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Thermophysiologicals of Jurassic marine crocodylomorphs inferred from the oxygen isotope composition of their tooth apatite

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isotopes, tooth apatite

Summary

Teleosauridae and Metriorhynchidae were thalattosuchian crocodylomorph clades that secondarily adapted to marine life and coexisted during the Middle to Late Jurassic. While teleosaurid diversity collapsed at the end of the Jurassic, most likely as a result of a global cooling of the oceans and associated marine regressions, metriorhynchid diversity was largely unaffected, although the fossil record of Thalattosuchia is poor in the Cretaceous. In order to investigate the possible differences in thermophysiology between these two thalattosuchian lineages, we analysed stable oxygen isotope compositions (expressed as $\delta^{18}\text{O}$ values) of tooth apatite from metriorhynchid and teleosaurid specimens. We then compared them to the $\delta^{18}\text{O}$ values of coexisting endothermic ichthyosaurs and plesiosaurs, as well as ecto-poikilothermic chondrichthyans and osteichthyans. The distribution of $\delta^{18}\text{O}$ values suggests that both teleosaurids and metriorhynchids had body temperatures intermediate between those of typical ecto-poikilothermic vertebrates and warm-blooded ichthyosaurs and plesiosaurs, metriorhynchids being slightly warmer than teleosaurids. We propose that metriorhynchids were able to raise their body temperature above that of the ambient environment by metabolic heat production, as endotherms do, but could not maintain a constant body temperature compared to fully homeothermic ichthyosaurs and plesiosaurs. Teleosaurids, on the other hand, may have raised their body temperature by mouth-gape basking, as modern crocodylians do, and benefited from the thermal inertia of their large body mass to maintain their body temperature above ambient one. Endothermy in metriorhynchids might have been a byproduct of their ecological adaptations to active pelagic hunting, and it probably allowed them to survive the global cooling of the Late Jurassic, thus explaining the selective extinction affecting Thalattosuchia at the Jurassic-Cretaceous boundary.

Introduction

Extant crocodylians are archosaurs that rely on environmental sources of heat in order to raise and maintain their body temperature by behavioural thermoregulation in a restricted range bracketed by “critical minimum” and “critical maximum” temperatures (Cowles and Bogert, 1944; Pough and Gans, 1982). Within this critical range, crocodylians tend to keep their body temperature within a narrower activity range from about 25°C to 40°C as determined empirically for a few extant species (see Markwick (1998) for a review). Consequently, the spatial and temporal distribution of crocodylians is limited by the temperatures of their living environments and by their seasonal fluctuations. Due to their rather conservative growth morphology and their restricted latitudinal distribution today, and in the geologic record, extant and fossil representatives of the crown group have been used as climate proxies for more than a century (Berg, 1965; Crichton, 1825; Markwick, 1998; Owen, 1850). Based on observations of extant representatives of crown group Crocodylia Owen, 1842, Markwick (1998) proposed that the occurrence of fossil representatives imply a living Mean Annual Air temperature (MAT) $\geq 14.2^{\circ}\text{C}$ and a Coldest Month Mean temperature (CMM) $\geq 5.5^{\circ}\text{C}$. These minimum limits have been tentatively used to constrain the climatic environment of long-extinct crocodylomorphs (Amiot et al., 2011), as well as the more distantly related clade Choristodera (Tarduno et al., 1998).

The crocodylomorph clade Thalattosuchia became secondarily adapted to marine life during the Mesozoic, and is subdivided into the families Teleosauridae Saint-Hilaire, 1831 and Metriorhynchidae Fitzinger, 1843. While teleosaurids retained a morphology reminiscent of typical semi-aquatic longirostrine crocodylomorphs, in having extensive osteoderm coverage and limbs adapted for terrestrial locomotion (Eudes-Deslongchamps, 1869), metriorhynchids had a more hydrodynamic body plan, with a hypocercal tail, and hydrofoil-like forelimbs (Fraas, 1902; Young et al., 2010). The bone histology of Callovian teleosaurids and metriorhynchids has been used to hypothesize that thalattosuchians were ectothermic (i.e. they rely on environmental sources of heat in order to raise their body temperature) and poikilothermic (i.e. their body temperature vary along

1
2 with that of their environment), with teleosaurids being capable of mouth-gape basking on shore,
3
4 whereas metriorhynchids thermoregulated differently by staying close to the water surface (Hua and
5
6 De Buffrénil, 1996). Hua and de Buffrénil (1996) did note that young metriorhynchids may have
7
8 had a faster growth rate than wild extant crocodylians.
9

