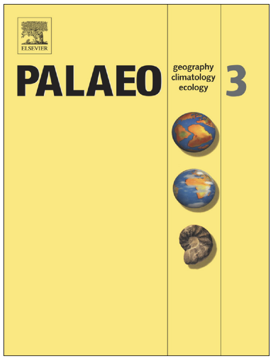

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The Effectiveness of Oxygen Isotopes in *Spinosaurus* Tooth Dentine for High-Resolution Palaeoenvironmental Reconstructions

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Abstract

Oxygen isotope compositions in tooth dentine of *Spinosaurus aegyptiacus* were investigated as a potential proxy for high-resolution reconstructions of palaeoenvironments in Cenomanian Cretaceous Morocco. The dentine was sampled sequentially along the tooth growth direction, and the successive $\delta^{18}O$ values exhibited cycles which likely tracked the oxygen isotope compositions of ingested water and inferred changes in additional palaeoenvironmental properties. A conceptual model of catchment palaeohydrology was reconstructed to explain the mechanisms of isotopic variation. Seasonally variable water balance in the catchment or changes in water sources throughout the extensive deltaic environments are the most likely explanations for the seasonal profiles. With analysis of isotopic change in the conceptual model and comparison with data of modern tropical and subtropical deltas, we found similarities between palaeoclimates and modern data, and effectively identified the wet and dry seasons represented by troughs and peaks in the $\delta^{18}O$ curves. These preliminary results demonstrated that palaeoenvironmental information at sub-seasonal resolution can be well preserved in theropod tooth dentine. The methodology developed in this study can be applied to the existing abundant reserves of theropod teeth to construct a Mesozoic palaeoclimatic database.

Key Words: Mesozoic; Kem Kem beds; palaeohydrology; geochemistry; teeth

demonstrated by the oxygen isotope analysis of serially sampled enamel of theropod teeth (Straight et al., 2004). This has the potential to provide a thus far unexplored archive for the reconstruction of late Mesozoic climates and environments. Here we present the first high-resolution isotopic dataset from *Spinosaurus aegyptiacus* to test the application of oxygen isotope compositions ($\delta^{18}O$) from carbonate-group of apatite in tooth dentine for palaeoenvironmental reconstruction.

Spinosaurus aegyptiacus was a large theropod species that primarily lived during the Cenomanian (Late Cretaceous) age (ca. 97 million years ago) in North Africa (Ibrahim et al., 2020a; Stromer, 1915). They were known for their unusual morphology (Gimsa et al., 2016; Hone and Holtz, 2017; Ibrahim et al., 2014a, 2020b). *Spinosaurus* populations were suggested to be highly abundant as their teeth make up a large proportion of local vertebrate assemblages (Goedert et al., 2016; Ibrahim et al., 2020a). Despite the abundance of teeth and the early discovery of this species (Stromer, 1915), the holotype was destroyed during the Second World War (Ibrahim et al., 2014a), and much of their anatomy and behaviour remains unknown or debated. Based on the evidence of flattened pedal claws, a vertically expanded tail, increased bone density compared to other theropods, and more negative $\delta^{18}O$ ratios compared to other theropod dinosaurs, *Spinosaurus* are believed to have led a semi-aquatic lifestyle (Amiot et al., 2010; Ibrahim et al., 2014a, 2020b). A highly specialized piscivore diet is supported by their elongated and mediolaterally compressed skull, retracted nostril position, conical-shaped teeth and Ca isotope compositions (Cuff and Rayfield, 2013; Hassler et al., 2018; Ibrahim et al., 2014a; Sasso et al., 2005; Vullo et al., 2016). Recent studies suggest the feeding strategy of *Spinosaurus* was most likely wading aquatic prey in shallow water (Hone and Holtz, 2021; Sereno et al., 2022). While all these intensive studies have explored their palaeontology and anatomy, very little is known about the environmental and ecological conditions to which *Spinosaurus* had adapted.

In this context, the oxygen isotopic composition of animal bioapatite can be used as an indicator of past climates and environments (Goedert et al., 2016; Kovács et al., 2012; Pryor et al., 2013). Large theropod species were suggested to be homoeothermic, and obtained body water through direct water ingestion (Barrick and Showers, 1994; Eagle et al., 2011; Fricke and Rogers, 2000). Therefore, the $\delta^{18}O$ values in their bioapatite carbonate were predominantly determined by $\delta^{18}O$ values of their ingested environmental water (Bryant and Froelich, 1995; Longinelli, 1984; Luz et al., 1984). In fact, both carbonate and phosphate groups in apatite formed from the same water source and present $\delta^{18}O$ values with an offset of around 8.5–9.0‰, and thus both can effectively reflect drinking water $\delta^{18}O$ values (Bryant et al., 1996; Domingo et al., 2015; Iacumin et al., 1996; Tütken et al., 2007). The isotope compositions of both materials can be diagenetic altered, with $\delta^{18}O_{CO3}$ ratios being more sensitive to inorganic solution exchange and $\delta^{18}O_{PO4}$ ratios being more sensitive to microbial activities (Pryor et al., 2013; Zazzo et al., 2004). Substantial isotopic exchange can occur between dental tissue and water by catalysis of organic enzymes (Ayliffe et al., 1994; Sharp, 2000). Consequently, the oxygen isotope analysis was restricted to phosphate of enamel

(Zazzo et al., 2004). Tooth carbonate, in comparison, is less influenced by such diagenesis but can be altered with abiotic carbonate exchanges with fluids (Zazzo et al., 2004). In this study, we chose to test the dentine carbonate as the material for palaeoenvironmental reconstructions. The $\delta^{18}O$ values in the environmental water, deduced from isotopic composition of dentine carbonate, were in turn likely primarily controlled by local to regional-scale environmental factors such as evaporation and precipitation amount or water/moisture sources (Dansgaard, 1964). These relationships between oxygen isotope compositions in *Spinosaurus* tooth carbonate and palaeoenvironmental conditions provide the conceptual framework for interpreting the palaeoclimatic implications of $\delta^{18}O$ values in *Spinosaurus* body water and thus tooth dentine.

2. Methods

2.1. Study Location

Three isolated teeth of *Spinosaurus* from the Kem Kem Beds, Morocco were analysed for this study (labelled as SP1, SP2 and SP3 respectively). The samples were acquired from international fossil dealers, who receive fossils from the Kem Kem beds collected by local excavators. The teeth were discovered in excavations site south of Taouz from sediments of the Kem Kem Group. However, no further information of the precise location or geological setting is available. Therefore, we describe here the stratigraphy of the entire Kem Kem beds in general and consider all units in the group as the potential discovery location of the samples.

The Cenomanian-age Kem Kem beds are a sequence of 150-200 m thick fluvial siltstones and sandstones that extend over 250 km at the southeastern border of Morocco (Ibrahim et al., 2014b; Sereno et al., 1996) (Figure 1). The Kem Kem beds are divided into the Lower Gara Sbaa and Upper Douira Formations based on their different lithologies. The Lower units are dominated by coarser sandstones while the upper units are finer-grained and also have greater lithological diversity (Cavin et al., 2010; Ibrahim et al., 2020a; Läng et al., 2013; Martill et al., 2011; Sereno et al., 1996). The Douira Formation also shows a fining-upwards sequence, which likely indicates the evolution of a palaeo-delta during the Cenomanian in North Africa, and a likely marine transgression at the Cenomanian-Turonian boundary (Guiraud et al., 2005; Ibrahim et al., 2020a; Martill et al., 2011). *Spinosaurus* remains were discovered in both formations and multiple excavation localities of the Kem Kem beds (Ibrahim et al., 2020a). Besides *Spinosaurus*, various aquatic and semi-aquatic vertebrate species were also discovered in this group, and they formed the majority of this faunal assemblage (Ibrahim et al., 2020a; Läng et al., 2013; Smith et al., 2023). The rich assemblage of aquatic species and low-energy fluvial sediments suggests that the Lower Kem Kem beds were a palaeo-delta fed by a vast river system flowing in a south-north direction, along with abundant overbank, lacustrine and tidal-flat palaeoenvironments (Guiraud et al., 2005; Ibrahim et al., 2014b, 2020a).

