



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

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### ABSTRACT

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

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### 1. Introduction

The enigmatic theropod dinosaur *Spinosaurus aegyptiacus* Stromer, 1915 has been interpreted as a piscivorous and semi-aquatic animal (e.g. Stromer, 1936; Taquet, 1984; Ibrahim et al., 2014; Arden et al., 2019), and more recently shown to have possessed a highly modified tail suited for propelling the animal through water (Ibrahim et al., 2020a). The hypothesis that this spectacular dinosaur was semi-aquatic – or even perhaps fully aquatic – has met with some opposition (e.g. Henderson, 2018; Hone and Holtz, 2019), not least because it challenges decade-old ideas on dinosaur ecology and evolution (Ibrahim et al., 2020a and papers therein). Evidence for an aquatic lifestyle hinges mainly on skeletal data, which provides compelling evidence, including a rearward position of the external nares, flattened pedal unguals and considerable divergence of pedal digits, a series of elongate neural spines on the caudal vertebrae giving the tail a fin-like morphology, a reduced pelvic girdle and hindlimb, with a

disproportionately short femur and osteoclerosis/pachyostosis of the skeleton (Ibrahim et al., 2020a), as well as circumstantial evidence for specialized sensory structures to detect prey in water (Ibrahim et al., 2014). Possession of a narrow, somewhat crocodile-like overall skull morphology and a dentition of simple conical teeth, often with pronounced apicobasal ridges, has also been interpreted as indicating a piscivorous diet (Stromer, 1936; Taquet, 1984; Ibrahim et al., 2014; McCurry et al., 2019). Comparisons with more distantly related forms – large piscivorous fish – have also been used to support piscivory in *Spinosaurus* (Vullo et al., 2016). Additional evidence from phylogenetic analysis suggest a very close relationship to the European *Baryonyx walkeri*, a spinosaurid in which possibly acid-etched lepidotid fish scales were discovered in the ribcage, providing potential evidence for a degree of piscivory in these animals (Charig and Milner, 1997). Isotopic evidence was also used to suggest an aquatic lifestyle for *Spinosaurus*, although the data was somewhat inconclusive (Amiot et al., 2010). Taken together, these diverse and independent lines of evidence all point toward a largely piscivorous – and aquatic – lifestyle. Here we present evidence from a taphonomic analysis of a new locality of the Kem Kem Group strata of south east Morocco that further strengthens a predominantly aquatic lifestyle for *Spinosaurus*.

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Most museum specimens of *Spinosaurus* from Morocco have been obtained from commercial sources, and generally lack precise locality or horizon data (Ibrahim et al., 2020a,b). Our field studies over the last 15 years in the Tafilalt region and Hamada du Kem Kem of south east Morocco reveal that a majority of this material comes from the top of the Ifezouane Formation of the Kem Kem Group. Many isolated teeth, occasional jaw fragments and, more rarely, other cranial and postcranial bones are dug by artisan miners from three or four event horizons characterised by mud-flake conglomerates with chaotic bedding, and sharp basal contacts. They are rarely more than 1 m thick, and often just a few centimetres, but may be extensive and traceable over several kilometres. The excavation of an associated skeleton by Ibrahim et al. (2020a) is an exception, as this specimen is one of only three associated dinosaurs reported from the Kem Kem Group (Ibrahim et al., 2020a,b), and it occurred at a slightly higher level in the sequence.

## 2. Locality and geological context

### 2.1. Locality

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

The Kem Kem Group strata represent an extensive fluvial system that can be traced in Morocco for at least 200 km from Zguilma in the south west to Aoufous and beyond to the Anoual Basin and the frontier with Algeria. In Algeria, coeval strata yield remarkably similar vertebrate assemblages both in terms of faunal diversity and taphonomy (Benyoucef et al., 2015; Ibrahim et al., 2020b). Vertebrate fossils occur at event horizons (likely flash-flood deposits and viscous sediment flows, as channel lags and as exceptionally rare isolated associated skeletons (Ibrahim et al., 2014, 2020a,b). The vertebrate assemblage is diverse (for a full faunal list see Cavin et al., 2010; Ibrahim et al., 2020b) and includes a wide variety of cartilaginous and bony fishes, archosaurs (dinosaurs, pterosaurs and crocodiles), turtles and snakes and lizards. There are anomalies such as a near absence of ornithischian dinosaurs and a lack of mammals, which have yet to be reported from the Kem Kem Group (Ibrahim et al., 2020b).

### 2.2. Geological context

The strata from which the fossils discussed here came comprise a suite of largely clastic red mudstones, fine sandstones and thin conglomerates (pebble and mud-flake) of the Kem Kem Group. They rest unconformably on folded Palaeozoic basement rocks and are overlain by marine carbonates of the Akrabou Formation that is well dated as middle Cenomanian to Turonian (Ettachfini and Andreu, 2004; Kennedy et al., 2008). In the north of the Tafilalt the Kem Kem Group has been divided into two formations, a lower Ifezouane Formation dominated by fine sands with event horizons yielding fossils vertebrates, and an upper Aoufous Formation that is comprised largely of variegated mudstones with thin-bedded sandstones. This latter formation generally lacks fossil vertebrates, except near Aoufous (Oum Tkout) where a thin horizon of laminated mudstones yields fully articulated skeletons of fish and amphibians in a lacustrine Konservat Lagerstätte (Dutheil, 1999; Cavin et al., 2010; Ibrahim et al., 2020b).