10
11 Martin et al. (2014) analysed the diversity of marine crocodylomorphs through the Mesozoic
12
13 and Paleogene, and observed a significant correlation between Sea Surface Temperatures (SST) and
14
15 generic diversity within four lineages, including the teleosaurids. Teleosaurids, at least European
16
17 representatives, experienced a diversity crash at the end of the Jurassic during a global cooling of
18
19 Tethyan waters (Lécuyer et al., 2003b), but according to Fanti et al. (2016) they may have
20
21 continued to survive until at least the Hauterivian along the southern coast of the Tethys Sea.
22
23 Metriorhynchids however, appear to have experienced an explosive radiation during the Callovian,
24
25 surviving through the Late Jurassic until the Aptian (Chiarenza et al., 2015). When metriorhynchids
26
27 became extinct is currently unclear. Young et al. (2010) hypothesized a two-step extinction for
28
29 Metriorhynchidae, first a diversity crash at the end Jurassic, then a final extinction during the cold
30
31 icehouse interval of the Valanginian (Pucéat et al., 2003). However, recent re-evaluations of
32
33 Cretaceous fossils and updated phylogenetic studies have disproved both steps of this hypothesis,
34
35 with post-Valanginian metriorhynchid specimens known and no fewer than four metriorhynchid
36
37 lineages crossed the Jurassic-Cretaceous boundary (Chiarenza et al., 2015; Ósi et al., 2018; Young
38
39 et al., 2014a). The global thalattosuchian fossil record however is still poor, the known diversity of
40
41 this clade is still heavily biased by the European rock record, as well as global marine record
42
43 sampling biases for specific time spans (e.g. Aalenian, Oxfordian, Early Cretaceous). Regardless of
44
45 the geologic megabiases, there is still a conspicuous diversity mismatch within Thalattosuchia that
46
47 raised the question whether metriorhynchids evolved a distinct thermoregulatory strategy, such as
48
49 endothermic capabilities that would explain their diversity and survival under cool SSTs (Martin et
50
51 al., 2014).
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1
2 In order to investigate the thermophysiology of metriorhynchids, we analysed the oxygen
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4 isotope composition of the enamel phosphate of their teeth ($\delta^{18}\text{O}_p$). Indeed, the $\delta^{18}\text{O}_p$ value of
5
6 vertebrate apatite (the mineral constituting bone, teeth and some fish scales) depends on the
7
8 animal's body water $\delta^{18}\text{O}_{bw}$ value, as well as its body temperature (Kohn, 1996; Longinelli and
9
10 Nuti, 1973a; Luz et al., 1984). For air breathing vertebrates, the body water has a $\delta^{18}\text{O}_{bw}$ value
11
12 controlled by oxygen input coming from drinking water, food and inhaled oxygen (through
13
14 metabolic water production), as well as oxygen loss as water vapour through transcutaneous
15
16 evaporation, sweat, exhaled vapour, and liquid water in urine and feces, some of these losses being
17
18 associated with oxygen isotope fractionation (Kohn, 1996; Langlois et al., 2003). A fractionation
19
20 equation that relates the apatite phosphate $\delta^{18}\text{O}_p$ value to that of body water and body temperature
21
22 (T_b) can be adapted from the phosphate-water temperature scale previously established by
23
24 Longinelli and Nuti (1973a) and recently updated by Lécuyer et al. (2013). Such equation has
25
26 proven to be valid for a large range of invertebrate and vertebrate bioapatites (Kolodny et al., 1983;
27
28 Lécuyer et al., 1996; Longinelli and Nuti, 1973b, 1973a):
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$$36 T_b (\text{°C}) = 117.4 - 4.5 (\delta^{18}\text{O}_p - \delta^{18}\text{O}_{bw}) \quad (1)$$

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41 This relationship is commonly used to reconstitute past SSTs based on fish apatite as most
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43 of them have a body temperature similar to that of their surrounding water, and a body water $\delta^{18}\text{O}_{bw}$
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45 value equal to ambient one (Dera et al., 2009; Lécuyer et al., 2003b; Picard et al., 1998; Pucéat et
46
47 al., 2003). Air-breathing vertebrates have a body water ^{18}O -enriched relative to environmental
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49 water, the magnitude of which depends on the amount of body water loss through exhaled $\text{H}_2\text{O}_{\text{vapor}}$
50
51 and transcutaneous evaporation. Direct measurements have shown that terrestrial mammals and
52
53 birds have body water from about 4‰ to 7‰ ^{18}O -enriched relative to their drinking water
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55 (Lazzerini et al., 2016; Longinelli, 1984; Wolf et al., 2013) whereas the body waters of semi aquatic
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1
2 to aquatic crocodylians, turtles and birds are about 2‰ to 3‰ ^{18}O -enriched relative to their drinking
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4 water (Amiot et al., 2007; Barrick et al., 1999; Lazzerini et al., 2016).
5

6 In this study we estimate the body temperatures of metriorhynchid and teleosaurid
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8 thalattosuchians recovered from five Jurassic localities in England and France. By comparing T_b of
9
10 thalattosuchians to those of associated ichthyosaurs or plesiosaurs, as well as to their ambient SST,
11
12 we show that metriorhynchids may have evolved some degree of endothermic-like
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14 thermophysiology, whereas teleosaurids retained a more typical ecto-poikilothermy.
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20 **Materials and methods**

21 **Sample collection**

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23 We analysed eighty-eight fossil teeth of Jurassic fish and marine reptiles for their oxygen
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25 isotope composition of phosphate ($\delta^{18}\text{O}_p$), as well as for their oxygen ($\delta^{18}\text{O}_c$) and carbon ($\delta^{13}\text{C}_c$)
26
27 isotope composition of apatite carbonate. The first English locality is Smallmouth Sands, Dorset
28
29 (**Figure 1**), from the lower part of the Kimmeridge Clay Formation dated as lower Kimmeridgian
30
31 (Young et al., 2014b). The second English locality is the Oxford Clay Formation Peterborough clay
32
33 pits, a world-famous fossiliferous collection of sites, dated to the middle Callovian, which has
34
35 yielded a rich marine fauna along with terrestrial elements (Martill and Hudson, 1991). The first
36
37 French locality is “Les Vaches Noires” of Normandy, dated as upper Callovian, where the “Marnes
38
39 de Dives” Formation crops out, consisting of marls where a rich fauna composed of marine and
40
41 terrestrial elements have been recovered (Lebrun and Courville, 2013). The second French locality
42
43 is the excavation of “Les Lourdines” near the eponymous quarry, dated as middle Callovian, which
44
45 is composed of white limestone (calcaire des Lourdines) where a marine fauna and some terrestrial
46
47 plants have been recovered (Barale et al., 1974). Finally, the locality of Cintheaux dated as
48
49 Bathonian consists of the “Pierre de Caen” limestone that has yielded a marine fauna with some
50
51 terrestrial elements (Riout, 1963). Studied tooth specimens include those of metriorhynchid and
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53 teleosaurid thalattosuchians, ichthyosaurs, plesiosaurs, as well as of chondrichthyans and
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1
2 osteichthyans (**Supplementary table 1**). When possible, tooth enamel was sampled using a
3
4 spherical diamond-tipped drill bit. For smaller teeth, the bulk enamel and dentin were ground using
5
6 an agate mortar and pestle.
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10 11 **Analytical techniques**

