatic lifestyle for *Spinosaurus* by Amiot et al. (2010), although the data was  
52 somewhat inconclusive. Taken together, these diverse and independent lines of evidence all point  
53 toward a largely piscivorous – and aquatic – lifestyle. Here we present evidence from a taphonomic  
54 analysis of a new locality of the Kem Kem Group strata of south east Morocco that further  
55 strengthens a predominantly aquatic lifestyle for *Spinosaurus*.

56

57 Most museum specimens of *Spinosaurus* from Morocco have been obtained from commercial  
58 sources, and generally lack precise locality or horizon data (Ibrahim et al., 2020a). Our field studies  
59 over the last 15 years in the Tafilalt region and Hamada du Kem Kem of south east Morocco reveal  
60 that a majority of this material comes from the top of the Ifezouane Formation of the Kem Kem  
61 Group. Many isolated teeth, occasional jaw fragments and, more rarely, postcranial bones are dug

62 by artisan miners from three or four event horizons characterised by mud-flake conglomerates with  
63 chaotic bedding, and sharp basal contacts. They are rarely more than 1 m thick, and often just a few  
64 centimetres, but may be extensive and traceable over several kilometres. The discovery of an  
65 associated skeleton by Ibrahim et al., (2020a) is an exception, as this specimen is one of only three  
66 associated dinosaurs reported from the Kem Kem Group (Ibrahim et al., 2020a), and it occurred at a  
67 slightly higher level in the sequence.

68

## 69 **2. Locality and geological context**

### 70 *2.1 Locality*

71 The data reported here was obtained from natural exposures at the foot of the Ikhf n'Oufza  
72 escarpment, the western extension of the Hamada du Meski between Goulmima and Er Rachidia on  
73 the northern margin of the Tafilalt Basin in south east Morocco. This locality lies within Errachidia  
74 Province near the village of Tarda on the eastern side of the Oued Tarda (Fig. 1). Exposure is  
75 extensive, patchily continuous for ~ 2.4 km, and has been quarried and mined in several places  
76 specifically for the extraction of fossils.

77 The Kem Kem Group strata represent an extensive fluvial system that can be traced in Morocco for  
78 at least 200 km from Zguilma in the south west to Aoufous and beyond to the Anoual Basin and the  
79 frontier with Algeria. In Algeria, coeval strata yield remarkably similar vertebrate assemblages both  
80 in terms of faunal diversity and taphonomy (Benyoucef et al., 2015; Ibrahim et al., 2020a,b).

81 Vertebrate fossils occur at event horizons (likely flash-flood deposits and viscous sediment flows, as  
82 channel lags and as exceptionally rare isolated associated skeletons (Ibrahim et al., 2014, 2020a,b).

83 The vertebrate assemblage is diverse (for a full faunal list see Cavin et al., 2010; Ibrahim et al.,  
84 2020b) and includes a wide variety of cartilaginous and bony fishes, archosaurs (dinosaurs,  
85 pterosaurs and crocodiles), turtles and snakes and lizards. There are anomalies such as a near  
86 absence of ornithischian dinosaurs and a lack of mammals, which have yet to be reported from the  
87 Kem Kem Group (Ibrahim et al., 2020a,b).

88

### 89 *2.2 Geological context*

90 The strata from which the fossils discussed here came comprise a suite of largely clastic red  
91 mudstones, fine sandstones and thin conglomerates (pebble and mud-flake) of the Kem Kem Group.  
92 They rest unconformably on folded Palaeozoic basement rocks and are overlain by marine

93 Carbonates of the Akrabou Formation that is well dated as Middle Cenomanian to Turonian  
94 (Ettachfini and Andreu, 2004; Kennedy et al., 2008). In the north of the Tafilalt the Kem Kem Group  
95 has been divided into two formations, a lower Ifezouane Formation dominated by fine sands with  
96 event horizons yielding fossils vertebrates, and an upper Aoufous Formation that is comprised  
97 largely of variegated mudstones with thin-bedded sandstones. This latter formation generally lacks  
98 fossil vertebrates, except near Aoufous (Oum Tkout) where a thin horizon of laminated mudstones  
99 yields fully articulated skeletons of fish and amphibians in a lacustrine Konservat Lagerstätte  
100 (Dutheil, 1999; Cavin et al., 2010; Ibrahim et al., 2020b).

101 At Tarda the base of the Kem Kem Group is not seen and the sequence commences with a series of  
102 greyish mudstones with thin beds of gypsum and thin (~20-50 mm thick) siltstones with halite  
103 pseudomorphs. These pass upwards into a sequence of massively bedded and cross bedded fine  
104 sandstones with occasional clay partings a few tens of centimetres thick. The sequence continues to  
105 be dominated by fine sandstones upwards until it passes into a series of variegated mudstones  
106 capped by a yellow weathering well-bedded limestone with *Thalassinoides*. This represents a brief  
107 marine intercalation but has only yielded a shelly fauna of very small bivalves resembling modiolids  
108 and a heterodont near Zrigat, a few kilometres to the east. This limestone is prominent in the  
109 landscape for its colour and also for producing the cap to a smaller plateau sitting lower than the  
110 dominating Hamada de Meski that forms the northern margin of the Tafilalt Basin. Above the thin  
111 yellowish limestone is a series of variegated (grey, blue-grey, orange, ochreous and red) sandstones  
112 that form the upper part of the Ifezouane Formation. These sandstones pass up into variegated  
113 mudstones with thin sandstones of the Aoufous Formation and are in turn capped by limestones of  
114 the Akrabou Formation that form the top of the Hamada du Meski. A preliminary sedimentary log  
115 for the exposure is provided in figure 2.

116 The Akrabou Formation limestones are dated as mid Cenomanian to Turonian on the basis of a  
117 diverse ammonite assemblage (Kennedy et al., 2008), but the age of the Kem Kem Group is not  
118 securely determined. Several authors, using the fossil vertebrates, have suggested a Lower  
119 Cenomanian age for the Kem Kem Group by comparing it with the Bahariya Formation of the  
120 Egyptian Western Desert (Sereno et al., 1996; Ibrahim et al., 2020b), but it may well be somewhat  
121 older, as there is a considerable thickness of strata and a number of disconformities between the  
122 vertebrate-bearing Ifezouane Formation and the base of the Akrabou Formation.

123

124 *2.3. Taphonomic context*

125 The two vertebrate-bearing horizons examined (Sites 1 and 2 [red and yellow stars respectively in  
126 Fig. 2]) differ sedimentologically and taphonomically. At Site 1 the vertebrate remains occur at the  
127 base of a brown weathering fine-grained lenticular sandstone channel that can be traced laterally for  
128 only a few tens of metres. The vertebrate remains often occur as broken fragments, are randomly  
129 orientated and brittle. Bone and dentine are white while enamel is pale yellow to orange. In places  
130 the sandstone is extremely well cemented by iron oxides, where it is a darker brown or buff colour.  
131 By contrast at Site 2 the vertebrate remains are restricted to a thin but laterally more continuous  
132 layer representing an event horizon more typical of other vertebrate-bearing horizons in the  
133 Ifezouane Formation, such as Ouzina and Begaa (e.g. Ibrahim et al., 2016; Martill et al., 2018  
134 respectively). At these localities fossil vertebrates occur in thin debris sheet flows that in places are  
135 mud-flake conglomerates, with matrix-supported clasts and chaotic bedding.

