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## THE MOSASAUR FOSSIL RECORD THROUGH THE LENS OF FOSSIL COMPLETENESS

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1 THE MOSASAUR FOSSIL RECORD THROUGH THE LENS OF FOSSIL  
2 COMPLETENESS

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3 9 **Abstract.** The quality of the fossil record affects our understanding of macroevolutionary  
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5 10 patterns. Palaeodiversity is filtered through geological and human processes, and efforts to  
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7 11 correct for these biases are part of a debate concerning the role of sampling proxies and  
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9 12 standardisation in models of biodiversity. Here, we analyse the fossil record of mosasaurs in  
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11 13 terms of fossil completeness as a measure of fossil quality, using three novel metrics of fossil  
12  
13 14 completeness with a compilation of 4,083 specimens. All metrics correlate with each other. A  
14  
15 15 new qualitative measure of character completeness (QCM), correlates with the phylogenetic  
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17 16 character completeness metric. Mean completeness by species decreases with specimen count,  
18  
19 17 and average completeness by substage varies significantly. Mean specimen completeness is  
20  
21 18 higher for species-named fossils than those identified to genus and family. The effect of  
22  
23 19 tooth-only specimens is analysed. Importantly, we find that completeness of species does not  
24  
25 20 correlate with completeness of specimens. Completeness varies by palaeogeography, North  
26  
27 21 American specimens showing higher completeness than those from Eurasia and Gondwana.  
28  
29 22 These metrics can be used to identify exceptional preservation, with specimen completeness  
30  
31 23 varying significantly by both formation and lithology. The Belgian Ciplly Formation displays  
32  
33 24 the highest completeness, and clay lithologies show higher completeness values than others.  
34  
35 25 Neither species diversity nor sea level correlates significantly with fossil completeness. A  
36  
37 26 GLS analysis using multiple variables agrees with this result. However, GLS shows that two  
38  
39 27 variables have significant predictive value for modelling averaged diversity, namely sea level  
40  
41 28 and mosasaur- and plesiosaur-bearing formations, the latter of which is redundant with  
42  
43 29 diversity. Mosasaur completeness is not driven by sea level, nor does completeness limit the  
44  
45 30 mosasaur diversity signal.

50 31  
51  
52 32 **Key words:** marine reptiles, mosasaur, fossil record quality, fossil completeness, sea level,  
53  
54 33 palaeodiversity.

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3 34 **MOSASAURIDAE** was a relatively short-lived, but diverse and abundant clade of marine  
4  
5 35 squamates that radiated in Late Cretaceous epicontinental seas and died out at the K/Pg  
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7 36 boundary (Debraga & Carroll 1993). The rise of mosasaurids (called ‘mosasaurs’ throughout  
8  
9 37 the paper) followed dramatic changes in the marine reptile fauna (Stubbs & Benton 2016),  
10  
11 38 including decreases in disparity of plesiosaurs in the Late Jurassic (Benson & Druckenmiller  
12  
13 39 2014) as well as the extinction of cryptoclidid plesiosaurs, ichthyosaurs (Bardet 1994, Fisher  
14  
15 40 *et al.* 2012) and thalattosuchian crocodiles (Young *et al.* 2010) in the Early to mid-  
16  
17 41 Cretaceous. Mosasauroids (aigialosaurids and dolichosaurids) arose in the Cenomanian as  
18  
19 42 relatively small swimming reptiles, followed by true mosasaurs in the Turonian (Bardet *et al.*  
20  
21 43 2008). As in other groups of marine reptiles (Massare 1994), the Mosasauridae showed  
22  
23 44 increasing adaptations to the marine environment through time (Motani 2009). The average  
24  
25 45 body size of mosasaurs increased through the Late Cretaceous, from 1–2 m in early semi-  
26  
27 46 terrestrial forms, to a gigantic 14–17 m in later forms (Polcyn *et al.* 2014; Stubbs & Benton  
28  
29 47 2016). They became increasingly efficient swimmers and filled niches vacated by some of the  
30  
31 48 aforementioned pelagic marine predators after their extinction (Motani 2005; Lindgren *et al.*  
32  
33 49 2007, 2009, 2011, 2013; Houssaye *et al.* 2013). Mosasaurs thrived in many marine  
34  
35 50 environments (Kiernan 2002), from rocky shores to pelagic shelves, including fresh water  
36  
37 51 environments (Holmes *et al.* 1999), and by the latest Cretaceous, they were the apex predators  
38  
39 52 in many complex ocean ecosystems (Sørensen *et al.* 2013). Accordingly, mosasaur fossils  
40  
41 53 have a widespread stratigraphic and global geographic distribution in a variety of  
42  
43 54 lithologically distinct Upper Cretaceous marine formations (Russell 1967).

48 55 Marine reptiles have figured in several studies that have contributed to the debate about  
49  
50 56 how to address biases in the fossil record (*e.g.* Benson *et al.* 2010; Benson & Butler 2011;  
51  
52 57 Cleary *et al.* 2015; Tutin and Butler 2017). Does the fossil record provide a reasonable picture  
53  
54 58 of mosasaur evolution (Polcyn *et al.* 2014), or is the record substantially biased by the  
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3 59 idiosyncrasies of preservation and collection (Benson *et al.* 2010; Benson & Butler 2011)?  
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5 60 Benson *et al.* (2010) identified serious megabiases affecting all Cretaceous marine reptiles,  
6  
7 61 including mosasaurs, and argued that their palaeodiversity signal was dependent on  
8  
9 62 geological sampling biases, meaning that the raw data said little about their true diversity.  
10  
11 63 Part of this result depended on residual diversity estimates using a method that has since been  
12  
13 64 severely criticised (Dunhill *et al.* 2014, 2018; Brocklehurst 2015; Sakamoto *et al.* 2017). Re-  
14  
15 65 analysis led Benson and Butler (2011) to identify that shallow marine tetrapods at least,  
16  
17 66 including most mosasaurs, showed close correlation between diversity and sea level and  
18  
19 67 continental area. Benson and Butler (2011) interpreted this as a ‘common cause’ effect (Peters  
20  
21 68 2005), analogous to a species-area effect; the fossil record and palaeodiversity of marine  
22  
23 69 reptiles fluctuated simultaneously as sea level rose and fell. These alternate viewpoints leave  
24  
25 70 an open question: is the mosasaur fossil record a fair representation of their true biological  
26  
27 71 signal or not?  
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31 72 One approach to understanding inadequacies of the fossil record is to consider the  
32  
33 73 specimens themselves – are they equally complete through all times and places, or do they  
34  
35 74 show variation (Benton *et al.* 2004; Smith 2007)? For example, Mannion & Upchurch (2010)  
36  
37 75 suggested that measures of fossil completeness could be used alongside other sampling  
38  
39 76 proxies to investigate the quality of the fossil record. Fossil completeness studies attempt to  
40  
41 77 quantify the quality of fossil specimens by assigning numerical metrics that reflect the  
42  
43 78 percentage of skeletal or phylogenetic character elements present in individual fossils or  
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45 79 whole groups of fossils.  
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48 80 Many recent analyses have used measures of fossil completeness. In taphonomic  
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50 81 studies, completeness can reflect post-mortem conditions and transport (Beardmore 2012a, b).  
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52 82 Aquatic vs. terrestrial deposits may preserve differently (Verriere *et al.* 2016) and, more  
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54 83 broadly, completeness may be related to lithology (Cleary *et al.* 2015). Completeness may be  
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3 84 related to body size; large fossils may be collected more often (Brown *et al.* 2013), or small  
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5 85 associated fossils may be preserved better at times (Brocklehurst *et al.* 2012). Completeness  
6  
7 86 may be affected by sea level (Mannion & Upchurch 2010; Cleary *et al.* 2015; Tutin & Butler  
8  
9 87 2017). Completeness can be used to measure collecting and naming biases through historical  
10  
11 88 time (Benton 2008a, b; Mannion & Upchurch 2010; Walther & Fröbisch 2013; Tutin &  
12  
13 89 Butler 2017) or as a direct metric to assess confidence in fossil record data in a single basin  
14  
15 90 through a key event (Benton *et al.* 2004). Finally, the fossil record of diversity may be  
16  
17 91 unbiased, or biased by completeness, either inversely (Brocklehurst & Fröbisch 2014; Smith  
18  
19 92 2007) or directly (Dean *et al.* 2016).

22 93 In this study, we explore a database of over 4000 mosasaur specimens and apply novel  
23  
24 94 methods of coding fossil completeness, to test whether fossil completeness is biasing the  
25  
26 95 measured richness of these organisms. We find that specimen completeness varies  
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28 96 enormously geographically, but is not correlated with species diversity or sea level. We find  
29  
30 97 that completeness does not limit the diversity signal in the mosasaur record.

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## 35 99 **MATERIALS AND METHODS**

### 37 100 *Data*

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39 101 *Specimens.* A mosasaur specimen database (Driscoll *et al.* 2018, **Data A**, **Data B**) includes all  
40  
41 102 scored specimens of Mosasauridae from collection visits and literature descriptions,  
42  
43 103 comprising **4083** mosasaur specimens. Mosasaur material is housed in at least 112 institutions  
44  
45 104 (Driscoll *et al.* 2018, **Appendix Table S1**), and 448 specimens were seen first-hand in these  
46  
47 105 collections (Driscoll *et al.* 2018, **Appendix Table S2**), including many referred, cited and  
48  
49 106 holotype specimens. Examination confirmed their description in the literature, even if some of  
50  
51 107 the elements showed abrasion or minor disintegration. In a few cases, elements originally  
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53 108 described with the specimen were not found on visiting the museums, and this was noted in  
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3 109 assessing skeletal completeness. Most specimens were identifiable, and scorings of the  
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5 110 holotype in the literature and observed first hand were identical, providing confidence that  
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7 111 measurements taken from the literature can be accurate. Catalogue descriptions as well as  
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9 112 photos from museum online collections databases (AMNH, GPIT, MCZ, SDMNH, TMP,  
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11 113 UAVPL, UCMP, USNM, UVER and YPM) were also used, and files containing museum  
12  
13 114 databases were obtained from LACM, FMNH, ALNHM and TMP.

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16 115 Additional specimen data **was** obtained from publications and monographs, including  
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18 116 original descriptions of holotypes (Driscoll *et al.* 2018, **Appendix Table S3**), as well as  
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20 117 secondary descriptions of non-type materials (e.g. Lydekker 1888; Camp 1942; Russell 1967;  
21  
22 118 Schultze *et al.* 1985; Kuypers *et al.* 1998; Bardet 2012; and others listed in Driscoll *et al.*  
23  
24 119 2018, **Appendix Table S7**). No publicly inaccessible or undocumented material was used in  
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26 120 the study. In total, over 4300 specimens were identified for study, but some were excluded  
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28 121 because of poor morphological data or lack of illustration.

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31 122 In this study, we used different subsets of the specimen lists. In many cases, we  
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33 123 considered all **4083** specimens. In other cases, we considered just those specimens that could  
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35 124 be assigned to named species, and excluded those that were assigned to genus alone (e.g.  
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37 125 *Mosasaurus* sp.) or to an even more general taxon (e.g. Mosasauridae indet.). **1044** specimens  
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39 126 were attributed to Mosasauridae indeterminate (i.e. family level), 731 specimens were  
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41 127 identified to generic level, and 2304 to species level. In the specimen list (Driscoll *et al.* 2018,  
42  
43 128 **Data B**), the specimens 1–843 and 1878–4073 are assigned to a named genus or named genus  
44  
45 129 and species, and specimens 843–**1887** are termed simply ‘Mosasauridae indet.’ Specimens  
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47 130 2416– 2544, for example are ‘*Mosasaurus* sp.’ More than 1400 of the **4083** specimens consist  
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49 131 only of isolated teeth, and these were included and excluded in different analyses.

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3 133 *Stratigraphic ranges.* The stratigraphic positions of many historical mosasaur specimens are  
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5 134 unknown. In some formations in which mosasaurs commonly occur, the stratigraphy and age  
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7 135 have been revised (e.g. Everhart 2001; Jagt 2005), and the revised date was used for  
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9 136 allocation to time bins. Mosasaurs generally occur in marine rocks, and often in close  
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11 137 association with zone fossils such as belemnites, ammonites or foraminifera, so enabling  
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13 138 correlation with short-term time zones that can be tied to radioisotopic ages in the standard  
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15 139 marine time scale. We compiled a list of 135 mosasaur-bearing formations from the specimen  
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17 140 search and cross-checked the age and stratigraphy of formations with the stratigraphic  
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19 141 literature (Driscoll *et al.* 2018, H). Many formation ages were already accurately represented  
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21 142 in the primary literature.

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24 143 The specimens were datable to different degrees of precision. 1726 mosasaur specimens  
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26 144 were datable to substage, and 2357 specimens were dated at best to two or more substages.  
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28 145 Because of the large amount of data, there were no substage time bins that did not contain  
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30 146 precisely assignable specimens.

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35 148 *Species list.* A list of valid species was assembled based on the primary scientific literature  
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37 149 (listed in Appendix in this manuscript), paying special attention to apomorphy-based  
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39 150 descriptions. Only species with clear taxonomic assignment and little disagreement on  
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41 151 taxonomy were used in this study. Our species list includes 74 valid species, and it agrees  
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43 152 broadly with a recent, independent compilation (Polcyn *et al.* 2014).

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48 154 *Specimen completeness metrics*

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50 155 *Background.* One of the most exact methods for scoring skeletal completeness in vertebrates  
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52 156 is to count the number of elements present compared to the total number of bones in the  
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54 157 skeleton. This has been done in some taphonomic studies, including *Archaeopteryx* (Kemp

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3 158 and Unwin 1997), a Triassic prolacertiform (Casey *et al.* 2007), and a Miocene salamander  
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5 159 (McNamara *et al.* 2012). However, this method is time-consuming and impractical when  
6  
7 160 many specimens are compared.

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9 161 Other quantitative methods have been developed for dealing with larger sample sizes.  
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11 162 Mannion & Upchurch (2010) presented two approaches to measure fossil completeness in  
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13 163 sauropods, a Skeletal Completeness Metric (SCM) that records the proportional completeness  
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15 164 of skeletons against a roster of elements that ought to be present, and a Character  
16  
17 165 Completeness Metric (CCM) that reports the number of phylogenetically informative  
18  
19 166 characters that are reported for each taxon. They suggested that SCM might be a more useful  
20  
21 167 metric in taphonomic studies comparing preservation in different geographic zones or facies,  
22  
23 168 etc., and CCM would be a better tool for comparing diversity patterns through time.

24  
25 169 Both SCM and CCM were subdivided into three individual measures: the best specimen  
26  
27 170 of a taxon, termed SCM1 or CCM1, the type specimen  $SCM_{ts}$  or  $CCM_{ts}$  and a composite  
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29 171 specimen that includes all preserved elements of the taxon from any number of specimens,  
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31 172 termed SCM2 and CCM2. These scores can be averaged over all taxa in a time bin, or all taxa  
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33 173 in a geological formation or geographic region, or for all representatives of a species or genus,  
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35 174 whether they occur in a single time bin or not.

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37 175 Another method, designed by Beardmore (2012a, b) for scoring fossil preservation in  
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39 176 marine crocodylomorphs, compared disarticulation and completeness, which are related to  
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41 177 environmental and preservational factors that were present at the time of death and burial. The  
42  
43 178 unmodified Beardmore index divides the skeleton into anatomical regions, giving each region  
44  
45 179 equal weight. This method can be quantitative, scoring every element present, but also allows  
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47 180 estimation of proportions of regions present; so this might be called a semi-quantitative  
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49 181 scoring system.  
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3 182 Cleary *et al.* (2015) used SCM1 and SCM2 (modified for the laterally crushed nature of  
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5 183 ichthyosaur fossils), but they also implemented a modified Beardmore skeletal completeness  
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7 184 metric (BSCM) in an investigation of fossil completeness in ichthyosaurs. These authors also  
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9 185 divided BCSM into best (BCSM1) and composite (BSCM2) specimen per species, and  
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11 186 averaged these values over all species assigned to stage level time bins.

13 187 Qualitative approaches can also be used to score fossil quality. For example, Benton *et al.*  
14  
15 188 (2004) and Benton (2008b) measured dinosaur specimen completeness using the ratio of  
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17 189 incomplete material (isolated elements or collections of bones) to complete material, such as  
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19 190 skulls or complete skeletons. This approach has been used successfully in several studies  
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21 191 (Fontaine *et al.* 2005; Smith 2007). Metrics such as SCM and CCM are more accurate than  
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23 192 qualitative scores (Brocklehurst *et al.* 2012), but qualitative metrics can be useful for  
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25 193 comparisons of diverse taxa or large sample sizes.  
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31 195 *Completeness metrics.* We used three completeness metrics. The Taphonomic Completeness  
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33 196 Metric (TCM) is based on Beardmore (2012a, b) and is a non-weighted method (Fig. 1). The  
34  
35 197 mosasaur skeleton is divided into nine anatomical regions, namely the skull, limbs (two  
36  
37 198 forelimbs and two hindlimbs), vertebral column (cervical, dorsal, caudal), and ribs, and each  
38  
39 199 region is given an arbitrary maximum score of 4, giving a total possible TCM of 36.

41 200 The Qualitative Completeness Metric (QCM) is based on Benton's (Benton *et al.* 2004;  
42  
43 201 Benton 2008a, b) qualitative description of dinosaur completeness and is weighted so that  
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45 202 skulls and jaws are afforded a higher weight than post-cranial elements, which is in  
46  
47 203 proportion to the distributions of characters used in phylogenetic analysis (e.g. Bell, 1993).  
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49 204 QCM is presented here (Table 1) as an estimate of character completeness when it is not  
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51 205 possible to examine every character present on individual elements. This is in accordance  
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53 206 with some previous studies (albeit using CCM) where each anatomical element present was  
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3 207 similarly assumed to contain all its characters (e.g. Brocklehurst *et al.* 2012). In contrast,  
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5 208 other analyses (e.g. Dean *et al.* 2016) used only the number of characters that could be  
6  
7 209 observed.

8  
9 210 In general terms, QCM is like CCM. Regions with higher numbers of phylogenetic  
10  
11 211 characters are given greater weight in both. The phylogenetic character list was derived from  
12  
13 212 the character matrix of Bell (Bell 1997; Bell & Polcyn 2005). This cladistic data matrix was  
14  
15 213 selected because it has more mosasaur characters than other matrices (e.g. LeBlanc *et al.*  
16  
17 214 2012). A table of anatomical elements and the number of their associated characters was  
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19 215 compiled by anatomical region for a test subset of 26 specimens of representative species  
20  
21 216 (Driscoll *et al.* 2018, Data D). For each of these specimens, the total score over all anatomical  
22  
23 217 regions was compared to the QCM fossil completeness metric (Driscoll *et al.* 2018, Data E).  
24  
25 218 This comparison tests the pre-weighted character total per specimen against an estimate of  
26  
27 219 character completeness provided by the QCM. Although not necessary for the analysis, a  
28  
29 220 weighted value of the character scores (assuming a maximum value of 9) for each specimen is  
30  
31 221 listed also, for comparison to QCM.

