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THE MOSASAUR FOSSIL RECORD THROUGH THE LENS OF FOSSIL COMPLETENESS

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Abstract. The quality of the fossil record affects our understanding of macroevolutionary patterns. Palaeodiversity is filtered through geological and human processes, and efforts to correct for these biases are part of a debate concerning the role of sampling proxies and standardisation in models of biodiversity. Here, we analyse the fossil record of mosasaurs in terms of fossil completeness as a measure of fossil quality, using three novel metrics of fossil completeness with a compilation of 4,083 specimens. All metrics correlate with each other. A new qualitative measure of character completeness (QCM), correlates with the phylogenetic character completeness metric. Mean completeness by species decreases with specimen count, and average completeness by substage varies significantly. Mean specimen completeness is higher for species-named fossils than those identified to genus and family. The effect of tooth-only specimens is analysed. Importantly, we find that completeness of species does not correlate with completeness of specimens. Completeness varies by palaeogeography, North American specimens showing higher completeness than those from Eurasia and Gondwana. These metrics can be used to identify exceptional preservation, with specimen completeness varying significantly by both formation and lithology. The Belgian Ciply Formation displays the highest completeness, and clay lithologies show higher completeness values than others. Neither species diversity nor sea level correlates significantly with fossil completeness. A GLS analysis using multiple variables agrees with this result. However, GLS shows that two variables have significant predictive value for modelling averaged diversity, namely sea level and mosasaur- and plesiosaur-bearing formations, the latter of which is redundant with diversity. Mosasaur completeness is not driven by sea level, nor does completeness limit the mosasaur diversity signal.

Key words: marine reptiles, mosasaur, fossil record quality, fossil completeness, sea level, palaeodiversity.

MOSASAURIDAE was a relatively short-lived, but diverse and abundant clade of marine squamates that radiated in Late Cretaceous epicontinental seas and died out at the K/Pg boundary (Debraga & Carroll 1993). The rise of mosasaurids (called 'mosasaurs' throughout the paper) followed dramatic changes in the marine reptile fauna (Stubbs & Benton 2016), including decreases in disparity of plesiosaurs in the Late Jurassic (Benson & Druckenmiller 2014) as well as the extinction of cryptoclidid plesiosaurs, ichthyosaurs (Bardet 1994, Fisher *et al.* 2012) and thalattosuchian crocodiles (Young *et al.* 2010) in the Early to mid-Cretaceous. Mosasauroids (aigialosaurids and dolichosaurids) arose in the Cenomanian as relatively small swimming reptiles, followed by true mosasaurs in the Turonian (Bardet *et al.* 2008). As in other groups of marine reptiles (Massare 1994), the Mosasauridae showed increasing adaptations to the marine environment through time (Motani 2009). The average body size of mosasaurs increased through the Late Cretaceous, from 1–2 m in early semi-terrestrial forms, to a gigantic 14–17 m in later forms (Polcyn *et al.* 2014; Stubbs & Benton 2016). They became increasingly efficient swimmers and filled niches vacated by some of the aforementioned pelagic marine predators after their extinction (Motani 2005; Lindgren *et al.* 2007, 2009, 2011, 2013; Houssaye *et al.* 2013). Mosasaurs thrived in many marine environments (Kiernan 2002), from rocky shores to pelagic shelves, including fresh water environments (Holmes *et al.* 1999), and by the latest Cretaceous, they were the apex predators in many complex ocean ecosystems (Sørensen *et al.* 2013). Accordingly, mosasaur fossils have a widespread stratigraphic and global geographic distribution in a variety of lithologically distinct Upper Cretaceous marine formations (Russell 1967).

Marine reptiles have figured in several studies that have contributed to the debate about how to address biases in the fossil record (*e.g.* Benson *et al.* 2010; Benson & Butler 2011; Cleary *et al.* 2015; Tutin and Butler 2017). Does the fossil record provide a reasonable picture of mosasaur evolution (Polcyn *et al.* 2014), or is the record substantially biased by the idiosyncrasies of preservation and collection (Benson *et al.* 2010; Benson & Butler 2011)? Benson *et al.* (2010) identified serious megabiases affecting all Cretaceous marine reptiles, including mosasaurs, and argued that their palaeodiversity signal was dependent on geological sampling biases, meaning that the raw data said little about their true diversity. Part of this result depended on residual diversity estimates using a method that has since been severely criticised (Dunhill *et al.* 2014, 2018; Brocklehurst 2015; Sakamoto *et al.* 2017). Re-analysis led Benson and Butler (2011) to identify that shallow marine tetrapods at least, including most mosasaurs, showed close correlation between diversity and sea level and continental area. Benson and Butler (2011) interpreted this as a 'common cause' effect (Peters 2005), analogous to a species-area effect; the fossil record and palaeodiversity of marine reptiles fluctuated simultaneously as sea level rose and fell. These alternate viewpoints leave an open question: is the mosasaur fossil record a fair representation of their true biological signal or not?

One approach to understanding inadequacies of the fossil record is to consider the specimens themselves – are they equally complete through all times and places, or do they show variation (Benton *et al.* 2004; Smith 2007)? For example, Mannion & Upchurch (2010) suggested that measures of fossil completeness could be used alongside other sampling proxies to investigate the quality of the fossil record. Fossil completeness studies attempt to quantify the quality of fossil specimens by assigning numerical metrics that reflect the percentage of skeletal or phylogenetic character elements present in individual fossils or whole groups of fossils.

Many recent analyses have used measures of fossil completeness. In taphonomic studies, completeness can reflect post-mortem conditions and transport (Beardmore 2012a, b). Aquatic vs. terrestrial deposits may preserve differently (Verriere *et al.* 2016) and, more broadly, completeness may be related to lithology (Cleary *et al.* 2015). Completeness may be related to body size; large fossils may be collected more often (Brown *et al.* 2013), or small associated fossils may be preserved better at times (Brocklehurst *et al.* 2012). Completeness may be affected by sea level (Mannion & Upchurch 2010; Cleary *et al.* 2015; Tutin & Butler 2017). Completeness can be used to measure collecting and naming biases through historical time (Benton 2008a, b; Mannion & Upchurch 2010; Walther & Fröbisch 2013; Tutin & Butler 2017) or as a direct metric to assess confidence in fossil record data in a single basin through a key event (Benton *et al.* 2004). Finally, the fossil record of diversity may be unbiased, or biased by completeness, either inversely (Brocklehurst & Fröbisch 2014; Smith 2007) or directly (Dean *et al.* 2016).

In this study, we explore a database of over 4000 mosasaur specimens and apply novel methods of coding fossil completeness, to test whether fossil completeness is biasing the measured richness of these organisms. We find that specimen completeness varies enormously geographically, but is not correlated with species diversity or sea level. We find that completeness does not limit the diversity signal in the mosasaur record.

MATERIALS AND METHODS

Data

Specimens. A mosasaur specimen database (Driscoll *et al.* 2018, Data A, Data B) includes all scored specimens of Mosasauridae from collection visits and literature descriptions, comprising 4083 mosasaur specimens. Mosasaur material is housed in at least 112 institutions (Driscoll *et al.* 2018, Appendix Table S1), and 448 specimens were seen first-hand in these collections (Driscoll *et al.* 2018, Appendix Table S2), including many referred, cited and holotype specimens. Examination confirmed their description in the literature, even if some of the elements showed abrasion or minor disintegration. In a few cases, elements originally described with the specimen were not found on visiting the museums, and this was noted in assessing skeletal completeness. Most specimens were identifiable, and scorings of the holotype in the literature and observed first hand were identical, providing confidence that measurements taken from the literature can be accurate. Catalogue descriptions as well as photos from museum online collections databases (AMNH, GPIT, MCZ, SDMNH, TMP, UAVPL, UCMP, USNM, UVER and YPM) were also used, and files containing museum databases were obtained from LACM, FMNH, ALNHM and TMP.

Additional specimen data was obtained from publications and monographs, including original descriptions of holotypes (Driscoll *et al.* 2018, Appendix Table S3), as well as secondary descriptions of non-type materials (e.g. Lydekker 1888; Camp 1942; Russell 1967; Schultze et al. 1985; Kuypers *et al.* 1998; Bardet 2012; and others listed in Driscoll *et al.* 2018, Appendix Table S7). No publicly inaccessible or undocumented material was used in the study. In total, over 4300 specimens were identified for study, but some were excluded because of poor morphological data or lack of illustration.

In this study, we used different subsets of the specimen lists. In many cases, we considered all 4083 specimens. In other cases, we considered just those specimens that could be assigned to named species, and excluded those that were assigned to genus alone (e.g. *Mosasaurus* sp.) or to an even more general taxon (e.g. Mosasauridae indet.). 1044 specimens were attributed to Mosasauridae indeterminate (i.e. family level), 731 specimens were identified to generic level, and 2304 to species level. In the specimen list (Driscoll *et al.* 2018, Data B), the specimens 1–843 and 1878–4073 are assigned to a named genus or named genus and species, and specimens 843–1887 are termed simply 'Mosasauridae indet.' Specimens 2416– 2544, for example are '*Mosasaurus* sp.' More than 1400 of the 4083 specimens consist only of isolated teeth, and these were included and excluded in different analyses.

Stratigraphic ranges. The stratigraphic positions of many historical mosasaur specimens are unknown. In some formations in which mosasaurs commonly occur, the stratigraphy and age have been revised (e.g. Everhart 2001; Jagt 2005), and the revised date was used for allocation to time bins. Mosasaurs generally occur in marine rocks, and often in close association with zone fossils such as belemnites, ammonites or foraminifera, so enabling correlation with short-term time zones that can be tied to radioisotopic ages in the standard marine time scale. We compiled a list of 135 mosasaur-bearing formations from the specimen search and cross-checked the age and stratigraphy of formations with the stratigraphic literature (Driscoll *et al.* 2018, H). Many formation ages were already accurately represented in the primary literature.

The specimens were datable to different degrees of precision. 1726 mosasaur specimens were datable to substage, and 2357 specimens were dated at best to two or more substages. Because of the large amount of data, there were no substage time bins that did not contain precisely assignable specimens.

Species list. A list of valid species was assembled based on the primary scientific literature (listed in Appendix in this manuscript), paying special attention to apomorphy-based descriptions. Only species with clear taxonomic assignment and little disagreement on taxonomy were used in this study. Our species list includes 74 valid species, and it agrees broadly with a recent, independent compilation (Polcyn *et al.* 2014).

Specimen completeness metrics

Background. One of the most exact methods for scoring skeletal completeness in vertebrates is to count the number of elements present compared to the total number of bones in the skeleton. This has been done in some taphonomic studies, including *Archaeopteryx* (Kemp and Unwin 1997), a Triassic prolacertiform (Casey *et al.* 2007), and a Miocene salamander (McNamara *et al.* 2012). However, this method is time-consuming and impractical when many specimens are compared.

Other quantitative methods have been developed for dealing with larger sample sizes. Mannion & Upchurch (2010) presented two approaches to measure fossil completeness in sauropods, a Skeletal Completeness Metric (SCM) that records the proportional completeness of skeletons against a roster of elements that ought to be present, and a Character Completeness Metric (CCM) that reports the number of phylogenetically informative characters that are reported for each taxon. They suggested that SCM might be a more useful metric in taphonomic studies comparing preservation in different geographic zones or facies, etc., and CCM would be a better tool for comparing diversity patterns through time.

Both SCM and CCM were subdivided into three individual measures: the best specimen of a taxon, termed SCM1 or CCM1, the type specimen SCM_{ts} or CCM_{ts} and a composite specimen that includes all preserved elements of the taxon from any number of specimens, termed SCM2 and CCM2. These scores can be averaged over all taxa in a time bin, or all taxa in a geological formation or geographic region, or for all representatives of a species or genus, whether they occur in a single time bin or not.

Another method, designed by Beardmore (2012a, b) for scoring fossil preservation in marine crocodylomorphs, compared disarticulation and completeness, which are related to environmental and preservational factors that were present at the time of death and burial. The unmodified Beardmore index divides the skeleton into anatomical regions, giving each region equal weight. This method can be quantitative, scoring every element present, but also allows estimation of proportions of regions present; so this might be called a semi-quantitative scoring system.

Cleary *et al.* (2015) used SCM1 and SCM2 (modified for the laterally crushed nature of ichthyosaur fossils), but they also implemented a modified Beardmore skeletal completeness metric (BSCM) in an investigation of fossil completeness in ichthyosaurs. These authors also divided BCSM into best (BCSM1) and composite (BSCM2) specimen per species, and averaged these values over all species assigned to stage level time bins.

Qualitative approaches can also be used to score fossil quality. For example, Benton *et al.* (2004) and Benton (2008b) measured dinosaur specimen completeness using the ratio of incomplete material (isolated elements or collections of bones) to complete material, such as skulls or complete skeletons. This approach has been used successfully in several studies (Fountaine *et al.* 2005; Smith 2007). Metrics such as SCM and CCM are more accurate than qualitative scores (Brocklehurst *et al.* 2012), but qualitative metrics can be useful for comparisons of diverse taxa or large sample sizes.

Completeness metrics. We used three completeness metrics. The Taphonomic Completeness Metric (TCM) is based on Beardmore (2012a, b) and is a non-weighted method (Fig. 1). The mosasaur skeleton is divided into nine anatomical regions, namely the skull, limbs (two forelimbs and two hindlimbs), vertebral column (cervical, dorsal, caudal), and ribs, and each region is given an arbitrary maximum score of 4, giving a total possible TCM of 36.

The Qualitative Completeness Metric (QCM) is based on Benton's (Benton *et al.* 2004; Benton 2008a, b) qualitative description of dinosaur completeness and is weighted so that skulls and jaws are afforded a higher weight than post-cranial elements, which is in proportion to the distributions of characters used in phylogenetic analysis (e.g. Bell, 1993). QCM is presented here (Table 1) as an estimate of character completeness when it is not possible to examine every character present on individual elements. This is in accordance with some previous studies (albeit using CCM) where each anatomical element present was similarly assumed to contain all its characters (e.g. Brocklehurst *et al.* 2012). In contrast, other analyses (e.g. Dean *et al.* 2016) used only the number of characters that could be observed.

In general terms, QCM is like CCM. Regions with higher numbers of phylogenetic characters are given greater weight in both. The phylogenetic character list was derived from the character matrix of Bell (Bell 1997; Bell & Polcyn 2005). This cladistic data matrix was selected because it has more mosasaur characters than other matrices (e.g. LeBlanc *et al.* 2012). A table of anatomical elements and the number of their associated characters was compiled by anatomical region for a test subset of 26 specimens of representative species (Driscoll *et al.* 2018, Data D). For each of these specimens, the total score over all anatomical regions was compared to the QCM fossil completeness metric (Driscoll *et al.* 2018, Data E). This comparison tests the pre-weighted character total per specimen against an estimate of character completeness provided by the QCM. Although not necessary for the analysis, a weighted value of the character scores (assuming a maximum value of 9) for each specimen is listed also, for comparison to QCM.

The final scoring method, Informal Completeness Metric (ICM), allows the inclusion of specimens that are associated only with general descriptions such as “skull”, or “axial elements,” or “appendicular skeleton”. The total possible ICM score is set arbitrarily at 5, with any mention of a skull scoring three points and any mention of axial and appendicular parts scoring one point each (Driscoll *et al*. 2018, Appendix Table S4).

Of the 4083 mosasaur specimens, 375 could be scored for only one or two of the three metrics (TCM, QCM and ICM). We compared all three methods as measures of fossil completeness. The equivalence of TCM values using all specimens vs. those exactly datable to single substages was also tested. Completeness scores were assigned to all holotype specimens (TCMh, QCMh and ICMh) and the best specimens (TCMb, QCMb and ICMb) of each species. In addition, a composite score (TCMc, QCMc and ICMc) for each species was calculated (Driscoll *et al.* 2018, Data C, D, and E).

Mosasaur fossil completeness

Time Series. Mean completeness scores were compiled and divided into time bins equivalent to Upper Cretaceous stratigraphic substages (Gradstein *et al.* 2012). For both species- and genus-level specimens, sampled in-bin taxa were compiled at the substage level and diversity was calculated. The terms "richness" and "diversity" are considered equivalent in this paper. Mean sea level for each Upper Cretaceous substage was calculated from Miller *et al.* (2005).

We assessed mean completeness for all specimens (TCMall, QCMall, ICMall) and for those specimens identified to species level (TCMsp, QCMsp, ICMsp), so excluding material only identifiable to higher taxonomic levels. Since there were so many specimens consisting of teeth alone, we compared completeness values across the above two time series, both with and without specimens consisting of teeth alone.

The mean completeness of all specimens for each species (TCMtot) was averaged over the time bins where those species occur (TCMav, QCMav, ICMav). This time series was compared to those derived from all specimens (TCMall, QCMall, ICMall), and to specimens named to species level (TCMsp, QCMsp, ICMsp). This compared the utility of using average completeness values assigned to whole species (in many cases from various time bins) to those derived from sampled-in-bin specimens. For clarity, a description of all the completeness metrics described in this study is listed (Table 2). No best, holotype or composite specimen scores were used for any time series analysis.

Mosasaur species and generic diversities are calculated based on specimen occurrences only, in substage-level time bins, so we do not use first-to-last ranges or include any Lazarus taxa, in this part of the analysis. In addition, we included five mosasaur species that were only assignable imprecisely to a range of two or three time bins, so we present also an "averaged" species diversity curve that includes these taxa counted as fractions. For example, *Plotosaurus bennisoni* is dated to the uppermost Lower Maastrichtian and/or lowermost Upper Maastrichtian, so its diversity is counted as 0.5 in both substages. We present the exact species and genus diversity curves as well as the "averaged" species diversity curve, together with comparisons among all curves and with sea level and completeness. TCMsp, QCMsp and ICMsp were compared with species and generic diversity, but not to "averaged" diversity so as not to make spurious comparisons between time bins that do not contain equivalent specimens.

Predicting diversity and completeness. To more fully understand the relationship between diversity and completeness, we used a multiple regression technique to compare the relationships between explanatory variables. A substage-level sampling proxy for explaining diversity and completeness was created and tested using mosasaur- and plesiosaur-bearing formations (MPBFs). These formations (Driscoll *et al.* 2018, Data I) were drawn from our mosasaur database and Upper Cretaceous plesiosaur data from unpublished research. We used GLS to check the relationship between mean TCM, diversity, sea level, formations and age by modelling TCM and diversity as a function of the other variables (i.e. TCMsp ~ species diversity + sea level + MPBFs + age; and "averaged" diversity ~ TCMav + sea level + MPBFs + age). We provide the raw data used for this analysis (Driscoll *et al.* 2018, Appendix Tables S5A, S6B).

Determinants of fossil completeness. Mean completeness scores were compared across several classes of taxonomic, biological, palaeogeographical, and lithological variables. TCM (instead of QCM) was used as a measure of preservation as affected by taphonomy. For most of these categorical variables, the data were much richer for specimens labelled as species, so TCMsp was the completeness metric used. Mean TCM was compared between specimens allocated to a maximum taxonomic resolution of family, genus or species. Tests both included and excluded specimens consisting of only teeth.

Mean TCMsp was assessed across different lithologies by assigning mosasaur-bearing formations to the categories chalk, sandstone, limestone, or clay, based on the predominant rock type of each formation. The specific lithology of individual specimens was not used. Mean TCMsp values of a few well-known and prolific mosasaur-bearing formations were calculated and compared. Differences in mean TCMsp between palaeogeographical regions (i.e. Eurasia, Gondwana, North America) were also analysed.

Finally, estimated body size for sample species was compared to the species mean completeness using mosasaur length estimates taken from Polcyn *et al.* (2014). For this analysis, mosasaurs were divided into three informal size groups: small (1–4 m), medium (4.5–7.5 m) and large (8 m or longer) because we did not have good quality individual measurements for each taxon, and for those with large sample sizes, we would have to consider a range of body sizes.

Sampling. A few representative sampling metrics were compiled to test the relationship between palaeontological sampling effort and fossil completeness. The number of specimens per species was used as one measure of sampling because it could be related to collector effort or availability of samples. The number of Google Scholar "hits" was tested as a measure of scientific interest (we recorded these on 1st December, 2017). The number of years since first discovery (i.e. naming of a species) was used to test scientific effort over historical time. Sampling or study effort could be related to absolute body length (Polcyn *et al.* 2014; Driscoll *et al.* 2018, Data A), and this was also compared with other variables.

Sampling and/or completeness might be related to rock outcrop area. For North American formations, this information is available at Macrostrat.org. The maps for representative North American mosasaur-bearing formations were double-checked against actual specimen locations. The average TCMsp by formation was compared to the rock area of these formations and their mosasaur species diversity. The number of formations (n) necessary to be confident about our results using the lowest p value (0.35) and highest r_s (0.6) was calculated using the method of Bonett and Wright (2000). Their work showed that a value of $n = 4$ is the smallest sample size that is adequate at this level of confidence; we have a value of $n = 5$ for our data.

Statistical tests

Differences in specimen completeness among categorical data (i.e. taxonomic rank, body size, lithology, palaeogeography etc.) were assessed using Wilcoxon tests and Kruskal-Wallis tests. Relationships between numerical data and paired time series were assessed using Spearman rank correlation tests. The correlation between completeness values across specimens was double-checked using the Kendall Tau-b test, which corrects for ties in the ranks across the thousands of specimens included. Time series were detrended using generalised differencing prior to correlation tests (using the gen.diff function of Graeme Lloyd; http://www.graemetlloyd.com/methgd.html), and these were corrected for false discovery rate (FDR) using the method of Benjamini and Hochberg (1995). Time series of completeness metrics were correlated with mosasaur diversity, sea level, and the various sampling proxies, with the aim of determining whether specimen completeness has any bearing on mosasaur diversity, and whether specimen completeness is driven by external factors such as sea level or sampling intensity. All statistical analyses were performed in R (v.3.3.0).