136

### 137 **3. Methods, aims and objectives**

138 During reconnaissance field work in the vicinity of Tarda in the northern Tafilalt of south east  
139 Morocco we discovered a bone bed at the base of a sandstone channel that had been exploited by  
140 local fossil diggers. Many large blocks of indurated sandstone lay around the abandoned diggings  
141 and all were rich in the teeth of *Spinosaurus*, rostral ‘teeth’ of the sawfish *Onchopristis* and circular  
142 vertebrae that we also attribute to *Onchopristis* (see Ibrahim et al., 2020b). Weathered spoil dumps  
143 from the small artisan mines were also collected and analysed for abundance data.

144

145 Just 1.5 kilometres distant we located an active mine site and met with a number of artisan fossil  
146 miners. One of us (DMM) purchased *all* of the fossils that a digger had obtained and put into a large  
147 sack (total number of elements = 1261). All of this material had been obtained from one  
148 stratigraphic level in the upper part of the Ifezouane Formation and is indicated as Site 2 on Fig. 1  
149 (stratigraphic nomenclature follows Ettachfini and Andreu, 2004).

150 Specimens cited in this work are accessioned in the following institutions: BSP, Staatliche  
151 Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und  
152 Geologie, Munich, Germany; DINO, Dinosaur National Monument, Utah, USA; FSAC, Département de  
153 Géologie, Faculté des Sciences Aïn Chock, Université Hassan II, Casablanca, Morocco; MIWG,  
154 Dinosaur Isle Museum, Sandown, Isle of Wight, UK; MN/UFRJ, Museu Nacional /Universidade  
155 Federal, Rio de Janeiro, RJ, Brazil; MNHN, Museum National d’histoire Naturelle, Paris, France;  
156 MSNM, Museo di Storia Naturale di Milano, Italy; MUCP, Museo de la Universidad Nacional del

157 Comahue, El Chocon Collection, Argentina: MUO, Museum of the University of Oklahoma, USA;  
158 NHMUK, Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde  
159 Stuttgart, Stuttgart, Germany; USP, University of Sao Paulo, SP, Brazil.

160

## 161 **4. Results.**

### 162 *4.1. Site 1*

163 Collecting from Site 1 at a horizon below the Yellow Limestone Member (See Figs 2, 3) in the lower  
164 Ifezouane Formation yielded a total of 926 vertebrate fossils, of which 317 (34.2%) were teeth  
165 (including *Onchopristis* rostral denticles) (Table 1A). Microvertebrate remains were not collected.  
166 We focussed our analysis on dental remains as all of these could be confidently assigned to a taxon  
167 at least at ordinal level or better (Table 1B, even when fragmentary). Only 6 distinct tooth  
168 morphotypes were present in the assemblage (Table 1B). Of these, the teeth of *Spinosaurus* (Figs. 4,  
169 5) comprised almost 48% of the total dental remains and 16.4% of the total vertebrate fossils from  
170 this site.

171 Although much of the dental material is fragmentary (see Figs 4, 5) it can easily be identified into  
172 broad taxonomic groups and sometimes genera. For *Spinosaurus* teeth we used criteria described  
173 and figured by Richter et al., (2013) and Hendrickx et al., (2019).

174 Thus, remarkably, *Spinosaurus* teeth were only slightly less numerous than the most common  
175 elements of the dental assemblage, the rostral denticles of the sawfish *Onchopristis numidus* (Table  
176 1A). The only other dinosaur present in the dental assemblage at this locality is the allosauroid  
177 *Carcharodontosaurus* sp., represented by a single broken tooth. The results show that *Spinosaurus*  
178 and *Onchopristis* are the most abundant fossils at this locality by a considerable margin (Fig. 6A, B).

### 179 *4.2. Site 2*

180 Site two yielded a more diverse assemblage than Site 1, where a total of 1261 vertebrate fossils  
181 were obtained. They were purchased from an artisan miner at his mine, and all originate from a  
182 single event horizon in the upper Ifezouane Formation occurring above the Yellow Limestone  
183 Member (Figs. 2, 3). We acknowledge that it is likely that this assemblage of fossils may have had  
184 some larger bones and more valuable larger teeth removed. It is likely that this would have been  
185 only a small number (pers. obs.). Of the material, 928 specimens (73.6%) represent dental remains  
186 (Table 2A, B). The diversity of teeth at this site is significantly greater than at site 1, with at least 12  
187 morphotypes represented. The most abundant tooth morphotype at Site 2 are the conical, faceted

188 teeth of *Spinosaurus* sp., (407 teeth) which comprised 43.9% of the dental sample and 32.3% of the  
189 total vertebrate material at this site. Although many of the *Spinosaurus* teeth are too fragmentary to  
190 be confidently placed within distinct morphotypes (*sensu* Richter et al., 2013), we were able to  
191 allocate 225 out of a total of 407 teeth (Fig. 7). The abundances of the three morphotypes  
192 approximate those of Richter et al (2013). The second most abundant dental remains are attributed  
193 to *Onchopristis* with a total of 375 (40.4%) rostral denticles (Fig. 6C, D).

194

#### 195 4.3. Comparisons between sites 1 and 2

196 Although there are considerable similarities between the two vertebrate assemblages, there are also  
197 some significant differences that likely reflect subtle differences in habitat preference between taxa  
198 and taphonomic filters such as size and density sorting. Dinosaur diversity is considerably greater at  
199 Site 2 than Site 1, but the numbers of non-spinosaurid dinosaur teeth are low, and combined they  
200 constitute no more than 4.2% of the total assemblage and 5.6 % of the dental assemblage. Where  
201 taxa are known from a single example we do not regard this as significant, and of those taxa that are  
202 common to both sites (Carcharodontosauridae; Spinosaurinae; *Onchopristis numidus*), only  
203 *Onchopristis* and *Spinosaurus* are found in any abundance. An intriguing discrepancy between the  
204 two sites is the lack of vertebrae attributable to *Onchopristis* at Site 2. These easily identified  
205 elements constitute 41% of the vertebrate remains at Site 1, and are reasonably common at many  
206 sites in the eastern and southern outcrops of the Kem Kem Goup (Ibrahim et al., 2020b). This  
207 discrepancy is unexpected and not easy to explain. We cannot rule out that the fossil digger at Site 2  
208 considered them to have no commercial value and left them in the mine, but this has not been our  
209 experience of other dig sites. An element of density sorting may be at play with the relatively light  
210 vertebrae having been winnowed away.

211

## 212 5. Discussion

213 The relative abundances of dental remains for the two distinct stratigraphic intervals collected at  
214 Tarda reveals that teeth of *Spinosaurus* occur in high abundance at both levels, but are exceptionally  
215 abundant at Site 1 where they constitute 48% of the dental remains. We know of no other dinosaur-  
216 bearing bone bed where such an abundance of dinosaur teeth occurs. The enhanced abundance of  
217 *Spinosaurus* teeth relative to other dinosaurs is likely a reflection of their aquatic lifestyle. An animal  
218 living much of its life in water is much more likely to contribute teeth to the river deposit than those  
219 dinosaurs that perhaps only visit the river for drinking and more casual feeding on its banks, or the

220 occasional carcass of a terrestrial dinosaur decomposing in the river. Similarly, the high abundance  
221 of rostral denticles of *Onchopristis* is hardly surprising, given that sawfish are fully aquatic animals,  
222 and that elasmobranchs are noteworthy for their efficiency in growing and replacing teeth  
223 (Slaughter and Springer, 1968). What is perhaps surprising is the rarity of other fish teeth, especially  
224 the more robust teeth of holosteans such as *Lepidotes* sp. and pycnodonts, although the latter are  
225 rare in the Kem Kem Group (Cooper and Martill, 2020), the former occur frequently and reached a  
226 large size.