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34  
35 222 The final scoring method, Informal Completeness Metric (ICM), allows the inclusion of  
36  
37 223 specimens that are associated only with general descriptions such as “skull”, or “axial  
38  
39 224 elements,” or “appendicular skeleton”. The total possible ICM score is set arbitrarily at 5,  
40  
41 225 with any mention of a skull scoring three points and any mention of axial and appendicular  
42  
43 226 parts scoring one point each (Driscoll *et al.* 2018, Appendix Table S4).

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45  
46 227 Of the 4083 mosasaur specimens, 375 could be scored for only one or two of the three  
47  
48 228 metrics (TCM, QCM and ICM). We compared all three methods as measures of fossil  
49  
50 229 completeness. The equivalence of TCM values using all specimens vs. those exactly datable  
51  
52 230 to single substages was also tested. Completeness scores were assigned to all holotype  
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54 231 specimens (TCMh, QCMh and ICMh) and the best specimens (TCMb, QCMb and ICMb) of

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3 232 each species. In addition, a composite score (TCMc, QCMc and ICMc) for each species was  
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5 233 calculated (Driscoll *et al.* 2018, **Data C, D, and E**).

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9 235 *Mosasaur fossil completeness*

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11 236 *Time Series*. Mean completeness scores were compiled and divided into time bins equivalent  
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13 237 to Upper Cretaceous stratigraphic substages (Gradstein *et al.* 2012). For both species- and  
14  
15 238 genus-level specimens, sampled **in-bin taxa** were compiled at the substage level and diversity  
16  
17 239 was calculated. The terms “richness” and “diversity” are considered equivalent in this paper.  
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19 240 Mean sea level for each Upper Cretaceous substage was calculated from Miller *et al.* (2005).

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22 241 We assessed mean completeness for all specimens (TCMall, QCMall, ICMall) and for  
23  
24 242 those specimens identified to species level (TCMsp, QCMsp, ICMsp), **so excluding material**  
25  
26 243 **only identifiable to higher taxonomic levels**. Since there were so many specimens consisting  
27  
28 244 of teeth alone, we compared completeness values across the above two time series, both with  
29  
30 245 and without specimens consisting of teeth alone.

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33 246 The mean completeness of all specimens for each species (TCMtot) was averaged over  
34  
35 247 the time bins where those species occur (TCMav, QCMav, ICMav). This time series was  
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37 248 compared to those derived from all specimens (TCMall, QCMall, ICMall), **and** to specimens  
38  
39 249 named to species level (TCMsp, QCMsp, ICMsp). This compared the utility of using average  
40  
41 250 completeness values assigned to whole species (**in many cases from various time bins**) to  
42  
43 251 those derived from sampled-in-bin specimens. For clarity, a description of all the  
44  
45 252 completeness metrics described in this study is listed (Table 2). No best, **holotype** or  
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47 253 composite specimen scores were used for any time series analysis.

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50 254 **Mosasaur species and generic diversities are calculated based on specimen occurrences**  
51  
52 255 **only, in substage-level time bins, so we do not use first-to-last ranges or include any Lazarus**  
53  
54 256 **taxa, in this part of the analysis. In addition, we included** five mosasaur species **that** were only  
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3 257 assignable imprecisely to a range of two or three time bins, so we present also an “averaged”  
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5 258 species diversity curve that includes these taxa counted as fractions. For example,  
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7 259 *Plotosaurus bennisoni* is dated to the uppermost Lower Maastrichtian and/or lowermost  
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9 260 Upper Maastrichtian, so its diversity is counted as 0.5 in both substages. We present the exact  
10  
11 261 species and genus diversity curves as well as the “averaged” species diversity curve, together  
12  
13 262 with comparisons among all curves and with sea level and completeness. TCMsp, QCMsp  
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15 263 and ICMsp were compared with species and generic diversity, but not to “averaged” diversity  
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17 264 so as not to make spurious comparisons between time bins that do not contain equivalent  
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19 265 specimens.  
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24 267 *Predicting diversity and completeness.* To more fully understand the relationship between  
25  
26 268 diversity and completeness, we used a multiple regression technique to compare the  
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28 269 relationships between explanatory variables. A substage-level sampling proxy for explaining  
29  
30 270 diversity and completeness was created and tested using mosasaur- and plesiosaur-bearing  
31  
32 271 formations (MPBFs). These formations (Driscoll *et al.* 2018, **Data I**) were drawn from our  
33  
34 272 mosasaur database and Upper Cretaceous plesiosaur data from unpublished research. We used  
35  
36 273 GLS to check the relationship between mean TCM, diversity, sea level, formations and age by  
37  
38 274 modelling TCM and diversity as a function of the other variables (i.e.  $TCM_{sp} \sim \text{species}$   
39  
40 275  $\text{diversity} + \text{sea level} + \text{MPBFs} + \text{age}$ ; and “averaged” diversity  $\sim TCM_{av} + \text{sea level} +$   
41  
42 276  $\text{MPBFs} + \text{age}$ ). We provide the raw data used for this analysis (Driscoll *et al.* 2018, **Appendix**  
43  
44 277 **Tables S5A, S6B**).  
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50 279 *Determinants of fossil completeness.* Mean completeness scores were compared across  
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52 280 several classes of taxonomic, biological, palaeogeographical, and lithological variables. TCM  
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54 281 (instead of QCM) was used as a measure of preservation as affected by taphonomy. For most  
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3 282 of these categorical variables, the data were much richer for specimens labelled as species, so  
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5 283 TCMsp was the completeness metric used. Mean TCM was compared between specimens  
6  
7 284 allocated to a maximum taxonomic resolution of family, genus or species. Tests both included  
8  
9 285 and excluded specimens consisting of only teeth.

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11 286 Mean TCMsp was assessed across different lithologies by assigning mosasaur-bearing  
12  
13 287 formations to the categories chalk, sandstone, limestone, or clay, based on the predominant  
14  
15 288 rock type of each formation. The specific lithology of individual specimens was not used.  
16  
17 289 Mean TCMsp values of a few well-known and prolific mosasaur-bearing formations were  
18  
19 290 calculated and compared. Differences in mean TCMsp between palaeogeographical regions  
20  
21 291 (i.e. Eurasia, Gondwana, North America) were also analysed.

22  
23  
24 292 Finally, estimated body size for sample species was compared to the species mean  
25  
26 293 completeness using mosasaur length estimates taken from Polcyn *et al.* (2014). For this  
27  
28 294 analysis, mosasaurs were divided into three informal size groups: small (1–4 m), medium  
29  
30 295 (4.5–7.5 m) and large (8 m or longer) because we did not have good quality individual  
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32 296 measurements for each taxon, and for those with large sample sizes, we would have to  
33  
34 297 consider a range of body sizes.

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37 298  
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39 299 *Sampling.* A few representative sampling metrics were compiled to test the relationship  
40  
41 300 between palaeontological sampling effort and fossil completeness. The number of specimens  
42  
43 301 per species was used as one measure of sampling because it could be related to collector effort  
44  
45 302 or availability of samples. The number of Google Scholar “hits” was tested as a measure of  
46  
47 303 scientific interest (we recorded these on 1<sup>st</sup> December, 2017). The number of years since first  
48  
49 304 discovery (i.e. naming of a species) was used to test scientific effort over historical time.  
50  
51 305 Sampling or study effort could be related to absolute body length (Polcyn *et al.* 2014; Driscoll  
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53 306 *et al.* 2018, Data A), and this was also compared with other variables.

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3 307 Sampling and/or completeness might be related to rock outcrop area. For North American  
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5 308 formations, this information is available at Macrostrat.org. The maps for representative North  
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7 309 American mosasaur-bearing formations were double-checked against actual specimen  
8  
9 310 locations. The average TCMsp by formation was compared to the rock area of these  
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11 311 formations and their mosasaur species **diversity**. The number of formations (n) necessary to  
12  
13 312 be confident about our results using the lowest p value (0.35) and highest  $r_s$  (0.6) was  
14  
15 313 calculated using the method of Bonett and Wright (2000). Their work showed that a value of  
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17 314  $n = 4$  is the smallest sample size that is adequate at this level of confidence; we have a value  
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19 315 of  $n = 5$  for our data.  
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24 317 *Statistical tests*

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26 318 Differences in specimen completeness among categorical data (i.e. taxonomic rank, body size,  
27  
28 319 lithology, palaeogeography etc.) were assessed using Wilcoxon tests and Kruskal-Wallis tests.  
29  
30 320 Relationships between numerical data and paired time series were assessed using Spearman  
31  
32 321 rank correlation tests. The correlation between completeness values across specimens was  
33  
34 322 double-checked using the Kendall Tau-b test, which corrects for ties in the ranks across the  
35  
36 323 thousands of specimens included. Time series were detrended using generalised differencing  
37  
38 324 prior to correlation tests (using the gen.diff function of Graeme Lloyd;  
39  
40 325 <http://www.graemetlloyd.com/methgd.html>), and these were corrected for false discovery rate  
41  
42 326 (FDR) using the method of Benjamini and Hochberg (1995). Time series of completeness  
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44 327 metrics were correlated with mosasaur **diversity**, sea level, and the various sampling proxies,  
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46 328 with the aim of determining whether specimen completeness has any bearing on mosasaur  
47  
48 329 **diversity**, and whether specimen completeness is driven by external factors such as sea level  
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50 330 or sampling intensity. All statistical analyses were performed in R (v.3.3.0).  
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3 331 Generalised least squares (GLS) is a multiple regression method for estimating the  
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5 332 unknown parameters in a linear regression model, and it can be used when there is a certain  
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7 333 degree of correlation between the residuals in a regression model. GLS has an advantage over  
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9 334 pairwise tests of correlation as it allows multiple explanatory variables to be examined  
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11 335 simultaneously and allows the addition or removal of additional variables to be assessed  
12  
13 336 quantitatively. Variables tested included diversity, sea level, TCM, age and formations.

15 337 GLS models were fitted in R using the package nlme (Pinheiro *et al.* 2017). As there  
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17 338 was evidence for heterogeneity in the spread of the residuals in some of the explanatory  
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19 339 variables, we applied a number of variance structures to the data and tested for the best fitting  
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21 340 model using the Akaike Information Criterion (AIC). The best fitting model for predicting  
22  
23 341 diversity contains a power of the covariate variance structure applied to the age data and the  
24  
25 342 best fitting model for predicting TCM contains a fixed variance structure applied to the age  
26  
27 343 data. Models were also fitted with an auto-regressive model of order 1 (AR-1) correlation  
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29 344 structure, which models the residual at time  $s$  as a function of the residual of time  $s-1$  (Zuur *et*  
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31 345 *al.* 2009). The models with the AR-1 structure were worse fits than the models without. This  
32  
33 346 is because of the common increasing trend of diversity, formations and sea level through  
34  
35 347 time. We therefore present both sets of models, with and without the autocorrelation structure  
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37 348 applied to the age parameter. Model fitting was achieved by comparing the full models with  
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39 349 models that drop each explanatory variable in turn and perform a likelihood ratio test. This  
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41 350 informs whether the dropped term has a significant influence on the fit of the model (Zuur *et*  
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43 351 *al.* 2009).

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50 353 *Institutional abbreviations.* ALNHM, Alabama Natural History Museum, Tuscaloosa,  
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52 354 Alabama, USA; AMNH, American Museum of Natural History, New York, USA; FMNH,  
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54 355 Field Museum of Natural History, Chicago, Illinois, USA; GPIT, University of Tübingen,  
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3 356 Tübingen, Germany; LACM, Los Angeles County Museum of Natural History, Los Angeles,  
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5 357 California, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge,  
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7 358 Massachusetts, USA; SDMNH, San Diego Museum of Natural History, San Diego,  
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9 359 California, USA; TMP, Royal Tyrell Museum of Palaeontology, Drumheller, Alberta,  
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11 360 Canada; UAVPL, University of Alberta Vertebrate Paleontology Lab, Edmonton, Alberta,  
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13 361 Canada; UCMP, University of California Museum of Paleontology, Berkeley, California,  
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15 362 USA; USNM, Smithsonian Institution National Museum of Natural History, Washington DC,  
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17 363 USA; UVER, University of Vermont Zadock Thompson Natural History Collection,  
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19 364 Burlington, Vermont, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.  
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366 **RESULTS**367 *Completeness scores*

28 368 The mean completeness scores for all specimens per species show a broad range of values for  
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30 369 different taxa: averages per taxon range as follows: TCM (1–21 **out of 36**), QCM (1–7 **out of**  
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32 370 **9**) and ICM (1–5 **out of 5**). Summaries are given of the overall mean TCM, QCM and ICM  
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34 371 scores for all mosasaur species (Driscoll *et al.* 2018, **Data A**), for all mosasaur specimens  
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36 372 (Driscoll *et al.* 2018, Data B) and by holotype, best specimen and species composite scores  
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38 373 (Driscoll *et al.* 2018, **Data F, G and H**, respectively). An overview of the completeness of the  
39  
40 374 various species and exemplary specimens is reviewed below and summarised (Table 3).  
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43 375 When the total character scores from the mosasaur phylogenetic matrix are compared to  
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45 376 QCM there is a very highly significant positive correlation (Spearman:  $r_s = 0.925$ ,  $p \ll 0.001$ )  
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47 377 derived from our 26 representative specimens, which remains significant after FDR correction  
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49 378 for multiple comparisons.  
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51 379 Statistical comparison of the completeness scores (TCM, QCM, ICM) across all  
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53 380 specimens shows highly significant positive correlations that were also significant after FDR  
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3 381 correction: TCM vs. ICM (Spearman:  $r_s = 0.74$ ,  $p \ll 0.001$ ), QCM vs. ICM (Spearman:  $r_s =$   
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5 382  $0.72$ ,  $p \ll 0.001$ ) and TCM vs. QCM (Spearman:  $r_s = 0.49$ ,  $p \ll 0.001$ ). The correlations  
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7 383 were also very highly significant using the Kendall tau-b test, with all  $p$  values  $< 0.001$ . The  
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9 384 metrics are so closely correlated with each other that all can be regarded as equivalent metrics  
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11 385 for recording fossil completeness data.

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13 386 A comparison of the completeness data (TCM) for all 4083 specimens versus the 1726  
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15 387 specimens datable to substage shows significant discrimination, as indicated by the Kruskal -  
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17 388 Wallis test ( $\chi^2 = 81.174$ ,  $df = 35$ ,  $p \ll 0.001$ ). These sets are not equivalent. At first, this  
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19 389 seems surprising, since the medians for these values are both 1; the mean TCM for single  
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21 390 substage specimens is 2.18, and for all specimens is 2.28. But this result is influenced by the  
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23 391 fact that the distribution of precisely datable specimens is skewed according to the level of  
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25 392 taxonomic assignment. Only 154/1034 (15%) of taxa assigned to Mosasauridae could be  
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27 393 dated precisely to substage, whereas for those identified to genus, this rises to 146/731 (20%),  
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29 394 and to 62% for specimens identified to species. However, when one compares the two sets of  
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31 395 data using only specimens named to species, there is no significant difference when using the  
32  
33 396 TCM of all specimens and those datable to precise substages (Kruskal-Wallis:  $\chi^2 = 41.94$ ,  $df =$   
34  
35 397  $32$ ,  $p = 0.124$ ). This shows that TCM<sub>sp</sub>, which necessarily leaves out many un-sampled  
36  
37 398 and/or un-datable specimens, can be trusted as a fair representation of the mean TCM for the  
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39 399 set of all specimens identified to species level. Note that comparisons like this, where some  
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41 400 data sets compared are subsets of each other, might be inadvisable; but in this case, the null  
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43 401 hypothesis was that the partial set of datable specimens should be equivalent to the set of all  
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45 402 specimens. We confirm this here in the comparison of substage-dated specimens with the  
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47 403 sample of all specimens.

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54 405 *Mosasaur fossil completeness*  
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3 406 *Time series.* Mean completeness of all mosasaur specimens varies through time, and there are  
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5 407 close similarities in the overall patterns through time for all three completeness metrics (Fig.  
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7 408 2). The same is true for mosasaur specimens named to species through time (Fig. 3).

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9 409 The time series of completeness metrics by substage all correlate significantly with each  
10  
11 410 other, both for all specimens and for those named as species. These correlations remain  
12  
13 411 significant after FDR correction. There is no bias in the overall pattern of mosasaur  
14  
15 412 completeness according to whether specimens have been assigned to named species or not.  
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17 413 Further, many of the rises and falls in the respective time series (Figs 2, 3) show statistically  
18  
19 414 significant differences between substages, both for named species and for all specimens.

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22 415 All patterns for the different metrics appear broadly similar, whether isolated teeth are  
23  
24 416 included or not, but the values without such teeth are inevitably always higher (over 1400 of  
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26 417 the 4083 specimens comprise isolated teeth only). The differences between time bins continue  
27  
28 418 to be significant (Figs 2, 3) regardless of whether the data include or exclude specimens  
29  
30 419 consisting of only a single tooth. The metric that is least changed by the removal of tooth-only  
31  
32 420 specimens is QCM.

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35 421 A difference between the ‘with teeth’ and ‘without teeth’ time series occurs in the late  
36  
37 422 Santonian for QCM, where the value excluding teeth is considerably higher (Fig. 2B). In the  
38  
39 423 early Campanian, a disproportionate number of tooth-only specimens (most likely from  
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41 424 *Prognathodon lutugini*) shift the ICM curve lower (Fig. 2C). The results are comparable also  
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43 425 for taxa named to species (Fig. 3), although the data set is smaller.

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46 426 There is an overall slightly declining trend in fossil completeness through time, with  
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48 427 completeness scores in the mid Cretaceous somewhat higher than those in the Maastrichtian.  
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50 428 However, the trend is modest, and perhaps dominated by the downturn from the early to late  
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52 429 Maastrichtian. For the whole data set, all three metrics show (Fig. 2) a high point in the  
53  
54 430 middle Coniacian, but this is based on a single specimen, and so the value is hardly

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3 431 meaningful. Further, there are no named mosasaur species datable exactly to the early  
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5 432 Coniacian (Fig. 3). For all specimens, the lowest average completeness is in the early  
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7 433 Santonian. The earliest true mosasaurs, found in the Turonian, have average completeness.  
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9 434 Later, completeness peaks in the late Santonian and drops to its lowest points in the early  
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11 435 Campanian and late Maastrichtian.

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13 436 For all three metrics, mean completeness (Table 4) for named species (TCMsp, QCMsp,  
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15 437 ICMsp) through time is correlated with overall completeness (TCMall, QCMall, ICMall) and  
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17 438 remains significant after FDR correction. Note that TCMsp and ICMsp are significantly  
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19 439 correlated with TCMav and ICMav after FDR correction, but other completeness metrics,  
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21 440 whether based on named specimens or all specimens, do not show significant correlations  
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23 441 with average species completeness (TCMav, QCMav, ICMav) analysed in specific time bins,  
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25 442 after FDR correction. For example, QCMsp does not correlate with QCMav. This indicates  
26  
27 443 that caution is required in interpreting time series that assume completeness values derived  
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29 444 from whole species-based values, such as averaged species completeness (TCMav, QCMav,  
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31 445 ICMav) are equivalent to specimen-based completeness averaged in single time bins.

