

Current Biology

Calcium Isotopic Evidence for Vulnerable Marine Ecosystem Structure Prior to the K/Pg Extinction

Highlights

- Calcium isotopes retain biogenic values in a Cretaceous marine vertebrate assemblage
- Isotopic variability in primary consumers parallels that of modern analogs
- A single calcium source for apex predators points to a Cretaceous wasp-waist food web
- Marine ecosystems were vulnerable prior to the K/Pg mass extinction

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In Brief

Martin et al. explored the trophic network of marine reptiles in a 66-million-year-old assemblage. Low calcium isotope ratios reveal that apex predators were feeding on a single calcium source, implying a wasp-waist food web. Such ecosystem structure is fragile in the modern world and helps explain extinctions during the end-Cretaceous biological crisis.



Calcium Isotopic Evidence for Vulnerable Marine Ecosystem Structure Prior to the K/Pg Extinction

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<http://dx.doi.org/10.1016/j.cub.2017.04.043>

SUMMARY

The collapse of marine ecosystems during the end-Cretaceous mass extinction involved the base of the food chain [1] up to ubiquitous vertebrate apex predators [2–5]. Large marine reptiles became suddenly extinct at the Cretaceous-Paleogene (K/Pg) boundary, whereas other contemporaneous groups such as bothremydid turtles or dyrosaurid crocodylomorphs, although affected at the familial, genus, or species level, survived into post-crisis environments of the Paleocene [5–9] and could have found refuge in freshwater habitats [10–12]. A recent hypothesis proposes that the extinction of plesiosaurians and mosasaurids could have been caused by an important drop in sea level [13]. Mosasaurids are unusually diverse and locally abundant in the Maastrichtian phosphatic deposits of Morocco, and with large sharks and one species of elasmosaurid plesiosaurian recognized so far, contribute to an overabundance of apex predators [3, 7, 14, 15]. For this reason, high local diversity of marine reptiles exhibiting different body masses and a wealth of tooth morphologies hints at complex trophic interactions within this latest Cretaceous marine ecosystem. Using calcium isotopes, we investigated the trophic structure of this extinct assemblage. Our results are consistent with a calcium isotope pattern observed in modern marine ecosystems and show that plesiosaurians and mosasaurids indiscriminately fall in the tertiary piscivore group. This suggests that marine reptile apex predators relied onto a single dietary calcium source, compatible with the vulnerable wasp-waist food webs of the modern world [16]. This inferred peculiar ecosystem structure may help explain plesiosaurian and mosasaurid extinction following the end-Cretaceous biological crisis.

RESULTS AND DISCUSSION

Following recent studies on modern marine vertebrates [17–20], we used calcium isotopes to assess trophic relationships among the diverse vertebrates that inhabit the Late Maastrichtian marine ecosystem of the Moroccan phosphatic basin. Calcium is a readily available and soluble element in seawater, amounting to about 420 ppm [21]. As a major element of bioapatite, it amounts to about 40% of tooth enamel, the most compact biological material. As measured in seawater, invertebrates, and vertebrates, a trophic level effect is observed showing decreasing calcium isotope values (expressed below as $\delta^{44/42}\text{Ca}$) with increasing trophic position [17–20]. Therefore, in the marine environment, the calcium isotope composition of mineralized biological tissues such as bone or teeth can be interpreted in terms of trophic inference. Case studies on marine fossil vertebrates have been restricted to Neogene assemblages and recover a similar trophic level effect as in the modern world [19, 20]. Given the high crystallinity of bioapatite in enamel and its high preservation potential, this method is applied here to older material [22, 23].

In this study, marine vertebrates comprising 16 species from a single level (C2) in the Benguerir section of the Ganntour Basin, Morocco (see [14] for stratigraphical details) were analyzed for calcium isotopes (see STAR Methods and Table S1). Importantly, the range of calcium isotope values measured in the Cretaceous vertebrate assemblage from the Benguerir section mirrors the trophic levels recovered in modern marine ecosystems [20]. This provides a robust case against a complete diagenetic overprinting of the biogenic isotope calcium composition. Results show identical calcium isotope values with or without pretreatment (Figure S2).

In the studied fossil assemblage (Figure 1), the least fractionated $\delta^{44/42}\text{Ca}$ value is represented by the marine turtle group ($-0.40 \pm 0.04\text{‰}$, 1SD, $n = 5$) and shows a $\Delta^{44/42}\text{Ca}$ relative to Late Maastrichtian seawater of -0.70‰ , which is identical to the $\Delta^{44/42}\text{Ca}$ between modern turtles and modern seawater. A second fossil group includes pycnodonts and teleost fishes with the barracuda-like *Enchodus* as well as two sawsharks of the genus *Pristiphorus* and has an intermediate mean value ($-0.57 \pm 0.12\text{‰}$, 1SD, $n = 8$) and a $\Delta^{44/42}\text{Ca}$ relative to Late

