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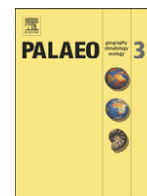
Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: Ecological and environmental significance

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ABSTRACT

In order to investigate mid-Cretaceous terrestrial climates of low paleolatitudes, Moroccan, Tunisian and Brazilian vertebrate apatites have been analyzed for their oxygen and carbon isotope compositions of phosphates ($\delta^{18}O_p$) and carbonates ($\delta^{18}O_c$, $\delta^{13}C_c$). At each site, coexisting theropod dinosaurs, titanosaurid sauropods, pterosaurs, crocodilians, turtles and fish have distinct $\delta^{18}O_p$ and $\delta^{13}C_c$ values reflecting their ecologies, diets and foraging environments. Oxygen isotope compositions of surface waters ($\delta^{18}O_w$) estimated from turtle and crocodile $\delta^{18}O_p$ values range from -5.0 ± 1.0‰ to -2.4 ± 1.0‰, which do not differ from mean annual rainwater values occurring today under inter-tropical sub-arid to arid climates. High water temperatures ranging from 21 ± 6 °C to 34 ± 2 °C deduced from fish $\delta^{18}O_p$ values are in agreement with those published for mid-Cretaceous low latitudes. Temporary or seasonal droughts are inferred from high $\delta^{18}O_p$ values of lungfish teeth, even though lower reptile $\delta^{18}O_p$ values suggest the use of distinct and most likely larger or regularly renewed bodies of water. Environmental conditions of the studied low latitude regions during the Aptian–Cenomanian interval were somewhat similar to those experienced today under semi-arid to arid tropical or equatorial climates, but with higher mean surface temperatures than present-day ones.

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1. Introduction

During the Cretaceous period (-135 to -65 Ma), important thermal fluctuations have been identified with an optimum during the mid-Cretaceous (Albian–Turonian), and cold episodes characterized by near freezing to freezing conditions in polar regions (e.g. Frakes, 1999; Price, 1999; Pucéat et al., 2003; Amiot et al., 2004). Elevated partial pressure of atmospheric CO_2, changes in oceanic circulation patterns in relation to plate motion and high sea levels most likely accounted for these peculiar climatic conditions (Haq et al., 1988; Barron et al., 1995; Berner and Kothavala, 2001). During the mid-Cretaceous thermal optimum, low equator-to-pole thermal gradient

(Huber et al., 1995), very high temperatures at low latitudes (Schouten et al., 2003) and episodically extreme climatic conditions in Saharan environments have been proposed (Russell and Paesler, 2003). According to these authors, mid-Cretaceous Saharan environments were characterized by a decline in productivity of terrestrial vegetation inferred from the relatively small size of herbivorous dinosaurs, highly productive waters deduced from the large size of fish and crocodilians, apparently a low vertebrate diversity and episodic climatic extremes taking mid-Cretaceous Saharan ecosystems near tolerance limits. If mid-Cretaceous Saharan ecosystems suffered such conditions, it raises the question of how the rather diverse and complex faunal associations shared water and food resources. Therefore, we analyzed the oxygen and carbon isotope compositions of Aptian to Cenomanian freshwater reptiles and fish from two North African and two Brazilian deposits in order to investigate climatic conditions as well as the habitats and foraging preferences of vertebrate faunas.

The first step consists in estimating mean air temperatures where dinosaurs, non-dinosaurian reptiles and fish coexisted. According to the studies performed by Barrick et al. (1999) and Amiot et al. (2007),

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the oxygen isotope composition of ambient waters can be inferred from that of turtle and crocodile apatite phosphate, which in turn can be used to calculate water temperature when combined to the isotopic composition of coexisting fish phosphate according to fractionation equations determined by Longinelli and Nuti (1973) and Kolodny et al. (1983). These water temperatures can be further compared to air temperatures estimated from the oxygen isotope compositions of ambient freshwaters that indirectly reflect the compositions of meteoric waters. Linked to the climate context, the strategies of terrestrial vertebrates for feeding on natural resources can be approached by the use of the carbon isotope composition of apatite carbonate that reflects the isotopic composition of food (e.g. Sillen and Lee-Thorp, 1994; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005 ; Fricke and Pearson, 2008; Tütken, in press).

1.1. Studied areas

Four deposits from inter-tropical paleolatitudes are considered (Fig. 1). Most samples were recovered from Moroccan deposits belonging to the lower Kem Kem beds (or Ifezouane Formation) in the Tafilalt region where extensive field exploration and collecting were carried out. This Formation, dated as Lower Cenomanian, represents fluvial deposits in deltaic environments (see Cavin et al. (2010) for a complete review). The other North African studied deposit is the Chenini Member of the Aïn Guettar Formation of Tunisia from which oxygen isotope compositions of phosphatic remains have been published (Amiot et al., 2006). The Chenini Member, dated as Upper Aptian to Lower Albian (Le Loeuff et al., 2010), also represents fluvio–deltaic environments with possibly mixed freshwater and marine influences (Anderson et al., 2007). Two sites were studied in Brazil, which are the locality of Laje do Coringa, constituted by estuarine deposits belonging to the Alcântara Formation of Lower Cenomanian age (Pedrão et al., 1993; Kellner et al., 2009), and the Araripe Basin from which a few samples come from the Crato and Romualdo formations, dated as Aptian to Albian (Pons et al., 1991; Fara et al., 2005).

1.2. Oxygen isotope composition of vertebrate apatites

The oxygen isotope compositions of apatite phosphate ($\delta^{18}O_p$) and carbonate ($\delta^{18}O_c$) from vertebrate bones, teeth and fish scales are a function of the $\delta^{18}O_{bw}$ value of the animal's body water as well as of its body temperature (Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984). The $\delta^{18}O_{bw}$ value is related to the $\delta^{18}O_w$ value of ingested water and to the animals' ecology and physiology. For most continental vertebrates, the main source of ingested oxygen is drinking or plant

water, which is meteoric water or water derived from it (D'Angela and Longinelli, 1990; Cormie et al., 1994; Kohn et al., 1996; Straight et al., 2004). As the $\delta^{18}O_w$ value of meteoric water depends on climatic parameters such as air temperature, humidity and amount of precipitation (Dansgaard, 1964; Gat, 1996; Grafenstein et al., 1996; Fricke and O'Neil, 1999), vertebrates thus indirectly record in their phosphatic tissues the climatic conditions of their living environment. It is noteworthy that the $\delta^{18}O_w$ value of surface waters can differ from that of precipitations due to local processes such as evaporation, mixing with ground waters or with rivers draining catchments with different water oxygen isotope compositions. Such processes complicate the interpretations in terms of climatic reconstructions. Physiological adaptations to a specific habitat (aquatic, semi-aquatic or terrestrial) also affect the $\delta^{18}O_{bw}$ value by controlling the magnitude of body input and output oxygen fluxes, some of them being associated with oxygen isotopic fractionations between apatite and water (Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996). From living and fossil communities of mammals, reptiles and fish, it has been observed that differences in the range of $\delta^{18}O_p$ values or in some cases differences in mean $\delta^{18}O_p$ values between coexisting aquatic or semi-aquatic vertebrates and terrestrial ones were related to their habitat use (Fricke and Rogers, 2000; Clementz and Koch, 2001; Clementz et al., 2003; Amiot et al., 2006, 2010). Ecological specificities such as plant–water use among herbivorous communities also affect the $\delta^{18}O_p$ value of vertebrates. Indeed, large differences in $\delta^{18}O_p$ values have been observed between coexisting herbivorous mammals that drink surface waters and those that only rely on water in plants, usually enriched in ^{18}O by several per mils relative to surface waters (Kohn et al., 1996). The $\delta^{18}O_w$ values of ingested water can be estimated from $\delta^{18}O_p$ values of fish, turtles and crocodilians by using PO_4–water fractionation equations established for extant species (e.g. Kolodny et al., 1983; Barrick et al., 1999; Amiot et al., 2007), the applicability of these equations to Mesozoic faunas having been tested successfully (Barrick et al., 1999; Amiot et al., 2004, 2009).

