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1 Sea surface temperature contributes to marine
2 crocodylomorph evolution

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9

10 **During the Mesozoic and Cenozoic, four distinct crocodylomorph lineages colonized the**
11 **marine environment. They were conspicuously absent from high latitudes, which in the**
12 **Mesozoic were occupied by warm-blooded ichthyosaurs and plesiosaurs. Despite a**
13 **relatively well-constrained stratigraphic distribution, the varying diversities of marine**
14 **crocodylomorphs are poorly understood because their extinctions neither coincided with**
15 **any major biological crises, nor with the advent of potential competitors. Here, we test**
16 **the potential link between their evolutionary history in terms of taxic diversity and two**
17 **abiotic factors, sea level variations and Sea Surface Temperatures (SST). Excluding**
18 **Metriorhynchoidea, which may have had a peculiar ecology, significant correlations**
19 **obtained between generic diversity and estimated Tethyan SST suggest that water**
20 **temperature was a driver of marine crocodylomorph diversity. Being most likely**
21 **ectothermic reptiles, these lineages colonized the marine realm and diversified during**
22 **warm periods, then declined or became extinct during cold intervals.**

23

24 Crocodylomorphs today show relatively narrow temperature tolerances, and their

25 geographic distribution, whether on land or in the sea, is limited by temperature range. They
26 are essentially tropical to subtropical organisms (*Alligator mississippiensis* and *Alligator*
27 *sinensis* being also known from warm-temperate zones) and their distribution in ancient
28 environments is usually taken as an indication of tropical to subtropical temperatures¹⁻³, a
29 crucial adjunct to climate models for the Cretaceous and Cenozoic⁴. This assumption that
30 crocodylomorphs are always tropical to subtropical indicators is based on their present
31 distribution. Indeed, crocodylomorphs are unique among Mesozoic marine reptiles because
32 some of them have living relatives. However, in the past, crocodylomorphs showed a far
33 wider range of habitats and adaptations than seen among their modern counterparts. Most
34 marine reptiles of the Mesozoic have no modern analogues, and processes affecting their rise
35 and demise have been much debated in the context of covariation of palaeodiversity and
36 sampling proxies⁵⁻⁷. The bias hypothesis (i.e. errors induced by human collection or
37 geological preservation) was put forward as the main explanation for palaeodiversity variation
38 in Mesozoic marine reptiles⁵. Closer analysis suggested differences in the fossil records of the
39 shelf and deep ocean, and that shallow marine tetrapod diversity was better explained by the
40 extent of flooded continental areas than by sampling error⁶. More recently, it has been
41 proposed that the extended extinction of unrelated marine reptile clades over the early
42 Cretaceous could equally be explained by climatic or biotic factors exclusive to a given
43 clade⁷. Another possibility is that marine reptile diversity could indirectly result from global
44 changes in ocean chemistry, deeply scrambling the biomass and the structure of trophic
45 chains, thus impacting again the diversity at the top of the food chain. There is therefore no
46 clear consensus about the role of extrinsic versus intrinsic factors on marine reptile
47 palaeodiversity in the Mesozoic.

48 In order to test the control of the two major factors, seawater temperature or sea-level
49 variations, on the diversity of marine crocodylomorphs, we have established a diversity

50 database (Supplementary data 1) of marine crocodylomorphs at the generic level using all
51 published occurrences worldwide from the Early Jurassic to the Late Eocene and compared
52 them to published sea-level curves and to an updated sea surface temperature (SST) curve
53 established from the oxygen isotope composition of fish teeth.

54 Our analyses recover significant support for the covariation of seawater temperatures
55 and the generic diversity of marine crocodylomorphs, excluding metriorhynchoids. A possible
56 interpretation of these findings is that the evolution of most marine crocodylomorphs depends
57 on environmental temperatures due to their ectothermic physiology. On the other hand, the
58 radiation of metriorhynchoids during cold SST intervals suggests a different ecological
59 strategy for this lineage.

60

61 **Results**

62 **Palaeodiversity.** The stratigraphic ranges of marine crocodylomorphs across the studied time
63 interval do not overlap, with the exception of marine eusuchians and Dyrosauridae, both of
64 which appeared at the very end of the Cretaceous. No marine crocodylomorph has ever been
65 reported from two intervals of the Cretaceous, the Hauterivian-Albian and the Coniacian-
66 Campanian. These gaps in the fossil record can be considered as true absences because marine
67 deposits of these ages are abundant (PaleoDB data) and have yielded remains of other marine
68 reptiles including ichthyosaurs, plesiosaurs or mosasaurs⁵, but have never yielded any
69 crocodylomorphs.

