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Physical drivers of mosasaur evolution

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ABSTRACT

Mosasaurs are marine squamates with a 32.5 million-year history from their appearance at 98 Ma to their extinction at the K–Pg boundary (65.5 Ma). Using a database of 43 generic and 94 species-level taxa, we compare the taxonomic diversity and patterns of morphological disparity in mosasaurs with sea level, sea surface temperature, and stable carbon isotope curves for the Upper Cretaceous to explore factors that may have influenced their evolution. No single factor unambiguously accounts for all radiations, diversification, and extinctions; however, the broader patterns of taxonomic diversification and morphological disparity point to niche differentiation in a "fishing up" scenario under the influence of "bottom-up" selective pressures. The most likely driving force in mosasaur evolution was high productivity in the Late Cretaceous, driven by tectonically controlled sea levels and climatically controlled ocean stratification and nutrient delivery. When productivity collapsed at the end of the Cretaceous, coincident with bolide impact, mosasaurs became extinct.

1. Introduction

The purpose of this contribution is to apply the fossil record of mosasaurs, an extinct clade of marine squamates, to understand physical drivers of evolution in the marine realm. Mosasaurs have a good fossil record extending through some 32.5 million years of the Late Cretaceous (Fig. 1) and the geology of this interval is well studied. Identifying physical drivers of evolution relies in large part on hypotheses derived from the circumstantial juxtaposition of observations and interpretations of Earth systems on the one hand, with biological transitions and phylogenetic patterns on the other hand. Ideally, physical conditions examined from a geological perspective can be directly related to biological change recognized in morphology, abundance, or distribution of species through time. However, it is only in rare cases that a specific evolutionary novelty can be directly related to a specific physical driver (e.g., Kinoshita et al., 1977; Okada et al., 1983; Ohno, 1984). In the case of inferences derived from the fossil record, uncertainties are common; thus, the reliance on circumstantial evidence is an expediency to facilitate discovery of patterns and explanatory, testable hypotheses and to investigate mechanisms of evolution in specific cases (Steeman et al., 2009; Marx and Uhen, 2010a,b; Pyenson et al., 2010; Ksepka and Thomas, 2012; Kelley et al., 2014–this volume). Here, we employ the rock and fossil records to interpret the evolutionary patterns seen in mosasaurs.

2. Background

2.1. The Late Cretaceous world

Mosasaurs appeared and evolved during a time of significant tectonic activity, which drove large swings in sea level, some estimates approaching nearly 300 m above Recent sea level during the Cenomanian–Turonian highstand (Seton et al., 2009). The separation of South America from Africa, beginning at about 130 Ma, heralded the opening of the South Atlantic and by the beginning of the Late Cretaceous, increase in sea level had created vast epicontinental seas (Fig. 2). This reorganization of the oceans was accompanied by a large increase in sea surface temperature in the mid-Cretaceous, peaking in the Cenomanian and gradually decreasing through the remainder of the Late Cretaceous (Friedrich et al., 2012). These physical parameters influenced rapid evolution in plankton size and species diversity in the mid-Cretaceous (Leckie et al., 2002) at or near so-called oceanic anoxic events (OAEs). These events were global in scale, relatively short-lived, and characterized by regional deposition of black shales. Handoh et al. (2003) concluded that anoxia is not strictly linked to the production of organic-rich sediments such as those deposited during OAEs, but most of these deposits can be linked to upwelling and thus are indicative of increased productivity. In the Cretaceous, as well as today, upwelling regions, currently comprising only 0.1% of ocean area (Meyers, 2006), were areas of high marine productivity. Jacobs et al. (2009, 2011) attributed the abundance of mosasaurs and other top consumers to a productive habitat resulting from coastal upwelling along the Angolan coast of Africa because the

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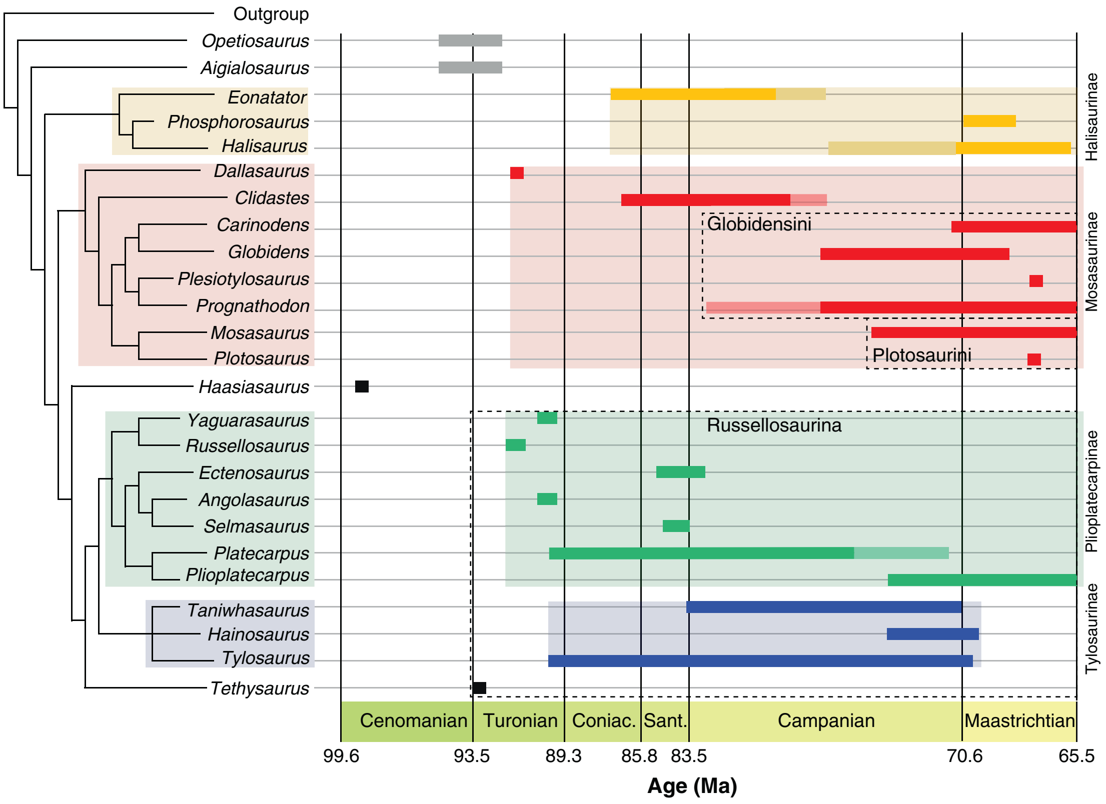

Fig. 1. Cladogram of mosasaur genera based largely on Bell (1997), Polcyn and Bell (2005a), Polcyn and Everhart (2008), and Polcyn et al. (2012). Subfamily membership indicated by muted color boxes, solid color bars indicate range, semitransparent bars indicate uncertainty in range or inferred ghost lineage.

paleolatitudes of those regions lay within the descending limb of the southern Hadley Cell. Trade winds of the Hadley Cells blowing across the African coast would result in upwelling then, as it does now (Fig. 2). Polcyn et al. (2010a) noted that the mosasaur-rich phosphate beds of Morocco occupied an analogous position in the descending limb of the northern Hadley Cell as that lying over the region of Angola in the Cretaceous. Upwelling productivity along the western coast of Africa has also been used to explain geochemical and sedimentological variations in OAE 2 as recorded in a deep-sea core in the southern Angola Basin (Dean et al., 1984; Forster et al., 2008). Upwelling zones contribute to the overall productivity of the ocean, but their level of productivity varies due to climatic effects on a variety of scales (Dupont et al., 2005; Meisel and Ulrich, 2011).