1.3. Carbon isotope composition of vertebrate apatites

Carbon isotope compositions of apatite from air-breathing vertebrates primarily reflect animal diets, with a ^{13}C-enrichment relative to ^{12}C that varies among animals. Indeed, ^{13}C-enrichments between apatite and diet of herbivorous and carnivorous terrestrial mammals were estimated in the range 10–15‰ and close to 9‰, respectively (Lee-Thorp et al., 1989; Tieszen and Fagre, 1993; Sillen and Lee-Thorp, 1994; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005). Similar ^{13}C-enrichments have been observed between reptile apatite and diet, namely 8–9‰ and 12‰ for carnivorous and herbivorous
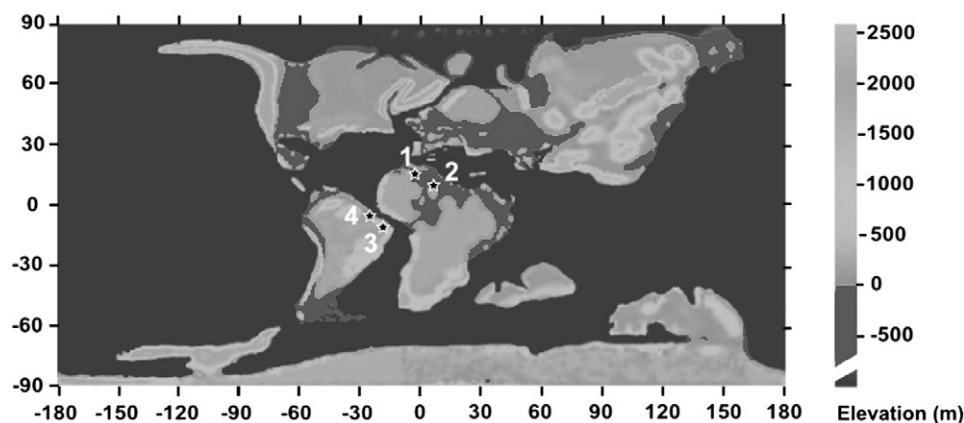

Fig. 1. Paleogeographic map of the mid-Cretaceous showing the geographic position of studied localities. Numbers refer to the following deposits: 1: Ifezouane Formation, Morocco; 2: Chenini Member, Tunisia; 3: Crato and Romualdo formations, Brazil; 4: Alcântara Formation, Brazil.

marine turtles, respectively, and about 9‰ estimated for crocodilians (Stanton, 2006). Higher ^{13}C-enrichment of 16‰ has been determined for large non flying birds (Von Schirnding et al., 1982; Johnson et al., 1998). According to some studies, variations in ^{13}C-enrichment between apatite and diet are primarily a result of differences in digestive physiology, rather than differences in the magnitude of fractionation between mineral and body fluid (Passey et al., 2005). In aquatic environments, the relationship between fish carbonate and diet δ^{13}C values is complicated as primary producers constituting the base of fish food webs have δ^{13}C values that can vary due to differences in productivity, dissolved CO_2 concentration, bicarbonate utilization, as well as variations in the mixing of atmospheric and respired CO_2 under different flow conditions (see Clementz and Koch (2001) for a review). Moreover, for some fish carbonate biogenic components such as otoliths, a substantial amount, if not all, of the carbon may also be derived from dissolved inorganic carbon (DIC) of the ambient water (McConnaughey et al., 1997; Thorrold et al., 1997). However, ^{13}C-enrichments of 10–16‰ between carbonate and diet have been observed for carnivorous sharks (Rau et al., 1983; Vennemann et al., 2001). Given the similarity with terrestrial mammals ^{13}C-enrichments between carbonate and diet, it was suggested that the carbon in the carbonate of shark teeth is compatible with a predominantly dietary source of carbon (Vennemann et al., 2001).

2. Sample collection

One hundred and one apatite remains consisting of theropod dinosaur teeth, titanosaurid sauropod teeth, pterosaur teeth, crocodilian teeth and osteoderms, turtle bony plates and fish teeth and scales, were recovered from two Brazilian (Araripe Basin, Crato and Romualdo formations, and Laje Do Coringa, Alcântara Formation) and six Moroccan localities (Tafilalt region, Kem Kem beds). Samples were collected as isolated specimens, cleaned and analyzed for their oxygen and carbon isotope compositions of phosphate and carbonate. Published $\delta^{18}O_p$ values of similar vertebrates remains coming from Tunisia (Chenini Member), Morocco (Kem Kem beds) and Brazil (Alcântara Formation) were added to the dataset (Amiot et al., 2006, 2010). Except for small teeth and scales for which bulk analyses were performed, enamel was preferentially selected. As reptile teeth are continuously replaced and take several months to grow (Erickson, 1996a,b), they can record seasonal variations in the $\delta^{18}O_w$ values of ingested surface water. In order to retrieve mean annual values of local waters, enamel was sampled from the base to the apex of each tooth and several teeth from each locality were analyzed. For each sample, the most mineralized apatite part was selected, namely reptile tooth enamel, dense bone layers from turtle shells and crocodilian osteoderms, and ganoine (an enamel-like apatitic tissue) covering the surface of fish scales. Sample description is reported in Table 1.

Calculation of past geographic coordinates of the sampling sites was made using the Apparent Polar Wander Path (APWP) of South American and African continents calculated by Besse and Courtillot (2002). This APWP was constructed using a selection of the best paleomagnetic poles available for South America and Africa that were averaged over 20-My time windows. Paleolatitudes and associated uncertainties are shown in Table 2. These uncertainties depend on the quality and number of magnetic poles used to build the APWP.

3. Analytical techniques

Measurements of oxygen isotope compositions of apatite phosphate consist in isolating the phosphate ions using acid dissolution and anion-exchange resin, according to a protocol derived from the original method published by Crowson et al. (1991) and slightly modified by Lécuyer et al. (1993). Silver phosphate was quantitatively precipitated in a thermostatic bath set at a temperature of 70 °C. After filtration, washing with double deionised water, and drying at 50 °C, 15 mg of Ag_3PO_4 was mixed with 0.8 mg of pure powder graphite. $^{18}O/^{16}O$ ratios were measured by reducing silver phosphates to CO_2 using graphite reagent (O'Neil et al., 1994; Lécuyer et al., 1998). Samples were weighed into tin reaction capsules and loaded into quartz tubes and degassed for 30 min at 80 °C under vacuum. Each sample was heated at 1100 °C for 1 min to promote the redox reaction. The CO_2 produced was directly trapped in liquid nitrogen to avoid any kind of isotopic reaction with quartz at high temperature. CO_2 was then analyzed with a Thermo-Finnigan MAT253 mass spectrometer at the Institute of Geology and Geophysics, Chinese Academy of Sciences. Isotopic compositions are quoted in the standard δ notation relative to V-SMOW. Silver phosphate precipitated from standard NBS120c (natural Miocene phosphorite from Florida) was repeatedly analyzed ($\delta^{18}O = 21.7 \pm 0.2$‰; n = 31) along with the silver phosphate samples derived from the fossil vertebrate remains.

