

Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs

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Received 5 January 2006; received in revised form 31 March 2006; accepted 13 April 2006

Available online 19 May 2006

Editor: H. Elderfield

Abstract

The much debated question of dinosaur thermophysiology has not yet been conclusively solved despite numerous attempts. We used the temperature-dependent oxygen isotope fractionation between vertebrate body water ($\delta^{18}\text{O}_{\text{body water}}$) and phosphatic tissues ($\delta^{18}\text{O}_p$) to compare the thermophysiology of dinosaurs with that of non-dinosaurian ectothermic reptiles. Present-day $\delta^{18}\text{O}_p$ values of vertebrate apatites show that ectotherms have higher $\delta^{18}\text{O}_p$ values than endotherms at high latitudes due to their lower body temperature, and conversely lower $\delta^{18}\text{O}_p$ values than endotherms at low latitudes. Using a data set of 80 new and 49 published $\delta^{18}\text{O}_p$ values, we observed similar and systematic differences in $\delta^{18}\text{O}_p$ values ($\Delta^{18}\text{O}$) between four groups of Cretaceous dinosaurs (theropods, sauropods, ornithomimids and ceratopsians) and associated fresh water crocodiles and turtles. Expressed in terms of body temperatures (T_b), these $\Delta^{18}\text{O}$ values indicate that dinosaurs maintained rather constant T_b in the range of endotherms whatever ambient temperatures were. This implies that high metabolic rates were widespread among Cretaceous dinosaurs belonging to widely different taxonomic groups and suggest that endothermy may be a synapomorphy of dinosaurs, or may have been acquired convergently in the studied taxa.

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Keywords: Cretaceous; oxygen isotopes; apatite; dinosaur; crocodile; turtle; thermophysiology

1. Introduction

Although they were traditionally considered as “cold-blooded” (ectothermic) reptiles, several lines of evidence suggest that dinosaurs may have been “warm-blooded”

(endothermic), like birds or mammals. Endothermy is a thermoregulatory strategy consisting in maintaining a high and constant body temperature (within ± 2 °C) through metabolic heat production, whereas in ectotherms, body temperature is linked to that of the environment and to behavioural thermoregulatory strategies. Various features of dinosaurs [1–3] have been used to suggest that at least several groups of dinosaurs possessed endotherm-like thermoregulatory strategies. Conversely, endothermy has

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been considered as unlikely in dinosaurs for physiological [4–7] and anatomical [8,9] reasons. For recent contrasting opinions on dinosaur thermophysiology, see Chinsamy and Hillenius [10] and Padian and Horner [11].

Oxygen isotope compositions of phosphate from biogenic apatites can be used to investigate the metabolic status of vertebrates. Rather constant intra-individual oxygen isotope compositions in bones of theropods and ornithischians have been considered as evidence of homeothermy, indicating an intermediate to high metabolic status [12–14]. However, these results have been questioned because of doubts about the preservation of pristine isotopic records in fossil bones [15]. Another approach is to test the metabolic status of dinosaurs by comparison with ectotherms [15,16]. Because oxygen isotope fractionation between phosphate and body water is temperature-dependent, co-existing endotherms and ectotherms having the same water strategies (i.e. similar water needs and origin of ingested water such as plant or drinking water) are expected to have distinct apatite $\delta^{18}\text{O}_p$ values. At the global scale, variations in the $\delta^{18}\text{O}$ values of vertebrate phosphate and body water are mainly controlled by variations in the compositions of drinking and food water. The ultimate source of oxygen is meteoric water, the $\delta^{18}\text{O}$ value of which decreases with increasing latitude and decreasing air temperatures [17–19]. Consequently, $\delta^{18}\text{O}_p$ values from both ectotherms and endotherms decrease with increasing latitude [16,20]. Moreover, as oxygen isotope fractionation between phosphate and water increases with decreasing temperatures, the $\delta^{18}\text{O}_p$ values of ectotherms are expected to be higher than those of associated endotherms at latitudes above 50° , due to their lower body temperature, and conversely, at low latitudes, ectotherms having body temperature comparable to or slightly higher than endotherms should display lower $\delta^{18}\text{O}_p$ values (Fig. 1). Based on such a comparison, it was concluded that some theropods were “warm-blooded” [16]. These conclusions, however, were challenged regarding possible differences in water strategies, diet and living environment, which could also explain the observed $\delta^{18}\text{O}_p$ offsets between crocodylians and theropods [21]. Nevertheless, it is now widely accepted that several groups of theropods possessed a kind of endothermy, but the metabolic status of the other groups of dinosaurs still remains unclear and highly debated [10,11].

2. Sample collection

Eighty samples were recovered from eleven Cretaceous localities at low paleolatitudes ranging from $12.4^{+3.5}_{-3.3}^\circ\text{N}$ to $39.8^{+4.2}_{-3.8}^\circ\text{N}$ (Fig. 2). Paleolatitudes of the

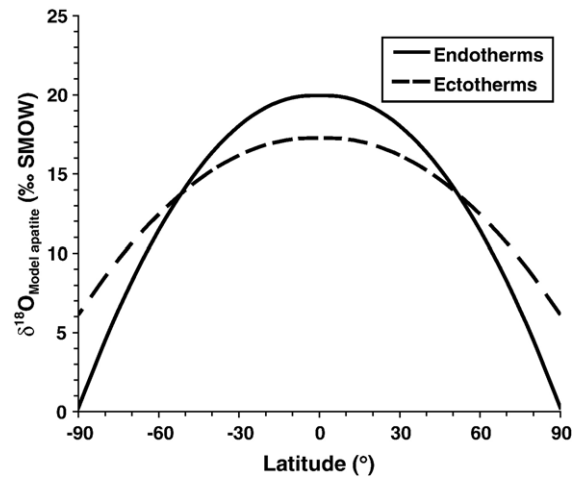


Fig. 1. Model curves of present-day $\delta^{18}\text{O}$ values of endothermic and ectothermic vertebrates as a function of latitude (endotherms: $\delta^{18}\text{O}_{\text{apatite}} = -0.0026L^2 + 0.0134L + 19.95$; ectotherms: $\delta^{18}\text{O} = -0.0015L^2 + 0.0076L + 17.28$, where L is the latitude). Curves are calculated using mean annual air temperatures and $\delta^{18}\text{O}$ values of weighted meteoric waters provided by the global network of weather stations operated by the IAEA–WMO (International Atomic Energy Agency – World Meteorological Organization [48]) combined with isotopic fractionation equations of mammals for endotherms ($\delta^{18}\text{O}_{\text{water}} = 1.11\delta^{18}\text{O}_{\text{mammals}} - 26.44$ [20]) and freshwater fish for ectotherms ($T(^{\circ}\text{C}) = 113.3 - 4.38(\delta^{18}\text{O}_{\text{fish}} - \delta^{18}\text{O}_{\text{water}})$ [49]).