2.2. The fossil record of mosasaurs

The earliest record of mosasaurs is from the Cenomanian, about 98 Ma (Polcyn et al., 1999, 2003; Jacobs et al., 2005a), and the clade went extinct around the Cretaceous–Paleogene boundary at 65.5 Ma (Jagt, 2005; Gallagher, 2005; Fernández et al., 2008; chronology follows Ogg et al., 2004). Phylogenetic relationships within the Mosasauridae are reasonably well understood (Bell, 1997a; Bell and Polcyn, 2005; Polcyn and Bell, 2005a; Polcyn and Everhart, 2008), and their paleobiology is being actively investigated from a number of perspectives, including new data from soft anatomy, evolutionary functional studies, and biomolecules (Lindgren et al., 2009, 2010, 2011a,b). Mosasaur fossils have been recovered from all continents (Russell, 1967; Bell, 1997b; Fig. 3) and across broad latitudes from near the Arctic (Lindgren and Siverson, 2002) to the Antarctic (Martin, 2006; Fernández and Gasparini, 2012) and in sediments deposited in both epicontinental seas and shelf environments adjacent to deep ocean basins (Fig. 3). Complementing this broad global distribution, there are specific areas that present sequences of mosasaur taxa in reasonably well-defined stratigraphic succession and large numbers, including the Western Interior Seaway of North America (Russell, 1967; Everhart, 2001), the North American Gulf and East Coasts (Kiernan, 2002; Gallagher, 2005), the Netherlands and Belgium (Jagt, 2005), Morocco (Bardet et al., 2010), and most notably with respect to our work, coastal Angola along the South Atlantic margin (Jacobs et al., 2006; Schulp et al., 2006, 2008; Jacobs et al., 2009; Mateus et al., 2009; Polcyn et al., 2010; Mateus et al., 2012).

2.3. Ecological models and physical drivers

The relationships between ecosystem dynamics and physical factors in modern marine communities are important for interpreting patterns from the fossil and rock record. Food webs in marine communities are complex, but population size at specific trophic levels can be viewed as being limited by either predation or by availability of prey; “top-down” and “bottom-up” forcing respectively. Top-down forcing and resulting trophic cascades may play a role in some community structures (Hairston et al., 1960; Estes et al., 2011), but in marine food webs, primary productivity in the form of plankton biomass, largely controls the relative abundance of organisms up the trophic chain as demonstrated by Frederiksen et al. (2006). Additionally, Croll et al. (2005) presented evidence linking intermittent coastal upwelling (and thus enhanced primary productivity in the form of plankton) to prey availability at intermediate trophic levels and increased whale abundance. These two examples taken from Recent marine ecosystems underscore the role of primary productivity in these communities (Frederiksen et al., 2006) and link ecosystem dynamics to physically controlled factors (Croll et al., 2005). Top down forces do play a role in population control in these communities and there are few examples where a particular population of organisms is subject to exclusively top-down or bottom-up forcing. In addressing the apparent heterogeneity present in food webs, Hunter and Price (1992; p. 725) succinctly

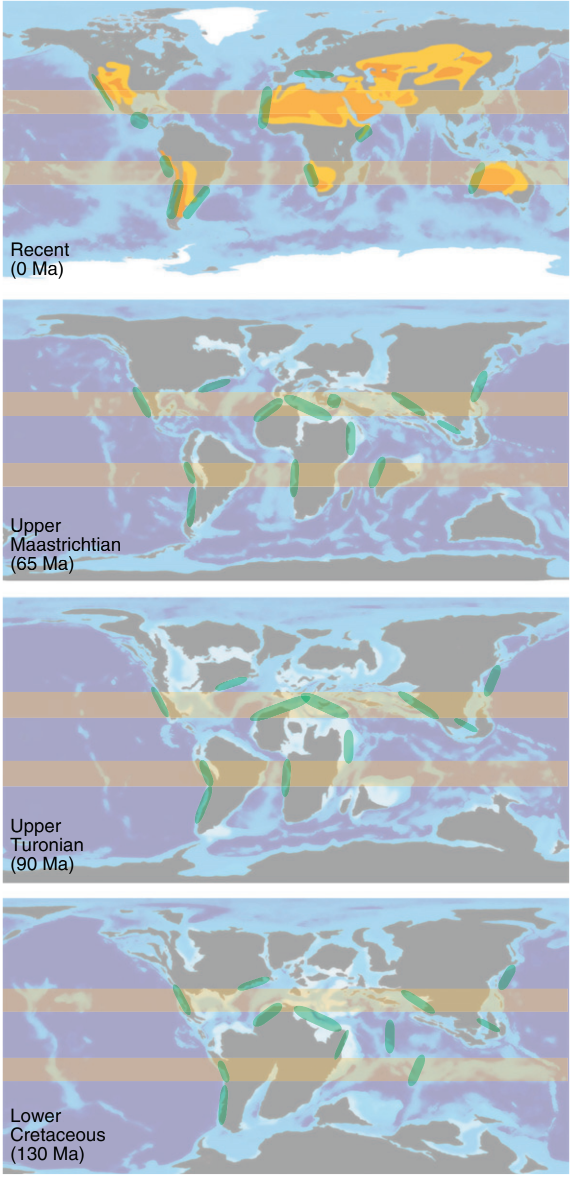

Fig. 2. Paleogeographic maps with schematic representation of upwelling areas and their relationship to the descending portions of the Hadley Cells between 15 and 30° latitude. Yellow horizontal bars = 15–30° Latitude; green ellipsoids = predicted upwelling areas. Base maps redrawn after Blakey (2008). Upwelling areas adapted from model based predictions of Barron (1985).

contrasted the relative roles of top-down versus bottom-up forces, stating "… the fundamental reality [is] that removal of higher trophic levels leaves lower levels present (if perhaps greatly modified). Whereas the removal of primary producers leaves no system at all." Similarly, the loss of prey species at intermediate levels in trophic chains can have significant impact on top predators. In exploring bottom-up forces controlling killer whale (*Orcinus orca*) populations, Ford et al. (2010) linked the availability of Chinook salmon (*Oncorhynchus tshawytscha*) to regional abundance. In this case, although killer whales do take other prey species, there appears to be an ecological specialization on this particular prey species and a clear linkage of prey species loss to population decline in the predator.

