Carbon isotope trends in north-west European mosasaurs (Squamata; Late Cretaceous)

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The carbon stable isotope composition ($\delta^{13}C$) of tooth enamel in mosasaurid squamates reflects aspects of their diet and diving behaviour. Here we present new $\delta^{13}C$ data for such marine squamates from the Maastrichtian of Denmark and compare these with results obtained in previous studies from the lower-latitude type area of the Maastrichtian Stage (latest Cretaceous; 72.1–66.0 Ma) in the south-east Netherlands and north-east Belgium. For the Danish samples, there is a weak correlation between mosasaur body size and $\delta^{13}C$ values, with larger-sized taxa having lower $\delta^{13}C$ values, comparable to what has previously been observed for mosasaurs from the Maastrichtian type area.

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Mosasaurs were a diverse, highly successful clade of marine squamates that were secondarily adapted to an aquatic life and were widely distributed during the last ~30 million years of the Cretaceous (Polcyn *et al.* 2014). These medium- to large-sized, agile predators fed on an extensive range of macroscopic prey, as is reflected in the wide variety of tooth morphologies. Although tooth morphology (e.g. Massare 1987; Schulp 2005), bite marks (e.g. Neumann & Hampe 2018), dental microwear (e.g. Holwerda *et al.* 2013), stomach contents (Martin & Fox 2007; Konishi *et al.* 2011) and eye size (Yamashita *et al.* 2015) may provide indirect or even direct evidence of hunting behaviour and dietary preferences, additional independent lines of evidence in reconstructing diet and trophic relationships are desirable.

Stable carbon and oxygen isotopes in tooth enamel have been used for evaluation of diet and other aspects of mosasaur palaeobiology (e.g. Robbins *et al.* 2008; Schulp *et al.* 2013). In the present contribution, we discuss the carbon isotope ($\delta^{13}C$) signatures recovered from tooth enamel of mosasaur teeth from the Maastrichtian of Denmark and compare these data with the pattern observed in the lower-latitude, but roughly coeval, type Maastrichtian ecosystem in the south-east Netherlands and north-east Belgium, as well as sites elsewhere.

Mosasaur teeth were continuously replaced, taking up to almost two years for each to form fully (Gren & Lindgren 2013). Tooth enamel is predominantly composed of hydroxyapatite, $Ca_{10}(PO_4)_6(OH)_2$, which contains less than 5 % by weight of carbonate (e.g. Koch *et al.* 1997). This structurally bound carbonate is precipitated in isotopic equilibrium with body fluids, which, prior to the formation of tooth enamel, becomes fractionated due to respiration (in which the lighter ^{12}C-isotope preferentially becomes liberated from the body pool) and during the formation of new enamel (DeNiro & Epstein 1978). Of this carbonate fraction, the stable isotope composition of carbon and oxygen ($\delta^{18}O$) can be measured. Robbins *et al.* (2008) and Schulp *et al.* (2013) noted that mosasaurs of larger body sizes generally had relatively low $\delta^{13}C$ values in comparison to smaller taxa, with juveniles having relatively higher values compared to conspecific adults. These $\delta^{13}C$ values mainly reflect diet, metabolic and physiological processes, whereas the $\delta^{18}O$ values would have been affected by temperature and the $\delta^{18}O$ values of ambient seawater. As such, the $\delta^{13}C$ and $\delta^{18}O$ signatures can be used to infer biological aspects of extinct squamates.

Schulp *et al.* (2013) focused their research on mosasaur teeth from the Upper Maastrichtian of the Netherlands and Belgium, while Robbins *et al.* (2008) used mosasaurid teeth from the Upper Cretaceous of Texas (USA) and Angola. Here we present the $\delta^{13}C$ signature from teeth of the full range of mosasaur genera represented in the Upper Cretaceous of Denmark, namely *Mosasaurus*, *Plioplatecarpus*, *Carinodens* and *Prognathodon*. On account of the similarities in assemblage between coeval faunas from Denmark and the Maastricht area, the present study aims to investigate whether a similar trend towards lower $\delta^{13}C$ in larger-sized mosasaurs exists in the Danish material. As this study constitutes a new data set from a more northern palaeolatitude, it also expands the latitudinal record of $\delta^{13}C$ signatures from mosasaur teeth.

Material and methods

Institutional abbreviations

NHMD: Natural History Museum of Denmark (Statens Naturhistoriske Museum), Copenhagen, Denmark; NHMM: Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; OESM: Østsjællands Museum, Store Heddinge, Denmark.

Geographical setting

During the Maastrichtian, the area of present-day Denmark was covered by a shallow (100–250 m deep) epicontinental sea (Lindgren & Jagt 2005; Einarsson 2018) in which mosasaurs ranked amongst the top predators. Since 1964, mosasaur tooth crowns have been recognized from Maastrichtian sedimentary rocks of Denmark (Lindgren & Jagt 2005; Fig. 1), corresponding to palaeolatitudes of ~44°N (reference frame from Van Hinsbergen *et al.* 2015; www.paleolatitude. org). Additional mosasaur material from the type Maastrichtian (south-east Netherlands, north-east Belgium; Mulder 2004) studied here corresponds to a palaeolatitude of *c.* 40°N during the latest Cretaceous (Van Hinsbergen *et al.* 2015; www.paleolatitude.org).

Localities, stratigraphy and specimens

The mosasaur teeth from Denmark analysed in the present study (Table 1) were collected at three localities: Stevns Klint, Møns Klint and Ålborg. In order to expand the existing data set from Schulp *et al.* (2013), additional material from the Maastrichtian type area around Maastricht, the Netherlands (Fig. 1), was assessed as well.