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

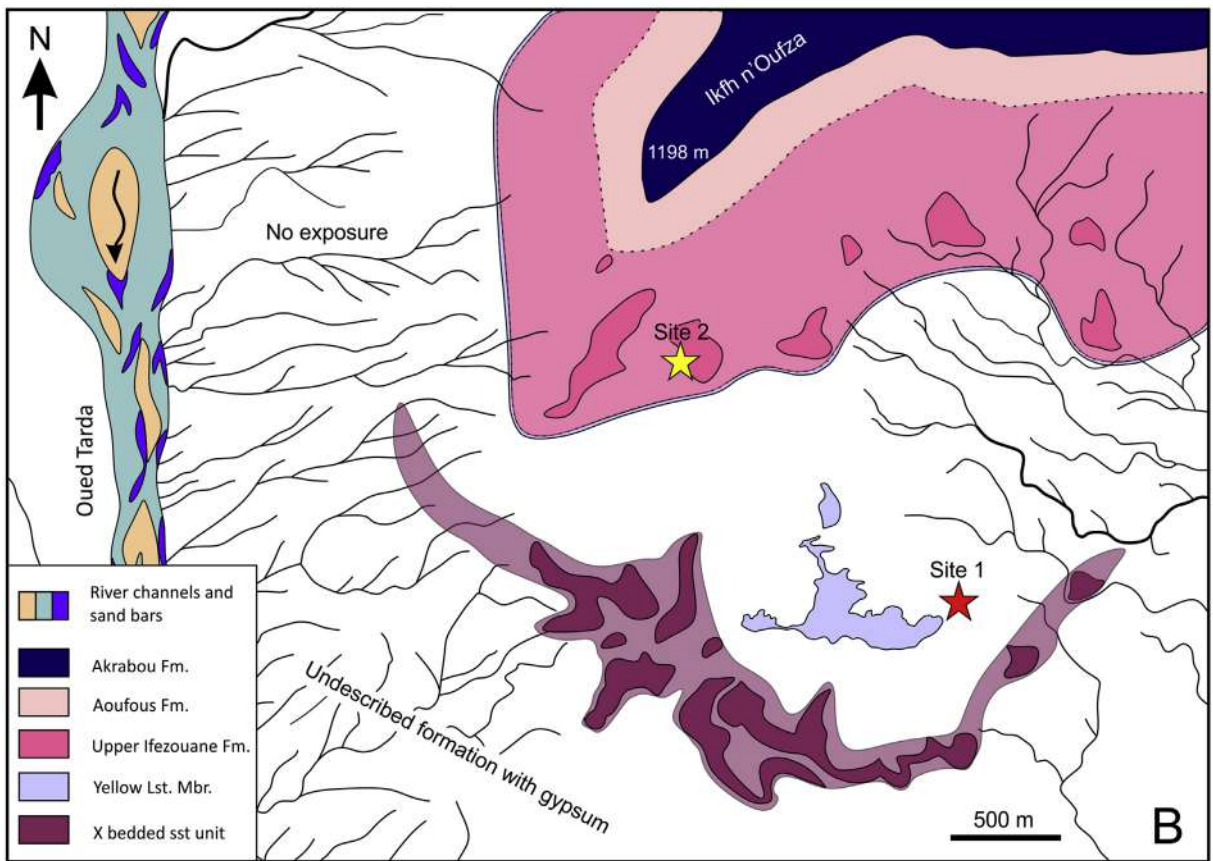
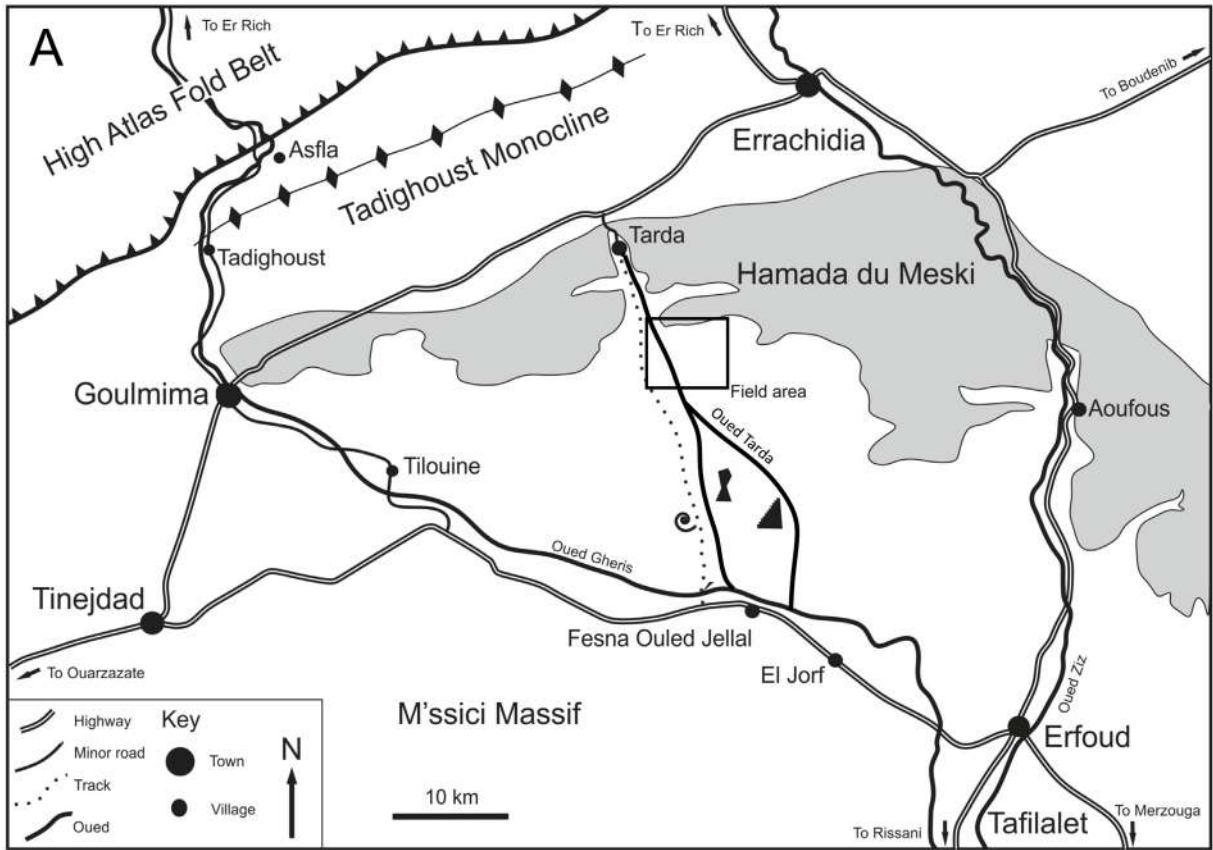
The Akrabou Formation limestones are dated as mid Cenomanian to Turonian on the basis of a diverse ammonite assemblage (Kennedy et al., 2008), but the age of the Kem Kem Group is not securely determined. Several authors, using the fossil vertebrates, have suggested a lower Cenomanian age for the Kem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

