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Climate, competition, and the rise of mosasauroid ecomorphological disparity

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Abstract: Mosasauroidea, prominent marine lizards (Squamata, Toxicofera) of the final 30 million years of the Cretaceous, have been extensively studied for their morphology, ecology and systematics in the past two centuries. However, the relative roles of biological and physical processes as drivers of their morphological diversification remain uncertain. Here we investigate the macroevolution of mosasauroid feeding and locomotory disparity using continuous characters measured from the mandible and forelimb as proxies. Patterns of morphospace occupation demonstrate important roles for innovation and niche partitioning in driving morphological disparity. The early evolution of Mosasauroidea is characterized by large shifts in morphology, especially elongation of the mandibular biting area and hydropedality. The later diversification of derived Mosasaurinae and Plioplatecarpinae is associated with a great expansion of morphospace, attributed to the acquisition of novel feeding and locomotory strategies. Temporally, disparity follows a top-heavy profile, possibly reflecting opportunism in the wake of the Cenomanian–Turonian anoxic event. The highest levels of disparity are found in the latest Cretaceous, associated with the radiation of derived mosasaurids alongside the persistence of more basal forms. Major morphological innovations are not associated with evolutionary rate shifts, which differentiates them from earlier marine reptiles, and may reflect constant and greater niche occupation in Late Cretaceous oceans. Linear modelling of potential physical drivers indicates a minor role for these processes, suggesting that biological drivers were the primary sculptors of mosasauroid morphological disparity.

Key words: Mosasauroidea, Aigialosauridae, macroevolution, ecomorphology, functional disparity, evolutionary drivers.

CONTEMPORARY oceanic ecosystems are dominated by sharks and secondarily aquatic tetrapods, most notably birds and mammals, which evolved from terrestrial ancestors to exploit marine habitats. In Mesozoic seas there were multiple lineages of marine reptiles (Pyenson *et al.* 2014; Kelley & Pyenson 2015; Reeves *et al.* 2021), the last of which, the mosasauroids, dominated oceanic ecosystems for the final *c.* 30 myr of the Cretaceous (Stubbs & Benton 2016; Reeves *et al.* 2021). Descendants of terrestrial squamates, and close relatives of either anguimorphs (Conrad *et al.* 2011) or snakes (Reeder *et al.* 2015; Paparella *et al.* 2018), mosasauroids are classically divided into plesiomorphic, semiaquatic 'aigialosaurs' and derived (predominantly) marine Mosasauridae; the former now commonly regarded as paraphyletic with respect to the latter (Russell 1967; Dutchak 2005; Caldwell 2012; Campbell Mekarski *et al.* 2019). Aigialosaur-grade taxa first arose in the Cenomanian, possibly from a dolichosaur-grade ancestor, and were limited in diversity (Paparella *et al.* 2018; Campbell Mekarski *et al.* 2019). However, following significant restructuring of marine ecosystems caused by the Cenomanian–Turonian Anoxic Event, the radiation of mosasaurids signalled the onset of mosasauroid dominion until the end of the Cretaceous (Ross 2009; Stubbs & Benton 2016).

The fate of lineages, their rise and fall, remains a fundamental question in palaeontology. Advances in statistical methods have permitted rigorous investigation of this topic, including in marine reptiles (Stubbs & Benton 2016; Moon & Stubbs 2020; Reeves *et al.* 2021). Mosasauroid functional macroevolution has not been studied in detail, despite apparent advantages including: (1) an exceptional fossil record, afforded by their marine habits, large size and cosmopolitan distribution (Driscoll *et al.* 2019); (2) being enthusiastically studied, with a large number of described taxa and a reasonably well resolved phylogeny; and (3) persisting in an environment that is well understood, with fine-scale stratigraphy that provides reliable temporal and driver data (Polcyn *et al.* 2014; Driscoll *et al.* 2019). Furthermore, the anatomy of mosasauroids is well documented (e.g. Russell 1967), particularly for the feeding and locomotory apparatus.

Mosasauroid jaws display considerable morphological diversity, ranging from the strongly kinetic jaws of plesiomorphic taxa (Callison 1967; Russell 1967) to the derived mandibles of shell-crushing *Globidens* and fish-eating *Plotosaurus* (LeBlanc *et al.* 2013, 2019). This mandibular variation reflects dietary diversity, with many taxa showing specialization towards certain prey (Schulp *et al.* 2013). Several studies have attempted to elucidate the evolutionary patterns of mosasauroid jaws. Ross (2009) applied the dental morphoguild concept of Massare (1987) to Mosasauridae and showed that early forms were predominantly of the generalist 'cut' guild, later to be augmented by some piscivorous 'pierce' guild taxa. However, only following the radiation of mosasaurines did guild diversity increase substantially, with taxa occupying five of the six marine reptile tooth guilds (Massare 1987; Ross 2009). Stubbs & Benton (2016), using continuous and discrete traits of the mandible and dentition to investigate functional disparity in Mesozoic marine reptiles, found that mosasauroid diversification did not follow an 'early burst' scenario, as in ichthyosaurs (Moon & Stubbs 2020), where high disparity was rapidly acquired and then followed by levelling or decline. Instead, initial mosasauroid disparity was low and increased continuously to the Cretaceous–Palaeogene (KPg) boundary, with the exceptionally high disparity of the Campanian and Maastrichtian attributed to diversification of feeding strategies, a product of niche partitioning and opportunism (Stubbs & Benton 2016). Importantly, both analyses concluded that mosasauroids became extinct at their evolutionary zenith, while they were still rapidly diversifying (Ross 2009; Stubbs & Benton 2016).

As descendants of terrestrial lizards with weight-bearing limbs, the locomotory anatomy of derived mosasauroids is strongly modified for an obligate marine existence, and convergent with other secondarily aquatic tetrapods (most notably ichthyosaurs; e.g. Lindgren *et al.* 2010). Such adaptations include elongation of the body to facilitate undulatory propulsion and the evolution of paddle-like limbs (Massare 1994; Kelley & Pyenson 2015). Under the classic view of mosasaur locomotion, an anguilliform profile and muscular tail facilitated propulsive undulation by the entire postcranium, while the limbs rested by the side, possibly to be used in sudden propulsive bursts (Massare 1994). Despite the apparent inefficiency of this locomotory mode, it matched the prevailing idea that mosasaurs were nearshore ambush predators that did not undertake sustained periods of intense activity. However, reanalysis of the caudal vertebrae of *Plotosaurus* has demonstrated that this taxon had a semi-lunate tail fluke with a fusiform profile, and thus used carangiform locomotion, not dissimilar to some derived ichthyosaurs. This ecomorphology suits sustained activity necessitated by pelagic cruising, the mode of life attributed to *Plotosaurus*

(Lindgren *et al.* 2007, 2008). Subsequent discoveries have demonstrated that these features are more widespread among mosasaurids, with caudal flukes and hydrodynamic body plans found in specimens of *Platecarpus* and *Prognathodon* (Lindgren *et al.* 2010, 2013). A high-fidelity fluke imprint of *Prognathodon* displays an aspect ratio similar to that of a moderately active carcharhinid shark (Lindgren *et al.* 2013).

The mosasauroid forelimb also became strongly modified for an aquatic lifestyle, transitioning from a basal 'plesiopedal' walking limb, with functional joints and digits, to a derived 'hydropedal' limb, sporting robust tablet-like epipodials, shortened long bones, immobile joints, and a paddle-like profile. Hydropedality only occurs in Mosasauridae and indicates adoption of obligatory marine habits, as this condition precludes terrestrial walking (Caldwell *et al.* 1995; Caldwell 1996; Bell & Polcyn 2005; Campbell Mekarski *et al.* 2019). However, it has been debated whether this condition in mosasaurs is homoplastic, or whether it could have arisen multiple times through convergence, which has evolutionary implications for other locomotory traits, such as the tail fluke. This debate is centred on the placement of critical taxa, such as *Dallasaurus*, which is recovered as a derived mosasaurine but possesses plesiomorphic limbs and girdles (Bell & Polcyn 2005). Ancestral state reconstruction has suggested that aquatically adapted limbs evolved ancestrally in Mosasauridae, and *Dallasaurus* may represent either reversion, poor postcranial data, or incorrect phylogenetic placement (Simões *et al.* 2017). Though other authors consider these results to be a phylogenetic artefact resulting from strong implied weighting and stress the importance of conservatism when investigating basal mosasauroid relationships and evolution (Madzia & Cau 2017). Following their acquisition, the hydropedal/hydropelvic limbs show increasing adaptation for marine locomotion, exemplified in the longipinnate paddles of *Plotosaurus* (Lindgren *et al.* 2007, 2011).

The feeding and locomotory strategies of an organism are vital components of its ecology. Previous studies of mosasauroids have generally interpreted the macroevolution of these traits without statistical analysis, often focusing on particular taxa. The few statistical studies on mosasaur feeding have been either in the broader context of marine reptiles as a whole (Stubbs & Benton 2016) or using restricted, guild-based characters (Ross 2009). No study has investigated the macroevolution of mosasauroid locomotion under a statistical framework. Furthermore, there has been conflict over the relative roles of biological and physical processes in driving mosasauroid evolution. For example, Polcyn *et al.* (2014) suggested that mosasauroid diversity and disparity were driven by extrinsic, physical processes, primarily the high productivity of Cretaceous oceans, based on a combination of:

(1) widespread transgression; (2) high sea surface temperatures; and (3) enhanced nutrient supply from increased precipitation and run-off. This combination of factors apparently drove high rates of niche and body size diversification in mosasaurids, in a textbook example of the 'Court Jester' hypothesis. Stubbs & Benton (2016), on the other hand, found a primary role for innate, biological or 'Red Queen' processes, such as competition, innovation and opportunity.

In this contribution, we analyse proxies for functional disparity of mosasauroid feeding and locomotion, using a suite of characters measured from the mandible and forelimb. We focus on the mandible as it is a useful proxy for feeding behaviour, with traits such as jaw leverage and robusticity linked to biomechanical principles, jaw performance and feeding ecology (Anderson *et al*. 2011). Locomotion in mosasauroids is a whole-body phenomenon, involving the axial column, pectoral and pelvic girdles, and limbs/paddles (Lindgren *et al*. 2007, 2010, 2011, 2013; Gutarra & Rahman, 2021). The vertebral column is incomplete in many specimens, making predictions of axial locomotory evolution problematic. Instead, here we focus on the morphology and function of the limbs and paddles. Limbs/paddles show trends associated with diversification into aquatic environments (Lindgren *et al*. 2007, 2011; Campbell Mekarski *et al*. 2019) and the aspect ratio of flippers (as measured from bony elements) has been used to infer locomotory performance (speed and manoeuvrability) in plesiosaurs (O'Keefe 2001). Aspect ratio is a well characterized predictor of the performance of aerodynamic surfaces (wings) in extant birds and quantifies the trade-off between efficiency and manoeuvrability in aerofoil and hydrofoil structures (Gutarra & Rahman 2021). We hypothesize that mosasauroids did not undergo an early burst in feeding and locomotory diversity, unlike other marine reptile groups; that the greatest disparity (in both traits) arose with the radiation of the disparate mosasaurines, possibly in association with major shifts in evolutionary tempo; and that biotic factors were important drivers in the evolution of mosasauroids, rather than solely physical drivers.

MATERIAL AND METHOD

Data collection

Not all mosasauroid taxa preserve mandibles and forelimbs suitable for use in a study such as this, and we could include only 41 taxa in the mandibular analysis and 33 taxa in the forelimb analysis (Cross *et al*. 2022). Measurements were taken primarily from figures in the literature, except in cases where we could acquire photographs directly from the institutions housing the original specimens. In addition, two 'dolichosaurs' were used as outgroups to help estimate the condition at the Mosasauroidea node. Ideally, measurements would have been taken from original specimens, but this was not possible for practical and financial reasons; in this case, visits to dozens of museums on most continents would have been required. Therefore, we chose to score characters from the literature, a common practice used in previous studies. Care was taken to ensure each character was scored multiple times and verified across multiple figures and images where possible. Both photographs and reconstructions were included, respectively accounting for 53% and 35% of the mandibular data, and 53% and 47% of the forelimb data. In addition, the mandible was sometimes figured as separate bones that were realigned in GIMP v.2.10.8, which accounts for the final 12% of mandibular data. The data are imperfect, and several taxa were included based on incomplete remains and could not be scored for all functional measurements. The number of taxa with missing data is 14% for the mandibular dataset and 23% for the forelimb dataset.

Functional characters

A total of 23 functional characters were used in this study, which aimed to reflect ecological adaptations to feeding and locomotion. The 11 mandibular characters were derived from previous studies of jaw functional macroevolution (Anderson *et al*. 2011, 2013; Stubbs *et al*. 2013; Button *et al*. 2014; Stubbs & Benton 2016; MacLaren *et al*. 2017), while the 12 limb-focused locomotory characters, measured from the humerus, radius and ulna, are novel contributions here. Characters were measured from images and reconstructions of specimens using ImageJ v.1.52a (Schneider *et al*. 2012); detailed descriptions are provided in Appendix S1.

Functional morphospace

To visualize functional differences among mosasauroid taxa, we performed a principal component analysis (PCA) on the mandibular and locomotory character datasets scaled to unit variance. PCA used the R multivariate statistics package FactoMineR v.2.3 (Lê *et al*. 2008), with the companion package missMDA (Josse & Husson 2016) used to impute missing data without affecting the results of the PCA (i.e. the imputed data carry no weight). The mandibular and forelimb datasets were subjected to separate PCAs, from which two visualizations of the data were created: the first includes all taxa and is used to contrast the functional characteristics of different clades, the second includes multiple plots representing geological stages and illustrates changes in morphospace occupation through time.

Phylogenetic trees and time-scaling

We produced a series of time-scaled phylogenies of Mosasauroidea plus a dolichosaur outgroup to estimate ancestral states and calculate evolutionary rates. The taxonomic and phylogenetic relationships of mosasauroids have been extensively explored (Bell 1997; Madzia & Cau 2017; Simões *et al.* 2017; Lively 2018; Jiménez-Huidobro & Caldwell 2019; LeBlanc *et al.* 2019). Although the monophyly of the traditional subfamilies is generally supported, their internal topologies and interrelationships are unresolved (Madzia & Cau 2017). Further, there is evidence of taxonomic inertia, where historical precedent leads to the retention of taxa even when there is insufficient diagnostic evidence. An example is *Clidastes*, where continued use of two poorly diagnosed species has obscured our understanding of the genus (Lively 2018). To account for these uncertainties, we tested three topologies: a maximum parsimony (MP) and a maximum likelihood (ML) tree from Simões *et al.* (2017), and a Bayesian-inference (BI) tree from Madzia & Cau (2017). Further, we wished to include several taxa that were not included in these phylogenies, so we used the results of other phylogenetic studies (Konishi & Caldwell 2011; Konishi *et al.* 2016; Jiménez-Huidobro & Caldwell 2019; LeBlanc *et al.* 2019), to position them informally in the phylogenies. The phylogenetic relationships of the dolichosaur outgroup were taken from Paparella *et al.* (2018).