For the oxygen and carbon isotope analysis of carbonate, about 10 mg of enamel, dentine or bone powder was pre-treated according to the procedure of Koch et al. (1997). Powders were washed with a 2% NaOCl solution to remove organic matter, followed by a 0.1 M acetic acid solution to remove diagenetic carbonates. The powder/solution ratio was kept constant to 0.04 g mL^{-1} for both treatments. Each treatment lasted for 24 h and samples were rinsed five times with distilled water. From the pre-treated powders a 2 mg aliquot was analyzed using a Thermo Finnigan Gasbench II following a procedure adapted after Spoetl and Vennemann (2003). Five drops of 100% orthophosphoric acid were added allowing the samples to react at 72 °C for 1 h under a He atmosphere before starting 10 measurement cycles of the isotopic composition of the produced CO_2 with a Finnigan MAT 253 continuous flow isotope ratio mass spectrometer. The measured carbon and oxygen isotopic compositions were normalized relative to the NBS-19 calcite standard. The normalization incorporates the CO_2-carbonate acid fractionation factor for calcite. Reproducibility for the carbon and oxygen isotopic compositions of apatite carbonate is better than ± 0.1‰ and ± 0.2‰, respectively. The carbon and oxygen isotopic compositions are expressed as δ-values relative to V-PDB for carbon and V-SMOW for oxygen.

4. Results

Oxygen and carbon isotope measurements of apatite phosphate and carbonate are reported in Table 1. The whole dataset ranges from 16.5‰ to 22.9‰ in $\delta^{18}O_p$ values, from 21.5‰ to 29.3‰ in $\delta^{18}O_c$ values and from −14.0‰ to −1.7‰ in $\delta^{13}C_c$ values. For each of the 9 localities, mean $\delta^{18}O_p$ values for each taxonomic group of reptiles are plotted against their calculated $\delta^{18}O_w$ value (Fig. 2). Significant $\delta^{18}O_p$ value differences are observed at any given locality between the various groups of reptiles, with range from 16.4‰ to 22.2‰ for dinosaurs (16.4‰ to 22.2‰ for spinosaurid theropods, 18.2‰ to 22.2‰ for other theropods and 19.2‰ to 19.9‰ for sauropods), from 18.3‰ to 22.9‰ for pterosaurs, from 17.5‰ to 19.9‰ for crocodilians and from 16.7‰ to 19.7‰ for turtles. Fish $\delta^{18}O_p$ values range from 19.2‰ to 22.3‰.

Oxygen isotope compositions of apatite carbonate at Laje do Coringa and Moroccan localities are roughly linearly correlated to $\delta^{18}O_p$ values, with a slope close to unity, whereas $\delta^{18}O_p$ and $\delta^{18}O_c$ values at Araripe basin locality show a large scattering (Fig. 3). Offsets can also be observed between mean $\delta^{13}C_c$ values of apatite carbonate from different taxonomic groups, especially between fish taxa that have $\delta^{13}C_c$ values ranging from −11.1‰ to −1.5‰, as shown in Fig. 4 where they are plotted against their corresponding $\delta^{18}O_p$ values. Reptile $\delta^{13}C_c$ values range from −12‰ to −7‰, indicating that they were feeding on C_3 plant-based foodwebs.

Table 1
Taxon, phosphatic tissue, location, and age are given along with oxygen and carbon isotope compositions of apatite phosphate and carbonate of mid-Cretaceous vertebrate samples.

Sample no.	Skeletal tissue	Taxon	Locality name	Country	Formation	Age	$\delta^{18}O_P$ (‰ V-SMOW)	$\delta^{18}O_C$ (‰ V-SMOW)	$\delta^{13}C_C$ (‰ V-PDB)	Data origin
BR13	Tooth bulk	cf. *Carcharodontosaurus*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.4	24.7	−11.1	This study
BR14	Tooth bulk	cf. *Carcharodontosaurus*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.9	26.6	−10.2	This study
BR15	Tooth bulk	cf. *Carcharodontosaurus*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	22.2	29.3	−8.4	This study
BR16	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.4	25.3	−7.9	This study
BR17	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.5	24.9	−7.5	This study
BR18	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.6	26.6	−4.3	This study
BR19	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.9	25.5	−9.0	This study
BR20	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.4	25.4	−6.8	This study
BR21	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.4	25.6	−7.1	This study
BR22	Tooth enamel	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.1	25.3	−6.4	This study
BR23	Tooth bulk	Spinosauridae	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	18.7	25.0	−4.0	This study
BR24	Tooth enamel	Crocodylia	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.2	26.1	−10.1	This study
BR25	Tooth bulk	Crocodylia	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.7	26.5	−9.8	This study
BR26	Tooth enamel	Crocodylia	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.1	25.5	−9.0	This study
BR27	Tooth bulk	Ceratodontiformes indet.	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.2	26.8	−8.0	This study
BR28	Tooth bulk	Ceratodontiformes indet.	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.5	25.8	−6.9	This study
BR29	Fin ray bone	*Mawsonia*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	19.1	25.0	−6.9	This study
BR30	Fin ray bone	*Mawsonia*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	18.8	24.9	−6.3	This study
BR31	Fin ray bone	*Mawsonia*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.2	25.5	−10.1	This study
BR32	Fin ray bone	*Mawsonia*	Laje do Coringa	Brazil	Alcântara Fm.	Early Cenomanian	20.2	26.5	−5.1	This study
BR01	Tooth enamel	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	21.0	26.7	−9.5	This study
BR02	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	20.4	23.2	−8.3	This study
BR03	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	20.7	25.1	−10.2	This study
BR04	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	21.5	26.3	−9.8	This study
BR05	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	21.2	25.9	−10.0	This study
BR06	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	21.4	24.8	−8.9	This study
BR07	Tooth bulk	Anhanguerid pterosaur	Araripe Basin	Brazil	Crato Fm.	Aptian–Albian	21.2	21.7	−7.5	This study
BR08	5 bulk teeth	*Neoproscinetes penalvai*	Araripe Basin	Brazil	Romualdo Fm.	Aptian–Albian	22.5	26.1	−1.7	This study
BR09	Tooth enamel	*Neoproscinetes penalvai*	Araripe Basin	Brazil	Romualdo Fm.	Aptian–Albian	22.5	22.6	−3.0	This study
BR10	Tooth enamel	*Neoproscinetes penalvai*	Araripe Basin	Brazil	Romualdo Fm.	Aptian–Albian	21.9	22.4	−1.5	This study
BR11	Scales	*Vinctifer*	Araripe Basin	Brazil	Romualdo Fm.	Aptian–Albian	19.9	24.5	−9.3	This study
BR12	Shell bone	*Araripemys*	Araripe Basin	Brazil	Romualdo Fm.	Aptian–Albian	19.7	21.5	−9.6	This study
M-BL-022	Tooth enamel	*Carcharodontosaurus saharicus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.0	-	-	Amiot et al. (2006)
M-BL-023	Tooth enamel	*Carcharodontosaurus saharicus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	18.2	-	-	Amiot et al. (2006)
M-BL-024	Tooth bulk	Theropoda	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.1	25.7	−8.5	This study
M-BL-025	Tooth bulk	Theropoda	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.0	25.6	−11.1	This study
M-BL-036	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.3	-	-	Amiot et al. (2006)
M-BL-041	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	20.6	27.6	−10.8	This study
M-BL-042	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.7	25.9	−9.5	This study
M-BL-043	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.6	26.3	−10.0	This study
M-BL-044	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.8	26.5	−14.0	This study
M-BL-045	Tooth enamel	*Spinosaurus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	19.1	25.9	−12.1	This study
M-BL-003bis	Tooth enamel	Anhanguerid pterosaur	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	18.3	24.3	−11.3	This study
M-BL-013	Osteoderm	Crocodylia	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	16.7	-	-	Amiot et al. (2006)
M-BL-038a	Tooth enamel	cf. *Sarcosuchus*	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	18.4	-	-	Amiot et al. (2006)
M-BL-040	Tooth enamel	Crocodylia	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	17.4	-	-	Amiot et al. (2006)
M-BL-014	Shell bone	Chelonia	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	16.7	-	-	Amiot et al. (2006)
M-BL-016	Shell bone	Chelonia	Bou Laalou	Morocco	Kem Kem beds	Early Cenomanian	17.2	-	-	Amiot et al. (2006)
M-KS-013	Tooth bulk	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.6	26.3	−9.4	This study
M-KS-023	Tooth enamel	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	20.7	-	-	Amiot et al. (2006)
M-KS-024	Tooth enamel	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.9	-	-	Amiot et al. (2006)
M-KS-028	Tooth enamel	*Carcharodontosaurus saharicus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.9	-	-	Amiot et al. (2006)
M-KS-015	Tooth bulk	Theropoda	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.6	25.6	−11.2	This study
M-KS-016	Tooth bulk	Theropoda	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.8	26.7	−7.6	This study

