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PALAIOS

Emphasizing the impact of life on Earth's history

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ABSTRACT: Oxygen isotope compositions of tooth enamel increments in theropod dinosaurs are investigated as potential proxies of climate seasonality. Six teeth of large carnivorous theropods collected from four Cretaceous formations deposited under contrasted climates have been sampled. These teeth have been analyzed for the oxygen isotope compositions of their apatite phosphate ($\delta^{18}O_p$) through incremental sampling performed along the major growth axis. Significant fluctuations in oxygen isotope compositions along the growth axis of each tooth are observed and interpreted as reflecting seasonality in ingested local surface water $\delta^{18}O_w$ values. Fluctuations in $\delta^{18}O_p$ values of theropod teeth from the Aptian of Thailand and Cenomanian of Morocco vary similarly to meteoric water $\delta^{18}O_{mw}$ values occurring today in sub-tropical regions subjected to large seasonal amounts of precipitations. A dinosaur tooth recovered from the more inland and mid-latitude Nemegt Formation of Mongolia shows a seasonal pattern similar to present-day cold temperate and continental climate. Finally, the high latitude and coastal Kakanaut Formation (Russia) experienced strongly dampened seasonal variations, most likely due to the influence of warm Pacific oceanic currents. Such conditions occur today in high latitude regions submitted to marine influence. These results further highlight the potential of using the oxygen isotope compositions of large theropod teeth to reconstruct past seasonal variations of terrestrial climates. Increased knowledge of past seasonality may help to better understand the complex interactions between climate and the dynamics of land biodiversity in terms of ecological adaptations, biogeography and the evolutionary history of organisms.

INTRODUCTION

Climate seasonality refers to the intra-annual fluctuations of physical parameters such as temperature or amounts of precipitation. In response to these variations, living organisms have developed various adaptations such as migration, hibernation, thermophysiology or reproductive strategies, which enable them to withstand seasonally extreme conditions such as freezing winters or drought periods. Therefore, the knowledge of seasonality is of paramount importance in order to understand some aspects of biodiversity dynamics or evolutionary trends (Tauber et al. 1986; Comeau et al. 2002; Altizer et al. 2006). Studies of past seasonality are limited by the scarcity of geological archives or proxies, most of which are based on the stable isotope compositions of fossilized organisms having prolonged or continuous growth (mollusk shells: Ivany et al. 2004; tree rings: McCarroll and Loader 2004; mammal teeth: Bernard et al. 2009; corals: Giry et al. 2012). When considering the Cenozoic Era, serial oxygen isotope analyses of hypsodont mammal teeth have been commonly used to reconstruct past seasonal variations of climate (e.g.,

Fricke et al. 1998; Fox and Fisher 2001; Zazzo et al. 2002; Bernard et al. 2009). However, during the Mesozoic Era, mammals were too small for their teeth to grow over a sufficient period of time to allow seasonal analysis. Consequently, available proxies of seasonality have been reduced to isotopic studies of marine organisms such as bivalves or cephalopods (e.g., Steuber et al. 2005; Lécuyer and Bucher 2006; Dutton et al. 2007). Stable oxygen isotope composition of theropod dinosaur tooth enamel may constitute a relevant proxy of seasonal variations of terrestrial climates. Indeed, theropod teeth are particularly abundant in the fossil record, and since theropods were homeothermic and carnivorous vertebrates, their tooth phosphate oxygen isotope composition is linearly related to that of local surface waters they drank (Amiot et al. 2004, 2011; Straight et al. 2004; Suarez et al. 2012, 2013, 2014; Domingo et al. 2013). Moreover, theropod teeth incrementally grew over several months depending on their size (up to 2.5 years for large adult tyrannosaurs; Erickson 1996b), and were continuously replaced throughout their life. Thus, each tooth increment records the oxygen isotope composition of recently ingested water,

i.e., surface waters (rivers, lakes, ponds) that mostly derive from local meteoric waters. In turn, meteoric waters have $\delta^{18}O$ values ($\delta^{18}O_{mw}$) reflecting both local air temperature and humidity (Dansgaard 1964; Rozanski et al. 1993). Thus, theropod dinosaur teeth should record seasonal variations in local meteoric water $\delta^{18}O_{mw}$ values integrated over their growth periods (Straight et al. 2004). It is noteworthy that the $\delta^{18}O$ value of surface waters ($\delta^{18}O_w$) can differ from that of local precipitations due to local processes such as evaporation, mixing with ground waters, mixing with river drainage catchments with different water oxygen isotope compositions, and orographic effect (e.g., Dutton et al. 2005). Such processes complicate the interpretations in terms of climatic reconstructions.

We have measured the oxygen isotope compositions of phosphate ($\delta^{18}O_p$) of enamel apatite incrementally sampled along six theropod teeth recovered from four sedimentary deposits for which distinct climate modes have been previously proposed. The measured $\delta^{18}O_p$ profiles have been compared to present-day seasonal records of $\delta^{18}O_{mw}$ values provided by climate stations operated by the International Atomic Energy Agency-World Meteorological Organization (IAEA-WMO) and discussed in terms of seasonal variations of air temperature, amounts of precipitation and continentality.

MATERIALS AND METHODS

Sample Collection

Enamel of six teeth of large theropods have been sampled and analyzed for their oxygen isotope composition of phosphate ($\delta^{18}O_p$). These teeth were recovered from four Cretaceous localities ranging in paleolatitude from about 16°N to 75°N (Fig. 1). One tooth, referred to *Spinosaurus aegyptiacus* (Mca) and another one attributed to *Carcharodontosaurus saharicus* (Mcb) come from the lower Cenomanian Ifezouane Formation at Khetitila Shrira, Morocco (Fig. 1B; Cavin et al. 2010). Tooth crown 'Mca' is 49 mm long from the apex to the base, whereas 'Mcb' is a 41 mm long fragment of a larger tooth. Two large theropod teeth, 'Ta' and 'Tb', have been recovered from the Thai localities of Khok Pha Suam and Ban Sapan Hin, respectively (Fig. 1A), both from the Aptian Khok Kruat Formation (Racey 2009; Racey and Goodall 2009). Sample 'Ta' is missing the tip, as well as a part of the root, and is 33 mm long. Sample 'Tb' is only missing the root and is 53 mm long. These teeth may belong to carcharodontosaurid theropods, which are the only non-spinosaurid large theropods hitherto recorded from the Khok Kruat Formation (Azuma et al. 2011). Tooth 'Mg' comes from the locality of Yagaan Khovil, Mongolia (Fig. 1C; Susuki and Watabe 2000; Watabe and Tsogtbaatar 2004). The associated fauna is characterized by the occurrence of large-sized tyrannosaurids and hadrosaurids and the bird-like small theropod *Avimimus*, which suggests that this locality belongs to the Maastrichtian Nemegt Formation (Jerzykiewicz and Russell 1991; Hasegawa et al. 2009). It is a fragmentary tooth measuring 53 mm along the growth axis. The frontal carina, which curves mesially toward the cervix and the wide denticles, which do not curve toward the apex, are both characteristics of Tyrannosauridae (Currie et al. 1990) but the tooth could not be identified at the generic level. Tooth 'R' comes from the Maastrichtian Kakanaut Formation at Kakanaut, in Northeastern Russia (Fig. 1C; Golovneva 1994, 2000; Rich et al. 2002; Godefroit et al. 2009); only its crown, 25 mm long, is preserved. As with the Mongolian tooth, the denticles of tooth 'R' are characteristic of Tyrannosauridae (Currie et al. 1990).