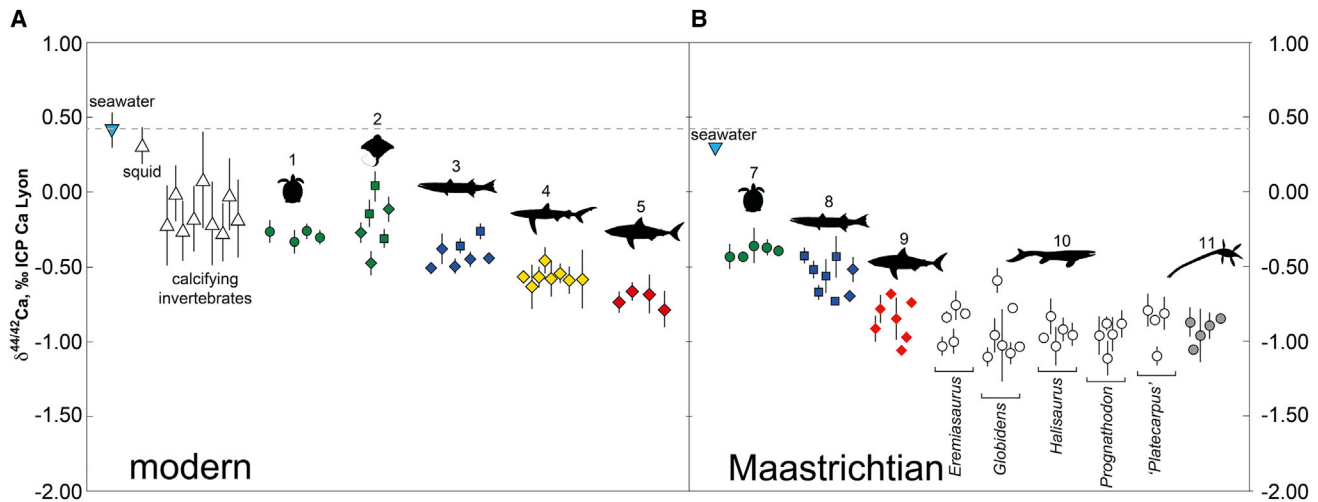


Figure 1. $\delta^{44/42}\text{Ca}$ Variability in Marine Ecosystems of the Modern World and the Maastrichtian

$\delta^{44/42}\text{Ca}$ data are given in ‰ relative to ICP Ca Lyon standard. For the modern dataset (A), data compilation is from the literature (see [19] for details), with the exception of modern marine turtles (this study). The fossil Maastrichtian dataset (B) is entirely new to this study. 1, modern marine turtles; 2, zooplanktivores; 3, primary piscivores; 4, secondary piscivores; 5, tertiary piscivores; 7, Maastrichtian marine turtles; 8, Maastrichtian primary piscivores; 9, Maastrichtian tertiary piscivores; 10, mosasaurs; 11, plesiosaurs. Triangles represent invertebrates; circles represent marine reptiles; squares represent teleost fishes; diamonds represent elasmobranchs. Error bars represent 2SD. See also Table S1.

Maastrichtian seawater of -0.87‰ , which is indistinguishable from the $\Delta^{44/42}\text{Ca}$ value observed between the modern primary piscivore group and modern seawater (-0.87‰). The group containing the large sharks *Cretolamna*, *Squalicorax*, and *Carcharias* ($-0.86 \pm 0.17\text{‰}$ 1SD, $n = 7$) has a $\Delta^{44/42}\text{Ca}$ relative to Late Maastrichtian seawater of -1.16‰ and is thus very close to the $\Delta^{44/42}\text{Ca}$ between modern tertiary piscivores and modern seawater (-1.13‰). Marine reptile calcium isotope values strongly overlap with the large sharks but display slightly lower values on average ($-0.93 \pm 0.12\text{‰}$ 1SD, $n = 31$). Values for the elasmosaurid plesiosaurian and the five mosasaurid genera are indistinguishable, suggesting that they indiscriminately fed on the same calcium source.

The relatively homogeneous calcium isotope values measured in marine reptile enamel imply that the calcium sources, i.e., prey, irrespective of their nature, had a comparable calcium isotope composition. Considering a systematic $\Delta^{44/42}\text{Ca}$ shift of about -0.14‰ from diet to consumer [20], our results point to a common calcium source for the diet of the large sharks and predatory marine reptiles. A single outlier (out of seven) is represented by a specimen of *Globidens*, which presents a relatively enriched calcium isotope composition relative to other marine reptiles, indicating a heavy calcium-rich food source for at least some individuals.

The calcium isotope data do not allow us to recognize any resource partitioning among predatory marine reptiles. Such results may instead reflect a single dietary source, or at least different dietary sources of identical trophic levels, which contrasts markedly with previous studies that documented an impressive diversity of trophic guilds based on mosasaurid tooth morphologies [7, 24]. For example, the massive bulbous dentition of *Globidens* has been hypothesized to serve a crushing function, whereas conical and/or blade-like teeth of other mosasaurid species and of elasmosaurid plesio-

saurians could serve puncturing or cutting functions [7]. This apparent discrepancy might be explained by the peculiar ecosystem structure of the Maastrichtian phosphatic deposits of Morocco.