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33 446 Both the sampled in-bin and “averaged” species diversity curves correlate significantly  
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35 447 with the generic diversity curves even after FDR correction (Table 4, Fig. 4A). Generic  
36  
37 448 diversity rises and falls, then upturns sharply from the mid Santonian onwards, and gently  
38  
39 449 rises through the Campanian to Maastrichtian, with only a slight increase through that span of  
40  
41 450 nearly 20 Myr. The species curves roughly follow the same pattern early on. The two curves  
42  
43 451 show a dramatic drop in diversity after the Turonian, corresponding to a low number of  
44  
45 452 assignable specimens; and in the early Coniacian none can be named to species level (e.g.  
46  
47 453 *Tylosaurus* indet.). Mosasaurid species diversity rises during the middle Coniacian, dropping  
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49 454 in the early Santonian, but then generally rises to the K/Pg boundary, with a slight drop in  
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3 455 the early Maastrichtian. Note that species diversity is at its highest during the late  
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5 456 Maastrichtian, with no hint of a pre-mass extinction diversity drop.

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7 457 For comparison, sea level (Fig. 4B) fluctuates in the Turonian through early Santonian,  
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9 458 concurrently with the **variability** in mosasaur diversity. The lowest sea level occurs in the  
10  
11 459 early Santonian, but it rises until the early Campanian, when it reaches its highest level. A  
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13 460 drop in sea level occurs in the early Maastrichtian, at the same time as a small drop in species  
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15 461 diversity. Species diversity is high during some times of relatively high sea level, but none of  
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17 462 the three diversity time series curves **correlates** in a statistically significant way with mean sea  
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19 463 level (Table 4) **in this comparison**. In like manner, none of the measures of completeness  
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21 464 shows any statistically significant correlations with sea level (Table 4).  
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26 466 *Predicting diversity and completeness.* GLS model fitting shows that a combination of **all**  
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28 467 **variables (e.g. sea level, mosasaur and plesiosaur bearing formations (MPBFs), TCM, and**  
29  
30 468 **age) best predict averaged diversity** (Driscoll *et al.* 2018, **Appendix Table S6A**). While sea  
31  
32 469 level and **MPBFs** appear positively related to **averaged** diversity (i.e. higher sea level or more  
33  
34 470 **MPBFs** sampled equals higher diversity), age is negatively related to diversity, i.e. mosasaur  
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36 471 diversity increases through time (Driscoll *et al.* 2018, **Appendix Table S6B**). However, once  
37  
38 472 we account for autocorrelation, we find that the best fitting model contains only sea level and  
39  
40 473 **MPBFs**, both of which are positively related to **averaged** diversity (Tables 5, 6). The best  
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42 474 fitting model for predicting **TCM<sub>sp</sub>** consists of **all variables (e.g. species diversity, sea level,**  
43  
44 475 **MPBFs and age)** (Driscoll *et al.* 2018, **Appendix Table S6A**). However, **none of these**  
45  
46 476 **variables appears to be significantly associated with TCM<sub>sp</sub>** (Driscoll *et al.* 2018, **Appendix**  
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48 477 **Table S6B**). When we account for autocorrelation, the best fitting model still for **TCM<sub>sp</sub>**  
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50 478 **contains all variables, but none is significant** (Tables 5, 6).  
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3 480 *Determinants of fossil completeness*

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5 481 *Taxonomic rank.* As might be predicted, mean TCM increases as one narrows taxonomy from  
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7 482 family to genus to species (Fig. 5A, B), and these differences are statistically highly  
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9 483 significant. Interestingly though, when all specimens including teeth were used in the  
10  
11 484 analysis, it was difficult to discriminate a significant difference in completeness between  
12  
13 485 genera and species (Fig. 5A), even though there was discrimination among all three  
14  
15 486 taxonomic categories when tested together. But, when the tests were repeated excluding  
16  
17 487 tooth-only specimens, there was clear discrimination (Fig. 5B). Among all 4083 specimens,  
18  
19 488 1044 were attributable to family only (Mosasauridae indet.), 731 to genera, and 2304 to  
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21 489 species.  
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26 491 *Lithology.* There are highly significant differences in TCMsp among specimens preserved in  
27  
28 492 different lithologies, with fossils preserved in clays displaying higher completeness than those  
29  
30 493 preserved in carbonate or coarse siliciclastic deposits (Fig. 6). These differences are much  
31  
32 494 smaller when specimens consisting only of teeth are left out of the analysis.  
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36  
37 496 *Palaeogeographic region.* The mean TCM of specimens identified as species varies  
38  
39 497 significantly by palaeocontinental region, with specimens from North America showing  
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41 498 higher completeness than those from Eurasia and Gondwana (Fig. 7). When tooth-only  
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43 499 specimens are excluded, there are no statistical differences.  
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48 501 *Formation.* Fossil completeness as measured by TCMsp varies significantly between different  
49  
50 502 geological formations. The Pierre Shale Formation in the western interior of the USA and the  
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52 503 Craie de Ciplu in Belgium have the most complete fossils (Fig. 8). The Maastrichtian  
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3 504 formations of the New Jersey Greensand and Maastricht Chalk yield the least complete  
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5 505 specimens.

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9 507 *Body size.* There are no significant differences in total mean species completeness (TCMtot)  
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11 508 between different body size classes derived from the estimated average body length of the  
12  
13 509 individual species concerned (Fig. 9).

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18 511 *Sampling.* Average species completeness correlates significantly and inversely with the  
19  
20 512 number of years elapsed since description, and inversely also with the number of specimens  
21  
22 513 per species (Table 7). The average completeness per species compared to the completeness of  
23  
24 514 the best specimen in a species correlates strongly for all three metrics. The best specimen  
25  
26 515 influences the average for a whole species. The total number of specimens per species shows  
27  
28 516 statistically significant positive variation with the number of years since description. The  
29  
30 517 number of Google Scholar “hits” for a species correlates strongly with the number of  
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32 518 specimens, as well as years elapsed since description. There is a trend for Google Scholar  
33  
34 519 “hits” to increase with estimated mosasaur body length, which is not quite statistically  
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36 520 significant using Spearman’s  $\rho$  ( $r_s = 0.26$ ,  $p = 0.052$ ).

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39 521 Results for North America rock outcrop area (Table 7) show no correlations between  
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41 522 regional diversity, formational outcrop area, or mean TCM by formation.

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46 524 *Overview of mosasaur fossil completeness.* The mean completeness (TCMtot) by species  
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48 525 using individual specimens ranged from 1.0 for those species known only from teeth, jaws or  
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50 526 individual bones to a high of 13.67 for *Hainosaurus bernardi* (Driscoll *et al.* 2018, Data A).  
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52 527 The scores by specimen type (Table 3; Driscoll *et al.* 2018, Data F–H) show that the average  
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54 528 holotype completeness is 8.1 for TCMh, which is approximately equivalent to 25% of the

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3 529 skeleton in the average mosasaur holotype. The highest scoring holotype is 32 for UPI R163,  
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5 530 *Eonatator sternbergii*. The lowest score for TCMh is 1.0 for several holotypes. The most  
6  
7 531 complete specimen is not always a holotype. *Platecarpus tympaniticus* (YPM 58129) from  
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9 532 the Kansas Chalk, with a TCMc of 36, is the most complete specimen in the database.  
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11 533 However, at least five other specimens scored over 30. Several species have perfect  
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13 534 composite scores, including some with soft tissue preservation (e.g. *Platecarpus tympaniticus*  
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15 535 and *Tylosaurus proriger*).

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18 536 The highest mean QCMtot was 5.6 for individual specimens of *Tethysaurus nopscai*. The  
19  
20 537 mean holotype completeness (QCMh) is 4.5; thus 50% of the phylogenetic characters occur in  
21  
22 538 the average type specimen. The highest QCMh is 8 (equivalent to a skull and most of the  
23  
24 539 skeleton) for several holotypes: *Eonatator sternbergii*, *Clidastes propython*, *Mosasaurus*  
25  
26 540 *missouriensis*, *Plotosaurus bennisoni* and *Latoplatecarpus willistoni*. The lowest QCMh for a  
27  
28 541 type specimen is 1.0 (but this a lectotype) for *Goronyosaurus nigeriensis*. Of note, the  
29  
30 542 composite score (QCMc) of *G. nigeriensis* is 8; multiple specimens make up for most of the  
31  
32 543 elements missing in most individual fossils. The best specimens of both *Tylosaurus proriger*  
33  
34 544 and *Platecarpus tympaniticus* both have QCMb scores of 9. The mean QCMc for all species  
35  
36 545 is 6.2. This indicates the composite character completeness of the average mosasaur species is  
37  
38 546 approximately equivalent to the score for a skull of that species. Multiple species have a  
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40 547 perfect QCMc. It should be noted, that at the time of this compilation, there were three  
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42 548 species with a QCMc only equal to 2.0, the lowest composite score, equivalent to a jaw  
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44 549 element, namely *Carinodens belgicus*, *Carinodens minalmimar* and *Igdamanosaurus*  
45  
46 550 *aegyptiacus*.

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50 551 The average TCMc for composite specimens is 15.7 (about 44 % of the skeleton). The  
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52 552 mean composite score for ICMc is 4.5/6, equivalent to some skull, axial and limb elements  
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54 553 available to describe the average mosasaur species.  
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5 555 **DISCUSSION**

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7 556 *Describing the mosasaur fossil record.* In this study, we have addressed one of the richest  
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9 557 vertebrate fossil records. Mosasaurs have attracted study for over two centuries, with the first  
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11 558 find, *Mosasaurus hoffmanni*, being described by Cuvier in 1808 (Russell 1967). Later  
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13 559 collectors noted their huge abundance: it is said that O. C. Marsh collected over 2,000 Kansas  
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15 560 mosasaur specimens (Everhart 2000), and Ikejiri *et al.* (2013) counted 1,563 Alabama  
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17 561 mosasaur specimens. An estimate of “literally thousands” of specimens of *Platecarpus* from  
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19 562 Kansas has been suggested (Konishi & Caldwell 2007). Our analysis of mosasaur diversity  
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21 563 through time complements previous studies (Polcyn *et al.* 2014; Ross 2009).

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24 564 It has been argued (Mannion & Upchurch 2010) that skeletal completeness metrics can  
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26 565 evaluate confidence in palaeontological data: as knowledge of the anatomy of a taxon  
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28 566 becomes more complete, with increased numbers of specimens, or more complete skeletons,  
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30 567 confidence in taxonomic assignments improves. In an ideal world, palaeontologists would  
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32 568 wait for relatively complete specimens before applying new taxonomic names, but in fact new  
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34 569 genera and species are often based on poor material. For example, in the case of echinoids  
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36 570 (Smith 2007), incomplete fossils were named more frequently than complete specimens, and  
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38 571 in the case of dinosaurs (Benton 2008a), the naming of species in the 19<sup>th</sup> century was  
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40 572 prodigious but quite inaccurate, and holotypes were on average much more incomplete before  
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42 573 1960 than after that date (Benton 2008b). **Brocklehurst & Fröbisch (2014) found, on the other**  
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44 574 **hand, that pelycosaurs named before 1900 were on average much more complete than those**  
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46 575 **named after that date.**

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50 576 Early in mosasaur palaeontology, many species were named based on inadequate  
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52 577 material, as can be seen by a perusal of invalid names listed by Russell (1967). Perhaps in the  
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54 578 19<sup>th</sup> century, names applied to scrappy material might by chance have been correct, as

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3 579 palaeontologists were naming the first ever mosasaur finds from newly identified geological  
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5 580 formations, but today, it is likely that new names applied to scrappy material risk being  
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7 581 synonyms of already named taxa.  
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11 583 *Using completeness scores in mosasaurs.* This is a specimen-, rather than taxon-based study.

13 584 Occurrence-based records that depend on presumed ranges of species were not used to place

15 585 specimens in time bins in the completeness calculations. This paper shows the utility of this

17 586 method, which might not have had enough power for statistical testing; the greatest risk was

19 587 with TCM, since the average completeness values are quite low. However, the analysis was

21 588 possible because of the large number of specimens in the database.  
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24 589 All three completeness metrics (TCM, QCM, TCM) correlated with each other, both

26 590 specimen by specimen and through the time series. A similar result was found with

28 591 ichthyosaur completeness, where SCM correlated with BSCM (Cleary et al 2015), a metric

30 592 similar to those used in this study. Our results suggest that even qualitative measures, such as

32 593 QCM and ICM, can be useful for comparing specimens and, because they correlate with TCM

34 594 (a quantitative metric) and with each other, any one of these metrics could be used to score

36 595 mosasaur fossils.  
38

39 596 TCM is based on true specimen in-bin averages, and thus it is likely driven by taphonomy

41 597 (Mannion & Upchurch 2010; Beardmore *et al.* 2012 a, b). TCM is similar to SCM, but it is

43 598 **not weighted volumetrically, but equally by anatomical region.** Weighting by size may

45 599 introduce an assumption that larger elements or regions are preserved more readily than

47 600 smaller ones. Disallowing such weighting then allows TCM to be used to test taphonomic or

49 601 preservational hypotheses.  
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52 602 QCM was developed as a proxy for phylogenetic completeness, and is somewhat

54 603 equivalent to CCM. QCM estimates phylogenetic completeness without having to score  
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3 604 characters on every element of a fossil specimen, because QCM is pre-weighted by character  
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5 605 density. In terms of the time involved in scoring, QCM can be assessed quickly from a  
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7 606 photograph or a fair description, whereas methods such as CCM require careful coding of all  
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9 607 skeletal elements. ICM, although less quantitative than the other metrics, was easily scored  
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11 608 and could discriminate mosasaur completeness in line with TCM and QCM values, even  
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13 609 when specimens could not be examined directly, or photos or more specific descriptions were  
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15 610 not available. This confirms its usefulness.

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18 611 It is important to note that there were some differences in our results when compared to  
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20 612 other studies using the SCM and CCM metrics. In most other fossil completeness studies (*e.g.*  
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22 613 Mannion & Upchurch 2010; Brocklehurst *et al.* 2012; Brocklehurst & Fröbisch 2014; Cleary  
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24 614 *et al.* 2015; Dean *et al.* 2016; Tutin & Butler 2017), **best and composite completeness values**  
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26 615 **for a species are calculated and then these values are generally assigned to time bins of the**  
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28 616 **species temporal range (usually based on first and last appearances). These completeness**  
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30 617 **values are then averaged in the various time bins. If there were only a single specimen**  
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32 618 **representing a species that is only assignable imprecisely to several time bins, there would be**  
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34 619 **no other alternative but to use this method. If the best specimen of a species or the composite**  
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36 620 **specimen cannot be assigned to an individual time bin, the result is the same as if the mean**  
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38 621 **completeness for a species did not vary over time bins. The large size of our data set allowed**  
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40 622 **for analysis using only exactly assignable in-bin specimens and avoided the need for proxies**  
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42 623 **of specimen completeness such SCM or CCM.**

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45 624 In our study, we chose not to include composite (TCMc, QCMc, ICMc), best (TCMb,  
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47 625 QCMb, ICMb), or holotype (TCMh, QCMh, ICMh) completeness metrics in the time series  
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49 626 analyses, to avoid calculating estimates of completeness from un-sampled specimens. In some  
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51 627 studies that used stage-level time bins (*e.g.* Cleary *et al.* 2015; Dean *et al.* 2016), best  
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53 628 specimen or composite specimen values were used, which involves some risk of  
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3 629 amalgamating disparate data across time bins. We provide data for holotype completeness  
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5 630 (TCMh, QCMh, ICMh), equivalent to SCMts, as well as best and composite specimen scores  
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7 631 average scores, lowest scores, etc. (Table 3), only for comparative purposes.  
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11 633 *Completeness and the mosasaur fossil record.* Most mosasaur species are very complete  
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13 634 (Driscoll *et al.* 2018, Data F–H), especially if one considers composite completeness by  
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15 635 species. On average, over 65% of the phylogenetic information is available for the average  
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17 636 mosasaur species. This is better than for anomodonts (Walther & Fröbisch 2013), otherwise  
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19 637 assumed to be rather complete, although anomodont skulls yield 82% of phylogenetic  
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21 638 characters on average, whereas postcranial characters account for only 4–9% of possible  
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23 639 totals. Our data show that through the history of mosasaur collecting there has not generally  
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25 640 been a bias in selecting well-preserved fossils. This is demonstrated by the fact that museums  
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27 641 curate thousands of incomplete specimens, indicated by the wide range of TCM and QCM  
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29 642 values (Driscoll *et al.* 2018, Data B). It should be noted that most of the QCM values are low  
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31 643 because there was not an over-representation of, say, skull material that would show bias in  
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33 644 collecting. QCM does not correlate with diversity (see below), and this is also an argument  
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35 645 that the best specimens do not bias the mosasaur record.  
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39 646 Because we included over 4,000 specimens of all completeness values, half of which  
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41 647 have TCM and QCM scores of 1 or 2, we were not sure at first whether the inclusion of such  
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43 648 low-scoring singleton specimens would distort our conclusions. On the other hand, we  
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45 649 reasoned that the inclusion of low-scoring elements should contain valuable information  
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47 650 concerning taphonomic drivers of preservation. Especially worrisome was the fact that so  
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49 651 many teeth were included as individual specimens.  
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52 652 These concerns were tested in several ways. Kendall tau-b correlation analysis comparing  
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54 653 completeness values over all specimens showed that, even though there were many  
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3 654 incomplete specimens, ties in the ranks did not affect analyses. All metrics are equally useful  
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5 655 for scoring. In any case, we analysed time series with and without teeth, and comparisons  
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7 656 remained statistically significant. It makes taphonomic sense that the inclusion of teeth in the  
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9 657 analysis of lithological variables increased the discrimination between rock types. The same  
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11 658 type of result occurred with the analysis of formational data, which again must vary by rock  
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13 659 type. Interestingly, leaving out tooth-only specimens obliterated the statistical differences  
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15 660 between palaeogeographic regions. European collections certainly do contain more teeth  
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17 661 (Driscoll *et al.* 2018, **Data B**) and perhaps European scientists have always identified more  
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19 662 specimens with teeth alone.

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22 663 It is reassuring that completeness scores are inversely proportional to category-level  
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24 664 discrimination, being best for specimens identified to species level, then poorer for those  
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26 665 identified to genus level, and worst for those assigned only to family. As noted before, the  
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28 666 difference between species and genus completeness is greatly enhanced when specimens  
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30 667 consisting of only teeth are excluded from the analysis. A few taxa have a very low  
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32 668 completeness score (e.g. *Tylosaurus ivoensis*), but all species with a species epithet have at  
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34 669 least some material that is separable by apomorphic characters (Bell 1995), the minimum  
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36 670 requirement for naming new taxa (Parham *et al.* 2012). It is perhaps true, that a species can be  
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38 671 identified by its teeth (Lindgren & Siverson 2002; Bardet *et al.* 2015), but in marine reptiles  
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40 672 the teeth are often homodont and lack variability, being in many cases convergently adapted  
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42 673 to diet (Massare 1987), and so may be of limited use taxonomically. When designing future  
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44 674 specimen-based studies, analyses with and without teeth would be recommended.