Analytical Method

The sampling technique followed the conventional method adopted by Bryant et al. (1996) and Fricke et al. (1998) for herbivorous mammals and adapted for theropods by Straight et al. (2004) based on different histological studies (Erickson 1996a, 1996b; Sander 1999, 2000). The teeth have been washed to remove traces of sediment. Then, enamel samples were collected using a spherical diamond-tipped drill bit (1 mm in diameter) perpendicularly to the major
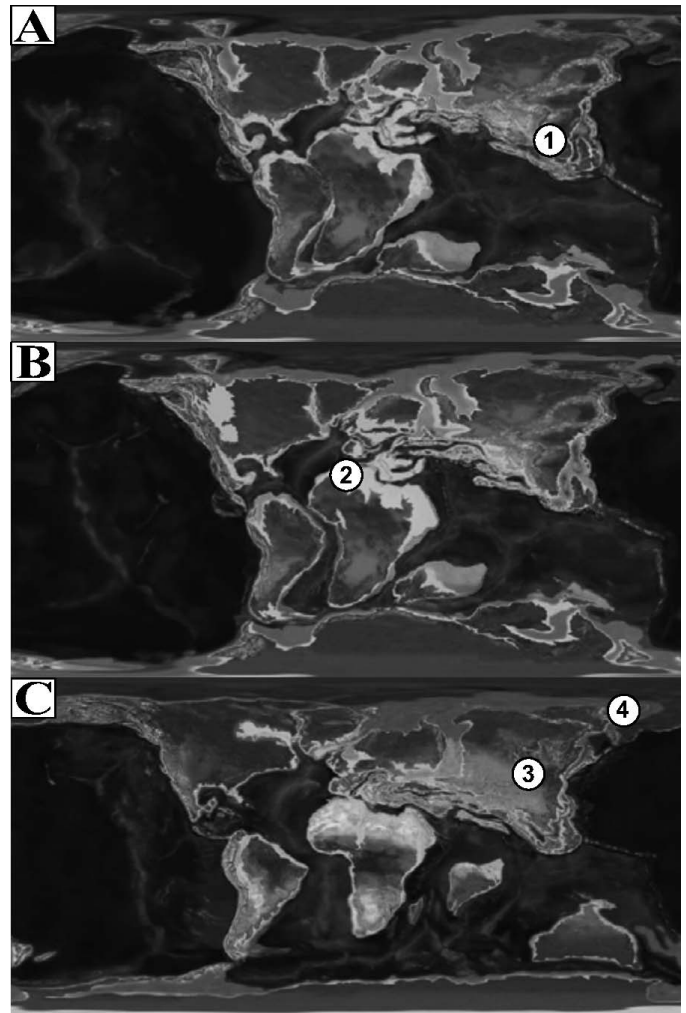

FIG. 1.—Paleogeographic maps (modified after Blakey 2015) showing the four Cretaceous localities from which the six theropod teeth have been recovered. **A**) Map of the Aptian showing the Thai localities of Khok Pha Suam (1) and Ban Sapan Hin (1) both belonging to the Khok Kruat Formation. **B**) Map of the Cenomanian showing the Moroccan locality of Khetitila Shrira (2) belonging to the Ifezouane Formation. **C**) Map of the Maastrichtian showing the Mongolian Yagaan Khovil locality (3) and the Russian Kakanaut locality (4) belonging respectively to the Nemegt Formation and the Kakanaut Formation.

growth axis (Fig. 2). The width of grooves was kept narrow and fixed for each tooth between 0.9 and 1.8 mm in order to both minimize time-averaging and collect a sufficient mass of enamel powder ranging between 2 and 3 mg.