227 Our results largely agree with those of Läng et al., (2013) who sampled the Ifezouane Formation in  
228 the southern Tafilalt and Benyoucef et al., (2015) who sampled the Algerian Kem Kem Group in the  
229 Guir Basin, although we note some differences. In the southern Tafilalt, amalgamated results for six  
230 horizons at three localities suggest that theropod remains (including *Spinosaurus*) constitute only  
231 ~6% of the assemblage. However, at the majority of their localities and horizons, the teeth of  
232 *Spinosaurus* outnumbered those of all other dinosaurs combined. In Algeria, Benyoucef et al. (2015)  
233 found that dinosaurs formed a much smaller component of all taxa reported from Béchar. However,  
234 in considering just the dinosaur remains, those identified as *Spinosaurus* represented 94% of the  
235 theropod dental assemblage. At Site 1 in Tarda *Spinosaurus* constitutes 99% of the theropod dental  
236 assemblage, and at Site 2 this value is 89%. Clearly *Spinosaurus* teeth are the most abundant  
237 dinosaur dental remains in the Kem Kem Group, over all of its outcrop. There are considerable  
238 differences in the relative abundances of non-dinosaurian remains between these localities, but  
239 discussion of this is beyond the scope of this analysis. We do add, however, that the similarity of  
240 distribution of vertebrate remains in the material collected from Site 1 compared to that  
241 collected by the miners at Site 2 is noteworthy, especially with regard to the distribution of  
242 remains of aquatic forms. Despite the difference in collecting methods (fossil miners vs  
243 research collecting), this strongly supports our observation that *Onchopristis* and  
244 *Spinosaurus* represent the largest components of the assemblages at both sites. It would  
245 seem odd surely, if the fossil collectors at Site 1 deliberately left behind the remains of  
246 *Onchopristis* and *Spinosaurus* (for researchers to find) while those at Site 2 collected only  
247 these taxa.

248

#### 249 5.1. Relative abundances

250 The abundance and availability of teeth for inclusion in a bone bed is controlled by both biological  
251 and taphonomic factors. Biological factors include tooth replacement, number of teeth per taxon,



252 longevity and number of individuals in population of the catchment area. In palaeontology many of  
253 these are unknowns, including even the total number of teeth in the jaws. For *Spinosaurus* the tooth  
254 count is estimated to be ~68-72 (see Table 3).

255 Theropod teeth were replaced on a regular basis, as they are in modern crocodylians (Currie, et al.,  
256 1990), where tooth replacement is irregular and affected by age and size of the individual crocodile,  
257 with irregularity of replacement increasing with age (Edmund, 1962). The functional life of each  
258 tooth differs from approximately nine months in anterior teeth, to sixteen in posterior teeth  
259 (Edmund, 1962). Teeth are replaced in waves from front to back in juveniles, and reversed in older  
260 individuals (Edmund, 1962). It has been suggested that theropods had a very similar tooth functional  
261 life to crocodylians of between nine and sixteen months per tooth. The presence of theropod teeth  
262 among some herbivorous dinosaur remains indicates that theropods may have lost one or more  
263 teeth in some feeding sessions, suggesting tooth replacement was rather constant and relatively  
264 rapid (Currie, et al., 1990). Erickson et al., (1996) notes a duration for replacement teeth of up to 777  
265 days for an adult *Tyrannosaurus*, while D'Emic et al., (2019) found as little as 56 days for  
266 *Majungasaurus* and 104 days for *Allosaurus*, both of which may be considered as tentative proxies  
267 for Kem Kem abelisaurids and *Carcharodontosaurus* respectively. We speculate that *Spinosaurus*  
268 may have had a tooth replacement duration within the 56 to 777 day range. We also note that the  
269 abelisaur with the highest tooth replacement rate has a low abundance in the Kem Kem Group  
270 (Tables 1, 2), suggesting perhaps that they were not an important part of this palaeobiotope.

271 The number of teeth in the jaw at any one time varies considerably between taxa in the Dinosauria,  
272 but for Spinosauridae it is probably between 68 and 72 (*Spinosaurus*) and 94 (*Baryonyx*) (Table 3).  
273 The total tooth count for *Carcharodontosaurus* is not known, but related allosauroids have total  
274 counts of between 60 and 80 (Table 3), which suggests that *Spinosaurus* is not particularly different  
275 from other theropods roaming the Kem Kem biotopes. Likewise, there is little reason to suspect that  
276 tooth shedding rates would be very different between *Spinosaurus* and *Carcharodontosaurus*  
277 (although of course they may have been), or the numbers of teeth during the course of their  
278 lifetime. Likely the greater abundance of *Spinosaurus* teeth compared to *Carcharodontosaurus* and  
279 the abelisaurids in the Kem Kem is that spinosaurids were present in greater numbers in this largely  
280 fluvial environment dominated by aquatic organisms (Ibrahim et al. 2020a,b and papers therein),  
281 and inhabited the sedimentary environment in which their teeth are preserved.

282 Of course, it is possible that the abundance of *Spinosaurus* remains in a fluvial deposit are the result  
283 of a wading heron-like ecology, snatching prey from shallow water as has been suggested by some  
284 authors (Taquet, 1984; Hone and Holtz, 2017, 2019; Henderson, 2018). An elongated skull and neck

285 relative to those of other large theropods is consistent with this interpretation (although these  
286 features are also consistent with diverse swimming birds). However, other aspects of the  
287 morphology of *Spinosaurus* are inconsistent with wading mode of life. Wading has developed  
288 independently several times in extant theropods, always converging on similar hindlimb  
289 morphologies. Wading birds are characterised by having hindlimbs that are longer, relative to body  
290 size, than those of other birds, with the tibiotarsus and tarsometatarsus disproportionately extended  
291 (Zeffer et al., 2003). Such a morphology increases foraging area (Baker, 1979) reduces drag,  
292 increasing efficiency while moving through water (Zeffer et al., 2003). These adaptations presumably  
293 also have the added benefit of reducing water disturbance that may alert potential aquatic prey to  
294 the presence of a predator.

295 In contrast, the hindlimbs of *Spinosaurus* are greatly shortened relative to body size, with  
296 disproportionate reduction of the femur (Ibrahim et al., 2014). Not only are these hindlimb  
297 proportions inconsistent with those of a wading animal, they suggest that *Spinosaurus* is more  
298 poorly adapted to a wading mode of life than any other non-avian theropod (perhaps with the  
299 exception of those paravians with elaborately feathered hindlimbs). Overall reduction in hindlimb  
300 length, that disproportionately affects the femur is consistent with only one form of avian  
301 locomotion: active swimming (Zeffer et al., 2003).

302 Taken in conjunction, both morphological analysis and now taphonomic data strongly support a  
303 predominantly aquatic mode of life for *Spinosaurus*.

