



## Body size estimation of Caimaninae specimens from the Miocene of South America

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### ABSTRACT

Living crocodylians are frequently regarded as morphologically and ecologically conservative, contrasting with the group's rich fossil record, which reveals a much higher diversity. In particular, Caimaninae is a striking example of such diversity, with only six extant species but a myriad of extinct taxa, exhibiting remarkable morphological variation. Their skulls vary substantially, with robust and flattened shapes, ranging from short to long snouts, and serve as a basis for many evolutionary studies in the group. Previous works have demonstrated that the skull is a good proxy to estimate the body size of extinct crocodylians. In this study, we estimate the body size of large Caimaninae specimens from the Miocene of South America, including *Purussaurus* and *Mourasuchus*. For that, we elaborated a comprehensive dataset of body size data collected from living crocodylians to generate regression equations. We performed regression analyses both including and excluding juvenile/subadult specimens, to account for the possible influence of ontogeny on the relationship between cranial measurements and body size. Furthermore, we also employed two different approaches (phylogenetic and non-phylogenetic) for estimating the body size of these Miocene caimanines. Our results indicate a significant influence of ontogeny on the body proportions of crocodylians, suggesting that datasets used for estimating the body size of extinct taxa should not include juvenile specimens. Moreover, the phylogenetic approach provided more conservative estimates, possibly as a result of the phylogenetic position of the analyzed taxa, given that the body size metrics are strongly phylogenetically structured in crocodylians. This is the first study to infer the body size of fossil caimanines using different methods and skeletal measurements, as well as a dataset comprised of solely adult crocodylians. In the light of our results, we also discuss the paleobiological implications of the large size of these Miocene caimanines.

### 1. Introduction

As with other crocodylian subgroups, Caimaninae has a currently low species richness, with only six species distributed mostly across South and Central America (Grigg and Kirshner, 2015). Most of the group displays relatively similar morphology and ecology, however the fossil record shows a much richer story, with more than 20 extinct species described. Even though most fossils are from South America, specimens from northern North America reveal a wider geographical range (Brochu, 1999, 2010, 2011; Scheyer et al., 2013; Pinheiro et al., 2013; Hastings et al., 2013, 2016; Salas-Gismondi et al., 2015; Bona et al., 2018; Cossette and Brochu, 2018; Cidade et al., 2019; Godoy et al.,

2021; Walter et al., 2021). The group also exhibited higher morphological disparity, including variable cranial shapes, which is reflected in different ecological roles played by its members (Salas-Gismondi et al., 2015; Wilberg, 2017; Cidade et al., 2019; Godoy, 2019). In particular, Caimaninae shows remarkable body size variation, ranging from the small *Tsoabichi greenriverensis* (less than a meter long; Brochu, 2010) to the giant *Purussaurus brasiliensis* (with an estimated body length of more than 12 m; Aureliano et al., 2015).

The Western Amazonian region, in northern South America, is well-known for its crocodylian-rich faunas during the Miocene (Brochu, 2003; Riff et al., 2010; Hoorn et al., 2010a; Cidade et al., 2019). The Miocene deposits of Colombia (middle Miocene, Honda Group),

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Venezuela (late Miocene, Urumaco Formation), and northern Brazil (late Miocene, Solimões Formation) stand out for the presence of numerous caimanine specimens (Scheyer et al., 2013; Salas-Gismondi et al., 2015; Scheyer and Delfino, 2016; Souza-Filho et al., 2018), many of which inhabited a huge lake denominated as Pebas and Acre Systems. Some of these taxa are also famously known for their large sizes and peculiar morphologies (e.g., *Purussaurus*, *Mourasuchus*, *Acrasuchus*). However, even though previous studies have estimated the body sizes of some South American Miocene caimanines (e.g., Aureliano et al., 2015; Scheyer et al., 2019; Solórzano et al., 2020; Cidade et al., 2020), some relevant specimens still lack reliable body size estimations, which precludes further investigations of the drivers behind the evolution of these large-sized caimanines.