70 Thalattosuchians comprise the first marine radiation, with three genera recorded in the
71 Toarcian, followed by a collapse in diversity during the Aalenian. This apparent peak is an
72 artefact of preservation due to a typical Lagerstätte effect⁵, further expressed with the absence
73 of record in the Aalenian, only recently recognized from new discoveries of other marine
74 vertebrates^{8,9}. A crocodylomorph assemblage containing both metriorhynchoids and

75 teleosaurids existed at least since the Bajocian when the first alleged metriorhynchoids are
76 recorded. From then, thalattosuchian diversity peaked in the Callovian with seven genera. A
77 diversity drop is recorded between the Callovian and the Oxfordian. The metriorhynchoid
78 burst in diversification took place during the Kimmeridgian-Tithonian interval, with five and
79 seven genera recorded respectively. While metriorhynchoids flourished, the diversity of
80 teleosaurids for this same interval dwindled to only two genera, *Machimosaurus* and
81 *Steneosaurus*. No teleosaurid has been reported thereafter. Finally, metriorhynchoid diversity
82 dropped in the Berriasian with two genera and the clade disappeared during the early
83 Hauterivian^{10,11,12}. Thalattosuchians have never been reported from younger rocks.

84 The present data compilation shows a gap in the record of marine crocodylomorphs
85 from the early Hauterivian to the Cenomanian, when some pholidosaurids colonized the
86 marine environment in the Cenomanian. They are not recorded after the Coniacian.

87 The last radiation of crocodylomorphs into the marine environment is Maastrichtian,
88 with five genera of Dyrosauridae and two genera of gavialoid eusuchians. Both Dyrosauridae
89 and gavialoids survived the end-Cretaceous events, Dyrosauridae becoming extinct some time
90 during the Ypresian. On the other hand, eusuchians seem to have radiated successively again
91 during the Eocene, Oligocene and Miocene, as gavialoids.

92

93 **Tests of correlation.** In comparisons of different data treatments, Spearman rank correlation
94 tests suggest some correlation of the palaeodiversity signal with the explanatory time series.
95 Out of the five explanatory time-series, SST show the greatest number (7) of significant
96 results for the correlation tests against the response variables (Table 1). This is closely
97 followed by the data for sea level reconstruction by Miller et al.¹³, with five significant
98 results. Then, the sea level estimate of Haq et al.¹⁴ shows only one significant correlation with
99 the response variable. Finally, the two subsequent explanatory variables (PaleoDB marine

100 formations and COSUNA formations) show non-significant correlations with the response
101 variables.

102 There appears to be no good match when either raw crocodylomorph species diversity
103 counts or phylogenetically corrected generic diversity counts are compared with SST. The
104 tested relations remain unmatched when applying various data transformations (time-scaling,
105 logarithmic, generalized differencing).

106 Significant correlations between SST and the response variables appear when
107 metriorhynchoid crocodylomorphs are excluded from the diversity count (NM dataset). In
108 terms of strength of correlation, Log_{10} (NMcroc) offers the best result, which is as good as the
109 correlation coefficients recovered for the sea level estimate of the Miller et al.¹³ curve versus
110 the response variables. Nevertheless, SST stands out from the sea level estimate of Miller et
111 al.¹⁴ when the response variables are phylogenetically corrected, with four significant
112 correlation coefficients (> 0.36) explained by SST, versus one significant correlation
113 coefficient (0.405) for Miller sea level (Table 1). Noteworthy in the results are significant
114 positive correlation coefficients obtained when considering SST or the sea level estimate of
115 Miller et al.¹³ against generalized differences of the diversity dataset without
116 metriorhynchoids (GD NMcroc and PC GD NMcroc in Table 1).