Generalised least squares (GLS) is a multiple regression method for estimating the unknown parameters in a linear regression model, and it can be used when there is a certain degree of correlation between the residuals in a regression model. GLS has an advantage over pairwise tests of correlation as it allows multiple explanatory variables to be examined simultaneously and allows the addition or removal of additional variables to be assessed quantitatively. Variables tested included diversity, sea level, TCM, age and formations.

GLS models were fitted in R using the package nlme (Pinheiro *et al.* 2017). As there was evidence for heterogeneity in the spread of the residuals in some of the explanatory variables, we applied a number of variance structures to the data and tested for the best fitting model using the Akaike Information Criterion (AIC). The best fitting model for predicting diversity contains a power of the covariate variance structure applied to the age data and the best fitting model for predicting TCM contains a fixed variance structure applied to the age data. Models were also fitted with an auto-regressive model of order 1 (AR-1) correlation structure, which models the residual at time s as a function of the residual of time s-1 (Zuur et al. 2009). The models with the AR-1 structure were worse fits than the models without. This is because of the common increasing trend of diversity, formations and sea level through time. We therefore present both sets of models, with and without the autocorrelation structure applied to the age parameter. Model fitting was achieved by comparing the full models with models that drop each explanatory variable in turn and perform a likelihood ratio test. This informs whether the dropped term has a significant influence on the fit of the model (Zuur *et al.* 2009).

Institutional abbreviations. ALNHM, Alabama Natural History Museum, Tuscaloosa, Alabama, USA; AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GPIT, University of Tübingen,

Tübingen, Germany; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; SDMNH, San Diego Museum of Natural History, San Diego, California, USA; TMP, Royal Tyrell Museum of Palaeontology, Drumheller, Alberta, Canada; UAVPL, University of Alberta Vertebrate Paleontology Lab, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, Smithsonian Institution National Museum of Natural History, Washington DC, USA; UVER, University of Vermont Zadock Thompson Natural History Collection, Burlington, Vermont, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

RESULTS

Completeness scores

The mean completeness scores for all specimens per species show a broad range of values for different taxa: averages per taxon range as follows: TCM (1–21 out of 36), QCM (1–7 out of 9) and ICM (1–5 out of 5). Summaries are given of the overall mean TCM, QCM and ICM scores for all mosasaur species (Driscoll *et al.* 2018, Data A), for all mosasaur specimens (Driscoll *et al.* 2018, Data B) and by holotype, best specimen and species composite scores (Driscoll *et al.* 2018, Data F, G and H, respectively). An overview of the completeness of the various species and exemplary specimens is reviewed below and summarised (Table 3).

When the total character scores from the mosasaur phylogenetic matrix are compared to QCM there is a very highly significant positive correlation (Spearman: $r_s = 0.925$, $p \ll 0.001$) derived from our 26 representative specimens, which remains significant after FDR correction for multiple comparisons.

Statistical comparison of the completeness scores (TCM, QCM, ICM) across all specimens shows highly significant positive correlations that were also significant after FDR correction: TCM vs. ICM (Spearman: $r_s = 0.74$, $p << 0.001$), QCM vs. ICM (Spearman: $r_s = 0.72$, $p << 0.001$) and TCM vs. QCM (Spearman: $r_s = 0.49$, $p << 0.001$). The correlations were also very highly significant using the Kendall tau-b test, with all p values < 0.001. The metrics are so closely correlated with each other that all can be regarded as equivalent metrics for recording fossil completeness data.

A comparison of the completeness data (TCM) for all 4083 specimens versus the 1726 specimens datable to substage shows significant discrimination, as indicated by the Kruskal - Wallis test ($\chi^2 = 81.174$, df = 35, $p << 0.001$). These sets are not equivalent. At first, this seems surprising, since the medians for these values are both 1; the mean TCM for single substage specimens is 2.18, and for all specimens is 2.28. But this result is influenced by the fact that the distribution of precisely datable specimens is skewed according to the level of taxonomic assignment. Only 154/1034 (15%) of taxa assigned to Mosasauridae could be dated precisely to substage, whereas for those identified to genus, this rises to 146/731 (20%), and to 62% for specimens identified to species. However, when one compares the two sets of data using only specimens named to species, there is no significant difference when using the TCM of all specimens and those datable to precise substages (Kruskal-Wallis: $\chi^2 = 41.94$, df = 32, $p = 0.124$). This shows that TCMsp, which necessarily leaves out many un-sampled and/or un-datable specimens, can be trusted as a fair representation of the mean TCM for the set of all specimens identified to species level. Note that comparisons like this, where some data sets compared are subsets of each other, might be inadvisable; but in this case, the null hypothesis was that the partial set of datable specimens should be equivalent to the set of all specimens. We confirm this here in the comparison of substage-dated specimens with the sample of all specimens.

Mosasaur fossil completeness

Time series. Mean completeness of all mosasaur specimens varies through time, and there are close similarities in the overall patterns through time for all three completeness metrics (Fig. 2). The same is true for mosasaur specimens named to species through time (Fig. 3).

The time series of completeness metrics by substage all correlate significantly with each other, both for all specimens and for those named as species. These correlations remain significant after FDR correction. There is no bias in the overall pattern of mosasaur completeness according to whether specimens have been assigned to named species or not. Further, many of the rises and falls in the respective time series (Figs 2, 3) show statistically significant differences between substages, both for named species and for all specimens.

All patterns for the different metrics appear broadly similar, whether isolated teeth are included or not, but the values without such teeth are inevitably always higher (over 1400 of the 4083 specimens comprise isolated teeth only). The differences between time bins continue to be significant (Figs 2, 3) regardless of whether the data include or exclude specimens consisting of only a single tooth. The metric that is least changed by the removal of tooth-only specimens is QCM.

A difference between the ‘with teeth’ and ‘without teeth’ time series occurs in the late Santonian for QCM, where the value excluding teeth is considerably higher (Fig. 2B). In the early Campanian, a disproportionate number of tooth-only specimens (most likely from *Prognathodon lutugini*) shift the ICM curve lower (Fig. 2C). The results are comparable also for taxa named to species (Fig. 3), although the data set is smaller.

There is an overall slightly declining trend in fossil completeness through time, with completeness scores in the mid Cretaceous somewhat higher than those in the Maastrichtian. However, the trend is modest, and perhaps dominated by the downturn from the early to late Maastrichtian. For the whole data set, all three metrics show (Fig. 2) a high point in the middle Coniacian, but this is based on a single specimen, and so the value is hardly meaningful. Further, there are no named mosasaur species datable exactly to the early Coniacian (Fig. 3). For all specimens, the lowest average completeness is in the early Santonian. The earliest true mosasaurs, found in the Turonian, have average completeness. Later, completeness peaks in the late Santonian and drops to its lowest points in the early Campanian and late Maastrichtian.

For all three metrics, mean completeness (Table 4) for named species (TCMsp, QCMsp, ICMsp) through time is correlated with overall completeness (TCMall, QCMall, ICMall) and remains significant after FDR correction. Note that TCMsp and ICMsp are significantly correlated with TCMav and ICMav after FDR correction, but other completeness metrics, whether based on named specimens or all specimens, do not show significant correlations with average species completeness (TCMav, QCMav, ICMav) analysed in specific time bins, after FDR correction. For example, QCMsp does not correlate with QCMav. This indicates that caution is required in interpreting time series that assume completeness values derived from whole species-based values, such as averaged species completeness (TCMav, QCMav, ICMav) are equivalent to specimen-based completeness averaged in single time bins.

Both the sampled in-bin and “averaged” species diversity curves correlate significantly with the generic diversity curves even after FDR correction (Table 4, Fig. 4A). Generic diversity rises and falls, then upturns sharply from the mid Santonian onwards, and gently rises through the Campanian to Maastrichtian, with only a slight increase through that span of nearly 20 Myr. The species curves roughly follow the same pattern early on. The two curves show a dramatic drop in diversity after the Turonian, corresponding to a low number of assignable specimens; and in the early Coniacian none can be named to species level (e.g. *Tylosaurus* indet.). Mosasaurid species diversity rises during the middle Coniacian, dropping in the early Santonian, but then generally rises the to the K/Pg boundary, with a slight drop in the early Maastrichtian. Note that species diversity is at its highest during the late Maastrichtian, with no hint of a pre-mass extinction diversity drop.

For comparison, sea level (Fig. 4B) fluctuates in the Turonian through early Santonian, concurrently with the variability in mosasaur diversity. The lowest sea level occurs in the early Santonian, but it rises until the early Campanian, when it reaches its highest level. A drop in sea level occurs in the early Maastrichtian, at the same time as a small drop in species diversity. Species diversity is high during some times of relatively high sea level, but none of the three diversity time series curves correlates in a statistically significant way with mean sea level (Table 4) in this comparison. In like manner, none of the measures of completeness shows any statistically significant correlations with sea level (Table 4).

Predicting diversity and completeness. GLS model fitting shows that a combination of all variables (e.g. sea level, mosasaur and plesiosaur bearing formations (MPBFs), TCM, and age) best predict averaged diversity (Driscoll *et al.* 2018, Appendix Table S6A). While sea level and MPBFs appear positively related to averaged diversity (i.e. higher sea level or more MPBFs sampled equals higher diversity), age is negatively related to diversity, i.e. mosasaur diversity increases through time (Driscoll *et al.* 2018, Appendix Table S6B). However, once we account for autocorrelation, we find that the best fitting model contains only sea level and MPBFs, both of which are positively related to averaged diversity (Tables 5, 6). The best fitting model for predicting TCMsp consists of all variables (e.g. species diversity, sea level, MPBFs and age) (Driscoll *et al.* 2018, Appendix Table S6A). However, none of these variables appears to be significantly associated with TCMsp (Driscoll *et al.* 2018, Appendix Table S6B). When we account for autocorrelation, the best fitting model still for TCMsp contains all variables, but none is significant (Tables 5, 6).

Determinants of fossil completeness

Taxonomic rank. As might be predicted, mean TCM increases as one narrows taxonomy from family to genus to species (Fig. 5A, B), and these differences are statistically highly significant. Interestingly though, when all specimens including teeth were used in the analysis, it was difficult to discriminate a significant difference in completeness between genera and species (Fig. 5A), even though there was discrimination among all three taxonomic categories when tested together. But, when the tests were repeated excluding tooth-only specimens, there was clear discrimination (Fig. 5B). Among all 4083 specimens, 1044 were attributable to family only (Mosasauridae indet.), 731 to genera, and 2304 to species.

Lithology. There are highly significant differences in TCMsp among specimens preserved in different lithologies, with fossils preserved in clays displaying higher completeness than those preserved in carbonate or coarse siliciclastic deposits (Fig. 6). These differences are much smaller when specimens consisting only of teeth are left out of the analysis.

Palaeogeographic region. The mean TCM of specimens identified as species varies significantly by palaeocontinental region, with specimens from North America showing higher completeness than those from Eurasia and Gondwana (Fig. 7). When tooth-only specimens are excluded, there are no statistical differences.

Formation. Fossil completeness as measured by TCMsp varies significantly between different geological formations. The Pierre Shale Formation in the western interior of the USA and the Craie de Ciply in Belgium have the most complete fossils (Fig. 8). The Maastrichtian formations of the New Jersey Greensand and Maastricht Chalk yield the least complete specimens.

Body size. There are no significant differences in total mean species completeness (TCMtot) between different body size classes derived from the estimated average body length of the individual species concerned (Fig. 9).

Sampling. Average species completeness correlates significantly and inversely with the number of years elapsed since description, and inversely also with the number of specimens per species (Table 7). The average completeness per species compared to the completeness of the best specimen in a species correlates strongly for all three metrics. The best specimen influences the average for a whole species. The total number of specimens per species shows statistically significant positive variation with the number of years since description. The number of Google Scholar "hits" for a species correlates strongly with the number of specimens, as well as years elapsed since description. There is a trend for Google Scholar "hits" to increase with estimated mosasaur body length, which is not quite statistically significant using Spearman's *rho* ($r_s = 0.26$, $p = 0.052$).

Results for North America rock outcrop area (Table 7) show no correlations between regional diversity, formational outcrop area, or mean TCM by formation.

Overview of mosasaur fossil completeness. The mean completeness (TCMtot) by species using individual specimens ranged from 1.0 for those species known only from teeth, jaws or individual bones to a high of 13.67 for *Hainosaurus bernardi* (Driscoll *et al.* 2018, Data A). The scores by specimen type (Table 3; Driscoll *et al.* 2018, Data F–H) show that the average holotype completeness is 8.1 for TCMh, which is approximately equivalent to 25% of the skeleton in the average mosasaur holotype. The highest scoring holotype is 32 for UPI R163, *Eonatator sternbergii*. The lowest score for TCMh is 1.0 for several holotypes. The most complete specimen is not always a holotype. *Platecarpus tympaniticus* (YPM 58129) from the Kansas Chalk, with a TCMc of 36, is the most complete specimen in the database. However, at least five other specimens scored over 30. Several species have perfect composite scores, including some with soft tissue preservation (*e.g. Platecarpus tympaniticus* and *Tylosaurus proriger*).

The highest mean QCMtot was 5.6 for individual specimens of *Tethysaurus nopscai.* The mean holotype completeness (QCMh) is 4.5; thus 50% of the phylogenetic characters occur in the average type specimen. The highest QCMh is 8 (equivalent to a skull and most of the skeleton) for several holotypes: *Eonatator sternbergii*, *Clidastes propython*, *Mosasaurus missouriensis*, *Plotosaurus bennisoni* and *Latoplatecarpus willistoni*. The lowest QCMh for a type specimen is 1.0 (but this a lectotype) for *Goronyosaurus nigeriensis*. Of note, the composite score (QCMc) of *G. nigeriensis* is 8; multiple specimens make up for most of the elements missing in most individual fossils. The best specimens of both *Tylosaurus proriger* and *Platecarpus tympaniticus* both have QCMb scores of 9. The mean QCMc for all species is 6.2. This indicates the composite character completeness of the average mosasaur species is approximately equivalent to the score for a skull of that species. Multiple species have a perfect QCMc. It should be noted, that at the time of this compilation, there were three species with a QCMc only equal to 2.0, the lowest composite score, equivalent to a jaw element, namely *Carinodens belgicus*, *Carinodens minalmimar* and *Igdamanosaurus aegyptiacus*.

The average TCMc for composite specimens is 15.7 (about 44 % of the skeleton). The mean composite score for ICMc is 4.5/6, equivalent to some skull, axial and limb elements available to describe the average mosasaur species.

DISCUSSION

Describing the mosasaur fossil record. In this study, we have addressed one of the richest vertebrate fossil records. Mosasaurs have attracted study for over two centuries, with the first find, *Mosasaurus hoffmanni*, being described by Cuvier in 1808 (Russell 1967). Later collectors noted their huge abundance: it is said that O. C. Marsh collected over 2,000 Kansas mosasaur specimens (Everhart 2000), and Ikejiri *et al.* (2013) counted 1,563 Alabama mosasaur specimens. An estimate of "literally thousands" of specimens of *Platecarpus* from Kansas has been suggested (Konishi & Caldwell 2007). Our analysis of mosasaur diversity through time complements previous studies (Polcyn *et al.* 2014; Ross 2009).

It has been argued (Mannion & Upchurch 2010) that skeletal completeness metrics can evaluate confidence in palaeontological data: as knowledge of the anatomy of a taxon becomes more complete, with increased numbers of specimens, or more complete skeletons, confidence in taxonomic assignments improves. In an ideal world, palaeontologists would wait for relatively complete specimens before applying new taxonomic names, but in fact new genera and species are often based on poor material. For example, in the case of echinoids (Smith 2007), incomplete fossils were named more frequently than complete specimens, and in the case of dinosaurs (Benton 2008a), the naming of species in the 19th century was prodigious but quite inaccurate, and holotypes were on average much more incomplete before 1960 than after that date (Benton 2008b). Brocklehurst & Fröbisch (2014) found, on the other hand, that pelycosaurs named before 1900 were on average much more complete than those named after that date.

Early in mosasaur palaeontology, many species were named based on inadequate material, as can be seen by a perusal of invalid names listed by Russell (1967). Perhaps in the 19th century, names applied to scrappy material might by chance have been correct, as palaeontologists were naming the first ever mosasaur finds from newly identified geological formations, but today, it is likely that new names applied to scrappy material risk being synonyms of already named taxa.

Using completeness scores in mosasaurs. This is a specimen-, rather than taxon-based study. Occurrence-based records that depend on presumed ranges of species were not used to place specimens in time bins in the completeness calculations. This paper shows the utility of this method, which might not have had enough power for statistical testing; the greatest risk was with TCM, since the average completeness values are quite low. However, the analysis was possible because of the large number of specimens in the database.

All three completeness metrics (TCM, QCM, TCM) correlated with each other, both specimen by specimen and through the time series. A similar result was found with ichthyosaur completeness, where SCM correlated with BSCM (Cleary et al 2015), a metric similar to those used in this study. Our results suggest that even qualitative measures, such as QCM and ICM, can be useful for comparing specimens and, because they correlate with TCM (a quantitative metric) and with each other, any one of these metrics could be used to score mosasaur fossils.

TCM is based on true specimen in-bin averages, and thus it is likely driven by taphonomy (Mannion & Upchurch 2010; Beardmore *et al.* 2012 a, b). TCM is similar to SCM, but it is not weighted volumetrically, but equally by anatomical region. Weighting by size may introduce an assumption that larger elements or regions are preserved more readily than smaller ones. Disallowing such weighting then allows TCM to be used to test taphonomic or preservational hypotheses.

QCM was developed as a proxy for phylogenetic completeness, and is somewhat equivalent to CCM. QCM estimates phylogenetic completeness without having to score characters on every element of a fossil specimen, because QCM is pre-weighted by character density. In terms of the time involved in scoring, QCM can be assessed quickly from a photograph or a fair description, whereas methods such as CCM require careful coding of all skeletal elements. ICM, although less quantitative than the other metrics, was easily scored and could discriminate mosasaur completeness in line with TCM and QCM values, even when specimens could not be examined directly, or photos or more specific descriptions were not available. This confirms its usefulness.

It is important to note that there were some differences in our results when compared to other studies using the SCM and CCM metrics. In most other fossil completeness studies (*e.g.* Mannion & Upchurch 2010; Brocklehurst *et al.* 2012; Brocklehurst & Fröbisch 2014; Cleary et. al. 2015; Dean *et al.* 2016; Tutin & Butler 2017), best and composite completeness values for a species are calculated and then these values are generally assigned to time bins of the species temporal range (usually based on first and last appearances). These completeness values are then averaged in the various time bins. If there were only a single specimen representing a species that is only assignable imprecisely to several time bins, there would be no other alternative but to use this method. If the best specimen of a species or the composite specimen cannot be assigned to an individual time bin, the result is the same as if the mean completeness for a species did not vary over time bins. The large size of our data set allowed for analysis using only exactly assignable in-bin specimens and avoided the need for proxies of specimen completeness such SCM or CCM.

In our study, we chose not to include composite (TCMc, QCMc, ICMc), best (TCMb, QCMb, ICMb), or holotype (TCMh, QCMh, ICMh) completeness metrics in the time series analyses, to avoid calculating estimates of completeness from un-sampled specimens. In some studies that used stage-level time bins (e.g. Cleary *et al.* 2015; Dean *et al.* 2016), best specimen or composite specimen values were used, which involves some risk of amalgamating disparate data across time bins. We provide data for holotype completeness (TCMh, QCMh, ICMh), equivalent to SCMts, as well as best and composite specimen scores average scores, lowest scores, etc. (Table 3), only for comparative purposes.

Completeness and the mosasaur fossil record. Most mosasaur species are very complete (Driscoll *et al.* 2018, Data F–H), especially if one considers composite completeness by species. On average, over 65% of the phylogenetic information is available for the average mosasaur species. This is better than for anomodonts (Walther & Fröbisch 2013), otherwise assumed to be rather complete, although anomodont skulls yield 82% of phylogenetic characters on average, whereas postcranial characters account for only 4–9% of possible totals. Our data show that through the history of mosasaur collecting there has not generally been a bias in selecting well-preserved fossils. This is demonstrated by the fact that museums curate thousands of incomplete specimens, indicated by the wide range of TCM and QCM values (Driscoll *et al.* 2018, Data B). It should be noted that most of the QCM values are low because there was not an over-representation of, say, skull material that would show bias in collecting. QCM does not correlate with diversity (see below), and this is also an argument that the best specimens do not bias the mosasaur record.

Because we included over 4,000 specimens of all completeness values, half of which have TCM and QCM scores of 1 or 2, we were not sure at first whether the inclusion of such low-scoring singleton specimens would distort our conclusions. On the other hand, we reasoned that the inclusion of low-scoring elements should contain valuable information concerning taphonomic drivers of preservation. Especially worrisome was the fact that so many teeth were included as individual specimens.

These concerns were tested in several ways. Kendall tau-b correlation analysis comparing completeness values over all specimens showed that, even though there were many incomplete specimens, ties in the ranks did not affect analyses. All metrics are equally useful for scoring. In any case, we analysed time series with and without teeth, and comparisons remained statistically significant. It makes taphonomic sense that the inclusion of teeth in the analysis of lithological variables increased the discrimination between rock types. The same type of result occurred with the analysis of formational data, which again must vary by rock type. Interestingly, leaving out tooth-only specimens obliterated the statistical differences between palaeogeographic regions. European collections certainly do contain more teeth (Driscoll *et al.* 2018, Data B) and perhaps European scientists have always identified more specimens with teeth alone.