The previous examples are taken from Recent snapshots of time; however, over geological time scales, if one mode of population regulation (either bottom-up or top-down) is more dominant than the other, those selection pressures may be reflected in the evolutionary patterns within a clade. Furthermore, the juxtaposition of the resulting evolutionary pattern (in this case taxonomic diversity and morphological disparity) through time, with that of the geological record, might then be extended to infer physical drivers of evolution. In mosasaurs, the drivers are those that control the parameters pushing the selection pressure. Specifically, physical factors of climate and oceanography that control upwelling and primary productivity are coupled through the food chain and thereby facilitate bottom-up pressure and presumably drive evolution.

3. Materials and methods

3.1. Approach

We compare taxonomic diversity, size, and other parameters, such as tooth form, diet, and isotopic indicators of niche differentiation, with the geologic record of oceanographic parameters, specifically sea-surface temperature, δ^{13}C ratios, sea-level, and oceanic anoxic events during the Late Cretaceous, to determine circumstances that might implicate physical drivers in mosasaur evolution.

3.2. Database

Our analysis is based on a dataset of 43 generic and 94 species-level taxa. We segregate those taxa into successive bins with a five million year duration because formal stages of the Late Cretaceous are of unequal lengths. Additionally, the binning window of five million years captures aggregate diversity for time slices appropriate for comparison with the geological record. Although mosasaur fossils are widespread, their occurrence in the field is not uniform in either space or time, and therefore taphonomic, geological, or collecting biases may be affecting the record to some degree (Benson et al., 2010). However, we use raw generic and species counts and do not include additional diversity from ghost lineages because the actual stratigraphic distribution of taxa is informative with respect to potential bias at the scale we are examining. Additionally, there are a number of other forms included in the database that are identifiable to subfamily and preserve characters that justify their retention as valid taxa for purposes of assessing diversity and thus are included in the taxonomic counts for time slices in which they appear; however, because their precise phylogenetic positions are unclear, ghost lineages cannot be confidently reconstructed (e.g. *Carinodens*, "*Platecarpus*" *ptychodon*, *Goronyosaurus*). Furthermore, we are dealing with an extinct group with relatively few major lineages, a scenario that has been demonstrated to yield superior results using taxonomic counts versus the phylogenetic method of estimating ghost lineage diversity in a simulation study (Lane et al., 2005). In that study, the taxonomic and phylogenetic methods of estimating diversity were compared using various sampling techniques and intervals and a known synthetic phylogeny. Although the phylogenetic method did perform slightly better in most cases, there were a number of scenarios in which the taxonomic method performed better, such as the one noted above. In almost all cases, the fluctuating patterns of diversity were recovered in both methods (see Lane et al., 2005; their Figs. 3–5) even in cases in which the magnitude of diversity recovered by the taxonomic and phylogenetic methods were different. Additionally, Lane et al. (2005) cautioned that the phylogenetic method is biased toward first occurrences and that last occurrences are underestimated, yielding their so-called "zombie lineages", which remain uncounted in either method. Therefore, given the issues noted above, we believe the use of the taxonomic method is conservative and justified.

We take temporal ranges from the literature and use either published measurements, estimates of body size based on preserved skull portions using the methods of Russell (1967) and Christiansen and Bonde (2002), or estimates of body size by comparison of preserved portions of vertebral columns. See supplemental information for taxon specific data.

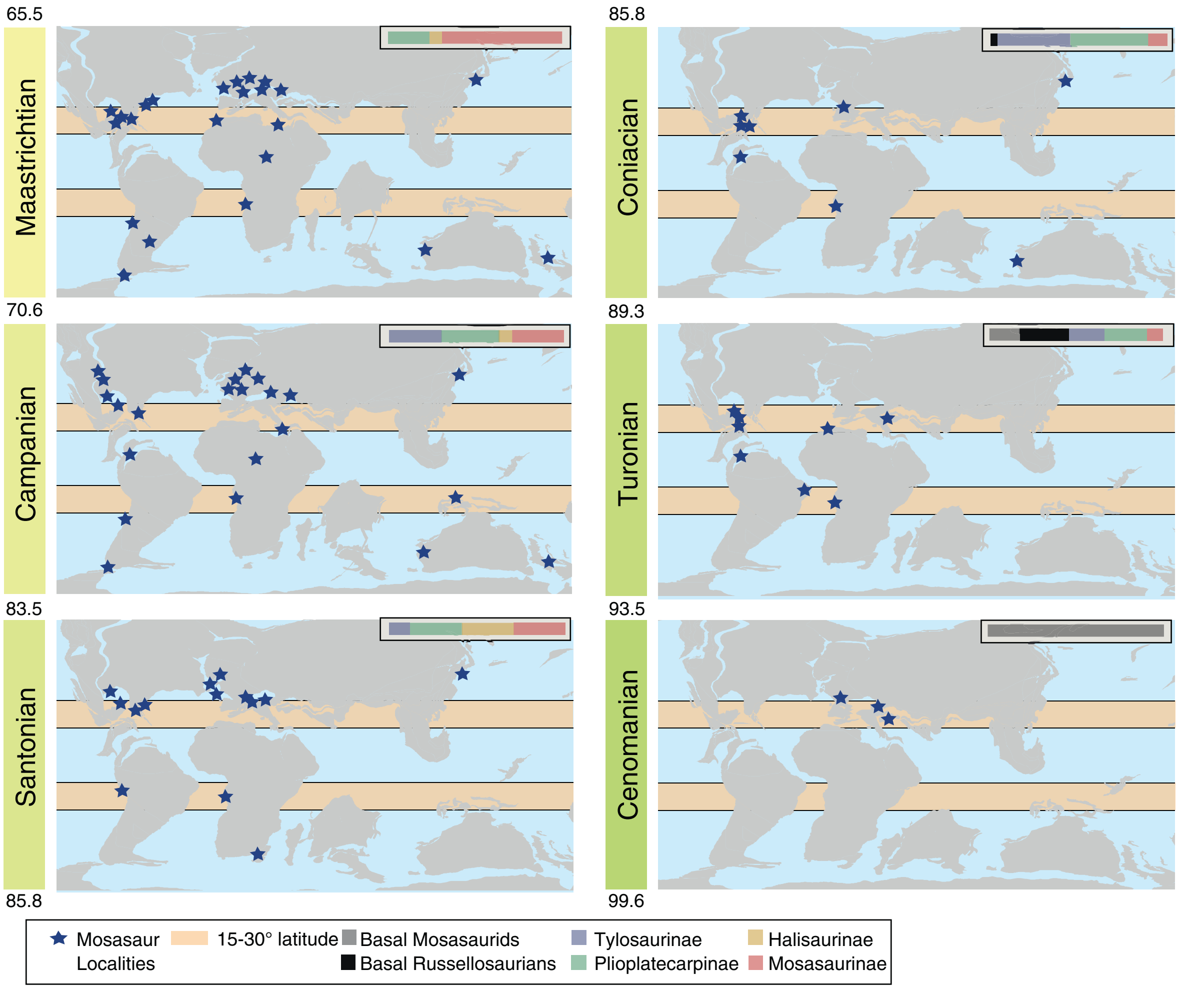

Fig. 3. Paleogeographic maps for Upper Cretaceous stages showing distribution of representative mosasaur localities and relative abundance of major clades per stage. Maps are cropped to display only 75°S to 75°N and 113°W to 166°E. Base maps generated at ODSN Plate Tectonic Reconstruction Website (Hay et al., 1999).