117 After correction with the Benjamini-Hochberg multiple comparisons and Bonferroni
118 correction, we found that all significant correlations (Table 1) ceased to be significant.
119 Perhaps the correction was too harsh, or at least any correlations that exist between the marine
120 crocodylomorph fossil record and the putative physical drivers are weak. There are clearly
121 problems with the time bins and palaeodiversity sample sizes used here. The temporal
122 distribution of the fossil record of marine crocodylomorphs is not as resolved as that of the
123 SST data. This means that variations in temperatures within these time bins cannot be
124 compared to the evolution of diversity at a finer stratigraphic scale, simply because the

125 stratigraphic distribution of the marine vertebrates can only be inferred using ghost ranges.
126 Nevertheless, these results do not invalidate the simple observation that marine
127 crocodylomorphs are present in the marine environment when warm SST prevail, but are
128 absent when cold SST are recorded. These are discussed below.

129

130 **Discussion**

131 No significant correlation between marine crocodylomorph diversity and Paleodb marine
132 formations is observed, under any manipulation of the time series, therefore suggesting that
133 the ups and downs in marine crocodylomorph diversity are not dominated by geological
134 sampling, but indicate some aspects of the original diversity signal and ought to be explained
135 by other external factors. The absence of significant correlation between marine
136 crocodylomorph diversity and the metric for continental flooding (COSUNA) contrasts with
137 previously published results, although it should be noted that the present diversity data sets
138 are necessarily small. A strong negative correlation was found between non-flooded surface
139 area and the taxic diversity of shallow environments⁶, a result predicted by the inverse
140 relation between non-flooded surface area and the number of shallow marine habitats. As
141 predicted by these results⁶, a positive and significant correlation would be expected in our
142 results between COSUNA and marine crocodylomorph diversity, but this is not the case. Our
143 dataset focuses on one group, marine crocodylomorphs, versus all marine reptiles in the case
144 of Benson and Butler⁶, who lump marine crocodylomorphs among shallow marine tetrapods.
145 Broad feeding scope and enhanced mobility in marine crocodylomorphs are strong indications
146 that their diversity should not have been significantly influenced by habitat modification,
147 despite significant modifications of the palaeogeography during the time under investigation.
148 Moreover, because of their freshwater origin, marine crocodylomorphs were certainly able to
149 live in freshwater drainages, as identified in some cases¹⁵, and could use the various food

150 resources available in the freshwater habitat. The combined role of ecology, physiology or
151 behaviour may therefore explain why marine crocodylomorph diversity does not show good
152 correlation with continental flooding. Pierce et al.¹⁶ suggested that thalattosuchian extinction
153 in the Early Cretaceous was driven by sea level fall. The present results show that marine
154 crocodylomorph diversity is at least partly affected by sea level variations. It is indeed
155 expected that coastal palaeogeography can be significantly modified by sea-level changes,
156 resulting in the appearance of new habitats and marine barriers, differing in size and marine
157 connection through time (e.g.¹⁷). How this is affecting crocodylomorph diversity is unknown
158 but should be considered. Correlations computed on the total diversity dataset of marine
159 crocodylomorphs with the sea level estimates are not significant. On the other hand, exclusion
160 of metriorhynchoids from the dataset leads to five significant correlations with the sea level
161 estimates of Miller et al.¹² and a single significant correlation with the sea level estimates of
162 Haq et al.¹⁴. These results underline that marine crocodylomorphs with varying adaptations
163 for offshore (e.g., teleosaurids) or pelagic swimming (metriorhynchoids) may be affected
164 differently by sea level variation. For instance, metriorhynchoid diversity alone seems to be
165 affected by sea level variation of Miller et al. (Fig. 1B), but there is no correlation
166 (Spearman's $\rho = 0.577$, $p = 0.13$), and perhaps the narrow temporal range (Pliensbachian-
167 Valanginian) prevents meaningful statistical testing. However, this hypothesis is unequally
168 supported by the two available sea level datasets (the one from Miller et al.¹³ being
169 incomplete from the Hettangian to Aalenian) and loses much support when the dataset is
170 phylogenetically corrected (Table 1). While sea level variation might partly explain the
171 diversity of marine crocodylomorphs, it is noteworthy that sea level is both influenced by
172 global tectonic activity (tectono-eustasy) and the growth and decay of polar ice caps
173 (glacio-eustasy). As the extension of the polar ice is ultimately controlled by global climate, a
174 drop in sea level could be related indirectly to a drop in marine crocodylomorph diversity, but

175 the underlying cause would be temperature change (Fig. 1C).