Estimating the body size of extinct crocodylians can be challenging, given the distinct body proportions of different subgroups, especially those phylogenetically distant from living crocodylians (Young et al., 2016; Godoy et al., 2016, 2019). Nevertheless, this issue is attenuated when skeletal measurements from extant crocodylians are used to estimate the body sizes of close extinct relatives, a practice that has been done by many studies, using different measurements to estimate body size (e.g., femoral length, vertebral measures, cranial width, orbito-dorsal cranial length, dorsal cranial length; Sereno et al., 2001; Hurlburt et al., 2003; Farlow et al., 2005; Aureliano et al., 2015; O'Brien et al., 2019; Iijima and Kubo, 2020). Among these, cranial measurements are more frequently used to estimate the body size of crocodylians given that cranial elements are more frequently available for the group (Mannion et al., 2019). Moreover, linear regressions are often used to construct allometric regression equations that translate the relationship between the skeletal measurement and body size (i.e., either total body length, snout-vent length, or body mass). In this context, comprehensive datasets are necessary for constructing such equations, which include measurements of many specimens of living crocodylians.

The body size of living crocodylians is directly related to ecological and physiological aspects of these animals' biology (Grigg et al., 1998; Seebacher et al., 1999; Hurlburt et al., 2003; Seymour et al., 2012, 2013), and estimating the body size of extinct crocodylians can provide us with important clues for inferring their ancient lifestyle and further features of the associated paleoenvironments (Aureliano et al., 2015; O'Brien et al., 2019; Cidade et al., 2020; Solórzano et al., 2020). In the case of Caimaninae, body size is a particularly relevant feature if we consider that some of its taxa are among the largest known crocodylians (Godoy et al., 2019; Scheyer et al., 2019). Additionally, the Miocene faunas of the Western Amazonia, which supported numerous large-size caimanine taxa, offer an interesting opportunity to investigate the possible drivers of the evolution of larger sizes in the group (Hoorn et al., 2010a; Cidade et al., 2019; Scheyer et al., 2019). In this study, we estimate the body sizes (i.e., body mass and total body length) of large-sized caimanine specimens from the Miocene of South America, using multiple approaches and accounting for potential biases caused by ontogeny. For that, we constructed a comprehensive dataset of living crocodylians with cranial and body size measurements, which served as the basis for the methods applied here. Our results allowed us to make comparisons between methods used, as well as to better understand and discuss the paleobiology of these large caimanines.

## 2. Material and method

### 2.1. Institutional abbreviations

Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela (CIAAP); Museu de Ciências da Terra, Rio de Janeiro, Brasil (DGM); Museo de Ciencias Naturales de Caracas, Caracas, Venezuela (MCNC); University of California Museum of Paleontology, Berkeley, USA (UCMP); Universidade Federal do Acre, Acre, Brasil (UFAC).

### 2.2. Fossils sampled and geological settings

We aimed to estimate the body size of some of the largest caimanines from the Miocene of South America (Honda Group, Urumaco Formation, and Solimões Formation; Fig. 1), culminating in a sample of nine specimens (Fig. 2), representing the genera *Purussaurus*, *Mourasuchus*, and *Acrasuchus* (Table 1). We used the software ImageJ to collect two cranial measurements (Fig. 3) from photographs of the fossil specimens: dorsal cranial length (DCL, measured from the tip of the snout to the posterior portion of the skull table) and skull width (or head width, HW, the width between the lateral margins of the quadrates).

The Miocene Western Amazonian region shows fine fluvial-lacustrine sediments, extensive wetlands, and flooding by mega lakes and swamps (Cozzuol, 2006; Hoorn et al., 2010a; Muniz et al., 2021). The Solimões Formation is an extremely rich in fossils and is an upper Miocene unit located in northwestern Brazil, recently dated to  $8.5 \pm 0.5$  Ma and  $10.89 \pm 0.13$  Ma (Bissaro-Júnior et al., 2019). The Urumaco Formation, in Venezuela, is also from the upper Miocene (Díaz de Gamero and Linares, 1989) and exhibits a similarly extraordinary fauna (Cozzuol, 2006; Sanchez-Villagra and Aguilera, 2006). Finally, the slightly older Honda Group is middle Miocene in age (Langston and Gasparini, 1997) and located in southern Colombia.

