Global ecomorphological restructuring of dominant marine reptiles prior to the K/Pg mass extinction

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ABSTRACT

Mosasaurid squamates were the dominant amniote predators in marine ecosystems during most of the Late Cretaceous. Evidence from multiple sites worldwide of a global mosasaurid community restructuring across the Campanian–Maastrichtian transition may have wide-ranging implications for the evolution of diversity of these top oceanic predators. In this study, we use a suite of biomechanical traits and functionally descriptive ratios to investigate how the morphofunctional disparity of mosasaurids evolved through time and space prior to the Cretaceous-Palaeogene (K/Pg) mass extinction. Our results suggest that the worldwide taxonomic turnover in mosasaurid community composition from Campanian to Maastrichtian is reflected by a notable increase in morphofunctional disparity on a global scale, but especially driven the North American record. Ecomorphospace occupation becomes more polarised during the late Maastrichtian, as the morphofunctional disparity of mosasaurids plateaus in the Southern Hemisphere and decreases in the Northern Hemisphere. We show that these changes are not associated with strong modifications in mosasaurid size, but rather with the functional capacities of their skulls, and that mosasaurid morphofunctional disparity was in decline in several provincial communities before the K-Pg mass extinction. Our study highlights region-specific patterns of disparity evolution, and the importance of assessing vertebrate extinctions both globally and regionally. Ecomorphological differentiation in mosasaurid communities, coupled with declines in other formerly abundant marine reptile groups, indicates widespread restructuring of higher trophic levels in marine food webs was well underway when the K-Pg mass extinction took place.

Keywords: Mosasauridae – morphometrics – provincialism – megapredator – ecomorphology – Cretaceous

44 **INTRODUCTION**

45 Marine ecosystems were dominated by reptiles during the entire Mesozoic (Motani 2002; Massare 1987;

46 Bardet 2012; Scheyer et al. 2014). Despite important turnovers at its base (Fischer et al. 2017; 2020), the Late

47 Cretaceous is no exception, as mosasaurid squamates rapidly diversified (Bardet et al. 2008; 2007; Polcyn et

48 al. 2014), achieving a cosmopolitan distribution prior to the Campanian (c.83.5 Mya) (Bardet et al. 2014;

49 Polcyn et al. 2014), and colonised several ecological guilds until their global extinction at the K/Pg boundary

50 mass extinction (66 Mya) (Martin et al. 2017). Prior to the Campanian, mosasaurid taxonomic richness saw a

51 steep increase (Polcyn et al. 2014), with speciation in the Western Interior Seaway (WIS) in central North

52 America triggering a diversification during the so-called 'Niobraran Age' (e.g. Kiernan 2002; Russell 1967).

53 High taxonomic richness persisted through the mid-Campanian (e.g. Driscoll et al. 2019), where an abrupt

54 taxonomic turnover is observed in central North American at the onset of the 'Navesinkan Age' (e.g. Russell

55 1993; Kiernan 2002). The abrupt shift observed in WIS mosasaurid community is mirrored in northern Europe

56 (Lindgren 2004), Japan (Tanimoto 2005; Sato et al. 2012), South America (Jiménez-Huidobro, Simões, and

57 Caldwell 2017), and to some extent in Oceania (Jiménez-Huidobro, Simões, and Caldwell 2017). Mosasaurids

58 seem to maintain a high diversity throughout the Maastrichtian, yet with varying assemblages (Cappetta et al.

59 2014). Despite abundant remains, it is unknown whether these changes in taxonomic composition resulted in

60 constriction of functional or ecomorphological variation of these top oceanic predators on provincial or global

61 scales leading up to the end-Cretaceous mass extinction.

62

63 For the first time, we explore global mosasaurid ecomorphological variation throughout the final chapter of

64 the Mesozoic (84–66 Mya) at both local and global scales, using a set of cranial and postcranial

65 measurements, including data from several tens of high-precision 3D models. Because of the strong

66 conservative forces governing mosasaurid bauplan evolution (e.g. hydrodynamic performance and phyletic

67 heritage; e.g. Stubbs and Benton 2016), we did not anticipate significant temporal changes in craniodental

68 morphofunctional disparity. Yet, we demonstrate polarisation of ecomorphospace occupation and significant

69 drops in mosasaur disparity just before the K/Pg mass extinction, most notably in the Northern Hemisphere.

70

MATERIAL AND METHODS

Taxonomic and Morphological Sampling

Skull and jaw material from 93 mosasaurid specimens were collected, representing 56 species and all subfamilies and tribes (Polcyn et al. 2014; Simões et al. 2017). The taxonomic composition of mosasaurid clades in this study follows the results of Simões et al. (2017); we consider halisaurines as basal mosasaurids, and treat Russellosaurina (including Tethysaurinae, Tylosaurinae, Plioplatecarpinae, and Yaguarasaurinae) and Mosasaurina (including Mosasaurinae) as monophyletic groups. Morphometric information was collected from two main sources: three-dimensional laser and structured light surface scans as well as photogrammetric models were the preferred methodology, supplemented with two-dimensional published images and first-hand photographs. Laser scanned specimens were digitised using a Creaform HandySCAN 300 handheld laser scanner at resolution 0.2–0.5mm; structured light scanning was performed using an Artec Eva handheld scanner, at resolution 0.5mm; photogrammed models were captured using a Nikon D3000 DSLR camera (burst mode with light-ring), with 3D models generated using Agisoft Metashape 1.6.3., scaled in MeshLab 2020.06 (Cignoni et al. 2008). All specimens are listed in Supplementary Information 1: Specimen List; 3D models will be provided in the open-source repository MorphoSource on peer-reviewed acceptance.