sampling sites are calculated using the method described by Besse and Courtillot [22] (see Amiot et al. [20] for details). The locality of Cherves-de-Cognac (France) is considered as Berriasian in age based on charophytes and ostracods [23]. The Khok Pha Suam locality (Thailand) is in the Khok Kruat Formation, considered as Aptian–Albian in age based on the occurrence of the freshwater hybodont shark *Thaiodus* [24]. Bateun el Hmama (Tunisia) is considered as early Albian in age [25]. The two Moroccan localities (Bou Laalou and Khetitila Srhira) belonging to the Kem–Kem beds are probably of early Cenomanian age (see review in [26]). The Slovenian locality of Košina is within a Campanian–Maastrichtian age bracket [27]. The French locality of Cruzy is late Campanian–early Maastrichtian in age [28]. The three French localities of Ausseing, Cassagnau 1 and Cassagnau 2 [29] are late Maastrichtian in age, like, possibly, the locality of Fântânele (Romania) [30].

Phosphatic fossil remains analyzed for their oxygen isotope compositions were collected as isolated specimens (shed teeth, turtle plates and crocodylian scutes). Dinosaur teeth belonged to animals of highly variable body size: very small theropods (with tooth crowns a few mm long), small ornithopods, and large theropods and sauropods. As reptile teeth are continuously replaced and take several months to grow [31,32], thus recording

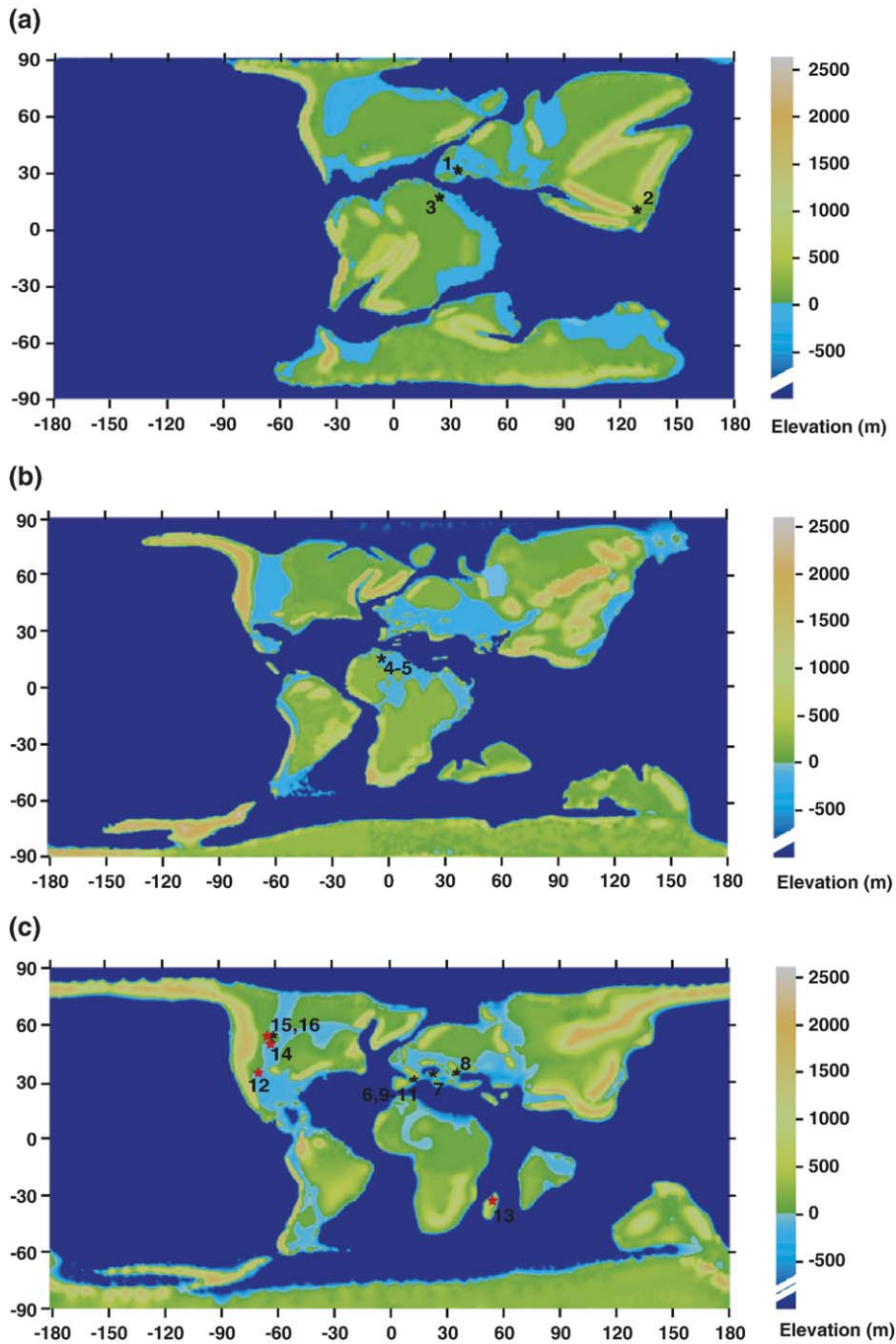


Fig. 2. (a) Early, (b) Middle and (c) Late Cretaceous paleogeographic maps showing the location of sites where vertebrate remains used for the geochemical analyses described in the present paper have been collected. Black asterisks correspond to sampling localities and red stars to published ones. Numbers refer to the following localities: (1) Cherves, Berriasian, France; (2) Khok Pa Suam, Aptian–Albian, Thailand; (3) Bateun el Hmaima, early Albian, Tunisia; (4) Bou Laalou, early Cenomanian, Morocco; (5) Khetitila Srhira, early Cenomanian, Morocco; (6) Cruzy, late Campanian, early Maastrichtian, France; (7) Košina, Campanian–Maastrichtian, Slovenia; (8) Fântânele, late Maastrichtian, Romania; (9) Ausseing, late Maastrichtian, France; (10) Cassagnau 1, late Maastrichtian, France; (11) Cassagnau 2, late Maastrichtian, France; (12) Texas, late Campanian – early Maastrichtian, United States [15,16]; (13) Madagascar, early Maastrichtian [16]; (14) Montana, Campanian, United States [12,16]; (15) Onefour, Alberta, late Campanian, Canada; (16) Alberta, late Campanian, Canada [16].