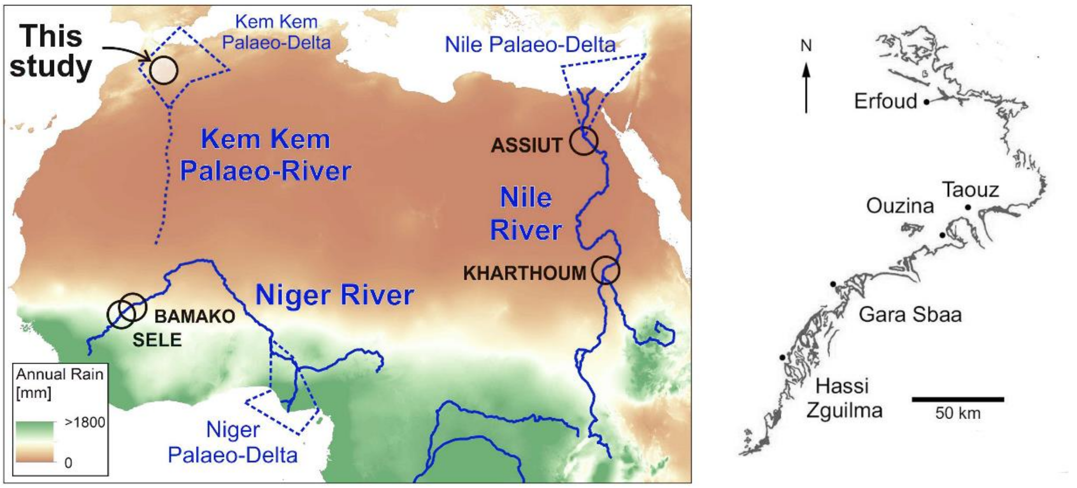


Figure 1. Information of the study location. **Left:** Map of North Africa with highlight of the location of the Kem Kem beds. The approximate locations of the major river deltas (Kem Kem river system, Palaeo-Nile delta and Palaeo-Niger delta outlined in dashed blue lines) during the Late Cretaceous were mapped based on Ibrahim et al., 2020a. The locations of several sites along modern Nile and Niger catchments were highlighted for further discussion in Section 4.3. **Right**: the Cretaceous outcrop at the Kem Kem region with several key fossil excavation sites, modified from Sereno et al. (1996). Data retrieved from: https://www.worldclim.org/data/index.html. Last access: 14/3/2024.

2.2. Preparations

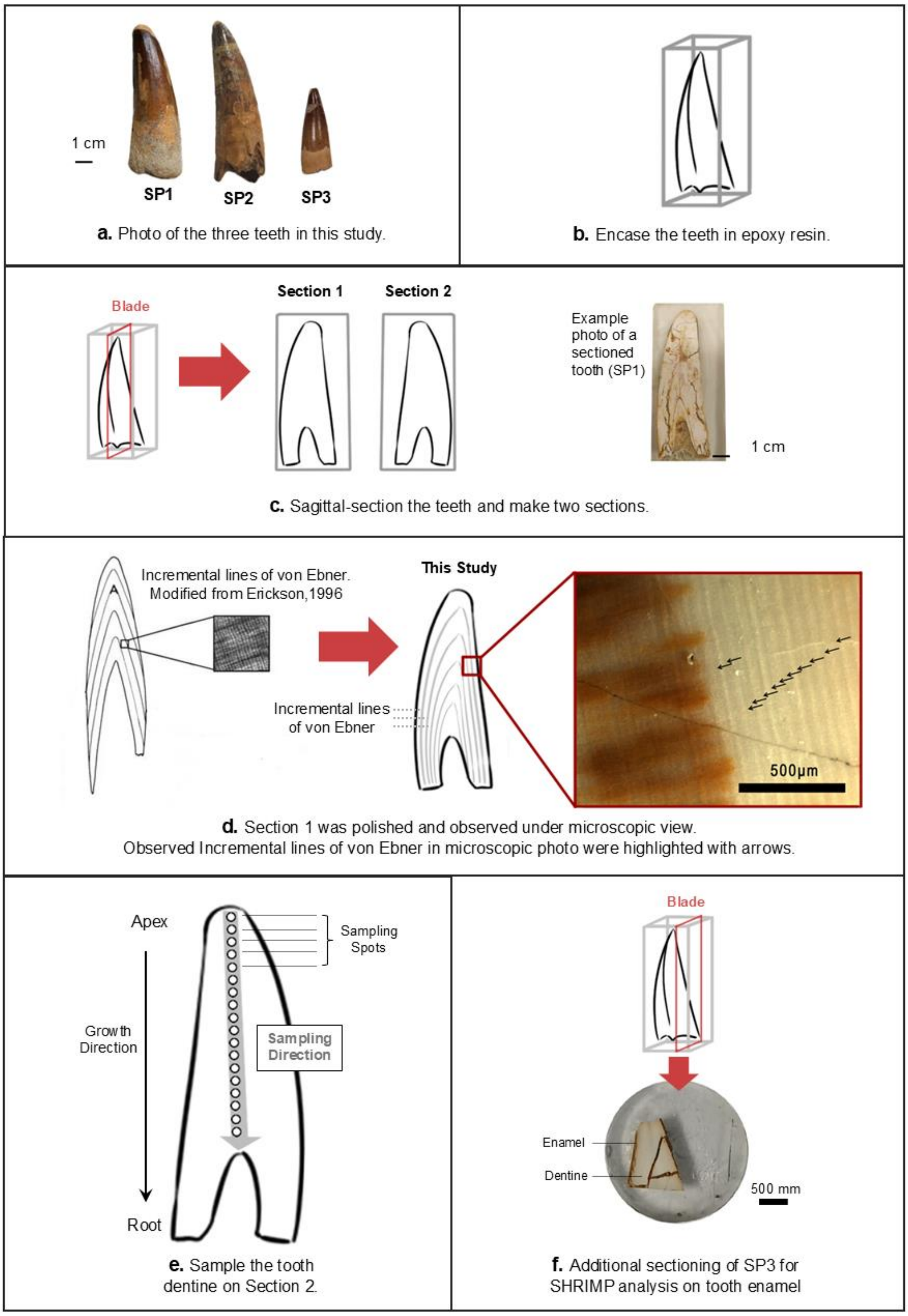
The samples were sectioned, polished and observed for incremental features before taking samples for isotopic analysis. The preparation steps are described below and also illustrated in Figure 2.

The *Spinosaurus* teeth were photographed (Figure 2a), and then embedded in epoxy resin (Figure 2b) before being sagittal-sectioned using a Buehler Isomet 1000 low-speed precision saw equipped with a 0.4 mm diamond coated blade. Each cut passed through the tip of the tooth, resulting in two sections of each tooth that are identical in shapes but mirrored (Figure 2c). The two sections were named Section 1 and Section 2 for different use.

Section 1 was used for observing growth lines. We wet polished Section 1 of each tooth with sandpaper of grit 600, and then observed them under a Wild M400 Photomacroscope with magnification 14.5-87.5x to observe the microstructure of *Spinosaurus* tooth dentine. In Figure 2d, the observed von Ebner lines were highlighted with arrows.

The tooth dentine of Section 2 was drilled using a 1 mm cylindrical diamond coated drill bit at approximately 1.5 mm resolution, using lines drawn perpendicular to the tooth height direction at approximately 1.5 mm spacing as a guide. The powdered samples, each weighing between 3 and 5 mg, were collected from the apex to the pulp cavity along a transect following the maximum growth axis and maximum tooth height (Figure 2e). These samples were pretreated following the methods developed by Balasse et al., 2002. They were first soaked in 2-3% NaOCl for 24 hours to remove organic materials, rinsed three times with distilled water before being reacted with 0.1M acetic acid for 4 hours to remove diagenetic carbonate, and then they were rinsed with the same procedure again. The pretreated samples were dried in a 40 °C oven overnight before being analyzed for $\delta^{18}O$ values with Isotope Ratio Mass Spectrometry (IRMS).

We also prepared an additional section from SP3 for Sensitive high-resolution ion microprobe (SHRIMP) analysis. A subsection of Sample SP3 was made by cutting longitudinally along the side of the tooth (Figure 2f). The secondary section was re-embedded in epoxy resin with a button mold so that the resin block could fit into the SHRIMP sample holder. The $\delta^{18}O$ values in tooth enamel on this section were analyzed to compare with those in tooth dentine for assessment of diagenesis.



a. Photo of the three teeth in this study.

b. Encase the teeth in epoxy resin.

c. Sagittal-section the teeth and make two sections.

d. Section 1 was polished and observed under microscopic view.
Observed Incremental lines of von Ebner in microscopic photo were highlighted with arrows.

e. Sample the tooth dentine on Section 2.

f. Additional sectioning of SP3 for SHRIMP analysis on tooth enamel

Figure 2. Graphic illustration of step by step preparations: a. Photographs of the three teeth used in this study; b. Schematic illustration of resin encasement; c. Schematic diagram showing the sectioning position and direction with an example of sectioned photo; d. Schematic illustration of the direction of von Ebner lines based on the illustration of their previous study of theropod tooth dentine (Erickson, 1996; Heckeberg and Rauhut, 2020; Kosch and Zanno, 2020) with observed incremental lines under microscopic view; e. Diagram showing sampling strategy for stable isotope analyses; f. Similar to c, a schematic diagram showing the additional sectioning and a photo of the re-encased sample which was analyzed using SHRIMP.