86

Linear Measurements and Functional Ratios

Twenty-four linear measurements were taken across the entire skull including dentition (Figure 1). Linear measurements on 3D scans were taken using the measurement tool in MeshLab 2020.06; measurements on 2D images were performed using the line measuring tool in ImageJ (Schneider, Rasband, and Eliceiri 2012). These measurements were then used to generate 16 functional ratios describing the craniodental architecture (Table 1). All these traits have clearly established functional importance or outcomes (Figure 1; for further details, see Supplementary Information 2: Functional Ratios). Examples include the ratio of mandibular lever arms (proxies for mechanical advantage, i.e. ratio of muscular input force to output force on prey items),

95   supratemporal fenestrae area (proxy for cross-sectional area of combined jaw adductor musculature), and

96   relative orbit size (amount of the skull dedicated to housing the eyeball).

97   A threshold of 40% trait completeness was applied to the sample, on each specimen; percentages of missing

98   data per species can be found in Supplementary Information 3: Species Coverage. A resultant craniodental

99   dataset with all 16 functional ratios was subjected to the 40% threshold. Following the threshold

100 computations, 18.2% of missing trait data was recorded, and the dataset included all 58 taxa studied. Trait

101 ratios were standardised using a z-transformation to assign all characters a mean of 0 and a variance of 1; data

102 which cleared the 40% completeness threshold were used to compute a Euclidean distance matrix for

103 ordination analyses and disparity calculation.

104

Ecomorphospaces

106 Ordination of trait data was visualised in two-dimensions in two ways: a principal coordinates analysis

107 (PCoA) and a non-metric multidimensional scaling approach (NMDS). PCoAs were performed using a

108 cailliez correction criterion to correct for negative eigenvalues (using ape v.5.3; Paradis, Claude, and

109 Strimmer 2004), and were preferred to principal components analysis (PCA) as PCoA allows missing values

110 in the Euclidean distance matrix. Comparisons between PCoA and non-metric multidimensional scaling

111 (NMDS) ordination demonstrated comparable patterns of ecomorphospace occupation. NMDS are used for

112 visualisation here as they pack more variation of the data into a two-dimensional graph. However, as NMDS

113 axes are not ideal to use as variables for disparity analyses because of their non-metric properties, all PCoA

114 axes were chosen for assessment of morphofunctional disparity in through time, within clades, and across

115 geographic regions. Comparative NMDS analyses were performed in 'vegan' v.2.5-6 (Oksanen et al. 2018);

116 graphical results from PCoA ecomorphospaces can be found in Supplementary Figure S1. Kernel 2D density

117 estimates were used to visualise density-based macroevolutionary landscapes, plotted onto NMDS

118 ecomorphospaces, following the methodology of Fischer et al. (2020). Moreover, mandible length (proxy for

119 body size) was used both in scaling datapoints to visually inspect the spread of large-sized mosasaurids, and

120 additionally to compare the spread of body sizes in mosasaurids through the Campanian-Maastrichtian.

121

Disparity

123   Morphofunctional disparity was calculated based on PCo axes. In addition, mosasaurid communities from

124   four geographically distinct regions were investigated: the Western Interior Seaway (WIS); Northern Tethys

125   Province (NTP); Southern Tethys Province (STP; Bardet 2012); and Weddellian Province (consisting of

126   South-East Oceania, the Antarctic peninsula and Patagonia; WP). Disparity was measured through time,

127   focusing on time bins bearing mosasaurid fossils during the latest Cretaceous: Early Campanian (83.60–77.85

128   Mya); Late Campanian (77.85–72.10 Mya); Early Maastrichtian (72.10–69.05 Mya); Late Maastrichtian

129   (69.05–65.50 Mya). The focus was made on these time periods as they encompassed the mosasaurid

130   taxonomic turnover in the mid-Campanian, and enabled the investigation of disparity in the lead up to the end-

131   Cretaceous mass extinction. Total disparity within mosasaurid clades and geographic regions during these

132   time periods was also calculated. Disparity analyses were performed in RStudio using the dispRity package

133   (v.1.5.0) (Guillerme 2018). The sum of variances (SoV) disparity metric was preferred, as it demonstrates

134   robusticity to sample size variation between time bins (Ciampaglio, Kemp, and McShea 2009). Alternative

135   disparity metrics (pairwise dissimilarity, PD; sum of ranges, SoR) were also tested to corroborate patterns

136   observed using SoV metric (Supplementary Table S1). Bootstrap iterations were set at 1000 repetitions;

137   additional bootstrapping procedures were performed to account for false positive results when testing for

138   significant differences (see Supplementary Table S1). Here, we adapt the terminology from population

139   ecology to assess disparity at the regional level (here termed 'α-disparity') and global level ('γ-disparity'). In

140   order to examine how mosasaurid ecomorphological disparity was differentiated across regional communities,

141   γ-disparity per time bin was divided by mean α-disparity across all provinces per time bin (following

142   population ecology methods e.g. Legendre 2008), creating 'ß-disparity'. Beta-disparity can be defined as a

143   measure of disparity differentiation; a high ß-disparity indicates a greater range of mean α-disparity values

144   within a specific time-bin, whereas low ß-disparity indicates more uniformity in mean α-disparity values,

145   suggesting less ecomorphological differentiation between disparities across communities. Mean bootstrap

146   estimates (1000 replications) were used as metrics for α- and γ-disparity calculations, and compared through

147   four time-bins (Early Campanian; Late Campanian; Early Maastrichtian; Late Maastrichtian). Changes in

148   disparity between subsequent time bins and between clades/geographic regions were tested for using non-

149   parametric Wilcoxon tests in the 'stats' package (v.4.0.3) (R Core Development Team 2008), with Bonferroni

150   corrections for multiple comparisons.