M-KS-009	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.8	26.6	−10.7	This study
M-KS-014	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.4	26.9	−8.9	This study
M-KS-006	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	16.9	–	–	Amiot et al. (2010)
M-KS-007	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	17.8	–	–	Amiot et al. (2006)
M-KS-008	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.8	–	–	Amiot et al. (2010)
M-KS-036	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	20.3	–	–	Amiot et al. (2006)
M-KS-037	Tooth enamel	*Spinosaurus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	17.3	–	–	Amiot et al. (2006)
M-KS-001a	Tooth enamel	Titanosauridae	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.9	26.7	−9.5	This study
M-KS-031	Tooth enamel	Crocodylia	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.8	–	–	Amiot et al. (2006)
M-KS-034	Tooth enamel	Crocodylia	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	16.5	–	–	Amiot et al. (2006)
M-KS-040	Tooth bulk	Crocodylia	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	17.8	–	–	Amiot et al. (2006)
M-KS-012	Shell bone	Chelonia	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	16.7	–	–	Amiot et al. (2006)
M-KS-019A	Scale ganoine	cf. *Lepidotes*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	21.1	28.0	−4.9	This study
M-KS-019B	Scale bulk	cf. *Lepidotes*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.4	25.4	−8.2	This study
M-KS-019C	Scale bulk	cf. *Lepidotes*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	18.6	25.7	−5.3	This study
M-KS-019D	Scale bulk	cf. *Lepidotes*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	20.4	25.3	−10.7	This study
M-KS-019E	Scale ganoine	cf. *Lepidotes*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	22.0	27.2	−4.6	This study
M-KS-025	Tooth bulk	cf. *Neoceratodus africanus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.1	25.4	−10.3	This study
M-KS-026	Tooth bulk	Dipnoi indet.	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.7	25.5	−10.1	This study
M-KS-027	Tooth bulk	cf. *Neoceratodus africanus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.9	26.1	−10.3	This study
M-KS-045	Tooth bulk	*Protopterus*	Khetitila Srhira	Morocco	Kem Kem beds	Early Cenomanian	19.9	25.9	−3.2	This study
M-CH-012n	Tooth enamel	*Carcharodontosaurus saharicus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	22.1	28.2	−9.6	This study
M-CH-013	Tooth enamel	*Carcharodontosaurus saharicus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	21.4	28.3	−8.3	This study
M-CH-014	Tooth bulk	Theropoda	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	20.9	26.2	−9.6	This study
M-CH-004	Tooth enamel	*Spinosaurus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	17.5	–	–	Amiot et al. (2010)
M-CH-007	Tooth enamel	*Spinosaurus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	18.4	–	–	Amiot et al. (2010)
M-CH-025	Tooth enamel	*Spinosaurus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	19.1	25.2	−12.5	This study
M-CH-036	Tooth enamel	*Spinosaurus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	17.8	24.2	−11.5	This study
M-CH-037	Tooth enamel	*Spinosaurus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	19.2	25.4	−11.5	This study
M-CH-006a	Tooth bulk	Titanosauridae	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	19.2	25.2	−11.1	This study
M-CH-005bis	Tooth enamel	Anhanguerid pterosaur	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	20.9	25.3	−8.5	This study
M-CH-010	Tooth enamel	Crocodylia	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	19.0	–	–	Amiot et al. (2006)
M-CH-011	Tooth bulk	Crocodylia	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	20.2	25.8	−11.2	This study
M-CH-029	Shell bone	Chelonia	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	18.6	–	–	Amiot et al. (2006)
M-CH-031	Shell bone	Chelonia	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	18.9	–	–	Amiot et al. (2006)
M-CH-024	Rostral tooth bulk	*Onchopristis numidus*	Chaaft	Morocco	Kem Kem beds	Early Cenomanian	21.3	–	–	This study
M-TA-017	Tooth enamel	*Carcharodontosaurus saharicus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	20.1	26.0	−9.0	This study
M-TA-019	Tooth enamel	*Carcharodontosaurus saharicus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.9	26.3	−9.1	This study
M-TA-026	Tooth enamel	*Spinosaurus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	18.6	26.1	−10.7	This study
M-TA-027	Tooth enamel	*Spinosaurus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	18.2	25.5	−9.8	This study
M-TA-028	Tooth enamel	*Spinosaurus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	18.4	25.7	−9.9	This study
M-TA-031	Tooth enamel	*Spinosaurus*	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.7	24.9	−7.7	This study
M-TA-020bis	Tooth bulk	Anhanguerid pterosaur	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.4	25.1	−7.9	This study
M-TA-021bis	Tooth bulk	Anhanguerid pterosaur	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.3	24.7	−10.2	This study
M-TA-030	Tooth bulk	Crocodylia	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.2	23.9	−9.1	This study
M-TA-004	Osteoderm	Crocodylia	Takemout	Morocco	Kem Kem beds	Early Cenomanian	20.5	25.5	−9.6	This study
M-TA-009	Shell bone	Chelonia	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.0	25.1	−10.7	This study
M-TA-011	Shell bone	Chelonia	Takemout	Morocco	Kem Kem beds	Early Cenomanian	19.7	24.8	−8.3	This study
M-JQ-008	Tooth bulk	Theropoda	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.3	22.9	−11.3	This study
M-JQ-009	Tooth bulk	Theropoda	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	20.2	24.5	−9.0	This study
M-JQ-010	Tooth bulk	Theropoda	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.9	23.8	−11.2	This study
M-JQ-038	Tooth enamel	*Spinosaurus*	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	18.9	24.6	−9.7	This study
M-JQ-039	Tooth enamel	*Spinosaurus*	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.3	24.0	−11.4	This study
M-JQ-040	Tooth enamel	*Spinosaurus*	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.7	24.2	−11.2	This study
M-JQ-001bis	Tooth bulk	Anhanguerid pterosaur	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	20.9	26.5	−10.1	This study
M-JQ-040A	Tooth bulk	Crocodylia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.3	25.3	−8.5	This study
M-JQ-040B	Tooth bulk	Crocodylia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	18.9	25.2	−9.8	This study
M-JQ-040C	Tooth bulk	Crocodylia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	18.7	24.7	−9.3	This study
M-JQ-017	Shell bone	Chelonia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	17.9	23.3	−10.0	This study

Table 1 (continued)