### 2.3. Dataset of living crocodylians

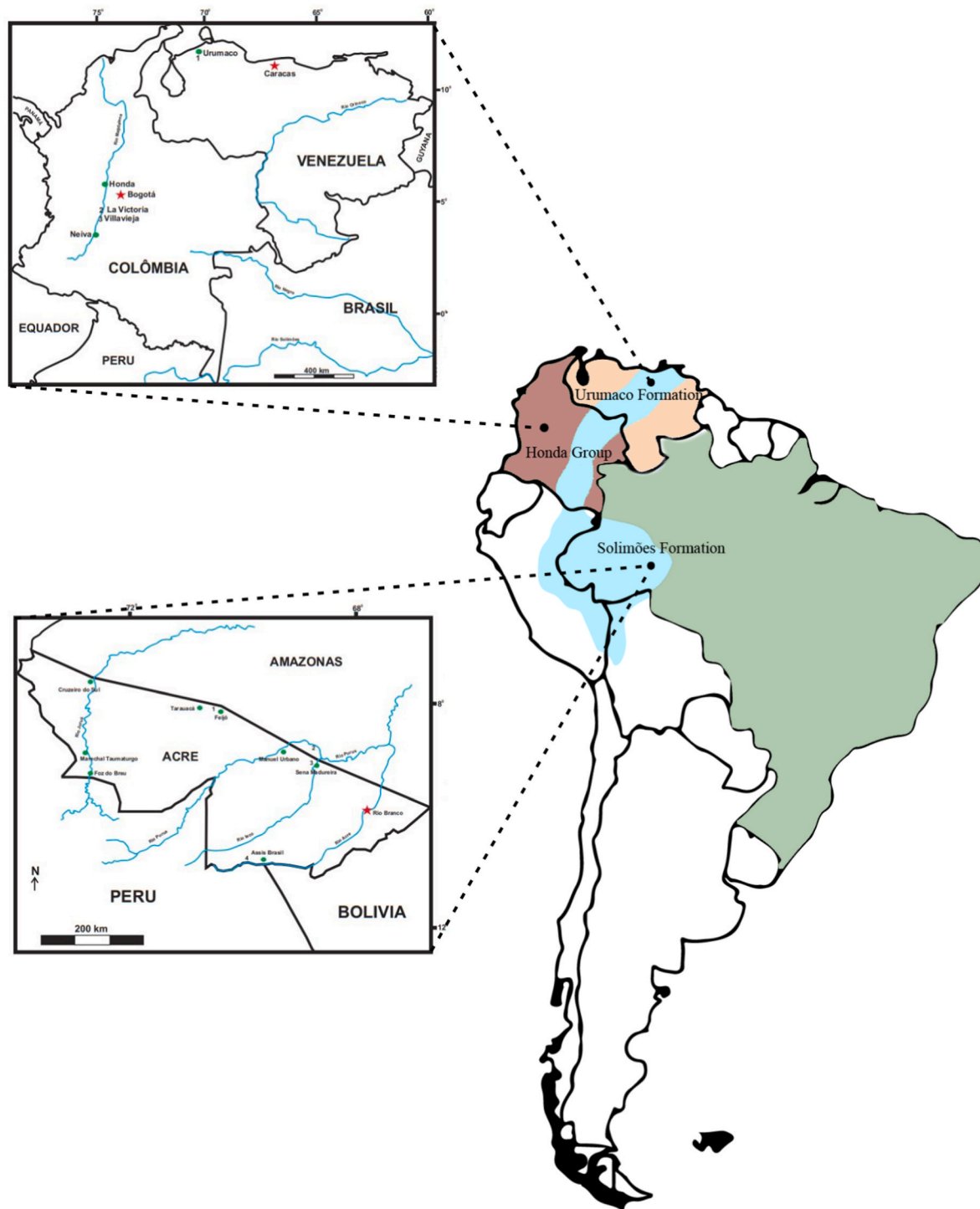
We sought a comprehensive dataset of measurements of living crocodylians to estimate the body size of extinct caimanines, from which we could regress the data to obtain the regression equations. Therefore, we constructed a dataset of 352 living crocodylian specimens, representing 24 species. This dataset includes captive and wild individuals, with males and females, as well as adults and juveniles. The majority of the data was collected from the literature (Woodward et al., 1995; Grigg et al., 1998; Verdade, 2000; Seymour et al., 2012; Godoy et al., 2019; Mannion et al., 2019; O'Brien et al., 2019), but also from living specimens, using a tape measure and a scale. The following measurements were collected: skull width (HW), dorsal cranial length (DCL), total length (TL, measured from the tip of the snout to the tip of the tail), and body mass (BM). The complete dataset is available in the Supplementary Material.