151

152   **RESULTS**

153   **Morphospace occupation**

154   We quantified mosasaurid craniodental disparity across the Campanian-Maastrichtian interval. Our aims were

155   to establish whether faunal transitions yielded changes in disparity in mosasaurids as well as whether global

156   and provincial mosasaurid disparity was in decline prior to the end-Cretaceous mass extinction. Most notably,

157   large 'megapredatory' taxa with cutting dentition, including almost all tylosaurines (Figure 2A; filled purple

158   squares), and the majority of large mosasaurines cluster in the ecomorphospace (Figure 2A). These results

159   suggest that overall skull functional morphology within these two (occasionally contemporaneous) clades of

160   megapredatory marine reptiles converged, despite numerous phylogenetic differences. A number of

161   brevirostrine mosasaurines occupy regions of positive NMDS axis 1, typified by relatively large

162   supratemporal fenestrae, deep jaws, blunt rostra and crushing dentition (e.g. *Globidens* spp.). The upper half

163   of ecomorphospace (positive values along NMDS axis 2) is occupied predominantly by primitive mosasaurids

164   (halisaurines, tethysaurines) and *Plioplatecarpus* spp., which all had large orbits, gracile skulls, and recurved,

165   piercing teeth (Figure 2A; see also Supplementary Figure S1); they constitute our 'grasping' cluster (Figure

166   2A & 2E).

167

168   The density of ecomorphospace occupation though time (Figure 2B-E) reveals a series of changes across the

169   Campanian-Maastrichtian interval. Many mosasaurines and russellosaurines occupy a large 'megapredatory'

170   region through the Early Campanian to the Early Maastrichtian. The majority of russellosaurines disappear

171   afterwards, strongly altering the pattern of ecomorphospace occupation (Figure 2E) by creating a clear divide

172   between two main clusters in the late Maastrichtian bin: the 'megapredatory' cluster, formed predominantly

173   by *Tylosaurus* and *Mosasaurus* and the 'grasping' cluster, formed by *Plioplatecarpus*, halisaurines, and the

174   Weddellian taxa *Taniwhasaurus oweni* and *Rikisaurus tehoensis*. In addition to this polarisation of mosasaurid

175   craniodental shape, a few taxa also evolved longirostrine (e.g. *Gavialimimus*) and brevirostrine (likely

176   durophagous; e.g. *Globidens* spp.) morphologies (Figures 2A-B). Our analyses of clade disparity add support

177   to the ecomorphospace signal, with decreases in tylosaurine, plioplatecarpine, and plotosaurin disparity

178   through the Maastrichtian (Supplementary Figure S2).

179

Evolution of skull size

181   Changes in mosasaurid communities also resulted in slight variation in skull size distributions (proxy for body

182   size) across the Campanian – Maastrichtian interval (Figure 2F). Early Campanian size distribution is notably

183   more uniform, with comparable densities of large and small mosasaurids (Figure 2F; blue line). By

184   comparison, density of smaller species is lower in the Late Maastrichtian, leading to a peak in mid-sized and

185   very large species (Figure 2F; yellow line). This pattern tracks the presence of multiple very large late

186   Maastrichtian tylosaurines and plotosaurins (a pattern mirrored in sharks; Cappetta et al. 2014), and highlights

187   the extinction of smaller species which were abundant during the Campanian (e.g. *Clidastes*,

188   *Plesioplatecarpus*) (Figure 2B-C). However, these differences are not significant, indicating that the changes

189   in ecomorphospace occupation and disparity we observe are not associated with strong changes in mosasaurid

190   size, but rather with the functional capacities of their skulls.

191

Spatiotemporal evolution of disparity

193   We find a significant increase in global (γ) ecomorphological disparity in mosasaurids (Figure 3A) coincident

194   with taxonomic turnovers known to have occurred at the mid-Campanian boundary (the 'Niobraran-

195   Navesinkan' transition; Lindgren 2004; Tanimoto 2005; Sato et al. 2012; Jiménez-Huidobro, Simões, and

196   Caldwell 2017; Kiernan 2002; Russell 1993). The observed increase in γ-disparity is common across all

197   disparity metrics we computed (sum of variances, sum of ranges, pairwise dissimilarity; Supplementary Table

198   S3). Our results demonstrate that γ-disparity of mosasaurid ecomorphologies increased from Early to Late

199   Campanian and continued increasing until the Early Maastrichtian, mirroring the expansion of the

200 craniodental ecomorphospace occupation (Figure 2B-D). Mosasaurid diversity (in this sample) somewhat

201 tracks fluctuations in disparity, but not to the same magnitude (Figure 3). By the Late Maastrichtian, γ-

202 disparity is higher than that recorded throughout the Campanian, despite fewer species being present in the

203 Late Maastrichtian (Figure 3A; Table 2).

204

205 While disparity increases on global (γ) and provincial (α) scales from the Campanian to the Maastrichtian

206 (Table 2), we observe significant declines in γ-disparity from early to late-Maastrichtian leading up to the K-

207 Pg mass extinction (Figure 3A-E). When examined at the provincial level (Figure 3B-E), the early–late

208 Maastrichtian transition records declines in α-disparity for all provinces (with the exception of STP; Table 2)

209 using almost all disparity metrics, reinforcing the global outlook of a significant decline in ecomorphological

210 disparity in mosasaurids in the latest Maastrichtian. This disparity decrease is found within all well-sampled

211 clades as well, no matter the disparity metric used, with the exception the pairwise dissimilarity metric which

212 slightly increased for the hyper-disparate group Globidensini through the Maastrichtian (Figure 2D-E). Sharp

213 decreases in tylosaurine and plioplatecarpine presence in the Western Interior Seaway contribute to the

214 decline in α-disparity in this region; by contrast, the presence of highly disparate globidensins in the Southern