Here, the structure of the Late Maastrichtian marine ecosystem, as inferred from calcium isotopes, differs in its composition from modern assemblages where apex predators are represented by birds and mammals but also by selachians. By contrast, our data point to a single dietary source for apex predators, suggesting a bottom-up control, with a considerable biomass sustaining an abundant and diversified assemblage of large apex predators. A comparable structure, known as a “wasp waist,” is observed in modern upwelling environments, where a large biomass of poorly diversified forage organisms (the intermediate trophic level) exerts a bottom-up control on diverse apex predators and exerts a top-down control on invertebrate preys [16, 25]. This inference is in perfect agreement with the sedimentological data from the study sites [26], which indicate that the studied fossiliferous phosphate strata were deposited under an upwelling environment. We therefore interpret our results as providing strong evidence for a wasp-waist structure in the studied Late Maastrichtian assemblage. As a caveat, it should be stressed that the structure of modern upwelling ecosystems has not yet been investigated using calcium isotopes.

Our results have implications for the extinction of marine reptiles at the K/Pg boundary. The latest Cretaceous was marked by a major expansion of phosphate deposits in the intertropical zone, interpreted as reflecting intensified upwellings related to the opening of the Atlantic Ocean [26]. In parallel, plesiosaurs and mosasaurs became particularly widespread, diversified, and abundant. Although the wasp-waist structure evidenced by our data for the Moroccan upwelling ecosystem deserves further testing in coeval marine assemblages, it can be reasonably hypothesized that a similar structure characterized many if

not all of these low-latitude upwelling ecosystems. If correct, this widespread wasp-waist structure may have rendered the latest Cretaceous ecosystems particularly vulnerable to environmental perturbations of the K/Pg. As a modern example, the drop in abundance and diversity of apex predators in modern upwelling environments is a result of sardine and anchovy overexploitation by industrial fisheries of the late 19th century [16]. Accordingly, the collapse of phytoplankton at the K/Pg boundary [1, 27] likely had a severe impact on intermediate and higher trophic levels occupied by selachians and marine reptiles [6]. This collapse would have been particularly detrimental to plesiosaurs and mosasaurs, which possessed a higher metabolic rate than crocodylomorphs or selachians [28], necessitating substantial caloric intake, hence a corresponding biomass available as prey. This may have been especially sustainable in upwelling zones, which are highly productive environments but are extremely vulnerable ecosystems in contrast to reef ecosystems [29]. The sudden environmental catastrophe disrupting primary productivity at the K/Pg boundary, combined with a widespread and vulnerable type of ecosystem, likely had drastic effects across apex predator communities. Together with models inferring biotic interactions in Cretaceous terrestrial ecosystems [30], our results highlight that the collapse of Maastrichtian marine ecosystems was timely and could have been partly explained by their vulnerable nature, characterized by a wasp-waist structure.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- METHOD DETAILS
 - Sample Collection
 - Analytical Methods
 - Modern Turtles
 - Seawater Calcium Evolution
 - Leaching Experiments
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.04.043>.

AUTHOR CONTRIBUTIONS

The project was conceived by J.E.M., P.V., T.T., N.B., and V.B. Specimens were retrieved in the field by P.V., N.B., F.K., and E.J. J.E.M. and P.V. sampled the specimens and conducted purification in the clean lab. J.E.M. and T.T. performed MC-ICP-MS measurements. All authors discussed the results. The first draft of the text was written by J.E.M., and P.V., T.T., N.B., V.B., F.K., and E.J. subsequently contributed to it.

ACKNOWLEDGMENTS

This work was performed under the convention “Cadre Phosphapal” of the cooperation between OCP, Ministère de l’Energie, des Mines, de l’Eau et de l’Environnement du Royaume du Maroc, Université Cadi Ayyad, Marrakech, Morocco and MNHN, France. We thank E. Robert (UMR CNRS 5276, LGLTPE)

for allowing us to sample modern turtle bone curated in the collections of Université Claude Bernard Lyon 1. The authors are grateful to the LABEX Lyon Institute of Origins (ANR-10-LABX-0066) of the Université de Lyon for financial support within the program “Investissements d’Avenir” (ANR-11-IDEX-0007) of the French government operated by the National Research Agency (ANR). For technical assistance with spectrometers, we thank E. Albalat, F. Arnaud-Godet, and P. Telouk. We also thank two reviewers who provided constructive comments that helped improve the content of this work.

Received: March 1, 2017

Revised: April 6, 2017

Accepted: April 20, 2017

Published: May 25, 2017

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Other		
Sr Resin (100-150 μm)	Triskem	Cat# SR-25-A
AG50W-X12 cationic resin (200-400 mesh)	Biorad	Cat# 1421651
Hydrochloric acid	Carlo Erba	Cat# UN1789
Nitric acid	Carlo Erba	Cat# UN2031

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Jeremy Martin (jeremy.martin@ens-lyon.fr).

