Climate constrains the evolutionary history and biodiversity of crocodylians

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The fossil record of crocodylians and their relatives (pseudosuchians) reveals a rich evolutionary history, prompting questions about causes of long-term decline to their present-day low biodiversity. We analyse climatic drivers of subsampled pseudosuchian biodiversity over their 250 million year history, using a comprehensive new data set. Biodiversity and environmental changes correlate strongly, with long-term decline of terrestrial taxa driven by decreasing temperatures in northern temperate regions, and biodiversity decreases at lower latitudes matching patterns of increasing aridification. However, there is no relationship between temperature and biodiversity for marine pseudosuchians, with sea-level change and post-extinction opportunism demonstrated to be more important drivers. A ‘modern-type’ latitudinal biodiversity gradient might have existed throughout pseudosuchian history, and range expansion towards the poles occurred during warm intervals. Although their fossil record suggests that current global warming might promote long-term increases in crocodylian biodiversity and geographic range, the ‘balancing forces’ of anthropogenic environmental degradation complicate future predictions.
ongoing climate change, with projected global warming of 2.0–4.8°C over the next century3, could have profound repercussions for crocodylian distributions and biodiversity. As ectotherms, living crocodylians are environmentally sensitive4, and 10 of the 23 extant species are at high extinction risk (http://www.iucncsg.org/; 2015). Ecological models can predict the responses of extant species distributions to rising temperatures. However, only the fossil record provides empirical evidence of the long-term interactions between climate and biodiversity5, including during intervals of rapid climate change that are potentially analogous with the present.

Pseudosuchia is a major reptile clade that includes all archosaurs closer to crocodylians than birds, and made its first fossil appearance nearly 250 million years ago, at the time of the crocodile–bird split5. Crocodylians, the only extant pseudosuchians, are semi-aquatic predators with low morphological diversity, and a tropically restricted geographic range (a band of ~35° either side of the Equator)6. Although often regarded as ‘living fossils’, the pseudosuchian fossil record reveals a much richer evolutionary history and high ancient biodiversity. This poses a key question about the drivers of long-term evolutionary decline in groups that were highly diverse in the geological past, especially given the extraordinary high biodiversity (~10,000 species) of the only other extant group of archosaurs, birds7. Over 500 extinct pseudosuchian species are known (this study), with a broader latitudinal distribution6 and a wider array of terrestrial ecologies than their living counterparts8,9. Several diverse lineages also independently invaded marine environments10. Body plans and feeding modes showed much higher diversity, including flippered taxa and herbivorous forms10–13, and body sizes varied from dwarfed species <1 m in length14, to giants such as Sarcosuchus, which reached around 12 m in length and weighed up to 8 metric tons15. Climate has often been proposed to have shaped pseudosuchian biodiversity through time,6,16,18, and the group’s geographic distribution over the past 100 million years has been used as evidence in palaeoclimatic reconstructions2.

Here we examine the effect of climate on spatiotemporal patterns in pseudosuchian biodiversity over their 250 million year history, using a comprehensive fossil occurrence data set. Our study is the first to analyse climatic drivers of pseudosuchian biodiversity through the group’s entire evolutionary history, applying rigorous quantitative approaches to ameliorate for uneven sampling across both time and space. Furthermore, this is the only comprehensive, temporally continuous fossil occurrence dataset for a major extant vertebrate group: equivalent estimates are congruent with observations of phylogenetic lineage divergence16,24,25, and indicate that both marine and non-marine crocodylomorph biodiversity declined across the J/K boundary (Figs 2 and 3a), including the extinction of teleosauroid thalattosuchians16,25. However, our subsampled estimates are congruent with observations of phylogenetic lineage survival16,24,25, and indicate that both marine and non-marine crocodylomorph biodiversity declined across the I/K boundary (Figs 2 and 3a), including the extinction of teleosaurid thalattosuchians16,25.