### 2.3. Taphonomic context

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

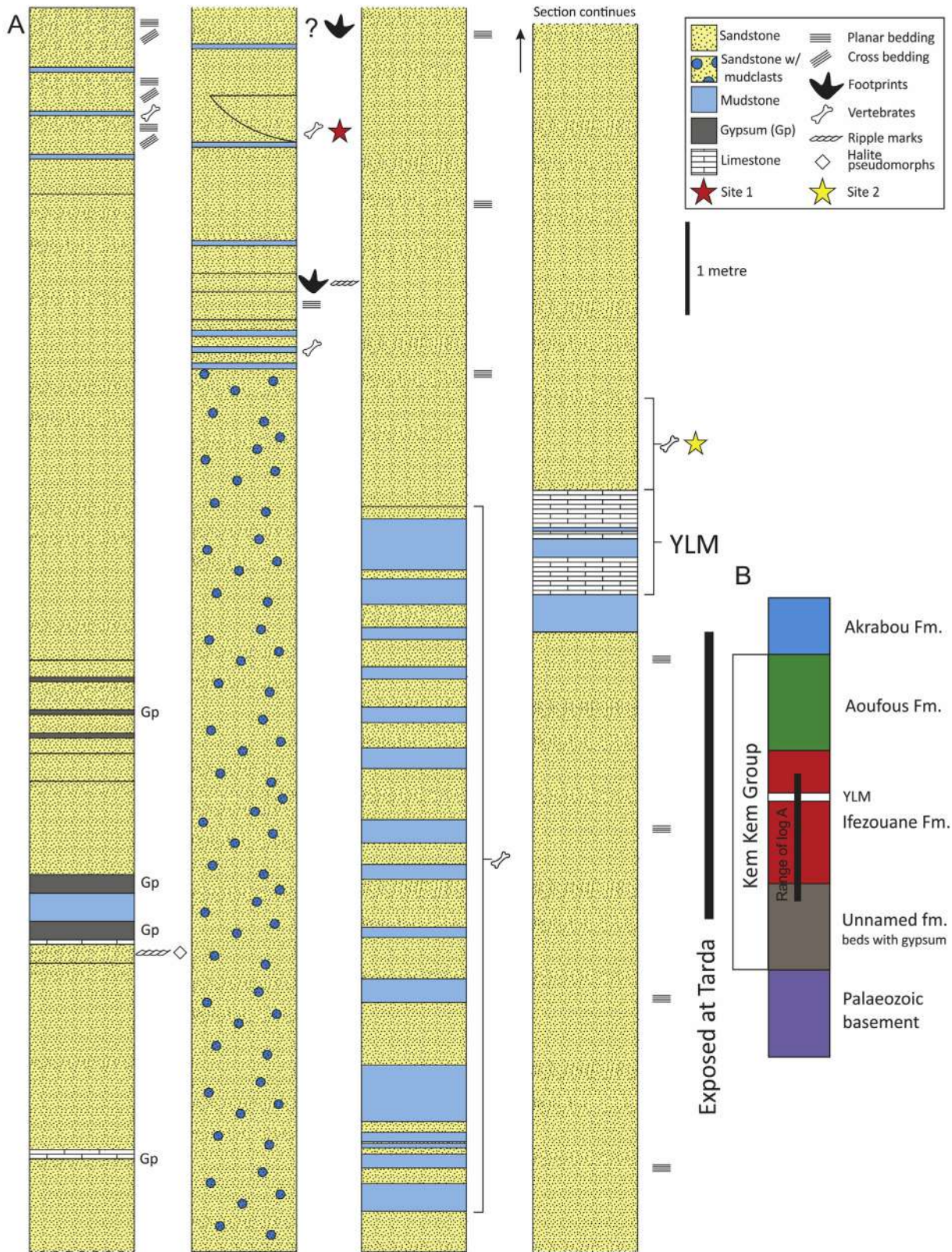
## 3. Methods, aims and objectives

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



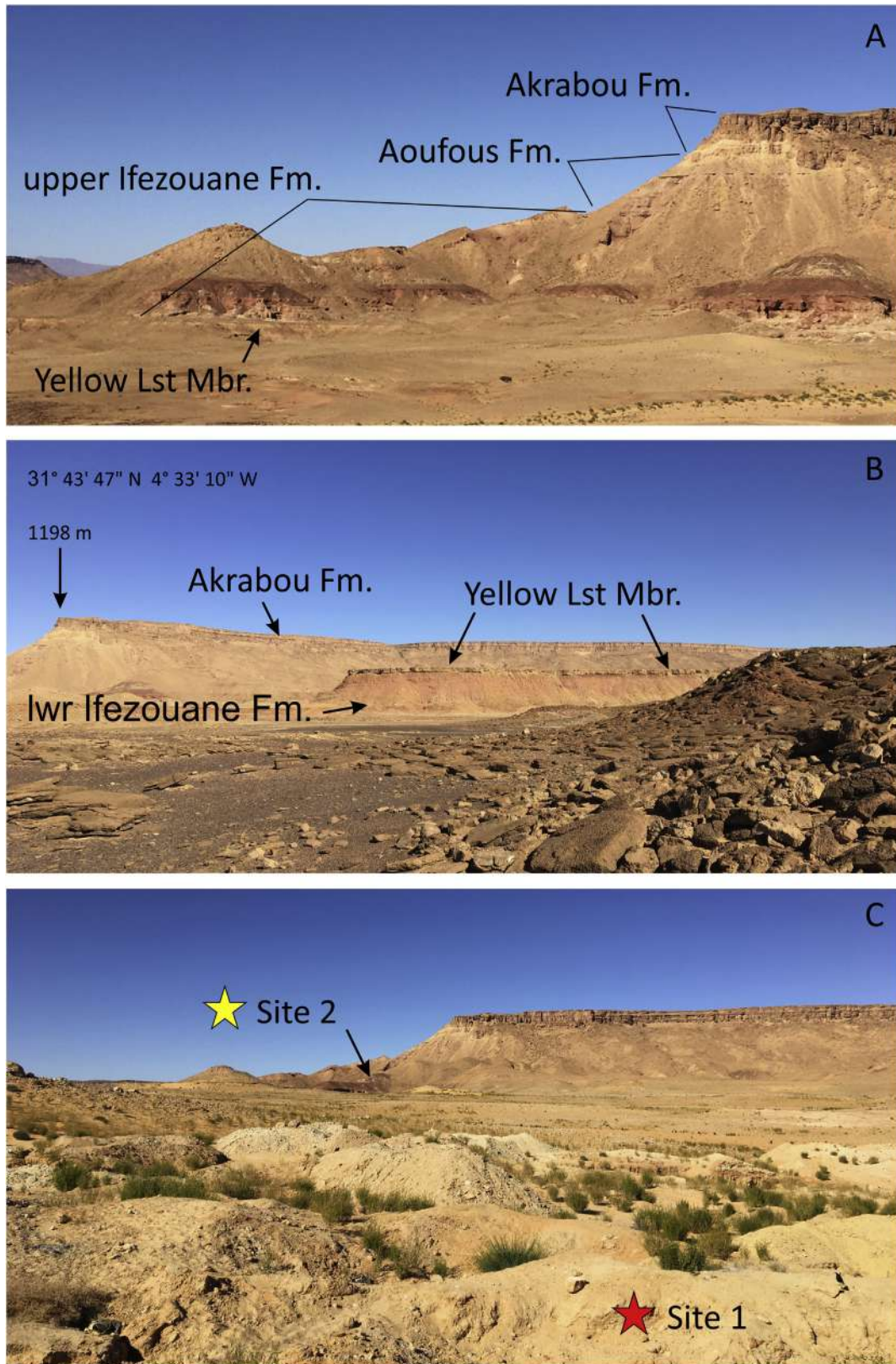
**Fig. 1.** Map of the Tarda locality with extensive exposures of the Kem Kem Group. A, General map of the northern Tafilalet showing the major towns and location of the Tarda Oasis with field area indicated by the box. B, Detailed map with schematic geological overlay. Sites one and two are indicated by red and yellow stars respectively. The uncoloured area corresponds to the lower Ifezouane Formation, but in many places this is concealed by alluvial fans. The red star is located on an outcrop on the flanks of a small plateau formed by the Yellow Limestone Member. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)





**Fig. 2.** Preliminary stratigraphic log for the region between Sites 1 and 2 near Tarda. A, Log through the Ifezouane Formation including the Yellow Limestone Member. B, Simplified stratigraphic scheme for the region with range strata visible at Tarda indicated by black line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)





**Fig. 3.** Photographs of exposures in the Tarda field area. A, View of the Ikhf n'Oufza escarpment taken from the small plateau shaded purple in Fig. 2. Site 2 is just a few metres to the east of this view. B, View looking north with the unnamed