3.3. Phylogeny and taxonomy

Fig. 1 is a cladogram of representative genera and taxonomic groupings modified from Bell (1997a), Bell and Polcyn (2005), Polcyn and Bell (2005a), Polcyn and Everhart (2008), and Polcyn et al. (2012). Early mosasaurs are variably placed at the base of the tree or in basal positions adjacent to subfamily groupings and are characterized by retention of primitive limbs and girdles and relatively primitive body form. Most taxonomic diversity is represented within four well-supported subfamilies (Halisaurinae, Plioplatecarpinae, Tylosaurinae, and Mosasaurinae), three of which were already established in the Turonian. Tylosaurines and plioplatecarpines were quite derived in the Middle to Upper Turonian of the Western Interior Seaway (WIS) of North America, share a close relationship, and along with *Tethysaurus* from the Lower Turonian of Morocco, form a clade referred to as Russellosaurina (sensu Polcyn and Bell, 2005a). Mosasaurines appear in the fossil record of the Middle Turonian WIS, represented by the one meter-long *Dallasaurus*, a primitive-limbed form, and only in the Coniacian do relatively derived mosasaurines appear, represented by the genus *Clidastes* (Polcyn et al., 2008). A well-supported clade currently composed of the genera *Prognathodon*, *Globidens*, and *Carinodens*, is referred to as Globidensini (sensu Bell, 1997a) and is the sister group of the clade composed of *Mosasaurus* and *Plotosaurus* and closely related forms, referred to as the Plotosaurini (sensu Bell, 1997a).

4. Results

4.1. Taxonomic diversity in mosasaurs

Fig. 4 illustrates the pattern of taxonomic diversification in mosasaurs through time at the subfamily, generic, and specific levels. Subfamily identity is established early in mosasaur history and regressions of both species and genera counts against time have significant R^2 values. We use these regressions and measure of fit as an illustrative aid, indicative of a long-term trend of diversification. Continuing improvement of the fossil record through fieldwork is likely to increase both correlation coefficients by providing data on portions of time now underrepresented, but the slopes of the curves for both genera and species of mosasaurs, as a group, are unlikely to change substantially. Nevertheless, the regression masks details of the pattern of taxonomic diversification, evident in a stage by stage examination at various taxonomic levels. Of note are the apparent declines in both genera and species in the Coniacian and the mid-Campanian, both followed by significant episodes of diversification. At the generic level, diversity increases from one at the base of the Cenomanian (~98 Ma) to ten in the Turonian (~93.5 to ~90 Ma), reduced to six or seven by the Coniacian (~85 Ma) and increases to 12 near the Santonian–Campanian boundary (~83.5 Ma). In the middle Campanian (~79 Ma), there appears to be a marked reduction, with only six genera represented, recovering to ten in the lower

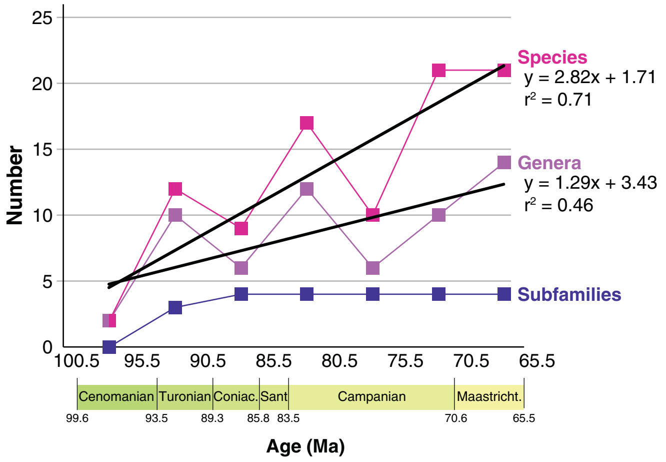

Fig. 4. Mosasaur taxonomic diversity through time at subfamily, genus, and species levels. See text for discussion and supplementary data for details on included taxa.

Maastrichtian (~70 Ma) to a maximum of 14 by the mid-Maastrichtian (~68 Ma).

At the specific level, there is a Coniacian decline in diversity as there is with genera, following an increase in the Turonian. Species diversity recovers to about 17 by the Santonian–Campanian boundary only to see a marked decline in the mid-Campanian. Maximum species diversity is attained in the lower part of the Maastrichtian, and appears to be retained through most of the stage. The marked drops in Coniacian and mid-Campanian are followed by significant diversification at both the generic and specific levels. However, the latter heralds the diversification of mosasaurines, a subfamily that exhibits both significant disparity in tooth form but also the greatest disparity in body size, reflecting increased niche differentiation at the expense of the tylosaurine–plioplatecarpine dominated assemblages, a pattern noted by previous workers (Russell, 1988; Lindgren and Siverson, 2004). There is a significant decline in diversity prior to the K–Pg boundary, not apparent at the scale of our analysis, but documented elsewhere (Gallagher, 2005; Gallagher et al., 2005; Jagt, 2005; Jagt et al., 2008). Typical terminal Maastrichtian assemblages on the east coast and WIS of North America, Northern Europe, and Angola in Africa preserve a taxon-reduced assemblage of some subset of the genera *Plioplatecarpus*, *Mosasaurus*, *Prognathodon*, *Carinodens*, and *Halisaurus*. The exception to this pattern is Morocco, apparently retaining significant taxonomic diversity to the K–Pg boundary (e.g. Jouve et al., 2008; Bardet et al., 2010).

4.2. Physical parameters and mosasaur diversity

Fig. 5 traces the diversity of mosasaurs through time compared to the Late Cretaceous record of sea level change, temporal secular variation of δ^{13}C, and sea surface temperature based on δ^{18}O. Comparison of mosasaur diversity with the curves in Fig. 5 reveals several key points. Mosasaurs originated in an interval of high sea levels and sea surface temperatures (Polcyn et al., 1999; Jacobs et al., 2005b; Bardet et al., 2008). Comparing the pattern of mosasaur diversity to the temperature curve of Friedrich et al. (2012) reveals that the initial radiation and subfamilial radiation of mosasaurs both occurred during the thermal maximum of the Late Cretaceous. This was also a time of notably high productivity as indicated by OAE 2. As cooling begins in the Coniacian, the geographic range of mosasaurs expands to include Japan and Australia (Fig. 3). There is an apparent decline in diversity coincident with temperature lows and the Campanian highstand. Mosasaurines, which appear in the Turonian as small-bodied forms (Bell and Polcyn, 2005), are endemic to the WIS until the mid-Campanian (Polcyn et al., 2008), at which time they first appear in Europe and the range of mosasaurs generally appears to expand to the high latitudes (Fig. 3). Their most intense acquisition of diversity and disparity occurred as sea levels were receding and sea surface temperatures were relatively lower. Only at the terminal Cretaceous do we see a reduction in diversity coincident with falling sea levels and temperature perturbations. Mosasaurs become extinct at the end of the Cretaceous during large-scale trophic collapse in the oceans, presumably due to the bolide impact.

