

On diving and diet: resource partitioning in type-Maastrichtian mosasaurs*

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Abstract

The carbon isotope composition of tooth enamel from all five mosasaur taxa known to date from the type Maastrichtian (southeast Netherlands, northeast Belgium) has been analysed. Differences in enamel $\delta^{13}\text{C}$ values between taxa suggest resource partitioning. Body size and $\delta^{13}\text{C}$ value correlate surprisingly well, with larger taxa having $\delta^{13}\text{C}$ values more depleted in the heavier ^{13}C isotope.

Keywords: Mosasauridae, Reptilia, carbon isotopes, Late Cretaceous

Introduction

During the Late Cretaceous, mosasaurs evolved to become highly diversified and successful marine carnivores (Polcyn et al., in press). Much like whales today, mosasaurs were lung breathers and agile divers (e.g., Rothschild & Martin, 2005). The mosasaur fauna from the Maastrichtian type area ranks among the best-studied in the world (e.g., Kuypers et al., 1998; Mulder, 2003). These reptiles were the apex predators of the type Maastrichtian marine ecosystem (e.g., Schulp, 2006). The presence of five taxa that exhibit a wide range of tooth morphologies suggests significant ecological specialisation among mosasaur species of that time interval.

To decipher better the ecological information locked in such fossil faunas, a variety of geochemical proxy records can be explored. Particularly valuable for such studies is a carbon isotope analysis of these remains. Carbon isotope ratios are affected by diet and habitat partitioning as well as by metabolic/physiologic processes (e.g., Koch et al., 1994). In the study of vertebrate fossils, the material generally preferred for carbon

isotope analysis is tooth enamel, because of its resistance to diagenetic alteration. Tooth enamel contains a small fraction of structurally bound carbonate that can be analysed for oxygen and carbon isotope composition (e.g., Bryant et al., 1996; Clementz & Koch, 2001).

Until now, only a single study targeted the carbon isotope composition of mosasaur teeth (Robbins et al., 2008). In that paper, it was suggested that $\delta^{13}\text{C}$ values generally decreased with body size. However, the wide range of taxonomic diversity, provenance, age, body size, presumed diets and palaeoenvironments of the taxa studied hampered a detailed interpretation of this pattern within an ecological context.

To constrain the ecological interpretation of carbon isotope compositions of mosasaur enamel better, we here present an analysis of tooth enamel $\delta^{13}\text{C}$ values for all known mosasaur taxa from a single site, with a narrow temporal range. Furthermore, we compare these isotope data to an extensive carbon isotope data set of shark teeth enamel (Van Baal et al., submitted), as well as various carbonate fossils from the same lithological sequence (Vonhof et al., 2011).

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Material and methods

Material

The mosasaur fauna from the Maastrichtian type area comprises five taxa (Jagt et al., 2008; Schulp et al., 2008), which range from the diminutive shellfish-eating *Carinodens belgicus* to the large *Mosasaurus hoffmanni* and *Prognathodon saturator*, which presumably fed on larger prey such as fish, squid, turtles and other marine reptiles (including mosasaurs) and possibly birds. All samples are from the Maastrichtian type area (near Maastricht, southeast Netherlands, and contiguous areas in northeast Belgium), and are in the collections of the Natuurhistorisch Museum Maastricht (NHMM). Specimen numbers are listed along with the reconstructed body lengths and $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in Table 1.

Table 1.