## 304 **6. Conclusions**

305 The teeth of *Spinosaurus* occur in high abundance in two bone-bearing horizons at the Tarda locality  
306 of the Kem Kem Group. The abundance of *Spinosaurus* at both levels in comparison to terrestrial  
307 dinosaurs such as the gigantic theropod *Carcharadontosaurus*, the somewhat smaller abelisaurids and  
308 sauropods is substantial. In the lower horizon, a channel-lag bone bed, teeth of *Spinosaurus*  
309 outnumber terrestrial dinosaur teeth by a factor of ~150 to 1. In addition, at this horizon the teeth of  
310 *Spinosaurus* are more abundant even than many aquatic and semi-aquatic animals such as bony  
311 fishes and crocodyliforms. At a slightly higher horizon in the same stratigraphic unit *Spinosaurus*  
312 teeth outnumber those of all other dental remains, and outnumber other dinosaur teeth by a factor  
313 of ~8 to 1. While all of the fossils collected from these horizons should be considered semi-  
314 autochthonous, it would seem that for such an abundance of teeth of *Spinosaurus* to occur, it is  
315 highly likely that this animal was living mostly within the river rather than along its banks. This  
316 conclusion is consistent with interpretations of *Spinosaurus*' palaeoecology based on anatomical  
317 evidence (Ibrahim, et al., 2014, 2020a). Furthermore, the channel-lag bone bed at Site 1 is the first

318 reported occurrence of a bone-bed dominated by dinosaur teeth, and represents a unique  
319 thanatocoenosis.

320

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327

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469

## 470 **Figure Captions**

471 **Fig. 1.** Map of the Tarda locality with extensive exposures of the Kem Kem Group. A, General map of  
472 the northern Tafilalt showing the major towns and location of the Tarda Oasis with field area  
473 indicated by the box. B, Detailed map with schematic geological overlay. Sites one and two are  
474 indicated by red and yellow stars respectively. The uncoloured area corresponds to the lower  
475 Ifezouane Formation, but in many places this is concealed by alluvial fans. The red star is located on  
476 an outcrop on the flanks of a small plateau formed by the Yellow Limestone Member.

477

478 **Fig. 2.** Preliminary stratigraphic log for the region between Sites 1 and 2 near Tarda. A, Log through  
479 the Ifezouane Formation including the Yellow Limestone Member. B, Simplified stratigraphic scheme  
480 for the region with range strata visible at Tarda indicated by black line.

481

482 **Fig. 3.** Photographs of exposures in the Tarda field area. A, View of the Ikfh n'Oufza escarpment  
483 taken from the small plateau shaded purple in Fig. 2. Site 2 is just a few metres to the east of this  
484 view. B, View looking north with the unnamed plateau capped by the Yellow Limestone Member  
485 and Ikfh n'Oufza in the distance. C, Site 2 seen from Site 1. The distance is just shy of 2 km.

486

487 **Fig. 4.** *Spinosaurus* teeth at Site 1. A, Thin section in PPL through sandstone bone-bed with spinosaur  
488 teeth. The tooth broken tooth in this image is a *Spinosaurus* crown tip with maximum diameter of  
489 2.5 mm. B, as A but seen in XPL. C, a bag full of broken *Spinosaurus* teeth abandoned by the fossil  
490 diggers at Site 1, presumably regarded as of no commercial value.

491

492 **Fig. 5.** Isolated vertebrate remains for Site 1 and Site 2 at Tarda, SE Morocco. Notice that the  
493 material is fragmentary, but not water worn. Hairline fractures in the material mean that specimens  
494 often fall apart when extracted, but some material was fragmented preburial, as seen in Fig. 4A, B.  
495 Scale bars = 10 mm. A, rostral denticle of *Onchoprisits cf. numidus*; B, Lamnid shark indet.; C,  
496 fragment of vomerine dentition from pycnodont; D, unidentified large fish tooth; E, lungfish dental  
497 plate; F, tooth of abelisaurid indet.; G, tooth of indeterminate theropod; H, tooth of *Spinosaurus* sp.;  
498 I, tooth of *Carcharodontosaurus* sp.; J, tooth of titanosauroid sauropod indet.; K, tooth of  
499 indeterminate ornithocheirid pterosaur; L, tooth of pholidosaurid crocodile; M, Tooth of *Elosuchus*

500 sp.; N, fragment of dorsal fin spine of hybodont shark; O, vertebra likely attributable to *Onchopristis*  
501 *numidus*; P, fragment of indeterminate turtle carapace; Q, teleost vertebra; R, holostean scale; S,  
502 indeterminate bone fragment.

503

504 **Fig. 6.** Pie charts displaying the relative abundance of vertebrate elements in assemblages from Sites  
505 1 and 2 of the Tarda locality. A, All vertebrate elements from Site 1; B, teeth only from Site 1; C, all  
506 vertebrate elements from Site 2; D, teeth only from Site 2. See also Tables 1A,B, and 2A,B, for  
507 numerical abundances. See Fig. 5 for identifications.

508

509 **Fig. 7.** *Spinosaurus* sp. tooth morphotypes at Site 2, Tarda, Morocco. The three morphotypes  
510 recognised by Richter et al., (2013) are Mt.1a-c. In the pie chart slightly less than half the teeth could  
511 not be confidently placed in a morphotype. Scale bars = 10 mm.

512

513 **Table 1.** Taxonomic abundances at Site 1. A, total taxonomic abundance; B, dental taxonomic  
514 abundance.