12 13 *Oxygen isotope analysis of biogenic apatite phosphate*

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15 Apatite powders have been treated following the wet chemistry protocol described by
16
17 Crowson et al. (1991) and slightly modified by Lécuyer et al. (1993). This protocol consists in the
18
19 isolation of phosphate (PO_4^{3-}) from apatite as silver phosphate (Ag_3PO_4) crystals using acid
20
21 dissolution and anion-exchange resin. For each sample, 20-30 mg of enamel powder was dissolved
22
23 in 2 mL of 2 M HF. The CaF_2 residue was separated by centrifugation and the solution was
24
25 neutralized by adding 2.2 mL of 2 M KOH. Amberlite™ IRN 78 anion-exchange resin beads were
26
27 added to the solution to isolate the PO_4^{3-} ions. After 24 hours, the solution was removed, the resin
28
29 was rinsed with deionized water and eluted with 27.5 mL of 0.5 M NH_4NO_3 . After 4 hours, 0.5 mL
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31 of NH_4OH and 15 mL of an ammoniacal solution of AgNO_3 were added and the solutions were
32
33 placed in a thermostated bath at 70 °C for 7 hours allowing for the precipitation of Ag_3PO_4 crystals.
34
35 Oxygen isotope compositions were measured using a high temperature elemental analyzer
36
37 interfaced in continuous flow mode to an isotopic ratio mass spectrometer (Fourel et al., 2011) at
38
39 the Plateforme d'Ecologie Isotopique du Laboratoire d'Ecologie des Hydrosystèmes Naturels et
40
41 Anthropisés (LEHNA – UMR5023, Université Claude Bernard Lyon 1). For each sample, 5
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43 aliquots of 300 µg of Ag_3PO_4 were mixed with 300 µg of pure graphite powder loaded in silver foil
44
45 capsules. Pyrolysis was performed at 1450 °C using a varioPYROcube™ Elemental Analyzer
46
47 (Elementar GmbH) interfaced in Continuous Flow mode with an Isoprime™ Isotopic Ratio Mass
48
49 Spectrometer (Elementar UK Ltd). Measurements have been calibrated against silver phosphate
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51 precipitated from the NBS120c (natural Miocene phosphorite from Florida), as well as against the
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53 NBS127 (Barium sulfate precipitated using seawater from Monterey Bay, California, USA). The
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1 value of NBS120c was fixed at 21.7‰ (V-SMOW) according to Lécuyer et al. (1993), and that of
2 NBS127 set at the certified value of 9.3‰ (V-SMOW; (Halas and Szaran, 2001; Hut, 1987)) for
3 correction of instrumental mass fractionation during CO isotopic analysis. Silver phosphate
4 precipitated from standard NBS120c along with the silver phosphate samples derived from fossil
5 bioapatites was repeatedly analyzed ($\delta^{18}\text{O}_p = 21.72 \pm 0.22\text{‰}$, $n = 20$) to ensure that no fractionation
6 occurred during the wet chemistry. Data are reported as $\delta^{18}\text{O}$ values with respect to V-SMOW (in
7 ‰ δ units).

Oxygen and carbon isotope analysis of biogenic apatite carbonate

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23 In order to remove potential organic contaminants as well as secondarily precipitated calcite,
24 about 10 mg of apatite powder was pre-treated following the protocol of Koch et al. (1997).
25 Powders were washed with a 2% NaOCl solution to remove organic matter, then rinsed five times
26 with double deionized water and air-dried at 40 °C for 24 hours. 0.1 M acetic acid was then added
27 and left for 24 hours, after which the powder was again rinsed five times with double deionized
28 water and then air-dried at 40 °C for 24 hours. The powder/solution ratio was kept constant at 0.04
29 g mL⁻¹ for both treatments. Stable isotope compositions of carbonate oxygen and carbon were
30 carried out at the Plateforme d'Ecologie Isotopique du Laboratoire d'Ecologie des Hydrosystèmes
31 Naturels et Anthropisés (LEHNA – UMR5023). The measurement were performed using an
32 isoFLOW system connected on line in continuous flow mode to a precisION mass spectrometer
33 (Elementar UK Ltd). For each sample, two aliquots of 2 mg of pretreated apatite powder were
34 loaded in LABCO Exetainer® 3.7 mL soda glass vials, round bottomed with exetainers caps
35 (LABCO UK Ltd) and were reacted with anhydrous phosphoric acid. The reaction took place at
36 90°C in a temperature regulated sample tray. The CO₂ gas generated during the acid digestion of the
37 carbonate sample was then transferred to the mass spectrometer via the centrION interface. A
38 calibrated CO₂ gas was used as a monitoring gas. Typical reproducibilities are 0.05‰ and 0.07‰
39 respectively for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements. For tooth apatite, the acid fractionation factor α
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(CO₂-apatite carbonate) of 1.00773 determined for the NBS120c phosphate rock reference material has been selected (Passey et al., 2007). Calibrated material used is Carrara Marble ($\delta^{18}\text{O}_{\text{V-PDB}} = -1.84\text{‰}$; $\delta^{13}\text{C}_{\text{V-PDB}} = +2.03\text{‰}$; (Fourel et al., 2016) NBS18 ($\delta^{18}\text{O}_{\text{V-PDB}} = -23.2\text{‰}$; $\delta^{13}\text{C}_{\text{V-PDB}} = -5.01\text{‰}$) and NBS120c ($\delta^{18}\text{O}_{\text{V-PDB}} = -1.13\text{‰}$; $\delta^{13}\text{C}_{\text{V-PDB}} = -6.27\text{‰}$; (Passey et al., 2007) Isotopic compositions are quoted in the standard δ notation relative to V-SMOW for oxygen and V-PDB for carbon.

Results

Oxygen isotope compositions of apatite phosphate ($\delta^{18}\text{O}_p$), apatite carbonate ($\delta^{18}\text{O}_c$) and carbon isotope compositions of apatite carbonate ($\delta^{13}\text{C}_c$) are reported in [Supplementary table 1](#) along with published $\delta^{18}\text{O}_p$ values of teeth and bones of marine vertebrates (Anderson et al., 1994; Bernard et al., 2010; Billon-Bruyat et al., 2005). Analysed teeth have $\delta^{18}\text{O}_p$ values ranging from 18.3‰ to 21.8‰ V-SMOW, $\delta^{18}\text{O}_c$ values ranging from 24.1‰ to 28.3‰ V-SMOW and $\delta^{13}\text{C}_c$ values ranging from -11.2‰ to 7.7‰ V-PDB. At the three sites of Smallmouth Sands, Peterborough and Les Vaches Noires, ichthyosaurs and plesiosaurs have slightly lower mean $\delta^{18}\text{O}_p$ values than those of co-occurring thalattosuchians ([Supplementary table 2](#)).