Trees were prepared for time-scaling in Mesquite v.3.61 (Maddison & Maddison 2019) to include relevant taxa for the locomotory and feeding analyses. Substage-level occurrence data were taken from Driscoll *et al.* (2019), with the maximum and minimum dates for substages from Ogg *et al.* (2016). Multiple time-scaling methods were employed to account for the effects of bias in any one method: the 'equal' (Lloyd *et al.* 2012), minimum branch length (MBL; Laurin 2004) and fossilized birth–death (FBD; Heath *et al.* 2014; Matzke & Wright 2016) approaches. Time-scaling with the equal and MBL dating methods was performed in R using the package paleotree v.3.3.25 (Bapst 2019). The 'minmax' data treatment setting was employed because the data consisted of possible occurrence ranges and not absolute occurrence dates. To account for this uncertainty, we produced ten time-scaled trees for each dating method/topology combination and compared these to ensure congruence. FBD time-scaling was undertaken in MrBayes v.3.2.7a (Ronquist *et al.* 2012), following the methods of Ballell *et al.* (2019).

Evolutionary rates analysis

The first principal component axes for the feeding and locomotory morphospace were subjected to evolutionary rates analyses in R to investigate the tempo of functional macroevolution. The fastANC function of phytools v.0.7-47 (Revell 2012) was used to estimate ancestral states on the time-scaled trees, using maximum likelihood methods. In addition, FossilBM v.1 (Silvestro *et al.* 2019), which employs a Bayesian framework, was used to estimate rate shifts across the phylogenies and distinguish evolutionary deviations from a Brownian (homogeneous rates) model of evolution. Tracer was used to check FossilBM outputs for convergence (Rambaut *et al.* 2018).

Stage-level disparity

The R package dispRity v.1.4.1 (Guillerme 2018) was used to investigate functional disparity through time from the feeding and locomotory datasets. This package was chosen because it permits flexible construction of analyses and is multifunctional, incorporating several disparity metrics, two of which are used here. We investigated disparity from the PCA scores generated, which reflects functional dissimilarity between taxa, using sum of variances (SoV) and sum of ranges (SoR) as the chosen metrics. SoV measures the spread of taxa in morphospace, whereas SoR reflects the amount of morphospace occupied (a proxy for morphovolume). Both variance-based and morphovolume disparity metrics have their relative strengths and weaknesses, and both are capable of biasing disparity analyses (Nordén *et al.* 2018). Thus, it is reasonable to use both metrics for comparison. The datasets were subsampled for 1000 bootstrap replicates to generate 95% confidence intervals, and rarefaction was applied to the SoR analysis, which is susceptible to sample size biases. Disparity was plotted by geological stage, using the occurrence data of Driscoll *et al.* (2019). This approach permits the identification of disparity highs and lows through time, which can be corroborated with the evolutionary rates analyses to investigate the broader patterns of mosasauroid macroevolution.

Phylogenetic time-sliced disparity

A second approach to calculating disparity, as outlined by Guillerme & Cooper (2018), is phylogenetic time-slicing. Here, disparity is calculated from a time-scaled phylogenetic tree for taxa extant at fixed points in time, removing the requirement to specify bins, which may implicitly bias the result. Furthermore, by incorporating branch data, time-slicing helps to combat issues associated with under-sampled time intervals by sampling directly from the ghost lineages. Here, we use the methods presented by Guillerme & Cooper (2018), implemented in the R package dispRity. The time-slicing approach was run on

60 trees. In each iteration, disparity was calculated at 10 equidistant dates, slicing through the phylogenies and sampling either the tips (observed fossils) or the ancestral nodes (estimated ancestral morphospace locations), based on relative proximity. In each iteration, the mean SoV from 100 bootstrap replicates was recorded and spaghetti-plots were generated to illustrate all iterations (Stubbs *et al.* 2021).

Clade-level disparity

In addition to the two methods of calculating temporal changes in disparity, we also investigated differences in disparity between different mosasauroid subclades. This was undertaken using dispRity v.1.4.1 (Guillerme 2018); taxa were binned by clade, and disparity calculated for their mandibular and forelimb PCA scores, using SoV with 1000 bootstrap replicates.

Generalized linear modelling of physical drivers

Polcyn *et al.* (2014) suggested that mosasauroid macro-evolution was driven by physical processes, but there has been no attempt to model physical drivers against pheno-typic variation. Here, we collated a substage-level time series of the three potential physical drivers outlined by Polcyn *et al.* (2014), spanning the Late Cretaceous. For eustatic sea level (SL) we used the curve of Miller *et al.* (2005), which provides full coverage for the Late Creta-ceous, though at lower resolution for the middle–early Santonian and middle Coniacian. Sea surface temperature (SST) data were taken from O'Brien *et al.* (2017), who collated published records of two palaeotemperature proxies, $\delta^{18}O$ and Tex86, to produce SST curves for the entire Cretaceous. The original study was focused on lati-tudinal differences, but we combined their latitude-specific temperature data to look at the global picture. The $\delta^{13}C$ record serves as a common proxy for oceanic primary productivity, and we used data from Cramer *et al.* (2009) to investigate this potential driver. The original dataset was broken down geographically, but again we combined this to look at the global trend. The physical driver records were averaged by geological substage to match the functional disparity scores.

We used generalized linear modelling within a Bayesian framework to infer the effect of sea level, sea surface tem-perature and primary productivity on each of the four-disparity metrics. A Shapiro–Wilk test was performed first to test for normality in the input variables. The disparity records were found to be non-normal, but the physical drivers could not be distinguished from a normal distri-bution. Following this, the model was implemented in R

and Stan (Stan Development Team 2020) using the pack-age brms v.2.14.0 (Bürkner 2017, 2018). Model parame-ters were set as: disparity was estimated from a log-normal likelihood distribution; priors for the three physi-cal drivers were standardized to determine their relative effects, and the coefficients were represented by normal distributions; a Student's-*t* distribution was used as a prior for the intercept (default in brms), and the standard deviation (σ) was set as a broad half-Cauchy distribution. The intercept represents the variation not described by the input parameter and the standard deviation indicates the variance of the relationship. Upon completion, priors were simulated to ensure the model sampled a realistic parameter space, and the MCMC chains were checked for convergence using estimated sample size (ESS > 200) and R-hat values (approaching 1.00), as reported in Stan and brms.

RESULTS

Morphospace

Jaw functional morphospace. The first two principal com-ponents account for 50.6% of the total variation and readily distinguish clades in morphospace (Fig. 1A; Fig. S3). PC1 accounts for 31.3% of the total variation and differentiates jaws based on their length, robusticity, and the relative sizes of various components, like the den-tal row. Negative values represent robust, elongate jaws, with long dental rows (e.g. *Mosasaurus*, *Prognathodon*), while positive values indicate shorter jaws, relatively larger muscle attachment sites and greater mechanical advan-tages (e.g. *Aigialosaurus*, *Selmasaurus*). PC2 accounts for 19.3% of total variation and differentiates jaws based on their opening capabilities and dental morphology. Positive values represent robust jaws with relatively large adduc-tors, high mechanical advantages, and often possessing low aspect-ratio teeth (e.g. *Globidens*), while negative values strongly discriminate jaws with high aspect-ratio teeth (e.g. *Plotosaurus*).

Mosasauroids occupy a distinct region of morphospace from dolichosaur-grade taxa, which is consistent with the prevailing view that the origin of the mosasaur skull lies among aigialosaur-grade taxa (Campbell Mekarski *et al.* 2019). The regions of morphospace occupied by 'aigialo-saurs' and basal mosasaurids (Halisaurinae, Tethysaurinae and Yaguarasaurinae) are restricted compared to the other groups, with basal mosasaurids overlapped by all three derived mosasaurid subfamilies. Plioplatecarpinae almost completely surround the basal mosasaurids, but cover an extended region, particularly along PC1 between 'aigialosaurs' and Mosasaurinae. Tylosaurines are nearly entirely overlapped by Mosasaurinae, which occupy the

FIG. 1. Functional morphospace for mosasauroid mandibles. A, functional morphospace described by PC1 and PC2, showing clade-level patterns of occupation. B–G, time-series illustrating morphospace occupation between geological stages; 'dolichosaurs' have been removed from these latter plots to focus on Mosasauroidea. A variant of A with taxon-specific labels is provided (Fig. S3). 'Aigialosaur', plioplatecarpine and mosasaurine skeletal diagrams redrawn from: Carroll & deBraga (1992), Holmes (1996) and LeBlanc *et al.* (2013).

largest region of morphospace and greatly expand on PC2, featuring the specialized mandibular anatomy of *Plotosaurus*, *Globidens* and *Prognathodon currii* (Christiansen & Bonde 2002; LeBlanc *et al.* 2013, 2019). Despite some overlap, mosasaurine and plioplatecarpine morphospace is strongly segregated and have different primary axes of variance (PC2 versus PC1 dominate).

Limb functional morphospace. The first two principal components account for 88.9% of the total variation (Fig. 2A; Fig. S4). PC1 accounts for 77.2% and distinguishes limbs based on characters linked to locomotory abilities. Negative values represent elongate propodials and epipodials, implying more plesiopedal locomotion found in plesiomorphic mosasauroids (e.g. *Aigialosaurus*), whereas positive values represent increasingly the short, robust pro- and epipodials of hydropedal morphology (e.g. *Plotosaurus*). PC2 accounts for 11.7% of the total variation and differentiates limb bones by their relative proportions and sizes. Positive values are associated with greater flaring of the distal humeral facet and a relatively larger ulna and radius, which are more equivalent in size to the humerus (e.g. *Plotosaurus*).

The plesiopedal 'aigialosaurs' occupy a distinct morphospace, with some taxa (e.g. *Portunatasaurus*) encroaching upon the positions of basal mosasaurids. The tentative mosasaurine *Dallasaurus* is located firmly among aigialosaur-grade taxa (Bell & Polcyn 2005), which is expected given its plesiomorphic limbs and girdles. Interestingly, 'aigialosaurs' are segregated from 'dolichosaurs' along PC2, the only other plesiopedal group in the analysis, as 'dolichosaurs' have more equal limb bone proportions. Basal mosasaurids occupy a small area of morphospace between aigialosaur-grade taxa and more derived, hydropedal taxa. Tylosaurines are found to cluster closely with these basal taxa, distinguished by broadly more positive PC1 scores, in a remarkably restricted morphospace. Plioplatecarpines occupy the second largest morphospace after mosasaurines, and more derived members of this clade converge upon their morphology. *Plotosaurus* and *Mosasaurus* are notable outliers with much higher values on PC1 resulting from their extensive hydropedal adaptations. Conversely, *Clidastes*, *Kourisodon*, *Prognathodon* and *Globidens* all score lower on PC1, closer to plioplatecarpines.

Temporal patterns of morphospace occupation. Morphospace occupation through time illuminates the tempo and mode of functional diversification (Figs 1B–G, 2B–G). Both mandible and limb morphospaces show similar patterns of occupation through time. The early evolution of mosasauroids (Cenomanian–Coniacian) shows clear directional shifts in the region occupied, and some

regions are vacated from one bin to the next, notably by the loss of aigialosaur-grade taxa. From the Coniacian onwards, however, morphospace occupation rapidly expands through innovation into new morphologies while retaining the older forms.

Functional disparity

Clade-binned disparity. Mosasaurines are the most disparate clade in both mandibular and forelimb traits, consistent with their broad morphospace occupation (Fig. 3). Plioplatecarpines also show relatively higher levels of disparity, particularly for forelimb traits, though notably lower than mosasaurines. 'Aigialosaurs' have reasonably disparate jaws, but more homogeneous limbs, while tethysaurines, yaguarasaurines, and tylosaurines are characterized by low levels of disparity for both traits.

Stage-binned disparity. Mandibular disparity is lowest in the early Late Cretaceous, but following a low-point in the Turonian, increases continually until the end-Maastrichtian, indicating a sustained period of ecomorphological diversification (Fig. 4A, B). Forelimb disparity follows a similar pattern with low values in the earlier stages, followed by expansion to the Campanian (Fig. 4C, D). Considering methodological differences between the SoR and SoV analyses, both metrics recover these temporal trends. We therefore suggest that this demonstrates a more or less continuous rise in disparity, for both traits, through the Late Cretaceous, similar to the result of Stubbs & Benton (2016).

Phylogenetic time-sliced disparity. Disparity is lowest in the earlier stages of the Late Cretaceous and increases continually until the end-Cretaceous, following a late Turonian or Coniacian expansion (Fig. 5). This pattern is observed for both the mandibular and forelimb datasets, although uncertainty exists over whether contraction or continued expansion of forelimb disparity occurred in the Maastrichtian. These results are congruent with those of the binned disparity analysis and therefore support a similar conclusion of continually increasing disparity through the Late Cretaceous.