It is reassuring that completeness scores are inversely proportional to category-level discrimination, being best for specimens identified to species level, then poorer for those identified to genus level, and worst for those assigned only to family. As noted before, the difference between species and genus completeness is greatly enhanced when specimens consisting of only teeth are excluded from the analysis. A few taxa have a very low completeness score (e.g. *Tylosaurus ivoensis*), but all species with a species epithet have at least some material that is separable by apomorphic characters (Bell 1995), the minimum requirement for naming new taxa (Parham *et al.* 2012). It is perhaps true, that a species can be identified by its teeth (Lindgren & Siverson 2002; Bardet *et al.* 2015), but in marine reptiles the teeth are often homodont and lack variability, being in many cases convergently adapted to diet (Massare 1987), and so may be of limited use taxonomically. When designing future specimen-based studies, analyses with and without teeth would be recommended.

A key discovery was that completeness of species as measured by TCMav does not necessarily correlate with completeness of specimens. Most studies on the completeness of the fossils have assigned various completeness scores to each species, but have treated these scores as a measure of preservation quality. The fact that the species-level scores for mosasaurs do not necessarily represent the quality of the preservation of the individual fossil specimens has important implications for how the results of these studies should be interpreted. The use of any whole species proxies for completeness that are derived from data outside of the time bin where the data is averaged will not necessarily be equivalent to analyses compiled from specimens in their home time bins. Results from species- and specimen-based studies will likely be more disparate with larger samples and shorter time bins. In addition, there could be links to correlations between completeness, the number of specimens and year since description: the completeness scores assigned to whole species will be a result of the accumulation of specimens assigned to that species, which we have shown are influenced by the history of discovery (= number of years since description).

Mosasaur completeness through time. Hundreds of specimens of mosasaurs are datable to substage, and the analysis shows that this subset of is a good representation of overall mosasaur species completeness. There are significant differences in completeness over time; but values in mean completeness from substage to substage are not unexpected, as the conditions for fossil preservation must vary in complex ways from fossil to fossil, formation to formation and taphonomic microenvironment to microenvironment. Because there are so many specimens in these time bins, from a wide geographic range, it is difficult to recognise any individual collections or formations that are driving these curves. The differences between time bins represent true in-bin mean values. We show here that using the average completeness of a species group (TCMav, QCMav, and ICMav) to calculate overall time bin completeness (TCMtot, QCMtot and ICMtot) is not generally warranted, at least for QCM in this dataset. Surprisingly, when TCMav was used to estimate species completeness by substage, it did correlate significantly with the mean TCMsp of the individual specimens in the time bin. This may indicate that multiple specimens of a single species tend to fossilise in similar ways.

It might have been predicted that mosasaur completeness would depend on sea level, as is the case for ichthyosaurs (Cleary *et al.* 2015) and plesiosaurs (Tutin & Butler 2017). However, we found no relationship between mosasaur skeletal completeness and average sea level in any of the time series analyses. There were some negative correlations (Table 4), but the correlation coefficients were extremely low, and not even near significant. Similarly, in GLS analysis, even though the best fitting model for predicting TCMsp included sea level, its predictive value was no better than the null model.

In cases where specimen quality depends on sea level, it might be predicted that the relationship would be positive, in that deep-water settings should provide better conditions for preservation than shallow waters, because the deep oceans are less subject to high-energy deposition, except through the medium of turbidity currents, and there are fewer scavengers than on the marine shelf. However, for ichthyosaurs (Cleary *et al.* 2015) and plesiosaurs, (Tutin & Butler 2017), completeness is inversely proportional to sea level, significantly so for the former, but not the latter. This inverse statistically insignificant relationship may also occur in marine crocodiles (Driscoll, unpublished), but the reasons for this relationship are not clear. As mentioned by Tutin & Butler (2017), the marine reptile fossil record is not particularly well sampled in the Jurassic and earliest Cretaceous, which might bias results. It is not clear whether this idea is confirmed by the absence of such a trend in the more intensively sampled and time-limited sample of mosasaurs, or whether different marine reptile groups show different preservation conditions.

We suggest here that the mosasaur fossil record is not much affected by lack of sampling (the exception being the early and mid Coniacian) and there is no correlation to changing sea level. For terrestrial tetrapods, a negative relationship between completeness and sea level was found for sauropod dinosaurs (Mannion & Upchurch 2010), which was explained by differences in sauropodomorph ecology; but there was no correlation for Mesozoic birds (Brocklehurst *et al.* 2012) or pterosaurs (Dean *et al.* 2016).

Explaining mosasaur macroevolution. In our first analysis, correlation results show no direct relationship between species or genus diversity and sea level, but our GLS results do show a significant contribution by sea level in the best fitting model explaining diversity. This compares with Polcyn *et al.* (2014), who argued that sea level at least partially drove mosasaur diversity, as mosasaur richness in their analysis trended in the same direction as sea level. The initial expansion of the clade might well have been triggered by the onset of major continental flooding in the early Late Cretaceous (Caldwell 2002). We suggest that any model of mosasaur macroevolution using environmental drivers will have to take more than sea level into account. The increase of mosasaur species richness combined with the quality of their fossil record makes a strong case for a model of marine reptile evolution in which mosasaur species steadily filled specific niches or expanded steadily into different biogeographic regions, once variability in global marine environmental drivers became stable in the Santonian. The almost level generic diversity curve in the latest Cretaceous shows that mosasaurs had become long-term and stable residents of the Cretaceous seas right up to the late Maastrichtian.

Neither species nor generic diversity through time correlated with skeletal completeness in mosasaurs for any of our metrics. In GLS modelling, the best-fitting auto-correlation model of completeness (TCMsp), species diversity was a predictive variable, but it was not statistically significant. This lack of correlation, confirming what Cleary *et al.* (2015) found also for ichthyosaurs, suggests that the quality of fossils does not drive our models of marine reptile diversity and it would be hard to construct a case that apparent changes in diversity are simply artefacts of the quality of fossils or the quality of nomenclature based on those fossils.

Sampling and redundancy. In most previous fossil completeness studies, sampling proxies have been used in multiple regression analysis of fossil completeness to help understand what is driving measured values of diversity and completeness. Variables such as collections, fossiliferous marine formations, dinosaur-bearing formations, marine tetrapod-bearing formations, pterosaur-bearing formations and other proxies have all been used. Much of this data is relatively accessible from the Paleobiology Database and/or the primary literature, but most of it is tallied at stage level. In our study, using substage-dated specimens, it was not possible to include the above proxies in our multiple regression analyses. Such a comparison will be interesting once a narrower time range analysis is possible. Instead, we developed an Upper Cretaceous substage-level proxy from mosasaur- and plesiosaur-bearing formations (MPBFs). Almost all plesiosaur-bearing formations also contained mosasaurs, so the data overlapped.

In all our best fitting GLS models, with and without auto-correlation, MPBFs correlated highly significantly with diversity. In the past, counts of fossiliferous formation were used as a proxy for sampling that combined geological and human biases (Benson *et al.* 2010). If MPBFs is considered as a proxy for geological megabiases, then our results could indicate that none of our diversity data is reliable enough to compare with any other time series, including sea level or completeness. However, the shape of the diversity curve, lack of evidence for lithological or regional correlates with specimen completeness, and the thousands of sampled fossils argue against jumping to this conclusion. Further, the data on fossil occurrence (collections, specimen counts, localities, formations) were collected at the same time as the data on diversity, and so there is a risk of tallying rock and fossil data that describe the same history of discovery, so pointing to redundancy (Benton *et al.* 2011; Benton 2015). The redundancy hypothesis for highly correlated rock and fossil data was confirmed in the case of the fossil records of the UK and the world by using statistical methods that identify not only correlation but also directionality of causation (Dunhill *et al.* 2014, 2018). Therefore, we cannot use the MPBF count as a sampling proxy because it is not an independent yardstick that represents either geological or human sampling. Our other variables, including fossil completeness, diversity and sea-level, are independent of one another. We have shown that fossil preservation, as measured by specimen completeness metrics, does not bias the fossil record of mosasaurs.

Explaining mosasaur completeness. We have compared completeness in the best-known mosasaur-bearing formations. Factors that might explain the differences include lithology, rock exposure and collecting biases. Comparing completeness among different outcrops and formations can be used as an aid in understanding Lagerstätten effects.

Our results for mosasaurs show many agreements with the study of the ichthyosaur fossil record by Cleary *et al.* (2015). In both studies, skeletons were more complete in fine-grained than coarse-grained sediments (Fig. 5), and this was expected because fossil completeness is partially dependent on taphonomy (Beardmore *et al.* 2012a, b) and post-depositional geological factors. This is supported by the fact that when low-completeness specimens consisting of only teeth are left out of calculations of mean completeness, the differences between lithologies are less evident. We expect, for example, that since sandstones are deposited in high-energy environments, which toss and abrade bone, specimens in sandstones would have smaller mean completeness values than those in lower-energy mudstones. Fine-grained sediments should preserve more detail. In fact, the New Jersey Greensands have the lowest completeness of the formations considered, and the Pierre Shale has a high average mean completeness value. A further contributor to the high quality of specimens in fine-grained sediments such as the Pierre Shale are their anoxic environments, with little scavenging (Kauffman & Sageman 1988).

The Pierre Shale covers thousands of square miles of the North American western interior, and produces some almost complete articulated fossils with soft tissue (personal observation; Carpenter 2006, 2008). The Pierre has yielded fewer specimens than the Niobrara or Greensand, but considering its greater mean completeness, the sheer size of the Pierre outcrop (311,000 km^2) in comparison to that of the Niobrara and Greensand (21,000 km^2 each) and its relative inaccessibility in remote regions of the North American western interior, suggests that complete specimens may yet be found. The Pierre Shale fossils have a higher mean completeness score than those from the Niobrara Chalk, but the latter formation is often considered a Lagerstätte (Bottjer 2002), and indeed some mosasaur soft tissue impressions are found (Lindgren *et al.* 2010). If average completeness could be considered one measure of a Lagerstätte, the Pierre should also be considered as such.

The Niobrara Chalk has experienced a great deal of collector effort (thousands of specimens; over 150 years of effort by hundreds of people), and is still yielding fresh finds, but no new species, barring those re-described, such as *Tylosaurus kansasensis*. Exposure (desert badlands) and accessibility are high. Most of the Niobrara species have probably been collected. Depending on average lithology and depositional environment, there may be a limit to the skeletal quality within any geological formation, and no amount of additional collecting can improve that. The fact that the mean TCM values between different formations are significantly different with and without tooth-only specimens supports the idea that in highly collected formations there may be a limit to average preservation values. Once enough rock is exposed and collected, lithofacies biodiversity reaches a peak (e.g. Smith & Benson 2013), and the known biodiversity then is limited by the ecology of the ancient environment and the preservation potential of the rocks, assuming collector effort and accessibility is high. Bones from the same family likely have similar preservation potential (Smith & McGowan 2011), so it is doubtful that there are missing taxa based on preservation alone.

Further to this theme, it might have been predicted that skeletal completeness and diversity would be related in some way to outcrop or exposure area; perhaps, for example, when the overall area of a geological formation is high, more skeletons of all kinds of completeness might be found, and so the mean completeness score might then rise, and thus perhaps biodiversity. In our preliminary analysis, the results show no significant correlation between completeness and diversity or outcrop area for North American formations (Table 8). This supports the idea that each formation is associated with an upper limit on preservation potential if there has been adequate exposure and collector effort.

The Craie de Ciply chalk from the Mons Basin in Belgium has the highest average skeletal completeness score. This Ciply chalk has produced many holotypes (Dollo 1904), and the blocks from that formation at the IRSNB contain highly articulated and well-preserved specimens, and very few single elements or partial fossils. This is striking when compared, for example, to the chalk at Maastricht, which has yielded many hundreds of disarticulated specimens, but the explanation, presumably to do with mode of deposition and rate of burial of the carcasses, is not clear. In this case, with all the almost complete skeletons available, perhaps less spectacular specimens were not deemed worthy of collection, or perhaps they do not exist. Neither lithology, outcrop area, nor the amount of collecting explains the completeness of these Belgian fossils, limited in area to quarries in a relatively small region.

The average completeness of mosasaur specimens has tended to decrease through research time, which was initially unexpected: specimens described and named many years ago tend to be more complete than those named more recently. The holotypes of species currently regarded as valid are typically rather complete specimens, and subsequently identified materials of many of these species may on average be less complete, and now more easily identifiable. Such specimens are not typically considered publishable material; and studies that use only published material to describe historical trends in fossil quality may not show the same result. The average-quality material found in many museums outnumbers more complete material. The inverse completeness trend may reflect that the holotypes of taxa named in former centuries were substantially complete and have been preferentially retained, whereas less complete materials were disposed of, or perhaps not collected at all in the early days of palaeontology when collectors were perhaps less assiduous in recording everything. Today, on the other hand, perhaps holotypes are of similar completeness, but museums retain enormous collections of less complete, referred specimens. Again, completeness does not continuously rise for a species as more specimens are collected, but we have not explored historical differences in completeness for specific formations.

Known fossil completeness of mosasaurs is best in North America and somewhat higher in Gondwana. Surprisingly, the well-known very complete European specimens do not significantly drive fossil completeness in Eurasia, nor does the relative number of specimens. When the tooth-alone specimens are left out of the analysis, there are no significant differences in completeness between the continents. North American collections in this analysis are relatively devoid of tooth specimens. We were not able to make a significant comparison of completeness in northern vs. southern hemispheres, as there are too few of the latter. For ichthyosaurs, Cleary *et al.* (2015) showed the well-studied northern hemisphere produced fossils of significantly higher quality than the southern hemisphere. The differences above are all likely sampling artefacts.

Larger mosasaurs do not show higher skeletal completeness than either small or medium-sized ones. One might hypothesise that larger specimens would be more complete, as in some dinosaurs (Brown *et al.* 2013). The situation here is different from that seen in other, smaller taxa such as birds or pterosaurs (Brocklehurst *et al*. 2012; Dean *et al*. 2016), where Lagerstätten may selectively preserve smaller specimens better than large specimens found in other deposits. This could be explained by the greater weight of their bones, the higher energy required by sedimentary flows to disarticulate a skeleton, the fact that larger specimens are easier to find, or they are preferentially collected. It is interesting to note that the number of Google Scholar hits per species showed a trend (although, not quite significant) with estimated body length, perhaps indicating preferential study of larger mosasaurs. For ichthyosaurs, Cleary *et al.* (2015) rather surprisingly found that medium-sized specimens were significantly more complete than small or large taxa: the incompleteness of small specimens was expected, but it was a surprise that larger specimens were also relatively incomplete.

CONCLUSIONS

Palaeobiology has been built on the idea that, in spite of limitations of the fossil record, biological information including patterns of diversity and macroevolution might be demonstrated with the proper analytical techniques. The mosasaur fossil record has been explored in terms of skeletal completeness, a study enabled and strengthened by the great abundance and quality of specimens. New completeness metrics, introduced here, adequately describe the preservation of the mosasaur fossil record. QCM, a novel and quick method for estimating fossil completeness correlates with true phylogenetic character completeness and can be used as a proxy for it.

Mosasaur fossils are found in all stratigraphic substages throughout their evolution, and neither skeletal nor phylogenetic completeness explains their diversity: fossil completeness does not bias the fossil record of mosasaurs and cannot be used as a proxy for diversity. A huge amount of both incomplete and well-preserved mosasaur material is identifiable, which is not the case for some other Mesozoic tetrapod groups. The mosasaur fossil specimen record contains thousands of teeth, which do not affect the general utility of the methods, but improve the resolution of completeness values in taphonomically related comparisons. Outcrop area, where data is available, does not explain mosasaur diversity. However, lithology has a role: skeletal completeness is higher in fine-grained than in coarse-grained sediments. There is no evidence to suggest that sea level drives mosasaur fossil completeness or mosasaur diversity. We do not detect any geological megabiases driving the fossil record of mosasaurs. Mosasaur species richness, based on specimens assignable to a single substage, rises steadily and smoothly from the late Coniacian to late Maastrichtian and correlates with the generic richness curve. Although ambiguous in this study, sea level may play a role in further models of mosasaur diversity. Low sampling in the mid Cretaceous makes the analysis of completeness difficult through this time range. Even considering this, mosasaurs appear unique among marine tetrapods in terms of the reliability of their fossil record.

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Appendix

Appendix. Species list for this study (Squamata, Mosasauridae) and the number of specimens included in the analysis; and mean completeness scores (TCM, QCM or ICM). Abbreviations: Camp = Campanian, Con = Coniacian, Maas = Maastrichthian, Sant = Santonian, Tur = Turonian. Completeness figures are rounded to two decimal places. The range is based on individual specimens that are datable to specific substages, except those with a "?", whose range is near a boundary, or "??", whose range is imprecise.

Genus	***Species***	**Number**	**TCM**	**QCM**	**TCM**	**Range**
Eonatator	*sp.*	1	2	1	1	Late Sant-Early Camp??
Eonatator	*sternbergii*	87	1.51	1.92	1.22	Early Camp
Eonatator	*cf. sternbergii*	1	2	3	3	Late Sant-Early Camp??
Halisaurus	*arambourgi*	33	5.64	2.76	3.25	Early-Late Maas
Halisaurus	*platyspondylus*	10	2.4	2	2	Early-Late Maas
Phosphorosaurus	*ortliebi*	1	2	3	3	Early Maas
Phosphorosaurus	*ponpetelegans*	1	10	7	4	Early Maas
Carinodens	*belgicus*	38	1.03	2	1.21	Late Maas
Carinodens	*minalmamar*	2	1.5	2	2	Late Maas
Clidastes	*liodontus*	21	8.47	5	3.67	Late Con-Early Camp
Clidastes	*moorevillensis*	4	6.67	4	3.67	Late Sant-Early Camp
Clidastes	*propython*	196	3.68	2.89	2.35	Early-Late Camp
Dallasaurus	*turneri*	3	7.33	3.33	3.33	Mid Tur
Globidens	*alabamensis*	16	1.47	2.44	1.53	Early-Late Camp
Globidens	*dakotensis*	1	8	6	4	Mid Camp
Globidens	*phosphaticus*	63	1.14	2.08	1.1	Early-Late Maas
Globidens	*schurmanni*	1	21	7	5	Late Camp
Igdamanosaurus	*aegyptiacus*	5	1	2	1	Early-Late Maas
Kourisodon	*sp.*	1	2	3	3	Late Camp
Kourisodon	*puntledgensis*	1	18	7	5	Late Sant
Moanasaurus	*mangahouangae*	5	6.6	5.2	3.6	Mid-Late Camp?
Mosasaurus	*beaugei*	110	1.03	2.02	1.04	Late Maas
Mosasaurus	*conodon*	123	3.53	2.49	1.81	Late Camp-Late Maas
Mosasaurus	*hobetsuensis*	1	13	3	3	Early Maas
Mosasaurus	*hoffmanni*	291	1.42	1.9	1.46	Early-Late Maas
Mosasaurus	*missouriensis*	11	9.9	5.4	4	Mid Camp-Late Camp
Mosasaurus	*mokoroa*	2	3.5	4.5	2.5	Mid Camp
Mosasaurus	*prismaticus*	1	2	3	3	Late Camp-Late Maas??
Plotosaurus	*sp*	1	1	2	1	Late Maas
Plotosaurus	*bennisoni*	50	4.59	2.19	1.86	Early Camp-Early Maas??
Plesiotylosaurus	*crassidens*	4	6.25	6	4	Early-Late Maas?
Prognathodon	*anceps*	6	1.17	2.17	1.67	Early Camp
Prognathodon	*currii*	8	2	2.63	1.38	Late Camp-Late Maas
Prognathodon	*kianda*	6	7	3.67	3.17	Late Maas
Prognathodon	*giganteus*	5	3	2.6	1.8	Early Maas
Prognathodon	*lutugini*	75	1.17	2.01	1.05	Early-Late Camp

Prognathodon	*mosasauroides*	2	1.5	2.5	2	Late Maas
Prognathodon	*overtoni*	12	8.58	5	4.08	Early-Late Camp
Prognathodon	*rapax*	13	1.91	1.92	2.27	Early-Late Maas
Prognathodon	*saturator*	4	5.75	3.25	2	Late Maas
Prognathodon	*sectorius*	30	1.03	2.03	1.07	Late Camp-Late Maas
Prognathodon	*solvayi*	7	5.71	3.29	3	Late Camp-Early Maas
Prognathodon	*waiparaensis*	3	4	4	3	Late Maas
Eremiasaurus	*heterodontus*	2	19	7	4.5	Late Maas
Angolasaurus?	*sp*	5	1	1	1	Late Maas
Angolasaurus	*bocagei*	4	6.5	5.5	3.75	Late Tur
Ectenosaurus	*sp.*	2	2	5.5	3	Late Con-Late Sant??
Ectenosaurus	*clidastoides*	7	9.33	3.57	3.57	Late Con-Mid Sant
Goronyosaurus	*nigeriensis*	26	1.42	1.69	1.35	Late Maas
Latoplatecarpus	*sp*	1	N/A	N/A	5	Mid-Late Camp
Latoplatecarpus	*nichollsae*	15	6.25	5	4.33	Late Sant-Mid Camp
Latoplatecarpus	*willistoni*	5	8.2	6.4	5	Mid Camp
Platecarpus	*ptychodon*	8	2	2.63	2	Late Maas
Platecarpus	*tympaniticus*	224	5.12	3.64	2.87	Early Sant-Mid Camp
Plesioplatecarpus	*planifrons*	30	6.33	4.14	3.76	Mid Con-Mid Sant
Plioplatecarpus	*houzeaui*	7	9.57	4.71	4.14	Early Maas
Plioplatecarpus	*marshi*	114	1.39	1.62	1.23	Late Maas
Plioplatecarpus	*depressus*	8	1.75	1.63	1.63	Early Maas
Plioplatecarpus	*peckensis*	1	11	6	4	Late Camp
Plioplatecarpus	*primaevus*	6	3.67	3.5	2.67	Mid-Late Camp
Selmasaurus	*johnsoni*	1	13	7	4	Early Sant
Selmasaurus	*russelli*	3	3	3.67	3	Late Sant-Early Camp
Tethysaurus	*nopcsai*	5	9.5	5.6	4.25	Mid Tur
Pannoniasaurus	*inexpectatus*	118	1	1.19	1.36	Early-Late Sant??
Hainosaurus	*bernardi*	3	13.67	4.67	4.33	Early Maas
Taniwhasaurus	*antarcticus*	1	14	6	4	Late Camp
Taniwhasaurus	*mikasaensis*	4	2	2	2	Late Sant-Early Camp??
Taniwhasaurus	*oweni*	17	1.76	1.88	1.65	Mid-Late Camp
Tylosaurus	*capensis*	1	2	3	3	Late Con-Early Sant??
Tylosaurus	*gaudryi*	1	3	3	3	Late Sant
Tylosaurus	*iembeensis*	2	2.5	2.5	3	Late Tur
Tylosaurus	*ivoensis*	206	1	1.94	1.01	Early Camp
Tylosaurus	*kansasensis*	16	8.86	5.38	3.88	Late Con
Tylosaurus	*nepaeolicus*	39	3.97	3.8	3.58	Late Con-Early Sant
Tylosaurus	*pembinensis*	12	4.25	3.5	3.42	Mid Camp
Tylosaurus	*proriger*	163	4.98	3.40	2.75	Early Sant-Late Camp
Romeosaurus	*fumanensis*	4	7	3.25	3.5	Mid Tur
Romeosaurus	*sorbinii*	1	2	3	3	Mid Tur
Russellosaurus	*coheni*	1	4	5	3	Mid Tur
Yaguarasaurus	*columbianus*	4	5.75	5	3.5	Mid Tur

TABLE 1. QCM method for scoring completeness. Presence or absence of a skull weights the score greatly. The skull contains 61% of characters used in the phylogenetic analysis of mosasaurs. A jaw fragment or tooth scores two points. Add total of parts present. There are nine points possible.