For each locality, SST has been calculated from the $\delta^{18}\text{O}_p$ values of fish using equation 1 ([Supplementary table 2](#)) considering that $T_b \approx T_{\text{sw}}$, and that $\delta^{18}\text{O}_{\text{bw}} \approx \delta^{18}\text{O}_{\text{sw}}$ (Kolodny et al., 1983). Because average seawater $\delta^{18}\text{O}_{\text{sw}}$ value may have varied between -1‰ and 0‰ V-SMOW depending on the amount of seawater stored as polar ice (Shackleton and Kennett, 1975), an average value of -0.5‰ was arbitrarily selected for temperature calculation, keeping in mind that the associated error in temperature calculation is about 2.3°C (based on the slope of 4.5 of equation 1).

The body temperature of studied marine reptiles have also been estimated using equation 1, and assuming a seawater-body water ¹⁸O-enrichment of 2‰, a general enrichment observed among semi-aquatic and aquatic air breathing vertebrates, including extant crocodylomorphs

(Amiot et al., 2007; Barrick et al., 1999; Lazzarini et al., 2016). While ichthyosaurs and plesiosaurs have a body temperature within the 32-40°C range compatible with their known endo-homeothermy (Bernard et al., 2010), teleosaurids have lower T_b ranging from 27°C to 31°C, and metriorhynchids show intermediate body temperatures ranging from 29°C to 37°C ([Supplementary table 2](#)).

Discussion

Original preservation of the stable isotope compositions

Before discussing the thermophysiological significance of the oxygen and carbon isotope compositions of vertebrate apatites, pristine preservation of the isotopic record needs to be assessed. Indeed, biotic and abiotic processes leading to the decomposition, burial and fossilization of living organisms may alter the original isotopic composition of bioapatite through processes of secondary precipitation, ion adsorption or dissolution–recrystallization of bioapatite (Blake et al., 1997; Kolodny et al., 1996; Lécuyer et al., 2003a; Trueman et al., 2003; Zazzo et al., 2004a, 2004b). Although no method can definitely demonstrate whether the original isotope compositions have been kept, several ways to assess the preservation state of the isotopic record have been proposed (Fricke et al., 1998; Iacumin et al., 1996; Kolodny et al., 1996; Lécuyer et al., 2003a; Pucéat et al., 2004; Tütken et al., 2008; Zazzo et al., 2004b). In modern skeletal tissues of vertebrates, carbonate and phosphate precipitate close to equilibrium with body water, so the $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values are positively correlated. Because isotopic exchange rates between carbonate-water and phosphate-water are significantly different, re-equilibration of both compounds during diagenesis is not expected and altered enamel should show isotopic shifts from the empirical $\delta^{18}\text{O}_p$ – $\delta^{18}\text{O}_c$ line. Therefore, it is expected that the distribution of pristine $\delta^{18}\text{O}$ values of fish and reptile tooth enamel should follow a line with a slope close to unity mimicking those established between the $\delta^{18}\text{O}_c$ and $\delta^{18}\text{O}_p$ values of modern mammals (Bryant et al., 1996; Chenery et al., 2012; Iacumin et al., 1996; Lécuyer et al., 2010; Zazzo et al., 2004b). Despite the narrow [range](#) in the distribution of oxygen isotope compositions (**Figure 2**), both $\delta^{18}\text{O}_c$ and $\delta^{18}\text{O}_p$ values fall within the range observed in

1
2 extant and fossil marine vertebrates (Kolodny and Luz, 1991; Lécuyer et al., 2003b; Vennemann et
3
4 al., 2001). This correlation shows that the oxygen isotope compositions of structural carbonate in
5
6 both tooth and bone apatites have preserved to a certain degree its original record.
7

8
9 A clue to the primary preservation of stable carbon isotope composition of apatite carbonate
10
11 is the systematic and significant difference in $\delta^{13}\text{C}_c$ values between fish and marine reptiles (**Figure**
12
13 **3**). Air breathing reptiles have $\delta^{13}\text{C}_c$ values mainly reflecting that of their diets with an isotope
14
15 fractionation that depends on their digestive physiology (Passey et al., 2005), as expected. In
16
17 aquatic environments, the relationship between fish carbonate and diet $\delta^{13}\text{C}$ values is complicated
18
19 as a substantial amount of the carbon may be derived from dissolved inorganic carbon (DIC) of
20
21 their ambient water (McConnaughey et al., 1997; Thorrold et al., 1997) with a higher $\delta^{13}\text{C}$ value
22
23 (Santos et al., 2011). Finally, the weight percentage of carbonate in analysed fossil apatites
24
25 (**Supplementary table 1**) lies within the expected biological range of modern vertebrate apatites of
26
27 2-13% (Brudevold and Soremark, 1967; Rink and Schwarcz, 1995; Vennemann et al., 2001). From
28
29 these lines of evidence, we can assume that oxygen isotope compositions of apatite phosphate and
30
31 carbonate have kept at least a significant part of their original information, and might be interpreted
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33 in **terms** of seawater temperature and thermophysiology.
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41 ***Body temperature reconstruction***

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43 In a previous study of marine reptile thermophysiology, Bernard et al. (2010) interpreted the
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45 oxygen isotope differences between marine reptiles and coexisting fish from a large range of water
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47 temperatures (estimated from 14°C to 34°C) in terms of T_b differences. They concluded that the
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49 three lineages Ichthyosauria, Plesiosauria and Mosasauridae were most likely endothermic and
50
51 homeothermic marine reptiles, although for mosasaurids this was later debated (Harrell Jr et al.,
52
53 2016; Motani, 2010). The method used in Bernard et al. (2010) cannot clearly identify the
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55 thermophysiology of thalattosuchians (**Figure 4**). Indeed, the available sample-set of thalattosuchian
56
57 specimens is restricted to five localities with a narrow range of low paleolatitudes from about 29°N
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59
60

1
2 to 36°N (**Supplementary table 2**; palaeolatitudes calculated using the online application of van
3
4 Hinsbergen et al. (2015)), as well as a narrow range of estimated paleotemperatures from 22±2°C to
5
6 27±2°C. Consequently, the sampled sites do not allow the two strategies of thermophysiology to be
7
8 clearly distinguished. Most metriorhynchids and teleosaurids show intermediate values between the
9
10 expected range for endotherms and ectotherms, with the exception of the metriorhynchids from the
11
12 middle Callovian of Les Lourdines which fall within the expected range of endotherms, and one
13
14 middle Callovian of Les Lourdines which fall within the expected range of endotherms, and one
15
16 teleosaurid from the Bathonian of Cintheaux, which has a typical ectotherm signature (**Figure 4**).