215 Tethys Province contributes toward more stable overall γ-disparity during the Maastrichtian (Figure 3A &

216 3D). Differentiation of disparity across regions (i.e. β-disparity) increases from early to late Maastrichtian

217 (Table 2); this increase in β-disparity can be attributed to several factors: decreases in α-disparity in several

218 (but crucially, not all) observed provinces; reductions in taxon count (Figure 3B-E); decreased occupancy of

219 previously commonly exploited niches (e.g. reduction of 'megapredators'; Figure 2E); and increased

220 endemism (e.g. Moroccan fauna of the STP; Strong et al. 2020; Lingham-Soliar 2002; Leblanc, Mohr, and

221 Caldwell 2019; Longrich, Bardet, Khaldoune, et al. 2021; Longrich, Bardet, Schulp, et al. 2021).

222

223 **DISCUSSION**

224 **The necessity for regional and global assessments of pre-extinction diversity and disparity**

225   The influence of localised faunal assemblages in the fossil record is well known to affect global patterns

226   diversity and disparity (i.e. Close et al. 2019; Upchurch et al. 2011; Condamine et al. 2021; etc.). For many

227   groups of large tetrapods, the global fossil record is not well resolved, whereas regional sampling in certain

228   geographic areas is strong, and consequent global biodiversity/disparity estimates can be heavily reliant on

229   those few regions (e.g. Brusatte et al. 2012; Sax and Gaines 2003; Benson et al. 2010; Cleary et al. 2015; etc.).

230   In many studies, including ours, it is clear that the sampling effort in North America over the past 150 years is

231   an important factor in estimating pre-Maastrichtian tetrapod diversity and disparity (e.g. Maidment et al. 2021;

232   Vavrek and Larsson 2010; Longrich, Scriberas, and Wills 2016). Regional diversity patterns are thus likely to

233   contain an important signal, as the highly-fragmented world of the Mesozoic and Cenozoic likely resulted in

234   ecosystems with distinct compositions and physico-chemical parameters (Zaffos, Finnegan, and Peters 2017).

235   This reality has often been overlooked when analysing tetrapod diversity and disparity patterns leading up to

236   and across the K/Pg mass extinction. Indeed, a series of studies on the extinction of non-avian dinosaurs have

237   recovered conflicting results (Brusatte et al. 2012; Condamine et al. 2021; Maidment et al. 2021; Dean,

238   Chiarenza, and Maidment 2020; Chiarenza et al. 2019; Vavrek and Larsson 2010), notably because of their

239   varying treatment of regional differences and their sampling.

240

241   Even though the fossil record of mosasaurids appears only weakly biased (Driscoll et al. 2019), and marine

242   reptile sampling indicators are generally excellent for the Campanian-Maastrichtian interval (Fischer et al.

243   2016), our results clearly indicate regional variations in the ecomorphological disparity patterns of

244   mosasaurids. The drivers of these differences should not necessarily be regarded as global; a telling example

245   are the provincial disparity patterns during the Maastrichtian (Figure 3B-E), which may be associated with the

246   magnitude of the environmental changes resulting from the sea level regressions. Indeed, the epicontinental

247   WIS greatly changed in extent and shape during the Maastrichtian (Berry 2017; Slattery et al. 2013), and this

248   region records the steepest decrease in α-disparity, while deeper basins such as Northern and Southern Tethys

249   Provinces were seemingly less affected (Bardet et al. 2014; Hornung, Reich, and Frerichs 2018; Lindgren

250   2004; Bardet 2012). In this context, focussing on the abundant North American record to reconstruct the

251   global diversity or disparity patterns of mosasaurids would result in a steeper late Maastrichtian decrease than

252   that which was computed for other regions, hence confounding regional and global factors at play prior to the

253   K/Pg mass extinction.

254

255   **Pre-K/Pg mosasaurid turnovers and crises**

256   The 'Niobraran-Navesinkan' (Early to Late Campanian) taxonomic transition from russellosaurine-to-

257   mosasaurine-dominated communities was initially identified in the Western Interior Seaway (WIS) (e.g.

258   Russell 1993), with similar turnovers identified in multiple other regions across the globe (Lindgren 2004;

259   Tanimoto 2005; Sato et al. 2012; Jiménez-Huidobro, Simões, and Caldwell 2017). We show that, far from

260   experiencing a global γ-disparity decline during this turnover, mosasaurids significantly increased in disparity

261   across this transition. However, this is in no small part due to the extinction of more 'generalist' and small-

262   sized plioplatecarpines and tylosaurines (Figure 3A). These extinctions in the WIS reduced the density of

263   'megapredatory' and 'generalist' ecomorphologies in the Late Campanian bin (Figure 2B-C), causing

264   increased polarisation of the remaining ecomorphologies exhibited by mosasaurid taxa. The removal of

265   common morphologies from a sample can impact disparity as much as the inclusion of highly disparate forms;

266   this is the case for a series of disparity metrics (but obviously not the sum of ranges). We observe this pattern

267   for mosasaurid γ-disparity through the Campanian (Figure 2B-C; Figure 3A). Actually, the increase in

268   morphofunctional disparity at the 'Niobraran-Navesinkan' transition is a phenomenon local to the Western

269   Interior Seaway, with a high enough amplitude to influence global patterns; other regions maintain stable

270   morphofunctional disparity through this interval (Figure 3; Table 2). The cause behind the abrupt shift in

271   mosasaurid community composition across the 'Niobraran-Navesinkan' is as yet unclear. A decrease in

272   oceanic temperature between the mid- and late-Campanian is coincident with the turnover (Polcyn et al. 2014;

273   Linnert et al. 2016), which essentially removed smaller species within multiple clades (e.g. *Selmasaurus*,

274   *Plesioplatecarpus*, *Tylosaurus kansasensis*). This seemingly selective extinction suggests that body size was