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48 675 **A key discovery was that completeness of species as measured by TCMav does not**  
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50 676 **necessarily correlate with completeness of specimens. Most studies on the completeness of**  
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52 677 **the fossils have assigned various completeness scores to each species, but have treated these**  
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54 678 **scores as a measure of preservation quality. The fact that the species-level scores for**  
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3 679 mosasaurs do not necessarily represent the quality of the preservation of the individual fossil  
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5 680 specimens has important implications for how the results of these studies should be  
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7 681 interpreted. The use of any whole species proxies for completeness that are derived from data  
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9 682 outside of the time bin where the data is averaged will not necessarily be equivalent to  
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11 683 analyses compiled from specimens in their home time bins. Results from species- and  
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13 684 specimen-based studies will likely be more disparate with larger samples and shorter time  
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15 685 bins. In addition, there could be links to correlations between completeness, the number of  
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17 686 specimens and year since description: the completeness scores assigned to whole species will  
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19 687 be a result of the accumulation of specimens assigned to that species, which we have shown  
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21 688 are influenced by the history of discovery (= number of years since description).  
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690 *Mosasaur completeness through time.* Hundreds of specimens of mosasaurs are datable to  
691 substage, and the analysis shows that this subset of is a good representation of overall  
692 mosasaur species completeness. There are significant differences in completeness over time;  
693 but values in mean completeness from substage to substage are not unexpected, as the  
694 conditions for fossil preservation must vary in complex ways from fossil to fossil, formation  
695 to formation and taphonomic microenvironment to microenvironment. Because there are so  
696 many specimens in these time bins, from a wide geographic range, it is difficult to recognise  
697 any individual collections or formations that are driving these curves. The differences  
698 between time bins represent true in-bin mean values. We show here that using the average  
699 completeness of a species group (**TCMav, QCMav, and ICMav**) to calculate overall time bin  
700 completeness (**TCMtot, QCMtot and ICMtot**) is not generally warranted, at least for QCM **in**  
701 **this dataset**. Surprisingly, when TCMav was used to estimate species completeness by  
702 substage, it did correlate significantly with the mean TCMsp of the individual specimens in

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3 703 the time bin. This may indicate that multiple specimens of a single species tend to fossilise in  
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5 704 similar ways.

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7 705 It might have been predicted that mosasaur completeness would depend on sea level, as is  
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9 706 the case for ichthyosaurs (Cleary *et al.* 2015) and plesiosaurs (Tutin & Butler 2017).  
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11 707 However, we found no relationship between mosasaur skeletal completeness and average sea  
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13 708 level in any of the time series analyses. There were some negative correlations (Table 4), but  
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15 709 the correlation coefficients were extremely low, and not even near significant. Similarly, in  
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17 710 GLS analysis, even though the best fitting model for predicting TCM<sub>sp</sub> included sea level, its  
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19 711 predictive value was no better than the null model.

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22 712 In cases where specimen quality depends on sea level, it might be predicted that the  
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24 713 relationship would be positive, in that deep-water settings should provide better conditions for  
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26 714 preservation than shallow waters, because the deep oceans are less subject to high-energy  
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28 715 deposition, except through the medium of turbidity currents, and there are fewer scavengers  
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30 716 than on the marine shelf. However, for ichthyosaurs (Cleary *et al.* 2015) and plesiosaurs,  
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32 717 (Tutin & Butler 2017), completeness is inversely proportional to sea level, significantly so for  
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34 718 the former, but not the latter. **This inverse statistically insignificant relationship may also**  
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36 719 **occur in marine crocodiles (Driscoll, unpublished)**, but the reasons for this relationship are not  
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38 720 clear. As mentioned by Tutin & Butler (2017), the marine reptile fossil record is not  
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40 721 particularly well sampled in the Jurassic and earliest Cretaceous, which might bias results. It  
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42 722 is not clear whether this idea is confirmed by the absence of such a trend in the more  
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44 723 intensively sampled and time-limited sample of mosasaurs, or whether different marine reptile  
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46 724 groups show different preservation conditions.

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49 725 We suggest here that the mosasaur fossil record is not much affected by lack of sampling  
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51 726 (the exception being the early and mid Coniacian) and there is no correlation to changing sea  
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53 727 level. For terrestrial tetrapods, a negative relationship between **completeness** and sea level  
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3 728 was found for sauropod dinosaurs (Mannion & Upchurch 2010), which was explained by  
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5 729 differences in sauropodomorph ecology; but there was no correlation for Mesozoic birds  
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7 730 (Brocklehurst *et al.* 2012) or pterosaurs (Dean *et al.* 2016).  
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11 732 *Explaining mosasaur macroevolution.* In our first analysis, correlation results show no direct  
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13 733 relationship between species or genus diversity and sea level, but our GLS results do show a  
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15 734 significant contribution by sea level in the best fitting model explaining diversity. This  
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17 735 compares with Polcyn *et al.* (2014), who argued that sea level at least partially drove  
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19 736 mosasaur diversity, as mosasaur richness in their analysis trended in the same direction as sea  
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21 737 level. The initial expansion of the clade might well have been triggered by the onset of major  
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23 738 continental flooding in the early Late Cretaceous (Caldwell 2002). We suggest that any model  
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25 739 of mosasaur macroevolution using environmental drivers will have to take more than sea level  
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27 740 into account. The increase of mosasaur species richness combined with the quality of their  
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29 741 fossil record makes a strong case for a model of marine reptile evolution in which mosasaur  
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31 742 species steadily filled specific niches or expanded steadily into different biogeographic  
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33 743 regions, once variability in global marine environmental drivers became stable in the  
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35 744 Santonian. The almost level generic diversity curve in the latest Cretaceous shows that  
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37 745 mosasaurs had become long-term and stable residents of the Cretaceous seas right up to the  
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39 746 late Maastrichtian.

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43 747 Neither species nor generic diversity through time correlated with skeletal completeness  
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45 748 in mosasaurs for any of our metrics. In GLS modelling, the best-fitting auto-correlation model  
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47 749 of completeness (TCM<sub>sp</sub>), species diversity was a predictive variable, but it was not  
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49 750 statistically significant. This lack of correlation, confirming what Cleary *et al.* (2015) found  
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51 751 also for ichthyosaurs, suggests that the quality of fossils does not drive our models of marine  
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3 752 reptile diversity and it would be hard to construct a case that apparent changes in diversity are  
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5 753 simply artefacts of the quality of fossils or the quality of nomenclature based on those fossils.  
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9 755 *Sampling and redundancy.* In most previous fossil completeness studies, sampling proxies  
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11 756 have been used in multiple regression analysis of fossil completeness to help understand what  
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13 757 is driving measured values of diversity and completeness. Variables such as collections,  
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15 758 fossiliferous marine formations, dinosaur-bearing formations, marine tetrapod-bearing  
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17 759 formations, pterosaur-bearing formations and other proxies have all been used. Much of this  
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19 760 data is relatively accessible from the Paleobiology Database and/or the primary literature, but  
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21 761 most of it is tallied at stage level. In our study, using substage-dated specimens, it was not  
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23 762 possible to include the above proxies in our multiple regression analyses. Such a comparison  
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25 763 will be interesting once a narrower time range analysis is possible. Instead, we developed an  
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27 764 Upper Cretaceous substage-level proxy from mosasaur- and plesiosaur-bearing formations  
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29 765 (MPBFs). Almost all plesiosaur-bearing formations also contained mosasaurs, so the data  
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31 766 overlapped.

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35 767 In all our best fitting GLS models, with and without auto-correlation, MPBFs correlated  
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37 768 highly significantly with diversity. In the past, counts of fossiliferous formation were used as  
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39 769 a proxy for sampling that combined geological and human biases (Benson *et al.* 2010). If  
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41 770 MPBFs is considered as a proxy for geological megabiases, then our results could indicate  
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43 771 that none of our diversity data is reliable enough to compare with any other time series,  
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45 772 including sea level or completeness. However, the shape of the diversity curve, lack of  
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47 773 evidence for lithological or regional correlates with specimen completeness, and the  
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49 774 thousands of sampled fossils argue against jumping to this conclusion. Further, the data on  
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51 775 fossil occurrence (collections, specimen counts, localities, formations) were collected at the  
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53 776 same time as the data on diversity, and so there is a risk of tallying rock and fossil data that  
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3 777 describe the same history of discovery, so pointing to redundancy (Benton *et al.* 2011; Benton  
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5 778 2015). The redundancy hypothesis for highly correlated rock and fossil data was confirmed in  
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7 779 the case of the fossil records of the UK and the world by using statistical methods that  
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9 780 identify not only correlation but also directionality of causation (Dunhill *et al.* 2014, 2018).  
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11 781 Therefore, we cannot use the MPBF count as a sampling proxy because it is not an  
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13 782 independent yardstick that represents either geological or human sampling. Our other  
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15 783 variables, including fossil completeness, diversity and sea-level, are independent of one  
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17 784 another. We have shown that fossil preservation, as measured by specimen completeness  
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19 785 metrics, does not bias the fossil record of mosasaurs.  
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24 787 *Explaining mosasaur completeness.* We have compared completeness in the **best-known**  
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26 788 mosasaur-bearing formations. Factors that might explain the differences include lithology,  
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28 789 rock exposure and collecting biases. Comparing completeness among different outcrops and  
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30 790 formations can be used as an aid in understanding Lagerstätten effects.  
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33 791 Our results for mosasaurs show many agreements with the study of the ichthyosaur fossil  
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35 792 record by Cleary *et al.* (2015). In both studies, skeletons were more complete in fine-grained  
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37 793 than coarse-grained sediments (Fig. 5), and this was expected because fossil completeness is  
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39 794 partially dependent on taphonomy (Beardmore *et al.* 2012a, b) and post-depositional  
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41 795 geological factors. This is supported by the fact that when low-completeness specimens  
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43 796 consisting of only teeth are left out of calculations of mean completeness, the differences  
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45 797 between lithologies are less evident. We expect, for example, that since sandstones are  
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47 798 deposited in high-energy environments, which toss and abrade bone, specimens in sandstones  
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49 799 would have smaller mean completeness values than those in lower-energy mudstones. Fine-  
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51 800 grained sediments should preserve more detail. In fact, the New Jersey Greensands have the  
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53 801 lowest completeness of the formations considered, and the Pierre Shale has a high average  
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3 802 mean completeness value. A further contributor to the high quality of specimens in fine-  
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5 803 grained sediments such as the Pierre Shale are their anoxic environments, with little  
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7 804 scavenging (Kauffman & Sageman 1988).  
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9 805 The Pierre Shale covers thousands of square miles of the North American western  
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11 806 interior, and produces some almost complete articulated fossils with soft tissue (personal  
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13 807 observation; Carpenter 2006, 2008). The Pierre has yielded fewer specimens than the  
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15 808 Niobrara or Greensand, but considering its greater mean completeness, the sheer size of the  
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17 809 Pierre outcrop (311,000 km<sup>2</sup>) in comparison to that of the Niobrara and Greensand (21,000  
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19 810 km<sup>2</sup> each) and its relative inaccessibility in remote regions of the North American western  
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21 811 interior, suggests that complete specimens may yet be found. The Pierre Shale fossils have a  
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23 812 higher mean completeness score than those from the Niobrara Chalk, but the latter formation  
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25 813 is often considered a Lagerstätte (Bottjer 2002), and indeed some mosasaur soft tissue  
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27 814 impressions are found (Lindgren *et al.* 2010). If average completeness could be considered  
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29 815 one measure of a Lagerstätte, the Pierre should also be considered as such.  
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33 816 The Niobrara Chalk has experienced a great deal of collector effort (thousands of  
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35 817 specimens; over 150 years of effort by hundreds of people), and is still yielding fresh finds,  
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37 818 but no new species, barring those re-described, such as *Tylosaurus kansasensis*. Exposure  
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39 819 (desert badlands) and accessibility are high. Most of the Niobrara species have probably been  
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41 820 collected. Depending on average lithology and depositional environment, there may be a limit  
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43 821 to the skeletal quality within any geological formation, and no amount of additional collecting  
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45 822 can improve that. The fact that the mean TCM values between different formations are  
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47 823 significantly different with and without tooth-only specimens supports the idea that in highly  
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49 824 collected formations there may be a limit to average preservation values. Once enough rock is  
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51 825 exposed and collected, lithofacies biodiversity reaches a peak (e.g. Smith & Benson 2013),  
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53 826 and the known biodiversity then is limited by the ecology of the ancient environment and the  
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3 827 preservation potential of the rocks, assuming collector effort and accessibility is high. Bones  
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5 828 from the same family likely have similar preservation potential (Smith & McGowan 2011), so  
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7 829 it is doubtful that there are missing taxa based on preservation alone.

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9 830 Further to this theme, it might have been predicted that skeletal completeness and  
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11 831 diversity would be related in some way to outcrop or exposure area; perhaps, for example,  
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13 832 when the overall area of a geological formation is high, more skeletons of all kinds of  
14  
15 833 completeness might be found, and so the mean completeness score might then rise, and thus  
16  
17 834 perhaps biodiversity. In our preliminary analysis, the results show no significant correlation  
18  
19 835 between completeness and diversity or outcrop area for North American formations (Table 8).  
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21 836 This supports the idea that each formation is associated with an upper limit on preservation  
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23 837 potential if there has been adequate exposure and collector effort.

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26 838 The Craie de Ciply chalk from the Mons Basin in Belgium has the highest average  
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28 839 skeletal completeness score. This Ciply chalk has produced many holotypes (Dollo 1904),  
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30 840 and the blocks from that formation at the IRSNB contain highly articulated and well-  
31  
32 841 preserved specimens, and very few single elements or partial fossils. This is striking when  
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34 842 compared, for example, to the chalk at Maastricht, which has yielded many hundreds of  
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36 843 disarticulated specimens, but the explanation, presumably to do with mode of deposition and  
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38 844 rate of burial of the carcasses, is not clear. In this case, with all the almost complete skeletons  
39  
40 845 available, perhaps less spectacular specimens were not deemed worthy of collection, or  
41  
42 846 perhaps they do not exist. Neither lithology, outcrop area, nor the amount of collecting  
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44 847 explains the completeness of these Belgian fossils, limited in area to quarries in a relatively  
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46 848 small region.

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49 849 The average completeness of mosasaur specimens **has tended** to decrease through  
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51 850 research time, which was **initially** unexpected: specimens described and named many years  
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53 851 ago tend to be more complete than those named more recently. The holotypes of species  
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3 852 currently regarded as valid are typically rather complete specimens, and subsequently  
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5 853 identified materials of many of these species may on average be less complete, and now more  
6  
7 854 easily identifiable. Such specimens are not typically considered publishable material; and  
8  
9 855 studies that use only published material to describe historical trends in fossil quality may not  
10  
11 856 show the same result. The average-quality material found in many museums outnumbers  
12  
13 857 more complete material. The inverse completeness trend may reflect that the holotypes of taxa  
14  
15 858 named in former centuries were substantially complete and have been preferentially retained,  
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17 859 whereas less complete materials were disposed of, or perhaps not collected at all in the early  
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19 860 days of palaeontology when collectors were perhaps less assiduous in recording everything.  
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21  
22 861 Today, on the other hand, perhaps holotypes are of similar completeness, but museums retain  
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24 862 enormous collections of less complete, referred specimens. Again, completeness does not  
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26 863 continuously rise for a species as more specimens are collected, but we have not explored  
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28 864 historical differences in completeness for specific formations.

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31 865 Known fossil completeness of mosasaurs is best in North America and somewhat higher  
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33 866 in Gondwana. Surprisingly, the well-known very complete European specimens do not  
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35 867 significantly drive fossil completeness in Eurasia, nor does the relative number of specimens.  
36  
37 868 When the tooth-alone specimens are left out of the analysis, there are no significant  
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39 869 differences in completeness between the continents. North American collections in this  
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41 870 analysis are relatively devoid of tooth specimens. We were not able to make a significant  
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43 871 comparison of completeness in northern vs. southern hemispheres, as there are too few of the  
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45 872 latter. For ichthyosaurs, Cleary *et al.* (2015) showed the well-studied northern hemisphere  
46  
47 873 produced fossils of significantly higher quality than the southern hemisphere. The differences  
48  
49 874 above are all likely sampling artefacts.

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53 875 Larger mosasaurs do not show higher skeletal completeness than either small or medium-  
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55 876 sized ones. One might hypothesise that larger specimens would be more complete, as in some

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3 877 dinosaurs (Brown *et al.* 2013). The situation here is different from that seen in other, smaller  
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5 878 taxa such as birds or pterosaurs (Brocklehurst *et al.* 2012; Dean *et al.* 2016), where  
6  
7 879 Lagerstätten may selectively preserve smaller specimens better than large specimens found in  
8  
9 880 other deposits. This could be explained by the greater weight of their bones, the higher energy  
10  
11 881 required by sedimentary flows to disarticulate a skeleton, the fact that larger specimens are  
12  
13 882 easier to find, or they are preferentially collected. It is interesting to note that the number of  
14  
15 883 Google Scholar hits per species showed a trend (although, not quite significant) with  
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17 884 estimated body length, perhaps indicating preferential study of larger mosasaurs. For  
18  
19 885 ichthyosaurs, Cleary *et al.* (2015) rather surprisingly found that medium-sized specimens  
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21 886 were significantly more complete than small or large taxa: the incompleteness of small  
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23 887 specimens was expected, but it was a surprise that larger specimens were also relatively  
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25 888 incomplete.  
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## 890 CONCLUSIONS

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

899 Mosasaur fossils are found in all stratigraphic substages throughout their evolution, and  
900 neither skeletal nor phylogenetic completeness explains their diversity: fossil completeness  
901 does not bias the fossil record of mosasaurs and cannot be used as a proxy for diversity. A

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3 902 huge amount of both incomplete and well-preserved mosasaur material is identifiable, which  
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5 903 is not the case for some other Mesozoic tetrapod groups. The mosasaur fossil specimen record  
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7 904 contains thousands of teeth, which do not affect the general utility of the methods, but  
8  
9 905 improve the resolution of completeness values in taphonomically related comparisons.  
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11 906 Outcrop area, where data is available, does not explain mosasaur diversity. However,  
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13 907 lithology has a role: skeletal completeness is higher in fine-grained than in coarse-grained  
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15 908 sediments. There is no evidence to suggest that sea level drives mosasaur fossil completeness  
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17 909 or mosasaur diversity. We do not detect any geological megabiases driving the fossil record  
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19 910 of mosasaurs. Mosasaur species richness, based on specimens assignable to a single substage,  
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21 911 rises steadily and smoothly from the late Coniacian to late Maastrichtian and correlates with  
22  
23 912 the generic richness curve. **Although ambiguous in this study, sea level may play a role in**  
24  
25 913 **further models of mosasaur diversity. Low sampling in the mid Cretaceous** makes the analysis  
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27 914 of completeness difficult through this time range. Even considering this, mosasaurs appear  
28  
29 915 unique among marine tetrapods in terms of the reliability of their fossil record.  
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41 920 completeness metric; and this in turn inspired ideas on how to apply it to mosasaurs. We  
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31 940 Data for this study are available in the Dryad Digital Repository: <https://doi.org/XXX>  
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## Appendix

