

The role of climate on the emergence of giant caimanines (Crocodylia, Alligatoroidea) from the Miocene western Amazonian region

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ABSTRACT

Extant caimanines include the six modern species of caimans, which occur predominantly in South and Central America and are mostly medium-sized crocodylians. Nevertheless, the fossil record of the group reveals a significantly higher diversity, with remarkable body size variation. In particular, the giants *Purussaurus* and *Mourasuchus*, from the Miocene western Amazonian region, are two of the most prominent representatives. Previous work has demonstrated a correlation between the body size of crocodylians and abiotic factors throughout the Cenozoic; however, this relationship is poorly understood, particularly within the Caimaninae lineage. Here, we explore evolutionary body size patterns within Caimaninae, investigating the potential influence of climatic factors. Using a phylogenetically-informed method, we estimated the body size of 33 caimanine specimens, coupled with climatic variables from a General Circulation Model to reconstruct deep-time patterns. Our results indicate that giant Miocene caimanines are restricted to warmer conditions, with significantly less seasonal temperature variation. This suggests that the unmatched climatic conditions of the Miocene western Amazonian region possibly allowed the emergence of unique palaeoecosystems, favouring the sustenance of these very large crocodylians.

1. Introduction

Body size plays a central role in the life history of crocodylians, affecting various aspects such as their ecology, physiology, and evolutionary history (Grigg et al., 1998; McClain and Boyer, 2009; Grigg and Kirshner, 2015; Godoy and Turner, 2020; Stockdale and Benton, 2021, 2022; Benson et al., 2022). Numerous studies have used body size as a metric for ecological investigations, shedding light on their lifestyles and palaeoenvironments (Serenio et al., 2001; Aureliano et al., 2015; O'Brien et al., 2019; Cidade et al., 2021; Paiva et al., 2022). However, the relation between body size and abiotic factors remains poorly understood. A recent work on crocodylian body size evolution identified a correlation between size increase and global temperature decrease

during the Cenozoic (Godoy et al., 2019). Nevertheless, these patterns have primarily been explored at broad phylogenetic and temporal scales, lacking resolution within more specific lineages.

Caimaninae represents a diverse crocodylian lineage, characterized by significant cranial disparity (Salas-Gismondi et al., 2015; Cidade et al., 2019; Godoy et al., 2019) and astonishing body size variation (Brochu, 2010; Aureliano et al., 2015; Paiva et al., 2022), both of which affects its ecology. Currently, the six living caimanine species are restricted to Central and South America, except for *Caiman crocodilus*, which is found in southern Mexico (Brochu, 1999; Grigg and Kirshner, 2015). Yet, the group had a broader distribution during the end of the Cretaceous and throughout the Cenozoic, including North America (Brochu, 1999, 2011; Scheyer et al., 2013; Salas-Gismondi et al., 2015;

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Bona et al., 2018; Cossette and Brochu, 2018; Cidade et al., 2019; Godoy et al., 2021; Stocker et al., 2021; Walter et al., 2021). The morphological disparity apex of the group likely occurred in the Miocene of northern South America (Scheyer et al., 2013; Salas-Gismondi et al., 2015; Scheyer and Delfino, 2016; Cidade et al., 2019). This epoch witnessed the Andean uplift, resulting in the formation of extensive fluvial lacustrine environments, characterized by two phases, the Pebas and Acre phases, during the Middle and Late Miocene, respectively (Hoorn, 2010; Hoorn et al., 2022; Latrubesse et al., 2010; Cidade et al., 2019), providing abundant resources for a very diverse fauna, probably unprecedented in other Cenozoic epochs. Important diversification events among vertebrates occurred during this time, including caimanines and other reptiles, amphibians, birds, and mammals (Aguilera, 2004; Cozzuol, 2006; Hsiou, 2010; Negri et al., 2009; Muniz et al., 2021; Guilherme et al., 2023; Stutz, 2023), as well as invertebrate lineages (such as molluscs and crustaceans; Gross et al., 2011, 2013; Sousa et al., 2021). Moreover, the Miocene was characterized by elevated temperatures (Böhme, 2003; Kaandorp et al., 2005; Super et al., 2018; Methner et al., 2020; Steinhorsdottir, 2021), akin to those of Paleocene-Eocene (Pearson et al., 2007; Mannion et al., 2015), possibly contributing to the high diversity of the ectothermic crocodylians.

Previous investigations on the body size of caimanines have mostly focused on Miocene taxa, which were notably large (Aureliano et al., 2015; Scheyer et al., 2019; Cidade et al., 2021; Paiva et al., 2022). Estimating the body size of species illuminates the evolutionary history of the group, particularly regarding cranial and body form variations, associated with their palaeoenvironments (Aureliano et al., 2015; O'Brien et al., 2019; Solórzano et al., 2020; Cidade et al., 2021; Paiva et al., 2022). Caimaninae exhibits a large range of ecomorphotypes (e.g., durophagous, top-predator, "gulp-feeder", and generalist; Aureliano et al., 2015; Salas-Gismondi et al., 2015; Cidade et al., 2017, 2021; Bona et al., 2018; Souza-Filho et al., 2018), which is also likely related to their body sizes. Furthermore, temperature fluctuations during their evolutionary history may also explain the observed diversity in body sizes, an aspect yet to be investigated.

In this study, we estimate the body size of caimanine species, across the entire evolutionary history of the group, exploring temporal patterns and conducting ancestral body size reconstructions. Additionally, we investigate potential climatic drivers related to the evolution of this trait, particularly those contributing to larger body sizes. We hypothesize that larger caimanines inhabit areas of relatively higher mean annual temperature. This study represents the first attempt to explore body size across the entire evolutionary history of Caimaninae, incorporating climate models to analyse the influence of environmental factors on body size variations.