176 Although based on now obsolete diversity counts, strong evidence for the influence of
177 climate on the evolution of crocodylomorphs has previously been detected⁴. It is expected that
178 crocodylomorphs, as ectotherms, are affected by temperature changes; this is reflected in the
179 marine environment by the temperature of their living medium (SST). No correlation between
180 SST and total marine crocodylomorph diversity is observed (Table 1), a result drastically
181 different when metriorhynchoids are excluded from the dataset (Table 1). In this case,
182 significant correlations are observed both with and without phylogenetic correction. The
183 average significant correlation value for SST is 0.380. Such a value implies that SST can only
184 partially explain the diversity of some marine crocodylomorphs and suggests that, with the
185 exclusion of metriorhynchoids, they were only able to colonize the marine environment when
186 ambient temperatures were favourable. According to present knowledge of the fossil record,
187 the marine environment was left vacant twice for several million years by crocodylomorphs,
188 in the Hauterivian-Albian and Coniacian-early Campanian intervals. Possibly, the marine
189 environment was not habitable. It is notable that crocodylomorphs colonised the marine
190 environment at the beginning of warming phases, with *Thalattosuchia* in the Toarcian,
191 *Pholidosauridae* in the Cenomanian and *Eusuchia* and *Dyrosauridae* in the Maastrichtian. On
192 the other hand, some drops in crocodylomorph diversity correspond to temperature declines
193 such as that of the Callovian affecting thalattosuchian diversity or the Valanginian-
194 Hauterivian boundary affecting metriorhynchoids. Concerning the extinction of
195 *Pholidosauridae* in the Turonian and *Dyrosauridae* in the Ypresian, a clear match between
196 SST and diversity is absent, even when considering fine-scale SST variations reconstructed
197 using other proxies^{18,19}. Among the considered marine crocodylomorph lineages, the
198 metriorhynchoids clearly stand out with an explosive radiation at the end of the Jurassic,
199 when SSTs continued to decrease. Comparatively, the other thalattosuchian group, the

200 teleosaurids, did not radiate and even went extinct before the Berriasian. Metriorhynchoids
201 appear to be morphologically different from any other marine crocodylomorphs, thus inviting
202 discussion about physiological adaptations in these different lineages (see below). The
203 statistical assessments retrieved in this study did not yield 1:1 correlations between SST and
204 marine crocodylomorph diversity, and as discussed below other factors might be involved in
205 the fluctuations in marine diversity. The aim of this study is not to prove that SST could
206 solely account for evolutionary patterns in climate-sensitive lineages, but rather to stress the
207 existence of a window of optimal temperatures in which these marine animals could thrive, as
208 defended in earlier studies⁴.

209 SST can be interpreted as a limiting factor, allowing crocodylomorphs to colonise new
210 environments when temperatures become favourable; or preventing crocodylomorphs from
211 widely thriving when temperatures fall. It is noteworthy that increasing marine water
212 temperatures also boost both biomass and biodiversity, thus increasing the amount of
213 resources for marine crocodylomorphs. Within that frame, other factors, including biotic ones
214 could impede speciation. One factor coming to mind is competition for resources or territory
215 among predators²⁰. Illustrating this, the demise of Pholidosauridae, and then of Dyrosauridae
216 might be paralleled with the rise of other large marine predators: mosasaurs in the mid-
217 Cretaceous or archaeocete marine mammals in the Paleogene. However, explaining the
218 turnover of vertebrates by competition for resources or territory should take into account the
219 body size factor. Body size is responsible for niche partitioning in large predators²¹ and it is
220 unlikely that pholidosaurids or dyrosaurids might have been worried by the small size of the
221 first mosasaurs and the first archaeocetes. Moreover, there are numerous instances of marine
222 crocodylomorphs coexisting with other large marine reptiles^{7,9}. Invoking competition for
223 resources or territory appears therefore unlikely as an explanation for the demise of marine
224 crocodylomorphs. Physiological specificities could represent other factors explaining the