The majority of the Danish teeth examined in the present study originate from the Møns Klint Formation (Surlyk *et al.* 2013), previously referred to the Tor Formation (Surlyk *et al.* 2006). This unit is characterized by thick sequences of marine chalk (Lindgren & Jagt 2005), as observed at Stevns Klint, that formed at water depths of ~100–200 m (Noe-Nygaard 1975) along the south-eastern margin of the Danish Basin. Stevns Klint comprises one of the best-preserved and most extensively studied records of Cretaceous–Palaeogene boundary sections and has therefore been recognized
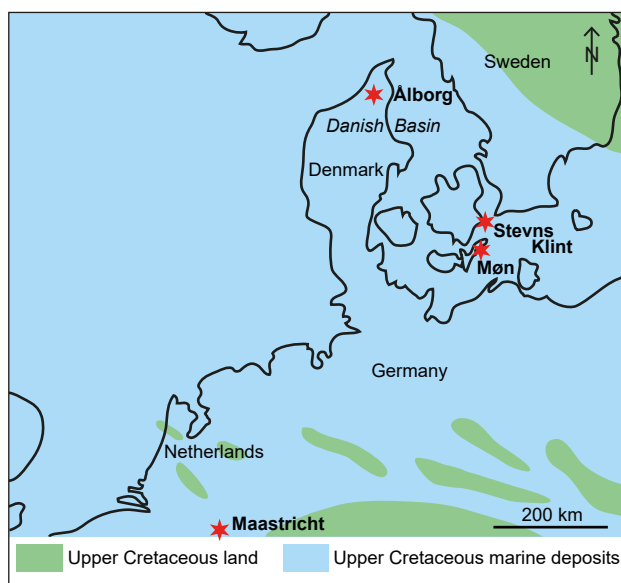

Fig. 1. Palaeogeography of north-west Europe during the Late Cretaceous, adapted from Blakey (2012), with indication of the localities of mosasaur teeth and tooth crowns analysed in the present study.
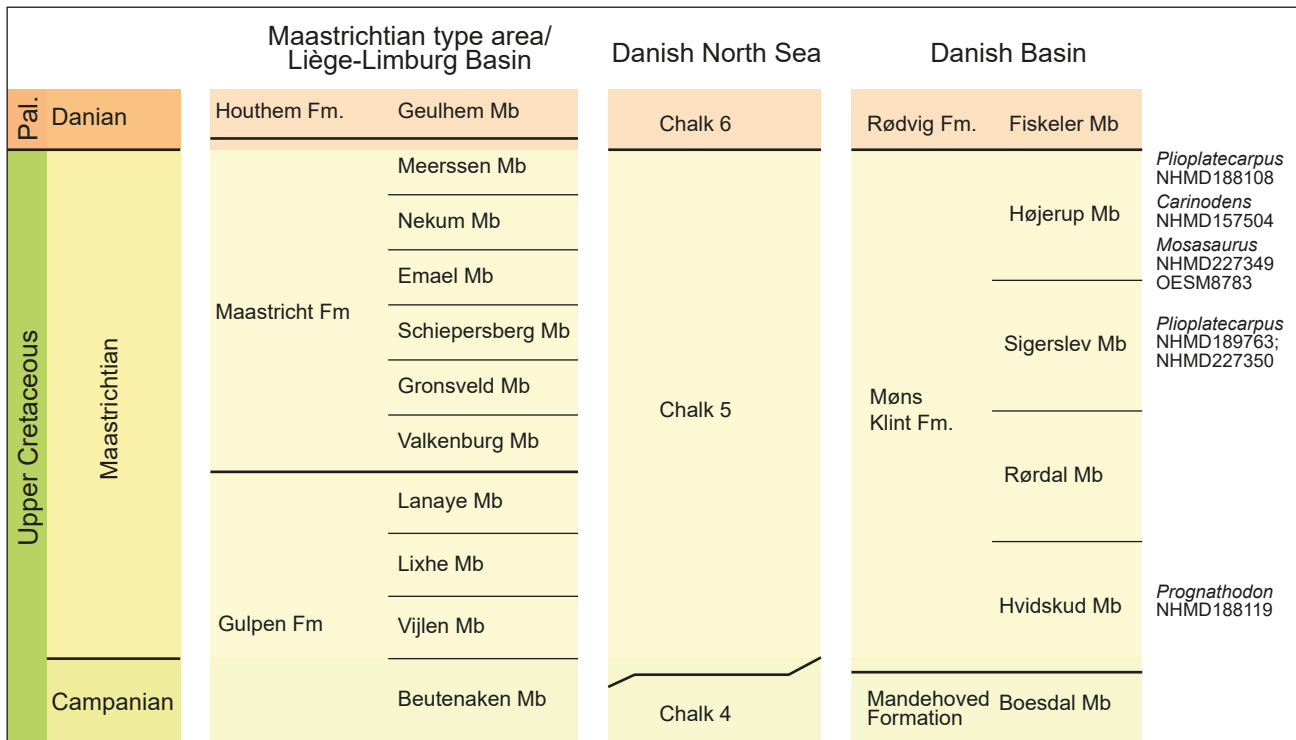
Fig. 2. Stratigraphy of the Danish Basin and the Maastrichtian type area (Liège-Limburg Basin) as well as lithostratigraphic scheme for the Danish North Sea (compare Lieberkind *et al.* 1982; Isaksen & Tonstad 1989; Van Adrichem Boogaert & Kouwe 1994; Niebuhr *et al.* 2007 and Surlyk *et al.* 2013). The record of *Prognathodon* NHMD 188119 is discussed by Giltaij *et al.* (2021).

as a UNESCO World Heritage Site (UNESCO website, accessed August 2020). The Møns Klint Formation spans the uppermost Maastrichtian up to the Cretaceous–Palaeogene boundary and has yielded several tooth crowns of at least three species of mosasaur (Bonde & Christiansen 2003).