2. Material and methods

2.1. Body size estimation

To estimate the body size of caimanine specimens, we applied the Bayesian approach proposed by O'Brien et al. (2019) and tested by Paiva et al. (2022), which uses head width to estimate total body length of crocodylians based on regression data of measurements collected from living specimens. This phylogenetic method accounts for the non-independence of the data (O'Brien et al., 2019; Paiva et al., 2022), considering that the species share an evolutionary history. In particular, we applied this method using the updated measurement dataset presented by Paiva et al. (2022), which includes 206 specimens of living crocodylians, 71 of which are caimanines (representing all living species). As the phylogenetic framework for this method, we updated the specimen-level tree topology of Paiva et al. (2022), by manually adding 24 extinct caimanine specimens/taxa as tips using Mesquite v. 3.70 (Maddison, 2008), following the phylogenetic hypothesis of Godoy et al. (2021) (Supplementary Material). In order to include fossil tips to a time-scaled phylogeny originally generated with molecular data, both

O'Brien et al. (2019) and Paiva et al. (2022) added near-zero lengths to branches with extinct taxa in their trees. Nevertheless, given that our tree includes a significantly higher number of fossil taxa, we took a different approach. We collected age information for all tips in our tree from the Paleobiology Database (PBDB) and the literature (see Supplementary Material), and time-calibrated the tree using the minimum branch length (*mbl*) method (Laurin, 2004), with a minimum length of 5 million years, obtaining time-calibrated trees from the unscaled topology (Supplementary Material). This procedure was done in R version 4.3.1 (R Core Team, 2023), using the *timePaleoPhy()* function from the R package *paleotree* v. 3.4.5 (Bapst, 2012).

Head width (HW, or skull width, measured as the linear distance between the extremes of the right and left quadrates) was collected for 33 extinct caimanines (Table S1), in which taxa previously recognized as juveniles were not included in this analysis. Specimens were sourced from the literature and photographs of museum collection, and measurements were collected using the software ImageJ. To minimize measurement error, we used photographs that include a scale bar, allowing for precise calibration and measurement using ImageJ. Additionally, potential measurement error that do persist is arguably minor compared to the different scales of magnitude observed in crocodylomorph and caimanine body size evolution (Godoy et al., 2019; Benson et al., 2022). Total length of extinct specimens was estimated using phylogenetic predictions by employing the BayesModelS method (Garland Jr. and Ives, 2000), which assumes a Brownian motion model of evolutionary change and uses Monte-Carlo Markov-Chain (MCMC) to obtain the estimates of an unknown value, in this case the body size (Garland Jr. and Ives, 2000; Nunn and Zhu, 2014; O'Brien et al., 2019; Paiva et al., 2022). The MCMC was run for 2,000,000 generations, discarding the first 500,000 as burn-in, and a thin of 1000. The BayesModelS implementation in R uses estimated phylogenetic signal values obtained using the *phylosig()* function from the *phytools* package v. 2.1–1 (Revell, 2012).

The data were natural log-transformed prior to the analysis to normalize data and reduce variance disparities, following recent debates (Benson et al., 2022; Stockdale and Benton, 2022). This approach is crucial for accurate comparisons, particularly given the significant skull variations and body sizes among caimanines. The method itself was employed using R functions made available by O'Brien et al. (2019) and Paiva et al. (2022), as well as R packages *car* v. 3.1–2 (Fox and Weisberg, 2019), *MASS* v. 7.3–60.2 (Venables and Ripley, 2002), *caper* v. 1.0.3 (Orme et al., 2018), *evomap* (Smaers and Mongle, 2014), and *rms* v. 6.8–1 (Harrell, 2017). The scripts for these steps are available in Supplementary Material.

2.2. Ancestral body size reconstructions

To explore deep-time patterns of body size evolution in Caimaninae, we used our body size estimations of extinct specimens and collected mean body size information for extant taxa from the literature (Grigg and Kirshner, 2015; O'Brien et al., 2019; Paiva et al., 2022). This allowed us to reconstruct ancestral body size values and map mean body size on the caimanine phylogeny. We manually constructed a species-level supertree by adding taxa to the topology of Godoy et al. (2021). This supertree differs from that used for the body size estimations, given that the former included specimens as tips. The final version of the tree comprises 41 crocodylian taxa, with 35 caimanines and six outgroups. An alternative topology was also constructed, including Late Cretaceous taxa from North America that are tentatively assigned to Caimaninae by some recent studies (*Albertochampsia langstoni*, *Brachychampsia montana*, *B. sealeyi*, and *Stangerochampsia mccabei*; Bona et al., 2018; Stocker et al., 2021). Subsequent analyses were performed on both topologies (reduced and complete supertrees, hereafter), to account for this phylogenetic uncertainty.

We time-calibrated these two topologies using a Bayesian approach with a fossilized birth-death (FBD) model (Heath et al., 2014; Zhang

et al., 2015; Didier and Laurin, 2020), following the protocol of Godoy et al. (2021), which in turn follows the recommendations of Matzke and Wright (2016) and Gearty and Payne (2020). Uniform priors were placed on the age of the root for both topologies, constrained between 83.5 and 83.6 Ma (complete supertree) and 70.6 and 70.7 Ma (reduced supertree), based on previous estimations of the Caimaninae origin (e.g., Bona et al., 2018; Godoy et al., 2021). We used the two supertrees as topological constraints and combined them with taxon ages data to create an empty morphological matrix using the *createMrBayesTipdatingNexus()* of the R package *paleotree* (Bapst, 2012), which generated command files to run the Bayesian analyses on MrBayes version 3.2.7 (Ronquist et al., 2012). For each supertree, two independent MCMC runs with four chains were run for 20 million generations, with the first 25 % discarded as burn-in. For each topology, the maximum clade credibility tree (MCCT) and 100 trees randomly selected from the posterior distribution were obtained for subsequent analyses. Ancestral body size values were estimated using maximum likelihood, by applying the *contMap()* function from the R package *phytools* v. 2.1–1 (Revell, 2012). Body size (log-transformed with a base of 10) was mapped on both the complete and the reduced supertrees, using the MCCT and also the 100 randomly sampled trees (Supplementary Material).