METHOD DETAILS

Sample Collection

The total number of analyzed samples is 55 (Table S1). To the exception of 5 fossil marine turtle bones, all fossil vertebrate samples consist of tooth enamel obtained from 6 specimens belonging to 3 species of teleost fishes ($n = 6$), 9 specimens belonging to 3 species of large elasmobranchs ($n = 9$), 5 elasmosaurid teeth and 26 specimens belonging to 5 species of mosasaurids ($n = 26$). In addition, modern turtle bone was also analyzed ($n = 4$, see below). For marine turtles, chips of compact cortical bone were obtained from osteons. Cubes of fossil tooth enamel were sampled under a binocular using the tip of a scalpel. Dentine was easily discarded, as enamel would perfectly detach along the dentine-enamel junction. In two pycnodont teeth, which are rounded and highly resistant to mortar pressure, both enamel and dentine could not be separated. All samples come from a single locality and a single level (C2) of the Benguerir section, Ganttour Basin, Morocco, about 67 million year old.

Analytical Methods

Chemical purification and analytical procedures follow what has been described in previous works [20, 31] using ion-exchange resins and purified acids (see Key Resources Table). The purified samples were measured on a Neptune Plus Multicollector Inductively Coupled Plasma Mass Spectrometer (MC-ICP-MS) at Laboratoire de Géologie de Lyon using the standard-sample bracketing method with ICP Ca Lyon as a standard [20, 31]. Isotopic compositions are expressed as delta values (in ‰) calculated using the $^{44}\text{Ca}/^{42}\text{Ca}$ ratio as follows:

$$\delta^{44/42}\text{Ca} = \left(\frac{(^{44}\text{Ca}/^{42}\text{Ca})_{\text{sample}}}{(^{44}\text{Ca}/^{42}\text{Ca})_{\text{ICP Ca Lyon}}} - 1 \right) \times 1000.$$

All samples fall on a Ca mass fractionation line (Figure S1). We report five independent measurements of NIST standard SRM 1486 (-1.00 ± 0.13 ‰, 2SD, $n = 30$; -1.06 ± 0.29 ‰, 2SD, $n = 29$; -1.00 ± 0.16 ‰, 2SD, $n = 14$; -1.03 ± 0.11 ‰, 2SD, $n = 9$; -1.02 ± 0.05 ‰, 2SD, $n = 14$) that are in good agreement with previously published values (-1.04 ± 0.11 ‰, 2SD [20]; -1.03 ± 0.13 ‰, 2SD [32]). Long-term reproducibility as measured for SRM 1486 is 0.12 ‰. All values obtained in this study fall on a mass fractionation line with a slope of 0.507 (Figure S1), in agreement with data from the literature [20]. The total range of measured values for $\delta^{44/42}\text{Ca}$ in fossil remains from the Benguerir section, Morocco is 0.75‰ from -0.36 ‰ to -1.10 ‰ (Figure 1 and Table S1). As in a previous study [20], taxonomic groups have overlapping values. The highest values of the dataset are part of the marine turtle group (median = -0.37 ‰, $n = 3$) and of the teleost fishes (median = -0.55 ‰, $n = 6$). The teleost group shows an outlier value (-0.89 ‰) for a pycnodont tooth. $\delta^{44/42}\text{Ca}$ values from large elasmobranch taxa are intermediate in the dataset (median = -0.82 ‰, $n = 6$) with a single outlier, *Pristiphorus*, showing a high value similar to those of the marine turtle and teleost groups (-0.52 ‰). The lowest values of the dataset were measured on marine reptile teeth (median = -0.96 ‰, $n = 16$).

Modern Turtles

In order to have comparable datasets between environments of the modern world and that of the Cretaceous, a set of modern turtle samples was added to the modern selachian dataset [20]. Four specimens from the collections of Paléontologie of Université Claude Bernard Lyon 1 and representing three species of marine chelonoids were sampled and analyzed for calcium isotopes. About half a milligram of skull bone was sampled on 1 specimen of *Caretta caretta* and 3 specimens of *Chelonia mydas*. *C. mydas* is a seagrass or algal grazer [33] and *C. caretta* feeds on invertebrates living on the surface [34]. The four turtle specimens analyzed here have an average value of -0.29 ± 0.03 ‰ (1SD, $n = 4$), which is slightly higher than the average value recovered for Maastrichtian marine turtles (-0.40 ± 0.04 ‰, 1SD, $n = 5$). Implications for the reconstruction of the Maastrichtian seawater calcium isotope value are discussed below.

Seawater Calcium Evolution

The primary source of calcium in the marine environment is seawater but its calcium isotope composition has not been constant over the Phanerozoic due to changes in continental weathering regime and precipitation of carbonates by different types of marine biocalcifiers [35, 36]. In the modern world, the abundance of aragonitic calcifiers explains the relatively high calcium isotope ratio for seawater [37]. During the Cretaceous, calcitic calcifiers were dominant leading to an estimated difference of 0.05 – 0.07 ‰ toward lower isotope ratios for seawater. However, such small difference may not be measurable within the range of analytical error.