seasonal variations in meteoric water $\delta^{18}\text{O}_w$ values, average values were obtained by analysing several teeth from each locality and by sampling enamel from the base to the apex of each tooth. The most compact bone parts were selected from turtle shells and crocodile scutes. In addition to the new eighty samples analyzed in the frame of this study, $\delta^{18}\text{O}_p$ data for Late Cretaceous vertebrates taken from the literature come from: 1) Fricke and Rogers [16] for theropod dinosaurs and crocodiles from Alberta, Montana, Texas and Madagascar; 2) Barrick et al. [12] for the ornithomimid dinosaurs *Orodromeus makelai*, *Hypacrosaurus stebingegi*, the ceratopsian dinosaurs *Montanoceratops sp.* and *Achelousaurus horneri* from Montana; and 3) Kolodny et al. [15] for turtles, crocodiles, carnosaurs and hadrosaurs from the Aguja Formation, Texas. The $\delta^{18}\text{O}_p$ values of the four groups of Cretaceous dinosaurs (theropods, sauropods, ornithomimids and ceratopsians) were compared with those of associated freshwater crocodiles and turtles recovered from the same fossil sites (Fig. 3).

Oxygen isotope compositions of ingested and body waters are only available for mammals and turtles [33,34]. Therefore, in order to determine the oxygen isotope enrichment between crocodylian body water and drinking water, blood and pond waters from 4 Nile crocodiles (*Crocodilus niloticus*) have been sampled at the Crocodile farm “La Ferme aux Crocodiles” near Pierrelatte in southeastern of France (Table 3).

3. Analytical techniques

Measurements of oxygen isotope ratios of apatite consist in isolating PO_4^{3-} using acid dissolution and anion-exchange resin, according to a protocol derived from the original method published by Crowson et al. [35] and slightly modified by Lécuyer et al. [36]. Silver phosphate is 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 are mixed with 0.8 mg of pure powder graphite. $^{18}\text{O}/^{16}\text{O}$ ratios are measured by reducing silver phosphates to CO_2 using graphite reagent [37,38]. Samples are weighed into tin reaction capsules, 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 GV Isoprime™ mass spectrometer at the Laboratory UMR CNRS 5125 ‘PEPS’, University Claude Bernard Lyon 1. 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 ($\delta^{18}\text{O} = 21.70 \pm 0.17\text{‰}$; $n = 15$) along with the silver phosphate samples derived from the Cretaceous vertebrate remains.

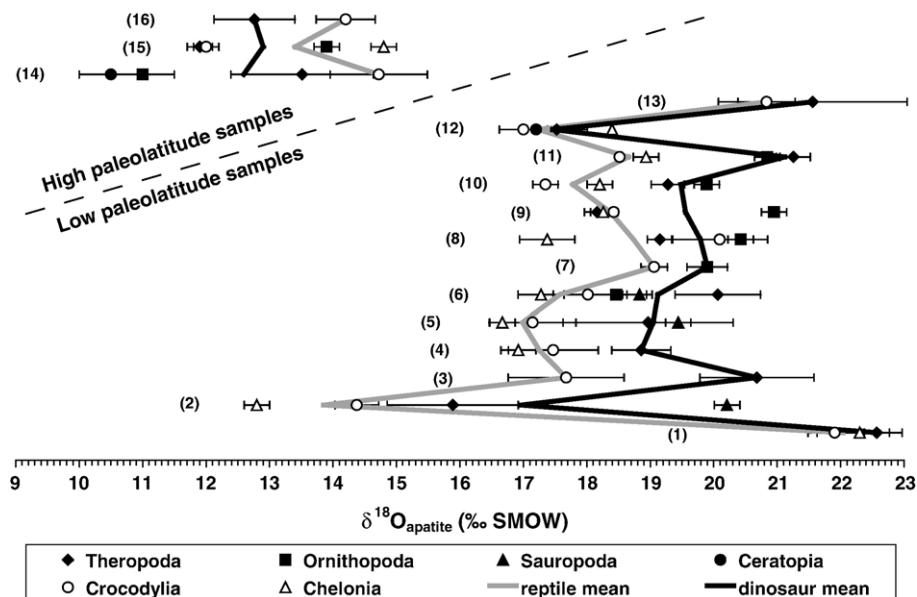


Fig. 3. Mean $\delta^{18}\text{O}$ values of phosphate from various Cretaceous vertebrate taxonomic groups vertically sorted by their relative stratigraphic age for high and low paleolatitudes localities (see Fig. 2 for the reference numbers of localities and stratigraphic ages). Note that mean dinosaur $\delta^{18}\text{O}$ values are systematically higher than those of co-existing crocodiles and turtles at low latitudes, this isotopic trend being reversed at high latitudes.

Table 1
Oxygen isotope composition of phosphate from Cretaceous dinosaurs, fresh water crocodylians and turtles