1214 *Appendix.* Species list for this study (Squamata, Mosasauridae) and the number of specimens  
 1215 included in the analysis; and mean completeness scores (TCM, QCM or ICM). Abbreviations:  
 1216 Camp = Campanian, Con = Coniacian, Maas = Maastrichthian, Sant = Santonian, Tur =  
 1217 Turonian. Completeness figures are rounded to two decimal places. The range is based on  
 1218 individual specimens that are datable to specific substages, except those with a “?”, whose  
 1219 range is near a boundary, or “??”, whose range is imprecise.  
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<i>Genus</i>	<i>Species</i>	Number	TCM	QCM	TCM	Range
<i>Eonatator</i>	<i>sp.</i>	1	2	1	1	Late Sant-Early Camp??
<i>Eonatator</i>	<i>sternbergii</i>	87	1.51	1.92	1.22	Early Camp
<i>Eonatator</i>	<i>cf. sternbergii</i>	1	2	3	3	Late Sant-Early Camp??
<i>Halisaurus</i>	<i>arambourgi</i>	33	5.64	2.76	3.25	Early-Late Maas
<i>Halisaurus</i>	<i>platyspondylus</i>	10	2.4	2	2	Early-Late Maas
<i>Phosphorosaurus</i>	<i>ortliebi</i>	1	2	3	3	Early Maas
<i>Phosphorosaurus</i>	<i>ponpetelegans</i>	1	10	7	4	Early Maas
<i>Carinodens</i>	<i>belgicus</i>	38	1.03	2	1.21	Late Maas
<i>Carinodens</i>	<i>minalmamar</i>	2	1.5	2	2	Late Maas
<i>Clidastes</i>	<i>liodontus</i>	21	8.47	5	3.67	Late Con-Early Camp
<i>Clidastes</i>	<i>moorevillensis</i>	4	6.67	4	3.67	Late Sant-Early Camp
<i>Clidastes</i>	<i>propython</i>	196	3.68	2.89	2.35	Early-Late Camp
<i>Dallasaurus</i>	<i>turneri</i>	3	7.33	3.33	3.33	Mid Tur
<i>Globidens</i>	<i>alabamensis</i>	16	1.47	2.44	1.53	Early-Late Camp
<i>Globidens</i>	<i>dakotensis</i>	1	8	6	4	Mid Camp
<i>Globidens</i>	<i>phosphaticus</i>	63	1.14	2.08	1.1	Early-Late Maas
<i>Globidens</i>	<i>schurmanni</i>	1	21	7	5	Late Camp
<i>Igdamanosaurus</i>	<i>aegyptiacus</i>	5	1	2	1	Early-Late Maas
<i>Kourisodon</i>	<i>sp.</i>	1	2	3	3	Late Camp
<i>Kourisodon</i>	<i>puntledgensis</i>	1	18	7	5	Late Sant
<i>Moanasaurus</i>	<i>mangahouangae</i>	5	6.6	5.2	3.6	Mid-Late Camp?
<i>Mosasaurus</i>	<i>beaugei</i>	110	1.03	2.02	1.04	Late Maas
<i>Mosasaurus</i>	<i>conodon</i>	123	3.53	2.49	1.81	Late Camp-Late Maas
<i>Mosasaurus</i>	<i>hobetsuensis</i>	1	13	3	3	Early Maas
<i>Mosasaurus</i>	<i>hoffmanni</i>	291	1.42	1.9	1.46	Early-Late Maas
<i>Mosasaurus</i>	<i>missouriensis</i>	11	9.9	5.4	4	Mid Camp-Late Camp
<i>Mosasaurus</i>	<i>mokoroa</i>	2	3.5	4.5	2.5	Mid Camp
<i>Mosasaurus</i>	<i>prismaticus</i>	1	2	3	3	Late Camp-Late Maas??
<i>Plotosaurus</i>	<i>sp</i>	1	1	2	1	Late Maas
<i>Plotosaurus</i>	<i>bennisoni</i>	50	4.59	2.19	1.86	Early Camp-Early Maas??
<i>Plesiotylosaurus</i>	<i>crassidens</i>	4	6.25	6	4	Early-Late Maas?
<i>Prognathodon</i>	<i>anceps</i>	6	1.17	2.17	1.67	Early Camp
<i>Prognathodon</i>	<i>currii</i>	8	2	2.63	1.38	Late Camp-Late Maas
<i>Prognathodon</i>	<i>kianda</i>	6	7	3.67	3.17	Late Maas
<i>Prognathodon</i>	<i>giganteus</i>	5	3	2.6	1.8	Early Maas
<i>Prognathodon</i>	<i>lutugini</i>	75	1.17	2.01	1.05	Early-Late Camp

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

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3 1222 **TABLE 1.** QCM method for scoring completeness. Presence or absence of a skull weights  
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5 1223 the score greatly. The skull contains 61% of characters used in the phylogenetic analysis of  
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7 1224 mosasaurs. A jaw fragment or tooth scores two points. Add total of parts present. There are  
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9 1225 nine points possible.

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

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

Metric	Sub-metric	Comment
		Taphonomic Completeness Metric - Total of scores from 8
TCM		regions.
		Qualitative Completeness Metric-Regions are weighted by
QCM		phylogenetic character density.
		Informal Completeness Metric-Scored only using skull,
ICM		axial and appendicular portions as regions.
	(TCM, QCM, ICM)tot	Total mean completeness of a <b>species, disregarding</b> 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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1232 **TABLE 3.** Summary of representative mosasaur completeness scores.

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

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3 1235 **TABLE 4.** Mean completeness comparisons by substage. Mean substage sea level (Miller  
4 1236 2005), species diversity (Species), generic diversity (Genus), and time-averaged species  
5 1237 diversity (Averaged) curves were compared. TCMav, QCMav and ICMav represent mean  
6 1238 substage completeness using average completeness for all specimens per species (TCMtot,  
7 1239 QCMtot, ICMtot) in the substage. TCMall, QCMall and ICMall are averages of all specimens  
8 1240 assigned to substage, regardless of species status. TCMsp, QCMsp, and TCMsp are average  
9 1241 completeness values per substage using only specimens with a designated species epithet.  
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	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*		

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1244 \* significant at  $p < 0.05$ ; \*\* significant after false discovery rate correction using method of  
1245 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 <b>averaged</b> diversity	TCM sea level <b>MPBFs</b>	<b>66.183</b>	<b>66.739</b>	<b>-26.091</b>
Best <b>averaged</b> diversity	<b>sea level</b> <b>MPBFs</b>	<b>60.251</b>	<b>61.435</b>	<b>-24.126</b>
Full <b>TCMsp</b>	diversity sea level <b>MPBFs</b>	<b>78.753</b>	<b>79.309</b>	<b>-32.376</b>
Best <b>TCMsp</b>	diversity <b>sea level</b> <b>MPBFs</b>	<b>78.753</b>	<b>79.309</b>	<b>-32.376</b>

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3 1249 **TABLE 6.** Summary of best-fitting GLS multiple regression models for predicting **averaged**  
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5 1250 diversity and **TCMsp** with autocorrelation structure for age parameter.

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

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21 1252

1253 **TABLE 7.** Correlation between species properties and completeness measures, **showing**  
 1254 **Spearman correlation coefficients.** Correlation tests were run over the following variables by  
 1255 species: average overall completeness by species (TCM, QCM and ICM); body length  
 1256 (Length) from Polcyn *et al.* (2014); Google Scholar “hits” (Google) for the species name;  
 1257 number of specimens **analysed** for that species (Specimens); and years since species first  
 1258 described (Years). Best of species (TCMb, QCMB, ICMb) and composite completeness  
 1259 (TCMc, QCMc, ICMc) were also compared to average species completeness values.

1260

	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

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1262 \* significant at  $p < 0.05$ ; \*\* significant after false discovery rate correction using method of

1263 Benjamini and Hochberg (1995).

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3 1265 **TABLE 8.** North American outcrop area vs. species diversity and mean species completeness

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5 1266 per **formation. There are** no significant correlations (Area vs. Diversity,  $r_s = 0.60$   $p = 0.35$ ;

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7 1267 Area vs. TCM,  $r_s = 0$ ,  $p = 1$ ; Diversity vs. TCM,  $r_s = 0.2$ ,  $p = 0.78$ )

8  
9 1268

Group	Area (km <sup>2</sup> )	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

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3 1270 **Figure Captions**

4  
5 1271 **FIG. 1.** Beardmore scoring method for mosasaur taphonomic completeness metric (TCM).

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7 1272 Each complete region of the skeleton (skull, ribs, forelimbs, hindlimbs and vertebrae (verts.)

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9 1273 including cervicals, dorsals, or caudals) is each worth 4 points, for a **maximum** possible score

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11 1274 of 36. Beardmore scoring **can assess** taphonomy. **Scoring is** as follows: 1. Count or

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13 1275 approximate number of elements for each region. 2. In incomplete skeletons, **score one** for

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15 1276 any girdle elements. 3. If vertebrae are undifferentiated, their score is the proportion present x

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17 1277 12 (**if** only two undifferentiated vertebrae, score = 2). 4. Any portion of a skull + any portion

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19 1278 of a jaw or **tooth = 2**. 5. Sum scores for each region. Skeletal image © Scott Hartman.

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24 1280 **FIG. 2.** Mosasaur specimen completeness by substage, **for specimens whose age is known.**

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26 1281 **Mean** completeness by substage was **calculated, according** to TCMall (A), QCMall (B), and

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28 1282 ICMall (C), **with** 95% confidence intervals, **except for** the early–middle Coniacian because

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30 1283 there are very few specimens. Completeness was plotted including and excluding specimens

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32 1284 consisting of only teeth. Statistics are shown here for specimens including teeth: TCMall vs.

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34 1285 QCMall (Spearman,  $r_s = 0.71$ ,  $p < 0.01$ ), TCMall vs. ICMall (Spearman,  $r_s = 0.77$ ,  $p < 0.01$ ),

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36 1286 QCMall vs. ICMall, (Spearman,  $r_s = 0.97$ ,  $p \ll 0.001$ ). When comparing differences between

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38 1287 time bins, TCMall (Kruskal-Wallis,  $\chi^2 = 597.73$ ,  $df = 12$ ,  $p < 0.001$ ), QCMall (Kruskal-

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40 1288 Wallis,  $\chi^2 = 219.08$ ,  $df = 12$ ,  $p < 0.001$ ), and ICMall (Kruskal-Wallis,  $\chi^2 = 529.56$ ,  $df = 12$ ,  $p$

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42 1289  $< 0.001$ ). For specimens *not* including teeth alone: when comparing differences between time

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44 1290 bins (TCMall, Kruskal-Wallis,  $\chi^2 = 30.05$ ,  $df = 12$ ,  $p = 0.003$ ; QCMall, Kruskal-Wallis,  $\chi^2 =$

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46 1291  $537.22$ ,  $df = 12$ ,  $p < 0.001$ ; ICMall, Kruskal-Wallis,  $\chi^2 = 38.38$ ,  $df = 12$ ,  $p = 0.001$ ).

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52 1293 **FIG. 3.** Comparing mosasaur species completeness by substage. **Mean and 95% confidence**

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54 1294 **intervals are plotted, and curves are plotted with and without teeth. Statistics for all specimens**

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3 1295 including teeth: TCMsp. vs. QCMsp (Spearman:  $r_s = 0.85$ ,  $p < 0.001$ ), TCMsp. vs. ICMsp  
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5 1296 (Spearman:  $r_s = 0.89$ ,  $p \ll 0.001$ ), QCMsp. vs. ICMsp (Spearman:  $r_s = 0.96$ ,  $p \ll 0.001$ ). In  
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7 1297 comparing completeness between time bins, TCMsp (Kruskal-Wallis,  $\chi^2 = 598.7904$ ,  $df = 11$ ,  
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9 1298  $p < 0.001$ ), QCMsp (Kruskal-Wallis,  $\chi^2 = 332.5136$ ,  $df = 11$ ,  $p < 0.001$ ), ICMsp (Kruskal  
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11 1299 Wallis:  $\chi^2 = 596.8376$ ,  $df = 11$ ,  $p < 0.001$ ). Statistics for all specimens *not* including teeth  
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13 1300 alone: TCMsp. – Kruskal-Wallis:  $\chi^2 = 28.13$ ,  $df = 11$ ,  $p = 0.003$ ), QCMsp (Kruskal-Wallis,  $\chi^2$   
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15 1301  $= 518.28$ ,  $df = 11$ ,  $p < 0.001$ ); ICMsp (Kruskal-Wallis,  $\chi^2 = 30.87$ ,  $df = 11$ ,  $p = 0.001$ ).  
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20 1303 **FIG. 4.** Mosasaur diversity and sea level through time. A. Generic and species diversity lines  
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22 1304 include only specimens with an exact substage assignment; the “averaged species” curve  
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24 1305 includes both in-bin species records, Lazarus taxa plus species based on specimens that could  
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26 1306 not be assigned to a stratigraphic substage with confidence, and so are averaged over all  
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28 1307 possible bins (e.g. two possible time bins, each species rated 0.5 per bin; three possible time  
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30 1308 bins, each species rated 0.33 per bin). B. Mean substage sea level from data available in  
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32 1309 Miller *et al.* (2005), and showing 95% confidence intervals.  
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37 1311 **FIG. 5.** Completeness by taxonomic rank. The mean completeness (TCM) was calculated for  
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39 1312 specimens in each category: Mosasauridae indeterminate, specimens identified to genus or  
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41 1313 identified to species. There are highly significant differences in TCM when comparing all  
42  
43 1314 three different taxonomic ranks (Kruskal-Wallis,  $\chi^2 = 95.62$ ,  $df = 2$ ,  $p < 0.001$ ). A. Results for  
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45 1315 all specimens including those consisting of a single tooth. In this case, there was no  
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47 1316 significant difference between completeness between genus and species specimens, because  
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49 1317 the median for each group = 1 (Wilcoxon:  $W=731307$ ,  $p = 0.09$ ). B. Plot for specimens *not*  
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51 1318 consisting of only teeth (Kruskal-Wallis,  $\chi^2 = 248.64$ ,  $df = 38$ ,  $p < 2.2e-16$ ). There are highly  
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53 1319 significant differences between groups, including genus and species.  
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5 1321 **FIG. 6.** Completeness by lithology. All specimens identified to species were assigned to the  
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7 1322 main lithology of their formation of origin. There are highly significant differences in TCM  
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9 1323 between different lithologies (Kruskal-Wallis,  $\chi^2 = 364.44$ ,  $df = 3$ ,  $p < 0.001$ ). Differences  
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11 1324 remain when specimens consisting of only teeth are left out, but are barely significant  
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13 1325 (Kruskal-Wallis,  $\chi^2 = 7.63$ ,  $df = 3$ ,  $p < 0.05$ ; plot not shown).

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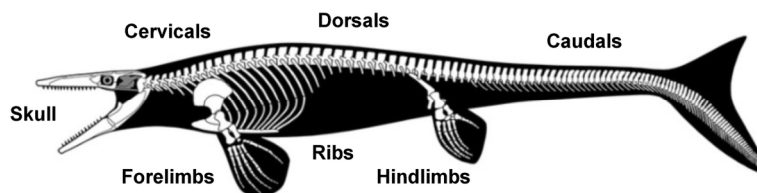
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18 1327 **FIG. 7.** Completeness by palaeogeographical region. Fossils named to species were divided  
19  
20 1328 by geographical origin. Because of a relative paucity of specimens, Africa, South America,  
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22 1329 Australia, New Zealand and Antarctic specimens were included in a “Gondwana” group.  
23  
24 1330 Mean TCM of species-named specimens showed highly significant differences between  
25  
26 1331 groups (Kruskal-Wallis,  $\chi^2 = 701.46$ ,  $df = 2$ ,  $p < 0.001$ ). When tooth-only specimens are left  
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28 1332 out of analysis, the differences are no longer significant (Kruskal-Wallis,  $\chi^2 = 0.9303$ ,  $df = 2$ ,  
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31 1333  $p = 0.63$ ; plot not shown).

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33 1334

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35 1335 **FIG. 8.** Completeness by well-known formations. There were over 100 formations to choose  
36  
37 1336 from. In this case, some of the best-known formations were compared. The mean TCM values  
38  
39 1337 for specimens named to species between formation groups showed highly significant  
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41 1338 differences (Kruskal-Wallis,  $\chi^2 = 595.89$ ,  $df = 5$ ,  $p < 0.001$ ). Differences remain when tooth-  
42  
43 1339 only specimens are left out (Kruskal-Wallis,  $\chi^2 = 32.05$ ,  $df = 5$ ,  $p < 0.001$ ; plot not included).

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48 1341 **FIG. 9.** Completeness by body size groups. There were no statistical differences between  
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50 1342 mean completeness (TCM<sub>tot</sub>) values of species among small, medium or large mosasaurs.

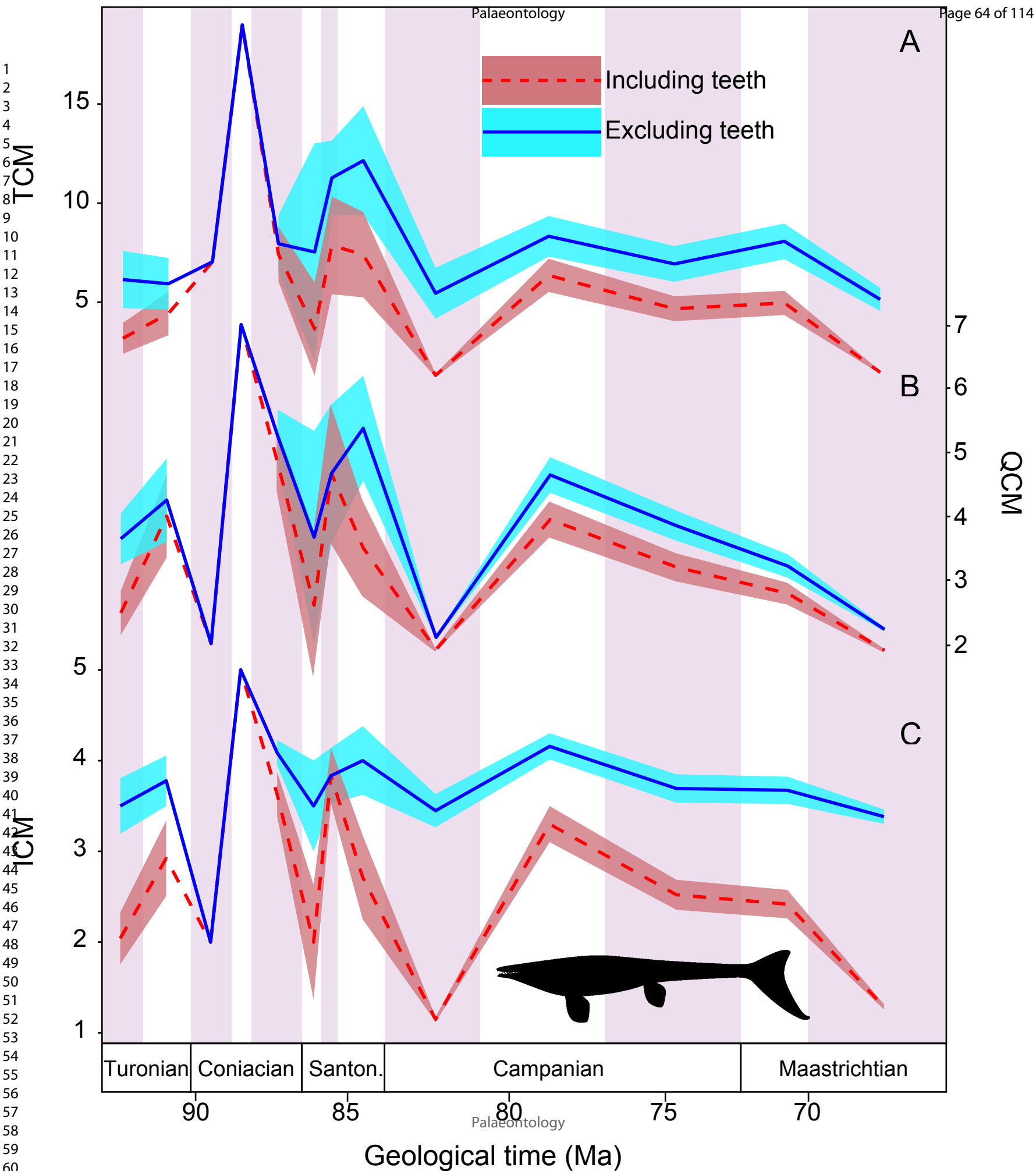


**Taphonomic Completeness Metric (TCM)**

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.