Taxon	Length (m)	Collection #	$\delta^{13}\text{C}$ value (‰ VPDB)	$\delta^{18}\text{O}$ value (‰ VPDB)
<i>Carinodens belgicus</i>	3 (adult)	NHMM 1980.6	-10.76	-3.97
	3 (adult)	NHMM 1980.7 (1)	-10.48	-2.28
	3 (adult)	-(2)	-10.42	
	2 (subadult)	NHMM 7354	-10.28	-3.55
<i>Plioplatecarpus marshi</i>	5.5 (adult)	NHMM 1984.88.1A	-11.07	-4.47
	5.5 (adult)	NHMM 1984.88.1B	-10.34	
<i>Prognathodon sectorius</i>	7 (subadult)	NHMM 1995 031	-9.92	-3.40
	8 (adult)	NHMM LV 150	-12.15	-3.11
<i>Prognathodon saturator</i>	12 (adult)	NHMM 1998 141 (1)	-12.57	-3.16
	12 (adult)	-(2)	-13.34	-3.35
	12 (adult)	-(3)	-13.56	-2.98
	12 (adult)	-(4)	-12.31	-2.75
	12 (adult)	-(5)	-12.30	-3.14
<i>Mosasaurus hoffmanni</i>	6 (juvenile)	NHMM 1317.02	-9.29	-3.20
	6 (juvenile)	NHMM MK 591	-7.14	
	10 (subadult)	NHMM 4560	-11.25	-3.79
	14 (adult)	NHMM 1446 (1)	-13.07	-4.70
	14 (adult)	-(2)	-12.98	-4.38
	14 (adult)	-(3)	-12.62	-4.00
	14 (adult)	-(4)	-13.81	-6.20
	14 (adult)	-(5)	-13.96	-4.44
	14 (adult)	-(6)	-13.44	-5.28
	14 (adult)	-(7)	-13.59	-4.00
	14 (adult)	-(8)	-14.86	-3.86
	14 (adult)	-(9)	-14.54	-3.86
	14 (adult)	-(10)	-13.71	-3.79
	14 (adult)	-(11)	-13.61	-6.18

Sampling protocol

Prior to sampling, all teeth were cleaned using acetone; enamel fragments were subsequently extracted under a binocular microscope by crushing the enamel surface and removing the fragments using tweezers and a surgical knife. All fragments were inspected microscopically; those with adhering dentine were removed and discarded. Teeth NHMM 1980.7, NHMM 1446 and NHMM 1998 141 were sampled multiple times in order to assess intra-tooth variability.

Analysis

Structural carbonate in mosasaur tooth enamel was analysed on a Thermo Finnigan Delta Plus mass spectrometer equipped with a Gasbench II preparation device. Samples (~100–400 μg) were placed in He-filled 4 ml exetainer vials, and were converted to CO_2 by reaction with concentrated phosphoric acid (H_3PO_4) at a temperature of 45 °C. Subsequently, the CO_2 -He gas mixture in the exetainer headspace is transported to the GASBENCH II by use of a He flow through a flushing needle system. Isotope values are reported as $\delta^{13}\text{C}$ vs VPDB. The reproducibility of routinely analysed laboratory CaCO_3 standards is better than 0.1‰ (1σ).

Mosasaur body size reconstructions

A previous study by Robbins et al. (2008) hinted at a correlation between mosasaur body size and $\delta^{13}\text{C}$ values; we therefore reconstructed the body size of the mosasaurs analysed in the present study. *Carinodens belgicus*, although not known from complete skeletons, should have attained overall body lengths of approximately 3 metres (Schulp et al., 2010). Total body length of *Prognathodon saturator*, as based on a partial skeleton, is reconstructed at ca 12 m (Christiansen & Bonde, 2002; Dortangs et al., 2002; Schulp, 2006). The largest specimen of *Mosasaurus hoffmanni* is suggested to have reached 17.6 m (Lingham-Soliar, 1995); a more conservative value, 14 m, is adopted to reflect the large, yet not extremely large, teeth in the present note. *Plioplatecarpus marshi* (see Lingham-Soliar, 1994; Kuypers et al., 1998) and *Prognathodon sectorius* (Schulp et al., 2008) are medium-sized taxa in the type Maastrichtian seas. No complete skeletons of either are known, but extrapolation of the proportions following mosasaur species outlined above, and consideration of the review in Christiansen & Bonde (2002), lengths of 5.5 and 8 m, respectively, appear reasonable estimates for body size of adult individuals. The reconstructed body length of subadult and juvenile specimens has been calculated on the basis of a linear size ratio comparison with adult teeth.