Sample no.	Nature	Taxon	Diet	Locality name	Country	Age	Paleolatitude (deg)	$\delta^{18}\text{O}$ (‰SMOW)	Source
F014	Dinosaur tooth enamel	Theropoda	C	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	21.5	This study
F016	Dinosaur tooth enamel	Theropoda	C	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	21.0	This study
F018	Dinosaur bulk tooth	Hadrosauridae	H	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	20.8	This study
F017	Crocodylian bulk tooth	<i>Thoracosaurus</i> sp.	C	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.5	This study
F019	Crocodylian osteoderm	<i>Thoracosaurus</i> sp.	C	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.6	This study
F015	Turtle osteoscuta	Chelonia	?	Cassagnau 2	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.9	This study
F008	Dinosaur bulk tooth	Theropoda	C	Cassagnau 1	France	Late Maastrichtian	34.7 (+3.7/–3.4)	19.0	This study
F010	Dinosaur tooth enamel	Theropoda	C	Cassagnau 1	France	Late Maastrichtian	34.7 (+3.7/–3.4)	19.5	This study
F012	Dinosaur bulk tooth	Hadrosauridae	H	Cassagnau 1	France	Late Maastrichtian	34.7 (+3.7/–3.4)	19.9	This study
F013	Crocodylian bulk tooth	<i>Thoracosaurus</i> sp.	C	Cassagnau 1	France	Late Maastrichtian	34.7 (+3.7/–3.4)	17.4	This study
F009	Turtle osteoscuta	Chelonia	?	Cassagnau 1	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.2	This study
AUS 240	Dinosaur bulk tooth	Theropoda	C	Ausseing	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.2	This study
F020	Dinosaur bulk tooth	Hadrosauridae	H	Ausseing	France	Late Maastrichtian	34.7 (+3.7/–3.4)	21.0	This study
F023	Crocodylian bulk tooth	<i>Acynodon</i> sp.	C	Ausseing	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.5	This study
F024	Crocodylian bulk tooth	<i>Musturzabalsuchus</i> sp.	C	Ausseing	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.4	This study
F022	Turtle osteoscuta	Chelonia	?	Ausseing	France	Late Maastrichtian	34.7 (+3.7/–3.4)	18.3	This study
R002	Dinosaur bulk tooth	Dromaeosauridae	C	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	19.2	This study
R005	Dinosaur bulk tooth	<i>Rhabdodon</i> sp.	H	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	20.4	This study
R008	Crocodylian bulk tooth	<i>Doratodon</i> sp.	C	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	19.3	This study
R001	Crocodylian bulk tooth	<i>Allodaposuchus</i> sp.	C	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	20.9	This study
R007	Turtle osteoscuta	<i>Kallokibotion bajazidi</i>	?	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	16.9	This study
R009	Turtle osteoscuta	<i>Kallokibotion bajazidi</i>	?	Fântânele	Romania	Late Maastrichtian	39.8 (+4.2/–3.8)	17.8	This study
F001	Dinosaur tooth enamel	<i>Tarascosaurus salluvicus</i>	C	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	20.7	This study
F002	Dinosaur tooth enamel	<i>Tarascosaurus salluvicus</i>	C	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	19.4	This study
F003	Dinosaur bulk tooth	<i>Rhabdodon priscus</i>	H	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	18.0	This study
F004	Dinosaur bulk tooth	<i>Rhabdodon priscus</i>	H	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	18.9	This study
F028	Dinosaur bulk tooth	<i>Ampelosaurus atacis</i>	H	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	18.8	This study
F031	Dinosaur bulk tooth	<i>Ampelosaurus atacis</i>	H	Cruzy	France	Late Campanian–Early Maastrichtian	35.5 (+5.1/–4.6)	18.9	This study
F005	Crocodylian	Crocodylia	C	Cruzy	France	Late Campanian–	35.5	18.6	This study

(continued on next page)

Table 1 (continued)

Sample no.	Nature	Taxon	Diet	Locality name	Country	Age	Paleolatitude (deg)	$\delta^{18}\text{O}$ (‰SMOW)	Source
F026	tooth enamel Crocodilian bulk tooth	Crocodylia	C	Cruzy	France	Early Maastrichtian– Late Campanian	(+5.1/–4.6) 35.5	17.5	This study
F007	Turtle osteoscuta	cf. <i>Foxemys</i>	?	Cruzy	France	Early Maastrichtian– Late Campanian	(+5.1/–4.6) 35.5	17.6	This study
F029	Turtle osteoscuta	cf. <i>Foxemys</i>	?	Cruzy	France	Early Maastrichtian– Late Campanian	(+5.1/–4.6) 35.5	17.5	This study
F030	Turtle osteoscuta	cf. <i>Foxemys</i>	?	Cruzy	France	Early Maastrichtian– Late Campanian	(+5.1/–4.6) 35.5	16.8	This study
CA001	Dinosaur bulk tooth	Theropoda	C	Onefour	Canada	Late Campanian	58.6 (+8.1/–7.2)	11.9	This study
CA010	Dinosaur bulk tooth	Ornithopoda	H	Onefour	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.9	This study
CA004	Crocodilian bulk tooth	Crocodylia	C	Onefour	Canada	Late Campanian	58.6 (+8.1/–7.2)	12.0	This study
CA006	Osteoscuta	Chelonia	?	Onefour	Canada	Late Campanian	58.6 (+8.1/–7.2)	14.8	This study
S001	Dinosaur bulk tooth	Hadrosauridae	H	Košina	Slovenia	Campanian– Maastrichtian	38.4 (+5.5/–4.9)	20.2	This study
S005	Dinosaur bulk tooth	Hadrosauridae	H	Košina	Slovenia	Campanian– Maastrichtian	38.4 (+5.5/–4.9)	19.6	This study
S002	Crocodilian bulk tooth	Crocodylia	C	Košina	Slovenia	Campanian– Maastrichtian	38.4 (+5.5/–4.9)	19.3	This study
S003	Crocodilian bulk tooth	Crocodylia	C	Košina	Slovenia	Campanian– Maastrichtian	38.4 (+5.5/–4.9)	18.8	This study
S006	Crocodilian bulk tooth	Crocodylia	C	Košina	Slovenia	Campanian– Maastrichtian	38.4 (+5.5/–4.9)	19.1	This study
M-BL-022	Dinosaur tooth enamel	<i>Carcharodontosaurus saharicus</i>	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	19.0	This study
M-BL-023	Dinosaur tooth enamel	<i>Carcharodontosaurus saharicus</i>	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	18.2	This study
M-BL-036	Dinosaur tooth enamel	<i>Spinosaurus aegypticus</i>	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	19.3	This study
M-BL-013	Crocodilian osteoderm	Crocodylia	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	16.7	This study
M-BL-038a	Crocodilian tooth enamel	cf. <i>Sarcosuchus</i>	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	18.4	This study
M-BL-040	Crocodilian tooth enamel	Crocodylia	C	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	17.4	This study
M-BL-014	Turtle osteoscuta	Chelonia	?	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	16.7	This study
M-BL-016	Turtle osteoscuta	Chelonia	?	Bou Laalou	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	17.2	This study
M-KS-023	Dinosaur tooth enamel	<i>Carcharodontosaurus saharicus</i>	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	20.7	This study
M-KS-028	Dinosaur tooth enamel	<i>Carcharodontosaurus saharicus</i>	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	18.9	This study
M-KS-007	Dinosaur tooth enamel	<i>Spinosaurus aegypticus</i>	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	17.8	This study
M-KS-036	Dinosaur tooth enamel	<i>Spinosaurus aegypticus</i>	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	20.3	This study
M-KS-037	Dinosaur tooth enamel	<i>Spinosaurus aegypticus</i>	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	17.3	This study
M-KS-001	Dinosaur tooth enamel	Titanosauridae	H	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	19.4	This study
M-KS-034	Crocodilian tooth enamel	Crocodylia	C	Khetitila Srhira	Morocco	Early Cenomanian	16.5 (+2.2/–2.1)	16.5	This study
M-KS-040	Crocodilian	Crocodylia	C	Khetitila	Morocco	Early Cenomanian	16.5	17.8	This study