17
18 Using equation 1 and assuming that thalattosuchians have a $\delta^{18}\text{O}_{\text{bw}}$ value of about 2‰ more
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20 positive than their ambient seawater, both metriorhynchids and teleosaurids have a body
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22 temperature above their environmental one, metriorhynchids being slightly warmer than
23
24 teleosaurids in average (**Supplementary table 2**; **Figure 5**). However, thalattosuchian T_b are
25
26 systematically below the calculated ones of co-occurring ichthyosaurs and plesiosaurs for which the
27
28 body temperature was calculated from the same equation 1 and using a body water $\delta^{18}\text{O}_{\text{bw}}$ value
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30 similar to that of thalattosuchians.
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34
35 An endothermic-like thermophysiology interpreted from metriorhynchid $\delta^{18}\text{O}_p$ values seems
36
37 likely according to their known morphology and ecology as active pelagic predators (Andrade et al.,
38
39 2010; Fernández and Gasparini, 2000; Hua and De Buffrénil, 1996; Massare, 1987; Young et al.,
40
41 2013, 2012). Active predation would require elevated metabolic rates compatible with an
42
43 endothermic thermophysiology. This seems plausible considering the large suite of evidence for an
44
45 endothermic ancestral condition for Archosauria, and a reversal within the crocodylomorph lineage
46
47 to an ectothermic state coming from different fields of biology, including developmental biology
48
49 (Seymour et al., 2004), physiology (Farmer and Sanders, 2010), anatomy (Summers, 2005),
50
51 palaeohistology (de Ricqlès et al., 2008), and phylogenetic signal extraction (Legendre et al., 2016).
52
53 Endothermy within metriorhynchids might have been inherited from their archosaur ancestors, and
54
55 “reactivated” along with the acquisition of morphological adaptations to active pelagic predation.
56
57
58 However, body temperature regulation seems to have been limited as observed T_b vary with varying
59
60

1
2 seawater temperature (**Figure 5**). Limited thermoregulatory capacities would be compatible with
3
4 the restricted range of paleolatitudinal occurrences compared to fully endo-homeothermic
5
6 ichthyosaurs and plesiosaurs having been found from equatorial to polar seas (Bardet et al., 2014).
7

8
9 Interpretation of the oxygen isotope composition of teleosaurid apatite in terms of body
10
11 temperature may be strongly biased by their possible semi-aquatic and eurhaline ecology, some
12
13 species having been found in estuarine or freshwater environments (Buffetaut, 1982; Martin et al.,
14
15 2019, 2016; Wilberg et al., 2019). As most teleosaurids retained a typical semi-aquatic
16
17 crocodylomorph morphology (external mandibular fenestrae, extensive osteoderm cover and limbs
18
19 adapted to terrestrial locomotion), it is hypothesized that they were ectothermic and poikilothermic
20
21 ambush predators spending most of their time motionless, and mouth-gape basking like modern
22
23 crocodylians. However, during the late Kimmeridgian-early Tithonian there is evidence for a
24
25 subclade of teleosaurids that became more pelagic (Foffa et al., 2019). The oxygen isotope
26
27 composition of teleosaurid apatite indicates that they kept a body temperature lower than that of
28
29 ichthyosaurs and plesiosaurs, but close to those of metriorhynchids. However, more estuarine living
30
31 environments can be characterized by more negative $\delta^{18}\text{O}$ values as a result of the mixing between
32
33 seawater and river waters having negative $\delta^{18}\text{O}$ values such as in the case of the San Francisco Bay
34
35 (Ingram et al., 1996). In this example, waters from the Sacramento river having $\delta^{18}\text{O}$ values
36
37 ranging from about -12‰ to -10‰ mix with seawater of 0‰ and results in estuarine waters that
38
39 can have $\delta^{18}\text{O}$ values of -3‰ to -10‰. Keeping this in mind, then the calculated body temperature
40
41 of teleosaurids living in estuarine environments would be lower, and their apatite $\delta^{18}\text{O}$ values would
42
43 fit within the expected range of ectotherms. Moreover, the possible semi-aquatic lifestyle of
44
45 teleosaurids could at least partly account for their elevated $\delta^{18}\text{O}_p$ values as a result of body water
46
47 loss through transcutaneous evaporation. In the studied localities where teleosaurid specimens were
48
49 found, fossil remains of continental vertebrates and plants have been found, indicating a proximity
50
51 to landmasses and a possible estuarine origin of teleosaurids. Gigantothermy and behavioural
52
53 thermoregulation may also account for the calculated body temperatures of teleosaurids close to
54
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1 those of metriorhynchids. Today, large marine crocodylians, such as ~1000 kg adult individuals of
2 the saltwater crocodile (*Crocodylus porosus*), are able to raise their body temperature well above
3 ambient temperatures through mouth-gape basking behaviours and can retain this elevation by the
4 thermal inertia of their large body size (Grigg et al., 1998; Seebacher et al., 1999). Large
5 teleosaurids may have used a similar behavioural thermoregulation as extant marine crocodiles (*C.*
6 *porosus*) and would have raised their body temperatures close to that of Jurassic metriorhynchids
7 and maintained it within a narrow range. This would explain the apparent tendency of teleosaurid-
8 fish isotope difference to parallel that of endo-homeothermic ichthyosaurs and plesiosaurs (Figure
9 4). Most metriorhynchid specimens were of smaller body-size than teleosaurids (Young et al., 2016,
10 2011), and metriorhynchids would have been unable to mouth-gape bask onshore (Young et al.,
11 2010).

12 Based on the available isotopic dataset, it seems likely that teleosaurids retained a typical
13 ecto-poikilothermic thermophysiology in agreement with their morphology and ecology, whereas
14 metriorhynchids may have been endothermic, being able to raise their body temperature above an
15 ambient one, and close to that of other warm-blooded marine reptiles. However, metriorhynchids
16 could not have achieved efficient thermoregulation as suggested from their varying body
17 temperature along with varying SST.