515

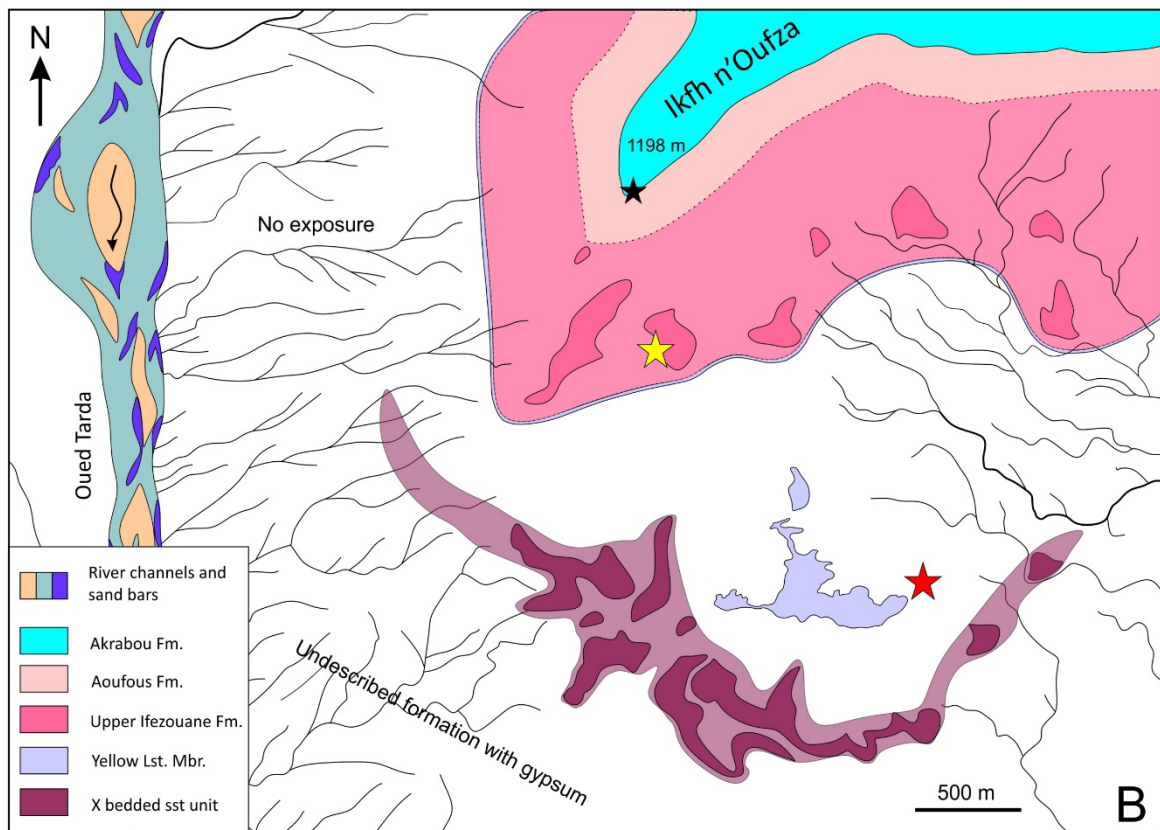
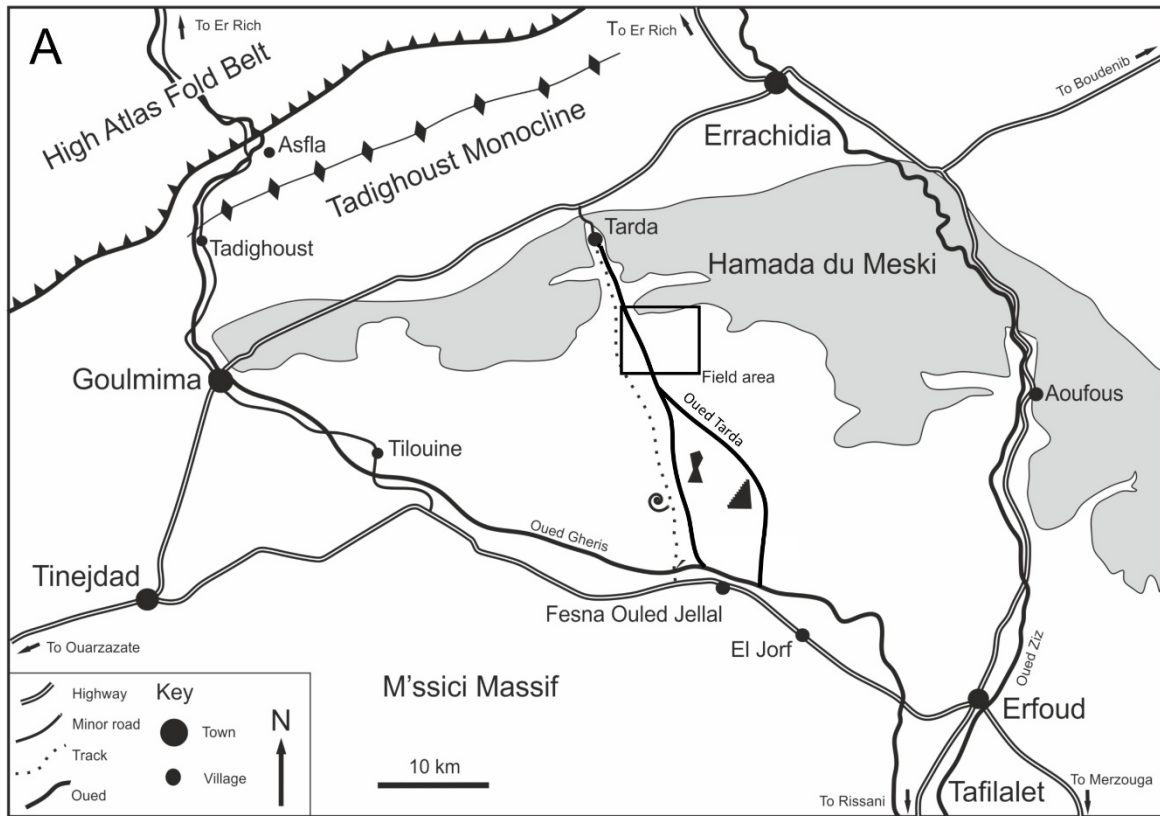
516 **Table 2.** Taxonomic abundances at Site 2. A, total taxonomic abundance; B, dental taxonomic  
517 abundance.

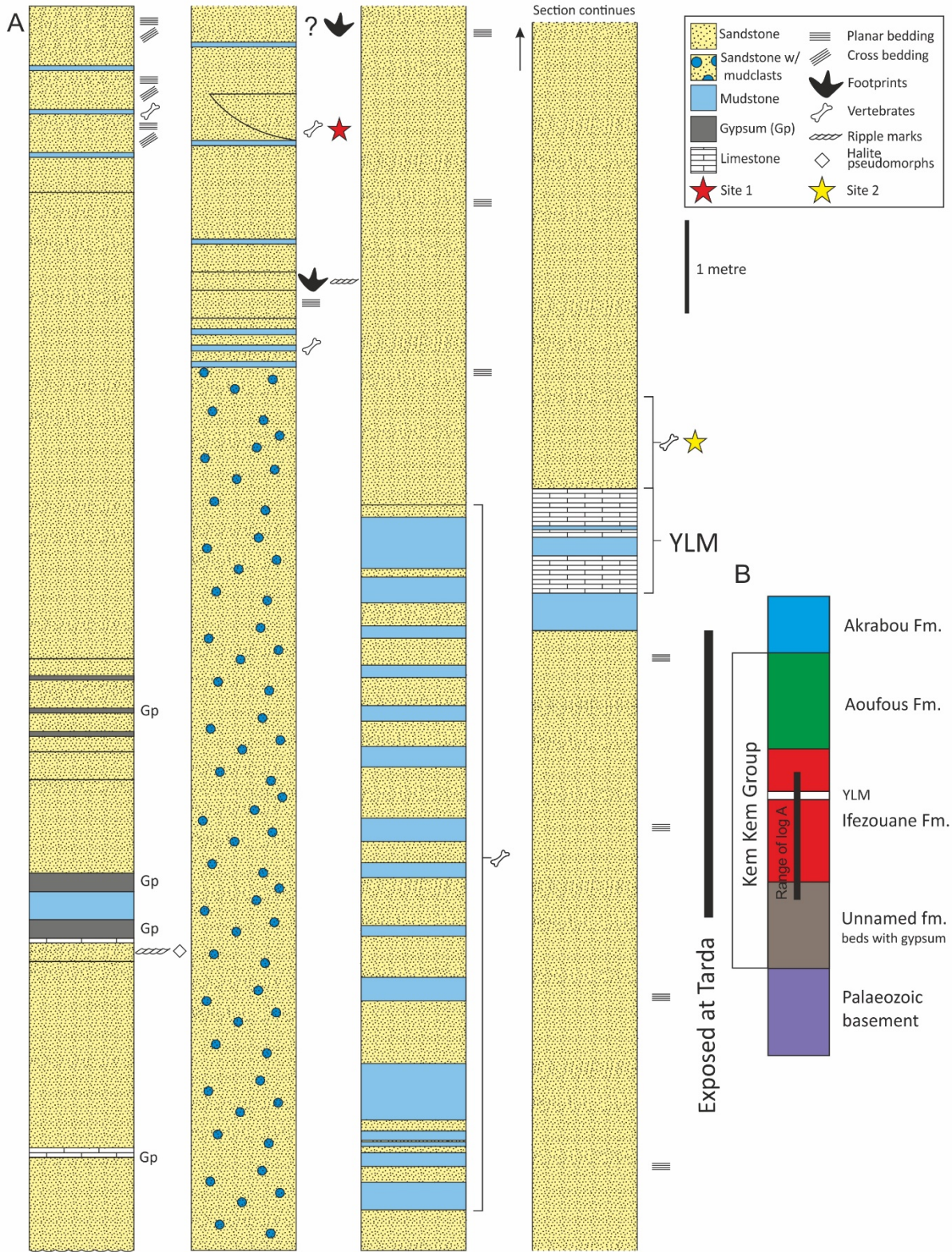
518

519 **Table 3.** Tooth counts for a variety of theropod dinosaurs from the Kem Kem Group with data from  
520 related forms from other localities. Asterisks indicate incomplete specimens where tooth count  
521 could be higher.