2.3. Palaeoclimate model reconstructions

Several studies have employed climate reconstructions to analyse the correlation of morphological patterns and environmental aspects within a study group. Prior investigations have examined the impact of climate on body sizes of crocodylomorphs and other reptiles, employing global parameters such as oxygen isotopes (e.g., Godoy et al., 2019; Farina et al., 2023), a proxy for temperature. More recently, climate models have been applied to directly reconstruct the climatic conditions of past environments (Ezcurra, 2010; Saltr e, 2016; Dunne et al., 2023). Using a General Circulation Model (HadCM3L) allows for a comprehensive description of the climatic conditions in which each species thrived (Dunne et al., 2023), instead of relying on global estimates, and incorporates an extensive set of climatic output variables.

We employed an updated version of the HadCM3L climate model (HadCM3BL-M2.1aD; Valdes, 2017), which has a horizontal resolution of 3.75° longitude x 2.5° latitude in the atmosphere and ocean, with 19 atmospheric and 20 oceanic levels using the Arakawa B-grid scheme. We used the MOSES2.1 land surface scheme and an interactive vegetation scheme, TRIFFID, which calculates the relative area of five plant functional types (broadleaf trees, needleleaf trees, shrubs, C3 [temperate] grasses and C4 [tropical] grasses) in each model gridbox, updated every 10 model days. We also refined the ozone scheme due to observed tropopause shifts in warm climates (Valdes et al., 2021), setting fixed ozone values for the troposphere (0.02 ppm), tropopause (0.2 ppm), and stratosphere (5.5 ppm). This modification minimally impacts global mean surface temperature under preindustrial conditions, but affects stratospheric temperature (~ -6 °C) and winds (~ -8 m/s). The model includes further updates, such as modified cloud condensation nuclei density and cloud droplet effective radius, following recent work (Kiehl and Shields, 2013; Sagoo et al., 2013). This modification raises temperatures at high latitudes, without substantially changing tropical temperatures, which reduces the pole-to-Equator temperature gradient in line with proxy observations of past warm climates (e.g., Hollis, 2019).

Model boundary conditions are specific for the Late Cretaceous (Maastrichtian and Campanian) and each geologic stage of the Cenozoic (Danian – Gelasian; 83.6–1.6 Ma), adjusting solar constant (Gough, 1981), proxy-based stage-specific atmospheric CO₂ (Rae et al., 2021), and palaeogeography (Lunt et al., 2016). Each simulation has been run for over 15,000 model years, with the last 6000 years using the new ozone and cloud updates. Each simulation is close to full equilibrium: (i) the globally and volume-integrated annual mean ocean temperature

trend is less than 1 °C per 1000 years; (ii) the global mean surface air temperature trend is less than 0.3 °C per 1000 years; and (iii) the net energy balance at the top of the atmosphere, averaged over a 100-year period at the end of the simulation, is less than 0.25 W m⁻². For input into the phylogenetic analysis, climatological means of temperature and precipitation are produced from the final 100-years of each simulation. The climate model used is identical to that used in Dunne et al. (2023) for the Late Triassic and Early Jurassic, and is archived as simulation set tfgs (experiment name containing a series of geological stage specific simulations) in the Providing Unified Model Access (PUMA) code archive.

Palaeoclimatic variables were assigned to extinct specimens based on their palaeocoordinates (i.e., estimated based on geographic locality stratigraphy of occurrences). For living taxa, average climatic variables were obtained from WorldClim database within 30 arc sec (Fick and Hijmans, 2017), crossing their latitude and longitude of occurrence. We mapped two climatic variables (Mean annual temperature [MAT] and mean annual precipitation [MAP]) on the caimanine tree using ancestral state reconstruction analyses (ancestral climate niche reconstruction), also using maximum likelihood and *phytools* (Revell, 2012). This was carried out on both the complete and the reduced supertrees, using the MCCT and also the 100 randomly sampled trees.

2.4. Statistical analyses

To investigate possible abiotic drivers of Caimaninae body size evolution, we tested for correlation between mean body size values and the following climatic variables: MAT, MAP and seasonal temperature variation (STV) of each variable, which is defined as the average temperature values of the three warmest months (WMMT) minus the average of the three coldest months (CMMT). The data were collected for each taxon and we used linear and phylogenetic regression analyses (i.e., ordinary least squares, OLS, and phylogenetic generalized least squares, PGLS) to investigate the relationship between the variables. The PGLS analyses were performed using both the complete and reduced supertrees, with the MCCT and also the 100 randomly sampled trees.

Finally, we also assessed if different body size categories exhibited significantly different climatic niches. For that, taxa were divided into two different body size categories: species larger or equal than three meters and smaller than three meters. These categories were based on our body size estimates of extinct caimanines, that can be roughly divided into these two groups. Similarly, living caimanines can be roughly divided in the same categories, since adults of “smaller” species (e.g., *Paleosuchus* and *Caiman*) have about 2.5 to 3 m, whereas adults of “larger” species (*Melanosuchus*) have more than that. We used raincloud plots to examine the distribution of the same three climatic variables (MAT, MAP and STV) across these two body size categories, and Mann-Whitney-Wilcoxon tests to verify for statistically significant differences, using the *wilcox.test()* R function.