275   an important factor in lineage survival across this local event (Figure 2B-C and 2F). By contrast, mosasaurid

276   assemblages from the Campanian elsewhere do not suggest clear reductions in smaller species at the mid-

277   Campanian boundary (Lindgren 2004; Jagt 2005), nor do they exhibit a radical shift in α-disparity (Table 2).

278

279 Later, a decrease in global γ-disparity and α-disparity is found within the Maastrichtian, in nearly all regions

280 and across all clades. When the differentiation of ecomorphological disparity between geographical regions is

281 considered (i.e. β-disparity; Table 2), it is clear that the Late Maastrichtian was a time of increased

282 regionalisation of mosasaurid disparity, rather than a consistent global decline. Communities of mosasaurids

283 in the WIS, NTP and WP are shown to be notably more homogeneous in the Late Maastrichtian than those of

284 the Early Maastrichtian (Figure 3B-E), with the WIS and WP communities represented by very few taxa

285 within only two tribes (Plotosaurini+Globidensini, and Plotoaurini+Tylosaurini respectively). By contrast, the

286 Late Maastrichtian mosasaurid community of the STP was comprised of a ecomorphologically diverse

287 assemblage of globidensins (e.g. *Globidens*), plotosaurins (*Mosasaurus* spp.), halisaurines (e.g. *Pluridens*),

288 and plioplatecarpines (e.g. *Gavialimimus*) (Strong et al. 2020; Leblanc, Caldwell, and Bardet 2012; Bardet et

289 al. 2004; Longrich, Bardet, Schulp, et al. 2021), yielding a high α-disparity in this region (Figure 3D). The

290 retention of disparate ecomorphologies of STP mosasaurids through the Maastrichtian drives the spike in β-

291 disparity observed in the Late Maastrichtian (Table 2), representing a peak in provincial differentiation. The

292 predominantly bimodal landscape of mosasaurids in the late Maastrichtian (Figure 2E) suggests that, while a

293 variety of niches were still being occupied by low densities of disparate mosasaurids, numerous Northern and

294 Southern Tethys mosasaurids exhibited 'megapredatory' or 'grasping' functional adaptations (Figure 2; also

295 Bardet 2012; Lindgren 2004; Bardet et al. 2014). Becoming increasingly apparent is the importance of the

296 Southern Tethys Province (including Afro-Arabia, Morocco, Niger-Nigeria, Angola and eastern Brazil) in

297 estimating late-Maastrichtian marine reptile diversity and disparity (e.g. Strong et al. 2020; Leblanc, Mohr,

298 and Caldwell 2019; Longrich, Bardet, Schulp, et al. 2021; Longrich, Bardet, Khaldoune, et al. 2021).

299 Understanding patterns such as these are vital for the accurate interpretation of faunal dynamics and functional

300 variation before and after extinction events. If only γ-disparity of mosasaurids were considered, then this

301 group could be interpreted as being in decline prior to their ultimate demise at the K/Pg boundary. However, it

302 is apparent that when both α- and β-disparities are taken into account, some regional communities were most

303 certainly declining in taxonomic diversity and ecomorphological disparity, whereas others were only

304 minimally affected on both counts.

305

How selective are the pre-K/Pg extinctions in marine reptiles?

307 The Early Maastrichtian is identified here as the time of greatest γ-disparity of mosasaurids (Figure 3A), with

308 expansion of ecomorphospace occupation by longirostrine and brevirostrine ecomorphologies, in addition to

309 an increase in halisaurine and plioplatecarpine species occupying new regions of ecomorphospace in the

310 'grasping' cluster (Figure 2A+D). This Early Maastrichtian rise in disparity appears to be driven by multiple

311 originations in the two Tethys Provinces (North and South). With regards to other marine reptile fauna,

312 ichthyosaurians and pliosaurids were long gone by the Late Maastrichtian (Schumacher 2011; Fischer et al.

313 2016; Bardet 1994), and the predominant marine reptiles in the Campanian-Maastrichtian were restricted to

314 xenopsarian plesiosaurians, mosasaurids, chelonioids, and crocodylians (e.g. Bardet et al. 2014). These clades

315 do not seem to follow a disparity pattern similar to that recovered here for mosasaurids. For example,

316 polycotylid plesiosaurians were already in decline in both phylogenetic diversity and ecomorphological

317 disparity during the Campanian-Maastrichtian interval (Fischer et al. 2018), with only the polycotyline

318 *Dolichorhynchops herschelensis* and the occultonectian *Sulcusuchus erraini* potentially being present during

319 the Maastrichtian (in addition to a handful of indeterminate remains; Sato 2005; Kaddumi 2006; O'gorman

320 and Gasparini 2013; Fischer et al. 2018). Robust evaluations of elasmosaurid disparity are still lacking, but the

321 range of phenotypes (either in terms of phylogenetic diversity, osteology or relative neck length) appears to

322 still be broad during the Maastrichtian, although within-Maastrichtian changes have not yet been computed

323 (Fischer et al. 2021). Similarly, within-Maastrichtian disparity dynamics have not been explored for marine

324 testudines, although previous assessments of testudines indicate a peak in cranial morphological variation in

325 the Maastrichtian (Foth and Joyce 2016; Foth, Ascarrunz, and Joyce 2017), and a consistent contribution to

326 the diversity of feeding morphologies across marine reptiles from Campanian to Maastrichtian (Stubbs and

327 Benton 2016). By contrast, aquatic crocodyliformes exhibit comparatively low disparity in the latest

328 Cretaceous. Dramatic declines in marine crocodyliform morphological disparity are known to have occurred

329 from Jurassic to Cretaceous, which potentially left niches open for mosasaurids to exploit during their own

330 radiation in the Cenomanian (Stubbs et al. 2013; Stubbs and Benton 2016). Subsequently, crocodyliform

331 morphological disparity was in decline throughout the late Cretaceous (Wilberg 2017; Stubbs et al. 2021); the

332 exception to this pattern were the aquatic dyrosaurid tethysuchians, which exhibited a rapid burst of

333 morphological evolution in the Maastrichtian (Stubbs et al. 2021), coinciding with increased regionalisation of

334 mosasaurid ecomorphological disparity revealed in this study. The increased endemism and expansion into

335 'grasping' and 'longirostrine' ecomorphologies by mosasaurids in the Late Maastrichtian combines with

336 isotopic analyses of trophic structure in the Maastrichtian of the Southern Tethys Province (Martin et al.