2.3. IRMS Analysis

The isotopic composition of the dentine samples was analyzed using an Analytical Precision AP2003 continuous-flow isotope ratio mass spectrometer at The School of Geography, Earth and Atmospheric Sciences, University of Melbourne. The atmosphere in the exetainers were first replaced with ultrapure helium gas with a purger, and then approximately 0.5 mL of 104% orthophosphoric acid was injected with a syringe. Samples were left to react with the acid for 30 minutes on a hot plate at 70 °C to produce headspace CO_2 gas, which was then analyzed by the mass spectrometer. Each sample was measured four times by the mass spectrometer. Although both $\delta^{18}O$ and $\delta^{13}C$ values were analyzed, only the oxygen isotopic results are reported and discussed in this study. The results are presented in delta (δ) notation in units of per mil (‰) relative to the Vienna Peedee belemnite (VPDB) standard, where:

$\delta = 1000 * (R_{sample} – R_{standard}) / R_{standard}$
$R_{oxygen} = {}^{18}O / {}^{16}O$

We used two calcium carbonate in-house standards (NEW1 and NEW12) and one international standard reference material (NBS-18) for calibration.. The uncertainty of each sample was the standard error calculated of the four measurements, which was approximately between 0.05 ‰ and 0.79 ‰. An outlier test was performed with boxplots to remove the outliers which were likely caused by measurement errors.

2.4. SHRIMP Analysis

The mount of sample SP3 was polished using 1200 grade SiC paper and 1 μm diamond paste. It was then washed with petroleum spirit, RBS solution and Millipore H_2O. The mount was then dried in a 60˚C vacuum oven for a minimum of 24 hours, then coated in high purity Al prior to SHRIMP analysis. The sample was analyzed with the SHRIMP at the Research School of Earth Science, Australian National University. The SHRIMP was operated in multi-collector, negative ion mode. A 15 kV, ∼3 nA Cs+ primary ion beam was focused to a 25 μm diameter spot on the Al-coated target, producing 200–250 pA of secondary $^{16}O^-$ (Aubert et al., 2012). Twenty two spots were analyzed in enamel along the direction of growth covering about 1 cm, and the distance between each sample was approximately 450 μm. Durango apatite was used as the standard for calibration of the results. The standard was analyzed first, then again after every six samples. Thus, five spots of standard were measured, producing an average value of 9.8‰ relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. The standard deviation for the standards is 0.08. For each sample, six scans were performed, and a bulk oxygen isotope composition with a combination of $\delta^{18}O_{PO4}$, $\delta^{18}O_{CO3}$ and $\delta^{18}O_{OH}$ ratios was measured. However, since $\delta^{18}O_{PO4}$ fraction is the dominant moiety measured (Aubert et al., 2012), we assume the results were similar to the enamel $\delta^{18}O_{PO4}$ ratios.

2.5. Assessment of Diagenesis

The degree of diagenesis was primarily assessed by comparing the offsets of $\delta^{18}O$ values in enamel and dentine. Enamel is the hardest material in teeth and can resist diagenesis over geological scales (Tütken et al., 2007; Zazzo et al., 2004). Various past studies have used stable isotopes in dinosaur tooth enamel to reconstruct Mesozoic environments, and the results show evidence of primary environmental signals (Amiot et al., 2010b; Barrick and Showers, 1994; Goedert et al., 2016; Thomas and Carlson, 2004). Therefore, comparing the $\delta^{18}O$ values in enamel and dentine from the same sample is a method for assessing diagenesis (Ayliffe et al., 1994; Sharp, 2000). Although this method does not unequivocally prove whether the primary minerals are fully preserved, it can still provide information on whether the dentine has been more significantly altered compared to the enamel.

Since the tooth dentine carbonate was analyzed with IRMS and the results are reported to the VPDB standard, and the enamel $\delta^{18}O_{SHRIMP}$ values were reported to the VSMOW standard, we converted the VPDB enamel values to VSMOW with existing equations for consistency in comparisons. The tooth dentine $\delta^{18}O$ values in VPDB standard was first converted to VSMOW standard using the equation developed by Coplen, (1988):

$$\delta^{18}O_{CO3/VSMOW} = 1.03091\ \delta^{18}O_{CO3/VPDB} + 30.91$$

We then converted the carbonate $\delta^{18}O$ values into phosphate following the methods used in Lüdecke et al. (2022). In mammals, the oxygen isotopic values in carbonate and phosphate can be converted using the equation by Iacumin et al. (1996) :

$$\delta^{18}O_{PO4} \approx 0.98\ \delta^{18}O_{CO3} - 8.5$$

The converted values can then be compared with the results from the SHRIMP analysis. We are aware that reptilians may have slightly different conversion equations than mammals due to physiological differences (Thomas and Carlson, 2004). However, the relationship in reptiles has not been adequately studied and there is no existing reptilian equations (Lüdecke et al., 2022). Furthermore, to assess whether the enamel $\delta^{18}O$ values in this study are valid, we also compared them to other studies which also analyzed the $\delta^{18}O$ values in *Spinosaurus* tooth enamel from Kem Kem beds, Morocco (Amiot et al., 2006, 2010a, b; Goedert et al., 2016).

3. Results

3.1. Isotopic Data

The IRMS $\delta^{18}O$ values in tooth dentine carbonate are presented here on the VPDB scale. There are 28 samples analyzed from SP1, and they range from -5.6‰ to -3.7‰ (Mean

= -4.7‰). The uncertainties range from 0.08‰ to 0.43‰. Three values are considered as outliers using boxplots and were removed. The sample numbers for SP2 and SP3 are 34 and 25, respectively, and no values from these two teeth were removed. The $\delta^{18}O$ values from SP2 range from -5.6‰ to -3.9‰ (Mean = -4.6 ‰), and they have greater uncertainties which are between 0.11‰ and 0.79‰. The results of SP3 were between -5.2‰ and -3.5‰ (Mean = -4.3‰), and the uncertainties range from 0.05‰ to 0.49‰. The values of the three teeth have no statistically significant differences (t test, $P > 0.05$). The SHRIMP measured $\delta^{18}O$ values in SP3 tooth enamel phosphate are presented here on the VSMOW scale. The values in the 22 samples range from 19.4‰ to 19.9‰, with an average value of 19.7‰. The uncertainties are between 0.04‰ and 0.16‰.

3.2. Comparison of Enamel and Dentine

The IRMS dentine $\delta^{18}O_{CO3}$ values of the three teeth were converted from VPDB to VSMOW scale using the equation in Section 2.5. As a result, the ranges of converted values for SP1, 2, and 3 are 25.1‰ ~ 27.1‰, 25.2‰ ~ 26.9‰, and 25.6‰ ~ 27.3‰, respectively. They were then compared to enamel $\delta^{18}O_{CO3}$ ratios measured by Amiot et al. (2010a) (Figure 3). The dentine $\delta^{18}O_{CO3/VSMOW}$ values of the three teeth overlap with the enamel $\delta^{18}O_{CO3}$ ratios, and show a lesser degree of variability.

For tooth SP3, the $\delta^{18}O_{CO3/VSMOW}$ values were further converted to $\delta^{18}O_{PO4}$, and the converted values are between 16.6‰ and 18.2‰. They were then compared to the SHRIMP measured $\delta^{18}O$ ratios in enamel, and the converted dentine $\delta^{18}O_{PO4}$ values are significantly lower ($p < 0.05$). Nonetheless, when they were compared to results from past studies, there is still a certain degree of overlap (Figure 3).