plateau capped by the Yellow Limestone Member and Ikhf n'Oufza in the distance. C, Site 2 seen from Site 1. The distance is just shy of 2 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 1A**

Tarda bone bed taxonomic abundance. Raw data n = 926.

Taxon	No. of Elements	%	Palaeoecology
<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
<b>Total specimens</b>	<b>926</b>	<b>99.9</b>	

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

Specimens cited in this work are accessioned in the following institutions: BSP, Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; DINO, Dinosaur National Monument, Utah, USA; FSAC, Département de Géologie, Faculté des Sciences Ain Chock, Université Hassan II, Casablanca, Morocco; MIWG, Dinosaur Isle Museum, Sandown, Isle of Wight, UK; MN/UFRJ, Museu Nacional/Universidade Federal, Rio de Janeiro, RJ, Brazil;

MNHN, Museum National d'histoire Naturelle, Paris, France; MSNM, Museo di Storia Naturale di Milano, Italy; MUCP, Museo de la Universidad Nacional del Comahue, El Chocon Collection, Argentina; MUO, Museum of the University of Oklahoma, USA; NHMUK, Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; USP, University of Sao Paulo, SP, Brazil.

#### 4. Results

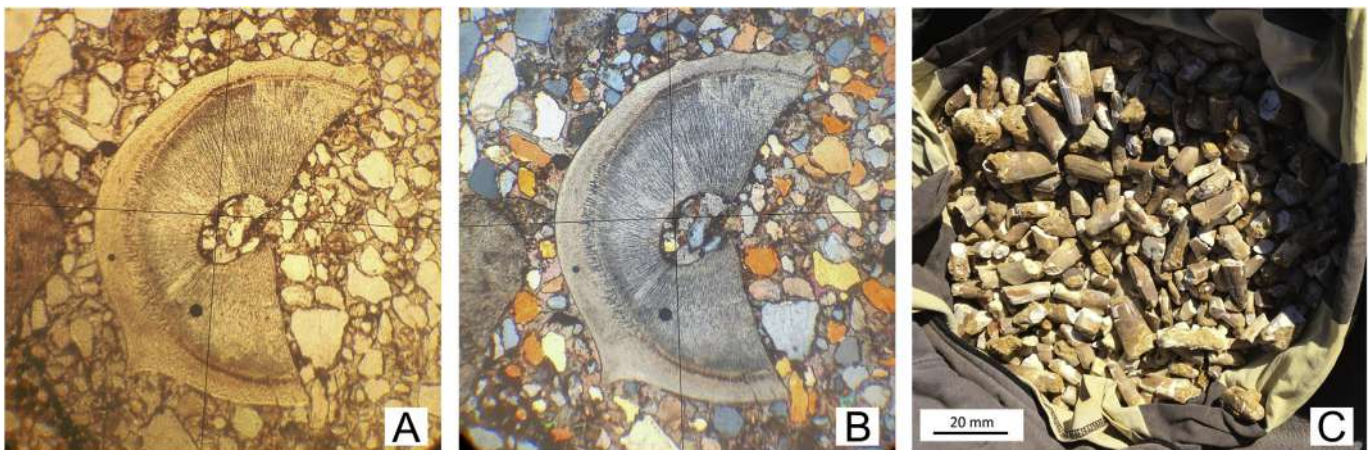
##### 4.1. Site 1

Collecting from Site 1 at a horizon below the Yellow Limestone Member (See Figs 2, 3) in the lower Ifezouane Formation yielded a total of 926 vertebrate fossils, of which 317 (34.2%) were teeth