Evolutionary rates and trends

Jaw rates and phylogenetic trends. Ancestral state estimates indicate two main shifts in jaw PC1 score across Mosasauroidea (Fig. 6A, B). The first is associated with functional innovation during the origin of mosasaurids from within 'aigialosaurs', while the second is attributed to
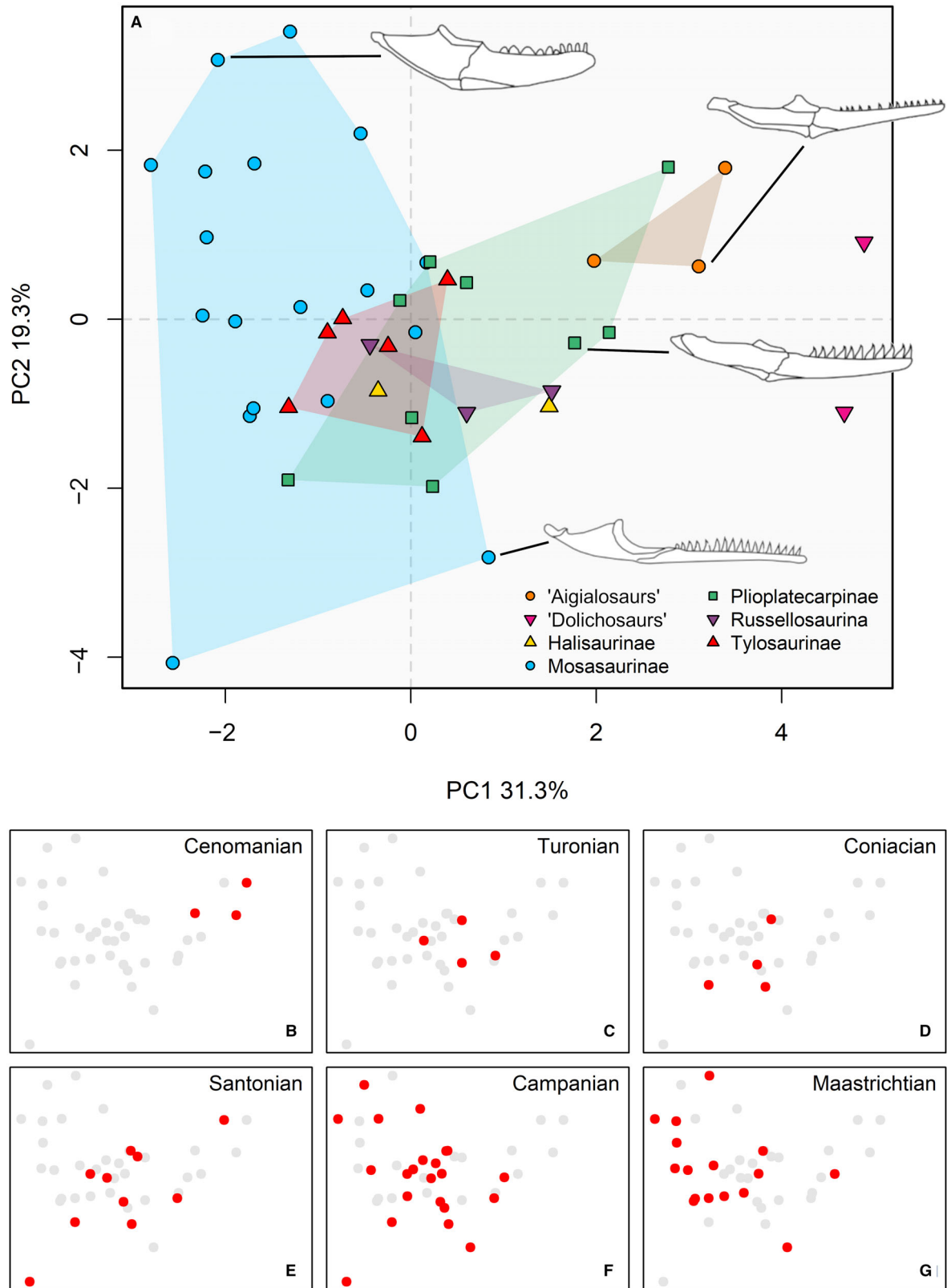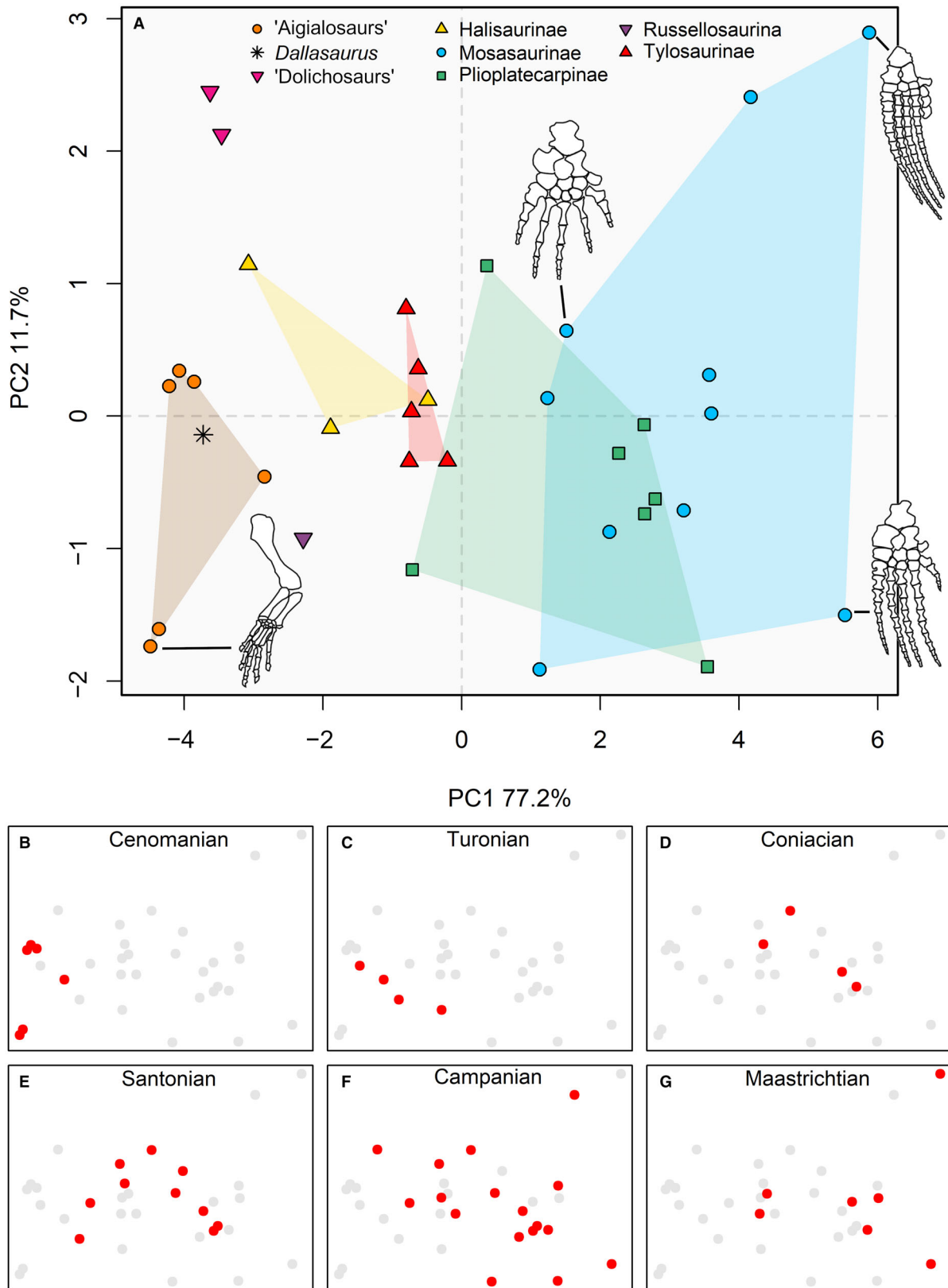
FIG. 2. Functional morphospace for mosasauroid forelimbs. A, functional morphospace described by PC1 and PC2, showing clade-level patterns of occupation. B–G, time-series illustrating stage-level morphospace occupation; 'dolichosaurs' have been removed. A variant of A with taxon-specific labels is provided (Fig. S4). Skeletal diagrams redrawn from Lindgren *et al.* (2011).
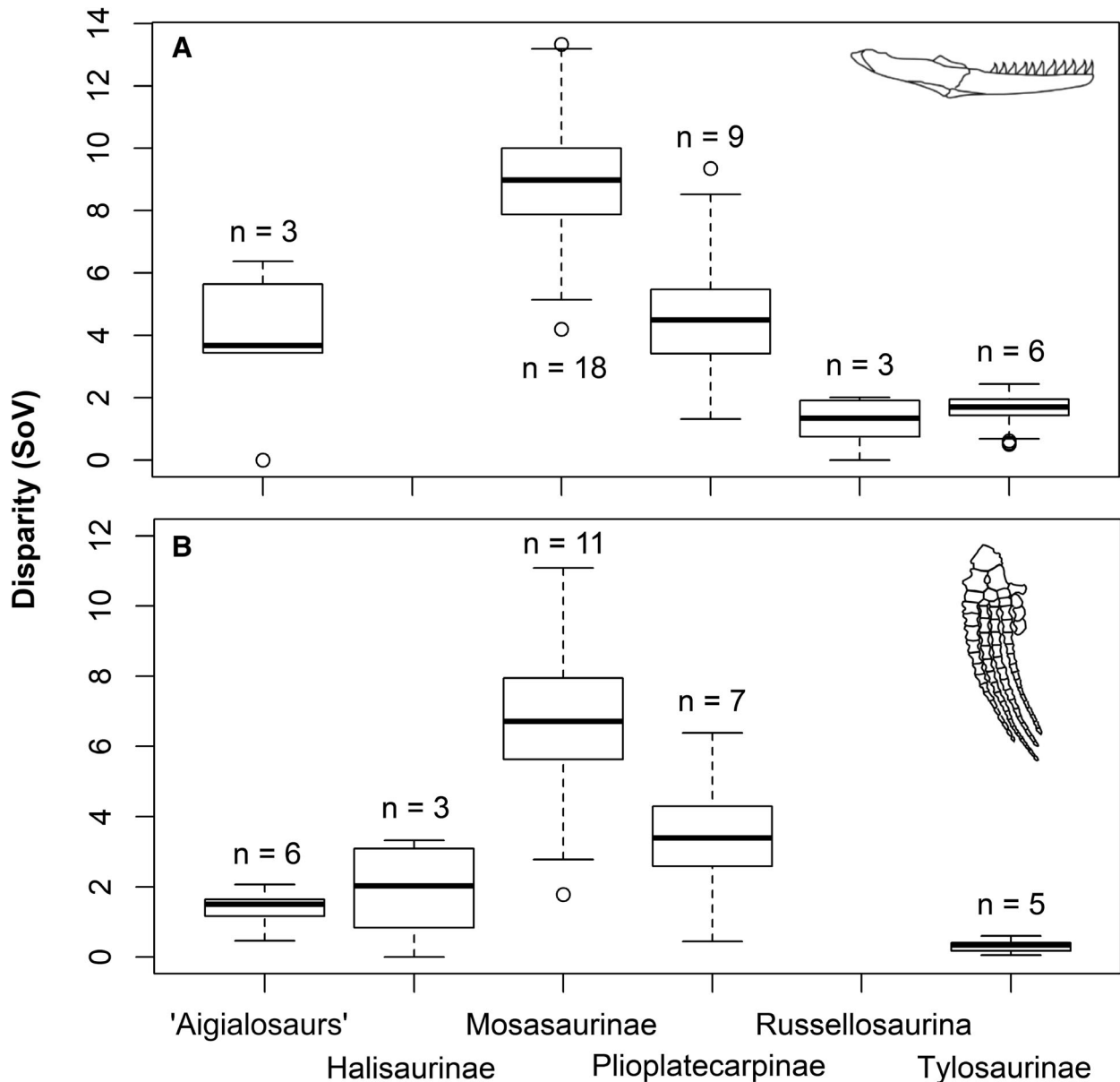
FIG. 3. Clade-level patterns of disparity using SoV metrics for mandibular traits (A) and forelimb traits (B). Mosasaurines are the most disparate clade for both trait categories, followed by plioplatecarpines. 'Aigialosaurs' and halisaurines show moderate disparity (although the former have fairly disparate mandibles). Tylosaurines and basal russellosaurines (comprising Tethysaurinae and Yaguarasaurinae and identified as Russellosaurina) have the lowest disparity. Disparity was not calculated for basal russellosaurine forelimbs or halisaurine mandibles, because of low sample sizes (n = 1 and n = 2 respectively).

innovation within Mosasaurinae, these patterns are common to all topologies and time-scaling methods. In addition, a shift within Tylosaurinae is variably recovered, though often it is purely restricted to the *Tylosaurus bernardi* + *Tylosaurus proriger* clade.

Irrespective of the apparent morphological shifts recovered by ancestral state reconstruction, FossilBM results demonstrate that these changes did not coincide with any positive rate shifts. Analysis of PC1 (Table 1) found the

greatest support for two rate shifts (61%), though there was also reasonable support for a single shift (37%); where a decrease in evolutionary rates occurring at or prior to the origins of Mosasauridae was most frequently recovered (81%). In addition, a single directional trend is observed on all tested trees.

Limb rates and phylogenetic trends. The ancestral state estimates suggest that limb PC1 shows a strong evolutionary
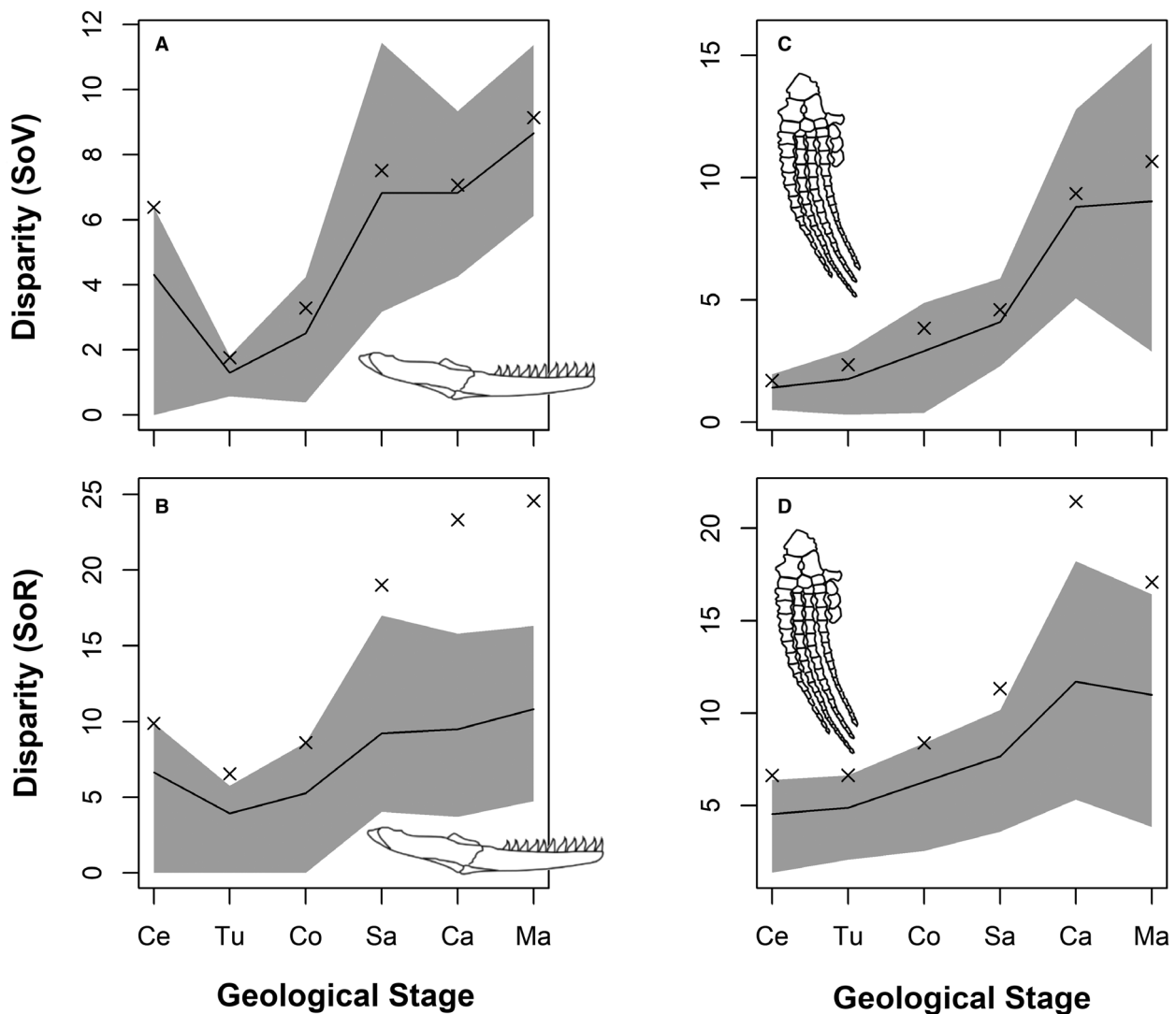
FIG. 4. Stage-level patterns of within-bin disparity using SoV and SoR metrics for the mandibular traits (A–B) and forelimb traits (C–D). The black line represents the mean bootstrapped disparity from 1000 replicates, with the 95% confidence estimates presented in grey. Crosses indicate the observed disparity. Mandibular disparity reaches a low point in the Turonian before increasing continually to the end-Maastrichtian. Conversely, forelimb disparity increases steadily throughout the Late Cretaceous, reaching the highest levels in the Campanian and Maastrichtian.

pattern (Fig. 6C, D). There is no major difference between plesiopedal 'aigialosaurs' and 'dolichosaurs'. However, a major shift on this component is associated with the origins of hydropedal morphology among the mosasaurids. Despite this, there was no consensus on the precise location at which this morphology first evolved, or whether it is a homoplastic trait, as it varied significantly between the topologies. This is seemingly conditional on the divergence estimate of *Dallasaurus*, which is morphologically more like aigialosaur-grade taxa than the inferred ancestral mosasaurid. Halisaurines and the basal russellosaurine *Romeosaurus* transitioned to more paddle-like limb

morphology, though to a lesser extent than in mosasaurines, plioplatecarpines and tylosaurines. Both mosasaurines and plioplatecarpines have evolved strongly hydropedal forelimbs, particularly the *Mosasaurus* + *Plotosaurus* clade.