Table 1 (continued)

Sample no.	Nature	Taxon	Diet	Locality name	Country	Age	Paleolatitude (deg)	$\delta^{18}\text{O}$ (‰SMOW)	Source
M-KS-012	bulk tooth Turtle	Chelonia	?	Srhira	Morocco	Early Cenomanian	(+2.2/–2.1) 16.5	16.7	This study
TU-001	osteoscuta Dinosaur tooth enamel	Theropoda	C	Srhira Bateun el Hmaima	Tunisia	Early Albian	(+2.2/–2.1) 12.4 (+3.5/–3.3)	20.0	This study
TU-002	Dinosaur tooth enamel	Theropoda	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	21.2	This study
TU-003	Dinosaur tooth enamel	Theropoda	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	20.3	This study
TU-004	Dinosaur tooth enamel	cf. <i>Spinosaurus</i>	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	22.2	This study
TU-006	Dinosaur tooth enamel	cf. <i>Spinosaurus</i>	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	19.8	This study
TU-005	Crocodylian tooth enamel	Crocodylia?	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	16.4	This study
TU-007	Crocodylian tooth enamel	Crocodylia	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	18.2	This study
TU-008	Crocodylian tooth enamel	Crocodylia	C	Bateun el Hmaima	Tunisia	Early Albian	12.4 (+3.5/–3.3)	18.4	This study
TH001	Dinosaur tooth enamel	Theropoda	C	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	15.5	This study
TH005	Dinosaur tooth enamel	Theropoda	C	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	14.9	This study
TH008	Dinosaur tooth enamel	Theropoda	C	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	17.3	This study
TH006	Dinosaur bulk tooth	Nemegtosauridae	H	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	20.2	This study
TH002	Crocodylian tooth enamel	Crocodylia	C	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	14.7	This study
TH007	Crocodylian tooth enamel	Crocodylia	C	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	14.0	This study
TH003	Turtle osteoscuta	Chelonia	?	Khok Pha Suam	Thailand	Aptian–Albian	24.3 (+1.9/–1.8)	12.8	This study
CHE-02-10	Dinosaur bulk tooth	cf. <i>Nuthetes</i>	C	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	22.6	This study
BG52	Crocodylian tooth enamel	<i>Goniopholis</i> sp.	C	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	22.1	This study
BG57	Crocodylian osteoderm	<i>Goniopholis</i> sp.	C	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	21.8	This study
BG58	Crocodylian osteoderm	<i>Goniopholis</i> sp.	C	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	21.3	This study
BG53	Crocodylian tooth enamel	<i>Pholidosaurus</i> sp.	C	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	22.4	This study
BG55	Turtle osteoscuta	? <i>Pleurosternon</i> sp.	?	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	21.6	This study
BG56	Turtle osteoscuta	? <i>Tretosternon</i> sp.	?	Cherves- de-Cognac	France	Berriasian	32.6 (+5.5/–4.8)	23.0	This study
–	Dinosaur tooth enamel	<i>Saurornitholestes</i>	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.0	[16]
–	Dinosaur tooth enamel	<i>Saurornitholestes</i>	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	18.3	[16]
–	Dinosaur tooth enamel	<i>Saurornitholestes</i>	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.5	[16]
–	Dinosaur tooth enamel	Ceratopsidae	H	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.2	[15]
–	Crocodylian tooth enamel	Crocodylian	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	16.8	[16]

(continued on next page)

Table 1 (continued)

Sample no.	Nature	Taxon	Diet	Locality name	Country	Age	Paleolatitude (deg)	$\delta^{18}\text{O}$ (‰SMOW)	Source
–	Crocodylian tooth enamel	Crocodylian	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.1	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	16.7	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	16.7	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.7	[16]
–	Turtle osteoscuta	Turtle	?	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	18.4	[15]
–	Dinosaur tooth enamel	<i>Carnosaura</i>	C	Texas	United States	Late Campanian– Early Maastrichtian	36.0 (+5.2/–4.6)	17.3	[15]
–	Dinosaur tooth enamel	<i>Majungatholus</i>	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	21.6	[16]
–	Dinosaur tooth enamel	<i>Majungatholus</i>	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	23.2	[16]
–	Dinosaur tooth enamel	<i>Majungatholus</i>	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	23.2	[16]
–	Dinosaur tooth enamel	<i>Majungatholus</i>	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	20.2	[16]
–	Dinosaur tooth enamel	<i>Majungatholus</i>	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	19.6	[16]
–	Crocodylian tooth enamel	Crocodylian	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	20.2	[16]
–	Crocodylian tooth enamel	Crocodylian	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	21.2	[16]
–	Crocodylian tooth enamel	Crocodylian	C		Madagascar	Early Maastrichtian	–32.0 (+3.2/–3.5)	21.1	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	12.9	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	12.5	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	13.5	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	13.1	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.8	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	11.8	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	15.4	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.1	[16]
–	Dinosaur bone	<i>Orodromeus makelai</i>	H	Montana	United States	Campanian	54.8 (+7.6/–6.8)	11.5	[12]
–	Dinosaur bone	<i>Hypacrosaurus stebingegi</i>	H	Montana	United States	Campanian	54.8 (+7.6/–6.8)	10.5	[12]
–	Dinosaur bone	<i>Montanoceratops</i>	H	Montana	United States	Campanian	54.8 (+7.6/–6.8)	11.0	[12]
–	Dinosaur bone	<i>Achelousaurus horneri</i>	H	Montana	United States	Campanian	54.8 (+7.6/–6.8)	10.0	[12]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.7	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	16.2	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	15.4	[16]

Table 1 (continued)

Sample no.	Nature	Taxon	Diet	Locality name	Country	Age	Paleolatitude (deg)	$\delta^{18}\text{O}$ (‰SMOW)	Source
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.1	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.7	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	15.0	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.9	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	13.4	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Montana	United States	Campanian	54.8 (+7.6/–6.8)	14.1	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	11.6	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.2	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	12.6	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.0	[16]
–	Dinosaur tooth enamel	<i>Albertosaurus</i>	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.4	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.9	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	13.6	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	14.6	[16]
–	Crocodylian tooth enamel	Crocodylian	C	Alberta	Canada	Late Campanian	58.6 (+8.1/–7.2)	14.7	[16]

Sample identification, location and stratigraphic age are reported along with calculated paleolatitudes and their associated uncertainties. Diet is indicated as C=carnivorous, H=herbivorous and ?=unknown diet.