18 **Concluding remarks**

19 The possible difference in thermophysologies between metriorhynchids and teleosaurids
20 inferred from their stable oxygen isotope composition of apatite can at least partly explain the
21 peculiar thalattosuchian biodiversity pattern of the Jurassic and Early Cretaceous (Martin et al.,
22 2014; Young et al., 2014a). Teleosaurid diversity crashed at the end of the Jurassic, a time of global
23 marine temperature decline, probably as a result of the temperature change or the global regression
24 affecting their ecological niches (Bardet et al., 2014). Endothermy may have helped
25 metriorhynchids to cope with global cooling, and due to their pelagic ecology, they might not have

1
2 been as affected by the marine regressions as teleosaurids. This may explain their success across the
3
4 Jurassic-Cretaceous boundary (Chiarenza et al., 2015; Tennant et al., 2017; Young et al., 2014a). At
5
6 this point, we cannot only speculate when metriorhynchids became extinction, or why. All we can
7
8 mention is that Jurassic metriorhynchids had an imperfect endothermic and poikilothermic
9
10 thermophysiology. We hope future studies will investigate whether the Late Jurassic pelagic
11
12 subclade of teleosaurids began to develop endothermic capabilities, and test whether Cretaceous
13
14 metriorhynchids, the most marine adapted of all thalattosuchians (Hua et al., 2000; Young et al.,
15
16 2010), evolved toward enhanced thermoregulatory abilities.
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21

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Figure Caption

Figure 1: Palaeogeography of Northwestern Europe during the Middle-Late Jurassic (modified from Pross et al. (2006). The red stars show the studied localities. 1: Peterboroug; 2: Smallmouth Sands; 3: Les Vaches Noires; 4: Les Lourdines excavation; 5: Cintheaux.

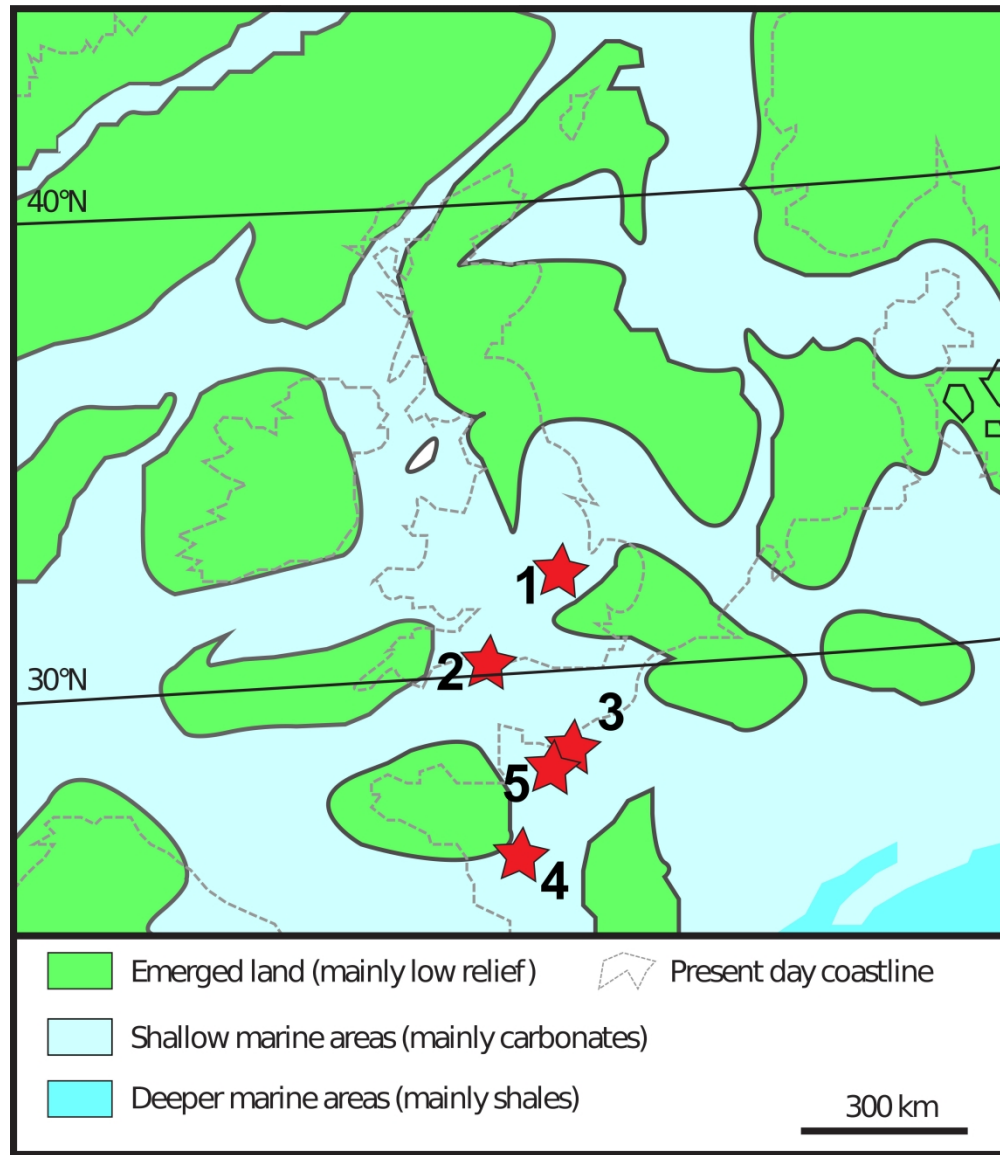
Figure 2: Oxygen isotope compositions of tooth phosphate reported against their corresponding oxygen isotope composition of structural carbonate, as well as published values of modern and fossil fish for comparison (Kolodny and Luz, 1991; Lécuyer et al., 2003b; Vennemann et al., 2001). The dashed line with a slope $a=1$ illustrates the correlation between oxygen isotope composition of phosphate and carbonate.

Figure 3: Carbon isotope compositions of apatite carbonates ($\delta^{13}C_c$) from fish and marine reptile samples. For each locality, the sizable difference between fish and coexisting marine reptiles $\delta^{13}C_c$ values is considered as evidence for primary preservation of the stable isotope compositions of studied specimens.