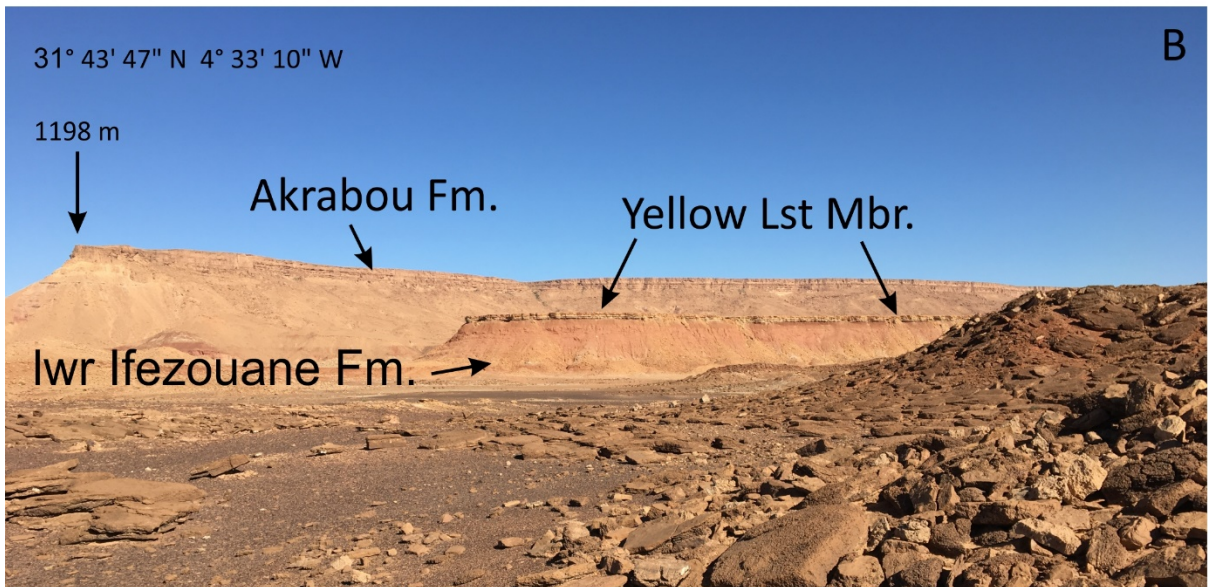
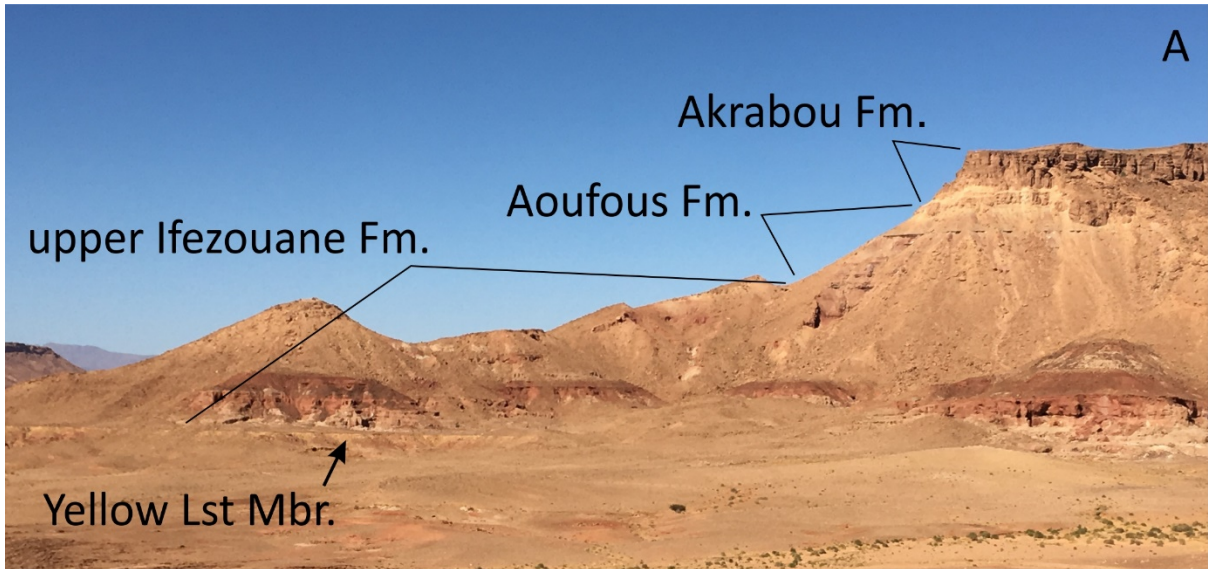
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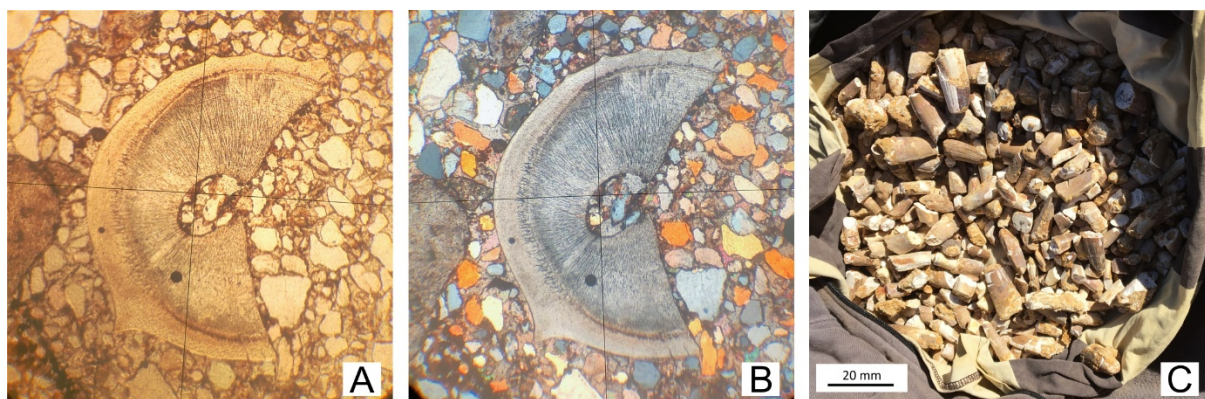