3. Results

3.1. Caimanine body size evolution

The phylogenetically-informed reconstruction of ancestral body sizes, using either the MCCT or a set of 100 randomly sampled trees, revealed relative variation in body size along the evolutionary history of the group (Figs. 1 and S1), although most (~70 %) of the ancestral values varied between 170 and 300 cm. The estimated ancestral body size of all caimanines was relatively small, independently of including or not the Late Cretaceous taxa of North America (*Brachychampsa* and its closest relatives; node 1; Fig. 1), with values varying between 208 and 249 cm (i.e., mean values of all 100 trees). Apart from *Melanosuchus niger*, the only extant caiman attaining a large size (i.e., more than 4 m in total length), the reconstructions indicate a clear discrepancy between most caimanine lineages and two specific clades containing solely

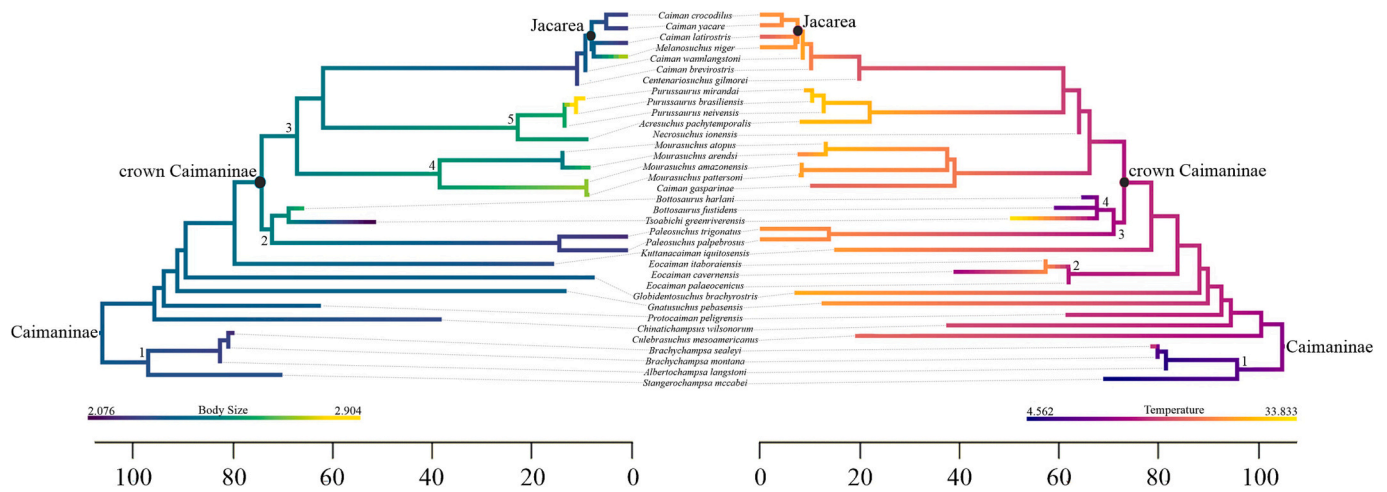


Fig. 1. Left, ancestral body size reconstructions (log-transformed values in cm) of Caimaninae. Right, mean annual temperature (in °C) mapped on the Caimaninae tree. The Maximum Clade Credibility Tree (MCCT) of the complete supertree is used for both representations. Numbers represent unnamed clades mentioned in the text. For the visualization of the ancestral reconstructions using the reduced supertree and the supertrees of 100 randomly generated trees, see Supplementary Material.

Miocene species from South America. Those include the four species of *Mourasuchus* (node 4; Fig. 1), and *Acrosuchus pachytemporalis* and the three *Purussaurus* species (node 5; Fig. 1). These two clades represent the apex of body size within Caimaninae, with no other lineage attaining such large sizes. Nevertheless, the estimated body size of the most recent common ancestor of these two clades (node 3; Fig. 1) is intermediate (~295 cm), similar to that estimated for the crown group node (~275 cm). It is worth mentioning that *Bottosaurus harlani* is the only North American taxon with a relatively large body size (~400 cm; Fig. 1).

3.2. Climate influence on caimanine body size

Geographically and temporally precise climate data allows for

testing possible correlations between body size and climatic variables, such as mean annual temperature (MAT), mean annual precipitation (MAP), and seasonal temperature variation (STV). Our PGLS results from 100 randomly trees show a significant correlation between mean body size and MAP (Table 1) when using the complete tree (i.e., including some putative Cretaceous caimanine from North America). Similarly, there is a significant correlation between mean body size and STV (Table 1), observed also using the simple linear regression model (OLS). The exclusion of the Cretaceous North American taxa from the analysis (i.e., reduced supertree topology), resulted in a significant correlation between size and temperature and seasonal temperature variation (see Table S2). This is particularly interesting because this seemingly important correlation only emerged after removing these taxa

Table 1

Regression results of mean body size values and climate models (mean annual temperature, MAT; mean annual precipitation, MAP; and seasonal temperature variation, STV) of the complete tree. Regression analyses include ordinary least squares (OLS), and phylogenetic generalized least squares (PGLS). PGLS* indicates the phylogenetic regression results of the model using the phylogenetic tree (among 100 trees) that received more support based on AIC scores. Significant p-values in underlined. For the regressions results of the reduced tree, see Table S2.