Figure 4: Model variation of the differences in the $\delta^{18}O_p$ values of tooth phosphate between marine reptiles and fish against the variation of the $\delta^{18}O_p$ values of fish teeth, assuming (1) an ectothermic and poikilothermic reptile [body water $\delta^{18}O_{bw}$ values 2‰ enriched relative to a seawater value and body temperature (T) equal seawater temperature]; (2) an endothermic reptile with body temperature ranging from 35°C to 39°C and body water 2‰ enriched relative to a seawater value ranging from -1‰ to 0‰ (modified from (Bernard et al., 2010). For comparison, metriorhynchoids and teleosaurids values are reported, along with newly measured (black border) and published (grey border) ichthyosaurs and plesiosaurs values.

1
2 **Figure 5:** Estimated body temperature of marine reptiles (left **axis**) and corresponding $\delta^{18}\text{O}_p$ values
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4 (right **axis**) are plotted against their environmental sea surface temperature estimated from fish
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6 $\delta^{18}\text{O}_p$ values.
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Figure 1: Palaeogeography of Northwestern Europe during the Middle-Late Jurassic (modified from Pross et al. (2006)). The red stars show the studied localities. 1: Peterborough; 2: Smallmouth Sands; 3: Les Vaches Noires; 4: Les Lourdines excavation; 5: Cintheaux.

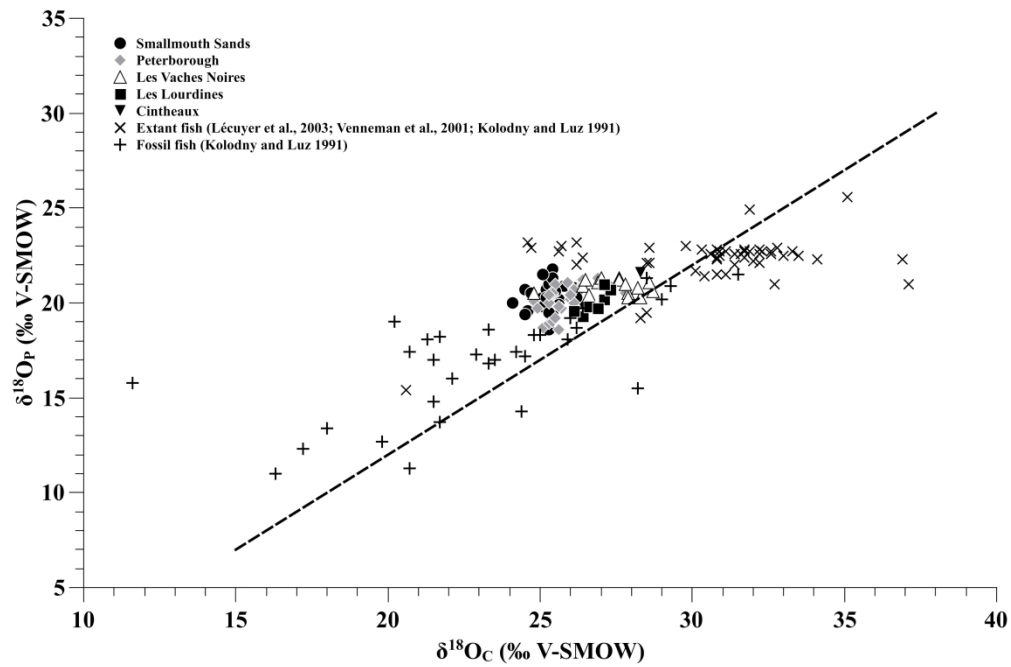


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297x196mm (300 x 300 DPI)

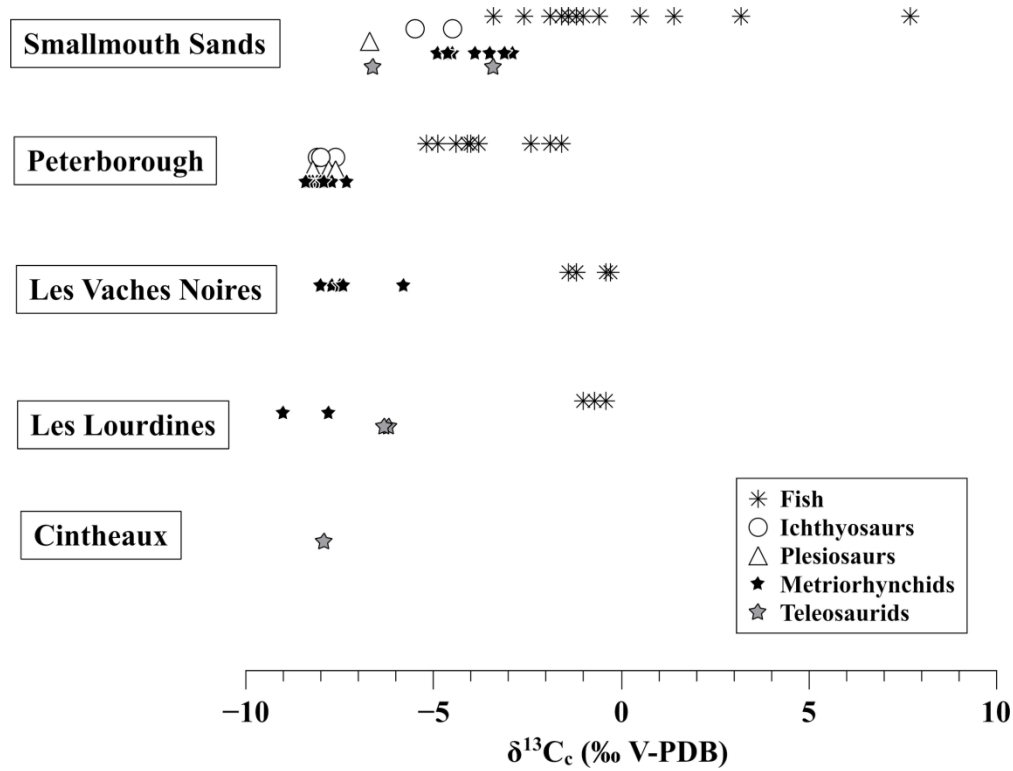


Figure 3: Carbon isotope compositions of apatite carbonates ($\delta^{13}C_c$) from fish and marine reptile samples. For each locality, the sizable difference between fish and coexisting marine reptiles $\delta^{13}C_c$ values is considered as evidence for primary preservation of the stable isotope compositions of studied specimens.