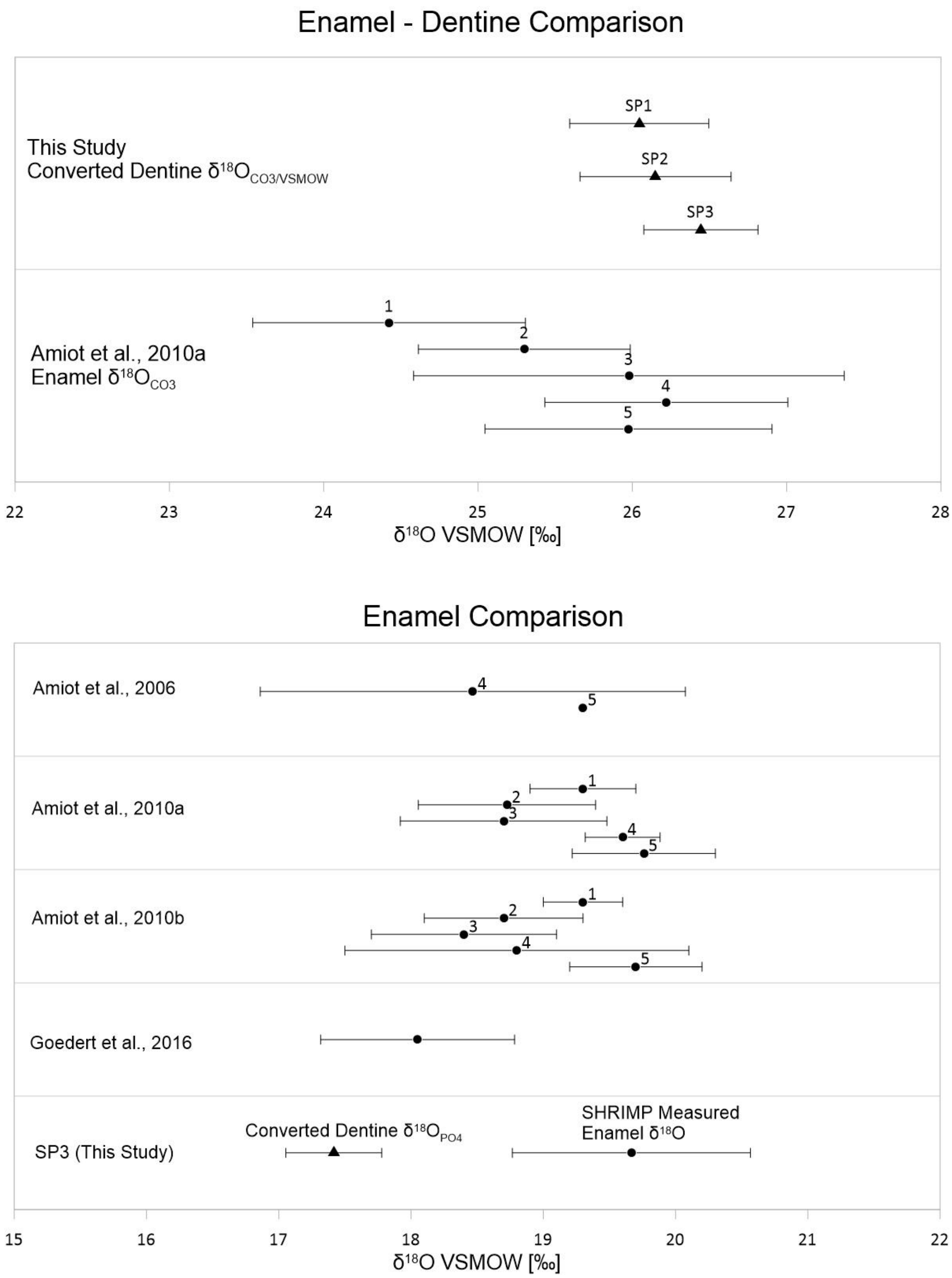


Figure 3.. The average values of the three teeth compared to results from *Spinosaurus* tooth enamel in past investigations. Error bars represent standard deviations. Dots: Measured values; Triangles: Converted values. Labelled numbers represent localities: 1 – Jebel Al Qabla; 2 – Takemout; 3 – Chaaft; 4 – Khetitila Srhira; 5 – Bou Laalou. The conversion equations were listed in Section 2.5.

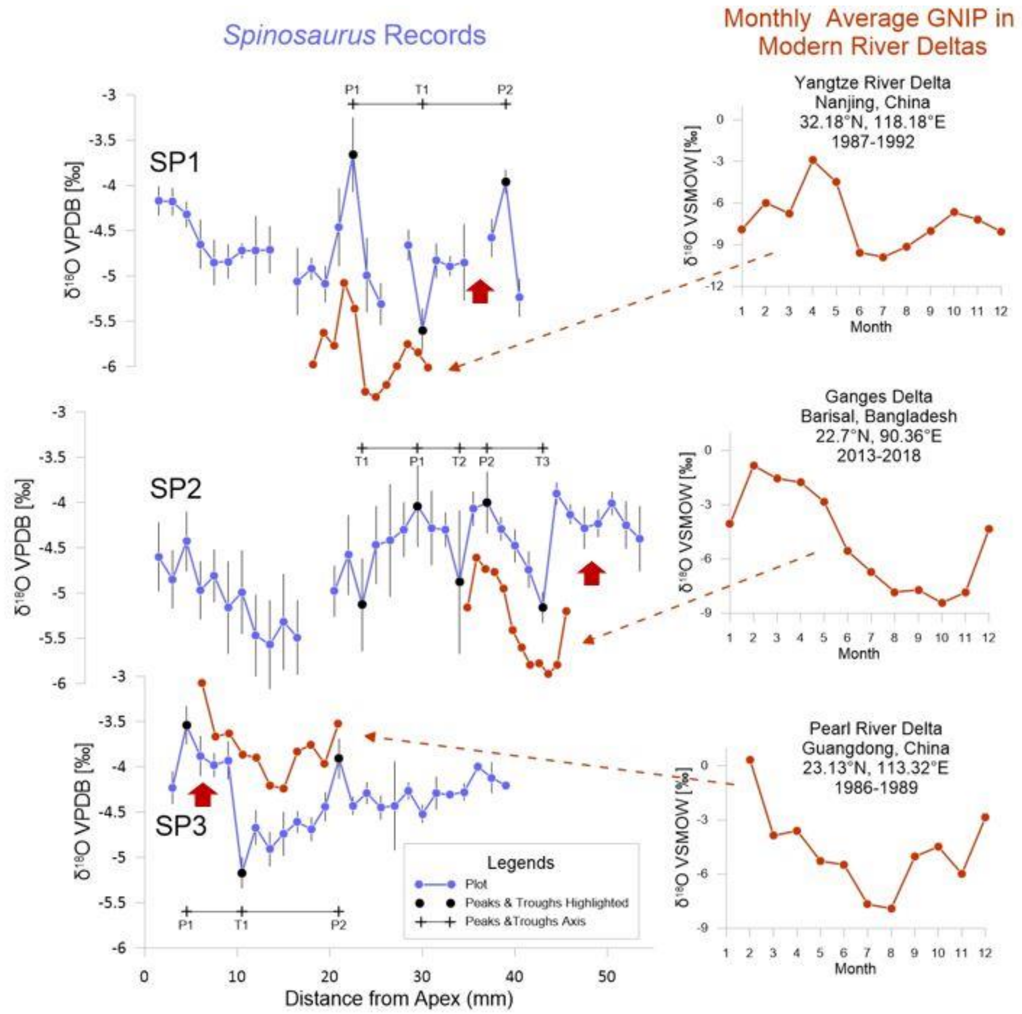


Figure 4. The sequential δ18O dentine carbonate values plotted against the incremental length of *Spinosaurus* dentine. Local peaks and troughs were highlighted with black dots, and they were also plotted on an axis with labels (abbreviations: p – peak, t – trough). The *Spinosaurus* records were also wiggle-matched (not to scale) to compare with monthly average δ18O values of Global Network of Isotopes in Precipitation (GNIP) in modern tropical and subtropical catchments (see discussion). Red arrows highlight the concaves which were discussed in Section 4.3. Data Retrieved from: https://nucleus.iaea.org/wiser/index.aspx. Last Access: 12/6/2023.

3.3. Sequential δ18O Variations

The sequential isotopic values of the three teeth were plotted against incremental length in Figure 4. The three gaps in SP1 were removed outliers as explained above, and the gap in the SP2 sequence was caused by a crack in the tooth where the materials were not drilled. All three curves show cyclicities at least in certain parts of them. The monthly average δ18O values of GNIP in modern tropical and subtropical river deltas were also plotted here, and their shapes were compared to the *Spinosaurus* records to show their similarities. This was discussed in Section 4. 3.

In SP1 and SP2, the curve at the right side of the first gap has a sinusoidal shape, and local peaks and troughs can be identified. They are highlighted with black dots and also labelled with a separate axis above with P representing “peak” and T representing “trough”. The curve at the left side of the first gap is less clear in cyclicity.