Excluding <i>Bottosaurus</i>				Including <i>Bottosaurus</i>			
MAT							
	OLS	PGLS	PGLS*		OLS	PGLS	PGLS*
Intercept	2.114	2.270	1.859	Intercept	2.206	2.314	2.452
Slope	0.011	0.004	0.024	Slope	0.008	0	0
p-value	0.07	0.59	<u>0.008</u>	p-value	0.16	0.97	0.33
R² adj.	0.10			R² adj.	0.04		
AIC		13.260	4.556	AIC		15.48	7.16
MAP							
	OLS	PGLS	PGLS*		OLS	PGLS	PGLS*
Intercept	2.386	2.365	2.394	Intercept	2.39	2.3	2.32
Slope	0.002	0.004	-0.026	Slope	0.004	0.003	-0.027
p-value	0.907	0.638	<u>0.008</u>	p-value	0.87	0.67	<u>0.007</u>
R² adj.	-0.04			R² adj.	-0.04		
AIC		13.339	4.498	AIC		15.29	5.38
STV							
	OLS	PGLS	PGLS*		OLS	PGLS	PGLS*
Intercept	2.517	2.333	2.522	Intercept	2.51	2.26	2.28
Slope	-0.009	0.001	-0.008	Slope	-0.008	0.003	0
p-value	<u>0.02</u>	0.69	<u>0.007</u>	p-value	<u>0.04</u>	0.5	0.97
R² adj.	0.17			R² adj.	0.12		
AIC		13.411	4.395	AIC		14.98	8.22

with a relatively low-temperature values, and whose inclusion into the group remains controversial (Brochu, 1999; Godoy et al., 2021; Walter et al., 2021).

Nevertheless, these are not the only taxa that could bias the analysis. Notably, *Bottosaurus harlani*, a large-sized Late Cretaceous taxon from North America, has an uncertain position within Caimaninae. Recent studies placed the species more highly nested in the group (Cossette and Brochu, 2018; Cossette, 2021; Godoy et al., 2021; Stocker et al., 2021; Bona et al., 2024), a position challenged by Walter et al. (2021) and Conedera et al. (2023), suggesting that it is instead an earlier branching

caimanine. This uncertainty underscores the potential impact of *Bottosaurus harlani* on the phylogeny and biogeography of the group. In the context of our analyses, *B. harlani* is a medium-to-large taxon inhabiting a relatively cold environment. Therefore, we explored the hypothesis of this species acting as an outlier and excluded it from the regression analyses. The results indicate consistently significant correlations (p -value < 0.05) between body size and all climatic variables (except for the MAP using the reduced supertree; Tables 1 and S2), Thus highlighting the substantial influence of temperature on the body sizes of caimanines. This finding adds complexity to the previous study of Godoy et al.