225 diversity pattern of marine crocodylomorphs. The prediction that ancient marine
226 crocodylomorphs were sensitive to seawater temperature variation is partly but not entirely
227 recovered in our results. That ancient marine crocodylomorphs were, as extant ones,
228 ectotherms, would require a full match between SST evolution and patterns of radiation-
229 extinction of the different crocodylomorph groups. Of particular relevance to the recovered
230 mismatch are Metriorhynchoidea, whose diversity does not match SST evolution. Indeed, the
231 Metriorhynchoidea appeared to radiate in the pelagic environment when Teleosauridae died
232 out and SST dropped at the end of the Jurassic. Whether metriorhynchoids retained
233 ectothermic characteristics is questionable and unanswered but could equally be linked to
234 drastic physiological changes such as reproductive strategies. Metriorhynchoidea display
235 extreme adaptations to marine life, with hypocercal tails and paddle-like limbs²², the latter
236 clearly not suited for land crawling. Extant crocodylomorphs need to come back onto land to
237 lay eggs, but if this could not be achieved by metriorhynchoids, a whole suite of physiological
238 adaptations would have been required, including live birth. As speculative as it may be, this
239 could explain their explosive radiation after the Callovian-Oxfordian temperature drop and
240 their survival after the end-Jurassic, while Teleosauridae drastically declined in diversity and
241 then disappeared. Live birth was widespread among ichthyosaurs²³ and has only recently been
242 reported for plesiosaurs²⁴ and mosasaurs²⁵. In the first two groups, $\delta^{18}\text{O}$ values of bone
243 phosphate tissue support the hypothesis of body temperature regulation²⁶. Whether
244 metriorhynchoids had some sort of endothermic capability would be consistent with our
245 results, also supported by their inferred hypercarnivorous diet²⁷, fulfilling the high metabolic
246 demand for protein. Although this remains to be tested (for example by analysing the $\delta^{18}\text{O}$
247 composition of metriorhynchoid bone phosphate), an intermediate metabolism could explain
248 both the delayed reaction to SST drops when teleosaurids disappeared, and also their demise
249 at the Hauterivian-Valanginian boundary when SST may have dropped below

250 metriorhynchoid tolerance. The temperature tolerance of metriorhynchoids would have been
251 better suited for cold temperatures than that of other marine crocodylomorphs, but remained
252 unparalleled to that of plesiosaurs and ichthyosaurs living in high-latitude cold
253 environments^{28,29,30}. No marine crocodylomorphs have ever been reported in these high-
254 latitude marine environments of the Jurassic and Cretaceous, whereas they were abundant in
255 contemporaneous lower latitude assemblages. This provides support for the first assumption
256 that marine crocodylomorphs were ectotherms, and therefore their capacity to diversify in the
257 marine environment was ultimately constrained by the evolution of sea surface temperatures.

258

259 **Methods**

260 **Diversity counts.** Marine crocodylian diversity counts were assessed at species and genus
261 level. Occurrences extend over the Hettangian to the Rupelian (Supplementary Data 1). To
262 begin with, species counts were retrieved from the literature for the Dyrosauridae and the
263 Eusuchia and updated from Benson et al.⁵ for the Thalattosuchia and Pholidosauridae. The
264 species raw count was included in the statistical analysis and a second set of analyses
265 excluded metriorhynchoids from the species count. In order to reduce taxonomic bias as much
266 as possible, another set of data considered only genera. This is because, across the different
267 lineages of marine crocodylians considered here, two have recently been revised in depth
268 leading to a burst of previously overlooked species diversity³³. Species diversity, and to a
269 lesser extent generic diversity, are unbalanced when comparing recently revised groups such
270 as metriorhynchoids or dyrosaurids, versus other groups such as the Teleosauridae, whose
271 taxonomic content has not been revised recently^{34,35}. Therefore, considering only genera in
272 the dataset allows smoothing out diversity counts across different lineages. An additional
273 approach was applied to this generic dataset for further refinement of the diversity:
274 phylogenetic correction, superimposed on the stratigraphy by filling ghost ranges of genera

275 (Supplementary Data 1). Phylogenetic corrections follows the topology recovered for
276 *Thalattosuchia*³³ and the topology recovered for *Dyrosauridae*³⁶. *Pholidosauridae* (2 marine
277 genera) are in comparison to *Thalattosuchia* and *Dyrosauridae* a relatively small marine
278 radiation with a larger ancestral freshwater stock. For this reason, no phylogenetic correction
279 could be applied here and only their ghost occurrence was added to the stratigraphic series.
280 Finally, phylogenetic correction was not applied to marine *Eusuchia* due to their controversial
281 phylogenetic relationships at the heart of the *Gavialis/Tomistoma* debate³⁷. Therefore, only
282 ghost ranges were added according to the stratigraphic distribution of taxa.