160x142mm (300 x 300 DPI)



Palaeontology

Including teeth  
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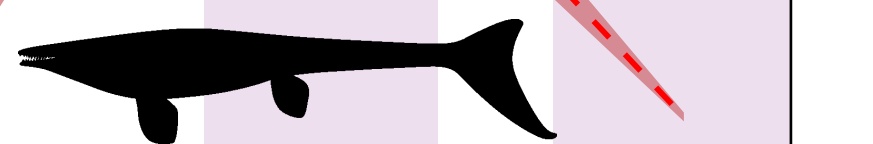
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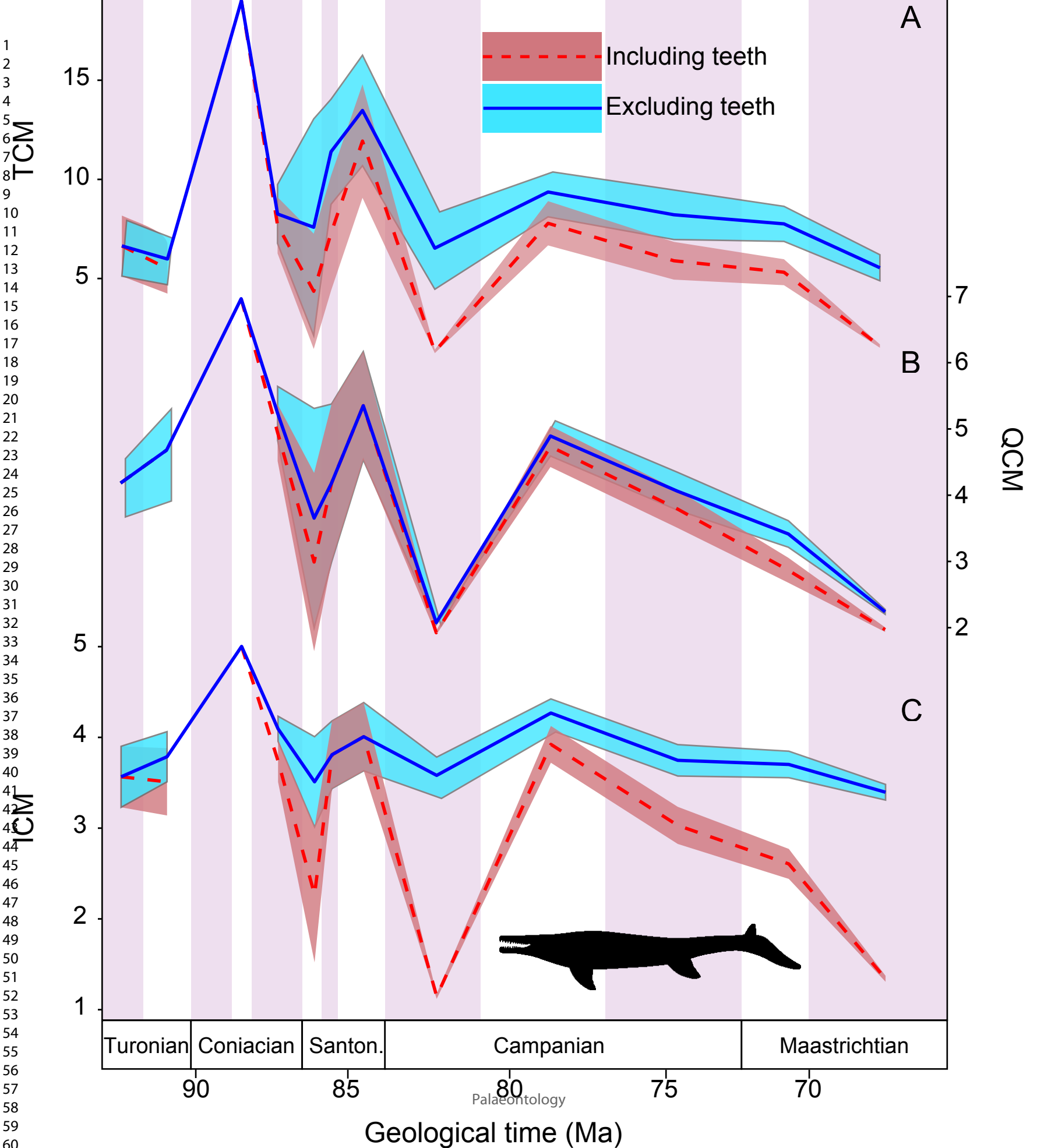
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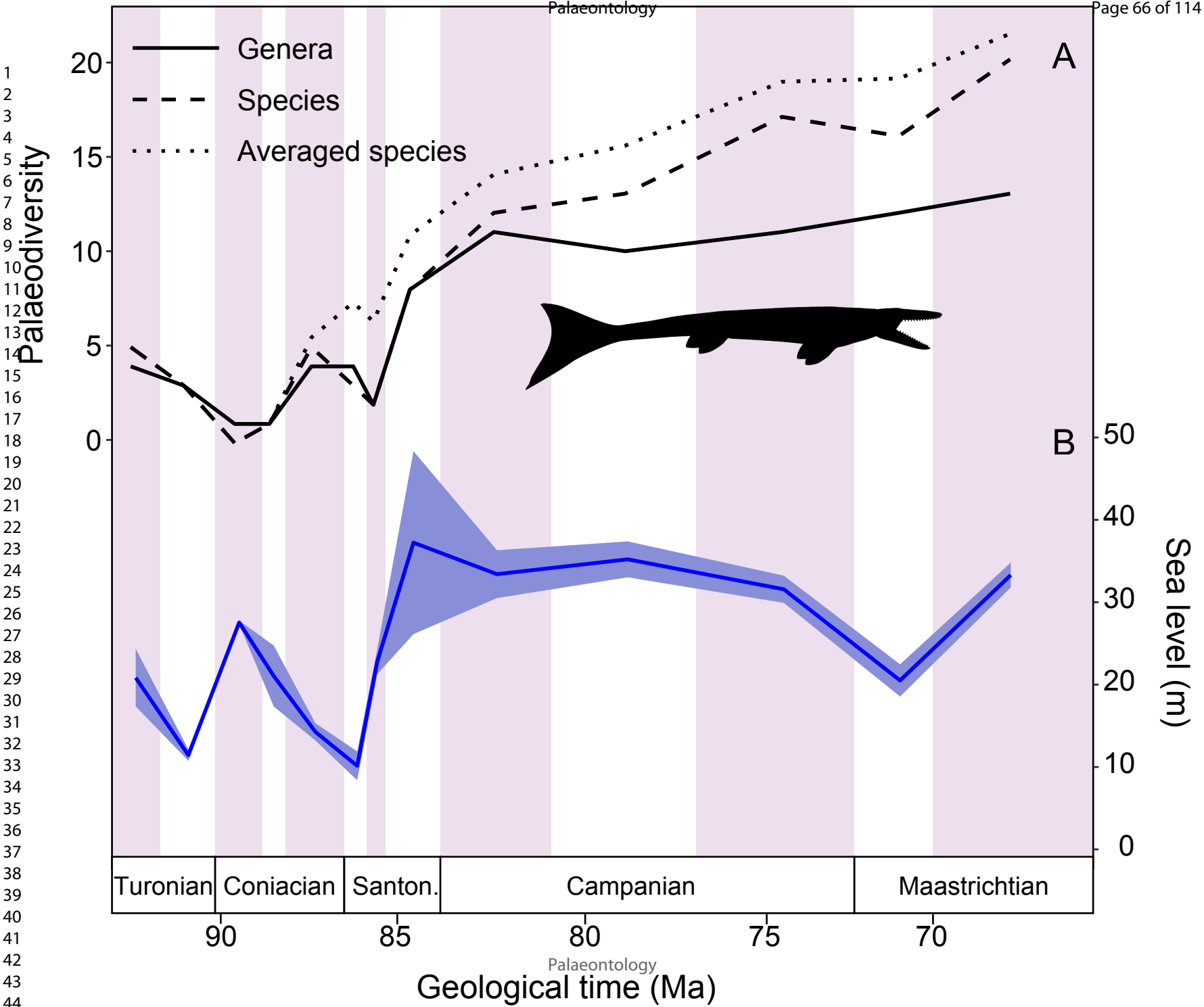
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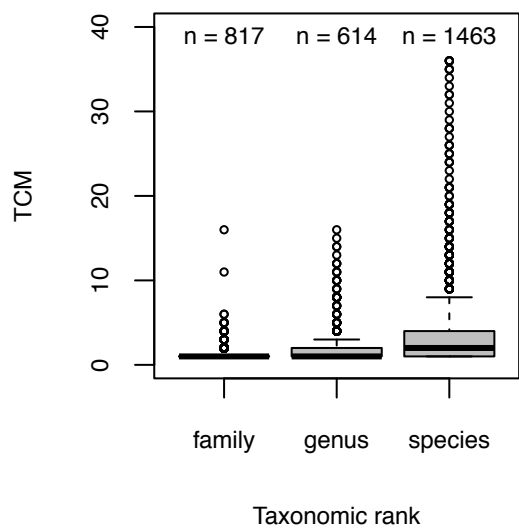
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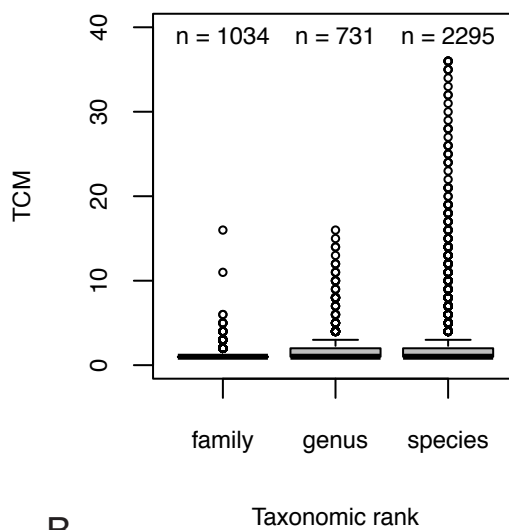


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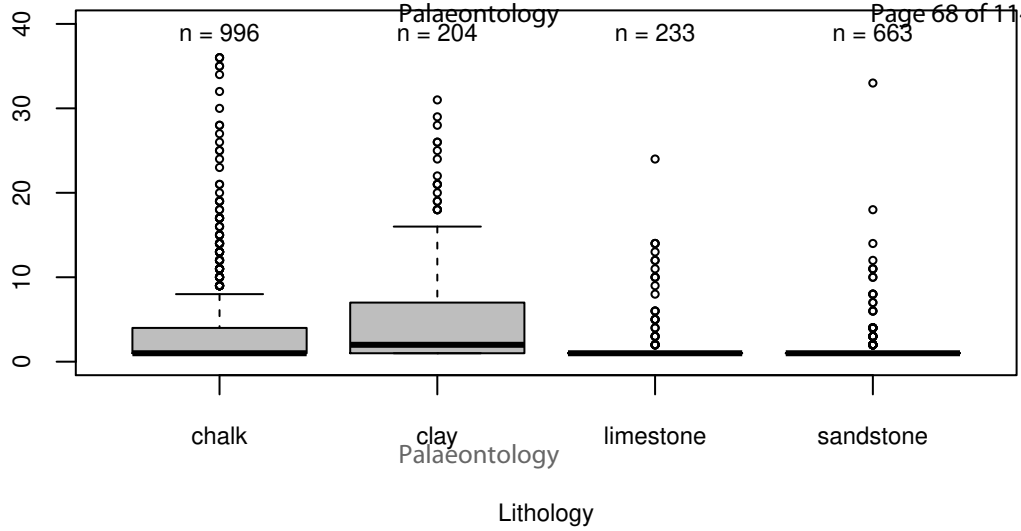


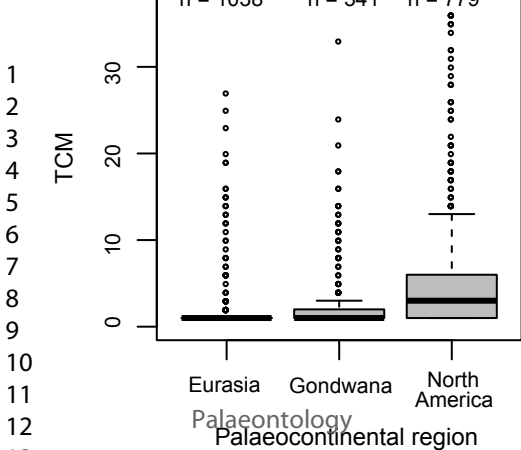
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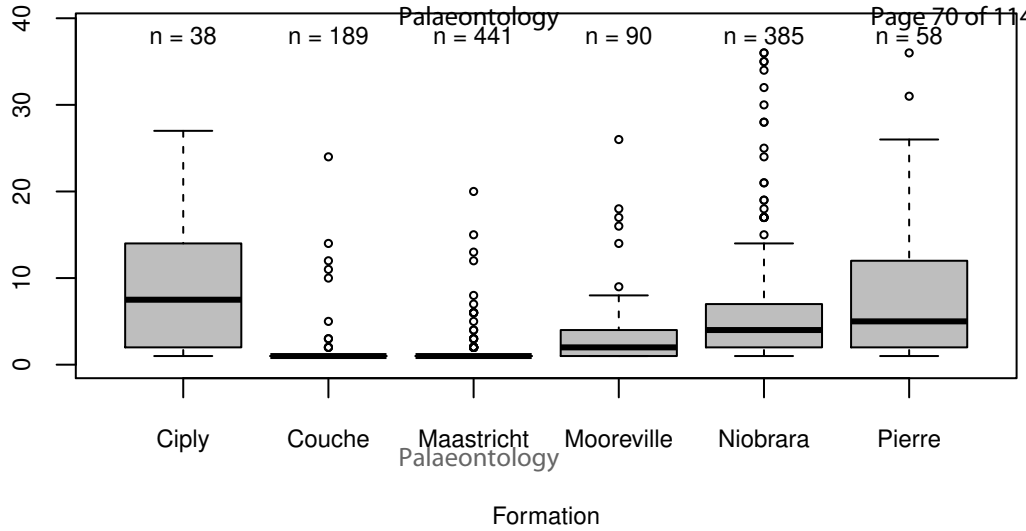
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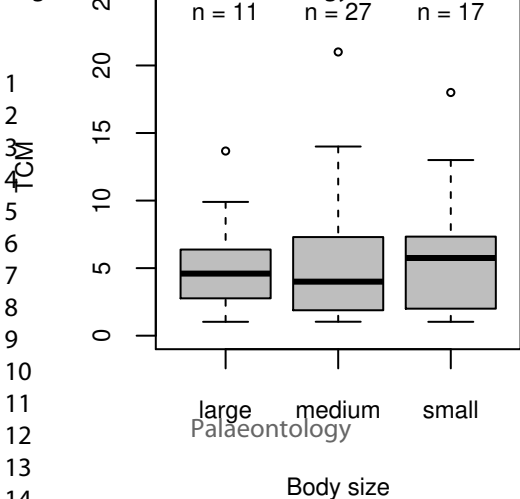
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3 **Supplementary Appendix for:**  
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6 **The mosasaur fossil record: through the lens of fossil completeness**  
7

8 Dan A. Driscoll, Alexander M. Dunhill, Thomas Stubbs and Michael J. Benton  
9

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11  
12 *Contents of the Supplementary Appendix*  
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15

16 TABLE S1. Institutional abbreviations of museums with mosasaur specimens (pp. 2–5).

17 TABLE S2. Museum specimens examined (pp. 5–9).

18 TABLE S3. Mosasaur holotype references (pp. 10–14).

19 TABLE S4. Specimen completeness using a simple method (ICM) (p. 15).

20 TABLE S5A. GLS data used to model TCM (p. 16).

21 TABLE S5B. GLS data used to model diversity (p. 16).

22 TABLE S6A. Summary of GLS analysis models without autocorrelation (p. 17).

23 TABLE S6B. Summary of the best fit GLS models for predicting TCM and Diversity without  
24 autocorrelation (p. 17).

25  
26 TABLE S7. Supplementary bibliography. References were used to find descriptions and  
27 figures of specimens, determine valid species; and determine geologic age and rock type of  
28 mosasaur-bearing stratigraphic units (pp. 18–31).  
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**TABLE S1.** Institutional abbreviations of museums with mosasaur specimens.