Each of the sampled powders was treated following the wet chemistry protocol described by Crowson et al. (1991), slightly modified by Lécuyer et al. (1993) and adapted by Bernard et al. (2009) for small sample weights (3 mg). This protocol consists of the wet chemical isolation of phosphate ions from apatite using acid dissolution and anion-exchange resin and subsequent precipitation as Ag_3PO_4 crystals. For each sample, 3 mg of enamel powder was dissolved in 1 mL of 2 M HF overnight. CaF_2 residue was separated by centrifugation and the solution was neutralized by adding 1 mL of 2 M KOH; 1.5 mL of Amberlite™ anion-exchange resin was added to the solution to separate the PO_4^{3-} ions. After 24 hours, the solution was removed and the resin was eluted with 6 mL of 0.1 M NH_4NO_3. After four hours, 0.1 mL of NH_4OH and 3 mL of an ammoniacal solution of $AgNO_3$ were added and the samples were placed in a thermostated bath at 70°C for six hours, allowing the precipitation of Ag_3PO_4 crystals. Oxygen isotope compositions were
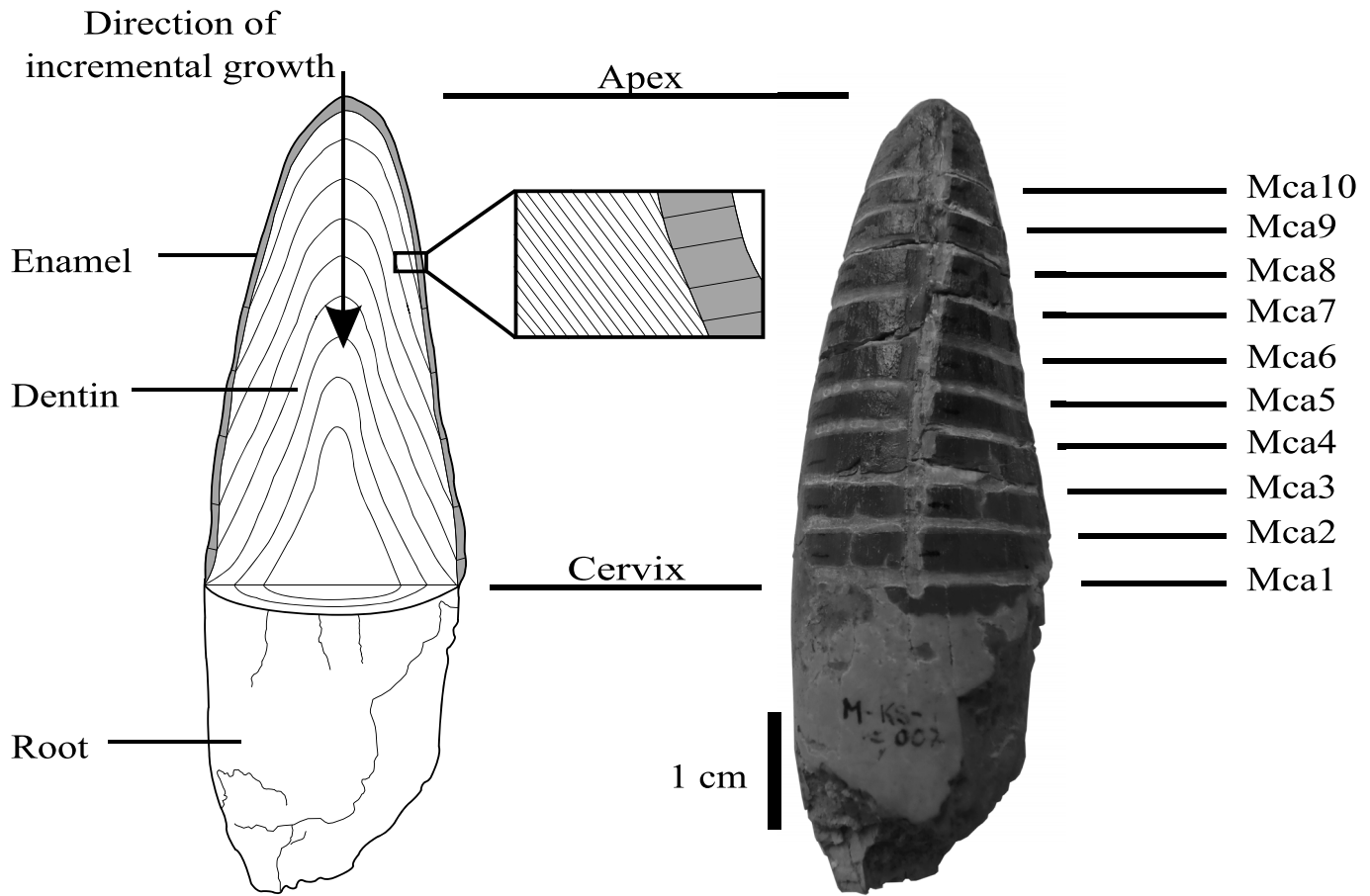
FIG. 2.—Schematic cross section (left) and picture (right) of the spinosaurid tooth (Mca) illustrating the sampling strategy adopted in this study. Dentin grows by cone-shaped increments adding up from the apex to the cervix of the crown. Each growth increment of dentin is associated with a circular band of enamel (see caption). The sampling strategy consisted in sampling enamel along inter-parallel bands perpendicularly to the major growth axis.

measured using a high temperature elemental analyzer (EA)-pyrolysis interfaced in continuous flow (CF) mode to an isotopic ratio mass spectrometer (IRMS) (EA-Py-CF-IRMS technique, Lécuyer et al. 2007; Fourel et al. 2011). For each sample, five aliquots of 350 to 400 μg of silver phosphate were mixed with 350–400 μg of pure powder graphite loaded in silver foil capsules. Pyrolysis was performed at 1450°C using a varioPYROcube[TM] Elemental Analyzer interfaced in continuous flow mode with an Isotopic Ratio Mass Spectrometer Isoprime[TM].

Measurements have been calibrated against the NBS120c standard (natural Miocene phosphorite from Florida). The value of NBS120c was fixed at 21.7‰ (V-SMOW) accordingly to Lécuyer et al. (1993) for correction of instrumental mass fractionation during CO isotopic analysis. Silver phosphate precipitated from the NBS120c standard was repeatedly analyzed ($\delta^{18}O_p$ = 21.7 $\pm$0.3‰, n = 16) along with the silver phosphate samples derived from the enamel to ensure that no fractionation occurred during the wet chemistry. The average standard deviation equals 0.26 $\pm$0.11‰.

RESULTS

Oxygen isotope compositions of enamel increments from the six theropod teeth are reported in Table 1. They range from 16.4‰ to 19.2‰ and from 19.2‰ to 22.0‰ for Moroccan *Spinosaurus* and *Carcharodontosaurus*, respectively. Thai teeth attributed to carcharodontosaurids have $\delta^{18}O_p$ values ranging from 13.5‰ to 17.1‰ and from 18.4‰ to 21.0‰. Mongolian and Russian tyrannosaurids have $\delta^{18}O_p$ values ranging from 11.1‰ to 14.0‰,

and from 10.3‰ to 11.9‰, respectively. For each tooth, the $\delta^{18}O_p$ values of enamel increments are plotted against their approximate time of growth (Fig. 3A, 4A, 5A, 6A) assuming a constant enamel growth rate of about 50 mm/yr (Erickson 1996a, 1996b; Straight et al. 2004). Each value corresponds to an enamel increment of 0.9 to 1.8 mm in width, corresponding to an isotopic composition averaged for about one to two weeks. Considering the analytical error to be about 0.3‰, observed intra-tooth variations ranging from 1.7‰ and 3.5‰ are assumed to be significant.

DISCUSSION

Preservation of the Original Oxygen Isotope Compositions

Secondary precipitation of apatite and isotopic exchange during microbially mediated reactions may alter the primary isotopic signal (Blake et al. 1997; Zazzo et al. 2004a, 2004b). However, apatite enamel has a low porosity and hence limited pore space for the precipitation of secondary minerals (Zazzo et al. 2004a, 2004b). Apatite enamel also has a very low organic matter content that makes it unsuitable for bacterial development. Furthermore, the pore size of dentin canals is probably too small for bacteria to penetrate and only cracks may create pathways to the heavily crystallized enamel (Kohn et al. 1999). Even on a geological time scale, inorganic isotopic exchange might not affect the oxygen isotope composition of phosphates as the covalent bond between oxygen and phosphate is very hard to break (Shemesh et al. 1983; Lécuyer et al. 1999).