**Table 1B**

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

Taxon	No. of Elements	%	Ecology
<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
<b>Total specimens</b>	<b>317</b>	<b>99.9</b>	



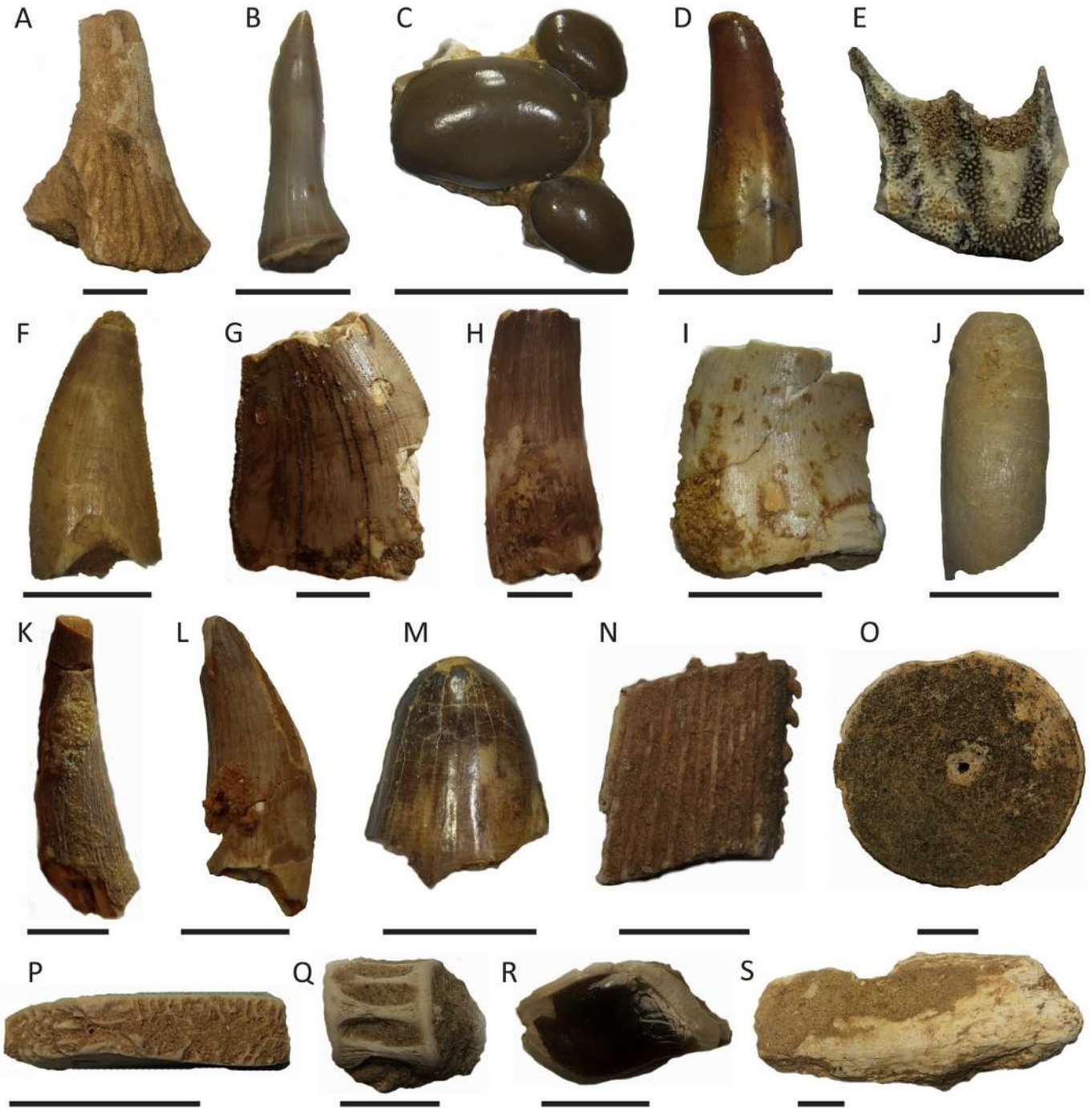
**Fig. 4.** *Spinosaurus* teeth at Site 1. A, Thin section in PPL through sandstone bone-bed with spinosaur teeth. The broken tooth in this image is a *Spinosaurus* crown tip with maximum diameter of 2.5 mm. B, as A but seen in XPL. C, a bag full of broken *Spinosaurus* teeth abandoned by the fossil diggers at Site 1, presumably regarded as of little commercial value.



(including *Onchopristis* rostral denticles) (Table 1A). Micro-vertebrate (<5 mm) remains were not collected. We focussed our analysis on dental remains as all of these could be confidently assigned to a taxon at least at ordinal level or better (Table 1B, even when fragmentary). Only 6 distinct tooth morphotypes were present in the assemblage (Table 1B). Of these, the teeth of *Spinosaurus*

(Figs. 4, 5) comprised almost 48% of the total dental remains and 16.4% of the total vertebrate fossils from this site.