	Skull	Skeleton
Fragments	2	1
Incomplete	3	2
Almost complete	5	
Complete	6	3

1229 **TABLE 2.** Description of completeness metrics used in this paper.

Metric	Sub-metric	Comment
TCM		Taphonomic Completeness Metric - Total of scores from 8 regions.
QCM		Qualitative Completeness Metric-Regions are weighted by phylogenetic character density.
ICM		Informal Completeness Metric-Scored only using skull, axial and appendicular portions as regions.
	(TCM, QCM, ICM)tot	Total mean completeness of a species, disregarding time bins.
	(TCM, QCM, ICM)sp	Mean metric from specimens named to species assignable to single time bins.
	(TCM, QCM, ICM)all	Mean metric from all specimens assignable to single bins, regardless of taxonomy.
	(TCM, QCM, ICM)av	The "tot" metric is calculated for each species, and this is averaged over every species in a time bin.
	(TCM, QCM, ICM)h	The metric of the holotype specimen.
	(TCM, QCM, ICM)b	The metric of the best specimen.
	(TCM, QCM, ICM)c	The metric of the composite-calculated using the best specimen plus any extra elements found in other specimens.

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TABLE 3. Summary of representative mosasaur completeness scores.

	Metric	Species	Specimen	Value
Highest Mean TCM	TCMtot	*H. bernardi*		13.67
Average Holotype TCM	TCMh	all		8.1
Average Composite TCM	TCMc	all		15.7
Highest Holotype TCM	TCMh	*E. sternbergii*	UPI R163	32
Most Complete Specimen	TCM	*P. tympaniticus*	YPM 58129	36
Highest Mean QCM	QCMtot	*T. nopscai*		5.6
Average Holotype QCM	QCMh	all		8
Highest Best Specimens	QCMb	*T. proriger,* *P. tympaniticus*	YPM 58129, AMNH FR221	9
Mean Composite Score	QCMc	all		6.2
Highest Composite Score	QCMc	many		36

TABLE 4. Mean completeness comparisons by substage. Mean substage sea level (Miller 2005), species diversity (Species), generic diversity (Genus), and time-averaged species diversity (Averaged) curves were compared. TCMav, QCMav and ICMav represent mean substage completeness using average completeness for all specimens per species (TCMtot, QCMtot, ICMtot) in the substage. TCMall, QCMall and ICMall are averages of all specimens assigned to substage, regardless of species status. TCMsp, QCMsp, and TCMsp are average completeness values per substage using only specimens with a designated species epithet.

	Sea Level	TCMall	QCMall	ICMall	TCMsp	QCMsp	ICMsp	Genus	Species
TCMall	-0.06								
QCMall	-0.2								
ICMall	-0.24								
TCMsp	0.04	0.75**							
QCMsp	-0.06		0.84**						
ICMsp	-0.01			0.69**					
Genus	0.04	-0.17	0.03	-0.04	0.15	0.24	0.37		
Species	0.22	-0.43	-0.01	-0.13	0.05	0.24	0.26	0.8**	
Averaged	0.13	-0.49	-0.04	-0.15				0.8**	0.98**
TCMav		0.58			0.81**				
QCMav			0.68*			0.53			
ICMav				0.6			0.64*		

* significant at $p<0.05$; ** significant after false discovery rate correction using method of Benjamini and Hochberg (1995).

1246 **TABLE 5.** Summary of GLS multiple regression analysis, showing the full and best models

1247 for predicting both diversity and TCM with autocorrelation structure for age parameter.

Model	Parameters	AIC	BIC	Log likelihood
Full averaged diversity	TCM sea level MPBFs	66.183	66.739	-26.091
Best averaged diversity	sea level MPBFs	60.251	61.435	-24.126
Full TCMsp	diversity sea level MPBFs	78.753	79.309	-32.376
Best TCMsp	diversity sea level MPBFs	78.753	79.309	-32.376

1248

1249 **TABLE 6.** Summary of best-fitting GLS multiple regression models for predicting averaged
1250 diversity and TCMsp with autocorrelation structure for age parameter.

Response	Parameters	Value	SE	t	*p*
Averaged diversity	intercept	-5.79	1.531	-3.782	0.004
	sea level	0.246	0.05	5.039	0.001
	MPBFs	0.521	0.024	21.774	< 0.001
TCMsp	intercept	7.01	4.312	1.625	0.14
	species diversity	-0.707	0.587	1.131	0.29
	sea level	0.17	0.15	-1.205	0.26
	MPBFs	0.116	0.333	0.347	0.74

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TABLE 7. Correlation between species properties and completeness measures, showing Spearman correlation coefficients. Correlation tests were run over the following variables by species: average overall completeness by species (TCM, QCM and ICM); body length (Length) from Polcyn *et al*. (2014); Google Scholar “hits” (Google) for the species name; number of specimens analysed for that species (Specimens); and years since species first described (Years). Best of species (TCMb, QCMb, ICMb) and composite completeness (TCMc, QCMc, ICMc) were also compared to average species completeness values.

	Specimens	Google	Length	TCM	QCM	ICM
Years	0.47**	0.55**	0.25	-0.28*	-0.34*	-0.30
Specimens		0.49**	0.25	-0.41**	-0.49**	-0.50**
Google			0.26	-0.05	-0.14	-0.19
Length				-0.08	-0.12	-0.19
TCMb				0.66**		
TCMc				0.04		
QCMb					0.50**	
QCMc					0.07	
ICMb						0.37**
ICMc						0.05

* significant at $p<0.05$; ** significant after false discovery rate correction using method of Benjamini and Hochberg (1995).

TABLE 8. North American outcrop area vs. species diversity and mean species completeness per formation. There are no significant correlations (Area vs. Diversity, $r_s = 0.60$ $p = 0.35$; Area vs. TCM, $r_s = 0$, $p = 1$; Diversity vs. TCM, $r_s = 0.2$, $p = 0.78$)

Group	Area (km^2)	Diversity	TCM
Pierre (NA)	310728	11	8.51
Niobrara (KS)	21091	10	5.35
Mooreville (AL)	315788	12	3.35
Monmouth (NJ)	21506	6	1.93
Moreno (CA)	23358	2	4.95

Figure Captions

FIG. 1. Beardmore scoring method for mosasaur taphonomic completeness metric (TCM). Each complete region of the skeleton (skull, ribs, forelimbs, hindlimbs and vertebrae (verts.) including cervicals, dorsals, or caudals) is each worth 4 points, for a maximum possible score of 36. Beardmore scoring can assess taphonomy. Scoring is as follows: 1. Count or approximate number of elements for each region. 2. In incomplete skeletons, score one for any girdle elements. 3. If vertebrae are undifferentiated, their score is the proportion present x 12 (if only two undifferentiated vertebrae, score = 2). 4. Any portion of a skull + any portion of a jaw or tooth = 2. 5. Sum scores for each region. Skeletal image © Scott Hartman.

FIG. 2. Mosasaur specimen completeness by substage, for specimens whose age is known. Mean completeness by substage was calculated, according to TCMall (A), QCMall (B), and ICMall (C), with 95% confidence intervals, except for the early–middle Coniacian because there are very few specimens. Completeness was plotted including and excluding specimens consisting of only teeth. Statistics are shown here for specimens including teeth: TCMall vs. QCMall (Spearman, $r_s = 0.71$, $p < 0.01$), TCMall vs. ICMall (Spearman, $r_s = 0.77$, $p < 0.01$), QCMall vs. ICMall, (Spearman, $r_s = 0.97$, $p << 0.001$). When comparing differences between time bins, TCMall (Kruskal-Wallis, $\chi^2 = 597.73$, df = 12, $p < 0.001$), QCMall (Kruskal-Wallis, $\chi^2 = 219.08$, df = 12, $p < 0.001$), and ICMall (Kruskal-Wallis, $\chi2 = 529.56$, df = 12, $p < 0.001$). For specimens *not* including teeth alone: when comparing differences between time bins (TCMall, Kruskal-Wallis, $\chi^2 = 30.05$, df = 12, $p = 0.003$; QCMall, Kruskal-Wallis,$\chi^2 = 537.22$, df = 12, $p < 0.001$; ICMall, Kruskal-Wallis,$\chi2 = 38.38$, df = 12, $p = 0.001$).

FIG. 3. Comparing mosasaur species completeness by substage. Mean and 95% confidence intervals are plotted, and curves are plotted with and without teeth. Statistics for all specimens

including teeth: TCMsp. vs. QCMsp (Spearman: $r_s = 0.85$, $p < 0.001$), TCMsp. vs. ICMsp (Spearman: $r_s = 0.89$, $p << 0.001$), QCMsp. vs. ICMsp (Spearman: $r_s = 0.96$, $p << 0.001$). In comparing completeness between time bins, TCMsp (Kruskal-Wallis, $\chi2 = 598.7904$, df = 11, $p < 0.001$), QCMsp (Kruskal-Wallis, $\chi2 = 332.5136$, df = 11, $p < 0.001$), ICMsp (Kruskal Wallis: $\chi2 = 596.8376$, df = 11, $p < 0.001$). Statistics for all specimens *not* including teeth alone: TCMsp. – Kruskal-Wallis: $\chi2 = 28.13$, df = 11, $p = 0.003$), QCMsp (Kruskal-Wallis, $\chi2 = 518.28$, df = 11, $p < 0.001$); ICMsp (Kruskal-Wallis, $\chi2 = 30.87$, df = 11, $p = 0.001$).

FIG. 4. Mosasaur diversity and sea level through time. A. Generic and species diversity lines include only specimens with an exact substage assignment; the “averaged species” curve includes both in-bin species records, Lazarus taxa plus species based on specimens that could not be assigned to a stratigraphic substage with confidence, and so are averaged over all possible bins (e.g. two possible time bins, each species rated 0.5 per bin; three possible time bins, each species rated 0.33 per bin). B. Mean substage sea level from data available in Miller *et al.* (2005), and showing 95% confidence intervals.

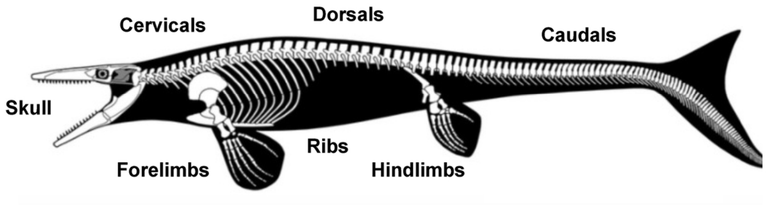
FIG. 5. Completeness by taxonomic rank. The mean completeness (TCM) was calculated for specimens in each category: Mosasauridae indeterminate, specimens identified to genus or identified to species. There are highly significant differences in TCM when comparing all three different taxonomic ranks (Kruskal-Wallis, $\chi^2 = 95.62$, df = 2, $p < 0.001$). A. Results for all specimens including those consisting of a single tooth. In this case, there was no significant difference between completeness between genus and species specimens, because the median for each group = 1 (Wilcoxon: W=731307, p = 0.09). B. Plot for specimens *not* consisting of only teeth (Kruskal-Wallis, $\chi^2 = 248.64$, df = 38, $p < 2.2e\text{-}16$). There are highly significant differences between groups, including genus and species.

FIG. 6. Completeness by lithology. All specimens identified to species were assigned to the main lithology of their formation of origin. There are highly significant differences in TCM between different lithologies (Kruskal-Wallis, $\chi^2 = 364.44$, df = 3, $p < 0.001$). Differences remain when specimens consisting of only teeth are left out, but are barely significant (Kruskal-Wallis, $\chi^2 = 7.63$, df = 3, $p < 0.05$; plot not shown).

FIG. 7. Completeness by palaeogeographical region. Fossils named to species were divided by geographical origin. Because of a relative paucity of specimens, Africa, South America, Australia, New Zealand and Antarctic specimens were included in a "Gondwana" group. Mean TCM of species-named specimens showed highly significant differences between groups (Kruskal-Wallis, $\chi^2 = 701.46$, df = 2, $p < 0.001$). When tooth-only specimens are left out of analysis, the differences are no longer significant (Kruskal-Wallis, $\chi^2 = 0.9303$, df = 2, $p = 0.63$; plot not shown).

FIG. 8. Completeness by well-known formations. There were over 100 formations to choose from. In this case, some of the best-known formations were compared. The mean TCM values for specimens named to species between formation groups showed highly significant differences (Kruskal-Wallis, $\chi^2 = 595.89$, df = 5, $p < 0.001$. Differences remain when tooth-only specimens are left out (Kruskal-Wallis, $\chi^2 = 32.05$, df = 5, $p < 0.001$; plot not included).

FIG. 9. Completeness by body size groups. There were no statistical differences between mean completeness (TCMtot) values of species among small, medium or large mosasaurs.



Taphonomic Completeness Metric (TCM)

Score:	0	1	2	3	4
Skull	Head is absent	A few elements remaining	Approx. 1/2 elements remaining	A few elements missing	Complete skull
Cervical vertebrae	0 vertebrae	1 or 2	3 or 4	5 or 6	7 vertebrae
Forelimbs	All bones absent	1 of 4 subunits present	2 of 4 subunits absent	3 of 4 subunits present	Humerus, radius, ulna and most phalanges
Ribs	No ribs	Extensive loss of ribs	Approx. 1/2 ribs	Approx. 3/4 ribs	Most ribs present
Dorsal vertebrae	0-2 vertebrae	10-25%	25-50%	50-75%	At least 12 present
Hindlimbs	All bones absent	1 of 4 subunits present	2 of 4 subunits present	3 of 4 subunits present	Femur, tibia, fibula and most phalanges
Caudal vertebrae	0-4 vertebrae	10-25%	25-50%	50-75%	>75%

Beardmore scoring method for mosasaur taphonomic completeness metric (TCM). Each complete region of the skeleton (skull, ribs, forelimbs, hindlimbs and vertebrae (verts.) including cervicals, dorsals, or caudals) is each worth 4 points, for a maximum possible score of 36. Beardmore scoring can assess taphonomy. Scoring is as follows: 1. Count or approximate number of elements for each region. 2. In incomplete skeletons, score one for any girdle elements. 3. If vertebrae are undifferentiated, their score is the proportion present x 12 (if only two undifferentiated vertebrae, score = 2). 4. Any portion of a skull + any portion of a jaw or tooth = 2. 5. Sum scores for each region. Skeletal image © Scott Hartman.

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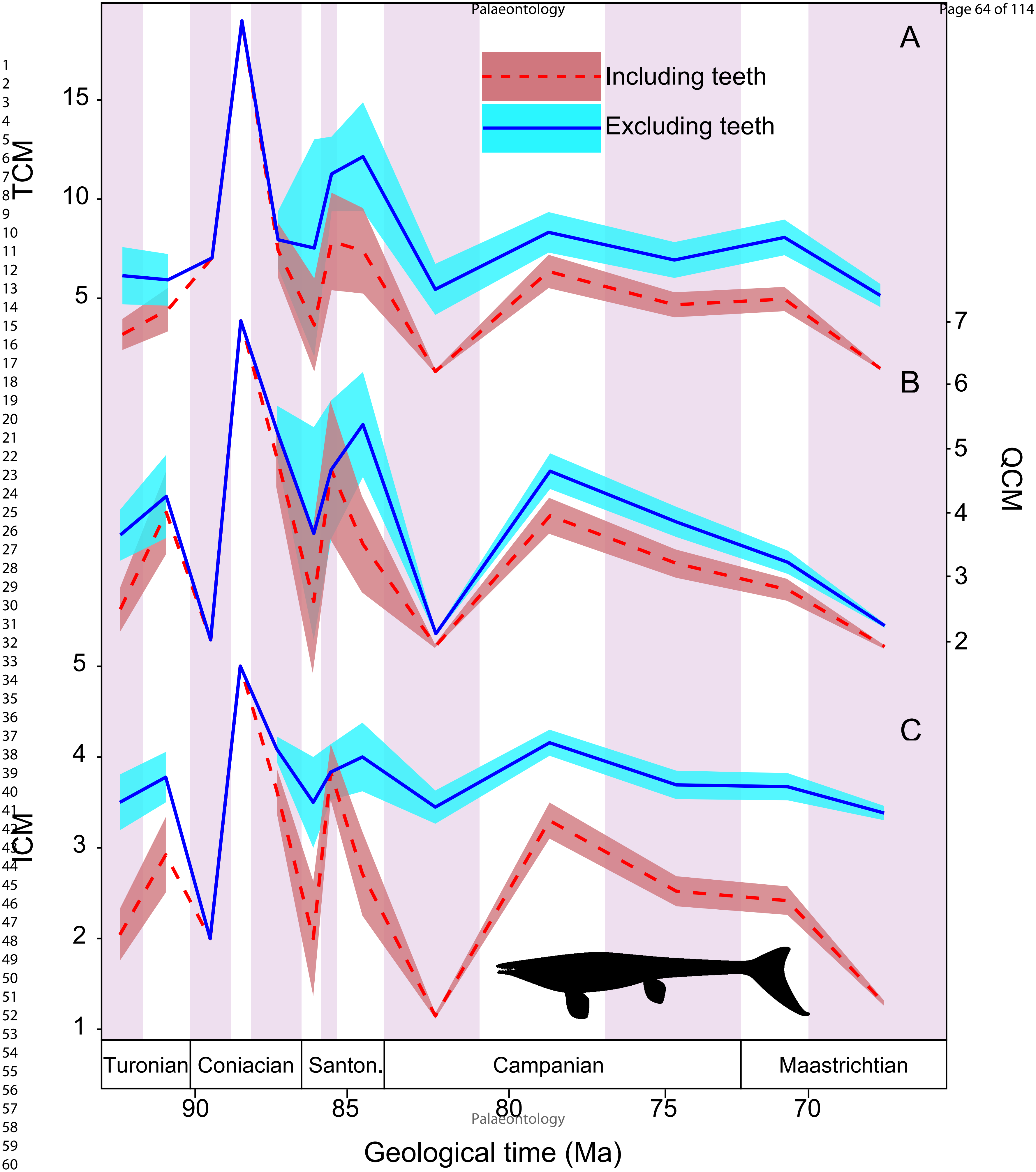
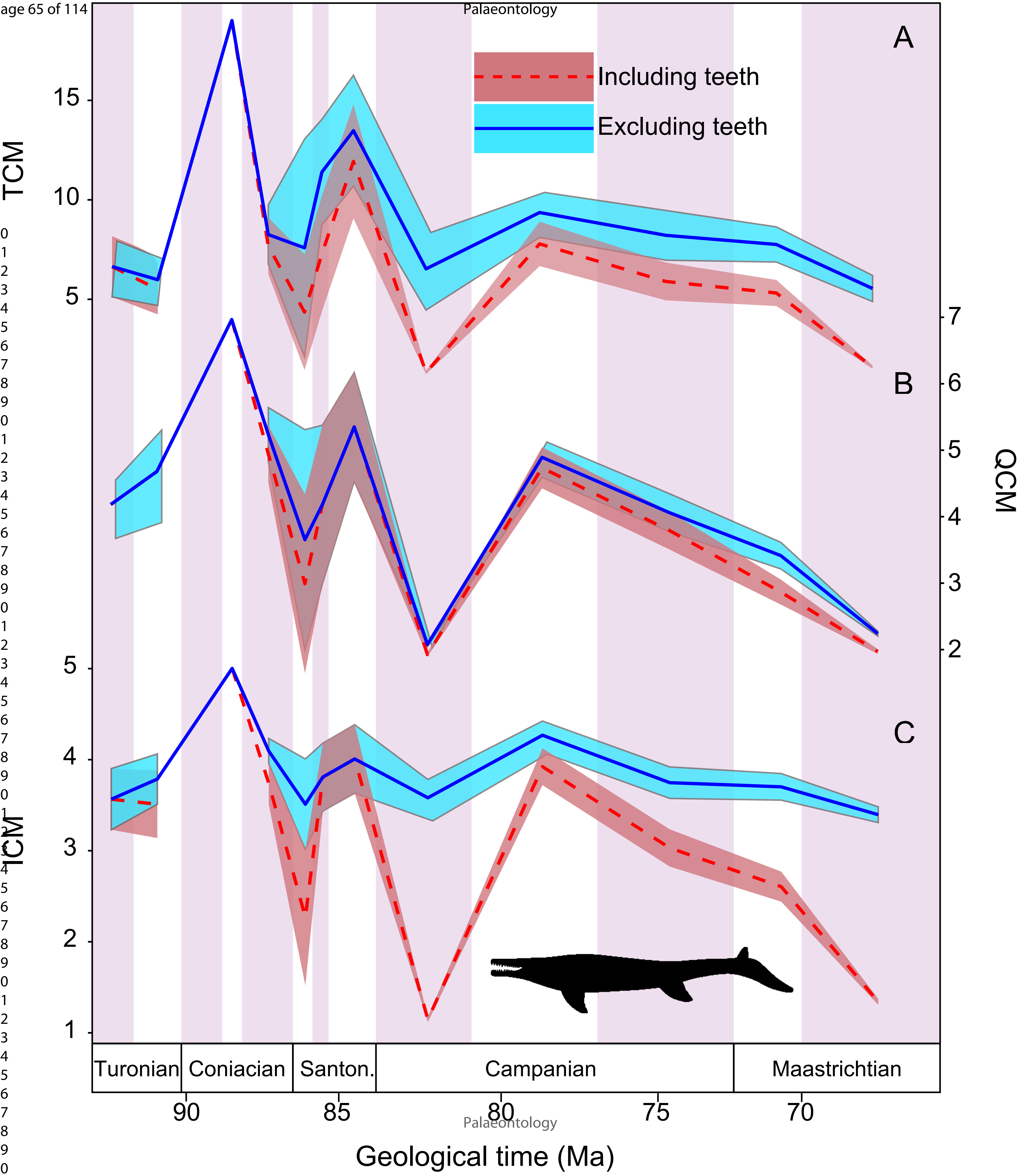