Crocodile blood samples were centrifuged to separate the plasma that was equilibrated with 20 μmol of CO_2 at 25 °C for 48 h. CO_2 was analysed with a GV IsoprimeTM mass spectrometer at the University of Lyon. Reproducibility of oxygen isotope measurements is better than 0.1‰.

4. Results

Oxygen isotope compositions of vertebrate phosphate are given in Table 1 and mean values for each taxonomic group are plotted on Fig. 3. Differences in oxygen isotope compositions between non-dinosaurian reptiles and dinosaurs (noted $\Delta^{18}\text{O}_{\text{dinosaurs} - \text{non-dinosaurian reptiles}}$) from each locality were tested for significance using a two-step procedure involving: (i) for each locality, a unilateral Student's *t*-test of the differences between two means, and (ii) for all localities, a Fisher's overall test for significance [39] (Table 2). For low latitude localities, $\delta^{18}\text{O}$ values of dinosaurs are significantly more positive than for non-

dinosaurian reptiles ($\chi^2=97.53$, $df=26$, $p<0.00001$). Conversely, for high latitude localities, $\delta^{18}\text{O}$ values of dinosaurs are significantly more negative than for non-dinosaurian reptiles ($\chi^2=28.95$, $df=6$, $p\approx 0.00006$). For the whole set of data, this $\Delta^{18}\text{O}$ value decreases from about +3 down to –2 with increasing paleolatitude (Fig. 4). It is noteworthy that the null difference occurs at a paleolatitude of about 50° in agreement with the present-day $\Delta^{18}\text{O}_{\text{endotherms} - \text{ectotherms}}$ curve.

5. Discussion

5.1. Preservation of the original oxygen isotope composition of reptile apatite?

Although no method is available to check whether the oxygen isotope composition of tooth phosphate was affected by diagenetic processes, several ways to assess the preservation state of primary isotopic record have been proposed (see [20] and references therein). Tooth

Table 2

Data used for statistical calculations at each fossil locality (Loc.)

Loc.	Reptiles			Dinosaurs			Student's <i>t</i> -test		Delta		Latitude		
	<i>N</i>	Mean	S.D.	<i>N</i>	Mean	S.D.	<i>t</i> value	<i>p</i> (unilateral)	Mean	S.D.	Mean	Max	Min
1	6	22.04	0.578	1	22.57	0.200	0.852	0.2166	0.53	0.624	32.6	38.10	27.80
2	3	13.85	0.896	4	16.97	2.252	2.516	0.0267	3.12	1.401	24.3	26.23	22.46
3	3	17.67	1.029	5	20.68	0.955	5.109	0.0032	3.01	0.716	12.4	15.90	9.10
4	5	17.25	0.676	3	18.86	0.524	3.762	0.0047	1.61	0.459	16.5	18.67	14.44
5	3	16.99	0.680	6	19.05	1.295	3.127	0.0084	2.06	0.815	16.5	18.67	14.44
6	5	17.57	0.610	6	19.16	0.954	3.342	0.0043	1.59	0.496	35.5	40.63	30.94
7	3	19.06	0.235	2	19.90	0.399	2.671	0.0378	0.84	0.274	38.4	43.91	33.52
8	4	18.74	1.621	2	19.79	0.797	1.068	0.1729	1.05	1.264	39.8	44.01	35.97
9	3	18.37	0.106	2	19.56	1.748	0.958	0.2044	1.19	0.925	34.7	38.41	31.30
10	2	17.78	0.536	3	19.48	0.405	3.824	0.0158	1.70	0.414	34.7	38.41	31.30
11	3	18.66	0.223	3	21.12	0.330	10.696	0.0002	2.46	0.230	34.7	38.41	31.30
12	6	17.23	0.658	5	17.46	0.479	0.660	0.2629	0.23	0.354	36.0	41.20	31.39
13	3	20.83	0.507	5	21.56	1.583	0.949	0.1898	0.73	0.968	32.0	35.46	28.82
14	9	14.72	0.790	11	12.59	1.666	3.757	0.0007	-2.13	0.606	54.8	62.44	48.01
15	2	13.40	1.500	2	12.90	1.000	0.392	0.7330	-0.50	1.275	58.6	66.67	51.38
16	9	14.20	0.460	5	12.80	0.640	4.312	0.0010	-1.40	0.294	58.6	66.67	51.38

Differences in oxygen isotope compositions between non-dinosaurian reptiles and dinosaurs were tested for significance in a two-step procedure involving: (i) for each locality, a unilateral Student's *t*-test of the differences between two means, and (ii) for all localities, a Fisher's overall test for significance [39]. Calculated paleolatitudes [22] and their associated uncertainties are also displayed.

enamel, considered as the biomineral most likely to preserve primary $\delta^{18}\text{O}_p$ record [15], was analysed preferentially. Here, the main argument supporting the preservation of pristine isotopic record is the significant

and systematic offsets observed between dinosaurs and ectothermic reptiles (turtles and crocodylians). These isotopic offsets, which decrease from about $+1.5 \pm 0.9\text{‰}$ to $-1.4 \pm 0.7\text{‰}$ with increasing latitude, most likely result