The calcium isotope value of seawater has been inferred for different time periods including the Jurassic and Cretaceous using fractionation factors between modern brachiopod calcite and seawater [35, 37]. However, for the Maastrichtian, no brachiopods have been analyzed yet and the inference is based on the fractionation factor between authigenic marine phosphate [38] and seawater, which appears to be less well constrained than that inferred from brachiopod calcite values [35, 37] but yields a $\delta^{44/42}\text{Ca}$ value of +0.26 ‰ for the lower Maastrichtian after conversion to ICP Ca Lyon has been applied.

Here, we calculate a fractionation factor between modern turtle bone ($-0.29 \pm 0.03\text{‰}$) and modern seawater (0.41‰ see Table 2 in [19]) using the equation presented in [35, 37]:

$$\alpha_{\text{tb-sw}} = (\delta^{44/42}\text{Ca}_{\text{tb}} + 1000) / (\delta^{44/42}\text{Ca}_{\text{sw}} + 1000) \quad (1)$$

where $\alpha_{\text{tb-sw}}$ corresponds to the fractionation factor between turtle bone (tb) and seawater (sw) and yields a value of 0.9993. Using $\alpha_{\text{tb-sw}}$ and the mean value for Maastrichtian turtle bone in this study (-0.40‰), we infer a calcium isotope value of +0.30 ‰ for seawater for the Late Maastrichtian. This value is close, albeit lower by about 0.1 ‰ than the modern seawater value (+0.41‰). This value is comparable with the value inferred from seawater for the lower Maastrichtian using the francolite-seawater fractionation factor [39] (+0.26 ‰ converted to ICP Lyon [37]). Considering a biotic fractionation factor between modern brachiopods and seawater [35, 40], the lower Maastrichtian calcium isotope inferred value is +0.39‰, which is nearly identical to the $\delta^{44/42}\text{Ca}$ value of seawater measured in the modern world.

Leaching Experiments

Four fossil samples comprising two turtle bones and two mosasaur enamel samples (Figure S2 and Table S1) were subjected to a test to assess the effect of diagenesis on the preservation of the original biogenic calcium isotopic composition. During mechanical sampling, the powder was split in half with one half for direct chemical purification and the other half for dilute acid etching. Acetic acid (0.1N) etching in an eppendorf tube takes 30 minutes after which the sample is rinsed three times with MQ water to remove potential CaCO_3 secondary precipitates. After this step, the leached sample undergoes chemical purification as any other samples treated in this study. The $\delta^{44/42}\text{Ca}$ measurements of the leached versus untreated pairs show no detectable differences (Table S1 and Figure S2).

QUANTIFICATION AND STATISTICAL ANALYSIS

Calcium isotope data discussed in the main text were analysed using non-parametric Wilcoxon-Mann Whitney tests. The errors discussed in the main text and featured in Figure 1, Figure S1, Figure S2, and Table S1 represent two standard deviations (2SD). The uncertainty displayed for parameters of the linear model (origin and slope) in Figure S1 are the 95% confidence intervals (2 standard errors) and were calculated using the linear model function of the software R.

Current Biology, Volume 27

Supplemental Information

**Calcium Isotopic Evidence for Vulnerable Marine
Ecosystem Structure Prior to the K/Pg Extinction**

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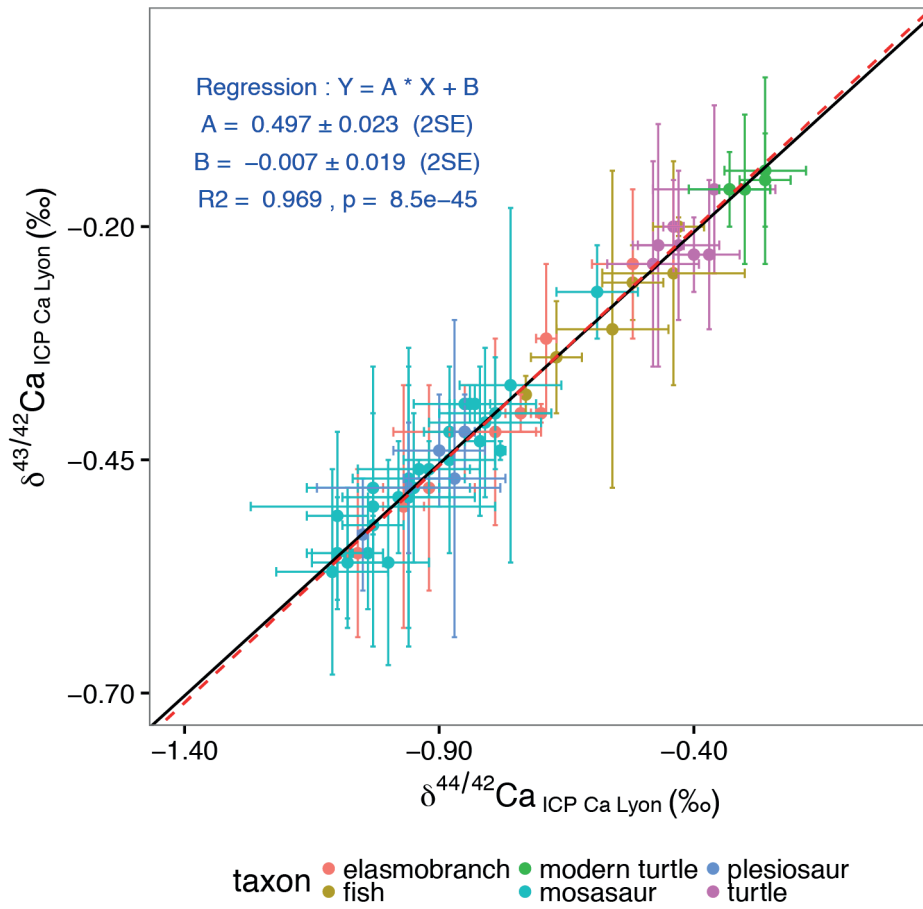