Two peaks and one trough were identified in the SP1 record, and are all V-shaped. The troughs in SP2 record are also sharp, while the peaks are smoother. The curve of SP3 has the opposite trend compared to the other two. The cyclicity can be identified in the first half of the curve where two peaks and a trough were present. The other half of the curve seems more averaged and shows much less variability.

4. Discussion

4.1. Sample Preservation

Physical and chemical transformations of sample materials may lead to isotopic exchange and loss of primary isotopic signals (Goedert et al., 2016; Keenan, 2016). Theropod tooth dentine was enveloped by enamel, the most resistant material to diagenetic alteration due to its low porosity and organic content (Ayliffe et al., 1994; Kohn, 1996; Tütken et al., 2007; Zazzo et al., 2004). The pore size is too small for bacteria to penetrate and only cracks on the enamel may expose dentine to diagenesis (Kohn, 1996). To date, no single method can conclusively assess whether the tooth material has been altered by diagenesis (Nelson et al., 1986). However, based on several lines of evidence, at least part of the primary isotopic signals from the tooth dentine seems to be preserved.

The first line of evidence is the comparison of $\delta^{18}O$ values between enamel and dentine. The dentine $\delta^{18}O_{CO3}$ values from this study are comparable to the enamel $\delta^{18}O_{CO3}$ values from Amiot et al. (2010a), and the converted dentine $\delta^{18}O_{PO4}$ values of SP3 also partly overlap with enamel values from other studies (Figure 3). The converted dentine $\delta^{18}O_{PO4}$ values are lower than the SHRIMP measured results from enamel, however this may be due to several reasons. First, despite it is assumed in this study that SHRIMP primarily measured the enamel $\delta^{18}O_{PO4}$ values, we are aware that the measurements still likely included certain influence from carbonates and OH groups. Therefore, the enamel $\delta^{18}O_{SHRIMP}$ values may be offset from the actual enamel $\delta^{18}O_{PO4}$ compositions. Also, one of the conversion equations was based on mammals rather than reptiles, and thus the actual data distribution of converted dentine $\delta^{18}O$ values could be either closer or further away from the enamel results. An additional explanation for the offset is the limited temporal duration represented by the enamel $\delta^{18}O$ values. Due to the limitations of mount size for the SHRIMP and the cost of instrument time, only a small fraction of enamel was analyzed. This is the reason for the small variations in the enamel $\delta^{18}O$ values compared to other studies. In Goedert et al. (2016), they sampled the enamel from the apex to the root, and there is more than one year of growth shown in their records. Thus, the $\delta^{18}O$ values in their study reflect environmental changes throughout different seasons. Certain samples from the other three studies also present relatively wide data distributions which might be due to the same cause (Figure 3). However, the temporal duration covered by the samples is unknow, since it is unclear whether the samples were serially sampled following the growth direction and at what resolution. In this study, all enamel samples were taken along a 9 mm transect, which had a much shorter time of growth. If the enamel was sampled from the apex to the root, as conducted for the dentine, the data distribution would be wider and also have a greater probability of overlapping with the converted dentine $\delta^{18}O$ values.

Also, all three tooth dentine carbonate profiles exhibited sinusoidal to quasi sinusoidal $\delta^{18}O$ variations which likely reflect seasonal environmental cycles (Figure 4). In most cases, complete diagenesis homogenizes the $\delta^{18}O$ values in all samples (Goedert et al., 2016; Metcalfe and Longstaffe, 2012). The results in tooth SP2 have greater uncertainties which make them less convincing. However, we are aware that, in certain situations, seasonal profiles can be preserved in diagenetically altered carbonates but the values are offset from the original composition (Moon et al., 2021). Therefore, in this study we primarily focus on interpreting the data variation pattern instead of the absolute values. In addition, there are observable dentine incremental lines in Figure 2d, suggesting some dentine material remained pristine despite not being a strong proof of minimal chemical alteration (Kolodny et al., 1996). Our stable isotope sampling spots are located along the central axis of the tooth, which is the innermost material and cracks are less frequent compared to the margins. Cracks and places of orange coloration were avoided during drilling, so the sampled powder was expected to be from material with the least degree of diagenetic alteration.

Overall, based on evidence from the enamel-dentine comparison, cross-study comparison, cyclicity that mimics seasonal environmental cycles and observable incremental lines, we conclude that a majority of the isotopic signals preserved in the dentine material are primary. We still assume there may be a mixture of dentine with some sedimentary material/secondary carbonate due to the fact that there is an offset between converted dentine $\delta^{18}O$ values and tested enamel $\delta^{18}O$ values, as well as part of the dentine in the tooth section which shows orange coloration (Figure 2c & d), indicating other materials are mixed in the tooth dentine despite such parts were avoided during drilling.

4.2. Isotopic Oscillations and Palaeoenvironments

Cycles of oxygen isotopic variations with several local peaks and troughs were detected in the serial tooth dentine samples. Through observation, there are at least two cycles in the record of SP2, and at least one cycle in SP1 and SP3. Due to the homoeothermic and obligate-drinking characteristics of large theropods (Barrick and Showers, 1994; Eagle et al., 2011), the isotopic ratios in *Spinosaurus* dentine should reflect those in its ingested environmental water (Bryant and Froelich, 1995; Longinelli, 1984; Luz et al., 1984). Thus, the temporal isotopic variations in *Spinosaurus* tooth were likely caused by $\delta^{18}O$ values in their ingested water, which in turn were controlled by seasonal changes in hydrology. Hydrological years were defined by identifying a sequential cycle of peak-trough-peak within the oxygen isotope profile. Starting from the first identifiable peak or trough, the distance between two peaks (or two troughs) is a full cycle and interpreted as one hydrological year (Roberts et al., 2019).

There are two possible explanations for the observed hydrological years in *Spinosaurus* dentine: 1) *Spinosaurus* moved through two different water sources annually; or 2) A seasonally variable water source that varied isotopically occurred in the area inhabited by *Spinosaurus* through the time of tooth growth. The isotopic variations could be caused by either of these explanations or a combination of both.

4.2.1. *Spinosaurus* Water Sources

Different aqueous environments coexisted in the Kem Kem delta, with both rapidly moving (lotic) river systems that flowed northward to the ocean and much rarer standing waters (lentic) represented by pond and floodplain deposits (Ibrahim et al., 2020a). We devised a schematic hydrological model for the delta, and divided it into two parts: the upland hydrologic catchment and lowland deltaic environment (Figure 5). In the upland, the primary water source for *Spinosaurus* was the lotic streams. Assuming the *Spinosaurus* lived in the upland of the Kem Kem delta, we may ignore the effects of the *Spinosaurus* drinking from different types of water sources due to the homogeneity of the hydrological environments. However, the water bodies may still experience a change of water source due to seasonal and continental effects (e.g., the source of precipitation was evaporated from different latitudes in different seasons) (Wright, 2013). In the lowlands, more diverse aqueous environments might occur, including: 1) perennial rivers with much slower current velocities; 2) floodplain lakes with connections to rivers; and 3) lakes that are mostly groundwater fed and evaporation driven. Contributions from different surface and/or subsurface water sources, each with distinct isotope compositions, determine the $\delta^{18}O$ values in these water bodies (Mook, 2001; Theakstone, 2003). Rainwater $\delta^{18}O$ values are more subject to seasonal changes than those of groundwater, which integrate the amount-weighted mean of effective rainfall through the year (Yeh and Lee, 2018). The rainwater is usually more enriched in ^{18}O than groundwater at most times of year, and can be more depleted during wet seasons (e.g., Yeh and Lee, 2018; Bedaso and Wu, 2021). Therefore, compared to groundwater-fed lakes, the oxygen isotopic composition of precipitation-dominated rivers and floodplain lakes are expected to be different in both data distribution and amplitude of seasonal variations (Mook, 2001).