4.3. Patterns of morphological disparity

Fig. 6 shows the distribution of mosasaur body size through time. Regression analyses of the largest and smallest taxa show a significant trend; as mosasaurs became larger, the total size disparity within the group also increased because representatives of smaller and intermediate sizes were retained as larger sized representatives evolved. Certain clades, such as the halisaurines and plioplatecarpines, maintain relatively small body size throughout most of their history. Tylosaurines attain large body size in the Turonian, with the genera *Tylosaurus* and *Hainosaurus* increasing in size throughout their history, while *Taniwhasaurus*, known from New Zealand, Antarctica, and southern South America, maintains a relatively small body-size. Within mosasaurines there is significant disparity in body size, beginning in the middle Campanian and expanding through the end of the Cretaceous. In the Maastrichtian, *Mosasaurus* achieves the largest body size, apparently replacing *Tylosaurus* and *Hainosaurus* in the size class.

5. Discussion

5.1. Biological factors and selection pressures

5.1.1. Life history

Factors that indicate bottom-up selection pressures include those that allow individuals to avoid predation by reducing vulnerability of the most endangered age groups, thereby facilitating recruitment into the breeding population and extension of breeding life. One such factor is ovoviviparity. As obligate marine organisms, mosasaurs were ovoviviparous, evidenced by young found in the body cavity of an adult (Bell et al., 1996; Bell and Sheldon, 2004), a condition attained early in the history of the clade (Caldwell and Lee, 2001). Another factor is rapid growth rate and early attainment of adult size in mosasaurs as shown by Pellegrini (2007).

5.1.2. Thermal physiology

Environmental temperature and the need for thermoregulation may also have also played a role in the evolution of the mosasaurs. The thermal maximum for the Late Cretaceous occurs during the Cenomanian–Turonian highstand, a time when a number of squamate groups entered the marine realm, including dolichosaurs, the first marine snakes, and mosasaurs (Polcyn et al., 1999; Tchernov et al., 2000; Rieppel et al., 2003; Haber and Polcyn, 2005; Jacobs et al., 2005b). With the exception of mosasaurs, these clades were largely restricted to the Cenomanian with the exception of dolichosaurs, which are present to at least the end of the Coniacian (Jacobs et al., 2005a; but see also Shimada and Belle, 2006). This initial radiation may have been driven in part by the thermal inertia the marine environment would offer a small-bodied (e.g. ~one meter-long) ectotherm. From an energetics perspective, consistent equable temperatures would free these basal mosasaurs from the temperature regulation required by terrestrial forms dealing with day–night cycles or at a minimum provide refuge from high terrestrial temperatures during this time. Cooling of the oceans followed and sea surface temperatures began a decline in the late Coniacian and were between about eight and 16 °C for the period between the mid-Campanian through the end of the Maastrichtian. Smaller forms (one to two meters in length) were restricted to the Cenomanian and Turonian. By the Coniacian, many mosasaur taxa had achieved relatively large body size (e.g., >3 m), and thus would

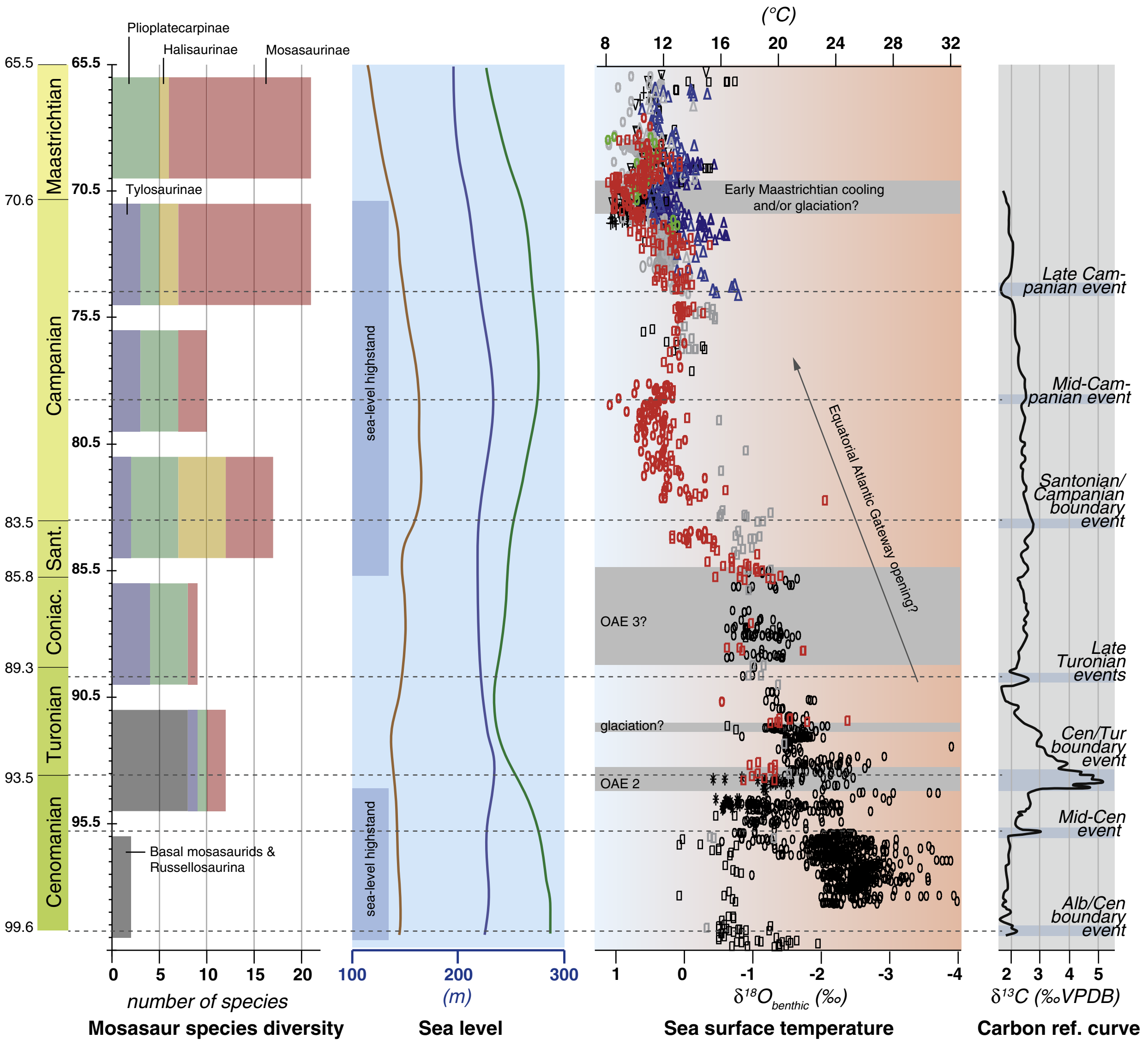

Fig. 5. Mosasaur taxonomic diversity compared with physical drivers. Sea level curves follow Seton et al. (2009) from published curves. Dark green is from Haq and Al-Qahtani (2005), blue curve taken from Haq et al. (1987), and the brown curve from Müller et al. (2008). Carbon reference curve after Jarvis et al. (2006). Sea surface temperature follows Friedrich et al. (2012). Annotation of curve sections follows respective references. See text for discussion.