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5	ALNHM	Alabama Natural History Museum, Tuscaloosa, AL USA
6	AMNH	American Museum of Natural History, New York City, NY USA
7	ANSP	Academy of Natural Sciences at Drexel University, Philadelphia, PA USA
8	AUMP	Auburn University Dept. Paleontology, Auburn, AL USA
9	BADL	Badlands National Park, Interior, SD USA
10	BSP	Bayerische Staatssammhung für Paläontologie, Munich, Germany
11	BMB	Booth Museum of Natural History, Brighton, UK
12		Dept. of Geosciences, Universidad Nacional de Colombia, Santafe de Bogota,
13		Colombia
14	BRV	
15	CCMGE	Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia
16	CAUK	Institut für Geowissenschaften der Christian-Albrechts-Universität, Kiel, Germany
17	CDM	Courtenay and District Museum, Courtenay, BC, Canada
18	CIT	California Institute of Technology (Now housed at LACM), Pasadena, CA USA
19	CM	Carnegie Museum, Pittsburgh, PA USA
20	CMN	Canadian Museum of Nature, Ontario, Canada
21	CM	Canterbury Museum, Christchurch, NZ
22	CPUC	Departamento de Geología of the Universidad de Concepción, Concepción, Chile
23	CVAI	Colección Vertebrados Asociación Isurus.
24	DMNH	Perot Museum (formerly Dallas Museum of Natural History), Dallas, TX USA
25	DMNS	Denver Museum of Nature and Science, Denver, CO USA
26	ENCI	ENCI Company Collection, Maastricht, Holland
27		East Texas State University (housed at UT Vertebrate Paleontology Lab),
28	ETSU	Commerce TX USA
29	FFM	Fick Fossil Museum, Oakley, KS USA
30	FGM	Fryxell Geology Museum, Augustana College, Rock Island, IL USA
31	FHSM	Sternberg Museum, Fort Hays, KS USA
32	FMNH	Field Museum of Natural History, Chicago, IL USA
33	GCB	Geo Centrum Brabant, Boxtel, Netherlands
34	GNS	GNS Paleontological Collection, Lower Hutt, New Zealand
35	GPIT	University of Tübingen, Tübingen, Germany
36	GSA(TC)	Geological Survey of Alabama, Tuscaloosa, AL USA
37	GZG	Geowissenschaftliches Zentrum der Universistät, Göttingen, Germany
38	HMG	Hobetsu Museum (Geology Collection), Mukawa City, Hokkaido Prefecture, Japan
39	HU	Hacetteppe University, Ankara, Turkey
40	HUJ	Hebrew University, Jerusalem, Israel
41	IAA	Instituto Antártico Argentino
42	IGNS	Institute of Geology and Natural Science, Lower Hutt, New Zealand
43	IGPUW	Instytut Geologii Podstawowej, Uniwersytet Warszawski, Warsaw, Poland
44	ING	Instituto Colombiano de Geologia
45		Institut für Paläontologie der Rheinische, Friedrich Wilhelms Universität, Bonn,
46		Germany
47	IPRFWU	
48	IRS(c)NB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
49	KHM	Kaikoura Historical Museum, Kaikoura, New Zealand
50	KrMG	Kristianstad Museum of Geology Kristiamstad, Sweden
51	KUVP	Biodiversity Institute and Natural History Museum, University of Kansas,
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3		Manhattan, KS, USA
4	LACM	Los Angeles County Museum of Natural History, Los Angeles, CA USA
5	LO, LR	Dept. Of Geology, Lund University, Lund, Sweden
6	MAPS	Monmouth Amateur Paleontological Society, Long Branch, NJ USA
7	MCM	Mikasa City Museum, Hokkaido, Japan
8		Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Alava,
9		Spain
10	MCNA	
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12	MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA USA
13	MKD	Muzeum Nadwiślańskie, Kazimierz, Dolny, Poland
14	MDM	Morden and District Museum, Manitoba, Canada
15	MEL	Museum Emmanuel Liais, Cherbourg, France
16	MGGC	Museo Geologico Giovanni Cappelini, Bologna, Italy
17	MGSN	Museum of Geological Survey of Nigeria
18	MGUAN	Geological Museum, Universidade Agostinho Neto, Luanda, Angola
19	MGUH	Geological Museum University of Copenhagen, Denmark
20	MiaMM	Miami Museum, Manitoba, Canada
21	MHNH	Museum National d'Histoire Naturelle, Paris, France
22	MML	Museo Municipal de Lamarque, Río Negro Province, Argentina
23	MMMN	Manitoba Museum of Man and Nature, Manitoba, Canada
24	MN	Museu Nacional, Rio de Janeiro, Brazil
25	MOR	Museum of the Rockies, Bozeman, MT USA
26	MP	Museo Geologico Jose Royo y Gomez of Ingeominas, Santafe de Bogota, Colombia
27	MPPVS	Museum of Paleontology and Prehistory, S. Anna d'Alfaedo, Italy
28	MTM	Magyar Természettudományi Múzeum, Budapest, Hungary
29	MU	University of Missouri, Columbia, MO USA
30	MUVP	Mansoura University Vertebrate Paleontology Center, Mansoura University, Egypt
31	NHMM	Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands
32	NHMUK	The Natural History Museum, London, England, UK
33	NHNV	Natural History Museum of Verona, Italy
34	NJGS	New Jersey Geological Survey Trenton NJ USA
35	NJSM	New Jersey State Museum, Trenton, NJ USA
36	NMMNH	New Mexico Museum of Natural History, Albuquerque, NM USA
37	NMNZ	National Museum of New Zealand, Te Papa, Wellington, New Zealand
38	NZGS	New Zealand Geological Survey, Lower Hutt, New Zealand
39	PA	Paleo-Angola Project, Southern Methodist University, Dallas, TX USA
40	OIGM	Oviedas Geological Museum, Asturias, Spain
41	OCP	Office Chérifien des Phosphates, Khouribja, Morocco
42	PMU	Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden
43	RE	Ruhr Museum, Essen, Germany
44	RGM	Rutgers Geology Museum Rutgers University NJ, USA
45	RMDC	Rocky Mountain Dinosaur Center, Woodland Park, CO USA
46	RMH	Roemer Museum, Hildesheim, Germany
47		Red Mountain Museum (housed at McWane Science Center), Birmingham, AL
48	RMM	USA
49	RMPZ	Swedish Museum of Natural History, Dept. of Palaeozoology, Stockholm, Sweden
50	SAM	South African Museum, Cape Town, South Africa
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SDMNH San Diego Museum of Natural History, San Diego, CA USA  
 South Dakota School of Mines and Technology Geology Museum, Rapid City, SD  
 SDSM(T) USA  
 Southern Environmental Museum, Birmingham Southern College, Birmingham, AL  
 SEM USA  
 SGU Geologic Survey of Sweden, Stockholm, Sweden  
 SGM Servicio Geologico Mexicano, Chihuahua, Mexico  
 SGMA Servicos de Geologia e Minas de Angola,  
 Saudi Geological Society, Paleontological Collection, Jiddah, Kingdom of Saudi  
 SGS 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  
 Texas Memorial Museum (at Vertebrate Paleontology Lab), University of Texas,  
 TMM 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  
 Smithsonian Institution National Museum of Natural History, Washington DC,  
 USNM USA  
 Université des Sciences Techniques du Languedoc, Vertebrate Paleontology  
 USTL Laboratory, Montpellier, France  
 UT Unversité de Tunis, Tunisia  
 University of Vermont Zadock Thompson Natural History Collection,  
 UVER 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	<i>Clidastes</i>	<i>liodontus</i>	DMNS	49925	<i>Clidastes</i>	<i>propyhton</i>
AMNH	221	<i>Tylosaurus</i>	<i>proriger</i>	DMNS	1582	<i>Mosasaurus</i>	sp
BMNH	R263	Mosasauridae	indet	DMNS	2851	<i>Mosasaurus</i>	sp
BMNH	R291a, b	Mosasauridae	indet	DMNS	28261	<i>Mosasaurus</i>	sp
BMNH	R876	Mosasauridae	indet	DMNS	43405	<i>Mosasaurus</i>	sp
BMNH	R1231	Mosasauridae	indet	DMNS	48169	<i>Mosasaurus</i>	sp
BMNH	R1232	Mosasauridae	indet	DMNS	48172	<i>Mosasaurus</i>	sp
BMNH	R1233	Mosasauridae	indet	DMNS	60861	<i>Mosasaurus</i>	sp
BMNH	R1253	Mosasauridae	indet	DMNS	45872	<i>Platecarpus</i>	sp
BMNH	R1620	Mosasauridae	indet	DMNS	48522	<i>Platecarpus</i>	sp
BMNH	R2573	Mosasauridae	indet	DMNS	1578	<i>Platecarpus</i>	<i>coryphaeus</i>
BMNH	5642	Mosasauridae	indet	DMNS	1579	<i>Platecarpus</i>	<i>coryphaeus</i>
BMNH	R9805	Mosasauridae	indet	DMNS	1581	<i>Platecarpus</i>	<i>coryphaeus</i>
BMNH	R9806	Mosasauridae	indet	DMNS	48616	<i>Platecarpus</i>	<i>ictericus</i>
BMNH	R9816	Mosasauridae	indet	DMNS	40988	<i>Platecarpus</i>	<i>tympaniticus</i>
BMNH	R10122	Mosasauridae	indet	DMNS	18352	<i>Prognathodon</i>	<i>overtoni</i>
BMNH	11591	Mosasauridae	indet	DMNS	2435	<i>Tylosaurus</i>	<i>proriger</i>
BMNH	11593	Mosasauridae	indet	DMNS	21813	<i>Tylosaurus</i>	<i>proriger</i>
BMNH	11599	Mosasauridae	indet	ETSU	L555	Mosasauridae?	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	?	<i>Globidens</i>	<i>fraasi</i>
BMNH	R11902	Mosasauridae	indet	ETSU	L569	<i>Clidastes</i>	sp
BMNH	R11903	Mosasauridae	indet	ETSU	4314	<i>Clidastes</i>	sp
BMNH	R11904	Mosasauridae	indet	ETSU	4349	<i>Clidastes</i>	sp
BMNH	R11905	Mosasauridae	indet	ETSU	4353	<i>Clidastes</i>	sp
BMNH	R11908	Mosasauridae	indet	ETSU	4354	<i>Clidastes</i>	sp
BMNH	R11910	Mosasauridae	indet	ETSU	4369	<i>Clidastes</i>	sp
BMNH	R11915	Mosasauridae	indet	ETSU	4370	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11917	Mosasauridae	indet	ETSU	4278	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11918	Mosasauridae	indet	ETSU	4281	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11919	Mosasauridae	indet	ETSU	4290	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11920	Mosasauridae	indet	ETSU	4293	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11921	Mosasauridae	indet	ETSU	4295	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11925	Mosasauridae	indet	ETSU	4307	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11926	Mosasauridae	indet	ETSU	L394	<i>Clidastes</i>	<i>propyhton</i>
BMNH	R11927	Mosasauridae	indet	ETSU	4329	<i>Mosasaurus</i>	sp
BMNH	R11929	Mosasauridae	indet	ETSU	4350	<i>Mosasaurus</i>	sp
BMNH	R11931	Mosasauridae	indet	ETSU	4288	<i>Platecarpus</i>	sp
BMNH	R11932	Mosasauridae	indet	ETSU	4306	<i>Platecarpus</i>	sp
BMNH	36557	Mosasauridae	indet	ETSU	4311	<i>Platecarpus</i>	sp
BMNH	37000	Mosasauridae	indet	ETSU	4312	<i>Platecarpus</i>	sp
BMNH	39423	Mosasauridae	indet	ETSU	4344	<i>Platecarpus</i>	sp
BMNH	39425	Mosasauridae	indet	ETSU	4347	<i>Platecarpus</i>	sp
BMNH	41383	Mosasauridae	indet	ETSU	L551	<i>Platecarpus</i>	sp
BMNH	42963	Mosasauridae	indet	ETSU	4327	<i>Platecarpus</i>	<i>ictericus</i>
BMNH	42977	Mosasauridae	indet	ETSU	4319	<i>Tylosaurus</i>	sp
BMNH	42999	Mosasauridae	indet	ETSU	4336	<i>Tylosaurus</i>	sp
BMNH	43193	Mosasauridae	indet	ETSU	4337	<i>Tylosaurus</i>	sp
BMNH	43194	Mosasauridae	indet	ETSU	4340	<i>Tylosaurus</i>	sp
BMNH	43200	Mosasauridae	indet	ETSU	4341	<i>Tylosaurus</i>	sp
BMNH	47954	Mosasauridae	indet	ETSU	4342	<i>Tylosaurus</i>	sp

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

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4	BMNH	5643	<i>Mosasaurus?</i>	sp	KUVP	85584	<i>Platecarpus</i> sp
5	BMNH	R264	<i>Mosasaurus</i>	sp	KUVP	85585	<i>Platecarpus</i> sp
6	BMNH	R820	<i>Mosasaurus</i>	sp	KUVP	85586	<i>Platecarpus</i> sp
7	BMNH	R1231	<i>Mosasaurus</i>	sp	KUVP	1007	<i>Platecarpus coryphaeus</i>
8	BMNH	R5884	<i>Mosasaurus</i>	sp	KUVP	4862	<i>Platecarpus coryphaeus</i>
9	BMNH	R5887	<i>Mosasaurus</i>	sp	KUVP	14285	<i>Platecarpus coryphaeus</i>
10	BMNH	R6376	<i>Mosasaurus</i>	sp	KUVP	14340	<i>Platecarpus coryphaeus</i>
11	BMNH	R10107	<i>Mosasaurus</i>	sp	KUVP	14341	<i>Platecarpus coryphaeus</i>
12	BMNH	R10110	<i>Mosasaurus</i>	sp	KUVP	66332	<i>Platecarpus coryphaeus</i>
13	BMNH	R10111	<i>Mosasaurus</i>	sp	KUVP	66336	<i>Platecarpus coryphaeus</i>
14	BMNH	R10112	<i>Mosasaurus</i>	sp	KUVP	66337	<i>Platecarpus coryphaeus</i>
15	BMNH	R10113	<i>Mosasaurus</i>	sp	KUVP	89853	<i>Platecarpus coryphaeus</i>
16	BMNH	R10114	<i>Mosasaurus</i>	sp	KUVP	27816	<i>Platecarpus ictericus</i>
17	BMNH	R10117	<i>Mosasaurus</i>	sp	KUVP	50093	<i>Platecarpus ictericus</i>
18	BMNH	R10118	<i>Mosasaurus</i>	sp	KUVP		<i>Plioplatecarpus</i> sp
19	BMNH	R10119	<i>Mosasaurus</i>	sp	KUVP	950	<i>Prognathodon overtoni</i>
20	BMNH	R10120	<i>Mosasaurus</i>	sp	KUVP		<i>Tylosaurus ?</i> sp
21	BMNH	R10121	<i>Mosasaurus</i>	sp	KUVP	1015	<i>Tylosaurus</i> sp
22	BMNH	42865	<i>Mosasaurus</i>	sp	KUVP	115002	<i>Tylosaurus</i> sp
23	BMNH	42873	<i>Mosasaurus</i>	sp	KUVP	86160	<i>Tylosaurus</i> sp
24	BMNH	42907	<i>Mosasaurus</i>	sp	KUVP	86643	<i>Tylosaurus</i> sp
25	BMNH	42909	<i>Mosasaurus</i>	sp	KUVP	1032	<i>Tylosaurus dyspelor</i>
26	BMNH	42947	<i>Mosasaurus</i>	sp	KUVP	1025	<i>Tylosaurus? proriger</i>
27	BMNH	42948	<i>Mosasaurus</i>	sp	KUVP	1089	<i>Tylosaurus? proriger</i>
28	BMNH	42952	<i>Mosasaurus</i>	sp	KUVP	947	<i>Tylosaurus proriger</i>
29	BMNH	42959	<i>Mosasaurus</i>	sp	KUVP	1016	<i>Tylosaurus proriger</i>
30	BMNH	42960	<i>Mosasaurus</i>	sp	KUVP	1017	<i>Tylosaurus proriger</i>
31	BMNH	42962	<i>Mosasaurus</i>	sp	KUVP	1020	<i>Tylosaurus proriger</i>
32	BMNH	42967	<i>Mosasaurus</i>	sp	KUVP	1029	<i>Tylosaurus proriger</i>
33	BMNH	42977	<i>Mosasaurus</i>	sp	KUVP	1013	<i>Tylosaurus proriger</i>
34	BMNH	R1224	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1033	<i>Tylosaurus proriger</i>
35	BMNH	R1226	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1050	<i>Tylosaurus proriger</i>
36	BMNH	42905	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1062	<i>Tylosaurus proriger</i>
37	BMNH	42929	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1075	<i>Tylosaurus proriger</i>
38	BMNH	42930	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	69546	Mosasauridae indet
39	BMNH	42931	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	145196	Mosasauridae indet
40	BMNH	42932	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	152196	Mosasauridae indet
41	BMNH	42933	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	152204	Mosasauridae indet
42	BMNH	42935	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	152206	Mosasauridae indet
43	BMNH	42936	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	152211	Mosasauridae indet
44	BMNH	42938	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1000	<i>Clidastes tortor</i>
45	BMNH	42941	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1022	<i>Clidastes velox</i>
46	BMNH	42942	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1026	<i>Clidastes westii</i>
47							<i>missouriensis</i>
48	BMNH	42943	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1034	<i>Mosasaurus</i> s
49	BMNH	42944	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	134401	<i>Plioplatecarpus</i> sp
50	BMNH	42945	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	152217	<i>Plioplatecarpus</i> sp
51	BMNH	42946	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1048	<i>Platecarpus</i> sp
52	BMNH	42948	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1159	<i>Tylosaurus proriger</i>
53	BMNH	42949	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1189	<i>Tylosaurus proriger</i>
54	BMNH	42950	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1195	<i>Tylosaurus proriger</i>
55	BMNH	42953	<i>Mosasaurus</i>	<i>camperi</i>	KUVP	1901	<i>Tylosaurus proriger</i>
56	BMNH	11590	<i>Mosasaurus</i>	<i>dekayi</i>	KUVP	5033	<i>Tylosaurus proriger</i>
57	BMNH	42929	<i>Mosasaurus</i>	<i>hoffmanni</i>	KUVP	28705	<i>Tylosaurus proriger</i>
58	BMNH	R4004	<i>Platecarpus</i>	?	KUVP	66129	<i>Tylosaurus proriger</i>
59							
60	BMNH	R271	<i>Platecarpus</i>	sp	IRSN B		Mosasauridae indet

1								
2								
3								
4	<b>BMNH</b>	R3041	<i>Platecarpus</i>	sp	<b>IRSN B</b>		Mosasauridae	indet
5								
6	<b>BMNH</b>	39424	<i>Platecarpus</i>	sp	<b>IRSN B</b>		<i>Mosasaurus</i>	<i>hoffmani</i>
7								
8	<b>BMNH</b>	R4003	<i>Platecarpus</i>	sp	<b>IRSN B</b>	3098	<i>Mosasaurus</i>	<i>lemonnieri</i>
9								
10	<b>BMNH</b>	R2837	<i>Platecarpus</i>	<i>coryphaeus</i>	<b>IRSN B</b>	3100	<i>Plioplatecarpus</i>	<i>houzeaui</i>
11								
12	<b>BMNH</b>	R2840	<i>Platecarpus</i>	<i>coryphaeus</i>	<b>IRSN B</b>	3107	<i>Plioplatecarpus</i>	<i>houzeaui</i>
13								
14	<b>BMNH</b>	R2833	<i>Platecarpus</i>	<i>ictericus</i>	<b>IRSN B</b>	3109	<i>Mosasaurus</i>	<i>lemonnieri</i>
15								
16	<b>BMNH</b>	R2838	<i>Platecarpus</i>	<i>ictericus</i>	<b>IRSN B</b>	3111	<i>Plioplatecarpus</i>	<i>houzeaui</i>
17								
18	<b>BMNH</b>	R4001	<i>Platecarpus</i>	<i>ictericus</i>	<b>IRSN B</b>	3113	<i>Mosasaurus</i>	<i>lemonnieri</i>
19								
20	<b>BMNH</b>	R4005	<i>Platecarpus</i>	<i>ictericus</i>	<b>IRSN B</b>	3117	<i>Mosasaurus</i>	<i>lemonnieri</i>
21								
22	<b>BMNH</b>	R813	<i>Plioplatecarpus</i>	sp	<b>IRSN B</b>	3119	<i>Mosasaurus</i>	<i>lemonnieri</i>
23								
24	<b>BMNH</b>	R5868	<i>Plioplatecarpus</i>	sp	<b>IRSN B</b>	3125	<i>Mosasaurus</i>	<i>lemonnieri</i>
25								
26	<b>BMNH</b>	42074	<i>Plioplatecarpus</i>	sp	<b>IRSN B</b>	3127	<i>Mosasaurus</i>	<i>lemonnieri</i>
27								
28	<b>BMNH</b>	42939	<i>Prognathodon</i>	sp	<b>IRSN B</b>	3152	<i>Plioplatecarpus</i>	<i>houzeaui</i>
29								
30	<b>BMNH</b>	48940	<i>Prognathodon</i>	sp	<b>IRSN B</b>	3153	<i>Mosasaurus</i>	<i>lemonnieri</i>
31								
32	<b>BMNH</b>	R822	<i>Taniwhasaurus</i>	<i>oweni</i>	<b>IRSN B</b>	3169	<i>Mosasaurus</i>	<i>lemonnieri</i>
33								
34	<b>BMNH</b>	R823	<i>Taniwhasaurus</i>	<i>oweni</i>	<b>IRSN B</b>	3186	<i>Mosasaurus</i>	<i>lemonnieri</i>
35								
36	<b>BMNH</b>	R824	<i>Taniwhasaurus</i>	<i>oweni</i>	<b>IRSN B</b>	3187	<i>Mosasaurus</i>	<i>lemonnieri</i>
37								
38	<b>BMNH</b>	R825	<i>Taniwhasaurus</i>	<i>oweni</i>	<b>IRSN B</b>	3188	<i>Plioplatecarpus</i>	<i>houzeaui</i>
39								
40	<b>BMNH</b>	R826	<i>Taniwhasaurus</i>	<i>oweni</i>	<b>IRSN B</b>	3193	<i>Mosasaurus</i>	<i>lemonnieri</i>
41								
42	<b>BMNH</b>	R2767	<i>cf. Tylosaurus</i>	sp	<b>IRSN B</b>	3210	<i>Mosasaurus</i>	<i>lemonnieri</i>
43								
44	<b>BMNH</b>	R5292	<i>cf. Tylosaurus</i>	sp	<b>IRSN B</b>	3211	<i>Plioplatecarpus</i>	<i>houzeaui</i>
45								
46	<b>BMNH</b>	R10939	<i>cf. Tylosaurus</i>	sp	<b>IRSN B</b>	3672	<i>Hainosaurus</i>	<i>bernardi</i>
47								
48	<b>BMNH</b>	R2947	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3857	<i>Mosasaurus</i>	<i>lemonnieri</i>
49								
50	<b>BMNH</b>	R2948	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3858	<i>Mosasaurus</i>	<i>lemonnieri</i>
51								
52	<b>BMNH</b>	R3625	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3859	<i>Plioplatecarpus</i>	<i>houzeaui</i>
53								
54	<b>BMNH</b>	R3626	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3860	<i>Mosasaurus</i>	<i>lemonnieri</i>
55								
56	<b>BMNH</b>	R4548	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3861	<i>Mosasaurus</i>	<i>lemonnieri?</i>
57								
58	<b>BMNH</b>	35615	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	3911	<i>Mosasaurus</i>	<i>lemonnieri</i>
59								
60	<b>BMNH</b>	35616	<i>Tylosaurus</i>	sp	<b>IRSN B</b>	4670	<i>Mosasaurus</i>	<i>lemonnieri</i>
	<b>BMNH</b>	35617	<i>Tylosaurus</i>	sp	<b>IRSN</b>	4672	<i>Prognathodon</i>	<i>solvayi</i>

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

TABLE S3. Mosasaur holotype references.