The Møns Klint Formation can be subdivided into four members (Fig. 2). The basal unit, the Hvidskud Member, is of early Maastrichtian age and consists of alternating white chalk and darker, slightly marly chalk beds. At Møns Klint, these beds yielded a diverse fossil assemblage, including sponges, bivalves and echinoids and, at several levels in the upper part of the member, bryozoans and foraminifera (Surlyk *et al.* 2013). At Store Stejlebjerg on Møns Klint, an isolated tooth crown (NHMD 188119) assigned to the genus *Prognathodon* Dollo, 1889 (Giltaij *et al.* 2021) was found loose in scree; this stems from the Hvidskud Member.

Overlying the Hvidskud Member is the Rørdal Member, which lacks the white chalk beds. Its reference section is at the Rørdal quarry near Ålborg (Surlyk *et al.* 2013). It is overlain by the Sigerslev Member, which comprises benthos-rich chalk in mounded bedding with nodular flint deposited below storm wave base in the sub-photic zone with oxygenated bottom waters (Hansen & Surlyk 2014). This is followed by a benthos- and flint-poor chalk horizon

with near-horizontal bedding suggestive of a very weak bottom current, overlain by a marker band of flint associated with a sea level drop (Surlyk *et al.* 2006; Hansen & Surlyk 2014; Milàn *et al.* 2018). Two specimens, both referred to the genus *Plioplatecarpus* Dollo, 1882, originate from the Sigerslev Member. One is a 28-mm-tall tooth crown from the cliff at Sigerslev at Stevns Klint (NHMD 189763; Fig. 3A–D), the other is a 12-mm-tall tooth crown from Stevns Kridtbrud, Stevns Klint (NHMD 227350; Fig. 3M). Both specimens are here referred to as *Plioplatecarpus* sp. on the basis of their relatively small size, marked recurvature and finely striated basal enamel surface.

The uppermost unit of the formation, the Højerup Member, consists of bryozoan-rich wackestone in southward-trending, asymmetrical mounds up to 35 m in length, deposited after the return of suberosive currents and a sea-level rise (Hansen & Surlyk 2014). This unit is about five metres in thickness at the southern end of Stevns Klint and becomes gradually thinner towards the north (Surlyk *et al.* 2006; Milàn *et al.* 2018). One shed tooth crown of *Carinodens minalmamar* (NHMD 157504) has been collected from the uppermost metre of this member at Mandehoved, Stevns Klint (Milàn *et al.* 2018).

A marginal tooth crown, referred to as *Plioplatecarpus* sp. (NHMD 188108) by Lindgren & Jagt (2005),

was recovered from a loose block of limestone on the beach north of Stevns Kridtbrud, Stevns Klint. The block had fallen from a section of the cliff only a few metres below the Cretaceous–Palaeogene boundary and can be assigned either to the Højerup Member or to the Sigerslev Member, making it possibly the youngest representative of *Plioplatecarpus* known to date (Bonde *et al.* 2008). It should be noted that Lindgren & Jagt (2005) erroneously noted this specimen to have been collected from the locality of Holtug Kridtbrud. Two additional teeth (OESM 8783 and NHMD 227349), both referred to the genus *Mosasaurus* (Conybeare, 1822), also stem from either the Højerup Member or the Sigerslev Member at Stevns Klint. OESM 8783 has recently been illustrated by Milàn *et al.* (2018), who assigned it to *M. hoffmanni* (Mantell, 1829). Although fragmentary, NHMD 227349 (Fig. 3I–L) is referred to as *Mosasaurus* with confidence on account of its relatively large size, slightly conical shape, coarse faceting of the enamel and the presence of a significant anterior carina.