### 2.4. The influence of ontogeny

As our dataset includes juvenile individuals, we accounted for a possible impact of ontogeny on the body proportions of crocodylians by creating two subsets: one with all specimens and another one excluding the juveniles. We used body size as a proxy for sexual maturity, depending on the species for selecting the adult specimens, following the literature (Verdade, 2000; Thorbjarnarson et al., 2001; Antelo, 2008; Da Silva and Lenin, 2010; Bezuijen et al., 2010; Cox, 2010; Fergusson, 2010; Platt et al., 2010; Targarona et al., 2010; Thorbjarnarson, 2010; Van Weerd, 2010; Webb et al., 2010; Gignac and Erickson, 2016; Shirley et al., 2017; Briggs-Gonzalez et al., 2017; Bashyal et al., 2021; Deem et al., 2021). Hatchlings have about 50 g of mass, approximately 30 cm in length, growing about "a foot a year" until reaching sexual maturity (7–15 years, depending on the species and sex; Grigg and Kirshner, 2015). This demonstrates the different body proportions at different ontogenetic stages. The resulting adults-only subset includes 206 specimens. We then accounted for the influence of ontogeny on the body proportions by comparing the regression coefficients of both the complete dataset and the adults-only subset (using t-tests). These regressions were used to investigate the relationships between the cranial measurement, DCL and HW, and the body size indices, TL and BM.