283 **Poorly known taxa from marginal setting.** A number of problematic crocodylians were not
284 included in the marine crocodylian diversity count because of uncertain taxonomic identity
285 and limited occurrence at a single locality in a marginal marine setting. These taxa are:
286 *Aigialosuchus villandensis* Persson, 1959³⁸ from the early Campanian of Blaksudden Ivö,
287 which is fragmentary and may well have been washed out in marginal marine deposits
288 together with dinosaurian teeth found in the same deposits. Moreover, according to the
289 morphology described by Persson (1959), *Aigialosuchus villandensis* can be considered
290 similar to contemporaneous freshwater eusuchians. *Crocodyleimus robustus* Jourdan 1862³⁹
291 from the Kimmeridgian of Cerin, France, possibly belongs to the *Pholidosauridae* but this has
292 not been substantiated yet. *Crocodyleimus robustus* occurs in a lagoonal mudstone and the
293 presence of atoposaurids in the same locality points to episodes of continental wash out into
294 this environment. Although *Pholidosauridae* diversified during the early Cretaceous, they
295 were restricted to freshwater environments. The genus *Anglosuchus* from the Great Oolite
296 (Bathonian) of Peterborough, UK has previously been referred to the *Pholidosauridae*^{40,41,42}
297 but these referrals have never been substantiated. The youngest teleosaurid was recorded from
298 the Valanginian of southern France⁴³. This specimen has recently been revised⁴⁴ and now

299 referred to a metriorhynchid. The youngest record of Teleosauridae is therefore Tithonian in
300 age, no record being substantiated for this group in the Cretaceous.

301 **Seawater temperature curve establishment.** Sea surface temperature curve for the
302 Hettangian – Rupelian interval has been established using both
303 published^{26,45,46,47,48,49,50,51,52,53} and new oxygen isotope composition of fish teeth
304 recovered from European, American, North African and Middle East localities
305 corresponding to the Western Tethys realm (Supplementary Data 1). In order to be
306 comparable, $\delta^{18}\text{O}_p$ values were all normalized to the most recently accepted value of
307 21.7‰ for the international standard NBS 120c⁵⁴. Values with maximum resolution at
308 the substage level were selected and an average value for the whole stage was
309 calculated. Seawater temperatures were then computed using the Phosphate-water
310 temperature scale⁵⁴ assuming an average $\delta^{18}\text{O}$ value of the ocean of -1‰:

$$311 \quad T(^{\circ}\text{C}) = 117.4(\pm 9.5) - 4.50(\pm 0.43) * (\delta^{18}\text{O}_{\text{PO}_4} - \delta^{18}\text{O}_{\text{H}_2\text{O}})$$

312 **Statistical assessment.** This dataset is then compared to the Sea Surface Temperature (SST)
313 curve (Fig. 1A) based on the compilation of new and published $\delta^{18}\text{O}$ values of fish tooth
314 apatite phosphate recovered from low to mid-latitude localities, and to sea level (Fig. 1B),
315 which was recalculated for each stratigraphic interval defined in Gradstein et al.³¹ along with
316 the values obtained from Haq et al.¹⁴ (Hettangian-Rupelian) and Miller et al.¹³ (2005)
317 (Bajocian-Rupelian). Marine crocodylomorph diversity is also confronted with another
318 physical factor, which is a metric for continental flooding⁵ compiled from MACROSTRAT
319 (COSUNA³²). Finally, in order to test possible taphonomic bias on the diversity of marine
320 crocodylomorphs, the number of marine geological formations was compiled from the
321 Paleobiology Database (PaleoDB) and compared to the diversity dataset. The stratigraphic
322 framework of Gradstein et al.³¹ is adopted here. We carried out a series of correlation tests to
323 determine the relationship between marine crocodylian diversity and paleoclimate. We

324 considered four forms of the diversity data, and for each of those, four variants on the data.