Sampling of palaeotropical non-marine crocodylomorphs is limited throughout the Jurassic–Cretaceous (Figs 3a and 4a). However, good sampling of terrestrial early Late Cretaceous North African crocodylomorphs inhabiting a low-latitude (18°N), semi-arid biome8,14 (Fig. 4b) indicates subsampled biodiversity levels comparable to those of palaeotropical forms in other Cretaceous time slices (Fig. 2a). Furthermore, sub-palaeotropical (24–28°S) South American crocodylomorphs of the Late Cretaceous Adamantina Formation were exceptionally diverse6,26, raising the possibility that pseudosuchians in fact reached their highest biodiversities in tropical environments during the mid-Cretaceous greenhouse world. In contrast to previous work6, this suggests that there was no palaeotropical diversity reached around 12 m in length and weighed up to 8 metric tons. Ecological models can predict the responses of extant species distributions to rising temperatures. However, only the fossil record provides empirical evidence of the long-term interactions between climate and biodiversity, including during intervals of rapid climate change that are potentially analogous with the present. Pseudosuchia is a major reptile clade that includes all archosaurs closer to crocodylians than birds, and made its first fossil appearance nearly 250 million years ago, at the time of the crocodile–bird split. Crocodylians, the only extant pseudosuchians, are semi-aquatic predators with low morphological diversity, and a tropically restricted geographic range (a band of ~35° either side of the Equator). Although often regarded as ‘living fossils’, the pseudosuchian fossil record reveals a much richer evolutionary history and high ancient biodiversity. This poses a key question about the drivers of long-term evolutionary decline in groups that were highly diverse in the geological past, especially given the extraordinary high biodiversity (~10,000 species) of the only other extant group of archosaurs, birds. Over 500 extinct pseudosuchian species are known (this study), with a broader latitudinal distribution and a wider array of terrestrial ecologies than their living counterparts. Several diverse lineages also independently invaded marine environments. Body plans and feeding modes showed much higher diversity, including flippered taxa and herbivorous forms, and body sizes varied from dwarfed species <1 m in length, to giants such as Sarcosuchus, which reached around 12 m in length and weighed up to 8 metric tons. Climate has often been proposed to have shaped pseudosuchian biodiversity through time, and the group’s geographic distribution over the past 100 million years has been used as evidence in palaeoclimatic reconstructions.

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from the Campanian into the Maastrichtian in both Europe and North America (Figs 2a and 3c), on the ~9 million-year timescale resolution of our study. This decrease in biodiversity prior to the K/Pg mass extinction event (66 Myr ago) mirrors the pattern seen in North American mammals29 and some dinosaur groups30. However, rather than signalling that a protracted global catastrophe caused the K/Pg mass extinction, this latest Cretaceous decline of crocodylomorphs tracks a long-term trend towards cooler temperatures through the Late Cretaceous31,32. This is consistent with the ‘background’ coupling between biodiversity and global climate observed throughout the late Mesozoic and Cenozoic (see below), and likely characteristic of the entire evolutionary history of Pseudosuchia.

The effect of the K/Pg mass extinction on crocodylomorphs has previously been perceived as minor or non-existent9,28, with any extinction temporally staggered33. However, several non-marine groups with high biodiversity before the boundary became extinct (most notably all non-sebecid notosuchians34), and only two clades (the marine dyrosaurids and terrestrial sebecids) survived alongside crocodylians28,35. Nevertheless, the extinctions of these groups, and other marine crocodylomorph taxa were balanced by rapid radiations of the three surviving clades in the early Paleocene19,28,34,36, including substantial range expansions of marine dyrosaurids36,37 and terrestrial alligatoroids28 into South America. Range expansions and increases in regional taxon counts among dyrosaurids35–37 and gavialoid crocodylians38 led to a substantial increase in global marine crocodylomorph biodiversity by the late Paleocene (Fig. 2c), with crocodylomorphs potentially benefiting from the extinction of many other marine reptiles at the K/Pg boundary36,39.

Biodiversity across the K/Pg boundary. The Cretaceous witnessed the non-marine radiations of notosuchians8,19,26 and eusuchians, with crocodylians diversifying from within Eusuchia during the Late Cretaceous (Santonian–Maastrichtian)9,28. Despite this, subsampled non-marine biodiversity decreased

Non-marine biodiversity and palaeotemperature. Relative changes in subsampled non-marine biodiversity in both North America and Europe track each other and the δ18O palaeotemperature proxy17,40 through the Cenozoic (Fig. 2a; Table 1). The relationship between these variables is characterised by near-zero, negative serial correlation for North American data, and high, negative serial correlation for European data. The occurrence of near-zero estimated serial correlation suggests links between high amplitude, long-term patterns, with weaker correspondence between low amplitude, short-term fluctuations. Nevertheless, a similar relationship is still recovered when serial correlation is assumed to equal zero, and for the European data when it is assumed to equal one (Table 1), demonstrating robustness of this result to statistical approach. Furthermore, the recovery of near-identical patterns of relative standing biodiversity from separate European and North American occurrence datasets suggests that our subsampling approach is effective in recovering a shared underlying biodiversity pattern.