Sample no.	Skeletal tissue	Taxon	Locality name	Country	Formation	Age	$\delta^{18}O_P$ (‰ V-SMOW)	$\delta^{18}O_C$ (‰ V-SMOW)	$\delta^{13}C_C$ (‰ V-PDB)	Data origin
M-JQ-018	Shell bone	Chelonia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	18.8	23.5	−9.5	This study
M-JQ-019	Shell bone	Chelonia	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	18.7	24.0	−9.5	This study
M-JQ-020	Tooth bulk	Neoceratodus africanus	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	20.2	24.9	−11.1	This study
M-JQ-036A	Scale ganoine	Stromerichthys	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	20.4	25.3	−2.7	This study
M-JQ-036B	Scale ganoine	Stromerichthys	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	20.1	23.8	−3.5	This study
M-JQ-036C	Scale ganoine	Stromerichthys	Jebel Al Qabla	Morocco	Kem Kem beds	Early Cenomanian	19.2	24.7	−5.7	This study
M-ZA-015	Tooth bulk	Theropoda	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	19.8	24.2	−10.7	This study
M-ZA-010	Tooth enamel	Anhanguerid pterosaur	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	22.9	–	–	This study
M-ZA-005	Osteoderm	Crocodylia	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	19.7	24.0	−12.0	This study
M-ZA-007	Shell bone	Chelonia	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	18.2	23.3	−10.3	This study
M-ZA-021A	Rostral tooth bulk	Onchopristis numidus	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	19.6	23.4	−8.2	This study
M-ZA-021B	Rostral tooth bulk	Onchopristis numidus	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	18.8	23.0	−6.2	This study
M-ZA-021C	Rostral tooth bulk	Onchopristis numidus	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	18.8	24.8	−8.7	This study
M-ZA-021D	Rostral tooth bulk	Onchopristis numidus	Zaouia	Morocco	Kem Kem beds	Early Cenomanian	19.6	23.1	−6.8	This study
TU-001	Tooth enamel	Theropoda	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	20.0	–	–	Amiot et al. (2006)
TU-002	Tooth enamel	Theropoda	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	21.2	–	–	Amiot et al. (2006)
TU-003	Tooth enamel	Theropoda	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	20.3	–	–	Amiot et al. (2006)
TU-004	Tooth enamel	cf. Spinosaurus	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	22.2	–	–	Amiot et al. (2006)
TU-006	Tooth enamel	cf. Spinosaurus	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	19.8	–	–	Amiot et al. (2006)
TU-005	Tooth enamel	cf. Spinosaurus	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	16.4	–	–	Amiot et al. (2006)
TU-007	Tooth enamel	Crocodylia	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	18.2	–	–	Amiot et al. (2006)
TU-008	Tooth enamel	Crocodylia	Bateun el Hmaima	Tunisia	Chenini Member	Late Aptian–Early Albian	18.4	–	–	Amiot et al. (2006)

Table 2
Locality name, paleolatitude and reconstructed environmental water $\delta^{18}O_w$ values calculated using the Amiot et al. (2007) and Barrick et al. (1999) oxygen isotope fractionation equations.

Locality	Paleolatitude			$\delta^{18}O_{water}$ (‰ V-SMOW)			
	mean	+	−	From crocodilians	From turtles	Average	Std. err.
Laje do Coringa	−5.0	1.7	11.9	−3.2	–	−3.2	1.0
Araripe Basin	−10.2	8.3	1.6	–	−2.4	−2.4	1.0
Bou Laalou	12.4	3.5	3.3	−4.7	−5.2	−5.0	1.0
Khetitila Srhira	16.5	2.1	2.2	−4.6	−5.4	−5.0	1.0
Chaaft	16.5	2.1	2.2	−3.0	−3.4	−3.2	1.0
Takemout	16.5	2.1	2.2	−2.8	−2.8	−2.8	1.0
Jebel Al Qabla	16.5	2.1	2.2	−3.5	−3.6	−3.6	1.0
Zaouia	16.5	2.1	2.2	−2.9	−4.0	−3.4	1.0
Bateun el Hmaima	16.5	2.1	2.2	−4.1	–	−4.1	1.0

5. Discussion

5.1. Preservation of pristine isotope compositions of fossil apatites

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). However, apatite crystals that make up tooth enamel or fish scale ganoine are large and densely packed, and isotopic exchange under inorganic conditions has little effect on the oxygen isotope composition of phosphates even at geological time scales (Kolodny et al., 1983; Lécuyer et al., 1999a). Turtle shell bone should be more susceptible to diagenetic alteration because hydroxylapatite crystals of bones are smaller and less densely intergrown than those of enamels (Kolodny et al., 1996), even though several case studies have shown that the original oxygen isotope composition seems to be preserved in Mesozoic and Cenozoic turtle remains (Barrick et al., 1999; Amiot et al., 2004, 2006; Matson and Fox, 2008; Amiot et al., 2009). Although no method is available to demonstrate definitely whether or not the oxygen isotope composition of fossil vertebrate phosphate was modified by diagenetic processes, several ways to assess the preservation state of the primary isotopic

record have been proposed (e.g. Iacumin et al., 1996; Kolodny et al., 1996; Fricke et al., 1998; Lécuyer et al., 2003; Pucéat et al., 2004; Zazzo et al., 2004b; Tütken et al., 2008). Here, the main argument supporting the preservation of the original oxygen isotope composition is the systematic offset observed between dinosaurs and ectothermic reptiles (turtles and crocodilians), most likely resulting from differences in ecology and physiology. The present dataset illustrates systematic offsets between semi-aquatic animals (turtles and crocodilians) and terrestrial ones (dinosaurs, except *Spinosaurus*), the latter having $\delta^{18}O_P$ values up to 2.7‰ higher than the values of crocodilians and turtles. If early diagenetic processes had occurred, they would have tended to homogenise $\delta^{18}O_P$ values of all vertebrate remains whatever the physiology and ecology of the corresponding taxa (Lécuyer et al., 2003). The second clue which favours at least a partial original preservation of both phosphate and carbonate values is the correlation between their two $\delta^{18}O$ values which roughly parallels the oxygen isotope fractionation line established for extant mammals (Iacumin et al., 1996; Zazzo et al., 2004b; Fig. 3). It is noteworthy that the large data scattering observed within Araripe Basin remains may indicate a partial modification of the pristine oxygen isotope compositions of apatite carbonate, which must therefore be considered with caution. Primary preservation of carbonate $\delta^{13}C_c$ values of apatite is more difficult to test. Here we assume an original preservation based on consistent value differences observed between taxonomic groups, and the low scattering of $\delta^{13}C_c$ values within each taxon compared to the inter-taxon variability. Indeed, mean $\delta^{13}C_c$ values range from −10.7‰ (spinosaurs) to −2.1‰ (*Neoproscinetes*) whereas standard deviations within most groups are of about ±1.0‰ with a maximum of ±2.3‰ for the ubiquitous fish *Lepidotes*.

5.2. Meaning of the oxygen and carbon isotope compositions of phosphate and carbonate

5.2.1. Crocodilians and turtles

Crocodilians and turtles from studied localities are identified as being semi-aquatic to aquatic species. Due to higher water turnover and lower transcutaneous water evaporation compared to terrestrial vertebrates, crocodilian and turtle $\delta^{18}O_P$ values are lower than those of coexisting terrestrial dinosaurs and pterosaurs, with two exceptions in Takemout and Zaouia localities where some crocodilian $\delta^{18}O_P$ values are close to theropod dinosaur ones. It is also noteworthy that $\delta^{18}O_P$ values of crocodilians are systematically higher than those of turtle for any given locality. This might be accounted for peculiar behaviour by crocodilians such as extensive basking in the sun or the fortuitous presence of terrestrial crocodilian remains within analyzed Moroccan samples such as *Hamadasuchus rebouli* (Buffetaut, 1994), sometimes difficult to identify from isolated osteoderms or anterior teeth. Although being ectothermic animals, and thus having body temperatures fluctuating along with environmental ones (e.g. Seebacher et al.,
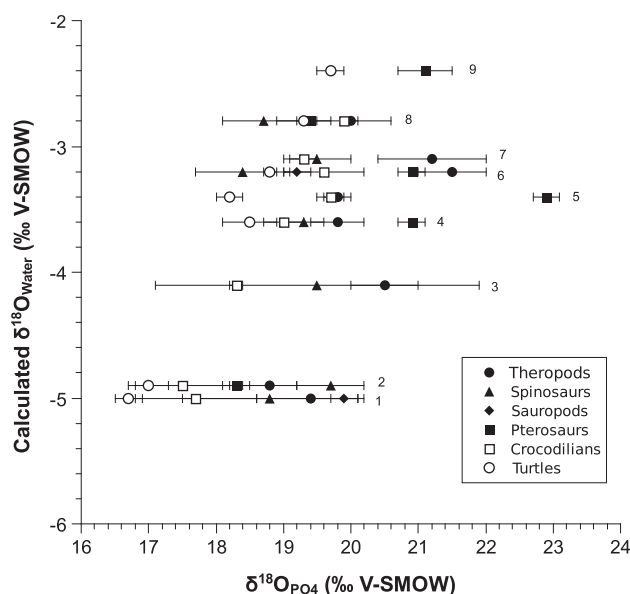