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



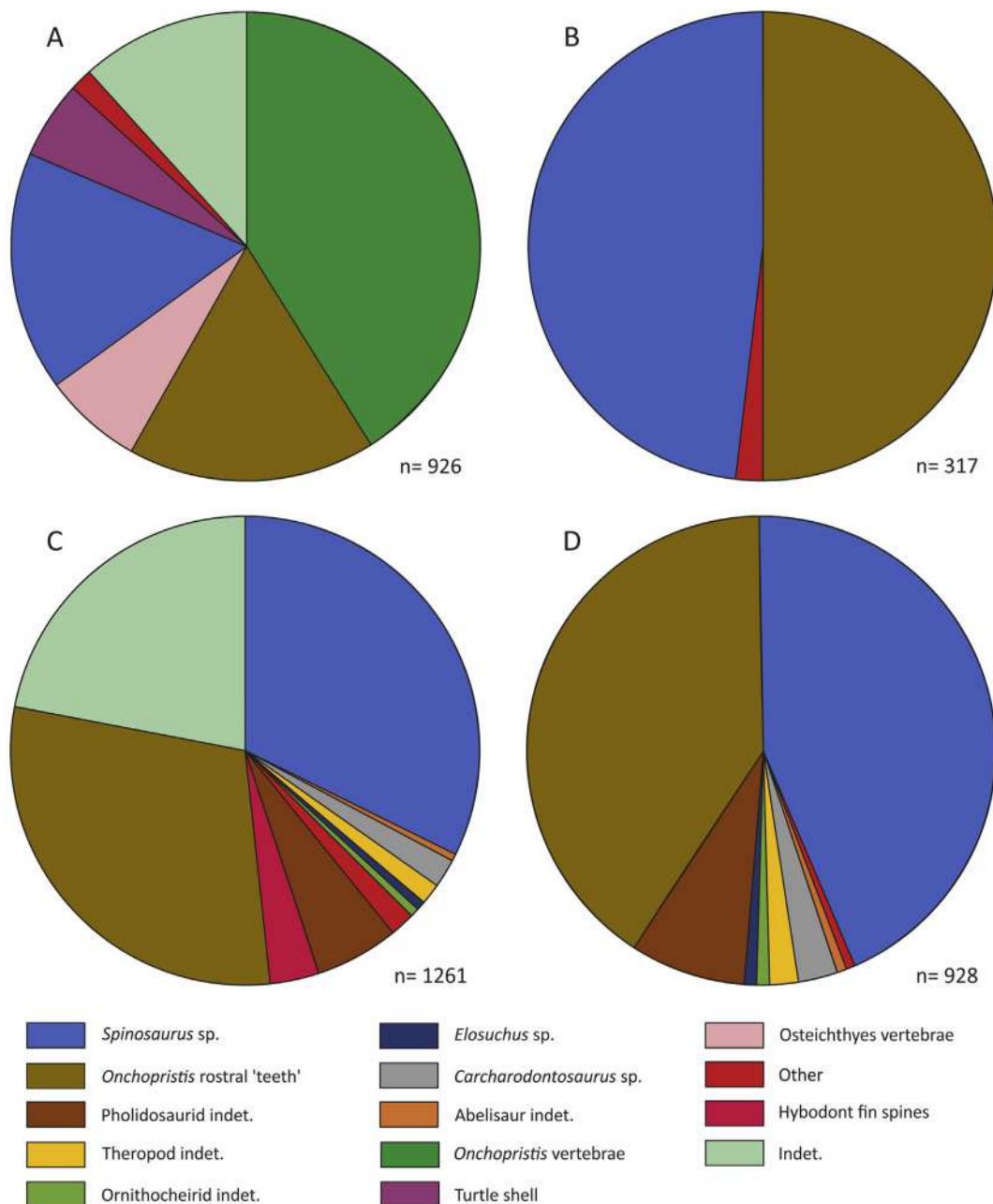
**Fig. 5.** Isolated vertebrate remains for Site 1 and Site 2 at Tarda, SE Morocco. Notice that the material is fragmentary, but not water worn. Hairline fractures in the material mean that specimens often fall apart when extracted, but some material was fragmented preburial, as seen in Fig. 4A, B. Scale bars = 10 mm. A, rostral denticle of *Onchopristis* cf. *numidus*; B, Lamnid shark indet.; C, fragment of vomerine dentition from pycnodont; D, unidentified large fish tooth; E, lungfish dental plate; F, tooth of abelisaurid indet.; G, tooth of indeterminate theropod; H, tooth of *Spinosaurus* sp.; I, tooth of *Carcharodontosaurus* sp.; J, tooth of titanosauroid sauropod indet.; K, tooth of indeterminate ornithocheirid pterosaur; L, tooth of pholidosaurid crocodile; M, Tooth of *Elosuchus* sp.; N, fragment of dorsal fin spine of hybodont shark; O, vertebra likely attributable to *Onchopristis numidus*; P, fragment of indeterminate turtle carapace; Q, teleost vertebra; R, holostean scale; S, indeterminate bone fragment.

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

#### 4.2. Site 2

Site two yielded a more diverse assemblage than Site 1, where a total of 1261 vertebrate fossils were obtained. They were purchased from an artisan miner at his mine, and all originate from a single event horizon in the upper Ifezouane Formation occurring above

the Yellow Limestone Member (Figs. 2, 3). We acknowledge that it is likely that this assemblage of fossils may have had some larger bones and more valuable larger teeth removed. It is likely that this would have been only a small number (pers. obs.). Of the material, 928 specimens (73.6%) represent dental remains (Tables 2A, B). The diversity of teeth at this site is significantly greater than at site 1, with at least 12 morphotypes represented. The most abundant tooth morphotype at Site 2 are the conical, faceted teeth of *Spinosaurus* sp., (407 teeth) which comprised 43.9% of the dental sample and 32.3% of the total vertebrate material at this site. Although many of the *Spinosaurus* teeth are too fragmentary to be confidently placed within distinct morphotypes (*sensu* Richter et al., 2013), we were able to allocate 225 out of a total of 407 teeth (Fig. 7). The abundances of the three morphotypes approximate those of Richter et al. (2013). The second most abundant dental remains are



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



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

Taxon	No.	%
<i>Spinosaurus</i> sp. teeth	407	32.3
<i>Spinosaurus</i> sp. neural spine frag.	1	0.1
Abelisauroidea 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
<b>Total</b>	<b>1261</b>	<b>100</b>

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

Taxon	No. of teeth	%
<i>Spinosaurus</i> sp.	407	43.9
Abelisauroidea	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
<b>Totals</b>	<b>928</b>	<b>100</b>

attributed to *Onchopristis* with a total of 375 (40.4%) rostral denticles (Fig. 6C, D).