The rate and trend estimations for forelimb evolution are like those for the mandibles, demonstrating that the results of the ancestral state reconstruction do not directly correspond to shifts in evolutionary rates (Table 2). Analysis of PC1 found a single rate shift to be most common (93%), with most shifts being slowdowns occurring before or at the origins of Mosasauridae (96%).
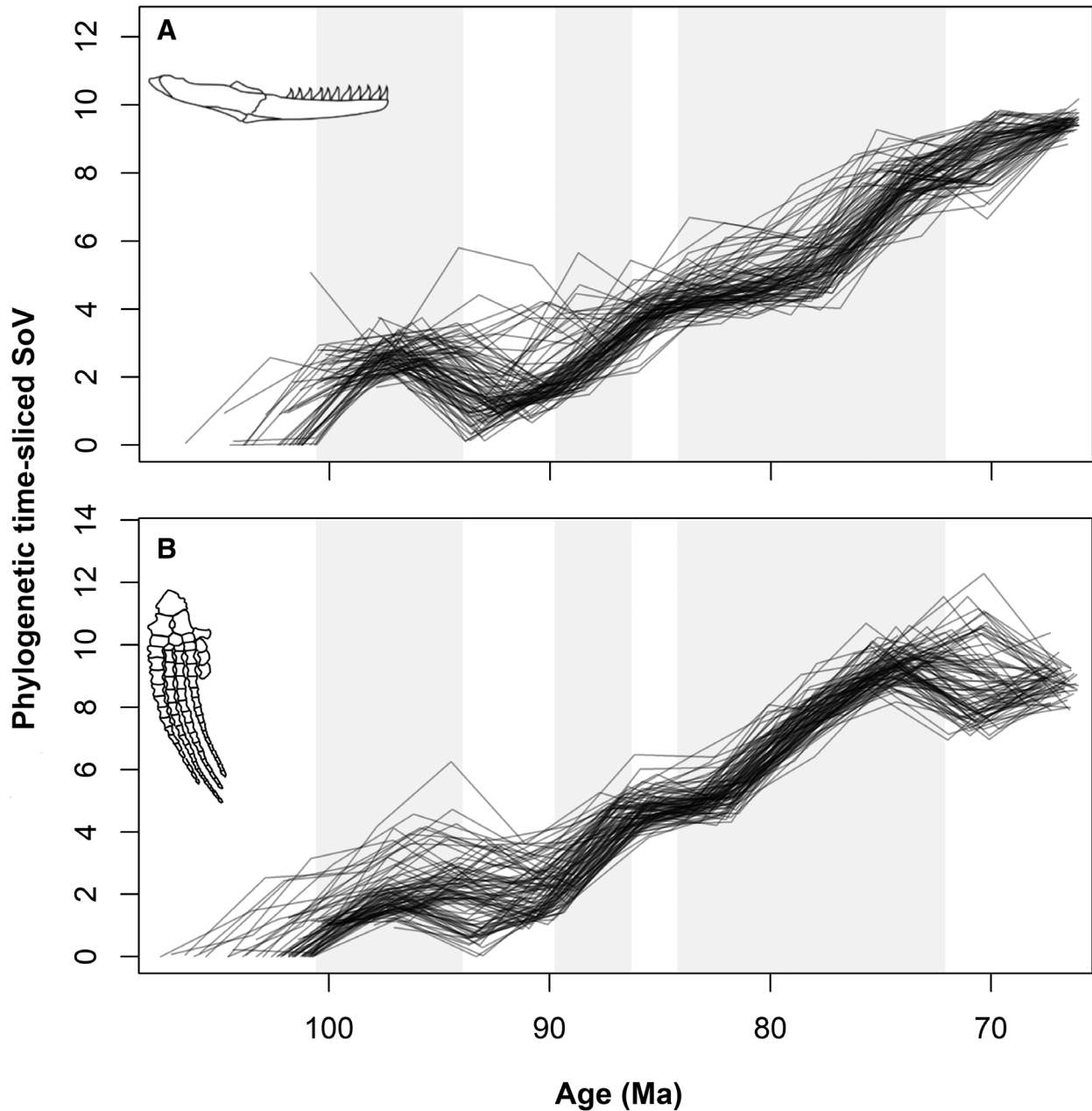
FIG. 5. Phylogenetic time-sliced disparity using 'equal' and minimum branch length dated topologies for the mandibular (A) and forelimb (B) datasets. These graphs follow the same patterns seen in Figure 4, however, by incorporating the ghost ranges, this metric counters the sampling issues encountered by the substage-level analysis.

Evolutionary trend analysis also favoured a single directional trend.

Physical driver modelling

The model reached convergence with all disparity metrics ($\hat{R} = 1.00$, ESS > 200), and prior simulation demonstrated that reasonable values were being sampled. Sampling of the posterior distribution produced small mean values for the driver coefficients (<1), for all combinations tested. These coefficients were lower than the estimated means for the intercept and standard deviation in all analyses (Fig. 7; Table 3). Plotting conditional effects demonstrated that negative correlations between drivers and disparity were most common, except for a positive correlation between

A

Eonatator sternbergi
Halisaurus arambourgi
Tethysaurus nopcsai
Russellosaurus coheni
Romeosaurus fumanensis
Plioplatecarpus houzeaui
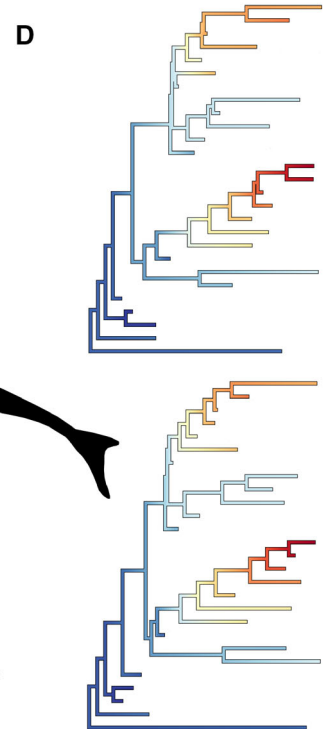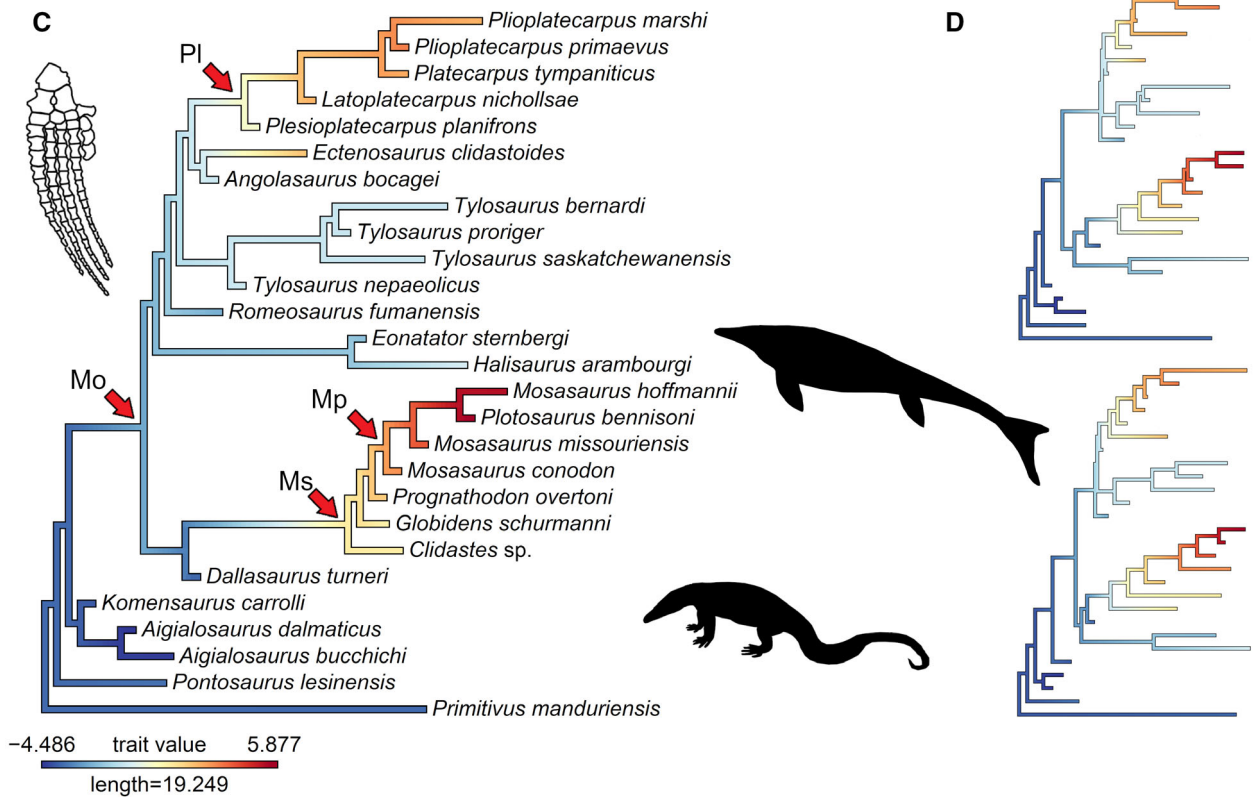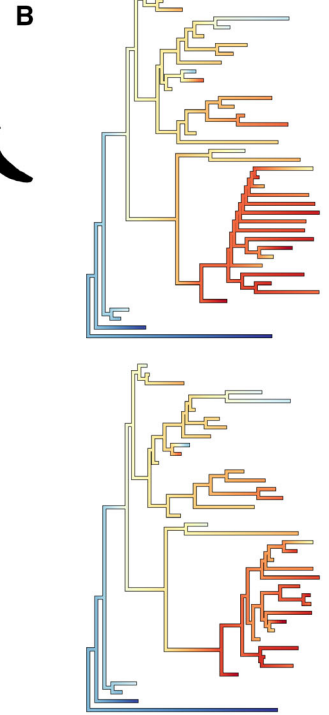*Plioplatecarpus primaevus*
Platecarpus tympaniticus
Latoplatecarpus willistoni
Latoplatecarpus nichollsae
Plesioplatecarpus planifrons
Selmasaurus johnsoni
Ectenosaurus clidastoides
Angolasaurus bocagei
Tylosaurus saskatchewanensis
Tylosaurus pembinensis
Tylosaurus proriger
Tylosaurus bernardi
Tylosaurus nepaeolicus
Taniwhasaurus antarcticus
Plotosaurus bennisoni
Mosasaurus hoffmannii
Mosasaurus missouriensis
Mosasaurus conodon
Plesiotylosaurus crassidens
Prognathodon waiparaensis
Prognathodon overtoni
Prognathodon saturator
Eremiasaurus heterodontus
Prognathodon solvayi
Prognathodon currii
Globidens simplex
Globidens schurmanni
Globidens phosphaticus
Prognathodon kianda
Clidastes propython
Aigialosaurus bucchichi
Aigialosaurus dalmaticus
Pontosaurus lesinensis
Primitivus manduriensis

Mo
Ty
Ms

−2.802   trait value   4.887
length=19.259

B

C

Pl
Plioplatecarpus marshi
Plioplatecarpus primaevus
Platecarpus tympaniticus
Latoplatecarpus nichollsae
Plesioplatecarpus planifrons
Ectenosaurus clidastoides
Angolasaurus bocagei
Tylosaurus bernardi
Tylosaurus proriger
Tylosaurus saskatchewanensis
Tylosaurus nepaeolicus
Romeosaurus fumanensis
Eonatator sternbergi
Halisaurus arambourgi
Mp
Mosasaurus hoffmannii
Plotosaurus bennisoni
Mosasaurus missouriensis
Mosasaurus conodon
Prognathodon overtoni
Globidens schurmanni
Clidastes sp.
Mo
Ms
Dallasaurus turneri
Komensaurus carrolli
Aigialosaurus dalmaticus
Aigialosaurus bucchichi
Pontosaurus lesinensis
Primitivus manduriensis

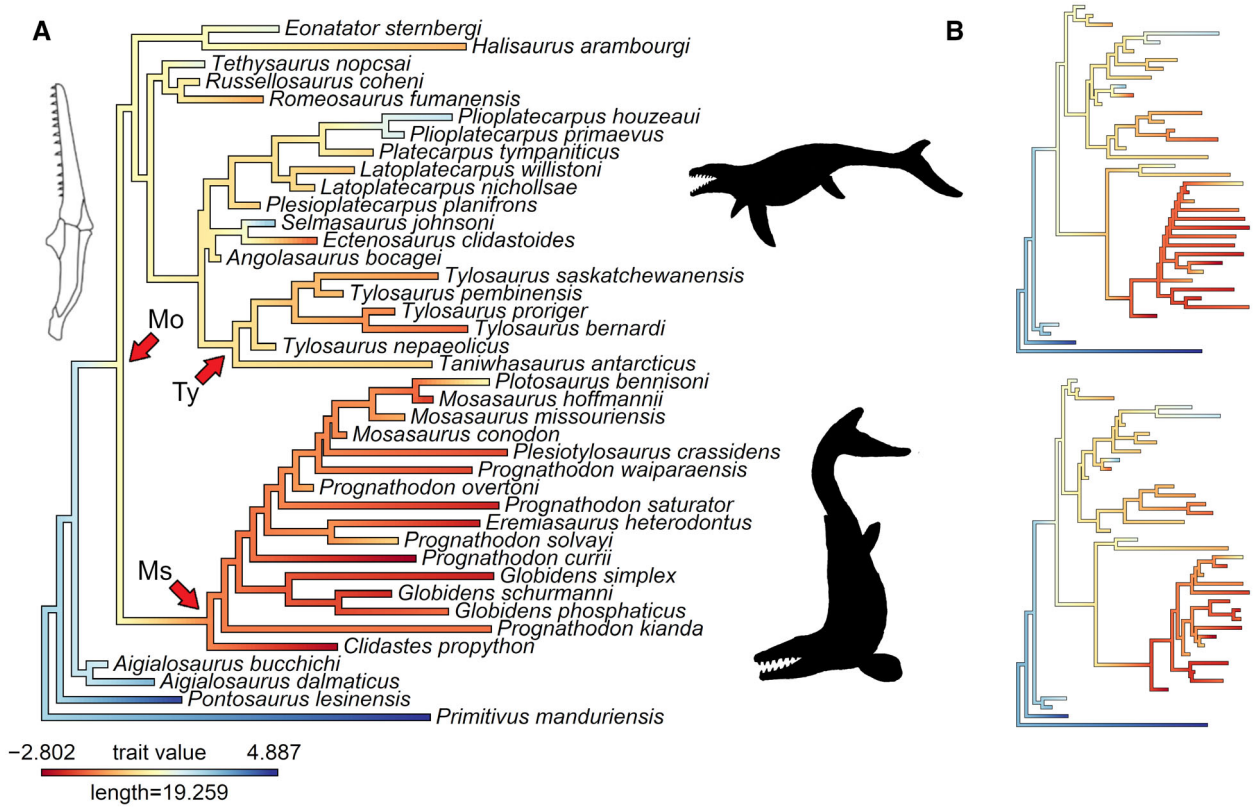−4.486   trait value   5.877
length=19.249

D

FIG. 6. Examples of ancestral state reconstructions using 'equal-dated' trees. A, evolution of mandibular PC1, with morphological shifts at Mosasauridae (Mo) and Mosasaurinae (Ms) highlighted; a shift within Tylosaurinae (Ty) is also variably recovered. B, alternative ancestral state reconstructions for mandibular PC1 using Maximum Likelihood (top) and Bayesian (bottom) topologies. C, evolution of forelimb PC1 with morphological shifts at Mosasauridae (Mo), within Plioplatecarpinae (Pl) and Mosasaurinae (Ms), and at the *Mosasaurus + Plotosaurus* (Mp) clade identified. D, alternative ancestral state reconstructions for forelimb PC1 using Maximum Likelihood (top) and Bayesian (bottom) topologies. Extremely similar results were recovered by minimum branch length and fossil birth–death time-scaling methods.