presumably be less sensitive to temperature variations. Additionally, Bernard et al. (2010) compared temperatures from stable oxygen isotopes of contemporaneous fish and marine reptile teeth, determining that some form of endothermy had evolved in mosasaurs, albeit not to the degree detected in plesiosaurs and ichthyosaurs, suggesting at least some mosasaurs were able to tolerate low temperatures that would be deleterious to extant squamates. Nonetheless, the mid-Campanian temperature low is coincident with a reduction in diversity, and therefore that cooling may have been a factor for at least some forms. Following the mid-Campanian decline in diversity, mosasaurines become the most diverse subfamily, dominating the relatively cooler oceans through the end of the Cretaceous.

Cooling and better-oxygenated bottom waters in the mid-Maastrichtian have also been suggested as the cause of the extinction of inoceramids (MacLeod, 1994), a clade of Upper Cretaceous bivalves. These bivalves have been reported as the prey item of the durophagous mosasaur genus *Globidens* (Martin and Fox, 2007), which also appears to become extinct in the mid-Maastrichtian (however, see Bardet et al., 2005, 2010) and may represent a case of temperature mediated prey item loss impacting predators up the trophic chain.

5.1.3. Disparity and niche differentiation

The distribution of mosasaur body size shown in Fig. 6 is similar to the increase in size variation through time in whales, and more broadly in vertebrates (Gillman, 2007), and was explained by an analogous retention of ancestral size ranges (Lindberg and Pyenson, 2006). This pattern indicates niche partitioning and expansion of ecological space by members of the clade throughout its geologic history. Within mosasaurs, size increase almost certainly exemplifies “fishing up prey size” (Lindberg and Pyenson, 2006), meaning larger food parcels are consumed rather than increasing consumption of massive amounts of small food items, because mosasaurs exhibit adaptations of active predators (Lindgren et al., 2011b). Large size and specialized feeding like that seen in baleen whales or ziphiid odontocetes has no analog in mosasaurs (Collin and Janis, 1997; Werth, 2006).

Further evidence for niche partitioning and ecological expansion is derived from preliminary analysis of $\delta^{13}C$ values in mosasaur tooth enamel (Robbins et al., 2008). Studies of tooth morphology, jaw function, and stomach contents (Massare, 1987; Ciampaglio et al., 2005; Schulp, 2005) demonstrate a variety of diets within mosasaurs, including invertebrates, fish, plesiosaurs, turtles, and even other mosasaurs. The isotopic values of carbon from tooth enamel varies

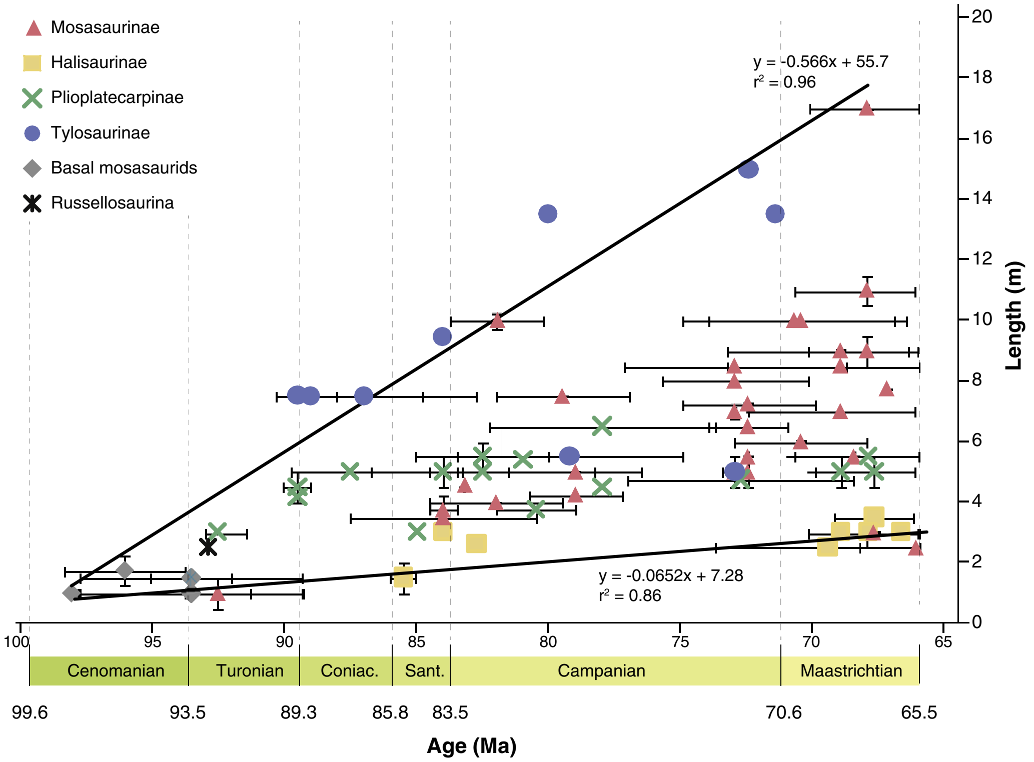

Fig. 6. Size disparity among mosasaurs over time. Symbols are plotted at mean age range and mean length, horizontal bars indicate range extent, vertical bars indicate size range where more that one value exists. See text for discussion and supplementary data for details on included taxa.

from 0 to 1‰ with each increasing trophic level (DeNiro and Epstein, 1978) and animals feeding at high trophic levels are expected to have higher (less negative) values in general.