Fig. 2. Mean oxygen isotope compositions of apatite phosphate ($\delta^{18}O_P$) from studied reptile taxa plotted against calculated environmental water $\delta^{18}O_w$ values. Numbers refer to the following localities: 1: Khetitila Srhira (Morocco); 2: Bou Laalou (Morocco); 3: Bateun el Hmaima (Tunisia); 4: Jebel Al Qabla (Morocco); 5: Zaouia (Morocco); 6: Chaaft (Morocco); 7: Laje do Coringa (Brazil); 8: Takemout (Morocco); 9: Araripe Basin (Brazil).
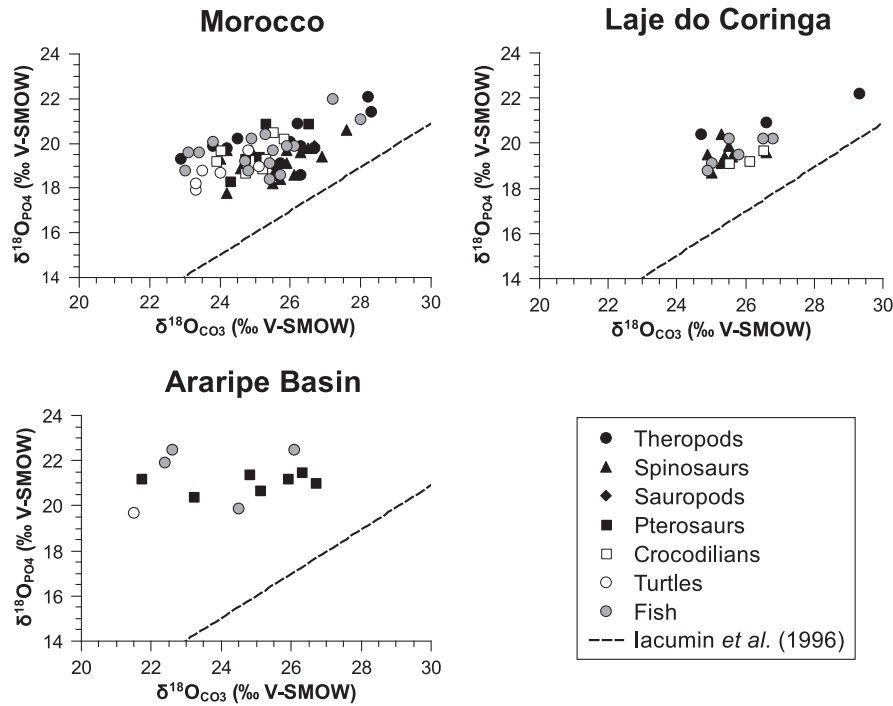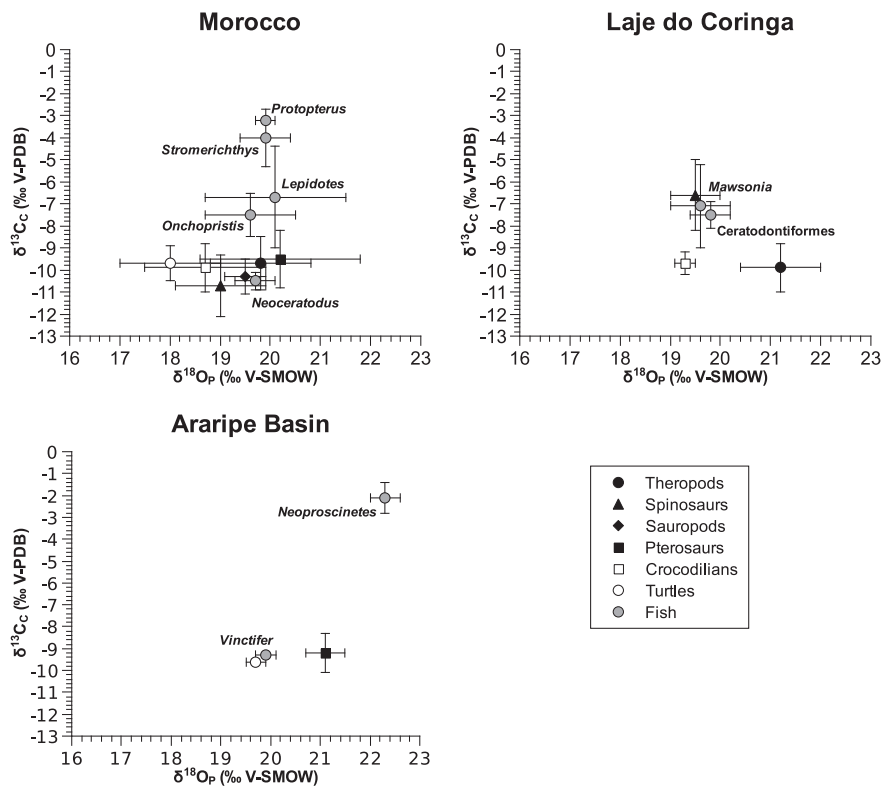
Fig. 3. Mean oxygen isotope compositions of apatite phosphate ($\delta^{18}O_p$) from studied vertebrate taxa plotted against their corresponding oxygen isotope composition of carbonate ($\delta^{18}O_c$), along with the phosphate–carbonate isotopic fractionation line established for extant herbivorous mammals (Iacumin et al., 1996).

2003), crocodilians and turtles synthesize bone and tooth phosphate under relatively narrow temperature ranges (Barrick et al., 1999; Amiot et al., 2007). Oxygen isotope compositions of environmental waters were estimated using empirical phosphate–water fractionation equations established for crocodilians and turtles (Barrick et al., 1999; Amiot

et al., 2007). Calculated $\delta^{18}O$ values of environmental waters range from −5‰ to −2.4‰, a range corresponding to continental surface water values observed nowadays at tropical to equatorial latitudes (IAEA/WMO, 2006). Carbon isotope compositions of both crocodilians and turtles range from −12.0‰ to −9.2‰. It is noteworthy that these values

Fig. 4. Mean oxygen isotope compositions of apatite phosphate ($\delta^{18}O_p$) from studied vertebrate taxa plotted against their corresponding carbon isotope composition of carbonate ($\delta^{13}C_c$).

fall within the larger range of $-18.1‰$ to $-4.1‰$ measured in extant crocodilians belonging to five different genera (Lécuyer et al., 2003; Stanton, 2006). Assuming a carbon isotope fractionation of 9‰ between crocodilian apatite and diet (a value calculated for carnivorous mammals; Lee-Thorp et al., 1989; Tieszen and Fagre, 1993), Stanton (2006) differentiated crocodilians feeding on preys based on C_4, C_3 and mixed plant foodwebs, highest $\delta^{13}C_c$ values corresponding to pure C_4-based diets. Diet of fossil turtles is difficult to assess from osteological features. Carbon isotope fractionations of 6–9‰ calculated between carnivorous turtle apatites and their diets, and of 12‰ between herbivorous ones and their diets have been proposed for extant marine turtles (Biasatti, 2004). Such isotopic fractionation values for both turtles and crocodiles indicate $\delta^{13}C$ values for their diet around $-20‰$, compatible with C_3-based foodwebs. Interestingly, the Brazilian turtle *Araripemys*, often considered as a marine turtle due to its flattened shell and its abundant presence in the saltwater deposits of the Romualdo member of the Santana Formation (e. g. Price, 1973; De Oliveira and Kellner, 2005), has both low $\delta^{18}O_P$ and $\delta^{13}C_c$ values more compatible with freshwater affinities. As only one sample was available for this study, definitive conclusions cannot be drawn, and a larger sample set must be analyzed in order to better understand the living environment of *Araripemys*.