TABLE 1. Summary of fossilBM rate analyses for mandibular PC1.

Shift number	95% CI	Proportion
1	1–3	0.29
1	1–4	0.08
2	1–3	0.19
2	1–4	0.41
2	1–5	0.01
3	1–4	0.01
3	2–5	0.01

Shift location	Direction	Proportion
Ectenosaurus + Selmasaurus	Increase	0.12
Mosasauridae	Decrease	0.29
Mosasauroidea	Decrease	0.52
Other	Increase	0.06

Shift number indicates the favoured number of rate shifts per tree, out of all runs, 95% CI represents the range of confidence intervals (set automatically at 0.95) from all runs favouring the specific shift number. The shift location corresponds to the node where the rate shift occurred, and direction demonstrates whether the observed shift was an increase or decrease in evolutionary rates. Trend analyses are not presented, as all topologies (100%) favoured a single directional evolutionary trend.

TABLE 2. Summary of fossilBM rate analyses for forelimb PC1.

Shift number	95% CI	Proportion
1	1–3	0.92
1	1–4	0.01
2	1–3	0.04
2	1–4	0.01
2	1–5	0.01

Shift location	Direction	Proportion
Mosasauroidea	Decrease	0.93
Mosasauridae	Decrease	0.03
Other	Increase	0.04

As in Table 1, trend analyses are not presented, as all topologies (100%) favoured a single directional evolutionary trend.

mandibular SoV and sea level, and between forelimb SoV and $\delta^{13}C$.

DISCUSSION

Tempo of mosasauroid macroevolution

Colonization of the marine realm should, theoretically, be associated with an 'early burst' macroevolutionary scenario, characterized by high rates of evolution and rapid acquisition of morphological variance, early in the evolution of a lineage (Hughes *et al.* 2013; Puttick 2018; Moon & Stubbs 2020). This might be expected for mosasauroids, but we did not identify such a disparity profile. Given that small sample sizes dominate the early time bins, where high rates of morphological diversification would be expected under an early burst, it could be argued that the disparity profiles reflect a sampling bias. We suggest that this is unlikely because of the strong congruence between the results of the time-binning and time-slicing methods; the latter being resistant to the biasing effects of small sample sizes (Guillerme & Cooper 2018). In addition, some authors have argued that early bursts may be an artefact of using cladistic characters for disparity analyses (e.g. Mongiardino Koch *et al.* 2017). Here, measured characters with known functional precedent were used instead, and these are considered to be more reliable for ecomorphological disparity studies (Anderson & Friedman 2012).

The second criterion of an early burst is an observation of high early rates of evolution, which we also did not find. A recent rate estimation of mosasauroids using cladistic characters found multiple shifts during their evolutionary history (Madzia & Cau 2020). However, differences between these results and ours can be attributed to their use of discrete cladistic characters, which inevitably introduces a phylogenetic signal into the rate estimations. It is also important to consider the potential effects of the 'dolichosaur' outgroup; these taxa are morphologically divergent and have substantial branch lengths (Figs 1, 2, 6). The rate estimations often recovered 'dolichosaurs' as having faster rates than mosasauroids; this might contribute to the apparent slow-down, but it is unlikely to explain entirely the absence of an early burst.
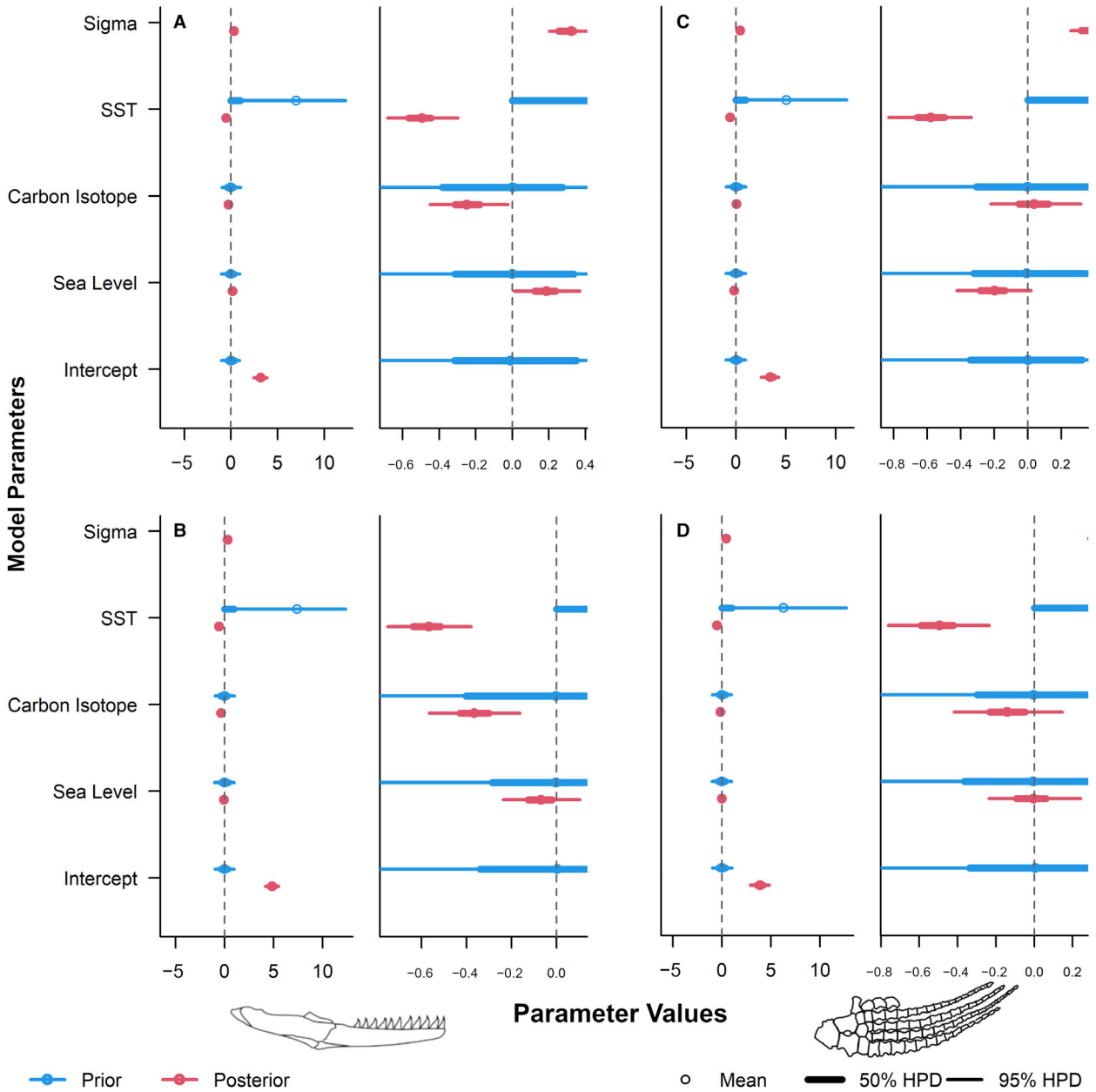
FIG. 7. Summary of parameters (prior and posterior estimates) from the generalized linear modelling of mosasauroid disparity and potential physical driver proxies. Two sub-plots are presented for each section, the full results are presented on the left plot, while the right-hand plot is focused on the posterior physical driver coefficients. A, mandibular SoV. B, mandibular SoR. C, forelimb SoV. D, forelimb SoR.

Considering these caveats, it is unlikely that large rate shifts occurred during mosasauroid evolution, as these should be picked out more frequently. Furthermore, our rate analyses corroborate the disparity profiles, with both showing steady diversification without an early burst. Therefore, we suggest that mosasauroids are unique among Mesozoic marine reptiles in displaying a protracted radiation, spanning the Late Cretaceous, which lacks major shifts in evolutionary tempo.

Evolution of jaw ecomorphology

The early part of mosasauroid evolution is characterized by the transition from a short, unspecialized mandible, with relatively large internal components (e.g. adductor attachment sites), to an elongate, specialized mandible, where the internal components are proportionally shorter (excluding the dental row; Fig. 1A). In Mosasauroidea, the lengthening of the mandible in absolute terms

TABLE 3. Output parameter estimates (mean, estimated error, 95% confidence range) for the generalized linear modelling of the physical driver data.

Disparity metric	Coefficient	Mean	Est. error	95% Range
Mandibular – SoV	Intercept	3.19	0.36	1.44
	SL	0.19	0.09	0.36
	$\delta^{13}C$	−0.25	0.11	0.45
	SST	−0.49	0.1	0.4
	σ	0.33	0.08	0.3
Mandibular – SoR	Intercept	4.84	0.34	1.36
	SL	−0.07	0.09	0.34
	$\delta^{13}C$	−0.37	0.1	0.41
	SST	−0.56	0.1	0.38
	σ	0.31	0.07	0.27
Forelimb – SoV	Intercept	3.43	0.45	1.82
	SL	−0.2	0.12	0.47
	$\delta^{13}C$	0.04	0.13	0.53
	SST	−0.58	0.12	0.49
	σ	0.42	0.09	0.36
Forelimb – SoR	Intercept	3.88	0.48	1.93
	SL	−0.01	0.12	0.48
	$\delta^{13}C$	−0.14	0.14	0.57
	SST	−0.5	0.13	0.54
	σ	0.45	0.1	0.39

Evolutionary drivers: SL, eustatic sea level; $\delta^{13}C$, carbon isotope proxy for palaeoproductivity; SST, sea surface temperature. Disparity metrics: SoV, sum of variance; SoR, sum of ranges.

co-occurred with proportional lengthening of the dental row. This elongation is the primary morphological distinction between 'dolichosaurs' and mosasauroids and between 'aigialosaurs' and mosasaurids, increasing substantially at each morphological grade. Aigialosaur-grade taxa have the shortest jaws among mosasauroids, with relatively large muscle attachment sites and higher mechanical advantages, suggesting that they were capable of proportionally higher bite forces. Ross (2009) assigned 'aigialosaurs' to the 'cut' dental morphotype guild, which, given their small size and unspecialized mandible, suggests that they were likely to have been generalists. Basal mosasaurids (Halisaurinae, Tethysaurinae and Yaguarasaurinae) group closely in morphospace, suggesting that this region represents an adaptive grade of the earliest mosasaurids (Bardet *et al.* 2005; Makádi *et al.* 2012; Palci *et al.* 2013). The tight clustering of these subfamilies indicates low disparity among early mosasaurid mandibles (Fig. 1A), supporting suggestions that other factors, specifically body size, might have accounted for differences in prey choice (Ross 2009). Elongation of the mandible was of key importance in the origin of Mosasauridae, suggesting that the dietary habits of early mosasaurids diverged from their aigialosaur-grade ancestors. Furthermore,

the outlying position of *Clidastes* in morphospace is attributable to mandibular elongation (Fig. 1A) prior to the increase in robusticity seen in later mosasaurines. Therefore, elongation was also important in the origins of the most disparate mosasauroid subclade.

Mandibular elongation has occurred multiple times in the evolution of marine tetrapods and has the adaptive benefit of increasing jaw closure speed, ideal for capturing agile aquatic prey (Stubbs & Benton 2016; McCurry *et al.* 2017; Ballell *et al.* 2019; Stubbs *et al.* 2021). In mosasauroids, this process co-occurred with lengthening of the dental row, which would serve to augment the elongated mandible as a high-velocity prey capture mechanism by presenting a larger area of teeth on which to ensnare prey. However, elongation lowered the mechanical advantage of the mandible, most notably in basal mosasaurids, which, paired with low robusticity and an unspecialized dentition, probably restricted them to softer prey items. Previous suggestions of halisaurine prey have included small fish and cephalopods (Bardet *et al.* 2015; Konishi *et al.* 2016). The primary driver of mandibular elongation was most likely to be adoption of obligatorily marine habits. 'Aigialosaurs' were capable of terrestrial locomotion, and there is no *a priori* reason to suggest they could not feed on land, a common feature in extant semiaquatic squamates (Mayes *et al.* 2005), which would account for their more generalized mandible. However, such possibilities would not be afforded to fully aquatic early mosasaurids, necessitating modification of the mandible to increase the efficiency of capturing agile aquatic prey. One possibility may be that an ecological opportunity arose following the Cenomanian–Turonian Anoxic Event, which caused a major turnover in marine communities that might have facilitated mosasauroid diversification (e.g. Bardet *et al.* 2008). However, we did not identify any evolutionary rate shift associated with the onset of mandibular elongation (Fig. 6A, B), so we cannot claim an example of ecological release, a part of the opportunism scenario.

Derived mosasaurids diversified to occupy substantial novel jaw morphospace (Fig. 1A). Tylosaurinae and Mosasaurinae are often considered the most derived groups, and show convergence in mandibular function towards large, robust jaws, with elongate tooth rows and the capacity for large gapes. Acquisition of this morphology is marked by a strong negative shift in the PC1 ancestral state reconstruction in both clades, but it remains unclear whether this condition is homoplastic amongst tylosaurines, as implied by some reconstructions (Fig. 6A, B). There are differences between tylosaurine and mosasaurine mandibles (Fig. 1A): the former are slightly less robust (more negative PC2 score), and their dental row is often shorter (though this is probably caused by the presence of an edentulous rostrum). Further, tylosaurine morphospace is considerably more restricted than that of

mosasaurines, reflecting lower overall disparity. Preserved stomach contents indicate that tylosaurines were apex predators of large vertebrates including, fish, sharks, seabirds and marine reptiles (Everhart 2004), a diet that is similar to that of some large mosasaurines (Konishi *et al.* 2011; Konishi *et al.* 2014). Therefore, this raises the possibility that large-bodied mosasaurines, particularly *Mosasaurus*, might have been in competition with tylosaurines. One argument against this is that tylosaurines may have incapacitated prey using their edentulous rostrum as a weapon (Konishi *et al.* 2018; Stewart & Mallon 2018), a feature absent from derived mosasaurines, which could indicate different feeding strategies.