A
B
C
Including teeth
Excluding teeth
TCM
15
10
5
TCM
5
4
3
2
1
QCM
7
6
5
4
3
2
Turonian
Coniacian
Santon.
Campanian
Maastrichtian
90
85
80
75
70
Geological time (Ma)


A
B
C
Including teeth
Excluding teeth
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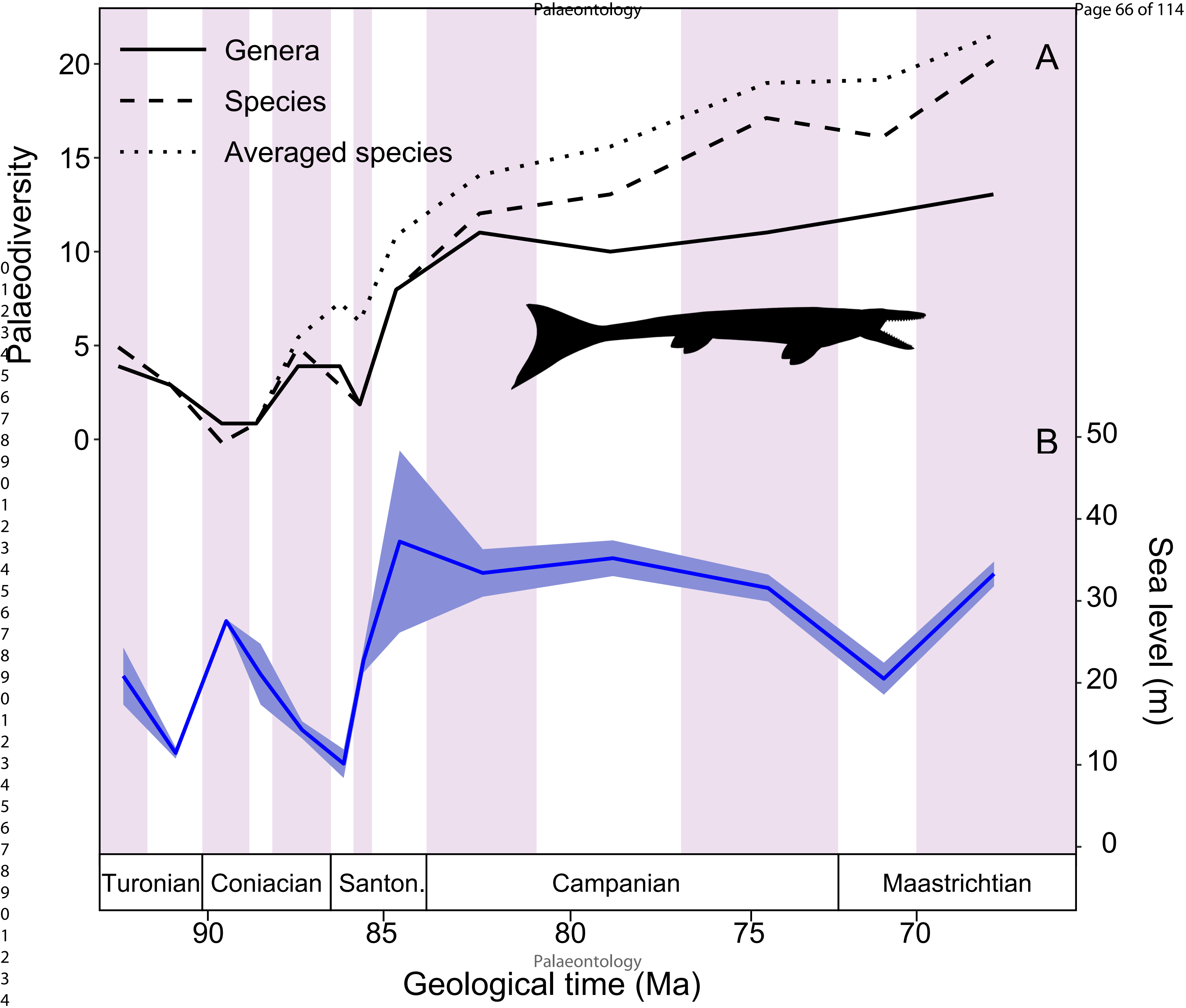
Coniacian
Santon.
Campanian
Maastrichtian
90
85
80
75
70
Geological time (Ma)


Genera
Species
Averaged species
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B
Palaeodiversity
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5
10
15
20
Sea level (m)
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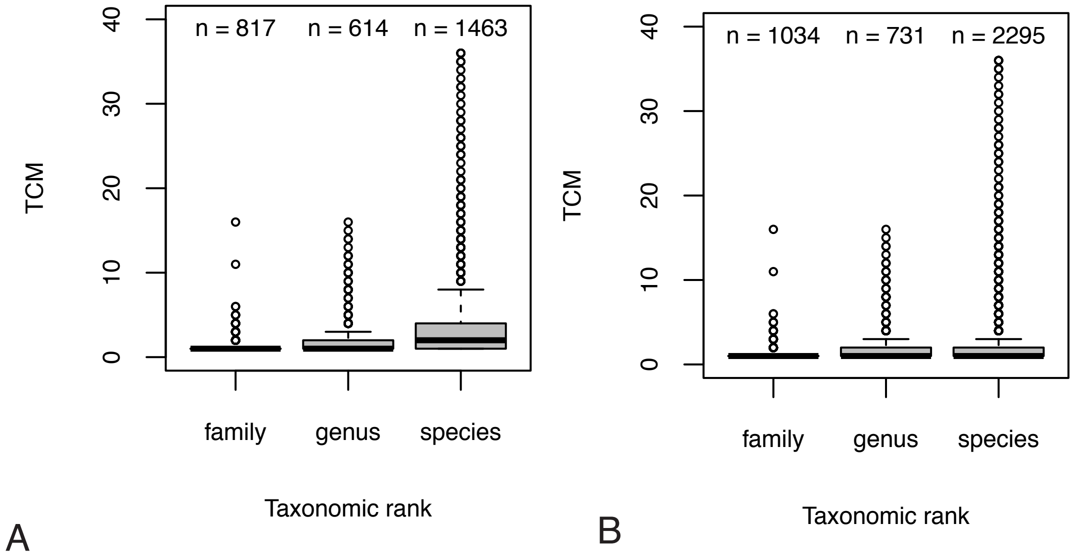
10
20
30
40
50
Turonian
Coniacian
Santon.
Campanian
Maastrichtian
90
85
80
75
70
Geological time (Ma)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genus
species
Taxonomic rank
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10
20
30
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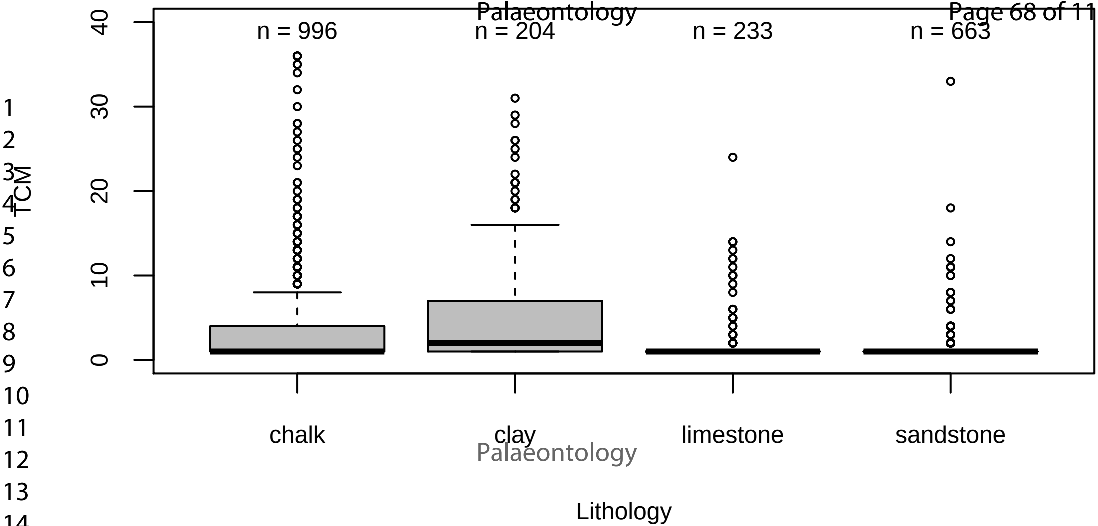
family
genus
species
Taxonomic rank
B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20
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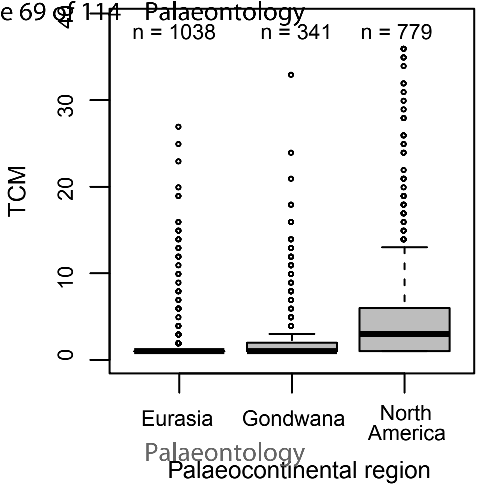
sandstone
Lithology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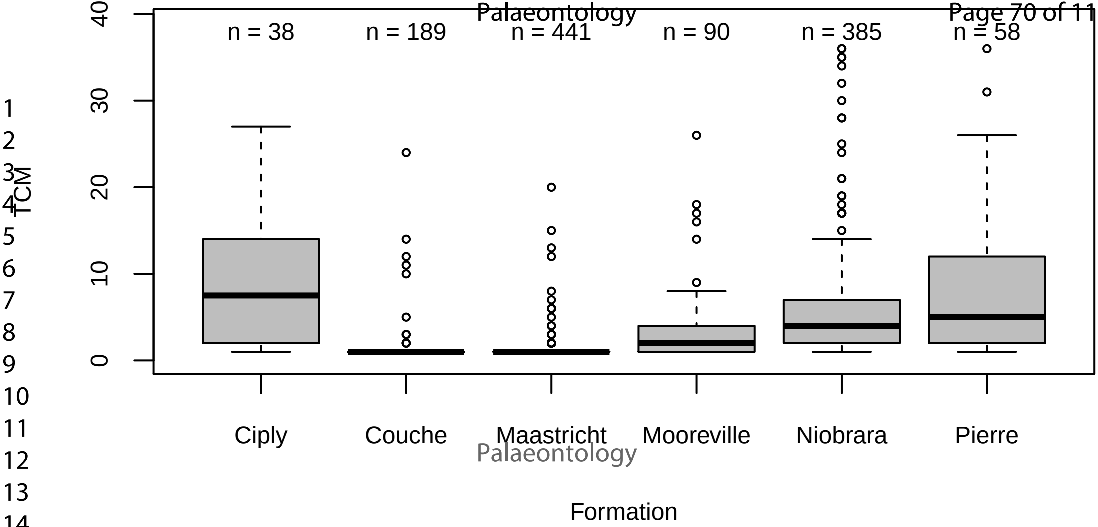
20
30
40
Eurasia
Gondwana
North America
Palaeocontinental region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n = 385
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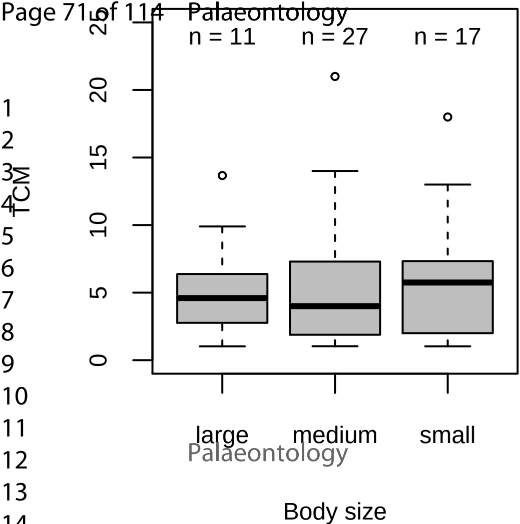
10
20
30
40
Ciply
Couche
Maastricht
Mooreville
Niobrara
Pierre
Formation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n = 17
TCM
0
5
10
15
20
25
large
medium
small
Body size

Supplementary Appendix for:

The mosasaur fossil record: through the lens of fossil completeness

Dan A. Driscoll, Alexander M. Dunhill, Thomas Stubbs and Michael J. Benton

Contents of the Supplementary Appendix

TABLE S1. Institutional abbreviations of museums with mosasaur specimens.

ALNHM	Alabama Natural History Museum, Tuscaloosa, AL USA
AMNH	American Museum of Natural History, New York City, NY USA
ANSP	Academy of Natural Sciences at Drexel University, Philadelphia, PA USA
AUMP	Auburn University Dept. Paleontology, Auburn, AL USA
BADL	Badlands National Park, Interior, SD USA
BSP	Bayerische Staatssammhung für Paläontologie, Munich, Germany
BMB	Booth Museum of Natural History, Brighton, UK
BRV	Dept. of Geosciences, Universidad Nacional de Colombia, Santafe de Bogota, Colombia
CCMGE	Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia
CAUK	Institut für Geowissenschaften der Christian-Albrechts-Universität, Kiel, Germany
CDM	Courtenay and District Museum, Courtenay, BC, Canada
CIT	California Institute of Technology (Now housed at LACM), Pasadena, CA USA
CM	Carnegie Museum, Pittsburgh, PA USA
CMN	Canadian Museum of Nature, Ontario, Canada
CM	Canterbury Museum, Christchurch, NZ
CPUC	Departamento de Geología of the Universidad de Concepcíon, Concepción, Chile
CVAI	Colección Vertebrados Asociación Isurus**.**
DMNH	Perot Museum (formerly Dallas Museum of Natural History), Dallas, TX USA
DMNS	Denver Museum of Nature and Science, Denver, CO USA
ENCI	ENCI Company Collection, Maastricht, Holland
ETSU	East Texas State University (housed at UT Vertebrate Paleontology Lab), Commerce TX USA
FFM	Fick Fossil Museum, Oakley, KS USA
FGM	Fryxell Geology Museum, Augustana College, Rock Island, IL USA
FHSM	Sternberg Museum, Fort Hays, KS USA
FMNH	Field Museum of Natural History, Chicago, IL USA
GCB	Geo Centrum Brabant, Boxtel, Netherlands
GNS	GNS Paleontological Collection, Lower Hutt, New Zealand
GPIT	University of Tübingen, Tübingen, Germany
GSA(TC)	Geological Survey of Alabama, Tuscaloosa, AL USA
GZG	Geowissenschaftliches Zentrum der Universistät, Göttingen, Germany
HMG	Hobetsu Museum (Geology Collection), Mukawa City, Hokkaido Prefecture, Japan
HU	Hacetteppe University, Ankara, Turkey
HUJ	Hebrew University, Jerusalem, Israel
IAA	Instituto Antártico Argentino
IGNS	Institute of Geology and Natural Science, Lower Hutt, New Zealand
IGPUW	Instytut Geologii Podstawowej, Uniwersytet Warszawski, Warsaw, Poland
ING	Instituto Columbiano de Geologia
IPRFWU	Institut für Paläeontologie der Rheinische, Friedrich Wilhelms Universität, Bonn, Germany
IRS(c)NB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
KHM	Kaikoura Historical Museum, Kaikoura, New Zealand
KrMG	Kristianstad Museum of Geology Kristiamstad, Sweden
KUVP	Biodiversity Institute and Natural History Museum, University of Kansas,

	Manhattan, KS, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA USA
LO, LR	Dept. Of Geology, Lund University, Lund, Sweden
MAPS	Monmouth Amateur Paleontological Society, Long Branch, NJ USA
MCM	Mikasa City Museum, Hokkaido, Japan
MCNA	Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Alava, Spain
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA USA
MKD	Muzeum Nadwiślanśkie, Kazimierz, Dolny, Poland
MDM	Morden and District Museum, Manitoba, Canada
MEL	Museum Emmanuel Liais, Cherbourg, France
MGGC	Museo Geologico Giovanni Cappelini, Bologna, Italy
MGSN	Museum of Geological Survey of Nigeria
MGUAN	Geological Museum, Universidade Agostinho Neto, Luanda, Angola
MGUH	Geological Museum University of Copenhagen, Denmark
MiaMM	Miami Museum, Manitoba, Canada
MHNH	Museum National d'Histoire Naturelle, Paris, France
MML	Museo Municipal de Lamarque, Río Negro Province, Argentina
MMMN	Manitoba Museum of Man and Nature, Manitoba, Canada
MN	Museu Nacional, Rio de Janeiro, Brazil
MOR	Museum of the Rockies, Bozeman, MT USA
MP	Museo Geologico Jose Royo y Gomez of Ingeominas, Santafe de Bogota, Colombia
MPPVS	Museum of Paleontology and Prehistory, S. Anna d'Alfaedo, Italy
MTM	Magyar Természettudományi Múzeum, Budapest, Hungary
MU	University of Missouri, Colombia, MO USA
MUVP	Mansoura University Vertebrate Paleontology Center, Mansoura University, Egypt
NHMM	Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands
NHMUK	The Natural History Museum, London, England, UK
NHMV	Natural History Museum of Verona, Italy
NJGS	New Jersey Geological Survey Trenton NJ USA
NJSM	New Jersey State Museum, Trenton, NJ USA
NMMNH	New Mexico Museum of Natural History, Albuquerque, NM USA
NMNZ	National Museum of New Zealand, Te Papa, Wellington, New Zealand
NZGS	New Zealand Geological Survey, Lower Hutt, New Zealand
PA	Paleo-Angola Project, Southern Methodist University, Dallas, TX USA
OIGM	Oviedas Geological Museum, Asturias, Spain
OCP	Office Chérifien des Phosphates, Khouribja, Morocco
PMU	Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden
RE	Ruhr Museum, Essen, Germany
RGM	Rutgers Geology Museum Rutgers University NJ, USA
RMDC	Rocky Mountain Dinosaur Center, Woodland Park, CO USA
RMH	Roemer Museum, Hildesheim, Germany
RMM	Red Mountain Museum (housed at McWane Science Center), Birmingham, AL USA
RMPZ	Swedish Museum of Natural History, Dept. of Palaeozoology, Stockholm, Sweden
SAM	South African Museum, Cape Town, South Africa