### 2.5. Body size estimation methods

All collected measurements were log-transformed prior to the

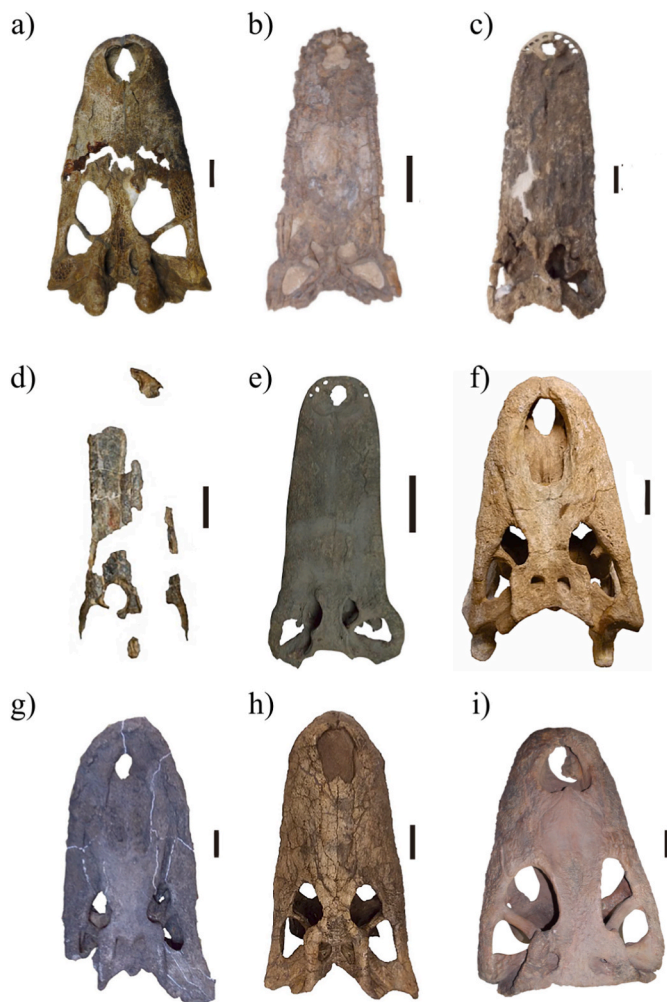


**Fig. 1.** Schematic image highlighting the provenance of the fossil specimens included in this study. Solimões Formation (Brazil), Honda Group (Colombia), and Urumaco Formation (Venezuela). Brazil, Colombia, and Venezuela are represented with green, red, and orange colors, respectively. The blue color represents the Pebas System, which extended through these three geological units. Modified from Hsiu (2010).

regression and body size estimation analyses (Gingerich, 2000). Two different approaches, a non-phylogenetic and a phylogenetic one, were applied to estimate the TL and BM of extinct Caimaninae. The non-phylogenetic method was solely based on linear regressions (ordinary least square; OLS), using the data collected from the living crocodylians included in our dataset, which were log<sub>10</sub>-transformed. We regressed both cranial measurements (DCL and HW) against both body size indices (TL and BM), using both the complete dataset and the adults-only subset. The regression results were used to obtain the

equations which were then applied to estimate TL and BM of the fossil specimens. The regressions were performed in R (version 4.1.3; R Core Team, 2022).

For the phylogenetic approach, we followed the protocol made available by O'Brien et al. (2019), which uses phylogenetically-informed Bayesian analyses to predict body size (TL and BM) from HW. O'Brien et al. (2019) reported high phylogenetic signals of body size metrics in Crocodylia, including HW, TL, and BM, therefore the usage of a phylogenetic approach to account for the

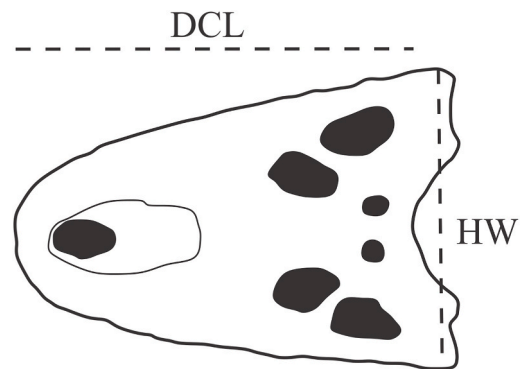


**Fig. 2.** Caimaninae fossil specimens measured in this present study; a) *Acresuchus pachytemporalis* (UFAC 2507, scale bar = 50 mm); b) *Mourasuchus amazonensis* (DGM 526-R, scale bar = 200 mm); c) *M. arendsi* (CIAAP-1297, scale bar = 100 mm); d) *M. atopus* (UCMP 38012, scale bar = 100 mm); e) *M. pattersoni* (MCNC-PAL-110 72 V, scale bar = 200 mm); f) *Purussaurus brasiliensis* (UFAC 1403, scale bar = 200 mm); g) *P. mirandai* (CIAAP-1369, scale bar = 100 mm); h) *P. neivensis* (UCMP 39704, scale bar = 100 mm); i) *Purussaurus* sp. (MCNC-PAL-112 72 V, scale bar = 100 mm). Skull pictures taken from Cidade (2019).

**Table 1**

Fossil caimanine specimens from the Miocene of South America included in our body size estimation analyses. Dorsal-cranial length (DCL) and skull width (HW) measurements in centimeters.