TABLE 1.—*Phosphate oxygen isotope composition of theropod dinosaur enamel increments reported along with the taxon name, location, age and the distance of the increment from the apex.*

Sample	Taxon	Locality name	Country	Formation	Age	Distance from apex (mm)	$\delta^{18}O_p$ (‰ V-SMOW)
Mca1	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	45.5	17.5
Mca2	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	41.5	17.4
Mca3	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	37.5	18.0
Mca4	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	34.0	18.8
Mca5	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	29.0	17.8
Mca6	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	25.0	19.0
Mca7	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	21.0	18.9
Mca8	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	16.0	19.2
Mca9	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	12.5	17.5
Mca10	*Spinosaurus aegyptiacus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	9.0	16.4
Mcb1	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	35.5	20.6
Mcb2	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	31.0	19.5
Mcb3	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	27.5	21.0
Mcb4	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	23.5	22.0
Mcb5	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	19.5	20.2
Mcb6	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	15.0	21.0
Mcb7	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	10.5	20.4
Mcb8	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	6.5	19.2
Mcb9	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Ifezouane	early Cenomanian	3.0	20.7
Ta1	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	26.0	13.5
Ta2	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	23.5	14.2
Ta3	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	19.5	14.9
Ta4	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	15.5	14.4
Ta5	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	11.5	15.2
Ta6	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	7.5	16.1
Ta7	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	3.5	17.1
Ta8	Carcharodontosauridae indet.	Khok Pha Suam	Thailand	Khok Kruat	Aptian	0.0	16.9
Tb1	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	45.0	20.9
Tb2	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	40.5	21.0
Tb3	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	36.5	21.0
Tb4	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	32.0	21.0
Tb5	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	28.0	19.7
Tb6	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	24.0	20.6
Tb7	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	20.0	19.6
Tb8	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	16.0	18.4
Tb9	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	12.5	18.9
Tb10	Carcharodontosauridae indet.	Ban Sapan Hin	Thailand	Khok Kruat	Aptian	7.0	19.3
Mg1	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	46.0	13.0
Mg2	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	41.5	13.3
Mg3	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	38.0	13.7
Mg4	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	34.0	14.0
Mg5	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	29.5	13.5
Mg6	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	25.5	13.5
Mg7	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	21.5	13.6
Mg8	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	18.0	13.9
Mg9	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	14.0	13.5
Mg10	Tyrannosauridae indet.	Yagaan Khovil	Mongolia	Nemegt	Maastrichtian	10.0	11.1
R0	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	21.0	10.7
R1	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	19.0	11.0
R1a	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	17.0	10.7
R2	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	15.0	10.3
R2a	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	13.0	10.3
R3	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	11.0	10.7
R3a	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	9.0	11.1
R4	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	7.0	11.9
R4a	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	5.0	10.7
R5	Tyrannosauridae indet.	Kakanaut	Russia	Kakanaut	Maastrichtian	2.0	10.4

To date, only one method is available to demonstrate directly whether or not the pristine oxygen isotope compositions of fossil vertebrate phosphate has been altered by diagenetic processes. This method is based on triple oxygen analysis (^{16}O, ^{17}O, ^{18}O) of phosphate of vertebrate apatite (Gehler et al. 2011). However, considering the analytical uncertainty at the time this study was carried out, the validity of the method was restricted to small mammals and it remains to be tested for large endotherms like dinosaurs.

The present dataset consists of phosphate oxygen isotope composition of tooth enamel only. The main arguments supporting the preservation of the original oxygen isotope compositions are the significant intra-tooth variations in
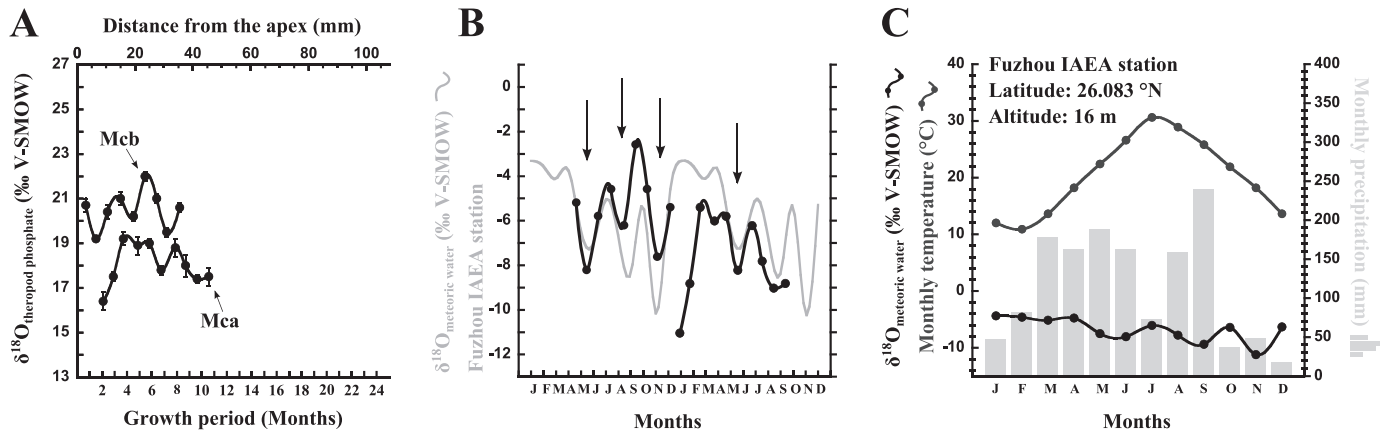
FIG. 3.—**A)** Oxygen isotope compositions of the Moroccan theropod samples 'Mca' and 'Mcb' enamel increments (black line with dots) are reported against their distance from the apex of the tooth, as well as their estimated duration of growth (in months). Vertical error-bars represent calculated standard deviations of 1σ. **B)** Same as A but the amplitude of the tooth profiles have been vertically stretched by 50%, which would correspond to a minimum dampening effect resulting from mineralization time and body water residence of large theropod dinosaurs (see discussion). Both tooth profiles have been arbitrarily fitted to the present-day meteoric water $\delta^{18}O_{mw}$ annual profile recorded by the Chinese IAEA/WMO station at Fuzhou (light gray line). Vertical arrows point to possible peaks of precipitation periods. **C)** Present-day monthly precipitation (gray bars), monthly temperatures (dark gray line with dots) and $\delta^{18}O_{mw}$ values of meteoric water (black line with dots) recorded at the Chinese IAEA/WMO station at Fuzhou.