Finally, one large tooth crown referred to as *Mosasaurus* cf. *hoffmanni* (NHMD 226499) stems from the Møns Klint Formation *sensu lato* near Ålborg. How-
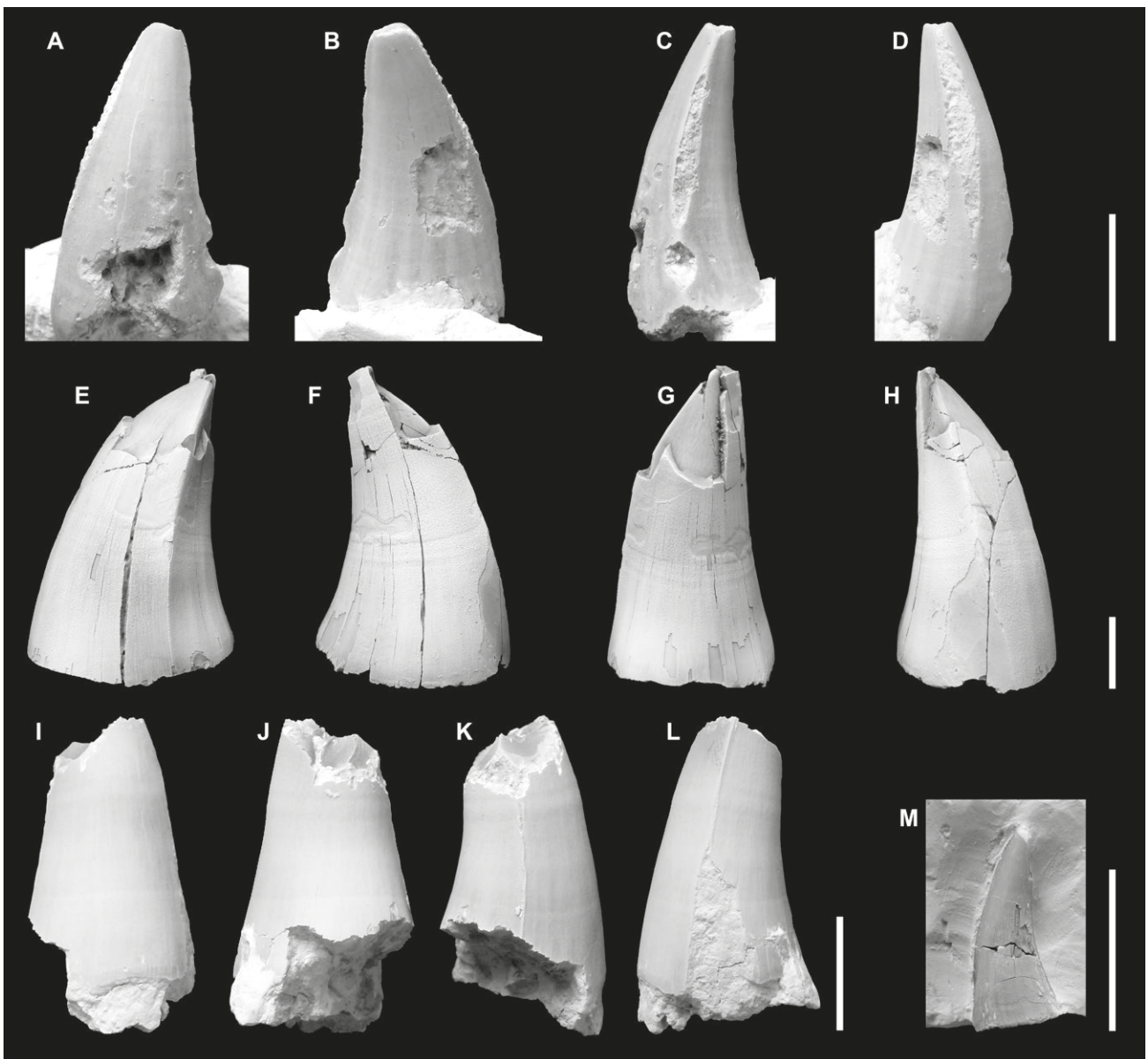

Fig. 3. Isolated mosasaurid tooth crowns. NHMD 189763, *Plioplatecarpus* sp. in labial (**A**), lingual (**B**), posterior (**C**) and anterior (**D**) views. NHMD 226499, *Mosasaurus* cf. *hoffmanni* in labial (**E**), lingual (**F**), posterior (**G**) and anterior (**H**) views. NHMD 227349, *Mosasaurus* sp. in labial (**I**), lingual (**J**), posterior (**K**) and anterior (**L**) views. NHMD 227350, *Plioplatecarpus* sp. in matrix (**M**). Scale bars equal 10 mm.

ever, the exact stratigraphic position is unknown (Lindgren & Jagt 2005; Fig. 3E–H).

The mosasaur teeth and tooth crowns from the Maastrichtian type area that have been analysed for the present study stem from the Maastricht and Gulpen Formations (Jagt & Jagt-Yazykova 2012; Schulp *et al.* 2013; Keutgen 2018; Fig. 2). While the Maastrichtian type locality is renowned for the historical discovery of the holotype of *Mosasaurus hoffmanni* in October 1778 (Pieters 2009; Homburg 2015), other species of mosasaur recovered from the uppermost strata include *Prognathodon sectorius* (Cope, 1871), *Prognathodon saturator* Dortangs *et al.* 2002, *Plioplatecarpus marshi* Dollo, 1882 and *Carinodens belgicus* (Woodward, 1891) (compare Jagt 2005; Schulp *et al.* 2013).