337 2017), suggesting increased dietary specialisation, as multiple predators coexisted and often fed upon prey

338 from a single trophic level . Patterns of taxonomic diversity and ecomorphological disparity across multiple

339 marine reptile groups indicate that wholesale (and in some cases fragile) restructuring of marine trophic webs

340 was underway before the K-Pg mass extinction event.

341

351

Author Contributions

353 JAM and VF conceived the study. JAM, RFB, and VF collected raw data. JAM and VF conducted statistical

354 analyses and designed figures. JAM, NB, and VF wrote the manuscript. All authors contributed to the final

355 manuscript.

356

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581

582 **Tables**

583 **Table 1.** Functional traits derived from linear measurements of mosasaurid skulls and jaws. Definitions,

584 calculations and diagrammatic representations for each trait can be found in the Supplementary Information 3:

585 Functional Ratios. % cov. = percentage of specimens represented by each trait. Percentages in italics fall

586 outside the completeness threshold of 40%.

Character	Function	% cov.
jaw depressor lever arm ratio	proxy for jaw opening mechanical advantage	77.2
jaw adductor lever arm ratio	proxy for jaw closing mechanical advantage	73.7
functional toothrow	defines proportion of jaw used for prey capture/processing	89.5
jaw robusticity	proxy for jaw bending resistance	85.9
supratemporal fenestra area	cross-sectional area of jaw adductor muscles	77.2
longirostry	defines hydrodynamic potential of pre-orbital snout	87.7
gullet size	proxy for volume of water expulsion, prey size etc.	80.7
tooth crown shape	proxy for tooth narrowing; hard vs. soft food items	96.5
tooth blade shape	describes dental compression; conical vs. blade-like teeth	61.4
tooth crown curvature	describes dental recurvature	96.5
nares position	proxy for ease of inhalation during steady-state swimming	78.9
relative orbit size	defines importance of vision for taxon	75.4
pupil size (sclerotic ring diameter)	defines amount of light able to enter the pupil	*15.8*
tympanic resonator area	proxy for area of quadrate available as resonator	73.7
premaxillary elongation	proxy for area available for anterior pressure sensation	75.4
parietal foremen	proxy for relative size of pineal eye	70.2

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589 **Table 2**. Mosasaurid population disparity (alpha, gamma and beta) from Early Campanian to Late