Figure S1. Triple isotope plot of all the data analysed in this study. All datapoints fall on a mass fractionation line (black line) in agreement with the 0.507 slope predicted by exponential mass fractionation law (indicated with the dashed red line). **Related to STAR Methods.**

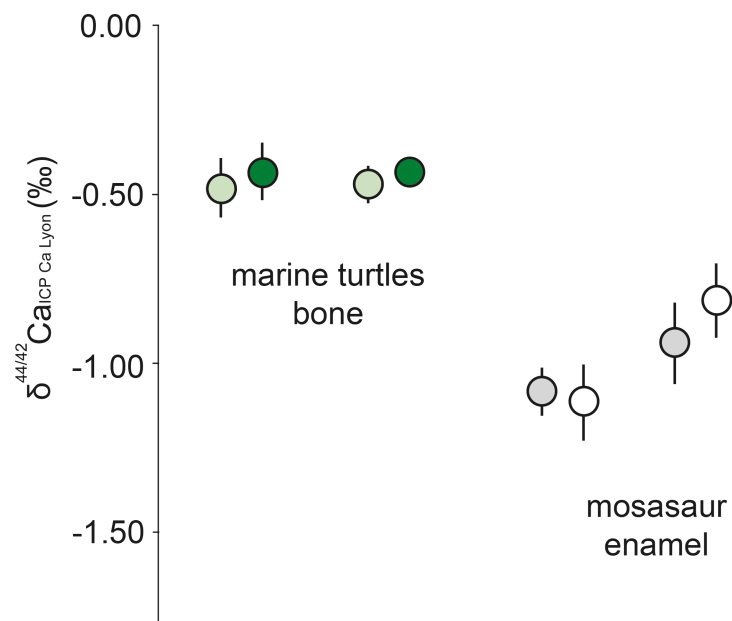


Figure S2. $\delta^{44/42}\text{Ca}$ values measured in this study for treated and untreated fossil samples. Comparison of $\delta^{44/42}\text{Ca}$ values measured on pairs of treated (to the left) versus untreated (to the right) samples (in ‰ relative to ICP Ca Lyon standard). Error bars represent 2SD. **Related to STAR Methods and Table S1.**