Mosasaurines are remarkable in occupying by far the largest functional morphospace (Fig. 1A). This is consistent with substantial innovation in the clade, especially their high mandibular and dental disparity, often considered fundamental to their success (Ross 2009; LeBlanc *et al.* 2013; Konishi *et al.* 2014). While both mosasaurines and tylosaurines display a positive shift in PC1 ancestral state reconstruction (Fig. 6A, B), mosasaurines surpass tylosaurines in most metrics associated with this axis (Fig. 1A), having the most elongate and robust mandibles and being capable of the largest gapes. However, while this trend may be an extension of processes extending back to 'aigialosaurs', mosasaurines hold the unique distinction of having differentiated substantially along PC2, suggesting diversification towards new prey types and feeding strategies.

Many mosasaurines show a preference for harder food items, particularly the durophagous taxa *Globidens* and *Carinodens*, whose mandibles and dentition were radically adapted for feeding on shelled invertebrates (Schulp 2005; Martin 2007; Martin & Fox 2007). The three species of *Globidens* included in this analysis show strongly positive PC2 scores (Fig. 1A), and form a tight cluster based on their exceptionally robust mandibles and low-aspect-ratio brachydont dentition. These characteristics are inferred as adaptations to resist high mechanical loads during feeding (Schulp 2005; Martin 2007; LeBlanc *et al.* 2019) and imply a powerful bite force. However, we note that while *Globidens* has high mechanical advantage and large adductor size compared to other mosasaurids, generally these traits vary little throughout the group, contrary to previous suggestions (e.g. LeBlanc *et al.* 2019). Indeed, the greatest variation in these traits occurs between short-jawed 'aigialosaurs' and long-jawed mosasaurids, which suggests that derived mosasaurines may have evolved other mechanisms to bolster force production, or reduce force requirements, that are not captured by our suite of functional characters. In the case of *Globidens*, derived species may have evolved a tripartite dentition, which served to puncture shells before crushing them, lowering the maximum forces required during processing (Martin 2007).

The paraphyletic genus *Prognathodon* is also considered to prefer harder prey items and occupies a similar region of morphospace to *Globidens* (Fig. 1A; Christiansen & Bonde 2002; Dortangs *et al.* 2002; Konishi *et al.* 2011). *Prognathodon* includes members with extremely robust crania and mandibles, some even likened to large tyrannosaurids in form and function (Christiansen & Bonde 2002; Dortangs *et al.* 2002). Unlike *Globidens*, *Prognathodon* was also an active predator (e.g. Konishi *et al.* 2011) and retains a relatively elongate dental row to assist prey capture. This morphology lowers mechanical advantage and implies a weaker bite force, which would be disadvantageous when processing harder food items. One solution may have been the evolution of bowed dentaries, which are common among *Prognathodon* species, and which increase mechanical advantage during biting by positioning prey towards the rear of the jaw (Rieppel & Labhardt 1979). This was also suggested by LeBlanc *et al.* (2019) and warrants further investigation with new functional characters. We also recommend that future quantitative analyses consider recent studies in mosasaurid dental morphology, microstructure, and chemistry, which demonstrate the teeth of some taxa were well adapted for withstanding high feeding stresses (Owocki & Madzia 2020).

Negative scores on PC2 are also attributed to feeding innovation in mosasaurines; with the exclusion of *Clidastes* (discussed earlier), *Plotosaurus* is the most differentiated along this axis. This taxon displays a suite of unique adaptations to facilitate ram feeding in a pelagic environment (LeBlanc *et al.* 2013) and is distinguished here primarily by its high-aspect-ratio teeth, but also by its adaptations for rapid jaw opening and low robusticity. This is consistent with the suggestion by LeBlanc *et al.* (2013) that the mandibles of *Plotosaurus* relied more on speed and precision than bite force, and that it specialized on a diet of small, soft prey.

The differentiation of mosasaurines along the PC2 axis reflects increasing specialization of the mandible and dentition, and niche partitioning between members of the clade (Fig. 1A). Konishi *et al.* (2014) suggested evidence for this, based on preserved gastric contents, among the contemporaneous mosasaurines *Prognathodon overtoni* and *Mosasaurus missouriensis*. In this analysis, *Mosasaurus* species are more negatively scored than *Prognathodon* on PC2 (excluding *Pr. kianda* and *Pr. solvayi*), confirming that *Mosasaurus* was more adapted for softer prey items.

An unexpected discovery was the considerable mandibular diversity of plioplatecarpines (Fig. 1A), forming the second largest cluster in morphospace, but barely discussed so far in terms of function. Plioplatecarpines are primarily differentiated along PC1, but also show reasonable divergence along PC2, suggesting a diversity of

feeding strategies and prey preferences. An interesting feature of this group is the apparent reversal in some taxa towards short jaws with high mechanical advantage. Such mandibles are capable of rapid opening and forceful closure but are not robust enough to withstand high mechanical loads. Undescribed material of the enigmatic plioplatecarpine 'Platecarpus' ptychodon (not included here) has indicated that this taxon was similarly specialized, and given its possible close relationship to *Selmasaurus*, which is considered here to be the most specialized plioplatecarpine, supports this position (Polcyn *et al.* 2016). However, the recently described *Gavialimimus* (also not included here), another close relative of *Selmasaurus* and possible source of Moroccan 'Pl.' ptychodon material, appears to possess a mandible modified for rapid prey capture, somewhat convergent with *Plotosaurus* (Strong *et al.* 2020). This stands in contrast to our results for *Selmasaurus* and demonstrates the need for further studies of plioplatecarpine feeding mechanics. The distinct mandibular anatomy of plioplatecarpines diverges substantially from mosasaurines and tylosaurines in morphospace, with the diversification of these clades occurring concurrently, consistent with niche partitioning.

The early history of mosasauroids is characterized by unidirectional evolution towards increased mandibular elongation and low levels of disparity (Figs 1B, 4A–B, 5A). Conversely, their later evolutionary history is characterized by a multidirectional radiation in morphospace (associated with novel feeding strategies and prey types) and far higher levels of disparity. The resulting disparity profile is characteristically 'top-heavy', in agreement with the result of Stubbs & Benton (2016), probably reflecting minimal vacant ecospace during the early evolution of the clade caused by the existence of established endemic competitors (Stubbs & Benton 2016; Reeves *et al.* 2021). During the Cenomanian and Turonian, plesiosaurs, sharks and large fish may have excluded the emerging mosasauroids from suitable niche space (Stubbs & Benton 2016; Madzia & Cau 2020). Therefore, the Cenomanian–Turonian Anoxic Event could have facilitated an opportunistic replacement by causing the extinction of such competitors although, as discussed previously, the absence of a rate shift at this point makes the idea uncertain (Tables 1, 2). Following the Turonian, disparity continued to rise to the Maastrichtian, driven by innovation alongside the retention of pre-existing morphologies. Disparity is highest in the terminal stages (Campanian and Maastrichtian), reflecting the radiation of the disparate mosasaurines and plioplatecarpines. The disparity profile matches the estimation of evolutionary rates and trends, which suggest mandibular evolution followed a single trajectory, and that the major phases of diversification were not associated with any significant rate shifts. Therefore, the rise in disparity probably reflects constant biological

forcing, whereby mosasauroids specialized their mandibles and dentitions in response to competition. In the case of mosasaurids, they diversified from the ancestral morphospace occupied by basal taxa to the new regions occupied by Tylosaurinae, Plioplatecarpinae, and Mosasaurinae, consistent with a niche partitioning scenario.

Evolution of the forelimb and locomotion

Our study introduces a suite of new characters of the forelimb aiming to reflect potential locomotory adaptation in mosasauroids. As these characters are novel, and as other body regions are involved in locomotion (including the primary propulsive apparatus), we provide a brief justification of our inference. The forelimbs of mosasauroids became radically modified throughout their evolution, with morphological differences related to changes in locomotory mode (Lindgren *et al.* 2007, 2011; Campbell Mekarski *et al.* 2019). This includes both the origin of the paddle from a walking limb, as well as its subsequent adaptation to different swimming styles in obligatorily marine taxa. 'Aigialosaurs' and basal mosasaurids were probably anguilliform swimmers, whereas some derived taxa were sub-carangiform or carangiform (Lindgren *et al.* 2007, 2011, 2013). In functionally analogous ichthyosaurs, such differences in locomotor mode are related to the propulsive cost of locomotion, where derived modes (e.g. carangiform) reduce the energetic cost of propulsion and are advantageous for sustained activity (Gutarra *et al.* 2019). In terms of marine tetrapod paddle morphology, high aspect-ratio fins are often associated with oceanic taxa (low drag, high stability), while low aspect-ratio fins are suited for rapid manoeuvring in more cluttered settings (O'Keefe 2001; Gutarra & Rahman 2021).

On PC1, the plesiopedal 'aigialosaurs' occupy the negative end of the axis, while the derived, carangiform *Plotosaurus*, is at the positive end (Fig. 2A). This distribution confirms that these characters serve as a proxy for swimming mode. However, because these morphologies are extremes, it is important to consider the positions of intermediate taxa. Basal mosasaurids plot closest to the 'aigialosaurs', between the latter and the derived mosasaurid subfamilies, consistent with their inferred locomotory modes and hydropedality (Lindgren *et al.* 2011; Polcyn *et al.* 2012; Campbell Mekarski *et al.* 2019). Indeed, of the halisaurines included in this analysis, *Halisaurus* results are substantially more positive on PC1 than *Eonatator*, which is consistent with evidence for more caudally driven propulsion (Polcyn *et al.* 2012). Among mosasaurines, basal taxa (e.g. *Clidastes*) are inferred to have had more anguilliform locomotion than moderately derived taxa (e.g. *Prognathodon*), which in turn were less

carangiform than *Plotosaurus* (Lindgren *et al.* 2007, 2011, 2013), a trend also observed here. Therefore, this suggests that limb morphospace PC1 axis functions as a good approximation of swimming mode, where positive scores are more carangiform and negative scores more anguilliform.

Though we suggest that our forelimb data provide a useful proxy for locomotion, the characters used herein are by no means exhaustive. Unlike feeding adaptations, which can be readily understood from the mandible and dentition, locomotory adaptations are far less regionalized. Propulsion, stability, control, streamlining and buoyancy all have strong bearings on the locomotory mode of a marine organism, and each is achieved by combinations of different anatomical regions. Future work would certainly benefit from the quantitative analysis of other anatomical regions. First and foremost, advances in caudal anatomy and propulsion may provide a valuable source of characters, albeit for a more restricted number of taxa (Lindgren *et al.* 2007, 2010, 2011, 2013). Likewise, limb girdle data could also be useful, following a sizeable body of literature demonstrating its critical role in the adoption of obligatory marine habits (Bell & Polcyn 2005; Caldwell & Palci 2007; Dutchak & Caldwell 2009).

Given that limb morphospace PC1 serves as a proxy for locomotory adaptation, both the functional morphospace and the ancestral state reconstructions demonstrate that mosasauroid evolution was characterized by a trend towards more aquatic adaptation (Figs 2, 6). This is reinforced by the trend analysis, which shows a single trend through mosasauroid evolution towards more positive PC1 scores (Fig. 2B). The earliest mosasauroids were strongly plesiopedal and employed anguilliform swimming alongside terrestrial locomotion (Carroll & Debraga 1992; Caldwell *et al.* 1995; Caldwell 1996; Campbell Mekarski *et al.* 2019). Subsequent modification of the plesiopedal limb produced an incipient hydropedal limb, a feature present in basal mosasaurids, which are recovered close to aigialosaur-grade taxa in morphospace. The acquisition of hydropedality is considered a major transition in mosasauroid evolution, but this is subject to a debate concerning its homology, with suggestions it may have arisen convergently multiple times (Caldwell 1996; Bell & Polcyn 2005; Dutchak & Caldwell 2009). In addition, analysis of the pelvic limb and girdle has shown that pelvic modifications probably restricted (or completely inhibited) terrestrial locomotion prior to the acquisition of truly hydropedal limbs (Caldwell & Palci 2007). This underpins the importance of testing these findings with alternative functional characters, though we suggest that girdle-based characters would be unsuited for independent analysis because they are probably uninformative on the derived swimming modes of Mosasauridae.

In terms of hydropedality, our results are inconclusive, being heavily dependent on the time-scaling method applied (Fig. 6). However, *Dallasaurus* is considered a reversal on most of the phylogenetic topologies analysed and therefore, should this taxon turn out not to be an early mosasaurine, it might be expected that all topologies would recover an ancestrally hydropedal Mosasauridae. Nonetheless, the proximity between basal mosasaurids and 'aigialosaurs' suggests that they employed anguilliform or near-anguilliform locomotion, which would restrict them to nearshore environments and suggest that they were not swimming in a sustained manner (Lindgren *et al.* 2007, 2011). The relatively expensive anguilliform propulsion of early mosasaurids probably favoured ambush predation tactics and could account for the strong shift towards longer dental rows, as a prey capture mechanism. This may in turn explain the apparent coupling of morphospace movement between feeding and locomotion during early mosasauroid evolution and suggest that opportunity also functioned as a driver for the early evolution of locomotion.

Following the origin of hydropedality, paddle-like limbs were increasingly modified to suit new locomotory modes, becoming effective control surfaces whose morphology varies in accordance with the functional demands of a specific mode (Lindgren *et al.* 2007, 2011). This is most pronounced in *Plotosaurus*, which had evolved a high-aspect longipinnate forelimb through extreme modification of the long bones and hyperphalangy, which afforded good stability with relatively low induced drag, to a body optimized for carangiform locomotion (Lindgren *et al.* 2007). Here, *Plotosaurus* is among the most positively scored taxa in PC1 (Fig. 2A), consistent with unique morphological characteristics that are attributed to colonization of the open oceans and sustained cruising locomotion (Lindgren *et al.* 2007, 2009). However, other mosasaurids appear to have modified their forelimbs and adopted new locomotory modes, most notably among the mosasaurines and plioplatecarpines. Many of these taxa are not considered to be especially oceanic, suggesting that derived locomotory strategies were not limited to oceanic taxa, but started to emerge in more coastal taxa, perhaps facilitating future conquest of open ocean habitats. This is congruent with recent analyses of exceptional specimens of moderately derived mosasaurids that show a suite of anatomical adaptations indicating heightened locomotor performance (Lindgren *et al.* 2010, 2011, 2013; LeBlanc *et al.* 2012; Cuthbertson *et al.* 2015). Indeed, for many such taxa, a high-aspect-ratio paddle may have been disadvantageous, restricting their manoeuvrability in denser coastal environments or throughout the water column, the latter shown to be ecologically important for some plioplatecarpines (Cuthbertson *et al.* 2015).