Paleogene non-marine biodiversity. These North American and European patterns indicate that non-marine crocodylomorphs remained diverse at temperate palaeolatitudes (30–60°) during the early Paleocene greenhouse world (66–41 Myr ago). There is no evidence for transient biodiversity increases driven by the short-term Paleocene–Eocene Thermal Maximum (56 Myr ago), possibly because the timescale of species origination and phenotypic divergence that would allow speciation to be recognisable in the fossil record is longer than that of this rapid climatic event (>5 °C in <10,000 years). Nevertheless, early Eocene crocodylomorphs expanded their palaeogeographic range to at least 75°N (Fig. 4a,c), coinciding with the sustained high temperatures of the Early Eocene Climatic Optimum (53–50 Myr ago)41. A major European and North American biodiversity peak during the middle Eocene (48–41 Myr ago;
Fig. 2a) is composed primarily of crocodylians, with sebecids, previously known only from South America 34, also present in Europe42. However, although this interval includes the short-term hyperthermal Mid-Eocene Climatic Optimum, the overall trend is one of cooling17, indicating a temporary decoupling of temperature and biodiversity. At temperate palaeolatitudes, a stark late Eocene–Oligocene (41–23 Myr ago) decline to unprecedentedly low biodiversity (Figs 2a and 3d) coincides with global cooling, the development of a strengthened latitudinal temperature gradient43, and the onset of Antarctic glaciation17. Unfortunately, southern hemisphere and palaeotropical (0–30°) sampling (Fig. 3d) is inadequate to determine additional patterns of Paleogene biodiversity, including the form of palaeolatitudinal biodiversity gradients. This also means that we cannot determine whether the correlation between palaeotemperature and non-marine biodiversity was restricted to northern temperate palaeolatitudes, or was a global pattern, during the Paleogene. If the latter is shown to have been the case, then we should...
ultimately expect to find extremely high Paleogene biodiversity in currently poorly sampled regions such as South America. Alternatively, temperature change might drive pseudosuchian biodiversity only at limiting, low–medium temperatures. At high, non-limiting temperatures, other factors such as aridity might become limiting, as suggested by low-latitude Cenozoic biodiversity patterns described below.

**Cenozoic marine biodiversity.** Marine crocodylomorph biodiversity decreased in the early Eocene (Fig. 2b), with the loss of basal gavialoids ('thoracosaurids') and decline in dyrosaurids, with the latter group becoming extinct in the middle–late Eocene.16,28,37 This observation conflicts with the conclusions of a recent study that did not use subsampling approaches16, the authors of which proposed that marine crocodylomorphs generally diversified during warm intervals. Furthermore, contrary to the findings of those authors16, there is no statistical relationship between the d18O palaeotemperature proxy and marine crocodylomorph biodiversity in any of our analyses, whether or not subsampling is applied (Table 2). This differs from the approach of Martin et al.16, who found correlations between their palaeotemperature proxy and marine crocodylomorph biodiversity, but only once metriorhynchoid thalattosuchians were excluded. They used this finding as evidence for an assertion that metriorhynchoids had a distinct biology from other marine crocodylomorphs. However, a more conservative reading of these results is that marine crocodylomorph biodiversity was not consistently linked to temperature over the studied interval. Instead, our analyses find strong, significant relationships between subsampled marine genus counts and eustatic sea level estimates of Miller et al.18 when including a 'phase' variable (see Methods) to distinguish the amplitude of thalattosuchian biodiversity patterns from that of stratigraphically younger marine radiations (Table 2). This regression model explains more than 60% of the variance in subsampled marine biodiversity. Directly counted marine genera have a marginally significant relationship with sea level (Table 2).
number of gavialoids 46 and tomistomines 28,47, before their biodiversity remained low through the remainder of the continental range expansion 36,39. Marine crocodylomorph marine crocodylomorphs, which show a substantial post-opportunism contributed to high biodiversity of early Paleogene important; for example, it is likely that post-extinction near-shore marine reptiles22. Other extrinsic factors might also be lineages49, and the presence of highly diverse sympatric occurrences declined to their approximate present day limits (Supplementary Fig. 5). The most poleward crocodylomorph both on the continents (Fig. 4) and in the marine realm clear evidence for latitudinal range contraction through time Mid-Miocene Climatic Optimum (15 Myr ago; Fig. 2a). There is higher palaeolatitude tetrapod faunas, and indicates that the onset of Arctic glaciation17. This is despite the occurrence of non-crocodylomorph-bearing fossil localities documenting the mega-wetlands52,53, driven by Andean uplift54. The overall dwindling of crocodylomorph biodiversity towards the present day tracks the late Cenozoic cooling trend17, increasing aridification52 and the rising predominance of grassland ecosystems during the late Neogene53, the Quaternary Ice Ages17 and presumably the more recent impact of human activity.