5.2.2. Dinosaurs

Theropod dinosaurs (except spinosaurs which are discussed below) were terrestrial homeotherm carnivorous dinosaur with an endotherm-like thermophysiology (Barrick and Showers, 1994; Fricke and Rogers, 2000; Amiot et al., 2006). As homeotherms and obligate drinkers, variations in their oxygen isotope compositions of phosphate and carbonate predominantly reflect variations in the drinking waters which overwhelm oxygen input from other sources such as food (Barrick and Showers, 1995; Barrick et al., 1996; Straight et al., 2004).

Spinosaurs were theropod dinosaurs with peculiar morphologies, the most striking features being their almost conical, crocodile-like teeth, elongated and narrow snout and their extremely tall vertebral neural spines indicating the presence of a dorsal sail. From these anatomical characteristics, these animals were supposed to be piscivorous, feeding on fish the way crocodilians do. The discovery of partially digested fish scales in the stomach region of a nearly complete skeleton of *Baryonyx* supported the hypothesis that these theropods ate preferentially fish (Charig and Milner, 1997), but not exclusively, as several direct evidence indicate that some other dinosaurs (Charig and Milner, 1997) and pterosaurs (Buffetaut et al., 2004) were also part of their diet. Although anatomical features indicate that spinosaurs were terrestrial and bipedal dinosaurs such as other theropods, it has been demonstrated that their $\delta^{18}O_P$ values are lower than the ones of coexisting terrestrial theropods and values within the range of crocodilians were most likely due to a semi-aquatic lifestyle consisting in spending most of daily time immersed (Amiot et al., 2009, 2010). Compared to other spinosaurs (including the ones from the Brazilian site of Laje do Coringa), those recovered from Morocco and Tunisia may have had a more complicated lifestyle, as their $\delta^{18}O_P$ values range from semi-aquatic reptile to terrestrial theropod ones. It is possible that peculiar environmental or ecological stresses forced them to alternate between semi-aquatic and terrestrial lifestyles (Amiot et al., 2010). It is noteworthy that the higher the $\delta^{18}O_w$ values of surface waters, the lower the spinosaur $\delta^{18}O_P$ values (Fig. 2). This may suggest that under dryer conditions, which are inferred from higher $\delta^{18}O_w$ values, spinosaurs would spend more time in water to circumvent drought-related stress. Titanosaurid sauropods from Morocco have $\delta^{18}O_P$ values similar to those of theropod dinosaurs, which strongly suggest that most of their oxygen input was from drinking water. If they had mostly relied on plant water, usually ^{18}O-enriched by several per mils relative to surface waters, their $\delta^{18}O_P$

values would have been significantly higher than those of coexisting theropods.

Studied dinosaurs have a restricted range in carbon isotope compositions from $-12‰$ to $-7‰$, which is expected for animals feeding on C_3 plant-based foodwebs. By comparing mean $\delta^{13}C_c$ values of both dinosaur tooth enamels and associated bulk sedimentary organic matter or fossil plant leaves, ^{13}C-enrichments of 18‰ have been proposed for hadrosaurs and ceratopsians (Fricke and Pearson, 2008), and 16‰ for sauropods (Tütken, in press). These ^{13}C-enrichments that are 3‰ to 8‰ higher than those of extant herbivorous mammals may account for distinct digestive physiologies including the incorporation of specific plant compounds and higher production of methane from the gastrointestinal tract of herbivorous dinosaurs. Indeed, the rate of ^{12}C-rich methane production and its loss during digestion and rumination can have an important influence on the enamel-diet ^{13}C-enrichment factor (Passey et al., 2005). Tütken (in press) also noted that the enamel-diet ^{13}C-enrichment of sauropod dinosaurs is similar to the bone-diet ^{13}C-enrichment of extant ostriches, both animals belonging to the same dinosaur lineage (Saurischia). Titanosaurid sauropods from Morocco have a mean $\delta^{13}C_c$ value of $-10.3 \pm 0.8‰$, suggesting that they were feeding on plants having a $\delta^{13}C$ value of about $-26‰$, falling within the C_3 plant range.

5.2.3. Pterosaurs

Studied Moroccan and Brazilian pterosaur teeth belong to the family Anhangueridae (Wang et al., 2009). According to their skull and tooth morphologies, these flying reptiles are considered to be fish eaters, fishing on the wing by seizing prey with their pointed jaws while flying above water surface (Campos and Kellner, 1985; Wellnhofer, 1991; Veldmeijer et al., 2007). As expected, their high $\delta^{18}O_P$ values are within the range of other terrestrial animals. Moreover, the large range of $\delta^{18}O_P$ values (from 18.3‰ to 22.9‰) suggests that they drank waters from different sources, including main river streams, evaporated water ponds and possibly marine waters while feeding. Moreover, their low and restricted $\delta^{13}C_c$ values ranging from $-11.3‰$ to $-7.5‰$ point to a diet with at least an important part of freshwater fish, as marine fish usually have more positive and variable $\delta^{13}C_c$ values (see discussion about fish $\delta^{13}C$ values below). However, as bulk teeth (enamel + dentine) only have been analyzed for their carbon isotope compositions, the possibility that diagenetic alteration is responsible for such $\delta^{13}C$ values cannot be totally excluded, dentine being more prone to such an alteration than enamel.

5.2.4. Fish

Early Cenomanian fish from Morocco and Brazil have high $\delta^{18}O_P$ values indicating that their phosphate precipitated from ^{18}O-enriched waters relative to those calculated from isotopic compositions of coexisting crocodilians and freshwater turtles. Indeed, the use of the fish phosphate–water temperature scale (Kolodny et al., 1983) gives anomalously low precipitation temperatures ranging from 3 °C to 13 °C assuming that fish were living in waters with $\delta^{18}O_w$ values of $-5‰$ to $-2.4‰$ as deduced from crocodilians and turtle $\delta^{18}O_P$ values. Therefore these fish $\delta^{18}O_P$ values suggest distinct aquatic environments. The euryhaline sawfish *Onchopristis numidus*, the semionotiform *Lepidotes* and the coelacanth *Mawsonia* might have shared their living environments between fresh and shallow marine waters. A similar lifestyle can be proposed for the poorly known *Stromerichthys*, which was also found in Cenomanian continental deposits of France (Vullo and Neraudeau, 2008), a geographic distribution suggesting its ability to venture in the open ocean. Therefore, we propose that their $\delta^{18}O_P$ values reflect seawater $\delta^{18}O_{sw}$ values (between $-1‰$ and $+1‰$) at temperatures ranging from 21 ± 6 °C (including the value of 16 °C inferred from one *Onchopristis* sample) to 34 ± 2 °C (Table 3), which is in good agreement with calculated Cenomanian sea surface temperatures of Western Tethys (Pucéat et al., 2003). Their $\delta^{13}C_c$

Table 3
Marine water temperatures estimated from the $\delta^{18}O_p$ values of fish using the equation of Kolodny et al. (1983).