$\delta^{18}O_p$ values along the growth axis that mimic seasonal patterns that can be observed nowadays under various climate regimes. If isotopic re-equilibration with diagenetic fluids occurred, it would have homogenized oxygen isotope compositions of all enamel increments within each tooth. Furthermore, four of these teeth (Mca, Mcb; Ta, Tb) come from deposits for which Amiot et al. (2009) and Amiot et al. (2010b) have demonstrated the preservation of the original oxygen isotope compositions of phosphatic remains based on the observation of expected $\delta^{18}O_p$ value differences between animals having various ecologies and physiologies (e.g., endothermic and terrestrial dinosaurs vs. ectothermic and semi-aquatic crocodilians and turtles). In this case, diagenetic alteration would have homogenized oxygen isotope compositions of all phosphatic remains and erased these biological differences (Lécuyer et al. 2003).

Based on these considerations, we assume that the $\delta^{18}O_p$ values of analyzed theropod teeth have at least partly preserved their original isotope compositions, and will be interpreted in terms of seasonal variations of the living environment of these dinosaurs.

Influences of Physiology and Ecology

Theropods were homeothermic vertebrates (Barrick and Showers 1994; Fricke and Rogers 2000; Amiot et al. 2006), which means that they maintained a relatively constant body temperature. Thus, the $\delta^{18}O_p$ value of their enamel is linearly related to the oxygen isotope composition of body water ($\delta^{18}O_{bw}$). As theropods were carnivorous, their body water came from ingested waters, most of them being surface waters, with a minor contribution of body water derived from their prey (Kohn 1996). It is worth noting that Kohn and McKay (2012) have observed that oxygen isotope compositions of apatite of fossil carnivores were systematically higher (4 to 5‰) than those of the associated herbivores. They tentatively explained this enrichment by either an unknown physiological
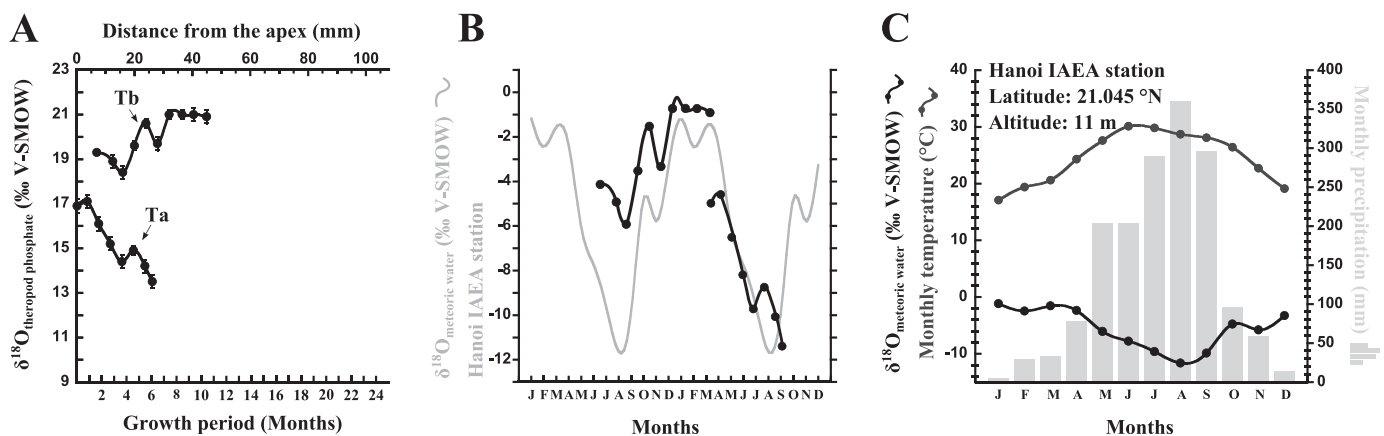

FIG. 4.—**A)** Oxygen isotope compositions of the Thai theropod samples 'Ta' and 'Tb' enamel increments (black line with dots) are reported against their distance from the apex of the tooth, as well as their estimated duration of growth (in months). Vertical error-bars represent calculated standard deviations of 1σ. **B)** Same as A but the amplitude of the tooth profiles have been vertically stretched by 50%, which would correspond to a minimum dampening effect resulting from mineralization time and body water residence of large theropod dinosaurs (see discussion). Both tooth profiles have been arbitrarily fitted to the present-day meteoric water $\delta^{18}O_{mw}$ annual profile recorded by the Vietnamese IAEA/WMO station at Hanoi (light gray line). **C)** Present-day monthly precipitation (gray bars), monthly temperatures (dark gray line with dots) and $\delta^{18}O_{mw}$ values of meteoric water (black line with dots) recorded at the Vietnamese IAEA/WMO station at Hanoi.
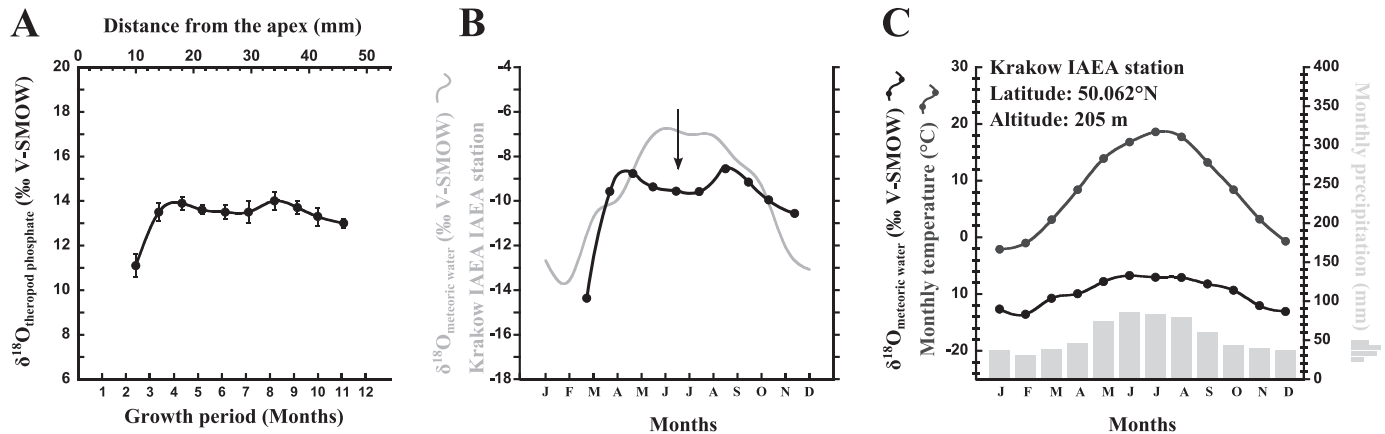
FIG. 5.—**A**) Oxygen isotope compositions of the Mongolian theropod sample 'Mg' enamel increments (black line with dots) are reported against its distance from the apex of the tooth, as well as its estimated duration of growth (in months). Vertical error-bars represent calculated standard deviations of 1σ. **B**) Same as A but the amplitude of the tooth profile has been vertically stretched by 50%, which would correspond to a minimum dampening effect resulting from mineralization time and body water residence of large theropod dinosaurs (see discussion). The tooth profile has been arbitrarily fitted to the present-day meteoric water $\delta^{18}O_{mw}$ annual profile recorded by the Polish IAEA/WMO station at Krakow (light gray line). The black arrow points to a drop in ingested $\delta^{18}O_{mw}$ values possibly due to the amount effect of summer rain. **C**) Present-day monthly precipitation (gray bars), monthly temperatures (dark gray line with dots) and $\delta^{18}O_{mw}$ values (black line with dots) recorded at the Polish IAEA/WMO station at Krakow.