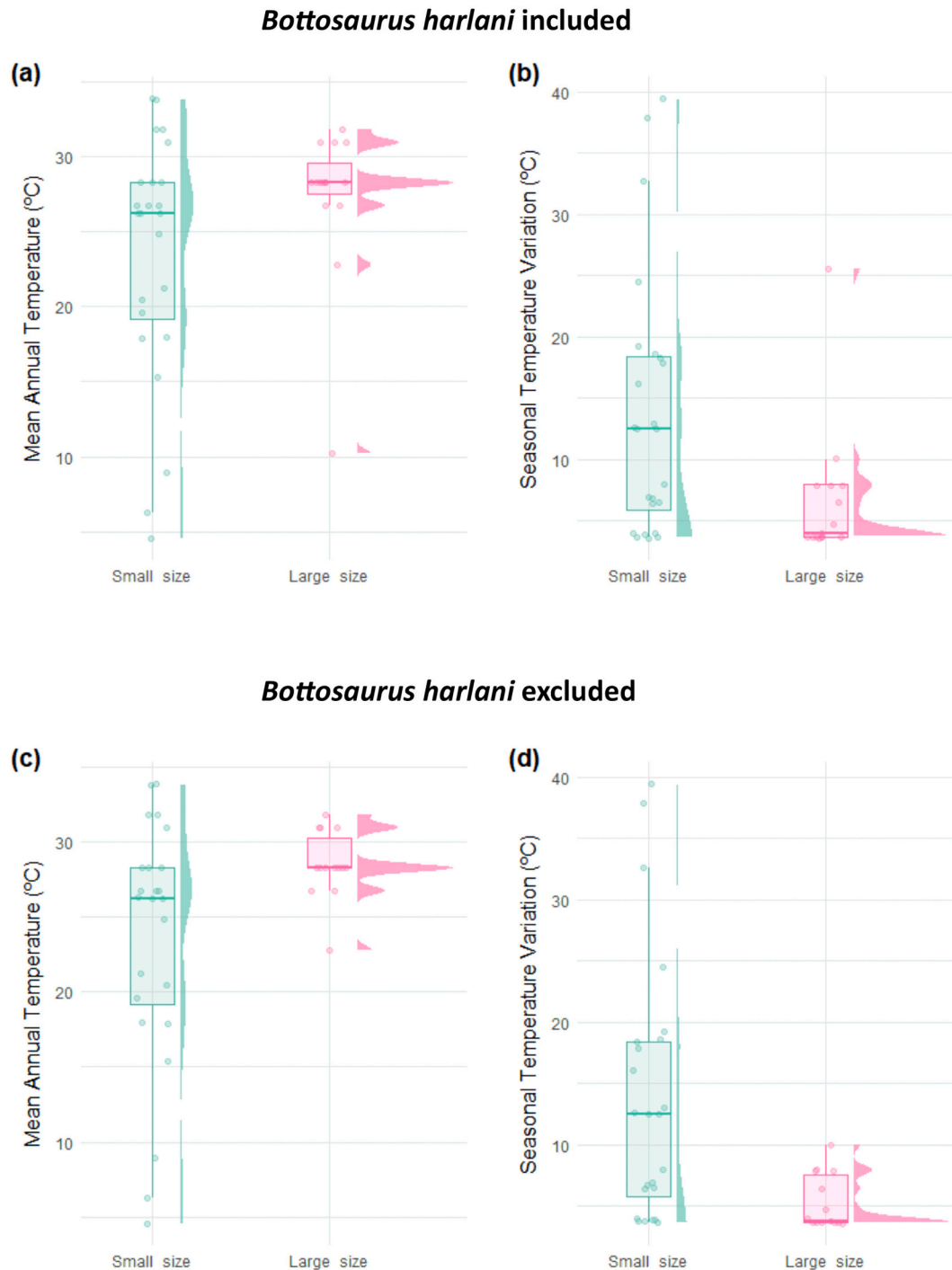


Fig. 2. Raincloud plots with values of mean annual temperature (a and c) and seasonal temperature variation (b and d) in °C across small (green) and large-sized (pink) caimanine species during the late Cretaceous and the Cenozoic, using the complete dataset. For the results of mean annual precipitation, see Fig. S11. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

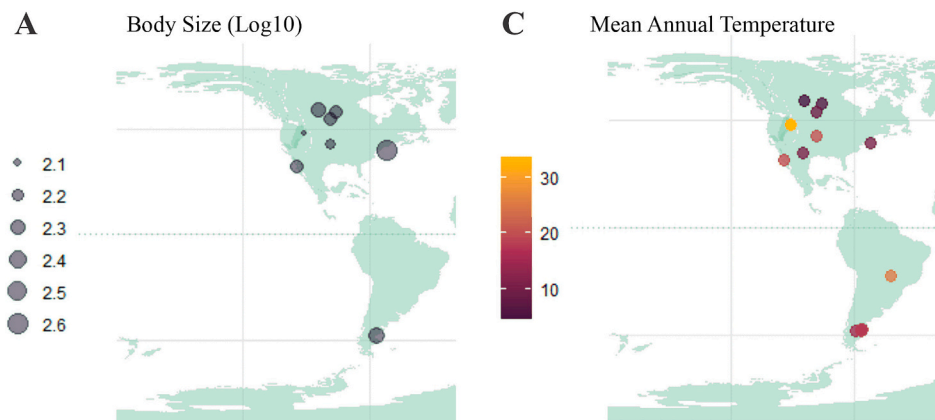
(2019), which found a correlation between global mean temperature and body size across the entire crocodylian clade. Godoy et al. (2019) described a correlation between average body size increase and global cooling in Crocodylia throughout the Cenozoic. Nevertheless, their analysis focused on all crocodylians rather than just on caimanines, suggesting that distinct patterns can be identified at different taxonomic levels. Moreover, they used global oxygen isotope ($\delta^{18}\text{O}$) data as a proxy for climatic conditions. In contrast, our analysis involves estimating climatic variables at more local geographic scales (based on the results from the General Circulation Model, HadCM3L; Saupe et al., 2019; Valdes et al., 2021; Dunne et al., 2023; Fenton et al., 2023), which is likely to be more appropriate for the specific region of each fossil site.

To further explore the relationship between body size and climate, we produced raincloud plots for two separate subsets: one with smaller (< 3 m) and another with larger (> 3 m) taxa. Interesting patterns arose from the plots with MAT and STV (Fig. 2), suggesting that seasonality of temperature, rather than precipitation, emerges as the predominant factor influencing body size in the group. Smaller caimanines are found in environments with both warm and cooler mean annual temperatures (Fig. 2a,c). Interestingly, they are also in regions with both high and low seasonal temperature variation (Fig. 2b,d), although most species are found in environments with relatively high mean temperatures and low seasonal variation. In contrast, larger species are only found in more restricted climatic conditions. While the temperature range for smaller species spanned from 4.5 °C to 33.8 °C, that of larger forms ranged from 10.1 °C to 31.8 °C. Therefore, although both size

categories tend to inhabit warm areas with relatively low seasonal variation, larger caimanines are excluded from other environments in which smaller ones are still found. The only exception to this pattern seems to be, once again, *Bottosaurus harlani*, which is a relatively large taxon living in restricted temperature conditions and high seasonal variation. When *B. harlani* is excluded from the plots (Fig. 2c,d), the differences between these two body size categories become statistically significant (p -value < 0.04; see Supplementary Material and Table S3).

Regarding the climate niche reconstructions, MAP results did not reveal any remarkable findings (see Supplementary Material). Low precipitation values were observed predominantly among extant individuals, whereas medium values were predominant in areas where Miocene species occur. Notably, the North American *Tsoabichi greenriverensis* is recorded in areas with high precipitation values. Nevertheless, interesting patterns emerged when MAT values were mapped on the Caimaninae tree (Fig. 1). Overall, relatively low temperatures were reconstructed for most of the older nodes (i.e., end Cretaceous/early Cenozoic; node 1), varying between 4.5 and 20.4 °C, contrasting with the values observed at the tips of the tree, which aggregate more extreme values, either higher or lower temperatures. For example, *Tsoabichi greenriverensis*, a small-sized caimanine (~119 cm), is associated with elevated temperature levels, unlike its ancestors which thrived in moderate or lower thermal conditions (node 4; Fig. 1). *Bottosaurus* and the common ancestor of the lineage comprising *Bottosaurus* spp. + *Tsoabichi greenriverensis* + *Paleosuchus* spp. were influenced by the exclusion of some early branching North American taxa (see