curation n°	age	consumer level	lab name	material	higher taxonomy	taxon	544/42Ca (‰)	2SD	543/42Ca (‰)	2SD	n
OCP-SA 1500	Maastrichtian	zooplanktivore	Ma-T1	bone	marine turtle	Bothremyidae indet.	-0.36	0.12	-0.16	0.09	4
OCP-SA 1501	Maastrichtian	zooplanktivore	Ma-T2	bone	marine turtle	Bothremyidae indet.	-0.40	0.04	-0.23	0.04	4
OCP-SA 1502	Maastrichtian	zooplanktivore	Ma-T3	bone	marine turtle	Chelonioidea indet.	-0.37	0.06	-0.23	0.08	5
OCP-SA 1503	Maastrichtian	zooplanktivore	Ma-T4	bone	marine turtle	indet.	-0.44	0.02	-0.20	0.05	3
OCP-SA 1504	Maastrichtian	zooplanktivore	Ma-T5	bone	marine turtle	indet.	-0.43	0.08	-0.22	0.08	3
OCP-SA 1505	Maastrichtian	primary	Ma-En1	tooth enamel	teleost fish	<i>Enchodus</i> sp. A	-0.43	0.05	-0.20	0.01	3
OCP-SA 1506	Maastrichtian	primary	Ma-En2	tooth enamel	teleost fish	<i>Enchodus</i> sp. A	-0.52	0.06	-0.26	0.04	3
OCP-SA 1507	Maastrichtian	primary	Ma-Enli1	tooth enamel	teleost fish	<i>Enchodus</i> sp. B	-0.67	0.05	-0.34	0.06	3
OCP-SA 1508	Maastrichtian	primary	Ma-Enli2	tooth enamel	teleost fish	<i>Enchodus</i> sp. B	-0.56	0.11	-0.31	0.17	3
OCP-SA 1509	Maastrichtian	primary	Ma-Py1	tooth enamel	teleost fish	Pycnodont	-0.73	0.00	-0.38	0.02	3
OCP-SA 1510	Maastrichtian	primary	Ma-Py2	tooth enamel	teleost fish	Pycnodont	-0.44	0.14	-0.25	0.12	3
OCP-SA 1511	Maastrichtian	primary	Ma-Pri1	tooth enamel	elasmobranch	<i>Pristiphorus</i> sp.	-0.70	0.02	-0.40	0.01	2
OCP-SA 1512	Maastrichtian	primary	Ma-Pri2	tooth enamel	elasmobranch	<i>Pristiphorus</i> sp.	-0.52	0.08	-0.24	0.08	3
OCP-SA 1513	Maastrichtian	tertiary	Ma-Cr1	tooth enamel	elasmobranch	<i>Cretolamna</i> sp.	-0.92	0.09	-0.48	0.11	3
OCP-SA 1514	Maastrichtian	tertiary	Ma-Cr2	tooth enamel	elasmobranch	<i>Cretolamna</i> sp.	-0.79	0.09	-0.42	0.10	4
OCP-SA 1515	Maastrichtian	tertiary	Ma-sq1	tooth enamel	elasmobranch	<i>Squalicorax</i> sp.	-0.69	0.02	-0.32	0.08	3
OCP-SA 1516	Maastrichtian	tertiary	Ma-sq2	tooth enamel	elasmobranch	<i>Squalicorax</i> sp.	-0.85	0.14	-0.42	0.05	3
OCP-SA 1517	Maastrichtian	tertiary	Car1	tooth enamel	elasmobranch	<i>Carcharias</i> sp.	-1.06	0.02	-0.55	0.09	2
OCP-SA 1518	Maastrichtian	tertiary	Car2	tooth enamel	elasmobranch	<i>Carcharias</i> sp.	-0.97	0.04	-0.50	0.13	2
OCP-SA 1519	Maastrichtian	tertiary	Car3	tooth enamel	elasmobranch	<i>Carcharias</i> sp.	-0.74	0.03	-0.40	0.02	2
OCP-SA 1520	Maastrichtian	tertiary	Ma-Ere1	tooth enamel	mosasaurid	<i>Eremiasaurus</i> sp.	-1.03	0.06	-0.52	0.01	3
OCP-SA 1521	Maastrichtian	tertiary	Ma-Ere2	tooth enamel	mosasaurid	<i>Eremiasaurus</i> sp.	-1.00	0.08	-0.56	0.11	3
OCP-SA 1522	Maastrichtian	tertiary	Ma-Ere3	tooth enamel	mosasaurid	<i>Eremiasaurus</i> sp.	-0.84	0.04	-0.39	0.02	3
OCP-SA 1523	Maastrichtian	tertiary	Ma-Ere4	tooth enamel	mosasaurid	<i>Eremiasaurus</i> sp.	-0.76	0.10	-0.37	0.19	2
OCP-SA 1524	Maastrichtian	tertiary	Ma-Ere5	tooth enamel	mosasaurid	<i>Eremiasaurus</i> sp.	-0.82	0.03	-0.43	0.08	3
OCP-SA 1525	Maastrichtian	tertiary	Ma-G1	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-0.78	0.01	-0.44	0.01	3
OCP-SA 1526	Maastrichtian	tertiary	Ma-G2	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-0.59	0.08	-0.27	0.05	3
OCP-SA 1527	Maastrichtian	tertiary	Ma-G4	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-1.03	0.24	-0.50	0.15	3
OCP-SA 1528	Maastrichtian	tertiary	Ma-G3	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-0.96	0.11	-0.47	0.10	3
OCP-SA 1529	Maastrichtian	tertiary	Ma-G5	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-1.10	0.06	-0.55	0.06	3
OCP-SA 1530	Maastrichtian	tertiary	Ma-G6	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-1.04	0.03	-0.55	0.06	4