effect or a greater incorporation of ^{18}O from food water or proteins of their prey items. Assuming that the contribution of prey water consumption is constant, this isotopic enrichment should not distort the intra-tooth isotopic variations. Thus, the $\delta^{18}O_p$ values of theropods reflect the $\delta^{18}O_w$ values of local environmental waters, assumed to be meteoric waters or derived from them.

Both enamel mineralization processes and body water residence time in large mammals have been recognized to dampen the oxygen isotope signal (Passey and Cerling 2002; Kohn 2004).

During the process of mineralization, the initial volume of enamel deposited is not fully mineralized and has a high protein content. Progressively, proteins are degraded and the mineral content increases. Thus, during the time it takes for the enamel to achieve maturation, it may incorporate oxygen from body water, which results from a time-averaged oxygen isotope composition of environmental water ingested by the animal. Moreover, water residence time in an animal's body increases with increasing body mass, thus affecting the resulting oxygen isotope composition of body water and apatite by dampening the environmental seasonal signal.

It is noteworthy that mammalian and reptilian enamels have differences and similarities in mineralization processes. For instance, in the scincid lizard *Chalcides viridanus*, ameloblast Tomes' processes (present in mammals) are lacking and enamel prisms do not form (Delgado et al. 2005). On the other hand, the maturation process, at least in *Chalcides viridanus*, progresses from the tip towards the base of the tooth similarly to that of mammals. Because no information about the duration of the maturation process is available, the related dampening effect is difficult to estimate. In theropods, the enamel is rather thin (~ 150 μm; Sander 1999) compared to that of large mammals. This difference of thickness could be associated with shorter duration of maturation for reptilian enamel, reducing the dampening as a result.

Kohn (2004) proposed that the dampening effect in large mammals such as bovids and horses should range between 40% and 70%. Bernard et al. (2009) have modeled the dampening effect for Pleistocene bison (*Bison priscus*) based on oxygen isotope analysis and predicted a dampening factor of about 50 to 55% for these 700 to 800 kg animals. In the case of theropods, this dampening is unknown. All analyzed teeth belong to large theropods of similar sizes, weighing between one to a few tons according to various estimates (e.g., Therrien and Henderson 2007). From the above-mentioned considerations, large theropod dinosaurs are assumed to have a shorter maturation time leading to reduced dampening effect, but a body water residence time larger than that

of modern large mammals, thus increasing the resulting dampening effect. Because neither effect can be quantified, a dampening of about 50% is assumed. We emphasize that the general seasonal pattern in terms of variations is not modified by this choice, but only the amplitude. Therefore, it is assumed that the measured amplitude of variations in theropod $\delta^{18}O_p$ values reflect seasonal variations of environmental water $\delta^{18}O_w$ values with a dampening of at least 50%. Figures 3B, 4B, 5B, 6B illustrate the possible restored amplitude in $\delta^{18}O$ values of waters ingested by theropods assuming a dampening effect of 50%.

It is also noteworthy that the $\delta^{18}O_p$ profile of the Moroccan carcharodontosaurid tooth 'Mcb' has an average $\delta^{18}O_p$ value more positive than that of the spinosaur tooth 'Mca'. This is likely the result of a distinct ecology, the spinosaur being semi-aquatic (Amiot et al. 2010a; Ibrahim et al. 2014), hence having enhanced water fluxes flushing through the body and being subjected to less water loss through evaporation than the apparently fully terrestrial carcharodontosaur. As a result, the spinosaur body water and apatite phosphate were less ^{18}O-enriched than those of the carcharodontosaur (Amiot et al. 2010a).