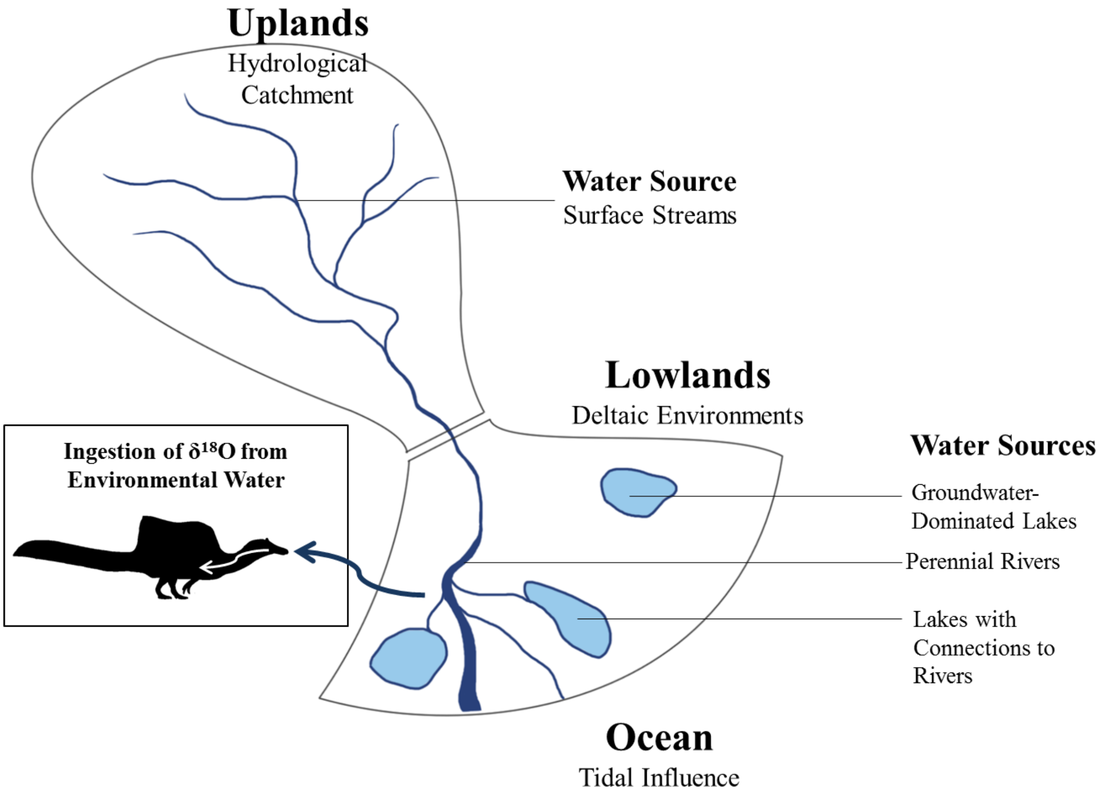


Figure 5. The schematic hydrological model in the Kem Kem delta, showing the possible water sources for the *Spinosaurus*.

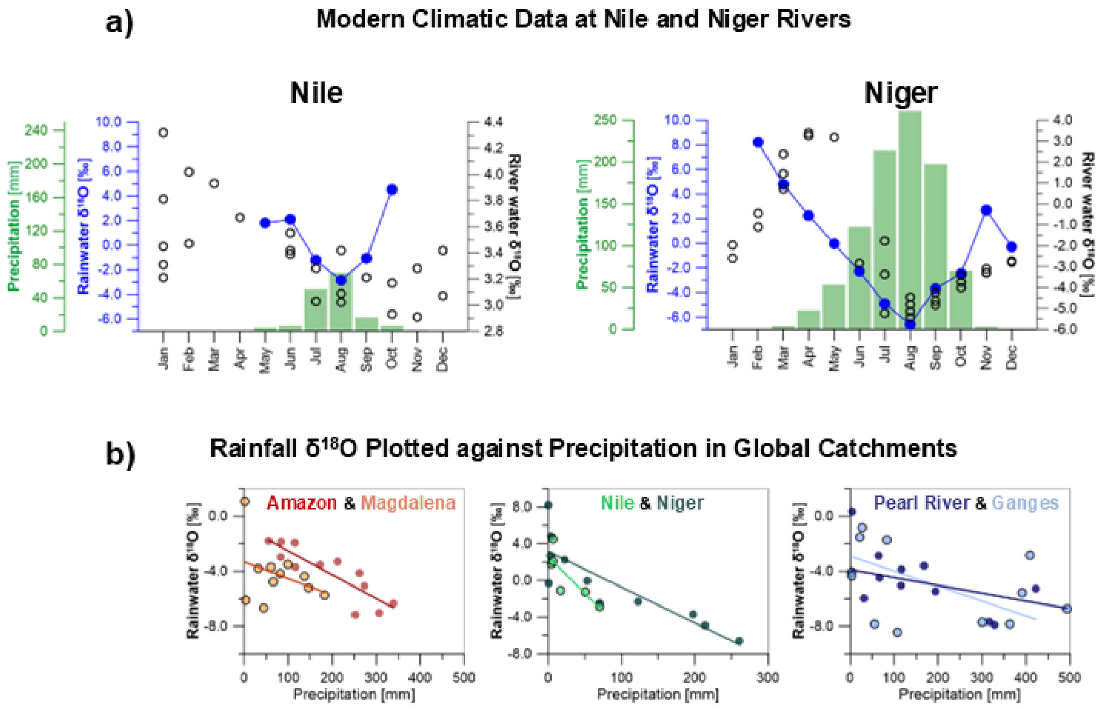
Besides regional mobility, the *Spinosaurus* also could have migrated on a much greater geographical scale; that is, moving between upland and lowland environments. This potential movement may cause substantial changes to ingested water $\delta^{18}O$ values, as river water $^{18}O/^{16}O$ ratios differ geographically, with progressive depletion of ^{18}O with increasing distance from the moisture source (Mook, 2001). During the Cretaceous, water would have evaporated from the tropical oceans surrounding the Kem Kem delta and transported to the Kem Kem delta catchment. Compared to the dominant $H_2{}^{16}O$ molecules, the heavier $H_2{}^{18}O$ molecules in vapor more readily condense and precipitate (Wright, 2013),so more $H_2{}^{18}O$ molecules rainout during air-mass transportation, which ultimately leads to depletion of rainwater in ^{18}O further into the catchment. Consequently, if the *Spinosaurus* migrated from upstream to downstream habitats, the $\delta^{18}O$ values in its ingested environmental water would become more positive and vice versa. However, the teeth analyzed in this study show evidence of no more than 3 years of growth based on the $\delta^{18}O$ patterns (Figure 4), whereas the process of long-range migration of *Spinosaurus* may not have been recorded in this relatively short time window. Therefore, it is assumed in this study that the *Spinosaurus* had only regional movements without long distance migration during the tooth formation time.

Estuarine and coastal environments could also be potential water sources for the *Spinosaurus*, which may bring further complexities in the $\delta^{18}O$ variation. The aqueous environment of the Kem Kem beds has been described as containing both freshwater and brackish settings (Ibrahim et al., 2020a). Massive amounts of dental rostrum of 'sawfish' *Onchopristis* were preserved in the fluvial sediments of the Kem Kem beds. Although the ecotype of *Onchopristis* is unknown, modern sawfish (*Pristis* spp.) are euryhaline and move between marine and freshwater habitats (Carlson et al., 2014; Whitty et al., 2017). The morphology of *Onchopristis* shares a convergent evolution with modern sawfish, and their habitat use has also been suggested to be potentially similar (Villalobos-Segura et al., 2021). Therefore, the presence of *Onchopristis* might suggest the river systems of the Kem Kem beds may have had a wide range of different salinities like the ecotype of modern sawfish. In addition, recently a juvenile plesiosaur (Family: *Leptocleididae*; Order: *Plesiosauria*) was discovered in the fluvial sediments of the Kem Kem beds (Bunker et al., 2022), which brought further evidence that the ocean was connected to the floodplain. The extent to which *Spinosaurus* dwelled in brackish/marine habitats is unknown; however, currently they are still generally considered as primarily of the freshwater ecotype due to the fluvial sediments in the Kem Kem beds and presence of certain species that likely lived exclusively in freshwater (e.g., *Neoceratodus*) (Ibrahim et al., 2020a). Additionally, the anatomy of *Spinosaurus* suggests they could not effectively propel or keep balance underwater, but instead were more adapted to wade in shallow-water environments (Hone and Holtz, 2021; Sereno et al., 2022). Therefore, in this study we assumed the *Spinosaurus* had no habitat use of brackish/marine environments although such environments existed in these formations. The changes in δ^{18}O values are therefore exclusively explained by the water balance in the riparian delta.