Note that at neither site were any invertebrate fossils encountered. Such remains are extremely rare in the Kem Kem Group, and are usually encountered only as internal moulds of rare unionid bivalves and as trace fossils in some of the thin sandstones (see Ibrahim et al., 2020b).

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

Although there are considerable similarities between the two vertebrate assemblages, there are also some significant differences that likely reflect subtle differences in habitat preference between taxa and taphonomic filters such as size and density sorting. Dinosaur diversity is considerably greater at Site 2 than Site 1, but the numbers of non-spinosaurid dinosaur teeth are low, and combined they constitute no more than 4.2% of the total assemblage and 5.6% of the dental assemblage. Where taxa are known from a single example we do not regard this as significant, and of those taxa that are common to both sites (*Carcharodontosauridae*; *Spinosaurinae*; *Onchopristis numidus*), only *Onchopristis* and *Spinosaurus* are found in any abundance. An intriguing discrepancy between the two sites is the lack of vertebrae attributable to *Onchopristis* at Site 2. These easily identified elements constitute 41% of the vertebrate remains at Site 1, and are reasonably common at many sites in the eastern and southern outcrops of the Kem Kem

Goup (Ibrahim et al., 2020b). This discrepancy is unexpected and not easy to explain. We cannot rule out that the fossil digger at Site 2 considered them to have no commercial value and left them in the mine, but this has not been our experience of other dig sites. An element of density sorting may be at play with the relatively light vertebrae having been winnowed away.

## 5. Discussion

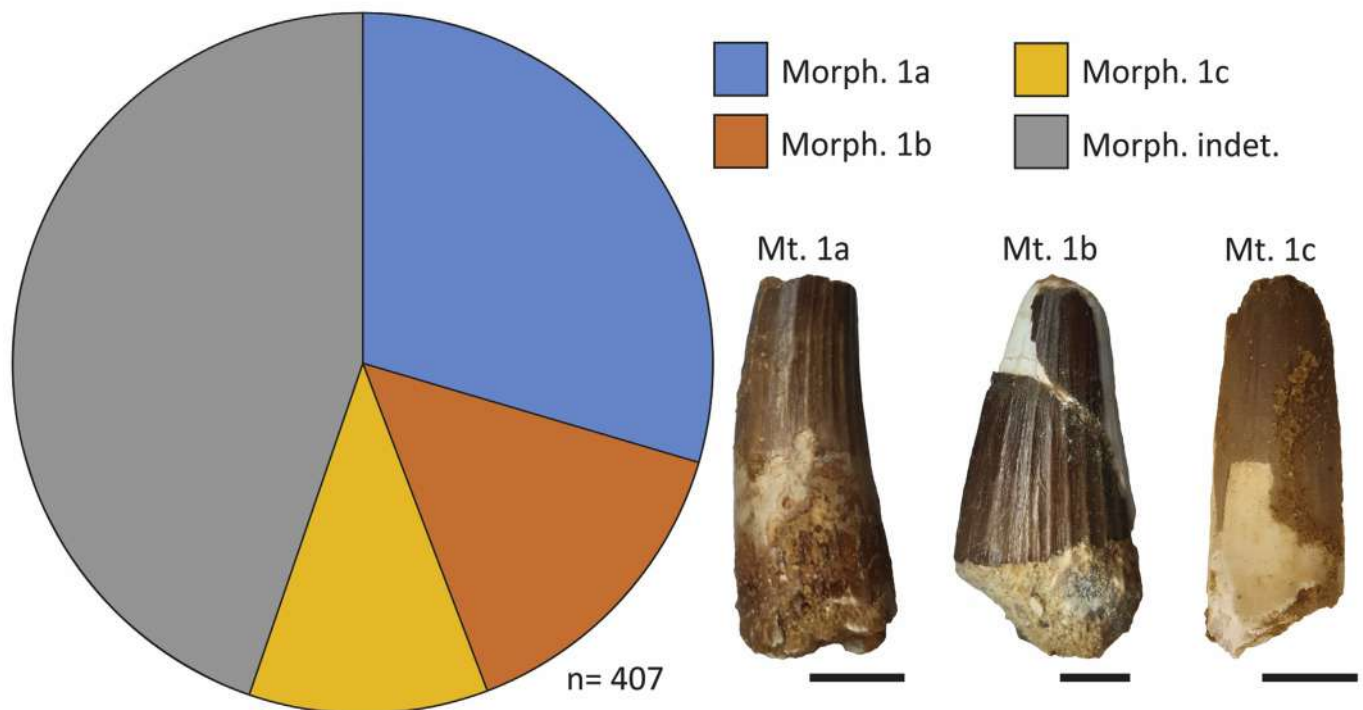
The relative abundances of dental remains for the two distinct stratigraphic intervals collected at Tarda reveals that teeth of *Spinosaurus* occur in high abundance at both levels, but are exceptionally abundant at Site 1 where they constitute 48% of the dental remains. We know of no other dinosaur-bearing bone bed where such an abundance of dinosaur teeth occurs. The enhanced abundance of *Spinosaurus* teeth relative to other dinosaurs is likely a reflection of their aquatic lifestyle. An animal living much of its life in water is much more likely to contribute teeth to the river deposit than those dinosaurs that perhaps only visit the river for drinking and more casual feeding on its banks, or the occasional carcass of a terrestrial dinosaur decomposing in the river. Similarly, the high abundance of rostral denticles of *Onchopristis* is hardly surprising, given that sawfish are fully aquatic animals, and that elasmobranchs are noteworthy for their efficiency in growing and replacing teeth (Slaughter and Springer, 1968). What is perhaps surprising is the rarity of other fish teeth, especially the more robust teeth of holosteans such as *Lepidotes* sp. and pycnodonts, although the latter are rare in the Kem Kem Group (Forey et al., 2011; Cooper and Martill, 2020 respectively), the former occur frequently and reached a large size.