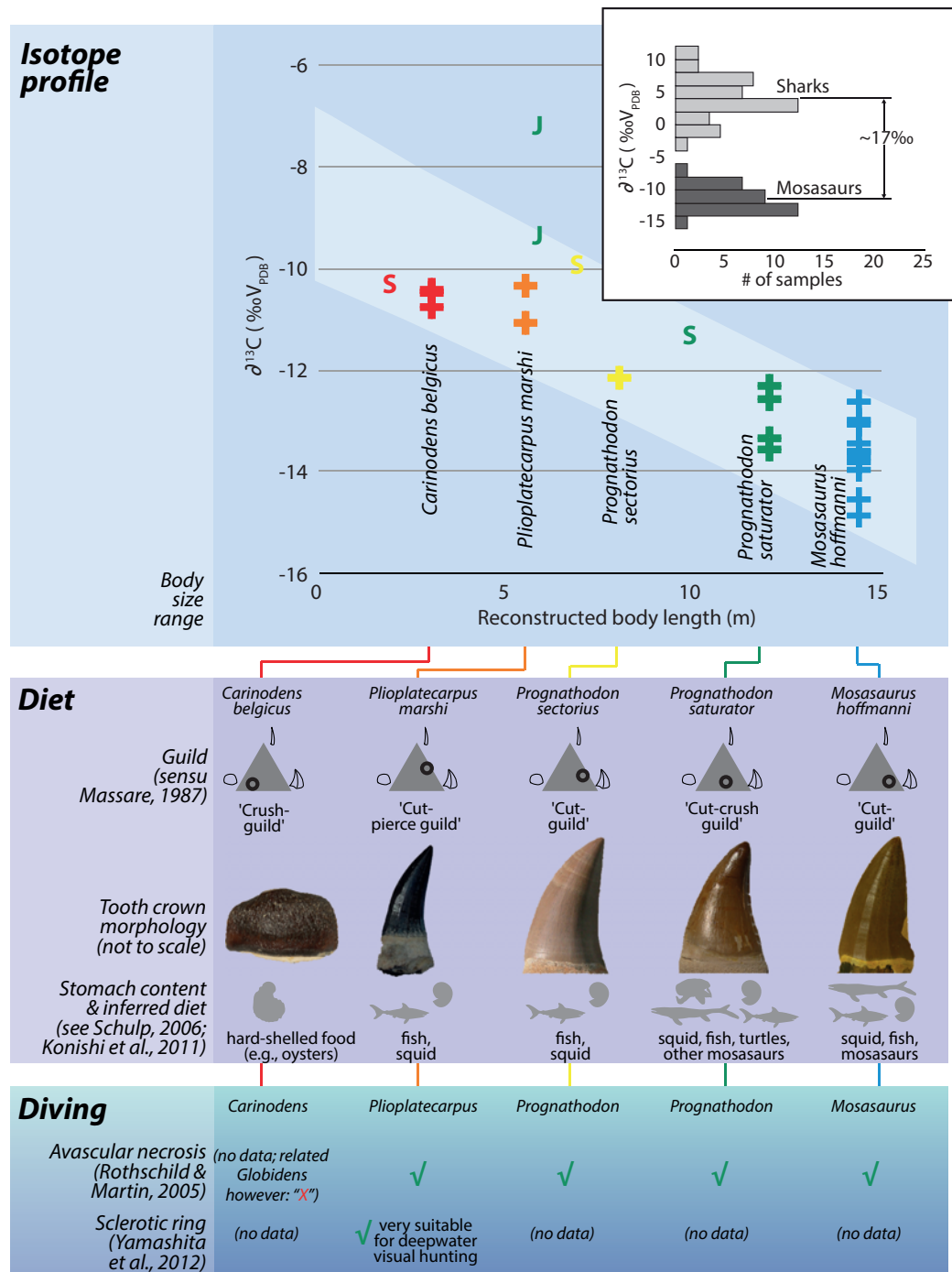
Results and discussion

Carbon isotope values of adult mosasaur teeth studied range from -10.3 to -14.9‰ (VPDB), which differ significantly from the shark fauna values ranging from -3.8 to 11.0‰ with a median of 4‰ relative to VPDB (Fig. 1). Similarly, mosasaur tooth $\delta^{13}\text{C}$ values are consistently lower by ~ 5 - 15‰ compared to all other skeletal carbonates analysed (e.g., belemnites, foraminifera) and diagenetic calcites from this site (Vanhof et al., 2011).