Late Cretaceous - Eocene



Miocene

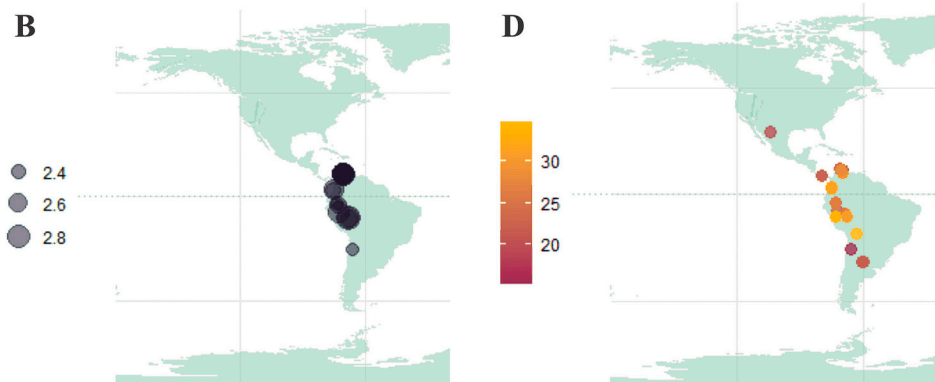


Fig. 3. Body size (log-transformed values in cm) and temperature (in °C) distribution of Caimaninae from the Late Cretaceous to the Eocene (A and C) and during the Miocene (B and D).

Supplementary Material). Typically, these taxa inhabit colder temperatures and their ancestral counterpart as well. However, it is unclear whether these taxa belong to Caimaninae (Bona et al., 2018; Rio and Mannion, 2021; Stocker et al., 2021) or lay outside the group (Brochu, 1999; Godoy et al., 2021; Walter et al., 2021).

From the Eocene onwards, most species were associated with warmer temperatures (higher than 15 °C), consistent with a more restricted latitudinal distribution, closer to the tropics (Fig. 3). This pattern is consistent with the environments inhabited by crocodylians today (Grigg and Kirshner, 2015). In particular, South American Miocene caimanines (e.g., *Purussaurus*, *Mourasuchus*, *Acrasuchus*, *Gnatusuchus*, *Globidentosuchus*, and *Kuttanacaiman*) thrived in elevated temperatures, likely influenced by the conditions of their habitat during that time (Fig. 3). The Miocene epoch is known for its high-temperature levels relative to today, and particular climatic conditions (Hoorn, 2010; Methner et al., 2020; Steinthorsdottir, 2021). The Andean uplift reached its peak in the middle Miocene, giving rise to a substantial water and sediment supply (Hoorn, 1993; Hoorn, 2010), developing a large lake, accompanied by a rich and diverse crocodylian fossil record, with numerous ecomorphotypes (Salas-Gismondi et al., 2015; Cidade et al., 2019). Among the sampled taxa, the Miocene caimanines from the western Amazonian region exhibit the highest temperature values, while also attaining impressively large sizes, such as *Mourasuchus* and *Purussaurus* (although smaller taxa also occur in the region, which indicates an increase in body size disparity). This is particularly interesting when assuming the topology used for our analyses (from Godoy et al., 2021), which displays these two genera in separate clades, suggesting that the evolution of such large sizes could have been achieved via convergence. However, alternative phylogenetic hypotheses do exist, placing these two taxa in the same clade (Bona et al., 2013, 2018; Salas-Gismondi et al., 2015; Cidade et al., 2017, 2018; Scheyer et al., 2019; Stocker et al., 2021; Walter et al., 2021). This suggests that the Miocene environments of the western Amazonian region might have offered the perfect biotic and abiotic conditions for such large crocodylians to succeed. The Pebas and Acre systems are hypothesized to be extremely resourceful wetland and fluvial environments (Hoorn, 2010; Hoorn et al., 2022; Latrubesse et al., 2010; Cidade et al., 2019). Our results reinforce the idea that the rich biodiversity exhibited by these ecosystems, including particularly large crocodylians, was possibly sustained by uniquely matching climate conditions.

4. Discussion

Caimanines with different lifestyles and ecomorphotypes were present in the Miocene western Amazonian region, represented by durophagous forms, semi-aquatic giant predators (*Purussaurus* species), “gulp-feeder” (*Mourasuchus* species), and generalists (Salas-Gismondi et al., 2015; Cidade et al., 2017, 2019). The temperature increases during the Miocene played a key role in the emergence of diverse ecomorphotypes, irrespective of size. According to Grigg and Kirshner (2015), different-sized species in similar environments result in minimal competition, a phenomenon observed in extant crocodylians. Like their extant counterparts, extinct caimanines were probably ectothermic animals, relying on environmental conditions for thermoregulation (Grigg et al., 1998; Seymour et al., 2004). Ectothermy likely conferred an energetic advantage for a semi-aquatic animal (Seymour, 2016; Gearty and Payne, 2020), but this hypothesis warrants further investigation. Nonetheless, we know that thermoregulation is a significant physiological factor influencing crocodylian size (Seymour et al., 2013), with higher temperature particularly affecting the thermoregulation of large crocodylians. Larger extant crocodylians exhibit a relatively smaller surface area, reducing heat loss or gain compared to smaller animals with proportionally larger surface areas (Markwick, 1998; Seebacher et al., 1999; Grigg and Kirshner, 2015). Additionally, as depicted in Fig. 3, the body size apex in the group is constrained by low-temperatures. This aligns with previous findings suggesting that high

biodiversity in crocodylomorphs, including their body size variation, is influenced by low or medium temperatures (Mannion et al., 2015; Godoy et al., 2019). Nevertheless, the relationship between body size and environmental temperature could entail a waste of resources reallocated for growth (Angilletta and Dunham, 2003; Stockdale and Benton, 2021), potentially intensifying competition, influencing niche availability and affecting other activities, guiding to a diversification in body sizes.