Neogene non-marine biodiversity. Temperate palaeolatitudinal biodiversity remained low among Neogene non-marine crocodylomorphs, although a minor peak might be coincident with the Mid-Miocene Climatic Optimum (15 Myr ago; Fig. 2a). There is clear evidence for latitudinal range contraction through time both on the continents (Fig. 4) and in the marine realm (Supplementary Fig. 5). The most poleward crocodylomorph occurrences declined to their approximate present day limits (35° N and S) by the late Miocene (Fig. 4a,d), coincident with the onset of Arctic glaciation17. This is despite the occurrence of non-crocodylomorph-bearing fossil localities documenting higher palaeolatitude tetrapod faunas, and indicates that crocodylomorph range contraction is not a sampling artefact.

Neogene terrestrial biodiversity of crocodylians was substantially higher in the palaeotropics of South America (Figs 2a and 3e), and has been attributed to hydrographic changes and the disappearance of the mega-wetlands52,53, driven by Andean uplift54. The overall dwindling of crocodylomorph biodiversity towards the present day tracks the late Cenozoic cooling trend17, increasing aridification52 and the rising predominance of grassland ecosystems during the late Neogene53, the Quaternary Ice Ages17 and presumably the more recent impact of human activity.

The future of crocodylians. Our findings show that the biodiversity of non-marine pseudosuchians has been strongly linked to both spatial and temporal temperature variation, as well as the spatial distribution of aridity, throughout the group’s evolutionary history. This can be demonstrated most clearly during the Cenozoic, where the long-term decline of crocodylomorphs at temperate latitudes over the last 50 million years has been driven by the descent into the modern-day icehouse world, and the geographic pattern of decline among palaeotropical taxa in the Neogene matches patterns of aridification in Africa and South America. As the Earth continues to warm, perhaps heading towards a greenhouse world comparable to that of the early Paleogene4, we might therefore expect that higher temperatures should promote long-term increases in crocodylian biodiversity and the expansion of the group’s latitudinal range outside of the tropics, as was the case for much of their Mesozoic and early Cenozoic history. However, in contrast to these earlier times, predictions of the distribution of their future biodiversity are complicated by the impact of human activity on habitat loss and fragmentation, which are likely to reduce the rate and magnitude of crocodylian range expansion4, especially into populated regions.

Table 2 | Results of generalised least squares regression of log$_{10}$ subsampled marine genus biodiversity (quorum = 0.4) on the $\delta^{18}$O palaeotemperature proxy of Prokoph et al.40 and estimated sea level18.