The divergence between mosasaurines and plioplatecarpines in the feeding analysis is not matched by divergence

of locomotory modes, and demonstrates that within these clades, derived aquatic locomotion was favoured irrespective of dietary niche (Fig. 2A). In addition, basal members are less positively scored on PC1 than derived ones, indicating that this was a trend driven by innovation. Therefore, it is interesting that tylosaurines do not display this pattern and are instead confined to a reduced morphospace, with an inferred locomotory mode like basal mosasaurids. This observation offers a solution to the possible competition between mosasaurines and tylosaurines suggested by the mandibular morphospace: differences in locomotor performance could indicate that these clades deployed different predation strategies and habitat preferences. The position of tylosaurines in morphospace close to basal mosasaurids with low-aspect-ratio paddles might indicate an ambush strategy with predominately anguilliform locomotion, suited to nearshore environments (Lindgren *et al*. 2007, 2011). Conversely, mosasaurines are identified as more carangiform locomotors and might have used sustained locomotion and pursuit predation. Interestingly, this trend is most pronounced for the *Mosasaurus* + *Plotosaurus* clade, the former inferred to have been a potential competitor with tylosaurines. These findings should also be considered in light of a body of evidence showing widespread paedomorphosis in tylosaurines, which is less pronounced in mosasaurines (Caldwell 1996; Jiménez-Huidobro *et al*. 2016, 2019). This is particularly relevant in the forelimb, where much of the tylosaurine mesopodium is unossified (Caldwell 1996), but also extends to the girdles and pelvic limb (Caldwell 1996; Jiménez-Huidobro *et al*. 2019). The presence of widespread cartilaginous material in the pelvic limb and girdle of *Tylosaurus* compared to *Mosasaurus* may indicate a reduced role for its paddle in locomotion (Jiménez-Huidobro *et al*. 2019). Our analysis of the pectoral limb is congruent with the idea that mosasaurines and tylosaurines used different locomotory modes, even if direct comparison between the limb segments is tenuous. We find *Mosasaurus* approaches the condition in *Plotosaurus*, where rigid, well-ossified longipinnate paddles provide an efficient control surface to accommodate the forces generated by carangiform locomotion. Conversely, *Tylosaurus* is considered to be far less adapted for sustained locomotion.

Of the less derived mosasaurines, *Globidens* and *Prognathodon* show no real increase in PC1 over more basal mosasaurines (e.g. *Clidastes*); these taxa are sufficiently distinct in their feeding anatomy to imply that they targeted different prey to tylosaurines and could co-occur with them without competing. Therefore, the locomotory adaptations of *Mosasaurus* (and *Plotosaurus*) probably relate to changes in hunting strategy, occurring in conjunction with colonization of more pelagic habitats, which favoured sustained activity. Under this scenario, competition and opportunity (new habitat) can be considered to be the drivers of morphological evolution.

Following the Turonian, forelimb disparity shows a consistent increase to the Maastrichtian, reflecting innovation and retention (Figs 2B, 4C–D, 5B). This disparity profile suggests great locomotory diversity in the latest Cretaceous, coinciding with the diversification of mosasaurines and plioplatecarpines, which are recovered here as the most disparate clades. Although these results support previous suggestions of rapid sequential acquisition of hydropedality and derived aquatic adaptation in Mosasauroidea (Lindgren *et al*. 2010; Campbell Mekarski *et al*. 2019), such innovations were not associated with any significant increase in evolutionary rates (Fig. 6C, D). Therefore, we suggest that the overarching pattern of mosasauroid locomotory evolution was a steady, directional trend towards sub-carangiform and carangiform modes and their corresponding paddle diversity, without any major shift in evolutionary tempo. Under this scenario, locomotory evolution follows the same general pattern as feeding evolution, suggesting that it was also driven by biological processes. Comparison of the feeding and locomotory morphospaces shows that many of the clades diversifying substantially in mandibular form (e.g. Mosasaurinae, Plioplatecarpinae) also diverged in forelimb morphology. Furthermore, the morphospace expansion of these traits follows a similar timing and pattern. This suggests that ecomorphological diversification was multifaceted, and locomotion played a key role in the specialization aspect of niche partitioning.

Drivers of mosasauroid macroevolution

We have demonstrated that innovation, competition, and possibly opportunism, were important drivers of mosasauroid ecomorphological disparity (Figs 1–6). Taken by itself, this is a classically 'Red Queen' view of biotically driven evolution. However, there remains the counterargument that evolution, particularly deep-time macroevolution, is driven instead by physical processes (Benton 2009). Polcyn *et al*. (2014) suggested that both the diversity and body size disparity of mosasaurs were driven by a combination of high primary productivity, sea level and temperatures, responsible for controlling trophic abundances.

We find that under both tested disparity metrics, the small coefficient values for each driver suggest a minimal role for physical processes in our model, although the relatively high standard deviations indicate wide error margins (Fig. 7). Therefore, despite conditional relationships, it appears that the physical drivers are incapable of explaining temporal changes in mosasauroid disparity, a view further reinforced by the comparably high mean for

the intercept, which implies substantial hidden effects unaccounted for by the proxy data. This suggests that in terms of functional disparity, mosasauroid macroevolution was driven primarily by biological rather than physical processes.

A final consideration is the role of other clades in driving mosasauroid evolution. Given that later mosasauroids were high in the trophic pyramid, competition and opportunity are the most important aspects. Madzia & Cau (2020) suggested that the extinction of brachauchenine pliosaurids might have permitted mosasauroids to invade their former ecospace opportunistically. This could account for the lack of an early burst in mosasauroid evolution and would support the suggestion of opportunism early in their evolution. However, this is difficult to justify given that the lack of rate shifts suggests that competitive release and radiation did not occur (Fig. 6), contrasting with earlier marine reptile evolution when unoccupied marine niches permitted colonizers to diversify rapidly (Stubbs & Benton 2016; Moon & Stubbs 2020; Reeves et al. 2021). Therefore, we suggest that opportunism remains a possible, but not definitive, driver in the early evolution of Mosasauroidea, and that interactions with other clades might have been important. However, the major phase of diversification, after the Coniacian, predominantly reflects innovation and competition, where mosasauroids appear to have been structuring their own evolution, as their own primary competitors.

CONCLUSION

The view that mosasauroid macroevolution was driven solely by the physical factors controlling productivity is challenged by analysis of functional characters of the mandible and forelimb. Patterns of morphospace occupation demonstrate the important role of mandibular elongation as a prey capture mechanism in the early evolution of mosasauroids, followed by broader morphological diversification in later taxa, particularly mosasaurines and plioplatecarpines, associated with new diets and feeding strategies. Remarkably similar patterns are observed in locomotory morphospace, where basal forms probably used ambush predation and anguilliform locomotion, while derived taxa evolved novel locomotory strategies in association with new foraging ranges and feeding mechanisms. Mandibular and locomotory diversification are therefore found to be linked and driven by innovation and competition between clades. Temporal disparity patterns are also similar for both traits. Disparity is lowest in the early stages (Cenomanian–Turonian), possibly caused by limited vacant ecospace in Cretaceous oceans. High disparity is observed in later stages (Campanian–Maastrichtian) and attributed to the diversification of the

disparate clades, alongside retention of plesiomorphic taxa, consistent with niche-partitioning. Single directional evolutionary trends are observed for all traits analysed, and no rate shifts are associated with major bursts of morphological diversification. This suggests that mosasauroid evolution was remarkably steady and lends credit to the idea that it was fundamentally more constrained than for other marine reptiles. Modelling of physical drivers reveals a limited role during mosasauroid diversification, demonstrating the biological drivers of competition, innovation, and possibly opportunity, to be more important.

Author contributions. All authors are responsible for conceptualization, methodology, validation, and all phases of writing. SRRC, TLS, and BCM are responsible for formal analysis, investigation, software, and visualization. MJB and EJR are responsible for project administration and, with TLS and BCM for supervision.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.8w9ghx3mc

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12590):

Appendix S1. Includes details of functional characters and a description of data files in the associated Dryad record (Cross et al. 2022), as well as Figures S1–S4.

REFERENCES

ANDERSON, P. S. L. and FRIEDMAN, M. 2012. Using cladistic characters to predict functional variety: experiments using early gnathostomes. *Journal of Vertebrate Paleontology*, **32**, 1254–1270.

ANDERSON, P. S. L., FRIEDMAN, M., BRAZEAU, M. D. and RAYFIELD, E. J. 2011. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature*, **476**, 206–209.

ANDERSON, P. S. L., FRIEDMAN, M. and RUTA, M. 2013. Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality. *Integrative & Comparative Biology*, **53**, 197–208.

BALLELL, A., MOON, B. C., PORRO, L. B., BENTON, M. J. and RAYFIELD, E. J. 2019. Convergence and functional evolution of longirostry in crocodylomorphs. *Palaeontology*, **62**, 867–887.

BAPST, D. W. 2019. paleotree: paleontological and phylogenetic analyses of evolution. R package v.3.3.25. https://cran.r-project.org/web/packages/paleotree/index.html

BARDET, N., PEREDA SUBERBIOLA, X., IAROCHENE, M., BOUYA, B. and AMAGHZAZ, M. 2005. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). *Zoological Journal of the Linnean Society*, **143**, 447–472.

BARDET, N., HOUSSAYE, A., RAGE, J.-C. and SUBERBIOLA, X. P. 2008. The Cenomanian-Turonian (late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. *Bulletin de la Société Géologique de France*, **179**, 605–622.

BARDET, N., HOUSSAYE, A., VINCENT, P., SUBERBIOLA, X. P., AMAGHZAZ, M., JOURANI, E. and MESLOUH, S. 2015. Mosasaurids (Squamata) from the Maastrichtian phosphates of Morocco: biodiversity, palaeobiogeography and palaeoecology based on tooth morphoguilds. *Gondwana Research*, **27**, 1068–1078.

BELL, G. L. Jr 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. 293–332. *In* CALLAWAY, M. W. and NICHOLLS, E. (eds.) *Ancient marine reptiles*. Academic Press.

BELL, G. L. and POLCYN, M. J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). *Netherlands Journal of Geosciences*, **84**, 177–194.

BENTON, M. J. 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science*, **323**, 728–732.

BÜRKNER, P.-C. 2017. brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, **80**, 1–28.

BÜRKNER, P.-C. 2018. Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, **10**, 395–411.

BUTTON, D. J., RAYFIELD, E. J. and BARRETT, P. M. 2014. Cranial biomechanics underpins high sauropod diversity in resource-poor environments. *Proceedings of the Royal Society B*, **281**, 20142114.

CALDWELL, M. W. 1996. Ontogeny and phylogeny of the mesopodial skeleton in mosasauroid reptiles. *Zoological Journal of the Linnean Society*, **116**, 407–436.

CALDWELL, M. W. 2012. A challenge to categories: "What, if anything, is a mosasaur?". *Bulletin de la Société Géologique de France*, **183**, 7–34.

CALDWELL, M. W. and PALCI, A. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. *Journal of Vertebrate Paleontology*, **27**, 863–880.

CALDWELL, M. W., CARROLL, R. L. and KAISER, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. *Journal of Vertebrate Paleontology*, **15**, 516–531.

CALLISON, G. 1967. Intracranial mobility in Kansas mosasaurs. *Palaeontological Contributions of Kansas University, Papers*, **26**, 1–15.

CAMPBELL MEKARSKI, M., JAPUNDŽIĆ, D., KRIZMANIĆ, K. and CALDWELL, M. W. 2019. Description of a new basal mosasauroid from the Late Cretaceous of Croatia, with comments on the evolution of the mosasauroid forelimb. *Journal of Vertebrate Paleontology*, **39**, 1–15.

CARROLL, R. L. and DEBRAGA, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66–86.

CHRISTIANSEN, P. and BONDE, N. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. *Journal of Vertebrate Paleontology*, **22**, 629–644.

CONRAD, J. L., AST, J. C., MONTANARI, S. and NORELL, M. A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). *Cladistics*, **27**, 230–277.

CRAMER, B. S., TOGGWEILER, J. R., WRIGHT, J. D., KATZ, M. E. and MILLER, K. G. 2009. Ocean overturning since the Late Cretaceous: inferences from a new benthic foraminiferal isotope compilation. *Paleoceanography*, **24**, PA4216.

CROSS, S. R. R., MOON, B. C., STUBBS, T. L., RAYFIELD, E. J. and BENTON, M. J. 2022. Data from: Climate, competition, and the rise of mosasauroid ecomorphological disparity. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.8w9ghx3mc

CUTHBERTSON, R. S., MADDIN, H. C., HOLMES, R. B. and ANDERSON, J. S. 2015. The braincase and endosseous labyrinth of *Plioplatecarpus peckensis* (Mosasauridae, Plioplatecarpinae), with functional implications for locomotor behavior. *The Anatomical Record*, **298**, 1597–1611.

DORTANGS, R. W., SCHULP, A. S., MULDER, E. W. A., JAGT, J. W. M., PEETERS, H. H. G. and DE GRAAF, D. T. H. 2002. A large new mosasaur from the Upper Cretaceous of The Netherlands. *Netherlands Journal of Geosciences*, **81**, 1–8.

DRISCOLL, D. A., DUNHILL, A. M., STUBBS, T. L. and BENTON, M. J. 2019. The mosasaur fossil record through the lens of fossil completeness. *Palaeontology*, **62**, 51–75.

DUTCHAK, A. R. 2005. A review of the taxonomy and systematics of aigialosaurus. *Netherlands Journal of Geosciences*, **84**, 221–229.

DUTCHAK, A. R. and CALDWELL, M. W. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901)(Squamata: Aigialosauridae) with comments on mosasauroid systematics. *Journal of Vertebrate Paleontology*, **29**, 437–452.

EVERHART, M. J. 2004. Plesiosaurs as the food of mosasaurs; new data on the stomach contents of a *Tylosaurus proriger* (Squamata; Mosasauridae) from the Niobrara Formation of Western Kansas. *The Mosasaur*, **7**, 41–46.

GUILLERME, T. 2018. dispRity: a modular R package for measuring disparity. *Methods in Ecology & Evolution*, **9**, 1755–1763.

GUILLERME, T. and COOPER, N. 2018. Time for a rethink: time sub-sampling methods in disparity-through-time analyses. *Palaeontology*, **61**, 481–493.

GUTARRA, S. and RAHMAN, I. A. 2021. The locomotion of extinct secondarily aquatic tetrapods. *Biological Reviews*, **97**, 67–98.

GUTARRA, S., MOON, B. C., RAHMAN, I. A., PALMER, C., LAUTENSCHLAGER, S., BRIMACOMBE, A. J. and BENTON, M. J. 2019. Effects of body plan evolution on the hydrodynamic drag and energy requirements of swimming in ichthyosaurs. *Proceedings of the Royal Society B*, **286**, 20182786.

HEATH, T. A., HUELSENBECK, J. P. and STADLER, T. 2014. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences*, **111**, E2957–E2966.

HOLMES, R. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the North American Western Interior Seaway. *Journal of Vertebrate Paleontology*, **16**, 673–687.

HUGHES, M., GERBER, S. and WILLS, M. A. 2013. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences*, **110**, 13875–13879.

JIMÉNEZ-HUIDOBRO, P. and CALDWELL, M. W. 2019. A new hypothesis of the phylogenetic relationships of the Tylosaurinae (Squamata: Mosasauroidea). *Frontiers in Earth Science*, **7**, 47.

JIMÉNEZ-HUIDOBRO, P., SIMÕES, T. R. and CALDWELL, M. W. 2016. Re-characterization of *Tylosaurus nepaeolicus* (Cope, 1874) and *Tylosaurus kansasensis* (Everhart, 2005): ontogeny or sympatry? *Cretaceous Research*, **65**, 68–81.