Taxon	Specimen number	Formation	DCL	HW
<i>Acresuchus pachytemporalis</i>	UFAC 2507	Solimões	53.2	34.0
<i>Mourasuchus amazonensis</i>	DGM 526-R	Solimões	113.5	59.0
<i>Mourasuchus arendsi</i>	CIAAP-1297	Urumaco	108.5	45.2
<i>Mourasuchus atopus</i>	UCMP 38012	Honda Group	71.2	27.0
<i>Mourasuchus pattersoni</i>	MCNC-PAL-110 72 V	Urumaco	108.1	52.9
<i>Purussaurus brasiliensis</i>	UFAC 1403	Solimões	140.6	98.0
<i>Purussaurus mirandai</i>	CIAAP-1369	Urumaco	122.8	78.6
<i>Purussaurus neivensis</i>	UCMP 39704	Honda Group	91.0	50.1
<i>Purussaurus</i> sp.	MCNC-PAL-112-72 V	Urumaco	88.8	65.7



**Fig. 3.** Dorsal cranial length (DCL) and skull width (HW) measurements, indicated by dashed lines. Drawing based on a *Purussaurus brasiliensis* specimen (UFAC 1403).

non-independence of allometric data in the group is justified. Phylogenetic generalized least squares (PGLS) regressions were used to analyze the relationship between HW and body size (TL and BM) in a phylogenetic context. Also, taking HW as the dependent variable, we used the BayesModelS method (Nunn and Zhu, 2014) to estimate TL and BM, together with confidence and prediction intervals. This method assumes a Brownian motion model of evolutionary change and uses Monte-Carlo Markov-Chain (MCMC) to estimate an unknown variable of a specimen in a given phylogenetic framework and from a dataset of measured variables (Garland and Ives, 2000; Nunn and Zhu, 2014; O'Brien et al., 2019).

We replaced the dataset used by O'Brien et al. (2019) with our own dataset of living specimens, which were transformed into natural logarithms. O'Brien et al. (2019) also estimated the BM of fossils using a 25% mass reduction, considering that their dataset contains only captive animals (given that the mass of captive crocodylians is, on average, 25% lower; Erickson et al., 2003, 2004). However, as our dataset contains both captive and wild crocodylian specimens and preliminary analyses did not demonstrate a significant difference when a 25% mass reduction was applied to the dataset, we decided not to reduce the mass of captive animals in our dataset. As the phylogenetic framework, we updated the extant crocodylian tree used by O'Brien et al. (2019), which in turn is a modified version of the molecular phylogeny (i.e., with sequences of nuclear genes and portions of mitochondrial genes) constructed by Erickson et al. (2012). Based on the phylogenetic hypothesis of Godoy et al. (2021), we manually included *Caiman yacare* to the tree using Mesquite (version 3.70; Maddison and Maddison, 2021), as well as the nine extinct caimanine taxa sampled in our study (Table 1). The final tree topology includes 31 crocodylian taxa (Fig. 4). As done by O'Brien et al. (2019), we added near-zero (0.0001) branch lengths to the added extinct species. The BayesModelS predictions use phylogenetic signals (both Pagel's  $\lambda$  and Blomberg's  $K$ ; Pagel, 1999; Blomberg et al., 2003), which were calculated prior to the analyses. We implemented a MCMC run for 2,000,000 generations, with the first 500,000 generations discarded as burn-in and a thin of 1000 to estimate the TL and BM of fossil caimanines. BayesModelS and PGLS analyses were implemented in R, using an adapted version of the scripts made available by O'Brien et al. (2019), which includes functions from R packages *car* (Fox and Weisberg, 2019), *MASS* (Venables and Ripley, 2002), *caper* (Orme et al., 2018), *evomap* (Smaers and Mongle, 2014), and *rms* (Harrell, 2017). The R codes used in our analyses are available as Supplementary Material.

### 3. Results

#### 3.1. The influence of ontogeny on crocodylian body proportions

We statistically assessed the influence of ontogeny on the relationship between the cranial measurements (DCL and HW) and body size (TL