Tooth morphology
Mosasaurs are typically considered secondary con-

sumers up to apex predators, having fed on ammonites, bony and cartilaginous fish, plesiosaurs, turtles and even other mosasaurs (Massare 1987; Schulp *et al.* 2013; Miedema *et al.* 2019). In addition to stable isotopes, tooth morphology can also be used as a proxy for mosasaur diet. Most mosasaurs had a more or less homodont type of dentition with conical teeth (Massare 1987; Lingham-Soliar 1995; Caldwell 2007; Robbins *et al.* 2008). Some species, such as *Carinodens*, had a more heterodont type of dentition, which indicates a more specialised foraging repertoire (Schulp 2005; Mulder *et al.* 2013). Prey with a hard shell or external armour required stout, low teeth, while more slippery prey called for more slender, sharp teeth for piercing and handling. The diversity in tooth morphology enables reconstruction of prey preferences; Massare (1987) divided tooth crowns into 'guilds', based on tooth morphology (Fig. 4); this division is followed here.
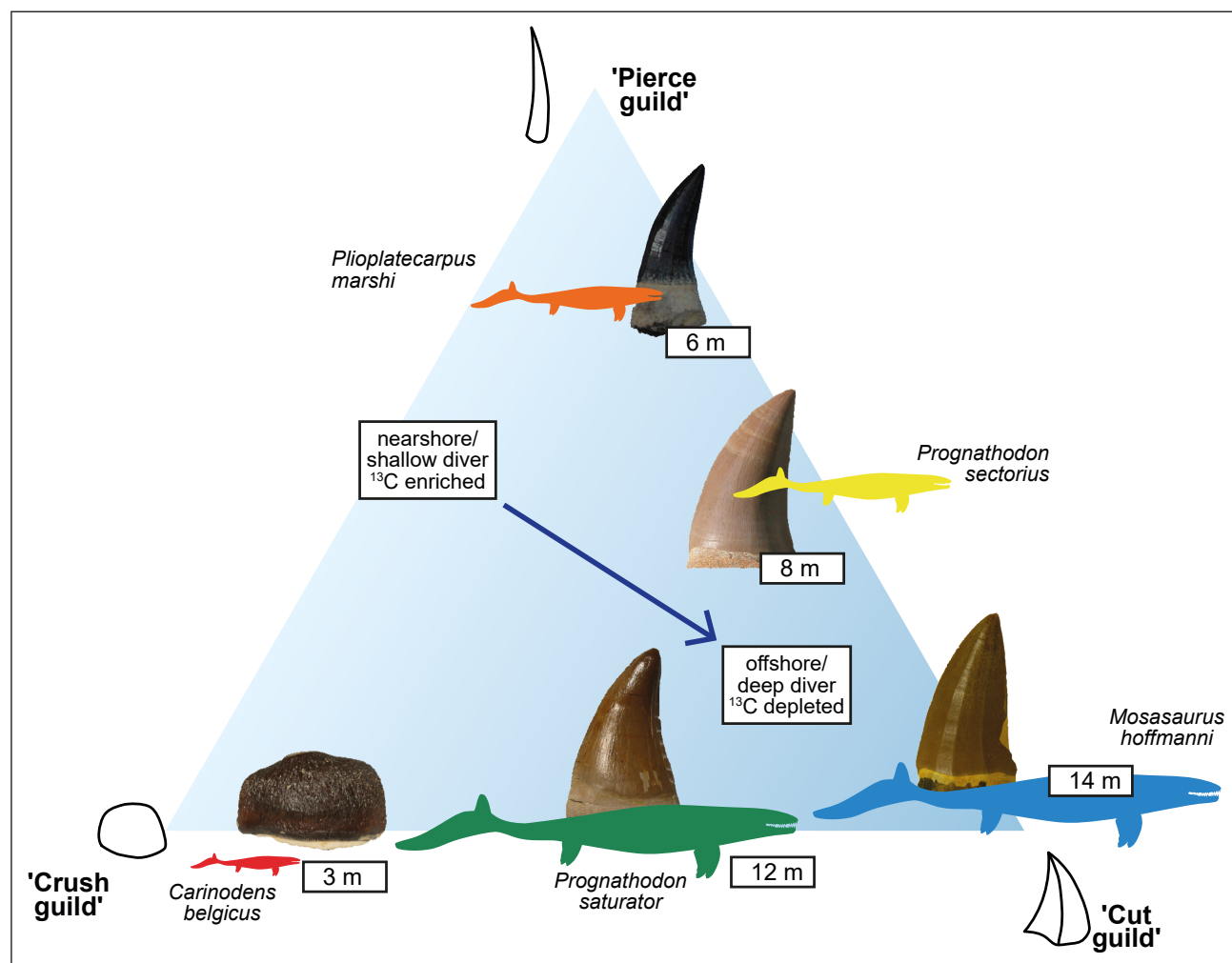

Fig. 4. Feeding strategies in mosasaurs, based on tooth morphology following Massare (1987), with the general ^{13}C isotope nearshore/offshore gradient (Robbins *et al.* 2008; Schulp *et al.* 2013) superimposed. Placement of mosasaur taxa follows Schulp *et al.* (2013); body lengths and example tooth images are based on assemblages from the Maastrichtian type area (Schulp *et al.* 2013); mosasaur silhouettes follow tail flukes as documented by Lindgren *et al.* (2013).

Body length reconstruction
As the dentition of mosasaurs is mostly homodont in nature, the body length of the individuals sampled could be roughly approximated using a linear relationship between tooth length and body length. As all the analysed teeth are detached from the jaws, we assume the teeth to be in either the seventh or eighth developmental stage (*sensu* Caldwell 2007). Body lengths (Table 1) were reconstructed following Russell (1967), Dortangs *et al.* (2002), Schulp *et al.* (2013) and Milàn *et al.* (2018).

Stable isotope analysis
Carbonate ions substitute into bioapatite in enamel, dentine and bone. Enamel is less porous, contains only a few percent of organic matter, and has larger and more stable crystals (*c.* 1000 × 130 × 30 nm) in comparison to bone or dentine (Cerling & Sharp 1996; Koch *et al.* 1997; Kohn *et al.* 1999; Koch 2007), which makes enamel less sensitive to diagenesis and therefore the preferred material for stable isotope analysis.