| Environment | Region | Independent variable | N | GLS | OLS (untransformed) |
|-------------|--------|----------------------|---|-----|---------------------|
|              |        |                      |   | Phi | Int.                | Slope | Int. | Slope | R$^2$ |     |     |
| Subsampled  |        |                      |   |     |                    |       |      |       |      |     |     |
| Marine      | Global | Prokopf $\delta^{18}$O | 12 | 0.68 | 0.26 | -0.05 (0.227) | 0.32 | -0.03 (0.539) | -0.06 |     |     |
| Marine      | Global | Prokopf $\delta^{18}$O + phase$^1$ | 12 | 0.88 | 0.25 | -0.05 (0.188) | 0.31 | -0.03 (0.581) | -0.17 |     |     |
| Marine      | Global | marine level         | 12 | 0.47 | 0.32 | 0.001 (0.159)  | 0.33 | 0.002 (0.114)  | 0.15  |     |     |
| Marine      | Global | marine level + phase$^1$ | 12 | -0.01 | 0.46 | 0.005** (0.002) | 0.46 | 0.005** (0.002) | 0.61  |     |     |
| Counted     |        |                      |   |     |                    |       |      |       |      |     |     |
| Marine      | Global | Prokopf $\delta^{18}$O | 18 | 0.57 | 0.64 | 0.047 (0.500)  | 0.67 | 0.067 (0.373) | -0.01 |     |     |
| Marine      | Global | Prokopf $\delta^{18}$O + phase$^1$ | 18 | 0.52 | 0.87 | 0.066 (0.331)  | 0.91 | 0.093 (0.184)  | 0.19  |     |     |
| Marine      | Global | marine level         | 18 | 0.72 | 0.60 | 0.004 (0.172)  | 0.62 | <0.000 (0.978)  | -0.06 |     |     |
| Marine      | Global | marine level + phase$^1$ | 18 | 0.54 | 0.89 | 0.005* (0.068) | 0.96 | 0.006** (0.047) | 0.30  |     |     |

*GLS* denotes generalised least squares regression incorporating a first-order autoregressive covariance model; OLS denotes ordinary least squares regression; `fd` indicates that first-differencing was applied to the input data series; phi is the serial correlation coefficient40; `Int.` is the y-intercept; R$^2$ is the adjusted R$^2$ of ordinary least squares regression, and comparable R$^2$ values cannot be computed for generalised least squares.; **significant at alpha = 0.05** (significance).

1including a binary variable indicating the Jurassic–Early Cretaceous marine radiation as ‘1’ and the Late Cretaceous–Cenozoic marine radiation as ‘2’.

slopes of the ‘phase’ variable in these regression models indicate that thalattosuchians attained higher biodiversity relative to sea level than did stratigraphically younger marine crocodylomorphs. Our results support previous observations that continental flooding, through eustatic sea level change, shaped the evolution of marine shelf biodiversity44,45, including that of near-shore marine reptiles22. Other extrinsic factors might also be important; for example, it is likely that post-extinction opportunism contributed to high biodiversity of early Paleogene marine crocodylomorphs, which show a substantial post-extinction biodiversity increase that was facilitated by inter-continental range expansion36,39. Marine crocodylomorph biodiversity remained low through the remainder of the Paleogene and early Neogene (Fig. 2b), comprising a small number of gavialoids46 and tomistomines28,47, before their present day restriction to non-marine environments.

Africa (Figs 2a and 3e), coincident with the formation of the Sahara Desert52 and sub-Saharan expansion of savannah environments53. A similar decline ensued in the post-Miocene palaetropics of South America (Figs 2a and 3e), and has been attributed to hydrographic changes and the disappearance of the mega-wetlands52,53, driven by Andean uplift54. The overall dwindling of crocodylomorph biodiversity towards the present day tracks the late Cenozoic cooling trend17, increasing aridification52 and the rising predominance of grassland ecosystems during the late Neogene53, the Quaternary Ice Ages17 and presumably the more recent impact of human activity.