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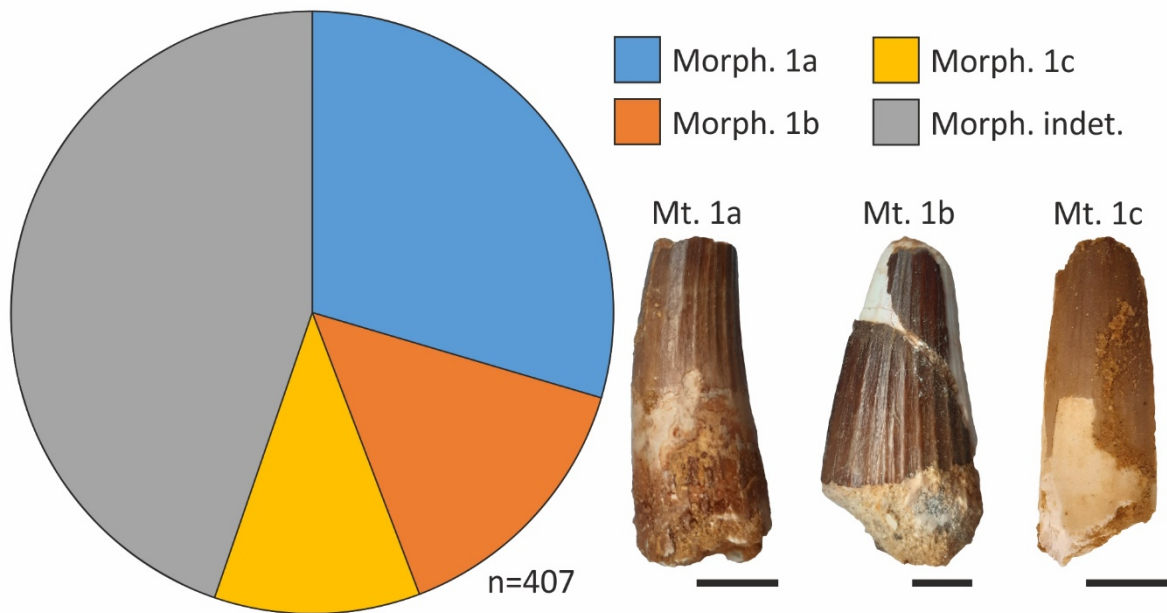


528

529



Morphotype	Abundance	%	% ex. indet.	% Richter, et al., 2012
1a	120	29.5	53.3	60.0
1b	60	14.7	26.6	22.0
1c	45	11.1	20.0	18.0
Indet.	182	44.7	N/A	N/A
<b>Total</b>	<b>407</b>	<b>100.0</b>	<b>99.9</b>	<b>100.0</b>



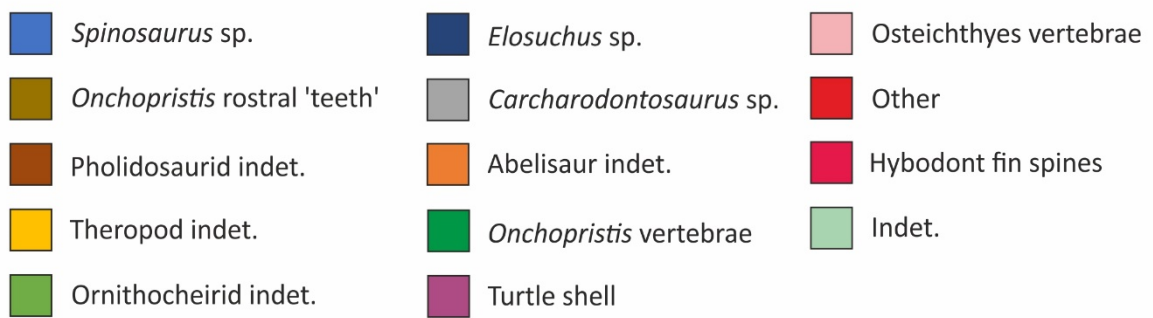
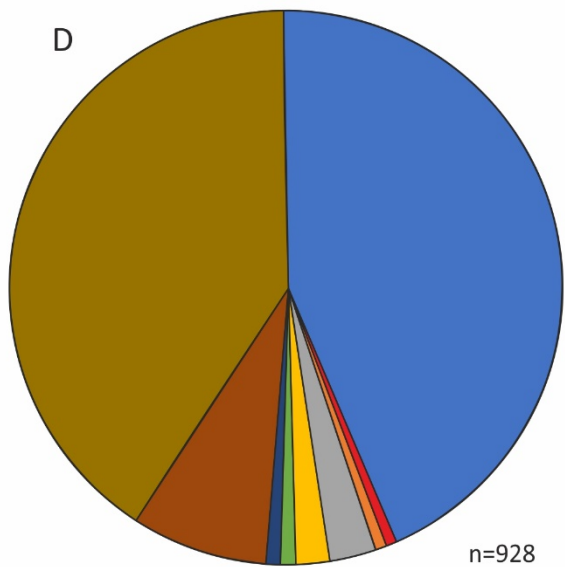
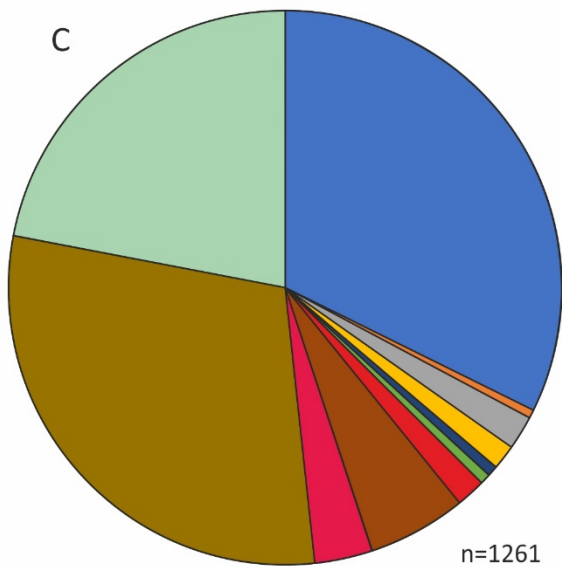
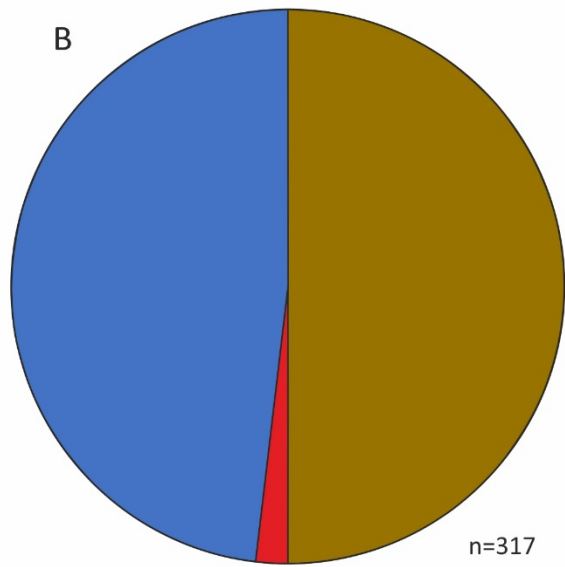
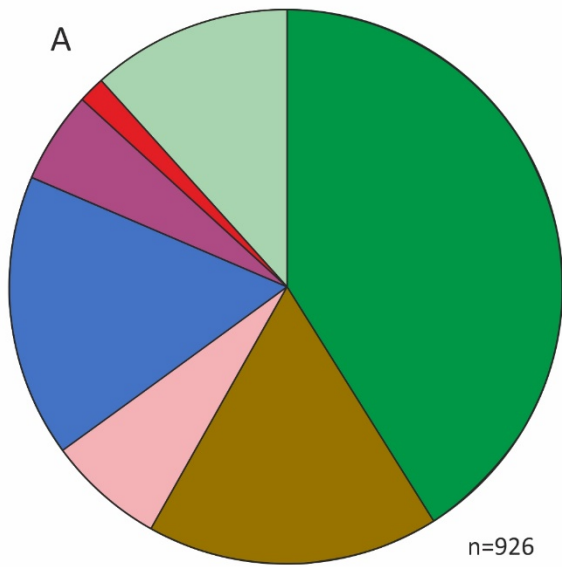






Table 1A. Tarda bone bed taxonomic abundance. Raw data n = 926.