325 The time series of crocodylian diversity was presented in these four formats: (1) total
326 species diversity; (2) phylogenetically corrected generic diversity, including ghost ranges; (3)
327 total species diversity minus metriorhynchids; and (4) phylogenetically corrected generic
328 diversity minus metriorhynchids. Phylogenetic correction is commonly done for studies of
329 fossil vertebrates^{6,55}: this consists of plotting a cladogram against geological time, and adding
330 Lazarus taxa (genera with a range above and below a time bin of interest) and ghost ranges
331 (minimal implied range at the base of a lineage implied by older fossils in the immediate
332 sister group).

333 Each of the four data formats was further considered in four forms: (1) raw data; (2)
334 time-corrected (total figures divided by durations of time bins); (3) logarithm (total data); and
335 (4) generalized-differenced total data. These modifications were to allow all possible
336 corrections for variable time bin duration, for any large-scale deviations from the mean
337 (logarithm transformation), and to distinguish overall trend from bin by bin variations
338 (generalized-differencing).

339 Pairwise tests of correlation were carried out between the response variables (diversity
340 time series) and the various possible explanatory time series (the new SST data, the Miller sea
341 level curve, the Haq sea level curve, PaleoDB marine formation counts, and COSUNA marine
342 formation counts). Pearson, Spearman, and Kendall correlation coefficients and significances
343 were calculated using R software v.2.14.1 (R Development Core Team, 2011), as in earlier
344 studies⁵⁶. Further, we recorded raw significance values, as well as those corrected for Type II
345 statistical errors, using the False Discovery Rate (FDR) approach⁵⁷, using an R script given in
346 Benton et al.⁵³, which runs numerous correlation tests with unadjusted and adjusted p values.

347

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496

497 **Author contributions**

498 All authors collected, analysed the data and wrote the manuscript.

499 **Conflict of interest**

500 There is no conflict of interests.

501 **Figure captions**

502 **Figure 1. Phylogenetically corrected generic diversity counts of marine**

503 **crocodylomorphs.** SST curve (A) and sea level curve of Miller et al. (2005)¹³ (B) plotted

504 against geological time. SST and sea level curve of Miller et al. (2005)¹³ are compared (C),

505 showing a close but imperfect co-variation.

506

507 **Table 1. Correlations of potential explanatory variables with different metrics**

508 **representing marine crocodylomorph diversity through the Mesozoic and Paleogene.**

509 Spearman rank correlations. Spearman's rho values are given, together with an indication of

510 significance provided when $p < 0.05$. Abbreviations: All crocodiles, raw species diversity; All

511 croc/time: raw species diversity corrected for time; Log10(allcroc), raw species diversity

512 corrected for Log10; GD allcroc: raw species diversity corrected for generalized differenced;

513 PC: phylogenetically corrected diversity; NM: No Metriorhynchoids.

514

	SST	Miller sea level	Haq sea level	PaleoDB marine formations	COSUNA formations
All crocodiles	0.067	0.169	-0.006	0.176	0.013
All croc/time	0.239	0.203	0.183	0.255	0.196
Log10(allcroc)	0.075	0.130	-0.023	0.137	-0.031
GD allcroc	0.067	0.169	-0.006	0.176	0.013
PC allcroc	0.078	0.116	-0.065	0.070	-0.093
PC all croc/time	0.347	0.205	0.235	0.218	0.190
PC log10(allcroc)	0.061	0.076	-0.104	0.024	-0.126
PC GD allcroc	0.078	0.116	-0.065	0.070	-0.093
NM crocodiles	0.366 ^(0.0431)	0.443 ^(0.0125)	0.242	0.145	0.138
NM croc/time	0.253	0.466	0.331	0.203	0.298
Log10(NMcroc)	0.430 ^(0.0158)	0.397 ^(0.0271)	0.230	0.031	0.071
GD NMcroc	0.365 ^(0.0431)	0.443 ^(0.0125)	0.242	0.145	0.138
PC NM crocodiles	0.367 ^(0.0423)	0.321	0.126	0.014	-0.018
PC NM croc/time	0.382 ^(0.034)	0.405 ^(0.0239)	0.369 ^(0.0411)	0.205	0.274

PC	0.382 ^(0.0338)	0.280	0.082	-0.080	-0.066
log10(NMcroc)					
PC GD NMcroc	0.367 ^(0.0423)	0.321	0.126	0.014	-0.018
TOTALS	7	5	1	0	0
SIGNIF.					
TOTALS NEG.	0	0	6	1	7

515
516