Prior to sampling, teeth were cleaned using ethanol in order to remove possible dirt, grease, and any residual flakes of sediment or glues and other residues from the enamel surface. Under an Olympus SZ60 optical microscope equipped with an Olympus Highlight 3000 fibre optic light source, tiny flakes (about 1 × 1 mm) of enamel were chipped off using a scalpel and put into vials after inspection for (and removal of) any remaining adhering dentine. Tooth crowns registered as NHMD 226499 and NHMM 1984089-1 were sampled in multiple locations in order to assess intra-tooth variability, and some samples of dentine were also included in order to document diagenesis. Samples of adhering matrix were taken to determine a background signal and examine possible diagenetic alteration. All samples are listed in Table 1. The structural carbonate in the enamel of mosasaur teeth was analysed using a Gasbench II connected to a Finnigan Delta+ mass spectrometer following the standard protocol at the Vrije Universiteit (Amsterdam) Earth Science stable isotope laboratory: samples were reacted with concentrated phosphoric acid (H_3PO_4) at 45°C for 24 hours to produce CO_2. Mixed with He, CO_2 was introduced to the mass spectrometer. Five samples of CO_2 monitor gas and ten subsamples of produced CO_2 were routinely analysed of each sample. A mean value of the samples was based on the last nine measurements. To monitor the accuracy of the analysis, ten samples with each a single grain of the VICS (VU In-house Carbonate Standard) were analysed in the same run as the samples and the international isotope standard IAEA-603. For the carbonate standards, the standard deviation (1σ) of the standard measurements is 0.08 ‰ and 0.14 ‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively.

For the individual enamel samples, the standard deviations of both averaged $\delta^{13}C$ and $\delta^{18}O$ values are below 0.4 ‰. The standard deviations of the measured $\delta^{13}C$ and $\delta^{18}O$ values of specimens NHMD 188119 and NHMM 001456 are larger than 0.5 ‰ and are therefore omitted from the dataset for interpretations. The $\delta^{13}C$ and $\delta^{18}O$ for the analysed bioapatite samples have a standard deviation ranging between 0.1 and 0.4 ‰ (Table 1). Hereafter, all reported results are reported as $\delta^{13}C$ and $\delta^{18}O$ values against the V-PDB scale.

Results

Isotope values
Table 1 shows the results of $\delta^{13}C$ and $\delta^{18}O$ analysis for structural carbonates of the tooth enamel as well as for the adhering matrix from Denmark. The $\delta^{13}C$ values in the Danish samples range from –11.1 to 0.2 ‰, whereas the $\delta^{18}O$ values range from –3.4 to –2.5 ‰.

The adhering carbonate sediments have $\delta^{13}C$ values between 0.1 and 2 ‰ and $\delta^{18}O$ values between –2.1 and –1.6 ‰. In case some of the adhering sediments would have remained, analysis of these samples would lead to considerably higher $\delta^{13}C$ values. This is less obvious for oxygen isotopes, which occur more or less in comparable ranges. Given the excess of oxygen in water, $\delta^{18}O$ values are expected to be more vulnerable to isotopic alteration than carbon isotopes during recrystallisation (Van Baal *et al.* 2013). Complementary to the Danish isotope data listed in Table 1 are $\delta^{13}C$ and $\delta^{18}O$ isotope analyses for structural carbonates in teeth from the Maastrichtian type area; $\delta^{13}C$ values range from –11.6 to –7 ‰ and $\delta^{18}O$ values range from –4.0 to –2.4 ‰.

The $\delta^{13}C$ values are plotted against the reconstructed body lengths of the sampled mosasaurs from Denmark and the Maastrichtian type area for the present study (Fig. 5). For comparison, these data have been plotted together with previously published datasets from the type Maastrichtian, USA and Angola (Schulp *et al.* 2013; Robbins *et al.* 2008). The $\delta^{13}C$ data show a negative relation with respect to body length, showing larger mosasaurs to have systematically lower $\delta^{13}C$ values. By combining both datasets from the Maastrichtian type area, we obtain a significant regression between reconstructed body length and $\delta^{13}C$ values, with a slope of –0.36 ‰ per metre body length. Some teeth considered to be from juvenile and subadult ontogenetic stages (indicated 'J' in Fig. 5) have not been included in the calculation of the regression line.

For the limited Danish mosasaur data (n = 6, juvenile specimen excluded), their reconstructed body

Table 1. Results of δ¹³C and δ¹⁸O stable isotope analysis for structural carbonates of the teeth sampled and of adhering matrix from Denmark and reconstructed body length.

Registration number	Species	Provenance	Member	δ¹³C	δ¹⁸O	Body length (m)
NHMD 157504	*Carinodens minalmamar*	Stevns Klint	Sigerslev	−6.28±0.13	−3.12±0.15	2
NHMD 227349	*Mosasaurus* sp.	Stevns Klint		−11.13±0.18	−2.48±0.18	10
OESM 8783	*Mosasaurus* sp.	Stevns Klint		−8.61±0.10	−2.62±0.14	8
OESM 8783	*Mosasaurus* sp.	Stevns Klint		−0.09±0.09	−2.05±0.16	[matrix]
NHMM 1984089-1	*Mosasaurus hoffmanni*	Maastricht		−10.32±0.29	−2.71±0.43	12
NHMM 1984089-1	*Mosasaurus hoffmanni*	Maastricht		−8.97±0.14	−3.38±0.18	12
NHMD 226499	*Mosasaurus* cf. *hoffmanni*	Ålborg		−6.94±0.37	−2.83±0.27	10
NHMD 226499	*Mosasaurus* cf. *hoffmanni*	Ålborg		−11.03±0.16	−2.74±0.15	10
NHMD 227350	*Plioplatecarpus* sp. juv.	Stevns Klint	?Sigerslev	0.24±0.30	−3.42±0.36	2.5
NHMD 189763	*Plioplatecarpus* sp.	Stevns Klint	?Sigerslev	−9.54±0.21	−2.82±0.19	5.5
NHMD 189763	*Plioplatecarpus* sp.	Stevns Klint	?Sigerslev	1.95±0.06	−1.61±0.09	[matrix]
NHMM 1997289	*Plioplatecarpus marshi*	Maastricht		−6.95±0.19	−2.40±0.23	5.5
NHMM 1997289	*Plioplatecarpus marshi*	Maastricht		−7.85±0.33	−4.01±0.27	5.5
NHMM 1998141-11	*Prognathodon saturator*	Maastricht	Upper Lanaye	−10.90±0.21	−2.67±0.18	12
NHMM 1998141-7	*Prognathodon saturator*	Maastricht	Upper Lanaye	−11.59±0.13	−2.52±0.06	12