<b>Taxon</b>	<b>No. of Elements</b>	<b>%</b>	<b>Palaeoecology</b>
<i>Onchopristis numidus</i> vertebrae	381	41.1	Aquatic
<i>Onchopristis numidus</i> rostral 'teeth'	159	17.2	Aquatic
Osteichthyes vertebrae	63	6.8	Aquatic
<i>Lepidotes</i> sp. teeth	3	0.3	Aquatic
<i>Spinosaurus</i> sp. teeth	152	16.4	Semi-aquatic to aquatic
<i>Carcharodontosaurus</i> sp. teeth	1	0.1	Terrestrial
Lungfish teeth	1	0.1	Aquatic Freshwater
Ganoid scales	2	0.2	Aquatic
Hybodont shark fin spine	2	0.2	Aquatic
Turtle shell	50	5.4	Aquatic
Crocodile tooth?	1	0.1	Semi-aquatic
Pterosaur bones	3	0.3	Aerial
Unidentifiable material	108	11.7	N/A
Total specimens	926	99.9	

Table 1B. Tarda bone bed taxonomic abundance of teeth by taxon. Raw data n = 317.

<b>Taxon</b>	<b>No. of Elements</b>	<b>%</b>	<b>Ecology</b>
<i>Onchopristis numidus</i> rostral 'teeth'	159	50.2	Aquatic
<i>Lepidotes</i> sp.	3	0.9	Aquatic
<i>Spinosaurus</i> sp.	152	47.9	Semi-aquatic to aquatic
<i>Carcharodontosaurus</i> sp.	1	0.3	Terrestrial
Lungfish	1	0.3	Aquatic Freshwater
Crocodile ?	1	0.3	Semi-aquatic
Total specimens	317	99.9	

Table 2A. Taxonomic abundances at Site 2. A, total taxonomic abundance.

<b>Taxon</b>	<b>No.</b>	<b>%</b>
<i>Spinosaurus</i> sp. teeth	407	32.3
<i>Spinosaurus</i> sp. neural spine frag.	1	0.1
Abelisauroida teeth	6	0.5
<i>Carcharodontosaurus</i> sp. teeth	25	2.0
Theropoda indet. teeth	19	1.5
Titanosauria teeth	3	0.2
Sauropoda indet. vert. frags	2	0.2
Ornithocheiridae teeth	8	0.6
Azhdarchidae jaw frag.	1	0.1
<i>Elosuchus</i> sp. teeth	8	0.6
Pholidosaurid indet. teeth	73	5.8
Crocodylomorpha indet. scutes	2	0.2
Serpentes trunk vertebrae	2	0.2
Hybodont shark fin spines	42	3.3
Lamniform shark tooth	1	0.1
<i>Onchopristis numidus</i> rostral 'teeth'	375	29.7
<i>Onchopristis numidus</i> rostral cartilage	2	0.2
<i>Aidachar pankowskii</i> tooth	1	0.1
Pycnodontiformes dentition	2	0.2
Holostean scales	4	0.3
Unidentified vertebrate material	277	22.0
Total	1261	100

Table 2B. Taxonomic abundances at Site 2. B, dental taxonomic abundance.

<b>Taxon</b>	<b>No. of teeth</b>	<b>%</b>
<i>Spinosaurus</i> sp.	407	43.9
Abelisauroidae	6	0.6
<i>Carcharodontosaurus</i> sp.	25	2.7
Theropoda indet.	19	2.0
Titanosauria indet.	3	0.3
Ornithocheiridae indet.	8	0.9
<i>Elosuchus</i> sp.	8	0.9
Pholidosauridae indet.	73	7.3
Lamniform shark	1	0.1
<i>Onchopristis numidus</i>	375	40.4
<i>Aidachar pankowskii</i>	1	0.1
Pycnodontiformes	2	0.2
Totals	928	100

Table 3. Tooth counts for a variety of theropod dinosaurs from the Kem Kem Group with data from related forms from other localities. Asterisks indicate incomplete specimens where tooth count could be higher.

<b>Taxon &amp; spec. no.</b>	<b>Dent. (l + r)</b>	<b>Premax. (l + r)</b>	<b>Max. (l + r)</b>	<b>Total count</b>	<b>Source</b>
<i>Spinosaurus aegyptiacus</i> Holotype BSP 1912 VIII 19	32	?	?		Stromer 1915; Smith et al., 2006
<i>Spinosaurus</i> cf. <i>aegyptiacus</i> MSNM V4047	?	12	24		Dal Sasso et al. (2005)
<i>Spinosaurus</i> sp. NHMUK 16665	?	14	*16+		Milner (2003)
Spinosauridae indet. FSAC-KK-7281	?	*10+	?		Lakin and Longrich (2019)
<i>Spinosaurus moroccanus</i> MNHN SAM 124	?	14	*18+		Taquet and Russell (1998)
cf. <i>Spinosaurus aegyptiacus</i> NHMUK PV R 16421	*34+	?	?		Milner (2003)
Compiled average for <i>Spinosaurus</i>	32	14	24	70	
" <i>Oxalaia quilombensis</i> " UFRJ MN 6117-V	?	14	?	14+	Kellner et al. (2011)
<i>Irritator challengeri</i> SMNS 58022	?	?	*20+	20+	Sues et al. (2002)
<i>Angaturama limai</i> USP GP/2T-5	?	14	*6+	20+	Kellner and Campos (1996)
<i>Baryonyx walkeri</i>	64	12/14	*16+	94+	Charig and Milner, 1997

NHMUK PV R  
9951

<i>Carcharodontosaurus saharicus</i> Holotype	?	?	*20 or 22+		Stromer (1931)
<i>Carcharodontosaurus saharicus</i> Neotype SGM-Din 1	?	?	*20+ Recon. at 24		Sereno et al. (1996)
<i>Carcharodontosaurus iguidensis</i> UCRC PV12	?	?	*20+		Brusatte and Sereno, 2007; see also Ibrahim et al., 2020b
<i>Carcharodontosaurus saharicus</i> NMC 41859	*8+	?	?		Ibrahim et al., 2020a, Ibrahim et al., 2020b
<i>Neovenator salerii</i> MIWG 6348	*26+	10	30	66+	Brusatte et al. (2008)
<i>Acrocanthosaurus atokensis</i> Holotype M.U.O. 8-0-S9	34	8	28	70	Stovall and Langston (1950)
<i>Allosaurus fragilis</i>	28-34 (Av. 32)	10	28-34		Madsen (1993)
<i>Allosaurus jimmadseni</i> DINO 11541	40	8	32	80	Chure and Loewen (2020)
<i>Giganotosaurus carolinii</i> Holotype MUCPv-Ch1	30	8	*24+	62+	Coria and Salgado (1995)
Estimated tooth count for <i>Carcharodontosaurus</i>	30	8	24	62	