Methods

Pseudosuchian occurrences data set. Following extensive work to ensure that occurrences and taxonomic opinions were consistent and up-to-date with the literature52, the Paleobiology Database (PaleoDB; http://paleobiodb.org) includes a near-comprehensive dataset of all published pseudosuchian occurrences spanning the Middle Triassic through to the Pleistocene, a period of nearly 250 million years. Pseudosuchian body fossil occurrences that could be assigned to genera (including...
genera were used so as to incorporate specifically indeterminate material, enabling us to include more data points in our analyses, and also to avoid problems with using species as a unit for estimating palaeobiodiversity58,59. This is especially pertinent to analyses of the pseudosuchian fossil record, where certain parts of the tree have been difficult to place in phylogenetic context due to a lack of intense taxonomic effort at the species level (for example, Thalattosuchia57), whereas other clades are composed primarily of monospecific genera (for example, Notosuchia26), and some groups have received relatively little attention (for example, Tomistominae63). Despite this issue, fluctuations in the number of genera and species are near-identical in the marine and non-marine realms (Supplementary Fig. 1). The sole exception to this pattern is that there is a continued increase in non-marine species numbers in our most recent time bin (Supplementary Fig. 1), in contrast to the decline that occurs in genera (Fig. 1; Supplementary Fig. 1). We also plotted ratios of non-marine species to genera through time, which shows no significant trend (Supplementary Fig. 2). However, the Neogene differs from eocene-miospian periods in post-Paleozoic history in having high species to genus ratios (Supplementary Fig. 2). We suggest that these deviations in the Neogene reflect the relative ease of recognizing modern species in the recent fossil record, with most living species belonging to just a small number of genera, whereas the Eocene were best considered a ‘Pull of the Recent’ type effect.

Extant genera, especially Alligator and Crocodylus, have been used as ‘wastebasket taxa’ for indeterminate or non-referable fossil species. Therefore, we modified occurrences of Crocodylus and Alligator before analysis, as explained in the Supplementary Methods. We also reviewed Cretaceous thalattosuchian occurrences, to help constrain marine crocodylomorph biodiversity over the J/K boundary (Supplementary Methods).

The resultant pseudosuchian data set was subdivided into non-marine (terrestrial plus freshwater; Supplementary Data 1) and marine taxa (Supplementary Data 2) using an amended version of a list of the names of Mesozoic–Ypresian tetrapod taxa presented in Benson et al. (in review). Environmental assignment (marine versus terrestrial; Supplementary Table 1) was based primarily on facies data recorded in the PaleOD and information presented in refs 16,28,46. Vélez-Juarbe et al.48 demonstrated the marine affinities of several late Oligocene–Neogene gavialoids, including Aṅkogavialis, Piscogavialis and Sipapiskeschus; these were omitted from the marine crocodylophian data set of Martin et al.54. In some cases, taxonomic placements were proposed in the absence of any data on marine occurrence. Although some stratigraphically older species currently included within Tomistoma were probably marine67, most occurrences (including the extant species T. schlegeli) are non-marine, or their environments are unknown; as such, we treat Tomistoma as non-marine.

**Subsampling protocol.** Pseudosuchian genera were assigned to approximately equal-length (9 million years) stratigraphic time bins (Supplementary Table 1 and Supplementary Data 3). Although there is variation in time bin duration, there is no significant trend of interval duration through time (Supplementary Fig. 3). We applied equal coverage or ‘shareholder quorum’ subsampling (SQS)58 to ameliorate the effect of unequal taxonomic sampling and to reconstruct paleobiodiversity. SQS tracks the ‘coverage’ of each subsampling pool represented by the taxa that have been drawn58. Coverage is the sum of the proportional frequencies of the taxa sampled in each time bin, and coverage of observed data is modified to estimate the coverage of the real taxonomic distribution for each sample pool. This is achieved by multiplying the average of the observed coverage by the fraction of occurrences representing non-singleton taxa58,59. Each interval can therefore only be subsampled to a maximum quorum level (i.e. amount of coverage) equal to Good’s u for that interval, meaning fewer time intervals/geographical regions can be subsampled at higher quorum levels. We used a quorum level of 0.4 for reported analyses, a level which recovers similar patterns to those at higher quorum levels based on marine invertebrate data sets58,59, and unreported analyses of our pseudosuchian data. The substantial advantage of SQS over other subsampling methods, such as classical rarefaction, is that it is robust to the tendency of those methods to ‘flatten out’ biodiversity curves58. It has been suggested that SQS can remove the effects of unequal taxonomic sampling and to reconstruct paleobiodiversity estimates are stronger than those with face value biodiversity counts (Tables 1 and 2). Furthermore, independent data on pseudosuchian biodiversity in the northern temperate latitudes from North America were used to test both methods across spatially extensive data sets. However, high levels of endemism are evident in non-marine pseudosuchian genera, which have wide geographic distributions, were analysed as a global data set. Therefore, we chose to analyse marine pseudosuchian genera, which were therefore analysed across a set of continental regions (Africa, Asia, Australasia, Europe, North America and South America) representing regional biotas of approximately equal geographic spread. For each continental region, we selected countries that were well-sampled and cohesive through time, and therefore the intervals that were used to determine the geographic spread of data relatively even among continents by excluding far-outlying countries (Supplementary Methods and Supplementary Table 2).