JIMÉNEZ-HUIDOBRO, P., CALDWELL, M. W., PAPARELLA, I. and BULLARD, T. S. 2019. A new species of tylosaurine mosasaur from the upper Campanian Bearpaw Formation of Saskatchewan, Canada. *Journal of Systematic Palaeontology*, **17**, 849–864.

JOSSE, J. and HUSSON, F. 2016. missMDA: a package for handling missing values in multivariate data analysis. *Journal of Statistical Software*, **70**, 1–31.

KELLEY, N. P. and PYENSON, N. D. 2015. Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science*, **348**, aaa3716.

KONISHI, T. and CALDWELL, M. W. 2011. Two new plioplatecarpine (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America, and a global phylogenetic analysis of plioplatecarpines. *Journal of Vertebrate Paleontology*, **31**, 754–783.

KONISHI, T., BRINKMAN, D., MASSARE, J. A. and CALDWELL, M. W. 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. *Journal of Vertebrate Paleontology*, **31**, 1026–1046.

KONISHI, T., NEWBREY, M. G. and CALDWELL, M. W. 2014. A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. *Journal of Vertebrate Paleontology*, **34**, 802–819.

KONISHI, T., CALDWELL, M. W., NISHIMURA, T., SAKURAI, K. and TANOUE, K. 2016. A new halisaurine mosasaur (Squamata: Halisaurinae) from Japan: the first record in the western Pacific realm and the first documented insights into binocular vision in mosasaurs. *Journal of Systematic Palaeontology*, **14**, 809–839.

KONISHI, T., JIMÉNEZ-HUIDOBRO, P. and CALDWELL, M. W. 2018. The smallest–known neonate individual of *Tylosaurus* (Mosasauridae, Tylosaurinae) sheds new light on the tylosaurine rostrum and heterochrony. *Journal of Vertebrate Paleontology*, **38**, e1510835.

LAURIN, M. 2004. The evolution of body size, Cope's Rule and the origin of amniotes. *Systematic Biology*, **53**, 594–622.

LÊ, S., JOSSE, J. and HUSSON, F. 2008. FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, **25**, 1–18.

LEBLANC, A. R. H., CALDWELL, M. W. and BARDET, N. 2012. A new mosasaurine from the Maastrichtian (Upper Cretaceous) phosphates of Morocco and its implications for mosasaurine systematics. *Journal of Vertebrate Paleontology*, **32**, 82–104.

LEBLANC, A. R. H., CALDWELL, M. W. and LINDGREN, J. 2013. Aquatic adaptation, cranial kinesis, and the skull of the mosasaurine mosasaur *Plotosaurus bennisoni*. *Journal of Vertebrate Paleontology*, **33**, 349–362.

LEBLANC, A. R. H., MOHR, S. R. and CALDWELL, M. W. 2019. Insights into the anatomy and functional morphology of durophagous mosasaurines (Squamata: Mosasauridae) from a new species of *Globidens* from Morocco. *Zoological Journal of the Linnean Society*, **186**, 1026–1052.

LINDGREN, J., JAGT, J. W. M. and CALDWELL, M. W. 2007. A fishy mosasaur: the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. *Lethaia*, **40**, 153–160.

LINDGREN, J., CALDWELL, M. W. and JAGT, J. W. M. 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942)(Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). *Journal of Vertebrate Paleontology*, **28**, 1043–1054.

LINDGREN, J., ALWMARK, C., CALDWELL, M. W. and FIORILLO, A. R. 2009. Skin of the Cretaceous mosasaur *Plotosaurus*: implications for aquatic adaptations in giant marine reptiles. *Biology Letters*, **5**, 528–531.

LINDGREN, J., CALDWELL, M. W., KONISHI, T. and CHIAPPE, L. M. 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. *PLoS One*, **5**, e11998.

LINDGREN, J., POLCYN, M. J. and YOUNG, B. A. 2011. Landlubbers to leviathans: evolution of swimming in mosasaurine mosasaurs. *Paleobiology*, **37**, 445–469.

LINDGREN, J., KADDUMI, H. F. and POLCYN, M. J. 2013. Soft tissue preservation in a fossil marine lizard with a bilobed tail fin. *Nature Communications*, **4**, 2423.

LIVELY, J. R. 2018. Taxonomy and historical inertia: *Clidastes* (Squamata: Mosasauridae) as a case study of problematic paleobiological taxonomy. *Alcheringa*, **42**, 516–527.

LLOYD, G. T., WANG, S. C. and BRUSATTE, S. L. 2012. Identifying heterogeneity in rates of morphological evolution: discrete character change in the evolution of lungfish (Sarcopterygii, Dipnoi). *Evolution*, **66**, 330–348.

MACLAREN, J. A., ANDERSON, P. S. L., BARRETT, P. M. and RAYFIELD, E. J. 2017. Herbivorous dinosaur jaw disparity and its relationship to extrinsic evolutionary drivers. *Paleobiology*, **43**, 15–33.

MADDISON, W. P. and MADDISON, D. R. 2019. Mesquite: a modular system for evolutionary analysis. v.3.61. http://www.mesquiteproject.org

MADZIA, D. and CAU, A. 2017. Inferring 'weak spots' in phylogenetic trees: application to mosasauroid nomenclature. *PeerJ*, **5**, e3782.

MADZIA, D. and CAU, A. 2020. Estimating the evolutionary rates in mosasauroids and plesiosaurs: discussion of niche occupation in Late Cretaceous seas. *PeerJ*, **8**, e8941.

MAKÁDI, L., CALDWELL, M. W. and ŐSI, A. 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. *PLoS One*, **7** (12), e51781.

MARTIN, J. E. 2007. A new species of the durophagous mosasaur *Globidens* (Squamata: Mosasauridae) from the Late Cretaceous Pierre Shale Group of central South Dakota, USA. *Geological Society of America Special Paper*, **427**, 177–198.

MARTIN, J. E. and FOX, J. E. 2007. Stomach contents of *Globidens*, a shell–crushing mosasaur (Squamata), from the Late Cretaceous Pierre Shale Group, Big Bend area of the Missouri River, central South Dakota. *Geological Society of America Special Paper*, **427**, 167–176.

MASSARE, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Paleobiology*, **7**, 121–137.

MASSARE, J. A. 1994. The mechanics and physiology of animal swimming. 133–149. *In* MADDOCK, L., BONE, Q. and RAYNER, J. M. V. (eds.) *Mechanics and physiology of animal swimming*. Cambridge University Press.

MATZKE, N. J. and WRIGHT, A. M. 2016. Inferring node dates from tip dates in fossil Canidae: the importance of tree priors. *Biology Letters*, **12**, 20160328.

MAYES, P. J., THOMPSON, G. G. and WITHERS, P. C. 2005. Diet and foraging behaviour of the semi-aquatic *Varanus mertensi* (Reptilia:Varanidae). *Wildlife Research*, **32**, 67–74.

McCURRY, M. R., WALMSLEY, C. W., FITZGERALD, E. M. G. and McHENRY, C. R. 2017. The biomechanical consequences of longirostry in crocodilians and odontocetes. *Journal of Biomechanics*, **56**, 61–70.

MILLER, K. G., KOMINZ, M. A., BROWNING, J. V., WRIGHT, J. D., MOUNTAIN, G. S., KATZ, M. E., SUGARMAN, P. J., CRAMER, B. S., CHRISTIE-BLICK, N. and PEKAR, S. F. 2005. The Phanerozoic record of global sea-level change. *Science*, **310**, 1293–1298.

MONGIARDINO KOCH, N., CECCARELLI, F. S., OJANGUREN AFFILASTRO, A. A. and RAMÍREZ, M. J. 2017. Discrete and morphometric traits reveal contrasting patterns and processes in the macroevolutionary history of a clade of scorpions. *Journal of Evolutionary Biology*, **30**, 814–825.

MOON, B. C. and STUBBS, T. L. 2020. Early high rates and disparity in the evolution of ichthyosaurs. *Communications Biology*, **3**, 68.

NORDÉN, K. K., STUBBS, T. L., PRIETO-MÁRQUEZ, A. and BENTON, M. J. 2018. Multifaceted disparity approach reveals dinosaur herbivory flourished before the end–Cretaceous mass extinction. *Paleobiology*, **44**, 620–637.

O'BRIEN, C. L., ROBINSON, S. A., PANCOST, R. D., SINNINGHE DAMSTÉ, J. S., SCHOUTEN, S., LUNT, D. J., ALSENZ, H., BORNEMANN, A., BOTTINI, C., BRASSELL, S. C., FARNSWORTH, A., FORSTER, A., HUBER, B. T., INGLIS, G. N., JENKYNS, H. C., LINNERT, C., LITTLER, K., MARKWICK, P., McANENA, A., MUTTERLOSE, J., NAAFS, B. D. A., PÜTTMANN, W., SLUIJS, A., VAN HELMOND, N. A. G. M., VELLEKOOP, J., WAGNER, T. and WROBEL, N. E. 2017. Cretaceous sea-surface temperature evolution: constraints from TEX_{86} and planktonic foraminiferal oxygen isotopes. *Earth-Science Reviews*, **172**, 224–247.

OGG, J. G., OGG, G. M. and GRADSTEIN, F. M. 2016. *A concise geologic time scale: 2016*. Elsevier.

O'KEEFE, R. F. 2001. Ecomorphology of plesiosaur flipper geometry. *Journal of Evolutionary Biology*, **14**, 987–991.

OWOCKI, K. and MADZIA, D. 2020. Predatory behaviour in mosasauroid squamates inferred from tooth microstructure and mineralogy. *Cretaceous Research*, **111**, 104430.

PALCI, A., CALDWELL, M. W. and PAPAZZONI, C. A. 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of northern Italy. *Journal of Vertebrate Paleontology*, **33**, 599–612.

PAPARELLA, I., PALCI, A., NICOSIA, U. and CALDWELL, M. W. 2018. A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. *Royal Society Open Science*, **5**, 172411.

POLCYN, M. J., LINDGREN, J., BARDET, N., CORNELISSEN, D., VERDING, L. and SCHULP, A. S. 2012. Description of new specimens of *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005 and the relationships of Halisaurinae. *Bulletin de la Société Géologique de France*, **183**, 123–136.

POLCYN, M. J., JACOBS, L. L., ARAÚJO, R., SCHULP, A. S. and MATEUS, O. 2014. Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **400**, 17–27.

POLCYN, M. J., BARDET, N., AMAGHAZ, M., GONÇALVES, O. A., HOUSSAYE, A., JOURANI, E., KADDUMI, H. F., LINDGREN, J., MATEUS, O., MESLOUHF, S., MORAIS, M. L., PEREDA-SUBERBIOLA, X., SCHULP, A., VINCENT, P. and JACOBS, L. L. 2016. An extremely derived plioplatecarpine mosasaur

from the Maastrichtian of Africa and the Middle East. *5th Triennial Mosasaur Meeting*. Museum of Evolution, Uppsala University.

PUTTICK, M. N. 2018. Mixed evidence for early bursts of morphological evolution in extant clades. *Journal of Evolutionary Biology*, **31**, 502–515.

PYENSON, N. D., KELLEY, N. P. and PARHAM, J. F. 2014. Marine tetrapod macroevolution: Physical and biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **400**, 1–8.

RAMBAUT, A., DRUMMOND, A. J., XIE, D., BAELE, G. and SUCHARD, M. A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **67**, 901–904.

REEDER, T. W., TOWNSEND, T. M., MULCAHY, D. G., NOONAN, B. P., WOOD, P. L., SITES, J. W. and WIENS, J. J. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. *PLoS One*, **10** (3), e0118199.

REEVES, J. C., MOON, B. C., BENTON, M. J. and STUBBS, T. L. 2021. Evolution of ecospace occupancy by Mesozoic marine tetrapods. *Palaeontology*, **64**, 31–49.

REVELL, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology & Evolution*, **3**, 217–223.

RIEPPEL, O. and LABHARDT, L. 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). *Herpetologica*, **35**, 158–163.

RONQUIST, F., TESLENKO, M., VAN DER MARK, P., AYRES, D. L., DARLING, A., HÖHNA, S., LARGET, B., LIU, L., SUCHARD, M. A. and HUELSENBECK, J. P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542.

ROSS, M. R. 2009. Charting the Late Cretaceous sea: mosasaur richness and morphological diversification. *Journal of Vertebrate Paleontology*, **29**, 409–416.

RUSSELL, D. A. 1967. Systematics and morphology of American mosasaurs. *Bulletin of the Peabody Museum*, **23**, 1–241.

SCHNEIDER, C. A., RASBAND, W. S. and ELICEIRI, K. W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

SCHULP, A. S. 2005. Feeding the mechanical mosasaur: what did *Carinodens* eat? *Netherlands Journal of Geosciences*, **84**, 345–357.

SCHULP, A. S., VONHOF, H. B., VAN DER LUBBE, J. H. J. L., JANSSEN, R. and VAN BAAL, R. R. 2013. On diving and diet: resource partitioning in type-Maastrichtian mosasaurs. *Netherlands Journal of Geosciences*, **92**, 165–170.

SILVESTRO, D., TEJEDOR, M. F., SERRANO-SERRANO, M. L., LOISEAU, O., ROSSIER, V., ROLLAND, J., ZIZKA, A., HÖHNA, S., ANTONELLI, A. and SALAMIN, N. 2019. Early arrival and climatically-linked geographic expansion of New World monkeys from tiny African ancestors. *Systematic Biology*, **68**, 78–92.

SIMÕES, T. R., VERNYGORA, O., PAPARELLA, I., JIMÉNEZ-HUIDOBRO, P. and CALDWELL, M. W. 2017. Mosasauroid phylogeny under multiple phylogenetic methods provides new insights on the evolution of aquatic adaptations in the group. *PLoS One*, **12**, e0176773.

STAN DEVELOPMENT TEAM 2020. *Stan Modeling Language Users Guide and Reference Manual*. v.2.21.2. https://mc-stan.org

STEWART, R. F. and MALLON, J. 2018. Allometric growth in the skull of *Tylosaurus proriger* (Squamata: Mosasauridae) and its taxonomic implications. *Vertebrate Anatomy Morphology Palaeontology*, **6**, 75–90.

STRONG, C. R., CALDWELL, M. W., KONISHI, T. and PALCI, A. 2020. A new species of longirostrine plioplatecarpine mosasaur (Squamata: Mosasauridae) from the Late Cretaceous of Morocco, with re-evaluation of the problematic taxon 'Platecarpus' ptychodon. *Journal of Systematic Palaeontology*, **18**, 1769–1804.

STUBBS, T. L. and BENTON, M. J. 2016. Ecomorphological diversifications of Mesozoic marine reptiles: the roles of ecological opportunity and extinction. *Paleobiology*, **42**, 547–573.

STUBBS, T. L., PIERCE, S. E., RAYFIELD, E. J. and ANDERSON, P. S. L. 2013. Morphological and biomechanical disparity of crocodile–line archosaurs following the end-Triassic extinction. *Proceedings of the Royal Society B*, **280**, 20131940.

STUBBS, T. L., PIERCE, S. E., ELSLER, A., ANDERSON, P. S. L., RAYFIELD, E. J. and BENTON, M. J. 2021. Ecological opportunity and the rise and fall of crocodylomorph evolutionary innovation. *Proceedings of the Royal Society B*, **288**, 20210069.