Diagenesis

Microscopic screening did not reveal preservational differences between teeth of different size or species. Previous studies of the effect of diagenetic alteration in isotope values of fossil shark teeth from this sequence have shown that, irrespective of excellent optical preservation, oxygen isotope values of tooth enamel structural carbonate are commonly altered, while the carbon isotopes of the same material consistently reflect primary signals (Van Baal et al., submitted). Due to the similarity of shark and mosasaur tooth enamel we postulate that the

Fig.1. Carbon isotope composition, body size, inferred diet and diving behaviour of the five mosasaur taxa known to date from the type Maastrichtian. The $\delta^{13}\text{C}$ values in mosasaur tooth enamel correlate closely with body length ($r^2 = 0.82$, $n = 27$); the difference between the medians of $\delta^{13}\text{C}$ values is shown; area within the 95% error bounds shaded; crosses represent adult specimens; 'J' data points are juveniles, 'S' are subadult. Typical analytical error (1SD): $\pm 0.1\text{‰}$. Inset: carbon isotope compositions of mosasaur and shark tooth enamel structural carbonate. A significant difference (t -test, $p < 0.001$, $n = 59$) exists between mosasaur and shark structural carbonate enamel $\delta^{13}\text{C}$ values from the Maastrichtian type area.



same applies to mosasaur tooth isotope data. We therefore exclude the oxygen isotope data of mosasaur tooth enamel structural carbonate from further interpretation, because we cannot rule out that these are diagenetically altered.

Shark vs mosasaur $\delta^{13}\text{C}$ values

The diagenetic considerations outlined above suggest that the observed $\sim 17\text{‰}$ offset between shark and mosasaur tooth enamel $\delta^{13}\text{C}$ values must reflect primary signals. As sharks and mosasaurs occupy somewhat comparable ranks in the food chain, dietary aspects can be ruled out as the main cause behind the large carbon isotopic difference observed. The fundamental difference between the two groups lies in the contrasting respiratory physiology between gill-respiring sharks and lung-breathing mosasaurs. As lung-breathers, mosasaurs likely experienced respiratory carbon isotope fractionation linked to holding breath during diving, which drives $\delta^{13}\text{C}$ to lower values (McConnaughey et al., 1997; Biasatti, 2004; Robbins et al., 2008). We therefore consider physiological factors, including respiratory fractionation, to be a major factor in the mosasaur tooth $\delta^{13}\text{C}$ values being lower than all other fossils analysed from the type Maastrichtian. Interestingly, the closest $\delta^{13}\text{C}$ value to values observed in mosasaurs was obtained from a cortical (dense) bone sample of another lung-breather, the sympatric marine turtle *Allopleuron hoffmanni* (Van Baal et al., submitted).

Body size

Within the mosasaur data set, body size and $\delta^{13}\text{C}$ values are remarkably well correlated (Fig. 1), with larger taxa having more depleted $\delta^{13}\text{C}$ carbon isotope compositions. If this body size correlation was primarily determined by trophic level differences between mosasaur taxa, then larger species, assumed to have generally occupied higher trophic levels, on the whole should have had higher $\delta^{13}\text{C}$ values (e.g., Clementz & Koch, 2001). In contrast, we have observed an opposite trend for which the following contributing factors can be considered:

Bohr effect – Isotopic fractionation through the Bohr effect is driven by elevated blood pCO_2 , the effect of which increases with prolonged and/or deeper diving (Biasatti, 2004). If mosasaurs with lower $\delta^{13}\text{C}$ values were more avid divers (either prolonged dives or diving relatively often), then part of the observed pattern could be explained through the Bohr effect, which is in line with the foraging range of the larger taxa extending to areas in deeper waters, further offshore.