Climate Seasonality Recorded by Theropod Teeth

Global paleogeography during the Cretaceous (Fig. 1), and partial pressure of atmospheric CO_2 (up to 1000 ppm according to Franks et al. 2014) were different from those of today, thus affecting the global water cycle and spatial distribution of marine and terrestrial surface temperatures (e.g., Ufnar et al. 2002; Amiot et al. 2004; Pucéat et al. 2007; Suarez et al. 2011). In this context, although it is likely that global Cretaceous climate modes may have had no modern equivalent, seasonal patterns of local temperature and precipitation do have present-day analogues. Keeping this in mind, the oxygen isotope profiles of theropod teeth were qualitatively compared to present-day records of seasonal variations in $\delta^{18}O_{mw}$ values provided by IAEA-WMO stations accessible via the Global Network of Isotopes in Precipitation (GNIP) database (Figs. 3C, 4C, 5C, 6C; IAEA/WMO 2015), assuming that intra-tooth variations in theropod $\delta^{18}O_p$ values reflect intra-annual fluctuations in meteoric water $\delta^{18}O_{mw}$ values. For consistency, stations at latitudes similar to the paleolatitudes of Cretaceous localities have been considered for comparison. It should be emphasized that each analyzed tooth does not record a complete seasonal pattern.
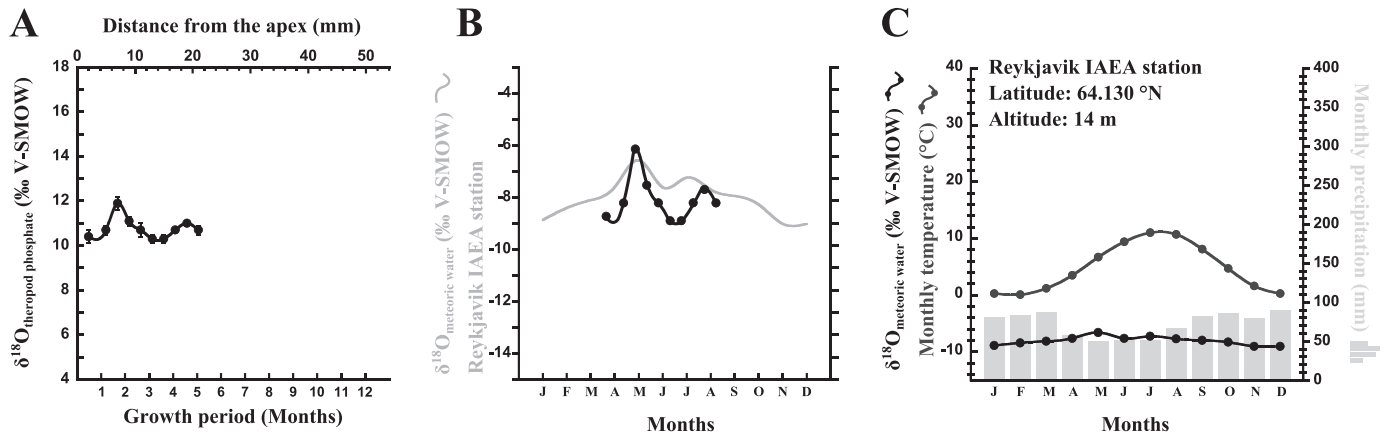
Fig. 6.—**A)** Oxygen isotope compositions of the Russian theropod sample 'R' enamel increments (black line with dots) are reported against its distance from the apex of the tooth, as well as its estimated duration of growth (in months). Vertical error-bars represent calculated standard deviations of 1σ. **B)** Same as A but the amplitude of the tooth profile has been vertically stretched by 50%, which would correspond to a minimum dampening effect resulting from mineralization time and body water residence of large theropod dinosaurs (see discussion). The tooth profile has been arbitrarily fitted to the present-day $\delta^{18}O_{mw}$ annual profile recorded by the Icelandic IAEA/WMO station at Reykjavik (light gray line). **C)** Present-day monthly precipitation (gray bars), monthly temperatures (dark gray line with dots) and $\delta^{18}O_{mw}$ values of meteoric water (black line with dots) recorded at the Icelandic IAEA/WMO station at Reykjavik.

$\delta^{18}O_p$ profiles of theropod teeth 'Mca' and 'Mcb' from Morocco appear to have spanned about nine and eight months of seasonal record, respectively (Fig. 3A). They are characterized by similar amplitudes of about 3‰, although the average $\delta^{18}O_p$ value of the carcharodontosaur tooth 'Mcb' is more positive than that of the spinosaur tooth 'Mca' as a result of different ecologies (see previous section). Both tooth profiles show several minima and maxima that are comparable to the $\delta^{18}O_{mw}$ values of present-day meteoric waters from regions subjected to a large amount of seasonal precipitation, such as that recorded in the East Asian station of Fuzhou, People's Republic of China (Fig. 3C). Moreover, Amiot et al. (2010b) estimated an average $\delta^{18}O_{mw}$ value of $-5.0 \pm 1.0‰$ for the locality of Khetitila Shrira from crocodile and turtle $\delta^{18}O_p$ values. This value falls within the range of variations of present-day $\delta^{18}O_{mw}$ values of meteoric water ($-3‰$ to $-10‰$; Fig. 3B) recorded by the station of Fuzhou and which is close to the mean annual value of $-5.5‰$. Under such climates, episodes of heavy rain during spring and summer lead to more negative $\delta^{18}O_{mw}$ values (the so-called amount effect). Similarities between the seasonal variations in $\delta^{18}O_{mw}$ values at Fuzhou and the raw (Fig. 3A) and "dampening-effect corrected" (Fig. 3B) $\delta^{18}O_p$ profiles of theropod teeth suggest that Moroccan paleoenvironments during the early Cenomanian were far from being as arid as traditionally viewed, but instead at least temporarily highly wet. Multiple and rapid (two to three month) fluctuations in the $\delta^{18}O_w$ values of local waters suggest that the precipitation regime was episodic rather than seasonal, as previously proposed by Russell and Paesler (2003).

The $\delta^{18}O_p$ profiles of Thai teeth 'Ta' and 'Tb' integrate about seven and nine months of seasonal record, respectively (Fig. 4A). They show large amplitudes in $\delta^{18}O_p$ values between 2.6‰ and 3.6‰, with 'Tb' having $\delta^{18}O_p$ values significantly higher than 'Ta'. Considering that these two teeth belong to individuals from the same taxon and were recovered from the same geological formation but from distinct localities (Khok Pha Suam and Ban Sapan Hin), the differences in the ranges of $\delta^{18}O_p$ values are probably the results of climate fluctuations on larger time scales (centennial or millennial). It is also possible that the two teeth reflect large intra-annual amplitudes of the local $\delta^{18}O_{mw}$ values such as those experienced today in monsoonal climates such as those of Southeast Asia. The present-day IAEA station of Hanoi, Vietnam (Fig. 4C), shows a seasonal $\delta^{18}O_{mw}$ profile compatible with those recorded by the two teeth 'Ta' and 'Tb' (Fig. 4A, 4B). Moreover, Amiot et al. (2009) estimated an average $\delta^{18}O_{mw}$ value of $-6.7‰$ from crocodile and turtle $\delta^{18}O_p$ values. This value falls within the range of variations of present-day $\delta^{18}O_{mw}$ values

of meteoric water ($-1‰$ to $-12‰$; Fig. 4B) recorded by the station at Hanoi and which is close to the mean annual value of $-5.7‰$. Under these climate conditions, $\delta^{18}O_{mw}$ values result from the large amounts of spring to summer precipitation corresponding to the summer monsoon. There is no clear consensus on climatic conditions that prevailed in northeastern Thailand during the deposition of the Khok Kruat Formation. It is, however, agreed that the depositional environment was a large flood plain with meandering river systems containing paleosols and silcretes indicative of aridity (Meesook 2000, 2011). The combination of both aridity markers and large hydrologic systems suggest that local climate was seasonal. Moreover, climates subjected to such large amounts of seasonal precipitation have previously been proposed for the Aptian Khok Kruat Formation of Thailand on the basis of both oxygen and carbon isotope compositions of vertebrate apatites (Amiot et al. 2009, 2015).