188x143mm (300 x 300 DPI)

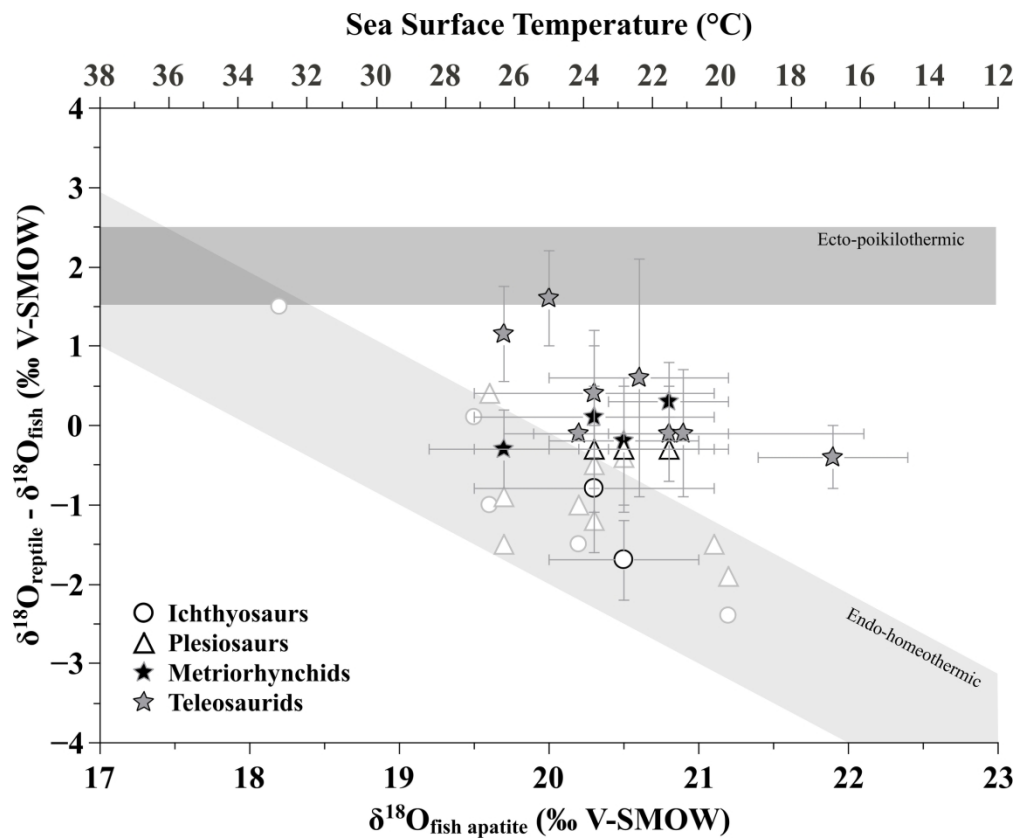


Figure 4: Model variation of the differences in the $\delta^{18}\text{O}_p$ values of tooth phosphate between marine reptiles and fish against the variation of the $\delta^{18}\text{O}_p$ values of fish teeth, assuming (1) an ectothermic and poikilothermic reptile [body water $\delta^{18}\text{O}_{\text{bw}}$ values 2‰ enriched relative to a seawater value and body temperature (T) equal seawater temperature]; (2) an endothermic reptile with body temperature ranging from 35°C to 39°C and body water 2‰ enriched relative to a seawater value ranging from -1‰ to 0‰ (modified from (Bernard et al., 2010)). For comparison, metriorhynchoids and teleosaurids values are reported, along with newly measured (black border) and published (grey border) ichthyosaurs and plesiosaurs values.

192x158mm (300 x 300 DPI)

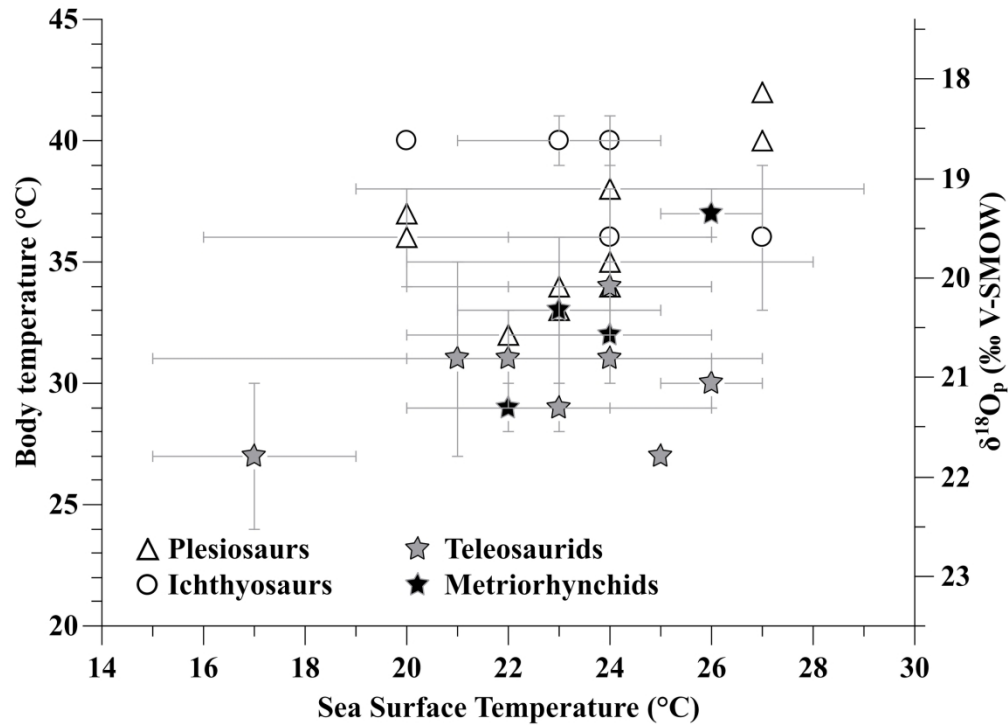


Figure 5: Estimated body temperature of marine reptiles (left axis) and corresponding $\delta^{18}\text{O}_p$ values (right axis) are plotted against their environmental sea surface temperature estimated from fish $\delta^{18}\text{O}_p$ values.

213x154mm (300 x 300 DPI)