Diet – Diet also has a marked impact on the carbon isotope composition of the animal. The range of food items of type Maastrichtian mosasaurs is fairly well constrained (Massare, 1987; Schulp, 2006 and references therein). The diminutive mosasaur *Carinodens* probably preyed on hard-shelled food such as small oysters (e.g., Schulp, 2005); the medium-sized *Prognathodon sectorius* and *Plioplatecarpus marshi* both have pointed teeth

with sharp carinae suited to process squid and fish (e.g., Kuypers et al., 1998). The much larger *Prognathodon saturator* was well equipped to deal with turtles (Dortangs et al., 2002; Konishi et al., 2011), whereas the large teeth of *Mosasaurus hoffmanni* could have handled virtually anything (Lingham-Soliar, 1995; Kuypers et al., 1998). In view of the fact that, for example, a diet high in lipids, such as that of marine turtles, can lower $\delta^{13}\text{C}$ values (Post et al., 2007), part of the pattern observed here can be attributed to dietary factors, as outlined in Fig. 1.

Foraging habitat

Diving behaviour and diet both have an impact on the $\delta^{13}\text{C}$ value as preserved in tooth enamel. Both factors can be considered as aspects of the more general concept of foraging habitat. Foraging habitats are known to correlate with the $\delta^{13}\text{C}$ signal, with nearshore settings being associated with higher $\delta^{13}\text{C}$ values (Clementz & Koch, 2001). Habitat partitioning alone accounted in extant marine mammals for a range in $\delta^{13}\text{C}$ values from around -13‰ in offshore marine settings to $\sim -6\text{‰}$ in kelp beds. This range is comparable to that observed here in mosasaurs.

Diving behaviour

In order to evaluate aspects of diving behaviour in mosasaurs further, two approaches have provided independent data. Bends-induced avascular necrosis is invariably present in bones of *Prognathodon*, *Mosasaurus* and *Plioplatecarpus* studied by Rothschild & Martin (2005), which is consistent with the diving behaviour discussed here. A second approach could also potentially provide independent evaluation of this hypothesis: Yamashita et al. (2012) evaluated the f -number of reconstructed mosasaur eyes. A lower f -number correlates to higher efficiency in capturing light, which would allow visual hunters to forage at deeper stretches of the photic zone. At this point, the limited data set of Yamashita et al. (2012) presents little overlap with the taxa discussed here, but the discrepancies between this approach and the conclusions by Rothschild & Martin (2005) are worthy of note. *Platecarpus* and *Clidastes* both have eyes that were adapted to visual foraging at deeper reaches of the photic zone, while the rather large *Tylosaurus* had much less well-developed lenses.

Ontogeny

In the type Maastrichtian marine ecosystem, juvenile mosasaur fossils are relatively rare, and so are juvenile shed (replaced) teeth, compared to the abundance of adult specimens (Kuypers et al., 1998). As a pilot, we have sampled a limited number of juvenile teeth, which have so far yielded considerably higher $\delta^{13}\text{C}$ values in comparison to adult specimens. However, more material and analyses would be required to evaluate this aspect of mosasaur ontogeny fully.

Conclusions

The five mosasaur taxa known from the type Maastrichtian show distinct partitioning in tooth enamel $\delta^{13}\text{C}$ values, with larger taxa preserving more negative values. This pattern compares favourably with previously published mosasaur $\delta^{13}\text{C}$ data, which showed a similar correlation between carbon isotope compositions and body size (Robbins et al., 2008). Carbon isotope composition of mosasaur tooth enamel of the type Maastrichtian has remarkably low $\delta^{13}\text{C}$ values compared to those of sharks from the same ecosystem. The large differences in $\delta^{13}\text{C}$ values can be explained by differences in respiratory physiology.

By analysing a relatively large sample of mosasaur teeth from different taxa but from the same age and area, we have been able to reduce the impact of spatio-temporal $\delta^{13}\text{C}$ variation in the data set significantly. This illustrates resource partitioning, reflected through the Bohr effect (McConnaughey et al., 1997; Biasatti, 2004), and thus diving/foraging behaviour, and through dietary specialisation, as important determinants in the carbon isotope composition as preserved in mosasaur tooth enamel.

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