SDMNH	San Diego Museum of Natural History, San Diego, CA USA
SDSM(T)	South Dakota School of Mines and Technology Geology Museum, Rapid City, SD USA
SEM	Southern Environmental Museum, Birmingham Southern College, Birmingham, AL USA
SGU	Geologic Survey of Sweden, Stockholm, Sweden
SGM	Servicio Geologico Mexicano, Chihuahua, Mexico
SGMA	Servicos de Geologia e Minas de Angola,
SGS	Saudi Geological Society, Paleontological Collection, Jiddah, Kingdom of Saudi Arabia
SMBU	Strecker Museum, Baylor University at Waco, TX USA
SMU	Schuler Museum, Southern Methodist University, Dallas, TX USA
TLAM	Timber Lake Museum Area Museum, Timber Lake, SD USA
TMA	University of Texas Arlington Collection, TX USA
TM	Teylers Museum, Haarlem, The Netherlands
TMM	Texas Memorial Museum (at Vertebrate Paleontology Lab), University of Texas, Austin, TX USA
TMP	Royal Tyrell Museum of Palaeontology, Drumheller, Alberta, Canada
TSJC	Trinidad State Junior College, Trinidad, CO USA
TSMHN	Teylers Strichtina Museum, Haarlem, Netherlands
UAVPL	University of Alberta Vertebrate Paleontology Lab, Edmonton, Alberta, Canada
UCBL	University Claude Bernard-Lyon, Villeurbanne, France
UCMP	University of California Museum of Paleontology, Berkeley, CA USA
UD	University of Damascus Geology Dept., Damascus, Jordan
UNO	University of New Orleans, LA USA
UP	University of Poitiers, France
UPI	University of Uppsala, Uppsala, Sweden
UPS	U. Paul-Sabatier, Toulouse, France
USNM	Smithsonian Institution National Museum of Natural History, Washington DC, USA
USTL	Université des Sciences Tecniques du Languedoc, Vertebrate Paleontology Laboratory, Montpellier, France
UT	Unversité de Tunis, Tunisia
UVER	University of Vermont Zadock Thompson Natural History Collection, Burlington, VT USA
WC	Williams College Williamstown, MA USA
WDC	Wyoming Dinosaur Center, Thermopolis, WY USA
YPM	Yale Peabody Museum, New Haven, CT USA
ZIN	Zoological Institute, Academy of Sciences, St. Petersburg, Russia

TABLE S2. Museum specimens examined

Museum	Number	Labelled Genus	Labelled Species	Museum	Number	Labelled Genus	Labelled Species
AMNH	192	*Clidastes*	*liodontus*	**DMNS**	49925	*Clidastes*	*propython*
AMNH	221	*Tylosaurus*	*proriger*	**DMNS**	1582	*Mosasaurus*	sp
BMNH	R263	Mosasauridae	indet	**DMNS**	2851	*Mosasaurus*	sp
BMNH	R291a, b	Mosasauridae	indet	**DMNS**	28261	*Mosasaurus*	sp
BMNH	R876	Mosasauridae	indet	**DMNS**	43405	*Mosasaurus*	sp
BMNH	R1231	Mosasauridae	indet	**DMNS**	48169	*Mosasaurus*	sp
BMNH	R1232	Mosasauridae	indet	**DMNS**	48172	*Mosasaurus*	sp
BMNH	R1233	Mosasauridae	indet	**DMNS**	60861	*Mosasaurus*	sp
BMNH	R1253	Mosasauridae	indet	**DMNS**	45872	*Platecarpus*	sp
BMNH	R1620	Mosasauridae	indet	**DMNS**	48522	*Platecarpus*	sp
BMNH	R2573	Mosasauridae	indet	**DMNS**	1578	*Platecarpus*	*coryphaeus*
BMNH	5642	Mosasauridae	indet	**DMNS**	1579	*Platecarpus*	*coryphaeus*
BMNH	R9805	Mosasauridae	indet	**DMNS**	1581	*Platecarpus*	*coryphaeus*
BMNH	R9806	Mosasauridae	indet	**DMNS**	48616	*Platecarpus*	*ictericus*
BMNH	R9816	Mosasauridae	indet	**DMNS**	40988	*Platecarpus*	*tympaniticus*
BMNH	R10122	Mosasauridae	indet	**DMNS**	18352	*Prognathodon*	*overtoni*
BMNH	11591	Mosasauridae	indet	**DMNS**	2435	*Tylosaurus*	*proriger*
BMNH	11593	Mosasauridae	indet	**DMNS**	21813	*Tylosaurus*	*proriger*
BMNH	11599	Mosasauridae	indet	**ETSU**	L555	Mosasuaridae?	indet
BMNH	R11895	Mosasauridae	indet	**ETSU**	4299	Mosasauridae	indet
BMNH	R11896	Mosasauridae	indet	**ETSU**	4272	Mosasauridae	indet
BMNH	R11897	Mosasauridae	indet	**ETSU**	L751	Mosasauridae	indet
BMNH	R11901	Mosasauridae	indet	**ETSU**	?	*Globidens*	*fraasi*
BMNH	R11902	Mosasauridae	indet	**ETSU**	L569	*Clidastes*	sp
BMNH	R11903	Mosasauridae	indet	**ETSU**	4314	*Clidastes*	sp
BMNH	R11904	Mosasauridae	indet	**ETSU**	4349	*Clidastes*	sp
BMNH	R11905	Mosasauridae	indet	**ETSU**	4353	*Clidastes*	sp
BMNH	R11908	Mosasauridae	indet	**ETSU**	4354	*Clidastes*	sp
BMNH	R11910	Mosasauridae	indet	**ETSU**	4369	*Clidastes*	sp
BMNH	R11915	Mosasauridae	indet	**ETSU**	4370	*Clidastes*	*propython*
BMNH	R11917	Mosasauridae	indet	**ETSU**	4278	*Clidastes*	*propython*
BMNH	R11918	Mosasauridae	indet	**ETSU**	4281	*Clidastes*	*propython*
BMNH	R11919	Mosasauridae	indet	**ETSU**	4290	*Clidastes*	*propython*
BMNH	R11920	Mosasauridae	indet	**ETSU**	4293	*Clidastes*	*propython*
BMNH	R11921	Mosasauridae	indet	**ETSU**	4295	*Clidastes*	*propython*
BMNH	R11925	Mosasauridae	indet	**ETSU**	4307	*Clidastes*	*propython*
BMNH	R11926	Mosasauridae	indet	**ETSU**	L394	*Clidastes*	*propython*
BMNH	R11927	Mosasauridae	indet	**ETSU**	4329	*Mosasaurus*	sp
BMNH	R11929	Mosasauridae	indet	**ETSU**	4350	*Mosasaurus*	sp
BMNH	R11931	Mosasauridae	indet	**ETSU**	4288	*Platecarpus*	sp
BMNH	R11932	Mosasauridae	indet	**ETSU**	4306	*Platecarpus*	sp
BMNH	36557	Mosasauridae	indet	**ETSU**	4311	*Platecarpus*	sp
BMNH	37000	Mosasauridae	indet	**ETSU**	4312	*Platecarpus*	sp
BMNH	39423	Mosasauridae	indet	**ETSU**	4344	*Platecarpus*	sp
BMNH	39425	Mosasauridae	indet	**ETSU**	4347	*Platecarpus*	sp
BMNH	41383	Mosasauridae	indet	**ETSU**	L551	*Platecarpus*	sp
BMNH	42963	Mosasauridae	indet	**ETSU**	4327	*Platecarpus*	*ictericus*
BMNH	42977	Mosasauridae	indet	**ETSU**	4319	*Tylosaurus*	sp
BMNH	42999	Mosasauridae	indet	**ETSU**	4336	*Tylosaurus*	sp
BMNH	43193	Mosasauridae	indet	**ETSU**	4337	*Tylosaurus*	sp
BMNH	43194	Mosasauridae	indet	**ETSU**	4340	*Tylosaurus*	sp
BMNH	43200	Mosasauridae	indet	**ETSU**	4341	*Tylosaurus*	sp
BMNH	47954	Mosasauridae	indet	**ETSU**	4342	*Tylosaurus*	sp

BMNH	48942	Mosasauridae	indet	**ETSU**	4350	*Tylosaurus*	sp
BMNH	49916	Mosasauridae	indet	**ETSU**	4358	*Tylosaurus*	sp
BMNH	R11928	*Angolasaurus*	sp	**ETSU**	4359	*Tylosaurus*	sp
BMNH	R5641	*cf. Clidastes*	sp	**ETSU**	4366	*Tylosaurus*	sp
BMNH	R473	*Clidastes*	sp	**ETSU**	4377	*Tylosaurus*	sp
BMNH	R3903	*Clidastes*	sp	**ETSU**	4390	*Tylosaurus*	sp
BMNH	R3904	*Clidastes*	sp	**ETSU**	L583	*Tylosaurus*	sp
BMNH	R3905	*Clidastes*	sp	**ETSU**	L567-2	*Tylosaurus*	sp
BMNH	R5641	*Clidastes*	sp	**ETSU**	4274	*Tylosaurus*	*proriger*
BMNH	R2946	*Clidastes*	*pumilis*	**ETSU**	4282	*Tylosaurus*	*proriger*
BMNH	R4537	*Clidastes*	*tortor*	**ETSU**	4283	*Tylosaurus*	*proriger*
BMNH	R4547	*Clidastes*	*tortor*	**ETSU**	4291	*Tylosaurus*	*proriger*
BMNH	R8697	*Globidens*	sp	**ETSU**	4324	*Tylosaurus*	*proriger*
BMNH	547	*Globidens*	*fraasi*	**ETSU**	4345	*Tylosaurus*	*proriger*
BMNH	R5658	*Goronyosaurus*	*nigeriensis*	**ETSU**	4346	*Tylosaurus*	*proriger*
BMNH	R5673	*Goronyosaurus*	*nigeriensis*	**ETSU**	4356	*Tylosaurus*	*proriger*
BMNH	R5674	*Goronyosaurus*	*nigeriensis*	**ETSU**	4357	*Tylosaurus*	*proriger*
BMNH	R5675	*Goronyosaurus*	*nigeriensis*	**ETSU**	4364	*Tylosaurus*	*proriger*
BMNH	R5676	*Goronyosaurus*	*nigeriensis*	**ETSU**	4375	*Tylosaurus*	*proriger*
BMNH	R5677	*Goronyosaurus*	*nigeriensis*	**ETSU**	4389	*Tylosaurus*	*proriger*
BMNH	R5678	*Goronyosaurus*	*nigeriensis*	**ETSU**	4395	*Tylosaurus*	*proriger*
BMNH	R5679	*Goronyosaurus*	*nigeriensis*	**ETSU**		*Tylosaurus*	*proriger*
BMNH	R5680	*Goronyosaurus*	*nigeriensis*	**ETSU**	4268	*Tylosaurus*	*proriger*
BMNH	R5681	*Goronyosaurus*	*nigeriensis*	**ETSU**	4275	*Tylosaurus*	*proriger*
BMNH	R5682	*Goronyosaurus*	*nigeriensis*	**ETSU**	4276	*Tylosaurus*	*proriger*
BMNH	R5683	*Goronyosaurus*	*nigeriensis*	**ETSU**	4279	*Tylosaurus*	*proriger*
BMNH	R5684	*Goronyosaurus*	*nigeriensis*	**ETSU**	4282	*Tylosaurus*	*proriger*
BMNH	R5688	*Goronyosaurus*	*nigeriensis*	**KUVP**	14263	*Platecarpus*	sp
BMNH	R8638	*Goronyosaurus*	*nigeriensis*	**KUVP**	14267	*Platecarpus*	sp
BMNH	R8640	*Goronyosaurus*	*nigeriensis*	**KUVP**	14273	*Platecarpus*	sp
BMNH	R8641	*Goronyosaurus*	*nigeriensis*	**KUVP**	14274	*Platecarpus*	sp
BMNH	R11912	*Goronyosaurus*	*nigeriensis*	**KUVP**	14276	*Platecarpus*	sp
BMNH	R11947	*Goronyosaurus*	*nigeriensis*	**KUVP**	14279	*Platecarpus*	sp
BMNH	R11958	*Goronyosaurus*	*nigeriensis*	**KUVP**	14281	*Platecarpus*	sp
BMNH	48939	*Hainosaurus*	sp	**KUVP**	14282	*Platecarpus*	sp
BMNH	49935	*Hainosaurus*	sp	**KUVP**	14283	*Platecarpus*	sp
BMNH	R1227	*Leiodon*	*anceps*	**KUVP**	14286	*Platecarpus*	sp
BMNH	R1228	*Leiodon*	*anceps*	**KUVP**	14287	*Platecarpus*	sp
BMNH	48943	*Leiodon*	*anceps*	**KUVP**	14342	*Platecarpus*	sp
BMNH	42937	*cf Liodon*	sp	**KUVP**	14343	*Platecarpus*	sp
BMNH	R2742	*Liodon*	sp	**KUVP**	14345	*Platecarpus*	sp
BMNH	R812	*Liodon*	*haumuriensis*	**KUVP**	50112	*Platecarpus*	sp
BMNH	R813	*Liodon*	*haumuriensis*	**KUVP**	55219	*Platecarpus*	sp
BMNH	R814	*Liodon*	*haumuriensis*	**KUVP**	63287	*Platecarpus*	sp
BMNH	R815	*Liodon*	*haumuriensis*	**KUVP**	63388	*Platecarpus*	sp
BMNH	R816	*Liodon*	*haumuriensis*	**KUVP**	66329	*Platecarpus*	sp
BMNH	R817	*Liodon*	*haumuriensis*	**KUVP**	69451	*Platecarpus*	sp
BMNH	R818	*Liodon*	*haumuriensis*	**KUVP**	69456	*Platecarpus*	sp
BMNH	R819	*Liodon*	*haumuriensis*	**KUVP**	84858	*Platecarpus*	sp
BMNH	R5473	*Lleiodon*	*mosasuroid*	**KUVP**	85583	*Platecarpus*	sp

			es				
BMNH	5643	*Mosasaurus?*	sp	**KUVP**	85584	*Platecarpus*	sp
BMNH	R264	*Mosasaurus*	sp	**KUVP**	85585	*Platecarpus*	sp
BMNH	R820	*Mosasaurus*	sp	**KUVP**	85586	*Platecarpus*	sp
BMNH	R1231	*Mosasaurus*	sp	**KUVP**	1007	*Platecarpus*	*coryphaeus*
BMNH	R5884	*Mosasaurus*	sp	**KUVP**	4862	*Platecarpus*	*coryphaeus*
BMNH	R5887	*Mosasaurus*	sp	**KUVP**	14285	*Platecarpus*	*coryphaeus*
BMNH	R6376	*Mosasaurus*	sp	**KUVP**	14340	*Platecarpus*	*coryphaeus*
BMNH	R10107	*Mosasaurus*	sp	**KUVP**	14341	*Platecarpus*	*coryphaeus*
BMNH	R10110	*Mosasaurus*	sp	**KUVP**	66332	*Platecarpus*	*coryphaeus*
BMNH	R10111	*Mosasaurus*	sp	**KUVP**	66336	*Platecarpus*	*coryphaeus*
BMNH	R10112	*Mosasaurus*	sp	**KUVP**	66337	*Platecarpus*	*coryphaeus*
BMNH	R10113	*Mosasaurus*	sp	**KUVP**	89853	*Platecarpus*	*coryphaeus*
BMNH	R10114	*Mosasaurus*	sp	**KUVP**	27816	*Platecarpus*	*ictericus*
BMNH	R10117	*Mosasaurus*	sp	**KUVP**	50093	*Platecarpus*	*ictericus*
BMNH	R10118	*Mosasaurus*	sp	**KUVP**		*Plioplatecarpus*	sp
BMNH	R10119	*Mosasaurus*	sp	**KUVP**	950	*Prognathodon*	*overtoni*
BMNH	R10120	*Mosasaurus*	sp	**KUVP**		*Tylosaurus ?*	sp
BMNH	R10121	*Mosasaurus*	sp	**KUVP**	1015	*Tylosaurus*	sp
BMNH	42865	*Mosasaurus*	sp	**KUVP**	115002	*Tylosaurus*	sp
BMNH	42873	*Mosasaurus*	sp	**KUVP**	86160	*Tylosaurus*	sp
BMNH	42907	*Mosasaurus*	sp	**KUVP**	86643	*Tylosaurus*	sp
BMNH	42909	*Mosasaurus*	sp	**KUVP**	1032	*Tylosaurus*	*dyspelor*
BMNH	42947	*Mosasaurus*	sp	**KUVP**	1025	*Tylosaurus?*	*proriger*
BMNH	42948	*Mosasaurus*	sp	**KUVP**	1089	*Tylosaurus?*	*proriger*
BMNH	42952	*Mosasaurus*	sp	**KUVP**	947	*Tylosaurus*	*proriger*
BMNH	42959	*Mosasaurus*	sp	**KUVP**	1016	*Tylosaurus*	*proriger*
BMNH	42960	*Mosasaurus*	sp	**KUVP**	1017	*Tylosaurus*	*proriger*
BMNH	42962	*Mosasaurus*	sp	**KUVP**	1020	*Tylosaurus*	*proriger*
BMNH	42967	*Mosasaurus*	sp	**KUVP**	1029	*Tylosaurus*	*proriger*
BMNH	42977	*Mosasaurus*	sp	**KUVP**	1013	*Tylosaurus*	*proriger*
BMNH	R1224	*Mosasaurus*	*camperi*	**KUVP**	1033	*Tylosaurus*	*proriger*
BMNH	R1226	*Mosasaurus*	*camperi*	**KUVP**	1050	*Tylosaurus*	*proriger*
BMNH	42905	*Mosasaurus*	*camperi*	**KUVP**	1062	*Tylosaurus*	*proriger*
BMNH	42929	*Mosasaurus*	*camperi*	**KUVP**	1075	*Tylosaurus*	*proriger*
BMNH	42930	*Mosasaurus*	*camperi*	**KUVP**	69546	Mosasauridae	indet
BMNH	42931	*Mosasaurus*	*camperi*	**KUVP**	145196	Mosasauridae	indet
BMNH	42932	*Mosasaurus*	*camperi*	**KUVP**	152196	Mosasauridae	indet
BMNH	42933	*Mosasaurus*	*camperi*	**KUVP**	152204	Mosasauridae	indet
BMNH	42935	*Mosasaurus*	*camperi*	**KUVP**	152206	Mosasauridae	indet
BMNH	42936	*Mosasaurus*	*camperi*	**KUVP**	152211	Mosasauridae	indet
BMNH	42938	*Mosasaurus*	*camperi*	**KUVP**	1000	*Clidastes*	*tortor*
BMNH	42941	*Mosasaurus*	*camperi*	**KUVP**	1022	*Clidastes*	*velox*
BMNH	42942	*Mosasaurus*	*camperi*	**KUVP**	1026	*Clidastes*	*westii*
BMNH	42943	*Mosasaurus*	*camperi*	**KUVP**	1034	*Mosasaurus*	*missourriensis*
BMNH	42944	*Mosasaurus*	*camperi*	**KUVP**	134401	*Plioplatecarpus*	*sp*
BMNH	42945	*Mosasaurus*	*camperi*	**KUVP**	152217	*Plioplatecarpus*	*sp*
BMNH	42946	*Mosasaurus*	*camperi*	**KUVP**	1048	*Platecarpus*	*sp*
BMNH	42948	*Mosasaurus*	*camperi*	**KUVP**	1159	*Tylosaurus*	*proriger*
BMNH	42949	*Mosasaurus*	*camperi*	**KUVP**	1189	*Tylosaurus*	*proriger*
BMNH	42950	*Mosasaurus*	*camperi*	**KUVP**	1195	*Tylosaurus*	*proriger*
BMNH	42953	*Mosasaurus*	*camperi*	**KUVP**	1901	*Tylosaurus*	*proriger*
BMNH	11590	*Mosasaurus*	*dekayi*	**KUVP**	5033	*Tylosaurus*	*proriger*
BMNH	42929	*Mosasaurus*	*hoffmanni*	**KUVP**	28705	*Tylosaurus*	*proriger*
BMNH	R4004	*Platecarpus*	?	**KUVP**	66129	*Tylosaurus*	*proriger*
BMNH	R271	*Platecarpus*	sp	**IRSNB**		Mosasauridae	indet

BMNH	R3041	*Platecarpus*	sp	**IRSN B**		Mosasauridae	indet
BMNH	39424	*Platecarpus*	sp	**IRSN B**		*Mosasaurus*	*hoffmani*
BMNH	R4003	*Platecarpus*	sp	**IRSN B**	3098	*Mosasaurus*	*lemonnieri*
BMNH	R2837	*Platecarpus*	*coryphaeus*	**IRSN B**	3100	*Plioplatecarpus*	*houzeaui*
BMNH	R2840	*Platecarpus*	*coryphaeus*	**IRSN B**	3107	*Plioplatecarpus*	*houzeaui*
BMNH	R2833	*Platecarpus*	*ictericus*	**IRSN B**	3109	*Mosasaurus*	*lemonnieri*
BMNH	R2838	*Platecarpus*	*ictericus*	**IRSN B**	3111	*Plioplatecarpus*	*houzeaui*
BMNH	R4001	*Platecarpus*	*ictericus*	**IRSN B**	3113	*Mosasaurus*	*lemonnieri*
BMNH	R4005	*Platecarpus*	*ictericus*	**IRSN B**	3117	*Mosasaurus*	*lemonnieri*
BMNH	R813	*Plioplatecarpus*	sp	**IRSN B**	3119	*Mosasaurus*	*lemonnieri*
BMNH	R5868	*Plioplatecarpus*	sp	**IRSN B**	3125	*Mosasaurus*	*lemonnieri*
BMNH	42074	*Plioplatecarpus*	sp	**IRSN B**	3127	*Mosasaurus*	*lemonnieri*
BMNH	42939	*Prognathodon*	sp	**IRSN B**	3152	*Plioplatecarpus*	*houzeaui*
BMNH	48940	*Prognathodon*	sp	**IRSN B**	3153	*Mosasaurus*	*lemonnieri*
BMNH	R822	*Taniwhasaurus*	*oweni*	**IRSN B**	3169	*Mosasaurus*	*lemonnieri*
BMNH	R823	*Taniwhasaurus*	*oweni*	**IRSN B**	3186	*Mosasaurus*	*lemonnieri*
BMNH	R824	*Taniwhasaurus*	*oweni*	**IRSN B**	3187	*Mosasaurus*	*lemonnieri*
BMNH	R825	*Taniwhasaurus*	*oweni*	**IRSN B**	3188	*Plioplatecarpus*	*houzeaui*
BMNH	R826	*Taniwhasaurus*	*oweni*	**IRSN B**	3193	*Mosasaurus*	*lemonnieri*
BMNH	R2767	*cf. Tylosaurus*	sp	**IRSN B**	3210	*Mosasaurus*	*lemonnieri*
BMNH	R5292	*cf. Tylosaurus*	sp	**IRSN B**	3211	*Plioplatecarpus*	*houzeaui*
BMNH	R10939	*cf. Tylosaurus*	sp	**IRSN B**	3672	*Hainosaurus*	*bernardi*
BMNH	R2947	*Tylosaurus*	sp	**IRSN B**	3857	*Mosasaurus*	*lemonnieri*
BMNH	R2948	*Tylosaurus*	sp	**IRSN B**	3858	*Mosasaurus*	*lemonnieri*
BMNH	R3625	*Tylosaurus*	sp	**IRSN B**	3859	*Plioplatecarpus*	*houzeaui*
BMNH	R3626	*Tylosaurus*	sp	**IRSN B**	3860	*Mosasaurus*	*lemonnieri*
BMNH	R4548	*Tylosaurus*	sp	**IRSN B**	3861	*Mosasaurus*	*lemonnieri?*
BMNH	35615	*Tylosaurus*	sp	**IRSN B**	3911	*Mosasaurus*	*lemonnieri*
BMNH	35616	*Tylosaurus*	sp	**IRSN B**	4670	*Mosasaurus*	*lemonnieri*
BMNH	35617	*Tylosaurus*	sp	**IRSN**	4672	*Prognathodon*	*solvayi*