The $\delta^{18}O_p$ profile of theropod tooth 'Mg' from Mongolia spans about eight months of seasonal record and shows a rapid rise from a low $\delta^{18}O_p$ value of 11.1‰ to higher values fluctuating between 13.5‰ and 14.0‰ over about five to six months, and then drops again (Fig. 5A). Considering the continental and mid-paleolatitude location of the sedimentary deposit where the tooth was recovered, it is likely that the seasonal fluctuation in $\delta^{18}O_{mw}$ values was mainly controlled by air temperature. Similar seasonality prevails today in areas experiencing continental climates. For example, the IAEA station of Krakow, Poland, records air temperature fluctuations that are similarly correlated to $\delta^{18}O_{mw}$ fluctuations (Fig. 5C). It is noteworthy that during the summer, a high amount of local precipitation, in the form of summer storms can be associated with a slight drop in $\delta^{18}O_{mw}$ values as already observed in several studies (Higgins and MacFadden 2004; Straight et al. 2004; Bernard et al. 2009). This effect could account for the ~0.5‰ drop in $\delta^{18}O_p$ values observed within the five to six months of $\delta^{18}O_p$ maxima (Fig. 5A) that may correspond to a larger drop of at least 1‰ considering the dampening effect due to body water residence time (Fig. 5B). High amounts of seasonal (summer?) precipitation are compatible with associated sedimentological criteria such as well-developed fluvial channels, mature caliche paleosols, as well as the lack of eolian dunes, which indicate seasonal climate (Jerzykiewicz and Russel, 1991).

The $\delta^{18}O_p$ profile of the theropod tooth 'R' from Russia spans about five months and shows the lowest amplitude in $\delta^{18}O_p$ values (1.6‰; Fig. 6A). During the Maastrichtian, the Kakanaut Formation was deposited in Far East Russia in the vicinity of the Pacific paleo-coast, at a paleolatitude of about 75°N (Fig. 1C). Similar patterns can be observed today in high-latitude coastal

regions as illustrated by the climate mode of the IAEA station of Reykjavik in Iceland (Fig. 6C). In these regions, the influence of the warm North Atlantic Current that continues the Gulf Stream brings warm waters from low latitudes. As a result, intra-annual air temperature variations are weakened, leading to low seasonal amplitudes in $\delta^{18}O_{mw}$ values (Fig. 6C). Conditions of comparable amplitude may have prevailed along the Pacific coast of northeastern Russia during the deposition of the Kakanaut Formation. Indeed, enhanced heat transfer toward polar regions through oceanic currents resulted in a globally warm Arctic Ocean as evidenced by paleobotanical studies (Herman and Spicer 1996; Spicer and Herman 2010). Moreover, it has been proposed that the Kakanaut paleoenvironments experienced low seasonality with 1500 to 1700 mm of annual precipitation equally distributed over the year and 10°C of mean annual temperature variation with temperatures as low as 3°C for the colder months (Golovneva 2000). It is noteworthy that the contemporaneous tooth from the Nemegt Formation of Mongolia, situated at a lower paleolatitude (~ 45°N), records a higher amplitude in $\delta^{18}O_p$ values than the Russian tooth situated at a higher paleolatitude (~ 75°N). This counter-intuitive observation may be due to the effect of continentality that significantly affects the seasonal amplitude of oxygen isotope composition of local meteoric waters (e.g., Dansgaard 1964). However, it cannot be excluded that the low amplitude in $\delta^{18}O_p$ values measured in the theropod tooth from the Kakanaut Formation could be the result of migratory behavior within dinosaur faunas, which is known to dampen intra-tooth oxygen isotope variations (e.g., Britton et al. 2009).

CONCLUSION

Oxygen isotope compositions of phosphate have been analyzed in increments sampled along the major growth axis of six large theropod dinosaur teeth. According to previously estimated theropod tooth growth rates, the studied teeth took between six and nine months to grow. Significant intra-tooth variation in $\delta^{18}O_p$ values are interpreted as reflecting seasonal variation in local surface waters. For the four Cretaceous localities from which the teeth have been recovered, different local climate patterns comparable to extant ones have been recognized. Theropod teeth from the early Cenomanian Ifezouane Formation of Morocco and from the Aptian Khok Kruat Formation of Thailand have $\delta^{18}O_p$ patterns reflecting warm climates subjected to large amounts of seasonal precipitation. Such climate seasonality can be observed today in Southeast Asia, for instance in South China or in Vietnam. The tyrannosaurid tooth recovered from the Maastrichtian Nemegt Formation of Mongolia has a $\delta^{18}O_p$ pattern most likely reflecting seasonal variation in local air temperatures in relation to its mid-latitude and continental location. Similar patterns occur today in regions far inland such as Central Europe. Finally, the tyrannosaurid tooth recovered from the Maastrichtian Kakanaut Formation of Far East Siberia shows a weaker intra-tooth $\delta^{18}O_p$ variation pattern despite its high paleolatitude (about 75°N). This might be due to the proximity of the fossil locality to the Pacific Ocean. Maastrichtian oceanic current circulation may have weakened the seasonal amplitude of air temperatures in coastal areas including the Kakanaut locality. High-latitude islands and coastal regions of the North Atlantic such as Iceland or west Norway experience similar amplitudes in air temperature and oxygen isotope composition of rain waters, buffered by the North Atlantic current. However, we consider all these interpretations cautiously as they rely on only one to two teeth analyzed per locality. More teeth from the same localities should be analyzed to assess the inter-annual variability along with inter-specific variability of oxygen isotope composition in order to draw firm conclusions. Nonetheless, following the previous attempt made by Straight et al. (2004), this study highlights the potential of using phosphate oxygen isotope composition of enamel from large theropod teeth to retrieve seasonal patterns of climate parameters for terrestrial environments during the Mesozoic. One further step would be to better constrain the oxygen isotope fractionation between theropod tooth phosphate and water, as well as physiological aspects of large theropod dinosaurs weighing a few tons, such as body water residence time. This would ultimately make it possible to quantitatively estimate seasonal amplitudes of local $\delta^{18}O_{mw}$ values and estimate intra-annual variations in air temperatures or amounts of precipitations.

Reconstructed seasonal variations in Cretaceous terrestrial climates present in this and previous studies reveal significant fluctuations from the intra-annual to the million year scale contrasting with the traditional view of a Mesozoic Era dominated by equable climatic conditions. Under such conditions, it is not surprising that dinosaurs, which benefited from sustained metabolic activity and thermoregulation (homeothermy), colonized all terrestrial environments from equatorial to polar regions and developed either adaptive or behavioral strategies to withstand local or temporal climate extremes that may have prevailed during the Mesozoic.

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