length and δ¹³C values follow a trend comparable to the larger (n = 30) Maastrichtian type area dataset. These trends from north-west Europe show a gentler slope compared to the trend observed by Robbins *et al.* (2008) based on mosasaurs from USA and Angola.

Discussion

The limited number of data points from Danish mosasaurs fall to a certain extent within the pattern previously observed in the relationship between reconstructed body length and δ¹³C values; however, the relatively large spread in data suggests that other factors besides body length likely played a role in the measured δ¹³C values of the specimens examined. Here we review possible factors that may have been influential on the measured δ¹³C values.

Diet
According to Kohn (1996), Koch *et al.* (1997), Kohn *et al.* (1999) and Koch (2007), an individual's diet primarily affects δ¹³C apatite values. Based on the blunt shape of the teeth (Fig. 4), the diet of the smallest mosasaur in our data set, *Carinodens*, presumably consisted of hard-shelled prey such as oysters, other bivalves and decapod crustaceans in (near) coastal environments, while the large-sized *Prognathodon saturator* may have fed on marine turtles, plesiosaurs, large-sized saurodontid teleosts and other mosasaurs farther offshore (Schulp & Jagt 2015). Medium-sized mosasaurs, such as *Plioplatecarpus marshi*, would have occupied an

intermediate trophic position between these two habitats, feeding on more slippery prey such as fish and squid (Schulp 2005). The largest mosasaurs, such as *Mosasaurus hoffmanni*, could have eaten virtually everything, opportunistically including other mosasaurs (e.g. Lingham-Soliar 1995). In general, δ¹³C values in tooth enamel increase by ~1‰ per trophic level (De-Niro & Epstein 1978; Polcyn *et al.* 2014); contrastingly, as previously observed by Robbins *et al.* (2008), Schulp *et al.* (2013) and the present study, larger mosasaurs have generally lower δ¹³C values. Teeth from juvenile and subadult ontogenetic stages would have occupied lower trophic levels, possibly more nearshore.

The negative trend of δ¹³C values towards larger mosasaurs such as *Prognathodon saturator* and *Mosasaurus hoffmanni* may be explained by a more lipid-rich diet of the larger mosasaurs (Post *et al.* 2007), which would tend to lower the overall δ¹³C values incorporated into bioapatite. Interestingly, coeval shark teeth from the Maastrichtian type area yield significantly higher δ¹³C values than mosasaurs, even though they would have occupied comparably high trophic levels (Schulp *et al.* 2013). The latter further supports that enamel largely preserves *in vivo* δ¹³C values and that, besides diet, other factors determine the δ¹³C signatures of the studied mosasaurs, such as habitat and migration.

Habitat
Robbins *et al.* (2008), Schulp *et al.* (2013) and Schulp & Jagt (2015) suggested that a habitat differentiation can be regarded as an important factor contributing to the δ¹³C signatures of mosasaurs, considering
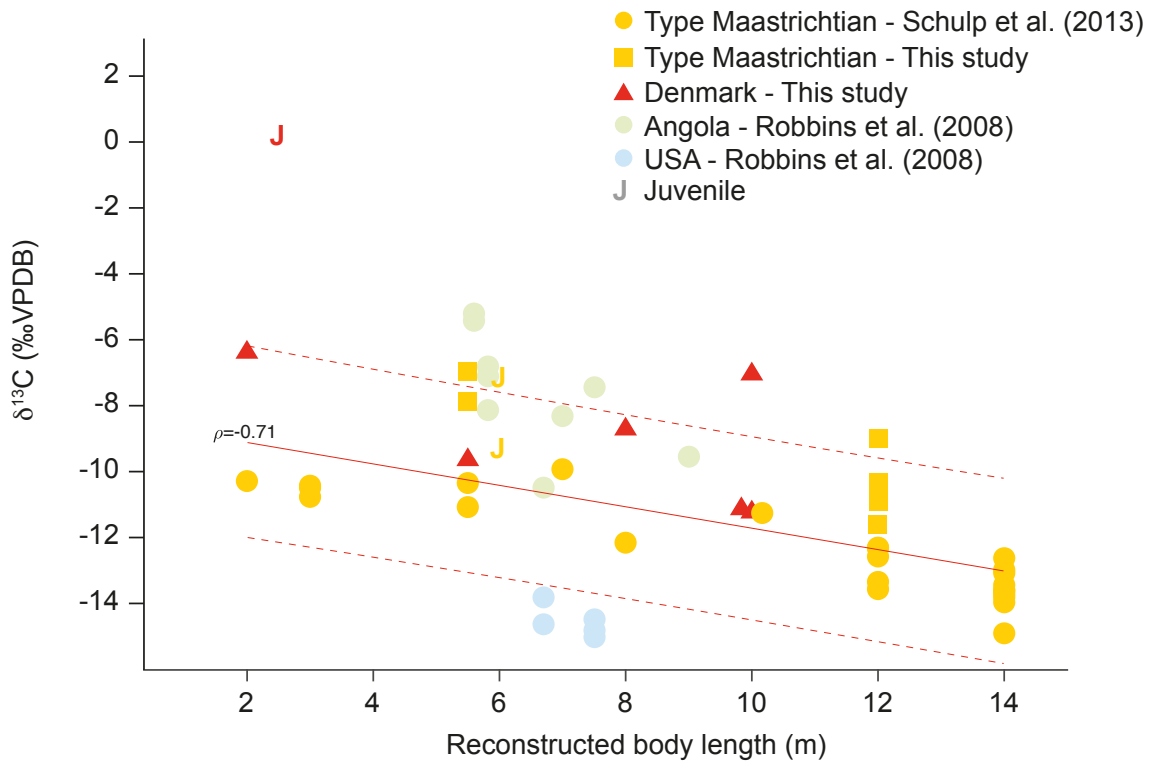
Fig. 5. Reconstructed mosasaur body length plotted against δ¹³C, with data from the Maastrichtian type area (Schulp *et al.* 2013), USA and Angola (Robbins *et al.* 2008), and analyses from the present study with material from Denmark and additional samples from the Maastrichtian type area. The red line represents a linear regression with a 99 % prediction interval (dashed lines) and Pearson's correlation coefficient of –0.71. Juveniles are not included in the regression line.