				B			
BMNH	35618	*Tylosaurus*	sp	**SMU**		*Mosasauridae*	indet
BMNH	35619	*Tylosaurus*	sp	**SMU**		*Mosasauridae*	indet
BMNH	35620	*Tylosaurus*	sp	**SMU**		*Mosasauridae*	indet
BMNH	35621	*Tylosaurus*	sp	**SMU**	72053	*Mosasauridae*	indet
BMNH	35624	*Tylosaurus*	sp	**SMU**	72208	*Mosasauridae*	indet
BMNH	35625	*Tylosaurus*	sp	**SMU**	72184	*Clidastes*	sp
BMNH	35626	*Tylosaurus*	sp	**SMU**	76499	*Mosasaurus*	*conodon*
BMNH	35727	*Tylosaurus*	sp	**SMU**	61799	*Platecarpus*	*coryphaeus*
BMNH	35634	*Tylosaurus*	sp	**SMU**	61767	*Platecarpus*	*cf somenensis*
BMNH	35635	*Tylosaurus*	sp	**SMU**	62046	*Tylosaurus*	sp
BMNH	35636	*Tylosaurus*	sp	**SMU**		*Tylosaurus*	*naepaolicus*
BMNH	40982	*Tylosaurus*	sp	**SMU**	76339	*Tylosaurus*	*naepaolicus*
BMNH	40983	*Tylosaurus*	sp	**SMU**	75374	*Tylosaurus*	*proriger*
BMNH	40984	*Tylosaurus*	sp	**SMU**	75586	*Tylosaurus*	*proriger*
BMNH	R3628	*Tylosaurus*	*dyspelor*	**TMM**	42035-1	Mosasauridae	sp
BMNH	R2949	*Tylosaurus*	*proriger*	**TMM**	42514-3	Mosasauridae	sp
DMNH	11872	*Clidastes*	sp	**TMM**	43414-1	Mosasauridae	sp
DMNH	12834	*Clidastes*	sp	**TMM**	43415-1	Mosasauridae	sp
DMNH	8769	*Latoplatecarpus*	*nichollsae*	**TMM**	43415-2	Mosasauridae	sp
DMNH	8561	*Platecarpus*	sp	**TMM**	43044-1	*Clidastes*	sp
DMNH	10408	*Platecarpus*	*planifrons*	**TMM**	3008-1	*Clidastes*	*propython*
DMNH	20114	*Platecarpus*	*planifrons*	**TMM**	30962-8	*Clidastes*	*propython*
DMNH	11409	*Tylosaurus*	*napaeolicus*	**TMM**	41934	*Globidens*	*alabamensis*
DMNH	1155	*Tylosaurus*	*proriger*	**TMM**	42921	*Halisaurus*	*platyspondylus*
DMNH	80298100	*Tylosaurus*	*proriger*	**TMM**	40566-1	*Halisaurus*	*sternbergi*
DMNH	8562	*Tylosaurus*	*proriger*	**TMM**	42352	*Liodon*	*sectorius*
DMNS	1723	Mosasauridae	indet	**TMM**	313-1	*Mosasaurus*	*maximus*
DMNS	2363	Mosasauridae	indet	**TMM**	40720-1	*Plotosaurus*	*bennisoni*
DMNS	2439	Mosasauridae	indet	**TMM**	42199-1	*Tylosaurus*	sp
DMNS	2443	Mosasauridae	indet	**TMM**	31051-64	*Tylosaurus*	*napaeolicus*
DMNS	22949	Mosasauridae	indet	**TMM**	43050-1	*Tylosaurus*	*napaeolicus*
DMNS	48871	Mosasauridae	indet	**TMM**	40601-1	*Tylosaurus*	*proriger*
DMNS	2360	*Clidastes*	sp.	**TMM**	40606-1	*Tylosaurus*	*proriger*
DMNS	47387	*Clidastes?*	sp	**TMM**	43046-1	*Tylosaurus*	*proriger*
				TMM	43047-1	*Tylosaurus*	*proriger*

TABLE S3. Mosasaur holotype references.

Author	**Year**	**Species List**	**Title**
Arambourg	1952	*Mosasaurus beaugei, Platecarpus ptychodon*	Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc – Algérie – Tunisie). Notes et Mémoires du Service Géologique du Maroc 92:1–372.
Bardet and Superbiola	2005	*Halisaurus arambourgi*	Bardet, N., X. Pereda Suberbiola, M. Iarochene, B. Bouya and M. Amaghzaz 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 et al	2005	*Globidens phosphaticus*	Bardet, N., X. P. Suberbiola, M. Iarochène, M. Amalik and B. Bouya 2005. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco, with description of a new species of *Globidens*. Netherlands Journal of Geosciences 84:167-175.
Bell and Polcyn	2005	*Dallasaurus turneri*	Bell, G. L. and M. J. Polcyn, 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.
Broom	1912	*Tylosaurus capensis*	Broom, R. 1912. On a species of *Tylosaurus* from the Upper Cretaceous beds of Pondoland. Annals of the South African Museum 7:332-3.
Camp	1942	*Plotosaurus bennisoni, Plesiotylosaurus crassidens*	Camp, C. L. 1942. California mosasaurs. University of California Memoirs 13:1-16.
Caldwell et al	2008	*Taniwhasaurus mikasaensis*	Caldwell, M. W., T. Konishi, I. Obata and K. Muramoto 2008. A new species of *Taniwhasaurus* (Mosasauridae, Tylosaurinae) from the Upper Santonian-Lower Campanian (Upper Cretaceous) of Hokkaido, Japan. Journal of Vertebrate Paleontology 28:339-348.
Christiansen and Bonde	2002	*Prognathodon curii*	Christiansen, P. and N. Bonde, 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22:629-644.
Cope	1869a	*Clidastes Propython, Plioplatecarpus depressus, Platecarpus tympaniticus*	Cope, E. D. 1869. On the reptilian ordcrs Pythonomorpha and Streptosauria. Boston Society of Natural History Proceedings 12:250-266.
Cope	1869b	*Tylosaurus proriger*	Cope, E. D. 1869. Remarks on *Holops brevispinus*, *Ornithotarsus immanis* and *Macrosaurus proriger*. Proceedings of the Academy of Natural Science Philadelphia 21: 123.
Cope	1869-70	*Prognathodon rapax*	Cope, E. D. 1869-1870. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. Transactions of the American Philosophical Society (issued in parts): 1:1-105; 2 (1870):106-235; 3(1870): i-vii, 236-232.
Cope	1871	*Prognathodon sectorius*	Cope, E. D. 1871. Supplement to the "Synopsis of the extinct Batrachia and Reptilia of North America." Proceedings of the American Philosophical Society 12:41-32.

Cope	1874	*Tylosaurus napaeolicus*	Cope, E. D. 1874. Review of the Vertebrata of the Cretaceous period found west of the Mississippi River. Bulletin of the United States Geological and Geographical Survey of the Territories Volume 1, Bulletin Number 2-First Series :13-48.
Cope	1881	*Mosasaurus conodon*	Cope, E. D. 1881. A new *Clidastes* from New Jersey. American Naturalist 15:586-587.
Crandell	1958	*Plioplatecarpus primaevus*	Crandell, D. R. 1958. Geology of the Pierre area, South Dakota. U. S. Geological Survey Professional Paper 307.
Cuthbertson et al	2007	*Latoplatecarpus (Plioplatecarpus) nichollsae*	Cuthbertson, R. S., J. C. Mallon, N. E. Campione and R. B. Holmes, 2007. A new species of mosasaur (Squamata: Mosasauridae) from the Pierre Shale (lower Campanian) of Manitoba. Canadian Journal of Earth Sciences 44:593-606.
Cuthbertson and Holmes	2015	*Plioplatecarpus peckensis*	Cuthbertson, R.S. and R. B. Holmes 2015. A new species of *Plioplatecarpus* (Mosasauridae, Plioplatecarpinae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of Montana, USA. Journal of Vertebrate Paleontology *35*:e922980.
Dollo	1882	*Plioplatecarpus marshi*	Dollo, L. 1882. Note sur l'ostéologie des Mosasauridæ. Bulletin du Musée d'Histoire Naturelle de Belgique 1:55-80.
Dollo	1885	*Hainosaurus bernardi*	Dollo, L. 1885. Le hainosaure. Revue des Questions Scientifiques 18:285–289.
Dollo	1889	*Plioplatecarpus houzeaui, Phosphorosaurus ortliebi, Prognathodon solvayi*	Dollo, L. 1889. Note sur les vertébrés récemment offerts au Musée de Bruxelles par M. Alfred Lemonnier. Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrogéologie 3:181-182.
Dollo	1904	*Prognathodon giganteus*	Dollo, L. 1904. Les mosasauriens de la Belgique. Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrogéologie, Mémoires,18:207-216.
Dollo	1913	*Carinodens belgicus*	Dollo, L. 1913. *Globidens Fraasi*, mosasaurien mylodonte nouveau du Maestrichtien (Cretac. supérieur) du Limbourg, et l'Ethologie de la Nutrition chez les mosasauriens. Archives de Biologie 28:09-626.
Dortangs, *et. al.*	2002	*Prognathodon saturator*	Dortangs, R. W., A. S. Schulp, E.W. Mulder, J. W. Jagt, H. H. Peeters and D. T. de Graaf 2002. A large new mosasaur from the Upper Cretaceous of The Netherlands. Netherlands Journal of Geosciences 81:1-8.
Everhart	2005	*Tylosaurus kansasensis*	Everhart, M. J. 2005. *Tylosaurus kansasensis*, a new species of tylosaurine (Squamata, Mosasauridae) from the Niobrara Chalk of western Kansas, USA. Netherlands Journal of Geosciences 84:231.
Fernandez and Martin	2009	*Taniwhasaurus antarcticus*	Fernandez, M. and J. E. Martin 2009. Description and phylogenetic relationships of *Taniwhasaurus antarcticus* (Mosasauridae, Tylosaurinae) from the upper Campanian (Cretaceous) of Antarctica. Cretaceous Research 30:717-726.
Gaudry	1892	*Prognathodon mosasauroides, Prognathodon anceps*	Gaudry, A. 1892. Les Pythonomorphes de France. Mémoires de la Société Géologique de France (Paléontologie) 10:13 and Pl. iv.

Gilmore	1912	*Globidens alabamensis*	Gilmore, C. W. 1912. A new mosasauroid reptile from the Cretaceous of Alabama. Proceedings of the United States National Museum, 40:479-484.
Goldfuss	1845	*Mosasaurus missouriensis*	Goldfuss, A. 1845. Der Schädelbau des Mosasaurus, durch Beschreibung einer neuen Art Gattung erläutert. Nova Acta Academiae Caesar Leopoldino-Carolinae Germanicae Natura Curiosorum 21:174–200
Konishi and Caldwell	2011	*Latoplatecarpus willistoni, (*and *L. nichollsae*-redescribed*)*	Konishi, T. and M. W. 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 *et. al.*	2015	*Phosphorosaurus ponpetelegans*	Konishi, T., M. W. Caldwell, T. Nishimura, K. Sakurai, and K. Tanoue 2015. 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
Lindgren and Siverson	2002	*Tylosaurus ivoensis*	Lindgren, J. and M. Siverson 2002. *Tylosaurus ivoensis*: a giant mosasaur from the early Campanian of Sweden. Transactions of the Royal Society of Edinburgh 93:73-93.
Lingham-Soliar	1991	*Igdamanosaurus aegypytiacus*	Lingham-Soliar, T. 1991. Mosasaurs from the upper Cretaceous of Niger. Palaeontology 34:653-670.
Makádi, Caldwell and Ősi	2012	*Pannoniasaurus inexpectadus*	Makádi, L., M. W. Caldwell and A. Ősi 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. PloS one 7:e51781.
Mantell	1829	*Mosasaurus Hoffmanni*	Mantell, G. 1829. A tabular arrangement of the organic remains of the country of Sussex. Transactions Geological Society London Series 2:201-216.
Marsh	1869	*Halisaurus platyspondylus*	Marsh, O. C. 1869. Notice of some new mosasauroid reptiles from the greensand of New Jersey. American Journal of Science, 2nd series 18:392-397.
Martin	2007	*Globidens schurmanni*	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. Special Papers-Geological Society of America 427:177-198.
Merriam	1894	*Clidastes liodontus, Ectenosaurus clidastoides*	Merriam, J. C. 1894. Über die Pythonomorphen der Kansas Kreide. Palaeontographica 41:1-39.
Nicholls	1988	*Tylosaurus pembinensis*	Nicholls, E. L. 1988. The first record of the mosasaur *Hainosaurus* (Reptilia: Lacertilia) from North America. Canadian Journal of Earth Sciences 25:1564-1570.
Nicholls and Mecker.	2002	*Kourisodon puntledgensis*	Nicholls, E. L. and D. Meckert 2002. Marine reptiles from the Nanaimo Group (Upper Cretaceous) of Vancouver Island. Canadian Journal of Earth Sciences 39:1591-1603.
Palci et al	2013	*Romeosaurus sorbinii, R. fumanensis*	Palci, A., M. W. Caldwell and C. A. Papazzoni 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of northern Italy. Journal of Vertebrate Paleontology 33:599-612.

Paramo	1994	*Yaguarasaurus columbianus*	Páramo, M. E. 1994. Positión sistemática de un reptil marinocon base en los restos fósiles encontrados en capas del Cretácico superior en Yaguará (Huila). Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales 9:63-80.
Polcyn *et. al.*	2010	*Globidens phosphaticus*	Polcyn, M. J., L. L. Jacobs, A. S. Schulp and O. Mateus 2010. The North African Mosasaur *Globidens phosphaticus* from the Maastrichtian of Angola. Historical Biology 22:175-185.
Polcyn and Bell	2005	*Russellosaurus coheni*	Polcyn, M. J. and G. L. Bell 2005. *Russellosaurus cohen*i n. gen., n. sp., a 92 million-year-old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. Netherlands Journal of Geosciences 84:321-333.
Polcyn andEverhart	2008	*Selmasaurus johnsoni*	Polcyn, M. J. and M. J. Everhart, M. J. 2008. Description and phylogenetic analysis of a new species of *Selmasaurus* (Mosasauridae: Plioplatecarpinae) from the Niobrara Chalk of western Kansas. Pp. 13-38 *in* M. J. Everhart, ed., Fort Hays Studies, Special Issue number three. Proceedings of the Second Mosasaur Meeting. Sternberg Museum of Natural History, Hays, Kansas.
Russell	1975	*Globidens dakotensis*	Russell, D. A. 1975. A new species of *Globidens* from South Dakota. Fieldiana Geology 33:235-256.
Schulp, Polcyn and Mateus	2008	*Prognathodon kianda*	Schulp, A. S., M. J. Polcyn, O. Mateus, L. L. Jacobs and M. L. Morais 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon*. In M. J. Everhart, ed. Proceedings of the Second Mosasaur Meeting, Fort Hays Studies Special Issue 3:1-12. Hays, KS.
Schulp, Bardet and Bouya	2009	*Carinodens minalmamar*	Schulp, A.S., N. Bardet, and B. Bouya 2009. A new species of the durophagous mosasaur *Carinodens* (Squamata, Mosasauridae) and additional material of *Carinodens belgicus* from the Maastrichtian phosphates of Morocco. Netherlands Journal of Geosciences 88:161-7.
Shannon	1975	*Clidastes moorevillensis, (Selmasaurus russelli)*	Shannon, S. W. 1975. Selected Alabama Mosasaurs. Unpublished Masters Thesis. University of Alabama.
Sakurai et. al.	1999	*Mosasaurus prismaticus*	Sakurai, K., T. Chitoku and N. Shibuya 1999. A new species of *Mosasaurus* (Reptilia, Mosasauridae) from Hobetsu, Hokkaido, Japan. Bulletin of the Hobetsu Museum 15: 53e66 (in Japanese, English abstract).
Suzuki	1985	*Mosasaurus hobetsuensis*	Suzuki, S. 1985. A new species of *Mosasaurus* (Reptilia, Squamata) from the Upper Cretaceous Hakobuchi Group in the Central Hokkaido, Japan. Monograph of the Association for Geological Collaboration in Japan 30: 45e66 (in Japanese, English summary).
Swinton	1930	*Goronyosaurus nigeriensis*	Swinton, W. E. 1930. On Fossil Reptilia from the Sokoto Province. Bulletin of the Geological Survey Nigeria 13:1-56.
Telles-Antunes	1964	*Angolasaurus bocagei, Tylosaurus iembensis*	Telles-Antunes, M. 1964. O Neocretacici eo Cenozoico do litoral de Angola; 1 Stratigraphica; repteis. Junta Invest. Port Ultramar, Lisbon.

Thevenin	1896	*Tylosaurus gaudry*	Thévenin, A. 1896. Mosasauriens de la Craie Grise de Vaux-Éclusier près Péronne (Somme). Bulletin de la Société Géologique de France, troisième mémoires série 24:900–916.
Welles and Gregg	1971	*Prognathodon waiparaensis, Mosasaurus mokoroa, Taniwhasautrus oweni*	Welles, S. P. and D. R. Gregg 1971. Late Cretaceous marine reptiles of New Zealand. Records of the Canterbury Museum 9:1–111.
Wiffen	1980	*Moanasaurus mangahouangae*	Wiffen, J. 1980. *Moanasaurus*, a new genus of marine reptile (Family Mosasauridae) from the Upper Cretaceous of North Island, New Zealand. New Zealand Journal of Geology and Geophysics 23:507-528
Williston	1897	*Prognathodon overtoni*	Williston, S. W. 1897. *Brachysaurus*, a new genus of mosasaurs. Kansas University Quarterly 6:95-98.
Williston	1898	*Platecarpus* (*Plesioplatecarpus* sensu Konishi) *planifons*	Williston, S. W. 1898. Mosasaurs. The University Geological Survey of Kansas 4:83-221, pls. 10-72.
Wright and Shannon	1988	*Selmasaurus russelli*	Wright, K. R. and S. W. Shannon 1988. *Selmasaurus russelli*, a new plioplatecarpine mosasaur (Squamata, Mosasauridae) from Alabama. Journal of Vertebrate Paleontology 8:102-107.
Wiman	1920	*Eonatator (Clidastes) sternbergi*	Wiman, C. 1920. Some reptiles from the Niobrara group in Kansas. Bulletin of the Geolological Insitute of Uppsala 18:9-18.
Yakovlev	1901	*(Prognathodon) Dollosaurus lutugini*	Yakovlev, N. N. 1901. Remains of the Late Cretaceous mosasaur from the south of Russia. Izvestiya Geologischeskogo Komiteta 20:407-522.

TABLE S4. Explaining specimen completeness using a simple method (ICM). Some museum databases list parts as “skull,” “axial elements,” or “appendicular elements”. A skull part is weighted higher than other elements. 1. A jaw fragment or tooth scores one point. 2. Add one point for "complete,” as in a “complete skeleton” etc. 3. Sum total for score (6 total points possible).

	Skull	Axial Skeleton	Appendicular Skeleton
Score	3	1	1

TABLE S5A. Data used in GLS analysis. The mean completeness of specimens named to species (TCMsp) in each substage was modelled with Miller average sea level, mosasaur species diversity of specimens assignable to single time bins and mosasaur and plesiosaur bearing formations.

Substage	Age (Ma)	TCMsp	Sea-level (m)	DIV by species	MPBFs
Late Maas	67.95	1.47	33.07	20	31
Early Maas	71	5.22	21.59	16	34
Late Camp	74.2	5.8	31.57	17	35
Mid Camp	78.5	7.7	35.21	13	25
Early Camp	82.1	1.2	33.41	12	26
Late Sant	84.4	11.88	38.06	8	17
Mid Sant	85.4	7.2	22.75	2	10
Early Sant	85.95	4.25	10.14	3	14
Late Con	87.1	7.6	14.26	5	9
Mid Con	88.25	19	21.05	1	7
Early Con	89.2		27.54	0	5
Late Tur	90.6	5.4	11.44	3	11
Mid Tur	92.05	6.56	20.84	5	5

TABLE S5B. Data used for GLS analysis. Averaged mosasaur species diversity is modelled with Miller average sea level, mean completeness of mosasaur species averaged in substages (TCMall) and mosasaur- plus plesiosaur-bearing formations.