Furthermore, the limited climatic range occupied by larger taxa is a consequence of the specific environmental conditions in which they thrived. Indeed, body size is related to many biological aspects, e.g., ecology, physiology, and evolutionary history (Grigg et al., 1998; Godoy et al., 2019; Gearty and Payne, 2020). Numerous studies have emphasized the significance of temperature concerning thermal physiology and body size (Seebacher et al., 1999; Mannion et al., 2015; Godoy et al., 2019). Large caimanines were predominant in the Miocene of South America (Cidade et al., 2019; Paiva et al., 2022), characterized by equatorial climates. That epoch includes two phases, the middle Miocene, marked by warmer temperatures, followed by a global cooling trend in the late Miocene (Zachos et al., 2008; Hoorn, 2010; Methner et al., 2020; Steinthorsdottir, 2021). Recent studies have investigated the influence of tectonics on environmental dynamics, potentially contributing to the increased diversity of North American mammals during the Cretaceous (Weaver et al., 2024) and the Miocene (Smiley et al., 2024). Similarly, the Andean uplift during the Cenozoic arguably played a key role on the diversity of South American crocodylians, particularly during the Miocene with the emergence of the mega-wetland system (Hoorn, 2010; Jaramillo, 2017; Sá et al., 2020). Additionally, the warm climate, in combination with these tectonic events, created a heterogeneous environment that further shaped crocodylian diversity, as seen in other groups (Smiley et al., 2024; Weaver et al., 2024). This dynamic setting was conducive to a high diversity of caimanines and also a wide range of body sizes. The Pebas and Acre phases played a pivotal role in resource availability (Böhme, 2003), fostering environmental conditions that supported the diversification of species into several ecomorphotypes, particularly ectothermic organisms like crocodylians (Böhme, 2003; Riff et al., 2009; Grigg and Kirshner, 2015; Cidade et al., 2019). This conducive environment probably allowed for the coexistence of such a rich diversity of species.

Therefore, the growth and diversification of Caimaninae during the Cenozoic were driven by a combination of environmental factors, including temperature fluctuations and greater resource availability. The disappearance of the mega-wetland systems due to the last Andean uplift phase likely led to a decrease in resources in the region. Combined with an event of global cooling, this resulted in a decline of caimanine diversity and, consequently, in the reduction of body size variation (Hoorn, 2010; Godoy et al., 2019). It is interesting to note that, although the Paleocene–Eocene thermal maximum (PETM) is also characterized by increased temperatures (Pearson et al., 2007; Mannion et al., 2015), the crocodylian fossil record of these epochs is relatively poorly known, hampering comprehensive large-scale studies (Mannion et al., 2015, 2019). Large caimanines were not the only crocodylomorphs living in this favourable Miocene environments. The terrestrial sebecids are represented by *Langstonia huilensis* and *Barinasuchus arveloi* (Langston, 1965; Paolillo and Linares, 2007). Furthermore, representatives of two other crocodylian lineages probably inhabited similar environments: the longirostrine and piscivorous crocodyloids (represented by the genera *Charactosuchus* and *Brasilosuchus*) and gryposuchine gavialoids (Vélez-Juarbe et al., 2007; Salas-Gismondi et al., 2015; Cidade et al., 2019). Other tetrapod groups also coexisted in this vast region, represented by birds (e.g., anhingids; Negri et al., 2009; Guilherme et al., 2023), mammals (e.g., marsupials, rodents, primates, xenarthra, notoungulata, and many others; Cozzuol, 2006; Stutz, 2023), anurans (e.g., *Pipa* sp. and *Rhinella* sp.; Muniz et al., 2021), turtles (e.g., Podocnemididae, Chelidae, and Testudinidae; Aguilera, 2004; Cozzuol, 2006), snakes (Boidae; Hsiou, 2010), and invertebrates (e.g., molluscs and

crustaceans; Gross et al., 2011, 2013; Sousa et al., 2021). By quantitatively demonstrating how such large-sized caimanine species depend on specific climatic conditions, our results provide further evidence that the Miocene western Amazonian region was a biodiversity hotspot, particularly for crocodylians, corroborating previous studies that documented such high diversity.

5. Conclusions

The reconstruction of ancestral body sizes across the evolutionary history of caimanines revealed that the common ancestor of most lineages probably exhibited small sizes. The main exceptions are the lineages including *Mourasuchus* and *Purussaurus*, which reached the apex of body sizes in the Miocene of South America. To explain such large sizes, we tested for correlations between body size values and climatic variables, and found significant correlations between mean annual temperature and mean body size, highlighting the influence of climate on caimanine body size evolution. In particular, our results indicate that larger species favored higher temperatures with less seasonal variation. This increase can be linked to the Miocene Climatic Optimum (Böhme, 2003; Steinhorsdottir, 2021). Environmental changes during the Miocene played a key role in diversity changes among crocodylian species. These changes fostered diverse ecomorphotypes, with gigantism observed in Miocene caimanines likely resulting from combined environmental conditions, supporting size increases during periods of rising temperatures. Therefore, we highlight that considering climatic conditions in evolutionary studies deepens our understanding of the intricate interplay between environmental factors and evolutionary processes, thereby underscoring the history of the studied group.

CRedit authorship contribution statement

Ana Laura S. Paiva: Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Pedro L. Godoy:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization. **Emma M. Dunne:** Writing – review & editing, Investigation. **Alexander Farnsworth:** Writing – review & editing, Investigation. **Paul J. Valdes:** Writing – review & editing, Investigation. **Daniel J. Lunt:** Writing – review & editing, Investigation. **Wilfried Klein:** Writing – review & editing, Supervision. **Max C. Langer:** Writing – review & editing, Supervision. **Annie S. Hsiou:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data is in the online repository.

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Appendix A. Supplementary data

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