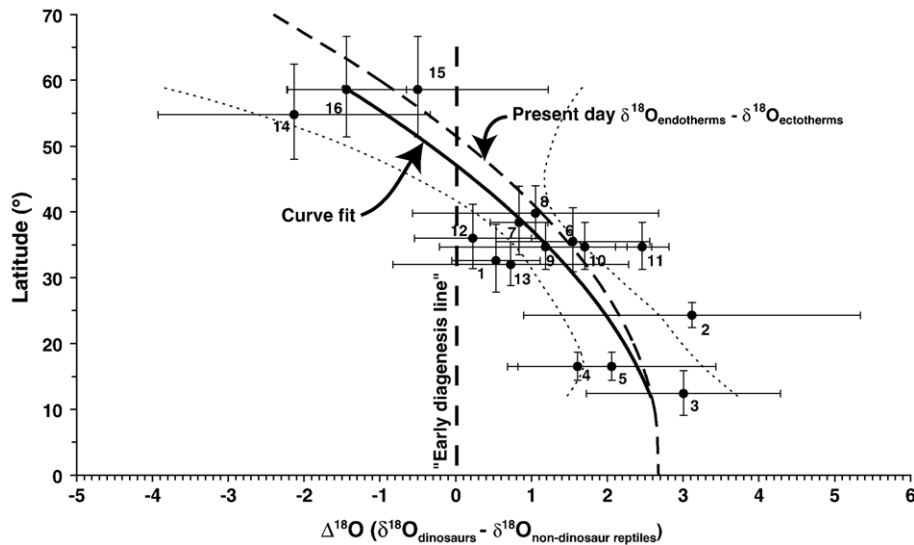


Fig. 4. Mean $\Delta^{18}\text{O}_p$ values ($=\delta^{18}\text{O}_{\text{dinosaurs}} - \delta^{18}\text{O}_{\text{non-dinosaurian reptiles}}$) for each studied locality plotted against absolute paleolatitude (see Fig. 2). The “early diagenesis line” corresponds to the expected $\Delta^{18}\text{O}$ values of phosphatic remains whose oxygen isotope composition was re-equilibrated by diagenetic aqueous fluids. The 95% non-parametric bootstrap confidence interval belts (dotted curves; estimated from 100,000 iterations) indicate that the regressed 2nd order polynomial curve (bold curve; multiple- $R^2=0.689$, Fisher's $F=14.41$, $p\text{-value}=5.0 \times 10^{-4}$) significantly differs from the “early diagenesis line” ($\Delta^{18}\text{O}=0$), whereas it cannot be distinguished from the present-day difference between $\delta^{18}\text{O}_{\text{endotherms}}$ and $\delta^{18}\text{O}_{\text{ectotherms}}$ as a function of latitude (dashed curve; $\Delta^{18}\text{O}=-1.1 \times 10^{-3}L^2+5.8 \times 10^{-3}L+2.677$).

from differences in vertebrate ecology and physiology. If early diagenetic processes had occurred, they would have homogenised $\delta^{18}\text{O}_p$ values of all vertebrate remains whatever the physiology and ecology of the corresponding taxa [40]. As $\delta^{18}\text{O}_p$ values published in Barrick et al. [12], Kolodny et al. [15], and Fricke and Rogers [16] follow the same consistent latitudinal trend as our values, we consider that they have most likely preserved their original isotopic composition.

5.2. Significance of the oxygen isotope composition of reptile apatite

Differences in $\delta^{18}\text{O}_p$ values of co-existing dinosaurs and ectothermic reptiles may be related both to thermophysiology and to water strategy. Unlike dinosaurs that were terrestrial animals, turtles and crocodiles are semi-aquatic reptiles. Therefore, dinosaur body waters may have been systematically more ^{18}O -enriched than those of crocodilians and turtles relative to environmental water. The best way to cast off this “water strategy” bias would have been to compare dinosaurs with terrestrial ectotherms such as lizards or snakes. However, lepidosaurian tooth material is so scarce that crocodilian and turtle remains that are abundant have been consequently preferred. Moreover, depending on diet, carnivorous and herbivorous dinosaurs may have had different $\delta^{18}\text{O}_p$ values. For example, plant leaves, which constitute the main source of food and water for some herbivores, have an oxygen isotope composition sensitive to environmental conditions. This is the case of relative air humidity which affects plant evaporation and shifts the water composition towards more positive $\delta^{18}\text{O}$ values. Herbivore body waters are in turn more or less enriched in ^{18}O relative to local precipitations, their $\delta^{18}\text{O}$ values are consequently increased by several permils depending on the variations in relative air humidity [41]. Such effects are however weak in the case of carnivores with an increase in $\delta^{18}\text{O}$ values in the range of a few tens of permil as predicted by the physiological model of Kohn [21,41]. Taking into account associated uncertainties, no such systematic and significant $\delta^{18}\text{O}_p$ differences are observed in the present data set between co-existing herbivorous and carnivorous dinosaurs. Our database reveals that the $\delta^{18}\text{O}_p$ values of dinosaurs are not systematically higher than those of co-existing crocodilians and turtles. The isotopic pattern shown in Fig. 4 partly results from differences in thermophysiology that are recorded in the $\delta^{18}\text{O}_p$ values as a function of the latitude, i.e. changes in mean air temperatures. Indeed, the similarity between the variations in $\Delta^{18}\text{O}_{\text{dinosaurs} - \text{non-dinosaurian reptiles}}$ values as a function of paleolatitude with those corresponding to the present-day model latitudinal $\Delta^{18}\text{O}_{\text{endotherms} - \text{ectotherms}}$

curve (Fig. 4) suggests that differences in body temperatures and water strategies between dinosaurs and associated crocodilians and turtles are similar to those observed between present-day terrestrial endotherms and semi-aquatic ectotherms. This suggests that, like extant mammals, dinosaurs possessed a high metabolism compared to proven ectothermic reptiles.

5.3. Estimation of dinosaur body temperature

Differences in body temperature between dinosaurs and the other reptiles may be inferred from the differences in both their mean $\delta^{18}\text{O}_p$ values and body water ^{18}O -enrichment relative to ingested water ($\Delta^{18}\text{O}_{\text{body water} - \text{ingested water}}$). Based on the few present-day data available so far, blood $\delta^{18}\text{O}$ values of *Crocodylus niloticus* (this study) and turtles [33] (Table 3) lead to estimate a mean $\Delta^{18}\text{O}_{\text{body water} - \text{ingested water}}$ of $2.5 \pm 1.1\%$ for these reptiles. In the case of mammals, similar measurements have also been performed, but so far only on humans and domestic pigs [34], leading to a mean $\Delta^{18}\text{O}_{\text{body water} - \text{ingested water}}$ value of $3.3 \pm 0.6\%$. Assuming that dinosaurs had an elevated metabolic rate comparable to that of extant mammals, the body water ^{18}O -enrichment

Table 3
Oxygen isotope compositions of body (blood plasma) and drinking waters from crocodiles, turtles [33], humans and domestic pigs [34]