Preliminary data presented in Fig. 7 (redrafted from Robbins et al., 2008) shows a correlation ($R^2 = 0.91$) between size and $\delta^{13}C$ value among *Dallasaurus*, *Clidastes*, and *Mosasaurus*, all mosasaurine mosasaurs; however, a decline in $\delta^{13}C$ values means less heavy isotope, a trend not consistent with climbing trophic levels as size increases. Therefore, the decrease in values might suggest an effect due to change in foraging range as recovered in Recent marine mammals (Clementz and Koch, 2001) or diving habits, as has been suggested for sea turtles (Biasatti, 2004). Within the globidensine mosasaurs *Globidens* and *Prognathodon*,

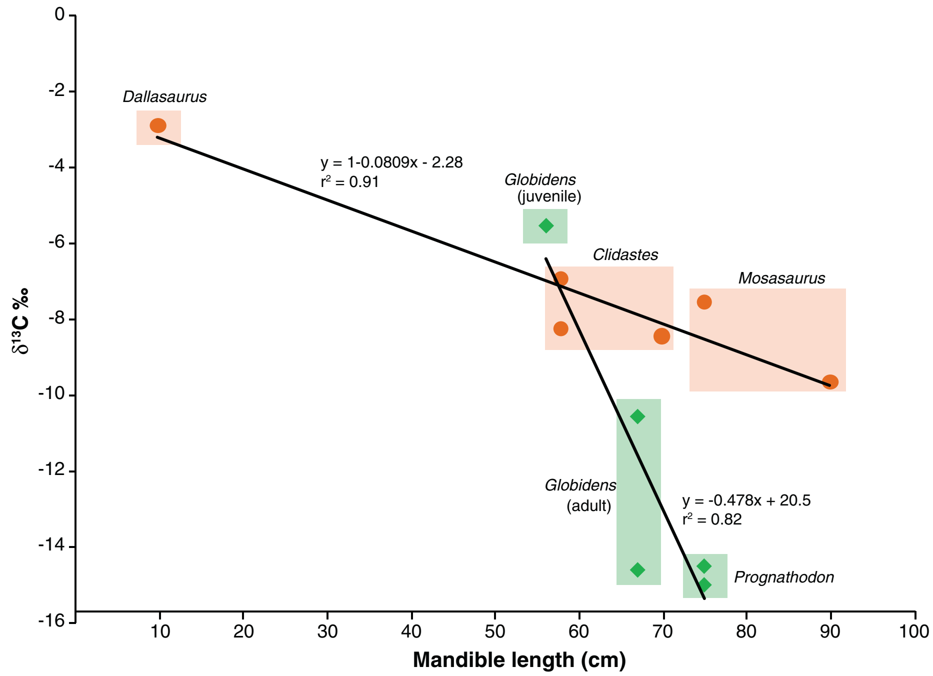

Fig. 7. $\delta^{13}C$ isotope values versus mandible length for selected mosasaur taxa redrawn from Robbins et al. (2008). The regression lines mirror phylogeny, and are calculated for mosasaurine mosasaurs both excluding *Globidens* and *Prognathodon* and for those two exclusively. See text for discussion.

the range of values is quite broad and beyond what would be expected only from trophic differences. The diet and tooth morphology of *Globidens* is distinct from other mosasaurines. It is durophagous and apparently fed low in the trophic chain on bottom dwelling bivalves (Martin and Fox, 2007), factors that may explain part or all of the variation. However, the range of values seen in *Globidens* juveniles as compared to adults may suggest ontogenetic change in diet (Robbins et al., 2008), as is also indicated by dental ontogeny (Polcyn and Bell, 2005b), as well as foraging range and diving habits. The other globidensine mosasaur included in the Robbins et al. (2008) study was *Prognathodon kianda*, which possesses teeth that are more suited for piercing and cutting, suggesting that foraging range and diving habits may account for the high negative values. The data in Fig. 7 are too few to be conclusive at a detailed level, but they are suggestive and present testable hypotheses, and they show a range of variation that is consistent with ecological diversification into new niches for the exploitation of food resources.

5.2. Mosasaurs as top-down drivers?

The occurrence of *Platecarpus* in the gut contents of *Tylosaurus* (Martin and Bjork, 1987) opens the possibility that apex mosasaurs may have applied top-down population pressure on prey species and thereby may have themselves been drivers of evolution within the clade. Gut contents are known from relatively small mosasaurs such as *Platecarpus* (Massare, 1987) and *Plotosaurus* (Camp, 1942); however, these are restricted to fish and other small prey items. Only in a large mosasaur like *Tylosaurus* (Martin and Bjork, 1987) are mosasaurs found in gut contents along with other prey items, which we take as evidence of active predation versus scavenging. At Bentiaba, Angola, almost all mosasaur remains show evidence of shark scavenging, although there are two cases of mosasaur-in-mosasaur gut contents in specimens in the PaleoAngola collection currently housed at Southern Methodist University in Dallas. As these are the only significant evidence for top-down population pressure in mosasaurs, albeit limited in time, we evaluate the implications more closely below.

Evidence that top predators can be a factor in structuring populations of marine mammals comes from studies of the dynamics of killer whales (*O. orca*) with their prey in the North Pacific, where baleen whale populations were decimated by the industrial whale fishery after World War II (Springer et al., 2003). Killer whales as a species have a broad and diverse diet that varies geographically but the diets of local populations are more fixed, at least in the short term (Barrett-Lennard and Heise, 2006). However, Springer et al. (2003) proposed that after decimation of their preferred food item, baleen whales, the diet of killer whales in the North Pacific opportunistically shifted to include more pinnipeds and sea otters and this top-down pressure is likely to have contributed to disruption of the food web and collapse of prey species populations.

If apex mosasaurs routinely preyed on other mosasaur species, one would expect more widespread taphonomic indicators on bones or from a more common occurrence of mosasaurs as stomach contents than currently exists. Throughout the record, mosasaurs as prey items of other mosasaurs are uncommon even in the cases in which gut contents are known. Nevertheless, obtaining the occasional mosasaur as prey might be anticipated within a “fishing-up prey” scenario. The record as known is more consistent with opportunistic capture of mosasaur prey within an indiscriminate diet of an apex mosasaur than with top-down pressures associated with an obligate prey preference restricting recruitment into the breeding population of the prey species.

Within mosasaurs as a whole, the pattern of size increase and concomitant size disparity through time, the niche differentiation indicated by stable isotopes, the diversity of tooth morphology among species, the record of gut contents, and the lack of evidence for red queen tracking (sensu Benton, 2009) between predator and prey, indicate that top-down pressure was irrelevant relative to bottom-up pressures.

5.3. Physical drivers and Cretaceous productivity

The kinds of evidence for bottom-up control of modern upper-trophic-level marine populations were reviewed by Hunt and McKinnell (2006). The effect of climate variation on a number of scales provides avenues for evaluating modern populations. On local scales, the demonstration that climate affects commercially valuable fish is evident of bottom-up pressure, because of the climatic impact on productivity and low trophic-level resources. In highly mobile top consumers, transient resource limitations may be mitigated by relocating to areas of more abundant food species. For species governed by bottom-up pressures, their abundance in the global ocean should be greatest where the resources are most abundant. In the fossil record, presence of large numbers of apex predators, significant taxonomic diversity, and morphological disparity should imply expanding use of resources and distribution in areas of high paleoproductivity.

During the Cretaceous increased rates of seafloor spreading and decrease in global ocean basin volume (Müller et al., 2008; Seton et al., 2009) created extensive epicontinental seas (Fig. 2). The development of these epicontinental seas increased the volume of marine photic zone as a function of increased surface area. The extensive shorelines of these epicontinental seas and their relatively shallow depth facilitated the introduction of nutrients from land (Weissert et al., 1998) and from bottom mixing. The rich and diverse fossil record of epicontinental seas testifies to their productivity.