Substage	Age (Ma)	DIV averaged	Sea-level (m)	TCMall	MPBFs
Late Maas	67.95	21.33	33.07	3.68	31
Early Maas	71	19	21.59	5.07	34
Late Camp	74.2	18.83	31.57	7.26	35
Mid Camp	78.5	15.5	35.21	7.97	25
Early Camp	82.1	14	33.41	3.57	26
Late Sant	84.4	10.83	38.06	11.88	17
Mid Sant	85.4	6.33	22.75	9.25	10
Early Sant	85.95	7.33	10.14	5.33	14
Late Con	87.1	5.5	14.26	6.51	9
Mid Con	88.25	1	21.05	19	7
Early Con	89.2	0	27.54		5
Late Tur	90.6	3	11.44	4.92	11
Mid Tur	92.05	5	20.84	6.07	5

TABLE S6A. Summary of GLS multiple regression analysis showing the full and best models for predicting both diversity and TCM. MPBFs means mosasaur and plesiosaur bearing formations.

Model	Parameters	AIC	BIC	Log likelihood
Full averaged diversity	TCMav sea level MBPFs age	55.563	55.184	-20.781
Best averaged diversity	TCMav sea level MPBFs age	55.563	55.184	-20.781
Full TCMsp	species diversity sea level MPBFs age	76.621	76.296	-32.31
Best TCMsp	species diversity sea level MPBFs age	76.621	76.296	-32.31

TABLE S6B. Summary of best fitting GLS multiple regression models for predicting diversity and TCM.

Response	Parameters	Value	SE	t	*p*
Averaged diversity	intercept	36.725	3.057	12.013	< 0.001
	TCMav	-0.22	0.068	-3.233	0.01
	sea level	0.138	0.014	9.576	< 0.001
	MPBFs	0.242	0.023	10.397	< 0.001
	age	-0.392	0.036	-10.924	< 0.001
TCMsp	intercept	48.049	45.459	1.057	0.36
	species diversity	-0.973	0.694	-1.402	0.2
	sea level	0.273	0.18	1.518	0.17
	MPBFs	-0.092	0.369	-0.248	0.81
	age	-0.456	0.492	-0.928	0.38

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Substage	Country	Region	Group	Formation
Mid Tur	USA	NM/CO/KS	Benton Group	Carlisle Shale
Mid Tur	USA	NM/CO/KS		Greenhorn LS
Mid Tur	USA	NM		Tres Hermanos
Mid Tur	USA	TX	Eagle Ford	"Eagle Ford"
Mid Tur	Mex	Puebla		Mexcala
Late Tur	USA	NM/CO/KS	Benton Group	Carlisle Shale
Late Tur	USA	W. TX	Terlingua Group	Boquillas
Late Tur	USA	TX	Eagle Ford	"Eagle Ford"
Late Tur	USA	TX	Eagle Ford	Arcadia Park
Late Tur	Mex	Puebla		Mexcala
Late Tur	Mexico	Nueva Leon		Vallecillo
Late Tur	England			Upper Chalk
Late Tur	Italy			Scaglia Rossi Veneta
Late Tur	Germany			Strehken
Late Tur	Angola			Itombe
Late Tur	Columbia			Villeta
Early Con	USA	TX	Austin Chalk	"Austin Chalk"
Early Con	USA		Niobrara	Ft.Hayes Ls
Early Con	USA	TX	Terlingua Group	Boquillas
Early Con	England			Upper Chalk
Early Con	Mexico	Monterrey		San Felipe
Mid Con	USA	TX	Austin Chalk	"Austin Chalk"
Mid Con	Mexico	Monterrey		San Felipe
Mid Con	Italy			Scaglia Rossi Veneta
Mid Con	USA		Niobrara	Lower
Mid Con	England			Upper Chalk
Mid Con	USA	TX	Terlingua Group	Boquillas
Mid Con	England			Upper Chalk
Late Con	USA		Niobrara	Lower
Late Con	USA	TX	Austin Chalk	"Austin Chalk"
Late Con	USA	AL/MS	Selma	Eutaw
Late Con	USA		Terlingua Group	Pen
Late Con	USA	TX	Terlingua Group	Boquillas
Late Con	Mexico	Monterrey		San Felipe
Late Con	Venezuela			Navay
Late Con	England			Upper Chalk
Late Con	Italy			Scaglia Rossi Veneta
Early San	USA	NM		Point Lookout Sandstone
Early San	USA	AL/MS	Selma	Eutaw
Early San	USA	TX	Austin Chalk	"Austin Chalk"

Early San	USA		Niobrara	Lower
Early San	USA	TX	Terlingua Group	Boquillas
Early San	USA	TX	Terlingua Group	Pen
Early San	USA	MT	Montana	Telegraph Creek
Early San	Canada	Alberta		Puskwakau
Early San	Mexico	Monterrey		San Felipe
Early San	England			Upper Chalk
Early San	Italy			Scaglia Rossi Veneta
Early San	Japan	Yezo	Yezo Group	Kashima
Early San	Japan			Tamayama
Early San	Russia			Penza region
Mid San	USA	Alabama/Miss	Selma	Eutaw
Mid San	USA	Kansas	Niobrara	Smoky Hill Chalk
Mid San	USA	TX	Terlingua Group	Boquillas
Mid San	USA	TX	Terlingua Group	Pen
Mid San	USA	TX	Austin Chalk	"Austin Chalk"
Mid San	Canada	Alberta		Puskwakau
Mid San	England			Upper Chalk
Mid San	France	Somme		Phosphatic Chalk
Mid San	Russia		Penza region	
Mid San	Japan	Yezo	Yezo Group	Kashima
Late San	USA	Kansas	Niobrara	Upper
Late San	USA	NM	Point Lookout Sandstone	
Late San	USA	AL/GA	Selma	Blufftown
Late San	USA	AL/MS	Selma	Mooreville Chalk
Late San	USA	TX	Austin Chalk	Dessau
Late San	USA	TX	Austin Chalk	"Austin Chalk"
Late San	USA	TX	Terlingua Group	Boquillas
Late San	USA	TX	Terlingua Group	Pen
Late San	Canada	Alberta		Puskwakau
Late San	Canada	Vancouver		Pender
Late San	England			Upper Chalk
Late San	France			Marnes de Bugarach
Late San	France			Marnes bleues de Sougraigne
Late San	France			Gres de Labastide
Late San	France	Somme		Phosphatic Chalk
Late San	Russia		Penza region	"Penza"
Late San	Japan	Yezo	Yezo Group	Kashima
Early Camp	USA	AL/GA	Selma	Blufftown
Early Camp	USA	AL/MS	Selma	Mooreville Chalk
Early Camp	USA	TX	Austin Chalk	"Austin Chalk"

Early Camp	USA	TX	Austin Chalk	Burditt
Early Camp	USA	TX	Austin Chalk	Roxton ls
Early Camp	USA	NM		Point Lookout Sandstone
Early Camp	USA	ARK		Brownstone Marl
Early Camp	USA	TX/ARK	Taylor Group	Ozan
Early Camp	USA	NC	Black Creek Grou	Tar Heel
Early Camp	USA	TX	Austin Chalk	Dessau
Early Camp	USA	NJ	Matawan Group	Merchantville
Early Camp	USA	TX	Tornillo	Aguja
Early Camp	USA	TX	Terlingua Group	Pen
Early Camp	USA	KS/CO/WY/NE/SD	Niobrara	Smoky Hill
Early Camp	USA	CO	Mesa Verde	Lewis Shale
Early Camp	Canada	Alberta		Puskwakau
Early Camp	Belgium		Spiennes Chalk	
Early Camp	England			Upper Chalk
Early Camp	France	Burgogne		White Chalk
Early Camp	Sweden			Kristianstad Basin
Early Camp	Saudi Arabia		Suqah Group	Adaffa Formation
Early Camp	Angola			Bentiaba
Early Camp	Japan	Yezo	Yezo Group	Kashima
Early Camp	Japan		Halebuchi Group	
Early Camp	NZ			Conway Siltstone
Early Camp	Antarctica			Santa Marta
Mid Camp	USA		Pierre Shale	
Mid Camp	USA	KS/SD	Pierre Shale	Sharon Springs
Mid Camp	USA	CO	Mesa Verde	Lewis Shale
Mid Camp	USA		Niobrara	Upper
Mid Camp	USA	AL/MS	Selma	Demopolis
Mid Camp	USA	AL/MS	Selma	Arcola Limstone
Mid Camp	USA	TX/ARK	Taylor Group	Ozan
Mid Camp	USA	NJ	Matawan Group	Marshalltown
Mid Camp	USA	NJ	Matawan Group	Woodbury
Mid Camp	USA	TX	Tornillo	Aguja
Mid Camp	USA	TX	Terlingua Group	Pen
Mid Camp	Canada	Manitoba	Pierre Shale	Pembina
Mid Camp	Canada	Alberta	Belly River	Oldman
Mid Camp	Canada	Alberta	Belly River	Dinosaur Park
Mid Camp	Canada	Alberta	Wapiti	Wapiti
Mid Camp	England			Upper Chalk
Mid Camp	Sweden			Kristianstad Basin
Mid Camp	Angola			Bentiaba

Mid Camp	Saudi Arabia		Suqah Group	Adaffa Formation
Mid Camp	Japan		Isumi Group	
Mid Camp	Japan	Yezo	Yezo Group	Kashima
Mid Camp	Japan		Halebuchi Group	
Mid Camp	NZ			Maungataniwaha ss
Mid Camp	NZ			Conway Siltstone
Mid Camp	Antarctica			Santa Marta
Late Camp	USA	AL/MS	Selma	Demopolis
Late Camp	USA	TX/ARK	Taylor Group	Ozan
Late Camp	USA	TX	Taylor Group	Wolfe City
Late Camp	USA	ARK	Taylor Group	Marlbrook Marl
Late Camp	USA	NJ	Monmouth Grou	Mt Laurel
Late Camp	USA	Tennessee		Coon Ck
Late Camp	USA	TX	Tornillo	Aguja
Late Camp	USA	TX	Terlingua Group	Pen
Late Camp	USA	MT	Montana	Judith River
Late Camp	USA		Pierre Shale	
Late Camp	USA	SD	Pierre Shale	Verendrye
Late Camp	US/Canada	MT/Alberta	Montana	Bear Paw
Late Camp	Canada	Alberta	Belly River	Dinosaur Park
Late Camp	Canada	Alberta	Wapiti	Wapiti
Late Camp	Canada	Alberta	Edmonton	
Late Camp	Mex	Coahuila		Cerro del Pueblo
Late Camp	Mex	Tamaulipas	Difunta	
Late Camp	Argentina			Allen
Late Camp	Argentina			Allen/Jagüel
Late Camp	Argentina			La Colonia
Late Camp	Netherlands, Belgium			Gulpen
Late Camp	England			Upper Chalk
Late Camp	France			Meudon Chalk
Late Camp	Spain			Vitoria
Late Camp	Turkey			Davutlar
Late Camp	Israel			Mishash
Late Camp	Saudi Arabia		Suqah Group	Adaffa Formation
Late Camp	Angola			Bentiaba
Late Camp	Japan		Isumi Group	
Late Camp	Japan		Isumi Group	Hiketa Fmn
Late Camp	Japan	Yezo	Yezo Group	Kashima
Late Camp	Japan		Halebuchi Group	
Late Camp	NZ			Maungataniwaha ss

Late Camp	NZ			Conway Siltstone
Late Camp	Antarctica			Santa Marta
Early Maas	USA	CA	Chico	Moreno
Early Maas	USA	MS/ALA/GA	Selma	Ripley Fm
Early Maas	USA	AL/MS	Selma	Bluffport Marl
Early Maas	USA	NC	Lumbee Group	Peedee
Early Maas	USA	NJ	Monmouth Grou	Navesink
Early Maas	USA	TX	Navarro Group	Neylandville
Early Maas	USA	AL/MS/LA	Navarro Group	Saratoga Chalk
Early Maas	USA	TX	Tornillo	Aguja
Early Maas	US/Canada	MT/Alberta	Montana	Bear Paw
Early Maas	Canada	Alberta	Montana	St Mary River
Early Maas	Canada	Alberta	Wapiti	Wapiti
Early Maas	alberta		Edmonton	
Early Maas	Mex	SLPotosi		Cardenas
Early Maas	Mex	Tamaulipas	Difunta	
Early Maas	Argentina			Paso del Sapo
Early Maas	Argentina			Allen
Early Maas	Argentina			Allen/Jagüel
Early Maas	Argentina			La Colonia
Early Maas	Netherlands, Belgium			Gulpen
Early Maas	Russia			Bereza Beds
Early Maas	Morocco			Couche 4
Early Maas	Morocco			Couche 5
Early Maas	Morocco			Couche 6
Early Maas	Angola			Bentiaba
Early Maas	Syria			Souknek Group
Early Maas	Jordan			Rouseifa Group
Early Maas	Saudi Arabia		Suqah Group	Adaffa Formation
Early Maas	NZ			Laidmore Fmn
Early Maas	NZ			Conway Siltstone
Early Maas	NZ			Maungataniwha ss
Early Maas	NZ			Katiki
Early Maas	Japan		Isumi Group	
Early Maas	Japan		Halebuchi Group	
Early Maas	Antarctica			Snow Hill
Late Maas	USA	AL/GA	Selma	Providence Sand
Late Maas	USA	AL	Selma	Prairie Bluff
Late Maas	USA	TX	Navarro Group	Corsicana
Late Maas	USA	NJ	Monmouth Grou	Mt Laurel

Late Maas	USA	NJ	Monmouth Grou	New Egypt
Late Maas	USA	NJ		Hornerstown
Late Maas	USA	MD		Severn
Late Maas	USA	CA	Chico	Moreno
Late Maas	USA	TX	Tornillo	Aguja
Late Maas	Mex	Tamaulipas	Difunta	
Late Maas	Chile			Quiriquina
Late Maas	Argentina			Paso del Sapo
Late Maas	Antarctica			López de Bertodano
Late Maas	Argentina			Allen
Late Maas	Argentina			Allen/Jagüel
Late Maas	France	Aquitaine		Nay Marl
Late Maas	France			Baculites ls
Late Maas	Spain			Raspay Fmn
Late Maas	Netherlands, Belgium			Maastricht
Late Maas	Netherlands, Belgium			Gulpen
Late Maas	Belgium			Ciply Phosphatic Chalk
Late Maas	Russia			Bereza Beds
Late Maas	Jordan			Rouseifa Group
Late Maas	Morocco			Couche II
Late Maas	Morocco			Couche III
Late Maas	Niger			Dukamaje Fmn
Late Maas	Angola			Bentiaba
Late Maas	Angola			Mucuio
Late Maas	NZ			Laidmore Fmn
Late Maas	NZ			Maungataniwha ss
Late Maas	Japan		Halebuchi Group	

Plesiosaur Material	Stage	Substage
Plesiosaur	Tur	Mid/Late
Plesiosaur	Tur	Mid
Plesiosaur	Tur	Mid
	Cen/Tur	
	Tur	
	Tur	Mid/Late
	Cen/San	
	Cen/Tur	
	Tur	Mid/Late
	Tur	
	Tur	Late
	Tur/Camp	Late/Late
	Tur/San	Mid/Early
Plesiosaur	Tur	Late
	Tur	Late
	Tur	Late
	Con/Camp	Early/Early
Plesiosaur	Con	Early
	Cen/San	
	Tur/Camp	Late/Late
	Con/San	Early/Early
	Con/Camp	Early/Early
	Con/San	Early/Early
	Tur/San	Mid/Early
Plesiosaur	Con/San	Mid/Early
	Tur/Camp	Late/Late
	Cen/San	
	Tur/Camp	Late/Late
Plesiosaur	Con/San	Mid/Early
	Con/Camp	Early/Early
	Con/San	Late/Mid
	Con/San	Ltae/Early
	Cen/San	
	Con/San	Early/Early
	Tur/Camp	
	Tur/Camp	Late/Late
	Con/San	Late/Early
Plesiosaur	San	Early/Early
	Con/San	Late/Mid
	Con/Camp	Early/Early

	Con/San	Mid/Early
	Cen/San	
	San/Camp	
	San	Early
	San/Camp	Early/Early
	Con/San	Early/Early
	Tur/Camp	Late/Late
	Con/San	Late/Early
	San/Camp	
Plesiosaur	San	Early
Plesiosaur	San	
	Con/San	Late/Mid
Plesiosaur	San/Camp	Mid/Early
	Cen/San	
	San/Camp	
	Con/Camp	Early/Early
	San/Camp	Early/Early
	Tur/Camp	Late/Late
	San	Mid/Late
Plesiosaur	San	
	San/Camp	
Plesiosaur	San/Early Camp	
	San/Camp	Early/Early
	San/Camp	Late/Early
	San/Camp	Late/Early
	San/Camp	Late/Early
	Con/Camp	Early/Early
	Cen/San	
	San/Camp	
	San/Camp	Early/Early
	San	Late
	Tur/Camp	Late/Late
	San	Late
	San	Late
	San	Late
	San	Mid/Late
Plesiosaur	San	
	Sant/Camp	
	San/Camp	Late/Early
	San/Camp	Late/Early
	Con/Camp	Early/Early

	Camp	Early?
	Camp	Early
	San	Early/Early
	Camp	Early/?
	Camp	Early/Late
	Camp	Early
	San/Camp	Late/Early
	Camp	Early
	Camp/Maas	
	San/Camp	
Plesiosaur	Camp	Early
Plesiosaur	Camp	Early/Mid
	San/Camp	Early
Plesiosaur	Camp	Early
	Tur/Camp	Late/Late
	Camp	Early
	Camp	Early/Mid
	Camp/Maas	Early/Early
	Camp/Maas	
	San/Camp	
	Camp/.Maas	
	Camp	Early/Mid
	Camp	Early/Late
	Camp	Mid/Late
Plesiosaur	Camp	Mid
	Camp	Early/Mid
	San/Camp	Late/Mid
	Camp	Mid/Late
	Camp	Mid
	Camp	Early/Late
	Camp	Mid
	Camp	Mid
	Camp/Maas	
	San/Camp	
	Camp	Mid
	Camp	Mid
	Camp	Mid/Late
	Camp/Maas	Mid/Mid
	Tur/Camp	Late/Late
	Camp	Early/Mid
	Camp/Maas	

	Camp/Maas	Early/Early
	Camp/Maas	Mid/Early
	Sant/Camp	
	Camp/.Maas	
Plesiosaur	Camp	Mid/Late
Plesiosaur	Camp	Early/Mid
	Camp	Early/Late
	Camp	Mid/Late
	Camp	Early/Late
	Camp	Late
	Camp	Late
	Camp	Late
	Camp	Late
	Camp/Maas	
	San/Camp	
	Camp	Late
	Camp	Mid/Late
	Camp	Late
Plesiosaur	Camp/Maas	Late/Early
	Camp	Mid/Late
	Camp/Maas	Mid/Mid
Plesiosaur	CampMaas	Late/Early
	Camp	Late
	Camp/Maas	Late/Late
	Camp/Maas	Late/Late
	Camp/Maas	Late/Late
Plesiosaur	Camp/Maas	Late/Early
	Camp/Maas	Late/Late
	Tur/Camp	Late/Late
	Camp	Late
	Camp	Late
	Camp	Late
	Camp	Late
	Camp/Maas	Early/Early
	Camp/Maas	
	Camp/Maas	Mid/Early
	Camp	Late
	Sant/Camp	
	Camp/.Maas	
Plesiosaur	Camp	Mid/ Late

Plesiosaur	Camp	Early/Mid
	Camp	Early/Late
	Maas	
	Maas	Early/Mid
	Maas	Early
	Maas	Early
	Maas	Early
	Maas	Early
	Maas	Mid
	Camp/Maas	
	Camp/Maas	Late/Early
	Maas	Early
	Camp/Maas	Mid/Mid
Plesiosaur	CampMaas	Late/Early
	Maas	Early
	Camp/Maas	Late/Late
	Maas	Late
	Camp/Maas	Late/Late
	Camp/Maas	Late/Late
	Camp/Maas	Late/Early
	Camp/Maas	Late/Late
	Maas	
	Maas	Mid
	Maas	Early
	Maas	Early
	Camp/Maas	
	Maas	Early
	Maas	
	Camp/Maas	Early/Early
	Maas	
Plesiosaur	Camp	Early/Mid
	CampMaas	Late/Late
Plesiosaur	Maas	Early
	Camp/Maas	Mid/Early
	Camp/Maas	
Plesiosaur	Maas	Early
	Maas	Late
	Maas	Late
	Maas	Mid/Late
	Camp	Late

	Maas	Late
	Maas	Late
	Maas	Late
Plesiosaur	Maas	
	Camp/Maas	
	Camp/Maas	Late/Late
Plesiosaur	Maas	Late
Plesiosaur	Maas	Late
Plesiosaur	Maas	Late
Plesiosaur	Camp/Maas	Late/Late
Plesiosaur	Camp/Maas	Late/Late
	Maas	Late
	Maas	Late
	Maas	Late
	Maas	Late
	Camp/Maas	Late/Late
	Maas	Late
	Maas	Late
	Maas	
	Maas	Late
Plesiosaur	Maas	Late
	Maas	Late
	Camp/Maas	
	Maas	Late
	Maas	
Plesiosaur	Camp/Maas	Late/Late
	Camp/Maas	