OCP-SA 1531	Maastrichtian	tertiary	Ma-G7	tooth enamel	mosasaurid	<i>Globidens</i> sp.	-1.08	0.07	-0.55	0.07	2
OCP-SA 1532	Maastrichtian	tertiary	Ma-H3	tooth enamel	mosasaurid	<i>Halisaurus</i> sp.	-0.98	0.02	-0.49	0.06	3
OCP-SA 1533	Maastrichtian	tertiary	Ma-H4	tooth enamel	mosasaurid	<i>Halisaurus</i> sp.	-0.83	0.12	-0.39	0.02	2
OCP-SA 1534	Maastrichtian	tertiary	Ma-H5	tooth enamel	mosasaurid	<i>Halisaurus</i> sp.	-1.03	0.13	-0.48	0.08	2
OCP-SA 1535	Maastrichtian	tertiary	Ma-H1	tooth enamel	mosasaurid	<i>Halisaurus</i> sp.	-0.92	0.08	-0.46	0.03	3
OCP-SA 1536	Maastrichtian	tertiary	Ma-H2	tooth enamel	mosasaurid	<i>Halisaurus</i> sp.	-0.96	0.08	-0.49	0.14	3
OCP-SA 1537	Maastrichtian	tertiary	Ma-Pro1	tooth enamel	mosasaurid	<i>Prognathodon</i> sp.	-0.96	0.13	-0.49	0.16	4
OCP-SA 1538	Maastrichtian	tertiary	Ma-Pro2	tooth enamel	mosasaurid	<i>Prognathodon</i> sp.	-1.11	0.11	-0.57	0.11	3
OCP-SA 1539	Maastrichtian	tertiary	Ma-Pro3	tooth enamel	mosasaurid	<i>Prognathodon</i> sp.	-0.95	0.11	-0.48	0.08	2
OCP-SA 1540	Maastrichtian	tertiary	Ma-Pro4	tooth enamel	mosasaurid	<i>Prognathodon</i> sp.	-0.88	0.09	-0.45	0.10	3
OCP-SA 1541	Maastrichtian	tertiary	Ma-Pro5	tooth enamel	mosasaurid	<i>Prognathodon</i> sp.	-0.88	0.05	-0.42	0.02	2
OCP-SA 1542	Maastrichtian	tertiary	Ma-Pus1	tooth enamel	mosasaurid	" <i>Platycarpus</i> " <i>ptychodon</i>	-1.10	0.06	-0.51	0.09	3
OCP-SA 1543	Maastrichtian	tertiary	Ma-Pus2	tooth enamel	mosasaurid	" <i>Platycarpus</i> " <i>ptychodon</i>	-0.81	0.11	-0.41	0.08	4
OCP-SA 1544	Maastrichtian	tertiary	Ma-Pus3	tooth enamel	mosasaurid	" <i>Platycarpus</i> " <i>ptychodon</i>	-0.79	0.11	-0.40	0.06	2
OCP-SA 1545	Maastrichtian	tertiary	Ma-Pus4	tooth enamel	mosasaurid	" <i>Platycarpus</i> " <i>ptychodon</i>	-0.85	0.02	-0.39	0.00	2
OCP-SA 1546	Maastrichtian	tertiary	Ma-P1	tooth enamel	elasmosaurid	indet.	-0.85	0.02	-0.42	0.04	3
OCP-SA 1547	Maastrichtian	tertiary	Ma-P2	tooth enamel	elasmosaurid	indet.	-0.87	0.10	-0.47	0.17	3
OCP-SA 1548	Maastrichtian	tertiary	Ma-P3	tooth enamel	elasmosaurid	indet.	-1.05	0.01	-0.53	0.06	3
OCP-SA 1549	Maastrichtian	tertiary	Ma-P5	tooth enamel	elasmosaurid	indet.	-0.96	0.18	-0.48	0.07	3
OCP-SA 1550	Maastrichtian	tertiary	Ma-P4	tooth enamel	elasmosaurid	indet.	-0.90	0.09	-0.44	0.06	3
OCP-SA 1538	Maastrichtian	tertiary	Ma-Pro2lea	tooth enamel	mosasaurid	<i>Prognathodon</i> sp. leached	-1.08	0.07	-0.56	0.07	4
OCP-SA 1543	Maastrichtian	tertiary	Ma-Pus2lea	tooth enamel	mosasaurid	<i>P. ptychodon</i> leached	-0.94	0.12	-0.46	0.01	2
OCP-SA 1503	Maastrichtian	zooplanktivore	Ma-T4lea	bone	marine turtle	indet.	-0.47	0.05	-0.22	0.13	3
OCP-SA 1504	Maastrichtian	zooplanktivore	Ma-T5lea	bone	marine turtle	indet.	-0.48	0.09	-0.24	0.11	3
UCBL-FSL-94808	modern	zooplanktivore	Chel1	bone	marine turtle	<i>Caretta caretta</i>	-0.26	0.08	-0.14	0.10	4
UCBL-FSL-532088	modern	zooplanktivore	Chel3	bone	marine turtle	<i>Chelonia mydas</i>	-0.33	0.08	-0.16	0.04	4
UCBL-FSL-532403	modern	zooplanktivore	Chel4	bone	marine turtle	<i>Chelonia mydas</i>	-0.26	0.05	-0.15	0.05	4
UCBL-FSL-532095	modern	zooplanktivore	Chel5	bone	marine turtle	<i>Chelonia mydas</i>	-0.30	0.05	-0.16	0.08	3

Table 1. Calcium isotope values (expressed as $\delta^{44}/^{42}\text{Ca}$ (in ‰) relative to standard ICP Ca-Lyon) measured in this study for marine vertebrates of the Maastrichtian of Morocco as well as for modern marine turtle bone. Institutional abbreviations: OCP-SA, Office Chérifien des Phosphates, Khouribga, Morocco; UCBL-FSL, Université Claude Bernard Lyon 1, Faculté des Sciences de Lyon, Villeurbanne, France. **Related to STAR Methods.**