590 Maastrichtian. Sum of variances metric used. Highest mean disparity values highlighted in bold. WIS =

591 Western Interior Seaway; NTP = Northern Tethys Province; STP = Southern Tethys Province; WP =

592 Weddellian Province.

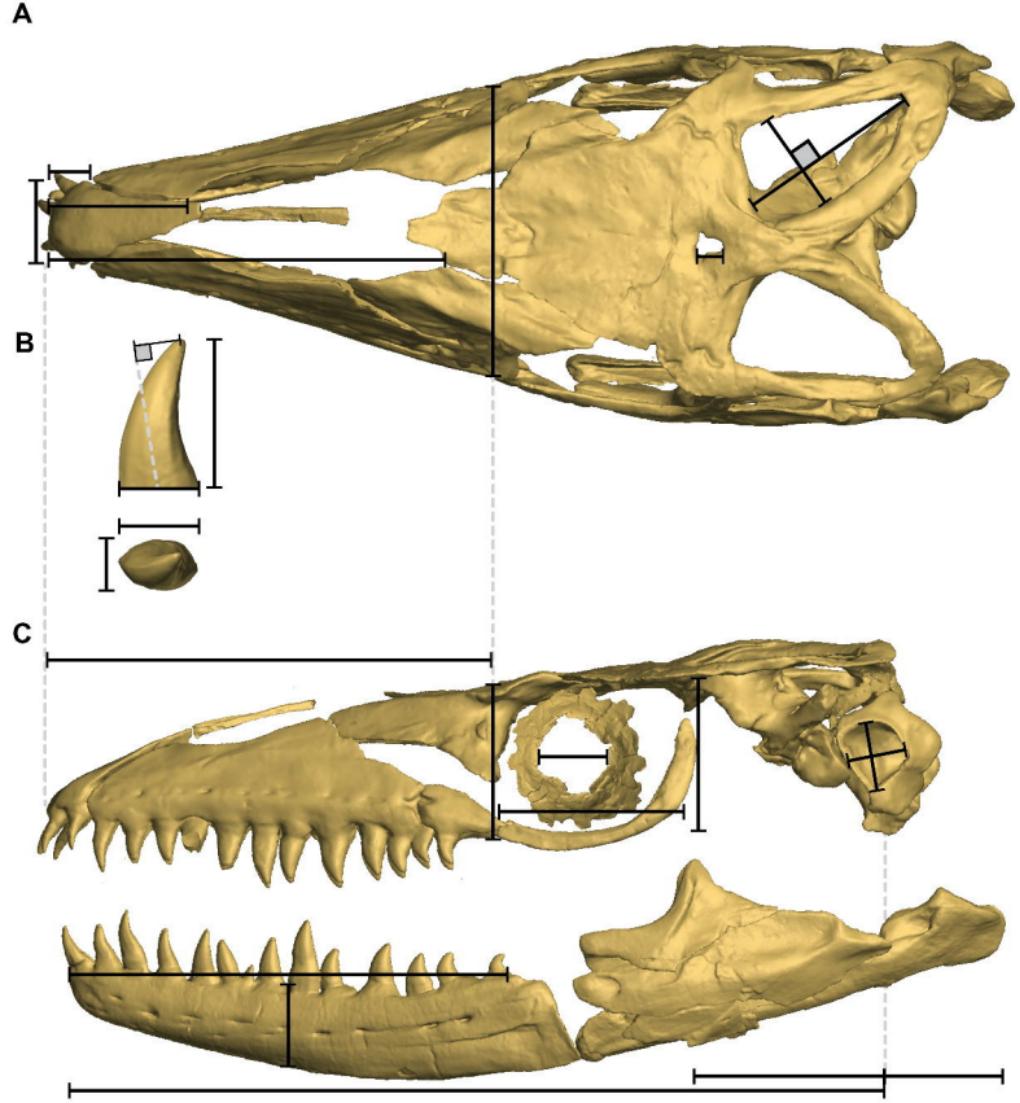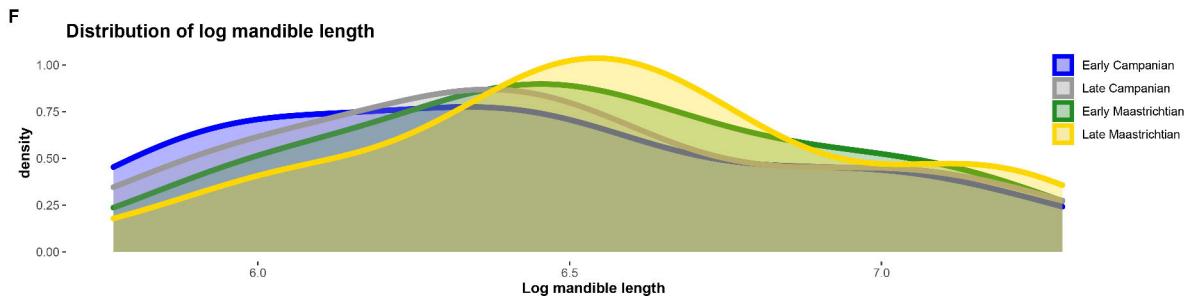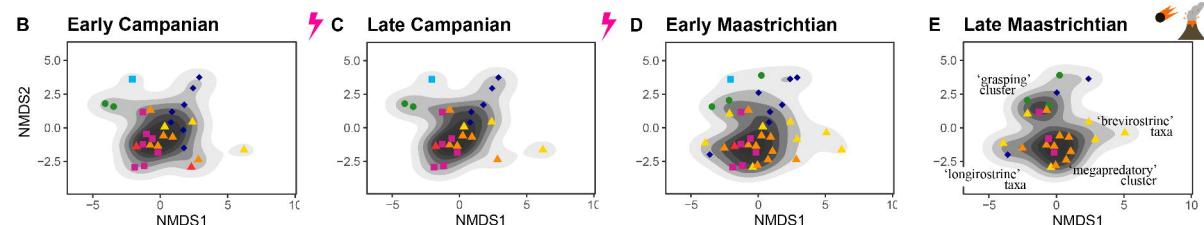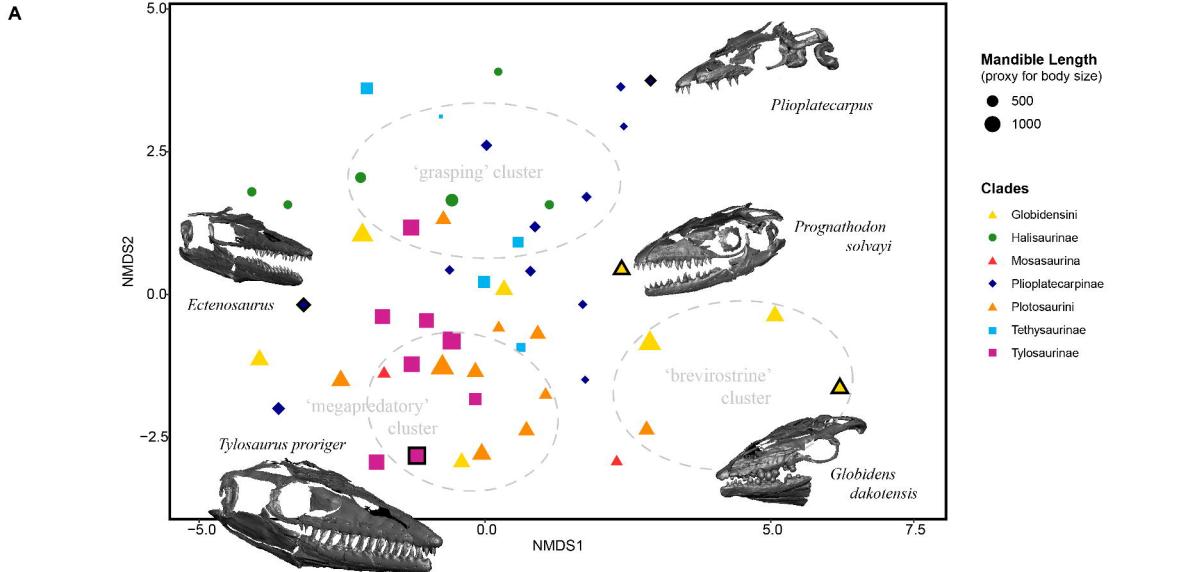| Disparity		Early Campanian	Late Campanian	Early Maastrichtian	Late Maastrichtian
gamma (γ)		18.90	19.30	**21.19**	20.12
	Mean	15.94	16.17	**19.26**	14.63
	WIS	*18.43*	***19.57***	*18.52*	*9.76*
alpha (α)	NTP	*22.03*	*21.60*	***23.35***	*17.50*
	STP	*10.22*	*10.44*	***22.04***	*21.51*
	WP	*13.07*	*13.06*	***13.13***	*9.75*
beta (β)		1.186	1.194	1.100	**1.375**