In addition to producing subsampled terrestrial and marine biodiversity curves through time, we also analysed the palaeolatitudinal distribution of terrestrial biodiversity. This was implemented through plots of subsampled regional biodiversity against the regional palaeolatitudinal centroid, as well as plots of downsampling curves within time bins (Fig. 3 and Supplementary Fig. 4). Plots of the palaeolatitudinal spread of all pseudosuchian and all tetrapod occurrences through time were also produced for non-marine (Fig. 4a) and marine taxa (Supplementary Fig. 5). Collections in the Paleobiology Database are assigned present-day coordinates and geological ages. These two pieces of information are combined with palaeogeographic rotation models provided by C. Scocete (http://www.scocete.com) to obtain reconstructed palaeogeographic positions for each occurrence.

**Correlation of biodiversity with palaeotemperature and sea level.** We compared subsampled genus biodiversities at a quorum of 0.4 to δ18O palaeotemperature proxies and sea level estimates 

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58,59. Marine pseudosuchian genera, which have wide geographic distributions, were analysed as a global data set. However, high levels of endemism are evident in non-marine pseudosuchian genera, which were therefore analysed across a set of continental regions (Africa, Asia, Australasia, Europe, North America and South America) representing regional biotas of approximately equal geographic spread. For each continental region, we selected countries that were well-sampled and cohesive through time, and therefore the intervals that were used to determine the geographic spread of data relatively even among continents by excluding far-outlying countries (Supplementary Methods and Supplementary Table 2).

In addition to producing subsampled terrestrial and marine biodiversity curves through time, we also analysed the palaeolatitudinal distribution of terrestrial biodiversity. This was implemented through plots of subsampled regional biodiversity against the regional palaeolatitudinal centroid, as well as plots of downsampling curves within time bins (Fig. 3 and Supplementary Fig. 4). Plots of the palaeolatitudinal spread of all pseudosuchian and all tetrapod occurrences through time were also produced for non-marine (Fig. 4a) and marine taxa (Supplementary Fig. 5). Collections in the Paleobiology Database are assigned present-day coordinates and geological ages. These two pieces of information are combined with palaeogeographic rotation models provided by C. Scocete (http://www.scocete.com) to obtain reconstructed palaeogeographic positions for each occurrence.
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Acknowledgements

We are grateful for the efforts of all those who have collected pseudosuchian data, and to all those who have also entered this data into the Paleobiology Database, especially J. Alroy, A. Behrensmeyer and M. Uhen. J. Alroy provided the PERL script used to perform subsampling analyses. K. Littler offered valuable insights on climatic data, and S. Peters provided constructive comments on methodological approach. P.D.M.’s research was supported by an Imperial College London Junior Research Fellowship and a Leverhulme Trust Early Career Fellowship (ECF-2014-662). R.J.B. received funding from the European Union’s Horizon 2020 research and innovation programme 2014–2018 under grant agreement 637483 (ERC Starting Grant: TERRA), as well as from a Marie Curie Career Integration Grant (PCIG14-GA-2013-630123). J.P.T. is funded by a NERC PhD studentship (EATAS G013 13). Part of the Cretaceous dataset was compiled by R.B.J.B. via Leverhulme Foundation Grant RPG-129, awarded to P. Upchurch. This is Paleobiology Database official publication number 235.

Author contributions

P.D.M., R.B.J.B. and R.J.B. conceived and designed the research. P.D.M., R.B.J.B., R.J.B., J.P.T. and M.T.C. compiled the data. R.B.J.B. carried out the analyses. P.D.M. and R.B.J.B. prepared the figures. All authors discussed the results and contributed to writing the manuscript.

Additional information

Supplementary Information accompanies this paper at http://www.nature.com/naturecommunications

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Mannion, P. D. et al. Climate constrains the evolutionary history and biodiversity of crocodylians. Nat. Commun. 6:8438 doi: 10.1038/ncomms9438 (2015).

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