4.2.2. Seasonal Isotopic Variation

Apart from potential movements between different aqueous environments, temporal variations of the isotope compositions in the same water body can also cause changes in *Spinosaurus* tooth δ^{18}O values. Nearly all natural water bodies, including streams, estuaries and lakes, experience seasonal oscillations of δ^{18}O values due to seasonally different water balances (Mook, 2001; Theakstone, 2003). The surface water isotopic content in a downstream catchment such as the Kem Kem delta, is determined by the sum of its water sources (input) as well as the water leaves the water body with fractionation (output) (Benson and Paillet, 2002; Mook, 2001). The input water sources for the Kem Kem river catchment may have included groundwater, upstream discharge and precipitation sourced from the ocean. Among these inputs, precipitation is assumed to have been the dominant source for both the Kem Kem delta and its upstream discharge. The isotopic composition of precipitation differs from those in surface runoff (Bedaso and Wu, 2021; Theakstone, 2003). Isotope compositions of surface runoff depend on those of the precipitation, and consequently a variation in isotope composition of precipitation would impact the seasonal values of the river water. The δ^{18}O values in rainwater have a negative relationship to the amount of precipitation. This is known as the amount effect, with extreme depletion of heavy isotopes during intense or prolonged rainfall events (Dansgaard, 1964). –Therefore, the negative δ^{18}O values in the *Spinosaurus* tooth dentine may be caused by seasonal increases in rainfall. The isotopic composition of groundwater has less seasonal variation (Bedaso and Wu, 2021; Yeh and Lee, 2018), and consequently would be expected to contribute little to the isotopic oscillations compared to precipitation. However, standing water in groundwater-fed lakes would have clear seasonal isotopic differences due to water evaporative fractionation, which is the primary process that significantly alters the isotopic composition of surface water (Benson and Paillet, 2002; Yeh and Lee, 2018). The δ^{18}O value has a positive correlation with temperature and humidity due to evaporation: $H_2{}^{16}O$ molecules are lighter and easier to evaporate, thus the river is left enriched with $H_2{}^{18}O$ when discharge reduces (Wright, 2013). Therefore, in both groundwater- and precipitation-dominated aqueous environments, the troughs (depletion) in the δ^{18}O curve are expected to represent rainy seasons and peaks (enrichment) represent dry seasons when evaporation is higher and there is less catchment discharge. Such relationships have been observed in modern semi-aquatic animals, as the δ^{18}O values in modern crocodile teeth also suggest depletion of heavy isotopes during wet seasons (Ascari et al., 2018).

Modern climatic and isotopic data were examined to test this hypothesis. During the Cenomanian, the palaeoenvironments of Northwestern Africa are envisioned as dominated by a vast river system that flowed northward into the Tethys Ocean, and the Kem Kem beds were a prograding delta formed downstream (Guiraud et al., 2005; Ibrahim et al., 2020a). However, currently there are no such major river systems west of the Nile River. Therefore, the closest modern references would be the Nile and Niger catchments, which likely would have already been formed during the Late Cretaceous (Ibrahim et al., 2020a). The monthly average precipitation, along with the δ^{18}O values of rainwater and river water in multiple sites along these two rivers are plotted in Figure 6. In both catchments, the heavy isotopes in rainwater and river water are more depleted during months of increased precipitation.



Latitude	10 °S ~ 10 °N		10 ~ 20 °N		20 ~ 30 °N	
River Delta	**Amazon**	**Magdalena**	**Nile**	**Niger**	**Pearl River**	**Ganges**
Site	Manaus, Brazil	Barranquilla, Colombia	Khartoum, Sudan	Bamako, Mali	Guangdong, China	Barisal, Bangladesh
Linear Coefficient	-0.017	-0.012	-0.081	-0.049	-0.011	-0.001
R²	0.75	0.12	0.68	0.74	0.42	0.15

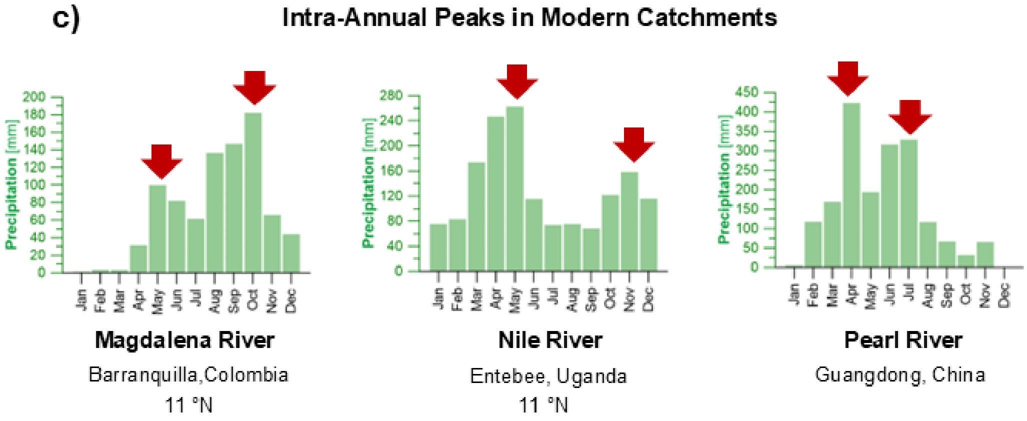


Figure 6. Climate and isotope data in modern tropical and subtropical river deltas. **a)** Left: monthly average precipitation and rainfall δ^{18}O values (Khartoum, Sudan), and river water δ^{18}O values (Assiut, Eygpt) of Nile River; Right: monthly average precipitation and rainfall δ^{18}O values (Bamako, Mali), and river water δ^{18}O values (Sele, Ethiopia) of Niger River. **b)** Scatter plots and a table showing the relationship between monthly average precipitation and rainfall

$\delta^{18}O$ values in tropical and subtropical river deltas. **c)** Monthly average precipitation in three modern river deltas with the intra-annual peaks highlighted with red arrows. Data Retrieved from: https://nucleus.iaea.org/wiser/index.aspx and http://www.ncdc.noaa.gov/ghcnm .Last Access: 12/6/2023.

We are aware of the temporal remoteness of the Late Cretaceous, so the use of the modern Nile and Niger rivers as analogues for the palaeo-delta of the Kem Kem beds should be interpreted cautiously. To address this issue, we compared data from additional modern river catchments worldwide. Since the latitude of the Kem Kem beds during the Cenomanian period was approximately 20°N (Scotese, 2014), we chose several modern tropical and sub-tropical river deltas for reference (Figure 6b & c), including the Amazon and Magdalena River Deltas that are close to the equator, as well as the Pearl River and Ganges Deltas between 20-30°N. For each site, we obtained monthly precipitation and oxygen isotopic data in rainwater from their local IAEA stations. In these tropical and sub-tropical deltas, the $\delta^{18}O$ values in rainfall also show an overall negative correlation to precipitation. Therefore, such correlations between $\delta^{18}O$ values and local precipitation are common in global tropical and subtropical catchments, at least in those dominated by precipitation (Figure 6). This further supports our hypothesis that the more negative $\delta^{18}O$ values in *Spinosaurus* tooth dentine carbonate likely reflect more humid environments in the Kem Kem beds.

4.3. Palaeoenvironmental Reconstruction

Based on the $\delta^{18}O$ profiles from the *Spinosaurus* tooth dentine, we aimed to interpret the isotopic values as an environmental proxy by analyzing their patterns of variability. The $\delta^{18}O$ amplitudes indicate pronounced inter-annual palaeoenvironmental differences.

The side close to the apex of tooth SP1 and SP2 isotopic profiles presents a decreasing slope with no observable cyclicity. This could be caused by a change of water source due to movement of the individual around the landscape. However, a more likely reason is that tooth growth rate was not uniform. The part closer to the apex of the tooth was formed during the earlier stage of tooth growth, and in the teeth of the living relatives of theropods, the crocodilians, the incremental lines near the apex are further away from each other, suggesting a faster growth rate (Kosch and Zanno, 2020). Despite the difference in growth rate, the resolution of each sampling spot is constant. Thus, each sampling spot at this part of the curve contains a shorter time of growth, and the decreasing trend could be a high-resolution record of transition from a dry season to a wet season. The shape of the curve from SP3, in contrast, has an opposite trend, where cyclicity is seen in the first half but not the rest. This is likely because SP3 is a much smaller tooth compared to the other two (Figure 2a). Therefore, with the same sampling resolution, each sample in SP3 could contain a greater temporal range. When we drilled near the root where the growth rate was slow, the sampling resolution became too low and thus the isotopic signal is likely time-averaged.