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

#### 5.1. Relative abundances

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

Morphotype	Abundance	%	% ex. indet.	% Richter et al., 2013
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>



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

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

Theropod teeth were replaced on a regular basis, as they are in modern crocodylians (Currie et al., 1990), where tooth replacement is irregular and affected by age and size of the individual crocodile, with irregularity of replacement increasing with age (Edmund, 1962). The functional life of each tooth differs from approximately nine months in anterior teeth, to sixteen in posterior teeth (Edmund, 1962). Teeth are replaced in waves from front to back in juveniles, and reversed in older individuals (Edmund, 1962). It has been suggested that theropods had a very similar tooth functional life to crocodylians of between nine and sixteen months per tooth. The presence of theropod teeth among some herbivorous dinosaur remains indicates that theropods may have lost one or more teeth in some feeding sessions, suggesting tooth replacement was rather constant and relatively rapid (Currie et al., 1990). Erickson et al.

(1996) note a duration for replacement teeth of up to 777 days for an adult *Tyrannosaurus*, while D'Emic et al. (2019) found as little as 56 days for *Majungasaurus* and 104 days for *Allosaurus*, both of which may be considered as tentative proxies for Kem Kem abelisaurids and *Carcharodontosaurus* respectively. We speculate that *Spinosaurus* may have had a tooth replacement duration within the 56–777 day range. We also note that the dinosaur with perhaps the highest tooth replacement rate – an abelisaur – has a low abundance in the Kem Kem Group (Tables 1 and 2), suggesting perhaps that these theropods were not an important part of this palaeobiotope.

The number of teeth in the jaws at any one time varies considerably between taxa in the Dinosauria, but for Spinosauridae it is probably between 68 and 72 (*Spinosaurus*) and 94 (*Baryonyx*) (Table 3). The total tooth count for *Carcharodontosaurus* is not known, but related allosauroids have total counts of between 60 and 80 (Table 3), which suggests that *Spinosaurus* is not particularly different from other theropods roaming the Kem Kem biotopes.



**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.

Taxon & spec. no.	Dent. (l + r)	Premax. (l + r)	Max. (l + r)	Total count	Source
<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)
<b>Compiled average for <i>Spinosaurus</i></b>	<b>32</b>	<b>14</b>	<b>24</b>	<b>70</b>	
" <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> NHMUK PV R 9951	64	12/14	*16+	94+	Charig and Milner, 1997
<i>Carcharodontosaurus saharicus</i> Holotype	?	?	*20 or 22+		Stromer (1931)
<i>Carcharodontosaurus saharicus</i> Neotype SGM-Din 1	?	?	*20+		Sereno et al. (1996)
			Recon. at 24		
<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., 2020 a, b
<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 jimmadeni</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)
<b>Estimated tooth count for <i>Carcharodontosaurus</i></b>	<b>30</b>	<b>8</b>	<b>24</b>	<b>62</b>	

Tooth shedding rates of *Spinosaurus* and *Carcharodontosaurus* may have been similar, but tooth shedding rate data is presently unavailable. Likely the greater abundance of *Spinosaurus* teeth compared to *Carcharodontosaurus* and the abelisaurids in the Kem Kem is that spinosaurids were present in greater numbers in this largely fluvial environment dominated by aquatic organisms (Ibrahim et al., 2020a,b and papers therein), and inhabited the sedimentary environment in which their teeth are preserved.

Of course, it is possible that the abundance of *Spinosaurus* remains in a fluvial deposit are the result of a wading heron-like ecology, snatching prey from shallow water as has been suggested by some authors (e.g. Taquet, 1984; Hone and Holtz, 2017; 2019; Henderson, 2018). An elongated skull and neck relative to those of other large theropods is consistent with this interpretation (although these features are also consistent with diverse swimming birds). However, other aspects of the morphology of *Spinosaurus* are inconsistent with a wading mode of life. Wading has developed independently several times in extant theropods, always converging on similar hindlimb morphologies. Wading birds are characterised by having hindlimbs that are longer, relative to body size, than those of other birds, with the tibiotarsus and tarso-metatarsus disproportionately extended (Zeffer et al., 2003). Such a morphology increases foraging area (Baker, 1979) and reduces drag, increasing efficiency while moving through water (Zeffer et al., 2003). These adaptations presumably also have the added benefit of reducing water disturbance that may alert potential aquatic prey to the presence of a predator.

In contrast, the hindlimbs of *Spinosaurus* are greatly shortened relative to body size, with disproportionate reduction of the femur

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

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

## 6. Conclusions

The teeth of *Spinosaurus* occur in high abundance in two bone-bearing horizons at the Tarda locality of the Kem Kem Group. The abundance of *Spinosaurus* at both levels in comparison to terrestrial dinosaurs such as the gigantic theropod *Carcharodontosaurus*, the somewhat smaller abelisaurids and sauropods is substantial. In the lower horizon, a channel-lag bone bed, teeth of *Spinosaurus* outnumber terrestrial dinosaur teeth by a factor of ~150 to 1. In addition, at this horizon the teeth of *Spinosaurus* are more abundant even than many aquatic and semi-aquatic animals such as bony fishes and crocodyliforms. At a slightly higher horizon in the same stratigraphic unit *Spinosaurus* teeth outnumber those of all other dental remains, and outnumber other dinosaur teeth by a factor of ~8 to 1. While all of the fossils collected from these horizons should be considered semi-autochthonous, it would seem that for such an abundance of teeth of *Spinosaurus* to occur, it is highly

likely that this animal was living mostly within the river rather than along its banks. This conclusion is consistent with interpretations of *Spinosaurus*' palaeoecology based on anatomical evidence (Ibrahim et al., 2014; 2020a). Furthermore, the channel-lag bone bed at Site 1 is the first reported occurrence of a bone-bed dominated by dinosaur teeth, and represents a unique thanatocoenosis.

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