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Figure Legends

Figure 1. Linear measurements of the mosasaurid skull used for quantitative trait comparisons and disparity analyses. Measurements on the skull and exemplar dentition are shown: **(A)** skull in dorsal aspect, **(B)** dentition in lateral and occlusal aspect, (C) skull in left lateral aspect. Filled squares denote measurements taken perpendicular to one another or to the edge of a bone. Black lines describe measurements used for trait quantification; dotted grey lines are used to clarify where specific measurements are recorded from and to. Functional traits and their ecomorphological importance are presented in Table 1. Models based on IRSNB R33b *Prognathodon solvayi*.
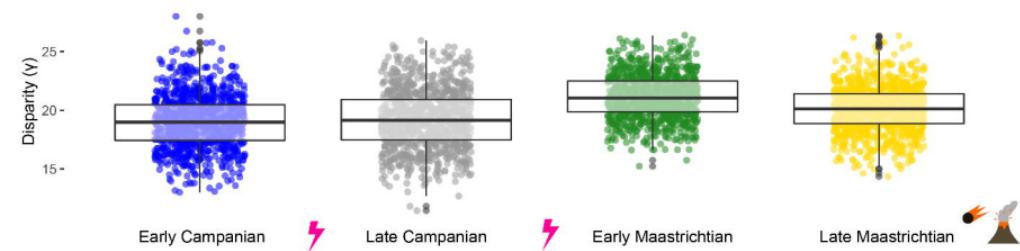
Figure 2. Functional ecomorphospace and size distribution in mosasaurids. Functional ecomorphospace occupation (based on NMDS axes) by all mosasaurids in the sample (**A**) with ecomorphological clusters and representative 3D models of skulls. Data points outlined in bold represent the placement of exemplar skulls; data point size represents relative skull size (based on mandible length). Functional ecomorphospace for each time bin through the Campanian-Maastrichtian (**B-E**) demonstrating changes in density and isolation of ecomorphological clusters in Late Maastrichtian (**E**). Size distribution of mosasaurids through the Campanian-Maastrichtian (**F**) demonstrating shifts in the density of small and mid-sized mosasaurids from Early Campanian (ECam) to Late Maastricthian (LMaa).

Figure 3. Global and provincial mosasaurid craniodental disparity through time. Global (γ) craniodental disparity of mosasaurids from Early Campanian to Late Maastrichtian (**A**) presented alongside raw sample diversity and provincial (α) disparity for the Maastrichtian of the Western Interior Seaway (**B**), Northern (**C**) and Southern (**D**) Tethys Provinces, and Weddellian Province (**E**). Approximate extent of provincial regions projected onto palaeomap, estimated for mid-Maastrichtian (72 Ma). Disparity estimates were generated using the sum of variances (SoV) metric; significant differences were recovered between all sequential time bins for both global and provincial datasets using pairwise Wilcoxon testing (see also Supplementary Table S1 & S3). Palaeomap provided by CR Schotese (PALEOMAP atlas for ArcGIS) (Scotese 2014).

A
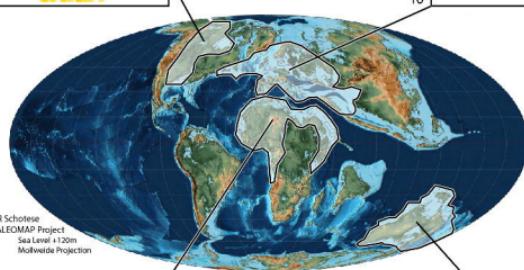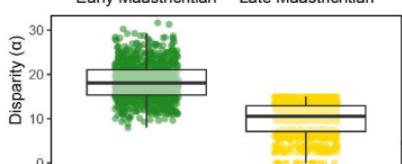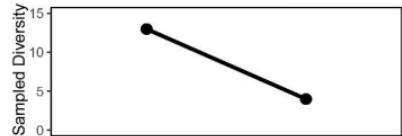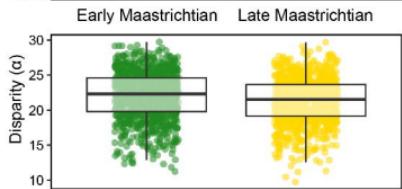
'grasping' cluster

Plioplatecarpus

Prognathodon solvayi

Ectenosaurus

'brevirostrine' cluster

'megapredatory' cluster

Tylosaurus proriger

Globidens dakotensis

Mandible Length
(proxy for body size)
● 500
● 1000

Clades
▲ Globidensini
● Halisaurinae
▲ Mosasaurina
◆ Plioplatecarpinae
▲ Plotosaurini
■ Tethysaurinae
■ Tylosaurinae

B Early Campanian

C Late Campanian

D Early Maastrichtian

E Late Maastrichtian

'grasping' cluster

'brevirostrine' taxa

'longirostrine' taxa

'megapredatory' cluster

F Distribution of log mandible length

■ Early Campanian
■ Late Campanian
■ Early Maastrichtian
■ Late Maastrichtian

A Global Mosasaurid Disparity

Early Campanian — Late Campanian — Early Maastrichtian — Late Maastrichtian

B Western Interior Seaway

C Northern Tethys Province

D Southern Tethys Province

E Weddellian Province

CR Schotese
PALEOMAP Project
Sea Level +120m
Mollweide Projection