Locality	Mawsonia			Neoproscinetes			Vinctifer			Lepidotes			Onchopristis			Stromerichthys		
$\delta^{18}O_{water}$ (‰ V-SMOW)	−1	1		−1	1		−1	1		−1	1		−1	1		−1	1	
	T°C		Std. err.	T°C		Std. err.	T°C		Std. err.	T°C		Std. err.	T°C		Std. err.	T°C		Std. err.
Laje do Coringa	23	32	3															
Araripe Basin				11	20	1	22	30	–									
Khetitila Srhira										21	30	6						
Chaaft													16	24	–			
Jebel Al Qabla																22	31	2
Zaouia													25	34	2			

values, higher than those of other continental vertebrates may derive from a carbon of marine origin such as dissolved inorganic carbon and organic carbon, usually having higher $\delta^{13}C$ values than freshwater carbon sources (Clayton and Degens, 1959). The two Moroccan lungfishes *Protopterus* and *Neoceratodus*, as well as the indeterminate ceratodontiform from Laje do Coringa (Brazil) also have high $\delta^{18}O_p$ values. As marine living environments for these fishes seem unlikely considering that fossil lungfish have been found quite exclusively in continental deposits since the Triassic (Cavin et al., 2007), it seems that their high $\delta^{18}O_p$ values might be due to temporary drought of their living environment, or to estivation behaviour. Indeed, African and South American lungfish are capable of surviving seasonal drying out of their habitats by burrowing into mud and estivating throughout the dry season (Fishman et al., 1986). According to this, they might have precipitated some parts of their tooth phosphate in equilibrium with ^{18}O-enriched evaporated waters. Assuming mean temperatures of continental environments in the 30–35 °C range (Russell and Paesler, 2003), their $\delta^{18}O_p$ values could reflect isotopic equilibrium with environmental waters having mean $\delta^{18}O_w$ values in the $+1$‰ to $+2$‰ range. Such differences in calculated $\delta^{18}O_w$ values between fish and crocodilian and turtles have also been observed in Early Cretaceous deposits of northeast Thailand. Indeed, these isotopic differences between fish and reptiles may reflect peculiar conditions experienced by fish during apatite mineralization such as temporary isolations from larger water bodies followed by intense evaporation. During periods of isolation of water bodies, tetrapods can move to other water bodies, whereas fish are trapped and record environmental changes in their phosphatic tissues (Amiot et al., 2009). Low $\delta^{13}C_c$ values of the Moroccan and Brazilian lungfishes are compatible with their freshwater living environments with the exception of the very positive value obtained from one *Protopterus* tooth that remains enigmatic in the framework of this study. The two fishes *Vinctifer* and *Neoproscinetes* from the Romualdo Formation of Brazil are considered to be either marine or species that lived in high saline waters. Their high $\delta^{18}O_p$ values are in agreement with their marine life, and the differences in both $\delta^{18}O_p$ and $\delta^{13}C_c$ values suggest differences in foraging environment and diets. *Neoproscinetes* is a durophageous fish according to its tooth morphology as well as its preserved gut contents found in some specimens (Kriwet, 2001), whereas *Vinctifer* possesses a well developed basket of gill rakers suggesting a filtering mode of feeding (Maisey, 1994). As marine shelled mollusks have significantly higher $\delta^{13}C_c$ values than marine plankton (Rau et al., 1989; Lécuyer et al., 2004; McConnaughey and Gillikin, 2008), such offset in diet $\delta^{13}C$ values is in good agreement with the difference observed between *Vinctifer* and *Neoproscinetes* $\delta^{13}C_c$ values.

5.3. Remarks on mid-Cretaceous Moroccan and Brazilian environmental conditions

Vertebrate $\delta^{18}O_p$ values are surprisingly not high enough to account for the expected hot or dry conditions that might have prevailed in Saharan environments during the mid-Cretaceous. Terrestrial dinosaurs would have undergone elevated transcutaneous evaporation, along with ingestion of waters from evaporated ponds (at least intermittently), thus leading to high $\delta^{18}O_p$ values. Such expected extremely positive values have been measured in phosphatic remains of extant desert faunas such as the Sahara sand viper *Cerastes vipera* which displayed $\delta^{18}O_p$ values up to 30‰ (Lécuyer et al., 1999b), or reptiles and mammals from Sibiloi National Park (Kenya), some of which having $\delta^{18}O_p$ values up to 32‰ (Schoeninger et al., 2000). Morevover, elevated $\delta^{18}O_p$ values of 26‰ were measured from theropod dinosaur teeth recovered from the Early Cretaceous of northeast Thailand where seasonal drought took place during this period (Amiot et al., 2009). Oxygen isotope compositions of environmental waters estimated from freshwater crocodilians and turtles are in the range of, or slightly lower than, values measured today in tropical and equatorial regions with semi-arid to arid climates (IAEA/WMO, 2006). It is also noteworthy that the $\delta^{13}C_c$ values of sauropods suggest a diet with a $\delta^{13}C$ value of -26 ± 1‰, which corresponds to C_3 plants not affected by stress conditions. Under environmental stresses such as elevated temperatures, light, salt or aridity, plant leaves tend to have higher $\delta^{13}C$ values as a result of reduced stomatal conductance leading to lower carbon isotope discrimination during photosynthesis (Farquhar et al., 1989). For example, $\delta^{13}C$ values as high as -20‰ have been measured from Mesozoic and Cenozoic fossil plants that lived under environmental stress (Bocherens et al., 1993). On the other hand, high $\delta^{18}O_p$ values measured in lungfish from Morocco and Brazil suggest that their water environments dried up temporaly or probably seasonally. From these considerations, it seems that the studied tropical to equatorial mid-Cretaceous environments were characterized by elevated temperatures reaching 34 °C (as deduced from high fish $\delta^{18}O_p$ values) in agreement with mean air temperatures previously proposed (Russell and Paesler, 2003). Water availability does not seem to have been a critical factor for plants and tetrapods as suggested by their carbon and oxygen isotope compositions, but seasonal or temporary drought might have trapped fish in small evaporating bodies of water where lungfish could have survived by burrowing into the mud.

6. Concluding remarks

Moroccan, Tunisian and Brazilian vertebrate apatites have been analyzed for their oxygen and carbon isotope compositions of phosphates ($\delta^{18}O_p$) and carbonates ($\delta^{18}O_c$, $\delta^{13}C_c$) in order to better understand mid-Cretaceous terrestrial climates of low paleolatitudes and to investigate the response of vertebrate faunas in terms of ecology. The following results are underlined:

- Oxygen isotope compositions of surface waters ($\delta^{18}O_w$) estimated from turtle and crocodile $\delta^{18}O_p$ values range from -5.0 ± 1.0‰ to -2.4 ± 1.0‰, which do not differ from mean annual rainwater values occurring today under inter-tropical sub-arid to arid climates.
- High water temperatures ranging from 21 ± 6 °C to 34 ± 2 °C deduced from fish $\delta^{18}O_p$ values are in agreement with those published for mid-Cretaceous low latitudes.

- At each site, coexisting theropod dinosaurs, titanosaurid sauropods, pterosaurs, crocodilians, turtles and fish have distinct $\delta^{18}O_p$ and $\delta^{13}C_c$ values reflecting their ecologies (terrestrial vs. aquatic), diets (water strategies) and foraging environments (marine vs. freshwater).
- Temporary or seasonal droughts are inferred from high $\delta^{18}O_p$ values of lungfish teeth, even though lower reptile $\delta^{18}O_p$ values suggest the use of distinct and most likely larger or regularly renewed bodies of water.
- Environmental conditions of the studied low latitude regions during the Aptian–Cenomanian interval were somewhat similar to those experienced today under semi-arid to arid tropical or equatorial climates, but with higher mean surface temperatures than present-day ones.
- The extreme conditions proposed by Russell and Paesler (2003) appear therefore unlikely for the studied areas and may have occurred further inland in the Aptian deposits of Niger where it has been suggested that dinosaurs were adapted to circumvent stress of heat and aridity (Russell and Paesler, 2003).

Acknowledgements

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