Sample no.	Taxon	$\delta^{18}\text{O}_{\text{body water}}$	$\delta^{18}\text{O}_{\text{water}}$	Source
SG001	<i>Crocodylus niloticus</i>	−6.8	−8.7	This study
SG002	<i>Crocodylus niloticus</i>	−7.1	−8.7	This study
SG003	<i>Crocodylus niloticus</i>	−7.5	−8.7	This study
SG004	<i>Crocodylus niloticus</i>	−7.2	−8.7	This study
172	<i>Chrysemys</i> sp.	−11.2	−15.0	[33]
502	<i>Chrysemys</i> sp.	−11.4	−15.0	[33]
211	<i>Chrysemys</i> sp.	−1.2	−3.8	[33]
156	<i>Chrysemys</i> sp.	−2.3	−6.2	[33]
5	<i>Homo sapiens</i>	−4.9	−9.5	[34]
12	<i>Homo sapiens</i>	−4.2	−8.0	[34]
36	<i>Homo sapiens</i>	−3.5	−7.2	[34]
13	<i>Homo sapiens</i>	−3.9	−7.2	[34]
10	<i>Homo sapiens</i>	−3.0	−6.3	[34]
10	<i>Homo sapiens</i>	−2.7	−5.5	[34]
6	<i>Homo sapiens</i>	−2.6	−5.5	[34]
15	<i>Sus scrofa</i>	−6.6	−10.0	[34]
3	<i>Sus scrofa</i>	−6.8	−10.0	[34]
5	<i>Sus scrofa</i>	−5.3	−8.0	[34]
10	<i>Sus scrofa</i>	−4.2	−8.4	[34]
7	<i>Sus scrofa</i>	−3.9	−7.2	[34]
4	<i>Sus scrofa</i>	−4.0	−6.7	[34]
3	<i>Sus scrofa</i>	−3.6	−6.3	[34]

difference of about 1‰ calculated between semi-aquatic reptiles (turtles and crocodylians) and mammals was subtracted from the observed offsets measured between dinosaurs and associated fossil turtles and crocodylians. Residual values of $+0.5 \pm 1\%$ and $-2.5 \pm 1\%$ are thus obtained for low and high latitude localities, respectively. Using the slope of the phosphate–water temperature scale [42], these residual $\delta^{18}\text{O}$ values correspond to a predicted mean body temperature for crocodylians and turtles about 2 °C higher than for dinosaurs at low latitudes. Applying the same method to high latitude samples, dinosaurs were about 10 °C warmer than associated crocodylians and turtles.

At low latitudes, present-day reptiles tend to warm their bodies, reaching temperatures close to those of mammals, in the 35–37 °C range, sometimes up to 38–39 °C [43], higher temperatures being lethal. If we assume that Cretaceous low latitude crocodylians and turtles had similar body temperatures, then the mean T_b of dinosaurs was in the 33–37 °C range, which encompasses the values of present-day endotherms. In cooler environments, reptiles being submitted to high temperature variations, their phosphatic tissues are deposited only when the body temperature is high enough. A minimum activity temperature of 26–28 °C has been measured on living crocodylians (see [43,44]). Assuming that Cretaceous high latitude crocodylians and turtles lived under similar conditions, then associated dinosaurs had a T_b of about 36–38 °C, statistically indistinguishable from that of their low latitude counterparts. These calculations strengthen the hypothesis that at least these Cretaceous dinosaurs were true endotherms and possessed a rather constant temperature similar to that of present-day mammals. Accordingly, at least the four studied groups of Cretaceous dinosaurs were most likely endothermic, or able to maintain a constant body temperature different from that of their environment.

Gigantothermy or mass homeothermy is an alternative hypothesis to endothermy for explaining dinosaur thermophysiology [45]. According to this hypothesis, very large ectotherms are able to maintain a stable body temperature even in relatively cold environments. Medium-sized to large species of Cretaceous dinosaurs may have possessed such thermal strategies. For polar dinosaurs from the north slope of Alaska, seasonal migrations of medium to large species and winter hibernation of small species have been proposed [6]. Assuming that only large dinosaurs could maintain a stable body temperature through gigantothermy, small supposedly ectothermic dinosaurs from high latitudes should have higher $\delta^{18}\text{O}$ values than large dinosaurs, in the range of crocodile and turtle values. However, all $\delta^{18}\text{O}$ values of small and large dinosaurs are lower than those of cro-

codylians and turtles, indicating that they had higher body temperatures, invalidating the hypothesis of gigantothermy for these taxa. Sauropods, the largest of all dinosaurs, have been considered either as simple ectotherms (the traditional view), as gigantothermic ectotherms [6,7] or as endotherms [1,46] on the basis of different kinds of evidence. Our $\delta^{18}\text{O}$ values of Cretaceous sauropod teeth are indistinguishable from other dinosaur values, a result which is more in accordance with endothermy than with gigantothermy.

6. Conclusion

The first salient result of this study is the absence of systematic difference observed between the four dinosaur taxa studied or between crocodile or turtle taxa possessing various diet or water strategies at any given site. This indicates, in the first order, that the $\delta^{18}\text{O}_w$ of drinking water and body temperature are the two main variables recorded in $\delta^{18}\text{O}_p$ values of these reptiles. Secondly, body temperatures estimated from $\delta^{18}\text{O}_p$ are similar for all the four groups of dinosaurs that have been studied, suggesting that they shared similar thermophysiology. As our samples cover a fairly wide spectrum, including theropods, sauropods, ornithomimids and ceratopsians, it would appear that endothermy was widespread among dinosaurs, at least in the Late Cretaceous, and not restricted to, for instance, the more bird-like forms. From a phylogenetic point of view, this suggests that endothermy may be a synapomorphy of dinosaurs as a whole, a feature acquired at a very early stage in the evolution of the group. An alternative but less parsimonious hypothesis is that endothermy may have been independently acquired in all or some of the four groups of Cretaceous dinosaurs we have sampled, as suggested by recent studies on prosauropod bone histology [47]. This could be tested by isotopic studies on a wider sample of dinosaurs, including earlier, pre-Cretaceous forms.

Acknowledgements

The authors thank the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois (Cruzy), the Espérasa Dinosaur Museum for providing French fossil samples, and Jean-Paul Billon-Bruyat, Larbi Boudad, Donald Brinkman, Zoltan Csiki, Irena Debeljak, Jim Gardner, Dan Grigorescu, Lahcen Kabiri, Adrijan Košir, Jean-Michel Mazin, Varavudh Suteethorn and Haiyan Tong who provided other samples from many parts of the world. The authors are also grateful to Dr. Samuel Martin, Luc Fougeirol ("La ferme aux crocodylians", Pierrelatte, France) and Dr. Kooby for providing

and preparing crocodile blood samples. This work was supported by the “ECLIPSE” and “ECLIPSE2” programs of the Centre National de la Recherche Scientifique and by the Jurassic foundation.

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