In the parts of the tooth where isotopic oscillations are clearer and more pronounced, all three teeth have sharp troughs, while the peaks are more variable. SP1 has sharp peaks, while the peaks at SP2 are more cuspate. These data points for SP2 have large uncertainties so they are less convincing. However, in the part of SP2 where the uncertainties are smaller, the record shows a similar trend to the patterns in the other two teeth (end of SP1 and start of SP3). Here, the $\delta^{18}O$ values become slightly more negative after the first peak, and are followed by another peak, resulting in a small concave shape before the profile reaches a trough (Figure 4). In the modern reference datasets, the monthly average precipitation data shows two intra-annual peaks in the hydroclimatic conditions of some tropical river deltas (e.g., Magdalena and Pearl River): there is a decrease interval in precipitation amount during the middle of the rainy season, resulting in two peaks in the same year. Such a phenomenon is also seen in a tropical upstream site of the Nile River (Figure 6c). With the deceasing interval extending for more than two months, the monthly rainfall pattern shows two wet season maxima in one year. In fact, a bimodal wet season is a typical feature of equatorial climates and reflects the biannual passage of the rain belt associated to the Inter-Tropical Convergence Zone. Therefore, an equatorial climate could be a possible interpretation for the concave pattern seen in the variation of *Spinosaurus* tooth dentine. This may suggest that the palaeoenvironmental conditions at the time that the Kem Kem beds were deposited were similar to climates of modern river deltas around 20°N.

This hypothesis is further supported by the direct comparison between the $\delta^{18}O$ profiles from *Spinosaurus* tooth dentine and modern records (Figure 4). At least part of the *Spinosaurus* $\delta^{18}O$ profiles have similar patterns to monthly average rainwater $\delta^{18}O$ in modern tropical and subtropical river catchments. This result agrees with a previous study undertaken by Goedert et al. (2016), who also discovered similarities between $\delta^{18}O$ values in *Spinosaurus* tooth enamel and rainwater isotopic data in Fuzhou, China (26.05°N, 119.31°E). It must be noted that such comparisons do not directly suggest that the palaeoclimates in Kem Kem beds were the same as the above localities, since the $\delta^{18}O$ variations in the *Spinosaurus* ingested water do not solely depend on rainfall (explained in Section 4.2.1.). Instead, we simply make the case that the variations of $\delta^{18}O$ values were caused by environmental changes, which supports that tooth dentine has preserved certain primary isotopic signal (see Section 4.1.). Nevertheless, the fact that the results developed from *Spinosaurus* tooth dentine and enamel from the two independent studies reached a similar conclusion gives further confidence in our hypotheses of both sample preservation and palaeoenvironmental interpretation.

Another argument that supports the tropical equatorial climate in the Kem Kem beds is that *Spinosaurus* remains, including the holotype, were also discovered in the Bahariya Formation in Egypt (Stromer, 1915). The Bahariya Formation was suggested to have a tropical climate as it was very close to the palaeo-equator during Cenomanian (Deaf, 2009; Scotese, 2014). Furthermore, mangrove deposits (Smith et al., 2001; Stromer,

1915) and morphological evidence from local flora also reflect tropical environments (Lyon et al., 2001). Although the mangrove deposit in the Bahariya Formation were not present in the Kem Kem beds (Ibrahim et al., 2020a), these two formations host very similar faunal assemblages (Ibrahim et al., 2020a; Sereno et al., 1996), suggesting similar palaeoclimatic conditions that allowed *Spinosaurus* and other aquatic species to flourish in both localities.

4.4. Research Potential & Limitations

Our exploratory data suggests that *Spinosaurus* tooth dentine effectively preserves sub-seasonal variations of oxygen isotopic signals that can be interpreted in palaeoenvironmental terms. In comparison to previous reconstructions which analyzed dinosaur tooth enamel, dentine as our choice of material has several advantages. First, dentine takes up most of the tooth volume and therefore it is easier to sample compared to the thin layer of enamel. Second, analyzing both enamel and dentine enables us to take advantage of more accessible samples, because some theropod teeth may have incomplete enamel preservation due to either life wear or physical and chemical alterations after death. Thus, the tooth dentine of *Spinosaurus* can be considered as an alternative material for palaeoenvironmental reconstructions in future studies. *Spinosaurus* teeth are abundant in the Kem Kem Group (Heckeberg and Rauhut, 2020; Ibrahim et al., 2020a) and relatively easy to obtain. Future research on these may include extracting sequential isotopic data from more *Spinosaurus* teeth to verify the findings of this study and obtain temporally longer datasets, as well as comparing the isotopic variations of teeth dated to different time windows and/or with known stratigraphic contexts reflecting all stages of delta evolution in the Kem Kem beds, to reconstruct palaeo-environmental and palaeo-climatic changes during the evolution of the Kem Kem delta. The same methodology may also be used for species from other formations for potential spatial and temporal comparisons of palaeoclimates. The oxygen isotopes in these teeth have the potential to generate a large database of high-resolution Mesozoic palaeoenvironmental reconstructions.

A major limitation in this study is the potential impact of diagenesis. Indeed, dentine is more susceptible to diagenesis compared to enamel. Therefore, we have attempted to assess diagenesis through various approaches, including enamel-dentine comparison, cross-study comparison, interpretation of isotopic variations and observation of incremental lines. The cross-study comparison shows our enamel results are consistent with other studies, and the enamel was likely well preserved. Enamel-dentine comparison suggests the dentine might have been diagenetically altered to some degree as the converted dentine values differ from tested enamel results. However, such comparison is limited by the indiscriminate measurement of $\delta^{18}O_{PO4}$, $\delta^{18}O_{CO3}$ and $\delta^{18}O_{OH}$ ratios in tooth enamel using the SHRIMP method, as well as inadequate study of phosphate-carbonate relationship in reptiles. Nevertheless, the converted dentine values partly overlap with enamel results from other studies. Overall, high-resolution isotopic variations caused by environmental changes can be recorded in dentine although the absolute $\delta^{18}O$ values may be offset. We would suggest caution when assessing diagenesis in future palaeoenvironmental reconstructions with dinosaur tooth dentine and recommend testing the $\delta^{18}O_{PO4}$ and/or $\delta^{18}O_{CO3}$ values from both dentine and enamel of the same tooth, as well as selecting samples with signs of good preservation (e.g., enamel completely preserved, no visible cracks, pristine dentine colour and easily observable von Ebner lines).

Another major challenge is the complexity of the aquatic systems in the Kem Kem beds. We were unable to definitively determine the potential brackish/marine influence on the oxygen isotopic ratios. This may be improved by cross-species comparison with other stable isotopes in future studies. For instance, sulphur isotopic ratios differ significantly in freshwater and marine environments due to different sources of dissolved minerals (Rees et al., 1978), and thus can be used to determine the salinity in the aqueous environments which the animal inhabited (Godbout et al., 2010; Goedert et al., 2018; Sayle et al., 2013). Carbon isotope compositions in aquatic species also vary substantially between lotic and lentic riparian environments (Finlay, 2004; Finlay et al., 1999). Comparing the isotopic values of *Spinosaurus* and their coexisting species of different ecotypes (e.g., between freshwater species like the *Neoceratodus* and potentially estuarine species like the *Onchopristis*. See Section 4.2.1) may allow better identification of different aquatic environments in their records, which ultimately help to better estimate the potential effects from changing water sources.

5. Conclusion

This study presents a high-resolution record of oxygen isotope variability in the tooth dentine of *Spinosaurus*, and demonstrates its potential to record palaeoenvironmental information. We captured pronounced $\delta^{18}O$ oscillations, with variations likely reflecting seasonal environmental changes in Late Cretaceous depositional setting of the Kem Kem beds in Morocco. From our preliminary analysis we reveal repeated wet and dry cycles, as well as inter-annual variations in seasonal amplitudes and seasonal transitions. These Late Cretaceous seasonal hydroclimatic variations recorded in the dentine of *Spinosaurus* teeth show certain similarities to the climates of modern tropical deltas. However, it must be noted that the relatively small dataset is limited in both temporal range and variability control, and thus sequential isotopic sampling of more teeth of *Spinosaurus* (and potentially other species as well) should be undertaken in future studies to allow more detailed and robust reconstructions. In future investigations, we recommend the sequential sampling and isotopic analysis of tooth dentine of *Spinosaurus* and other theropod species from broader temporal and geographical ranges, to generate a large quantitative database for Mesozoic palaeoenvironments and palaeoclimates at different localities and during different periods of time.

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Statement of Competing Interests

The authors declare no known competing interests.

Statement of Data Availability

Data presented in the article is attached in the supplementary materials.

Author Contributions

Planning: all coauthors ; sample acquisition: ZL; laboratory work: ZL, AP, KL; Funding: AP, KL; isotopic data processing: RD; data interpretation: ZL, AP, JHM; graph production: ZL, JHM; manuscript drafting: ZL, with reviews and inputs from all coauthors.

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Highlights

- Theropod tooth dentine can be used for palaeoenvironmental reconstructions.

- $\delta^{18}O$ records from *Spinosaurus* dentine carbonate reflect local climatic changes.
- The $\delta^{18}O$ records suggest palaeoclimates in the Kem Kem beds share certain similarities to modern tropical and subtropical river deltas.