Author	Year	Species List	Title
Arambourg	1952	<i>Mosasaurus beaugei</i> , <i>Platecarpus ptychodon</i>	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	<i>Halisaurus arambourgi</i>	Bardet, N., X. Pereda Suberbiola, M. Iarochene, B. Bouya and M. Amaghazaz 2005. A new species of <i>Halisaurus</i> from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the <i>Halisaurinae</i> (Squamata: Mosasauridae). Zoological Journal of the Linnean Society 143:447-472.
Bardet et al	2005	<i>Globidens phosphaticus</i>	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 <i>Globidens</i> . Netherlands Journal of Geosciences 84:167-175.
Bell and Polcyn	2005	<i>Dallasaurus turneri</i>	Bell, G. L. and M. J. Polcyn, 2005. <i>Dallasaurus turneri</i> , 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	<i>Tylosaurus capensis</i>	Broom, R. 1912. On a species of <i>Tylosaurus</i> from the Upper Cretaceous beds of Pondoland. Annals of the South African Museum 7:332-3.
Camp	1942	<i>Plotosaurus bennisoni</i> , <i>Plesiotylosaurus crassidens</i>	Camp, C. L. 1942. California mosasaurs. University of California Memoirs 13:1-16.
Caldwell et al	2008	<i>Taniwhasaurus mikasaensis</i>	Caldwell, M. W., T. Konishi, I. Obata and K. Muramoto 2008. A new species of <i>Taniwhasaurus</i> (Mosasauridae, Tylosaurinae) from the Upper Santonian-Lower Campanian (Upper Cretaceous) of Hokkaido, Japan. Journal of Vertebrate Paleontology 28:339-348.
Christiansen and Bonde	2002	<i>Prognathodon curii</i>	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	<i>Clidastes Propython</i> , <i>Plioplatecarpus depressus</i> , <i>Platecarpus tympaniticus</i>	Cope, E. D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. Boston Society of Natural History Proceedings 12:250-266.
Cope	1869b	<i>Tylosaurus proriger</i>	Cope, E. D. 1869. Remarks on <i>Holops brevispinus</i> , <i>Ornithotarsus immanis</i> and <i>Macrosaurus proriger</i> . Proceedings of the Academy of Natural Science Philadelphia 21: 123.
Cope	1869-70	<i>Prognathodon rapax</i>	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	<i>Prognathodon sectorius</i>	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	<i>Tylosaurus napaolicus</i>	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	<i>Mosasaurus conodon</i>	Cope, E. D. 1881. A new <i>Clidastes</i> from New Jersey. American Naturalist 15:586-587.
Crandell	1958	<i>Plioplatecarpus primaevus</i>	Crandell, D. R. 1958. Geology of the Pierre area, South Dakota. U. S. Geological Survey Professional Paper 307.
Cuthbertson et al	2007	<i>Latoplatecarpus (Plioplatecarpus) nichollsae</i>	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	<i>Plioplatecarpus peckensis</i>	Cuthbertson, R.S. and R. B. Holmes 2015. A new species of <i>Plioplatecarpus</i> (Mosasauridae, Plioplatecarpinae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of Montana, USA. Journal of Vertebrate Paleontology 35:e922980.
Dollo	1882	<i>Plioplatecarpus marshi</i>	Dollo, L. 1882. Note sur l'ostéologie des Mosasauridæ. Bulletin du Musée d'Histoire Naturelle de Belgique 1:55-80.
Dollo	1885	<i>Hainosaurus bernardi</i>	Dollo, L. 1885. Le hainosaure. Revue des Questions Scientifiques 18:285-289.
Dollo	1889	<i>Plioplatecarpus houzeaui, Phosphorosaurus ortliebi, Prognathodon solvayi</i>	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	<i>Prognathodon giganteus</i>	Dollo, L. 1904. Les mosasauriens de la Belgique. Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrogéologie, Mémoires, 1 8:207-216.
Dollo	1913	<i>Carinodens belgicus</i>	Dollo, L. 1913. <i>Globidens Fraasi</i> , 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	<i>Prognathodon saturator</i>	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	<i>Tylosaurus kansasensis</i>	Everhart, M. J. 2005. <i>Tylosaurus kansasensis</i> , a new species of tylosaurine (Squamata, Mosasauridae) from the Niobrara Chalk of western Kansas, USA. Netherlands Journal of Geosciences 84:231.
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	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 MPBFs 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	<i>p</i>
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"

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3	Early San	USA		Niobrara	Lower
4	Early San	USA	TX	Terlingua Group	Boquillas
5	Early San	USA	TX	Terlingua Group	Pen
6	Early San	USA	TX	Terlingua Group	Pen
7	Early San	USA	MT	Montana	Telegraph Creek
8	Early San	Canada	Alberta		Puskwakau
9	Early San	Canada	Alberta		Puskwakau
10	Early San	Mexico	Monterrey		San Felipe
11	Early San	England			Upper Chalk
12	Early San	Italy			Scaglia Rossi Veneta
13	Early San	Italy			Scaglia Rossi Veneta
14	Early San	Japan	Yezo	Yezo Group	Kashima
15	Early San	Japan			Tamayama
16	Early San	Russia			Penza region
17					
18	Mid San	USA	Alabama/Miss	Selma	Eutaw
19	Mid San	USA	Kansas	Niobrara	Smoky Hill Chalk
20	Mid San	USA	TX	Terlingua Group	Boquillas
21	Mid San	USA	TX	Terlingua Group	Pen
22	Mid San	USA	TX	Terlingua Group	Pen
23	Mid San	USA	TX	Austin Chalk	"Austin Chalk"
24	Mid San	Canada	Alberta		Puskwakau
25	Mid San	Canada	Alberta		Puskwakau
26	Mid San	England			Upper Chalk
27	Mid San	France	Somme		Phosphatic Chalk
28	Mid San	Russia		Penza region	
29	Mid San	Japan	Yezo	Yezo Group	Kashima
30					
31	Late San	USA	Kansas	Niobrara	Upper
32	Late San	USA	NM	Point Lookout Sandstone	
33	Late San	USA	AL/GA	Selma	Blufftown
34	Late San	USA	AL/GA	Selma	Blufftown
35	Late San	USA	AL/MS	Selma	Mooreville Chalk
36	Late San	USA	TX	Austin Chalk	Dessau
37	Late San	USA	TX	Austin Chalk	"Austin Chalk"
38	Late San	USA	TX	Terlingua Group	Boquillas
39	Late San	USA	TX	Terlingua Group	Boquillas
40	Late San	USA	TX	Terlingua Group	Pen
41	Late San	Canada	Alberta		Puskwakau
42	Late San	Canada	Vancouver		Pender
43	Late San	Canada	Vancouver		Pender
44	Late San	England			Upper Chalk
45	Late San	France			Marnes de Bugarach
46	Late San	France			Marnes bleues de Sougraigne
47	Late San	France			Gres de Labastide
48	Late San	France			Gres de Labastide
49	Late San	France	Somme		Phosphatic Chalk
50	Late San	Russia		Penza region	"Penza"
51	Late San	Japan	Yezo	Yezo Group	Kashima
52					
53	Early Camp	USA	AL/GA	Selma	Blufftown
54	Early Camp	USA	AL/MS	Selma	Mooreville Chalk
55	Early Camp	USA	TX	Austin Chalk	"Austin Chalk"
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3	Early Camp	USA	TX	Austin Chalk	Burditt
4	Early Camp	USA	TX	Austin Chalk	Roxton ls
5	Early Camp	USA	NM		Point Lookout Sandstone
6	Early Camp	USA	ARK		Brownstone Marl
7	Early Camp	USA	TX/ARK	Taylor Group	Ozan
8	Early Camp	USA	NC	Black Creek Group	Tar Heel
9	Early Camp	USA	TX	Austin Chalk	Dessau
10	Early Camp	USA	NJ	Matawan Group	Merchantville
11	Early Camp	USA	TX	Tornillo	Aguja
12	Early Camp	USA	TX	Terlingua Group	Pen
13	Early Camp	USA	KS/CO/WY/NE/SD	Niobrara	Smoky Hill
14	Early Camp	USA	CO	Mesa Verde	Lewis Shale
15	Early Camp	Canada	Alberta		Puskwakau
16	Early Camp	Belgium		Spiennes Chalk	
17	Early Camp	England			Upper Chalk
18	Early Camp	France	Burgogne		White Chalk
19	Early Camp	Sweden			Kristianstad Basin
20	Early Camp	Saudi Arabia		Suqah Group	Adaffa Formation
21	Early Camp	Angola			Bentiaba
22	Early Camp	Japan	Yezo	Yezo Group	Kashima
23	Early Camp	Japan		Halebuchi Group	
24	Early Camp	NZ			Conway Siltstone
25	Early Camp	Antarctica			Santa Marta
26	Mid Camp	USA		Pierre Shale	
27	Mid Camp	USA	KS/SD	Pierre Shale	Sharon Springs
28	Mid Camp	USA	CO	Mesa Verde	Lewis Shale
29	Mid Camp	USA		Niobrara	Upper
30	Mid Camp	USA	AL/MS	Selma	Demopolis
31	Mid Camp	USA	AL/MS	Selma	Arcola Limstone
32	Mid Camp	USA	TX/ARK	Taylor Group	Ozan
33	Mid Camp	USA	NJ	Matawan Group	Marshalltown
34	Mid Camp	USA	NJ	Matawan Group	Woodbury
35	Mid Camp	USA	TX	Tornillo	Aguja
36	Mid Camp	USA	TX	Terlingua Group	Pen
37	Mid Camp	Canada	Manitoba	Pierre Shale	Pembina
38	Mid Camp	Canada	Alberta	Belly River	Oldman
39	Mid Camp	Canada	Alberta	Belly River	Dinosaur Park
40	Mid Camp	Canada	Alberta	Wapiti	Wapiti
41	Mid Camp	England			Upper Chalk
42	Mid Camp	Sweden			Kristianstad Basin
43	Mid Camp	Angola			Bentiaba
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3	Mid Camp	Saudi Arabia		Suqah Group	Adaffa Formation
4	Mid Camp	Japan		Isumi Group	
5	Mid Camp	Japan	Yezo	Yezo Group	Kashima
6	Mid Camp	Japan		Halebuchi Group	
7	Mid Camp	NZ			Maungataniwaha ss
8	Mid Camp	NZ			Conway Siltstone
9	Mid Camp	Antarctica			Santa Marta
10					
11	Late Camp	USA	AL/MS	Selma	Demopolis
12	Late Camp	USA	TX/ARK	Taylor Group	Ozan
13	Late Camp	USA	TX	Taylor Group	Wolfe City
14	Late Camp	USA	ARK	Taylor Group	Marlbrook Marl
15	Late Camp	USA	NJ	Monmouth Group	Mt Laurel
16	Late Camp	USA	Tennessee		Coon Ck
17	Late Camp	USA	TX	Tornillo	Aguja
18	Late Camp	USA	TX	Terlingua Group	Pen
19	Late Camp	USA	MT	Montana	Judith River
20	Late Camp	USA		Pierre Shale	
21	Late Camp	USA	SD	Pierre Shale	Verendrye
22	Late Camp	US/Canada	MT/Alberta	Montana	Bear Paw
23	Late Camp	Canada	Alberta	Belly River	Dinosaur Park
24	Late Camp	Canada	Alberta	Wapiti	Wapiti
25	Late Camp	Canada	Alberta	Edmonton	
26	Late Camp	Mex	Coahuila		Cerro del Pueblo
27	Late Camp	Mex	Tamaulipas	Difunta	
28	Late Camp	Argentina			Allen
29	Late Camp	Argentina			Allen/Jagüel
30	Late Camp	Argentina			La Colonia
31		Netherlands,			
32	Late Camp	Belgium			Gulpen
33	Late Camp	England			Upper Chalk
34	Late Camp	France			Meudon Chalk
35	Late Camp	Spain			Vitoria
36	Late Camp	Turkey			Davutlar
37	Late Camp	Israel			Mishash
38	Late Camp	Saudi Arabia		Suqah Group	Adaffa Formation
39	Late Camp	Angola			Bentiaba
40	Late Camp	Japan		Isumi Group	
41	Late Camp	Japan		Isumi Group	Hiketa Fmn
42	Late Camp	Japan	Yezo	Yezo Group	Kashima
43	Late Camp	Japan		Halebuchi Group	
44	Late Camp	NZ			Maungataniwaha ss
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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 Group	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
	Netherlands,				
Early Maas	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 Group	Mt Laurel

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3	Late Maas	USA	NJ	Monmouth Group	New Egypt
4	Late Maas	USA	NJ		Hornerstown
5	Late Maas	USA	MD		Severn
6	Late Maas	USA	CA	Chico	Moreno
7	Late Maas	USA	TX	Tornillo	Aguja
8	Late Maas	Mex	Tamaulipas	Difunta	
9	Late Maas	Chile			Quiriquina
10	Late Maas	Argentina			Paso del Sapo
11	Late Maas	Antarctica			López de Bertodano
12	Late Maas	Argentina			Allen
13	Late Maas	Argentina			Allen/Jagüel
14	Late Maas	France	Aquitaine		Nay Marl
15	Late Maas	France			Baculites ls
16	Late Maas	Spain			Raspay Fmn
17		Netherlands,			
18	Late Maas	Belgium			Maastricht
19		Netherlands,			
20	Late Maas	Belgium			Gulpen
21	Late Maas	Belgium			Ciply Phosphatic Chalk
22	Late Maas	Russia			Bereza Beds
23	Late Maas	Jordan			Rouseifa Group
24	Late Maas	Morocco			Couche II
25	Late Maas	Morocco			Couche III
26	Late Maas	Niger			Dukamaje Fmn
27	Late Maas	Angola			Bentiaba
28	Late Maas	Angola			Mucuio
29	Late Maas	NZ			Laidmore Fmn
30	Late Maas	NZ			Maungataniwha ss
31	Late Maas	Japan		Halebuchi Group	
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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	Late/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

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	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	
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	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	
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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	
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	San/Camp	Late/Early
	San/Camp	Late/Early
	Con/Camp	Early/Early

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4		Camp	Early
5		San	Early/Early
6		Camp	Early/?
7		Camp	Early/Late
8		Camp	Early
9		San/Camp	Late/Early
10		Camp	Early
11		San/Camp	Late/Early
12		Camp	Early
13		Camp/Maas	
14		San/Camp	
15		Camp	Early
16	Plesiosaur	Camp	Early
17	Plesiosaur	Camp	Early/Mid
18		San/Camp	Early
19	Plesiosaur	Camp	Early
20		Tur/Camp	Late/Late
21		Camp	Early
22		Camp	Early/Mid
23		Camp/Maas	Early/Early
24		Camp/Maas	
25		San/Camp	
26		Camp/.Maas	
27		Camp	Early/Mid
28		Camp	Early/Late
29		Camp	Mid/Late
30		Camp	Mid
31		Camp	Early/Late
32		Camp	Mid/Late
33	Plesiosaur	Camp	Mid
34		Camp	Early/Mid
35		San/Camp	Late/Mid
36		Camp	Mid/Late
37		Camp	Mid
38		Camp	Early/Late
39		Camp	Mid
40		Camp	Mid
41		Camp/Maas	
42		San/Camp	
43		Camp	Mid
44		Camp	Mid
45		Camp	Mid
46		Camp	Mid/Late
47		Camp/Maas	Mid/Mid
48		Tur/Camp	Late/Late
49		Camp	Early/Mid
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	Camp/Maas	Mid/Early
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Plesiosaur	Camp	Early/Mid
	Camp	Early/Late
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	Camp	Early/Late
	Camp	Late
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	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
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Plesiosaur	Camp	Mid/ Late

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

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3		Maas	Late
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7	Plesiosaur	Maas	
8		Camp/Maas	
9		Camp/Maas	Late/Late
10		Camp/Maas	Late/Late
11	Plesiosaur	Maas	Late
12	Plesiosaur	Maas	Late
13	Plesiosaur	Maas	Late
14	Plesiosaur	Maas	Late
15	Plesiosaur	Camp/Maas	Late/Late
16	Plesiosaur	Camp/Maas	Late/Late
17		Maas	Late
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25		Camp/Maas	Late/Late
26		Maas	Late
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28		Maas	Late
29		Maas	
30		Maas	Late
31		Maas	Late
32	Plesiosaur	Maas	Late
33		Maas	Late
34		Camp/Maas	
35		Maas	Late
36		Maas	
37		Maas	
38	Plesiosaur	Camp/Maas	Late/Late
39		Camp/Maas	
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