the higher δ¹³C values nearshore compared to more offshore marine ecosystems (Vennemann *et al.* 2001; Koch 2007). Consequently, larger-sized mosasaurs such as *Prognathodon* that preferred more offshore habitats would have lower δ¹³C values than taxa that were associated with more nearshore, shallow-water settings. *Mosasaurus* has slightly higher δ¹³C values in comparison to *Prognathodon*, which would place it in a more nearshore setting (Schulp *et al.* 2013). In accordance, skeletal remains of *Mosasaurus* outnumber those of *Prognathodon* by orders of magnitude, indicating that they were abundantly present in the shallow-marine ecosystem of the type Maastrichtian (Schulp & Jagt 2015). Furthermore, Mulder *et al.* (1998), Mulder (2003) and Jagt (2005) have previously noted that as fully nektic animals mosasaurs, including *Mosasaurus hoffmanni*, could have easily migrated through the Cretaceous Boreal Sea during the Late Cretaceous. A migratory behaviour of *Prognathodon* could cause isotopic signatures that differ greatly from the environment a specimen is buried in (e.g. Kohn *et al.* 1999).

The recent addition of *Prognathodon* to the Danish mosasaur record (Giltaij *et al.* 2021) underscores the resemblance between the Danish and Dutch fossil faunal assemblages, previously evident from other mosasaur taxa, which were situated ~4° latitude apart during the late Maastrichtian (Milàn *et al.* 2018). The Danish isotope data fall largely in the δ¹³C trend of the mosasaurs from the Maastrichtian type area (Fig. 5), highlighting the possible similarity between both mosasaur populations. The expected latitudinal effect on the δ¹³C values in marine ecosystems (~0.02 ‰ per degree latitude; Rau *et al.* 1982; Fang *et al.* 2016), is indeed too small to cause a significant difference in the isotope signatures of the Danish and type Maastrichtian mosasaurs.

Respiratory physiological effects
Beside the dietary and habitat influences, the observed δ¹³C trend can be further attributed to respiratory physiological effects. Prolonged and rapid repeated breath-hold diving of extant and extinct Squamata and marine turtles elevates the CO_2 pressure in blood, leading to lower δ¹³C values in the skeletal material (the so-called Bohr effect; Biasatti 2004; Robbins *et al.* 2008; Van Baal *et al.* 2013; Schulp *et al.* 2013; Janssen 2017). Consequently, mosasaurs that hunted for prey further offshore or at greater depths would have needed to make more prolonged or frequent dives,

which would be expressed by lower δ¹³C signatures. Larger divers store more oxygen relative to their consumption rate, due to their lower mass-specific metabolic rates (Verberk *et al.* 2020). Intensive diving behaviour of some mosasaur genera is also supported by independent lines of evidence, such as the occurrence of avascular necrosis and reconstructions of mosasaur eyes (Martin & Rothschild 1989; Schulp *et al.* 2013 and references therein; Yamashita *et al.* 2015). The obtained relationship between δ¹³C values and body size is less steep as observed by Robbins *et al.* (2008) in two distinct mosasaur populations from USA and Angola, which therefore might have been more strongly affected by the aforementioned factors related to diet and habitat than those in the present study.

Conclusions

The inverse relationship between δ¹³C values of mosasaur tooth enamel and their reconstructed body length is complemented by the new data from the Maastrichtian type area. For the Danish samples, there is only a weak correlation between mosasaur body size and δ¹³C values. This trend can be partly attributed to environmental and biological factors, such as diet and habitat differentiation, but the Bohr effect appears to be a dominant factor. The obtained relationship between δ¹³C in tooth enamel and body size seems to be less affected by other factors than that found by Robbins *et al.* (2008), who analysed mosasaurs from very different settings. The weak correlation for the Danish mosasaurs can partly be attributed to the low sample number (n = 6) compared to the type Maastrichtian dataset (n = 30). Future research with a more extensive dataset would expand the knowledge about these similar mosasaur populations.

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