The most striking feature of the Late Cretaceous δ^{13}C curve (Fig. 5) is the conspicuous spike that characterizes oceanic anoxic event 2 (OAE 2), a widespread episode of laminated, highly organic shale deposition at the Cenomanian–Turonian boundary (93.5 Ma). No simple model explains the deposition of this black shale, although stagnant oxygen-depleted bottom waters insufficient to oxidize organic matter raining from above have been suggested, coincident with reduced productivity in the upper levels of the ocean (Bralower and Thierstein, 1984; de Graciansky et al., 1984).

More recently, however, the causes of high productivity, which facilitates the rain of organic matter to the sea floor, have become a focus of investigation (Leckie et al., 2002). Meyers (2006), utilizing biomarkers, δ^{15}N, and redox-sensitive metals, hypothesized that surface salinity stratification during intervals of increased rainfall and surface runoff enhanced microbial primary production in an expanded oxygen minimum zone that extended into the photic zone. The organic matter produced in the productive stratum rained down and was deposited at depth, contributing to the black shale. Thus, anaerobic microbial activity augmenting and alternating with phytoplankton photosynthesis maintained productivity over long intervals during the Cretaceous. Additional support for this hypothesis comes from evidence of microbial nitrogen fixation seen in cores taken at Ocean Drilling Program sites on the Demerara Rise in the equatorial Atlantic (Meyers et al., 2008). In that study, the activity of the microbes was attributed to thermohaline stratification and the biologically useful fixed nitrogen that resulted served to fertilize primary production. These processes leading to high productivity were linked to precessional cycles and warm temperatures that increased rainfall, but were also considered sensitive to smaller variations in climate that increased rainfall. Moreover, numerical models indicate that precessional forcing of the Late Cretaceous climate influenced precipitation and river discharge in Africa (Floegel and Wagner, 2006), which were suggested to trigger tropical Atlantic black shale formation. This is consistent with the notion of anaerobic microbial productivity being enhanced at times of thermohaline stratification and augmenting planktonic productivity in the oxygenated photic zone.

High productivity seems to be characteristic of the entire Late Cretaceous; however, it is possible that OAE 2 represents a particularly productive interval. The temperature curve for the Late Cretaceous (Fig. 3) shows especially high sea-surface temperatures during the first half of the Late Cretaceous, including the interval containing OAE

2. High temperatures and high sea levels causing epicontinental seas contributed to the remarkably high productivity of the Late Cretaceous. Some models place tropical sea-surface temperatures at > 30 °C, which would place a considerable strain on marine tetrapods (Jacobs et al., 2005b). In the modern ocean, Tittensor et al. (2010) concluded that temperature and coastline length were the primary large-scale environmental correlates of diversity, and consistent with the idea that these factors facilitate species richness over evolutionary and ecological timescales. Further, the temperature regime, tectonic setting, and sea levels of the Cretaceous have long been considered the cause of productivity leading to the production of massive amounts of oil formed during this interval (Irving et al., 1974). These physical circumstances are consistent with high productivity driven bottom-up selection in predators evolving progressively larger body size. The common driver underlying the broader pattern of increasing diversity and disparity appears to be high productivity and availability of prey items, whether in the epicontinental seas or upwelling areas, both of which are caused by physical parameters of geological and oceanographic context.

5.4. Mosasaurs and the K–Pg extinctions

We have made the argument that mosasaur evolution was controlled largely by bottom-up pressures, and that productivity resulting from geological and environmental conditions resulted in abundant food resources in the Cretaceous marine realm, thus defining the physical drivers of mosasaur evolution through this chain. Geological and environmental conditions, including high global temperature and high sea stands with extensive epicontinental seas, were the physical drivers of productivity and therefore the primary physical drivers of early mosasaur evolution. Following the Campanian diversification of mosasaurines, mosasaurs are found in significant numbers in sediments that were deposited in high productivity upwelling zones (e.g., Morocco and Angola), but they are also relatively common in other productive settings (e.g., the Western Interior Seaway of North America). A test, and an explanation of the demise of mosasaurs, is to examine marine productivity at the end of the Cretaceous when mosasaurs became extinct.

The K–Pg event is widely accepted as being initiated by a bolide impact, although the exact conditions of the bolide impact resulting in differential extinction are difficult to model. Within the marine realm, $\delta^{13}C$ excursions at or following the K–Pg boundary, and the difference between $\delta^{13}C$ values of benthic and planktonic species, clearly indicate a severe drop in productivity, the onset of a "Strangelove Ocean" (Hsü et al., 1982; Magaritz, 1989; Zachos et al., 1989; D'Hondt et al., 1998). A catastrophic drop in planktonic productivity at the K–Pg boundary would affect species up the food chain, including mosasaurs (Bardet, 1994, 1995; Gallagher, 2003), which we have argued were evolutionarily driven by bottom-up selection pressures throughout the history of the clade.

Adams et al. (2004) determined through statistical comparison of recovery models that while the unproductive "Strangelove Ocean" would be of short duration, the ensuing "Living Ocean" would take as long as three million years, and perhaps two recovery stages, to reach pre-impact levels of ocean surface productivity, the duration, they concluded, being attributable to as yet unknown biological factors. In our studies of the stratigraphic distribution of mosasaurs in Angola, and in all published reports of the youngest occurrence of mosasaurs in other stratigraphic sections (Gallagher, 2005; Gallagher et al., 2005; Jagt, 2005; Jagt et al., 2008; Jouve et al., 2008; Bardet et al., 2010), there is no unequivocal record of mosasaurs postdating the K–Pg boundary. Thus, the initial drop in marine productivity, driven by impact, appears to have resulted in the demise of the mosasaurs (Gallagher, 2003).

5.5. Summary

The Late Cretaceous appears to have been a time of remarkable primary productivity in the marine realm that was transferred up the trophic web to the top consumers. Thus, the physical drivers of that productivity, notably warm climate and high sea stands, were also the physical drivers of the early evolution of mosasaurs (Polcyn et al., 1999; Jacobs et al., 2005b; Bardet et al., 2008). The unusual productivity represented by OAE 2 may have triggered a cascade of niche differentiation guided by bottom-up population dynamics and fishing-up the food chain. Mosasaur life history patterns, including ovoviviparity, rapid growth, and high mobility, reduced the threat of top-down predation and mitigated local and transient reduction of prey abundance by allowing mosasaurs to seek food resources elsewhere. Our work in Angola and a review of other K–Pg boundary sections containing mosasaurs (Gallagher, 2005; Gallagher et al., 2005; Jagt, 2005; Jacobs et al., 2006; Jagt et al., 2008) suggest the possibility of a diversity decline prior to the extinction of mosasaurs; however, that pattern is not obvious from the scale of analysis in this study and its elucidation must await further research. Regardless, the collapse of marine productivity at the end of the Cretaceous, coincident with bolide impact, resulted in the total demise of mosasaurs (Bardet, 1994, 1995; Gallagher, 2003).

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Appendix A. Supplementary data

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