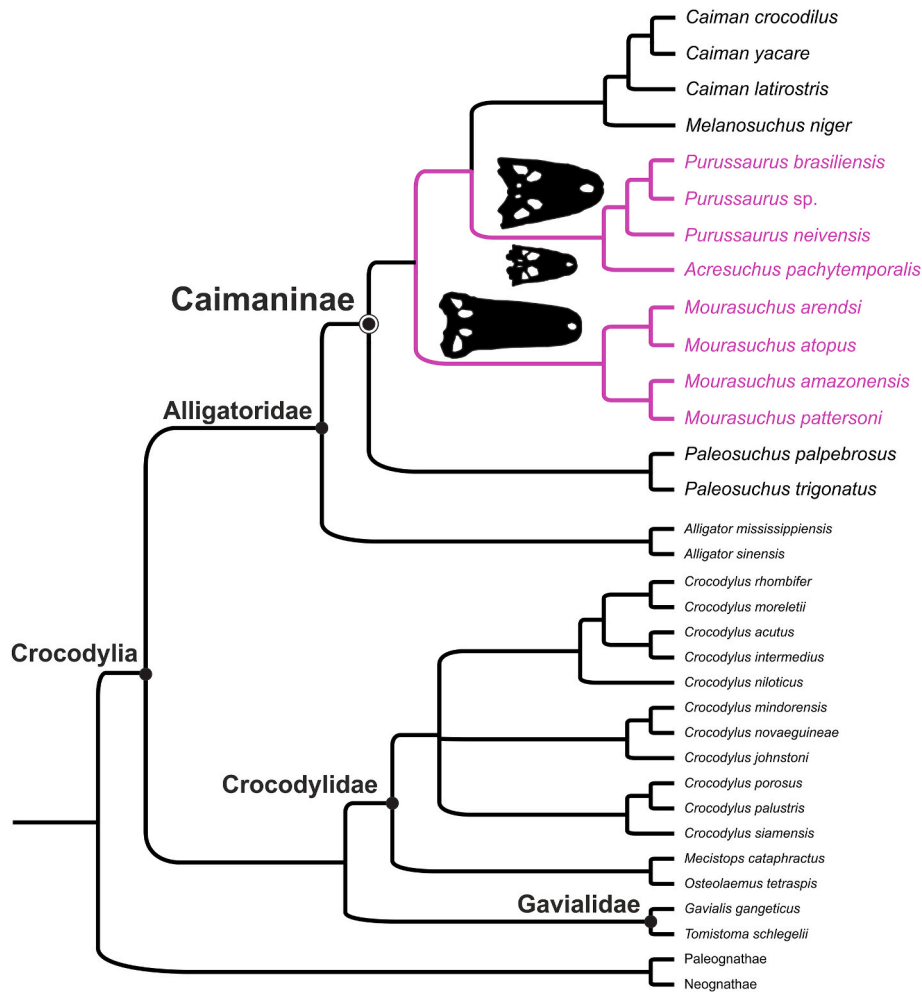


Fig. 4. Crocodylian tree topology used for the phylogenetic body size estimation, modified from O'Brien et al. (2019). The tree includes branch lengths, following O'Brien et al. (2019), but these are not represented in this figure.

and BM) of living crocodylians by comparing the regression coefficients when using the complete dataset or the adults-only subset. Overall, OLS results showed strong relationships between the two cranial measurements (HW and DCL) and both TL and BM, in agreement with previous works (e.g., Sereno et al., 2001; Hurlburt et al., 2003; O'Brien et al., 2019). Also, the results with the complete dataset show that the body size indices are slightly more strongly correlated with HW than with DCL.

Although apparently similar results are found independently of the dataset used, slightly weaker correlations are found when the adults-only subset is used. Indeed, the t-tests reveal significant differences in the regression results when comparing the two datasets, with the only exception of the relationship between HW and TL (Fig. 5, Table 2). These results indicate a significant influence of ontogeny on the relationships between cranial measurements and body size indices. Therefore, we used solely the adults-only subset for both non-phylogenetic and phylogenetic body size estimation approaches.

### 3.2. Non-phylogenetic body size estimation

The OLS results using the adults-only subset allowed us to create equations that describe the relationship between the cranial measurements (HW and DCL) and TL, as well as an equation describing the relationship between TL and BM. The equations can be found below:

$$(1) \log_{10}(\text{TL}) = \log_{10}(\text{DCL}) * 0.875 + 1.209$$

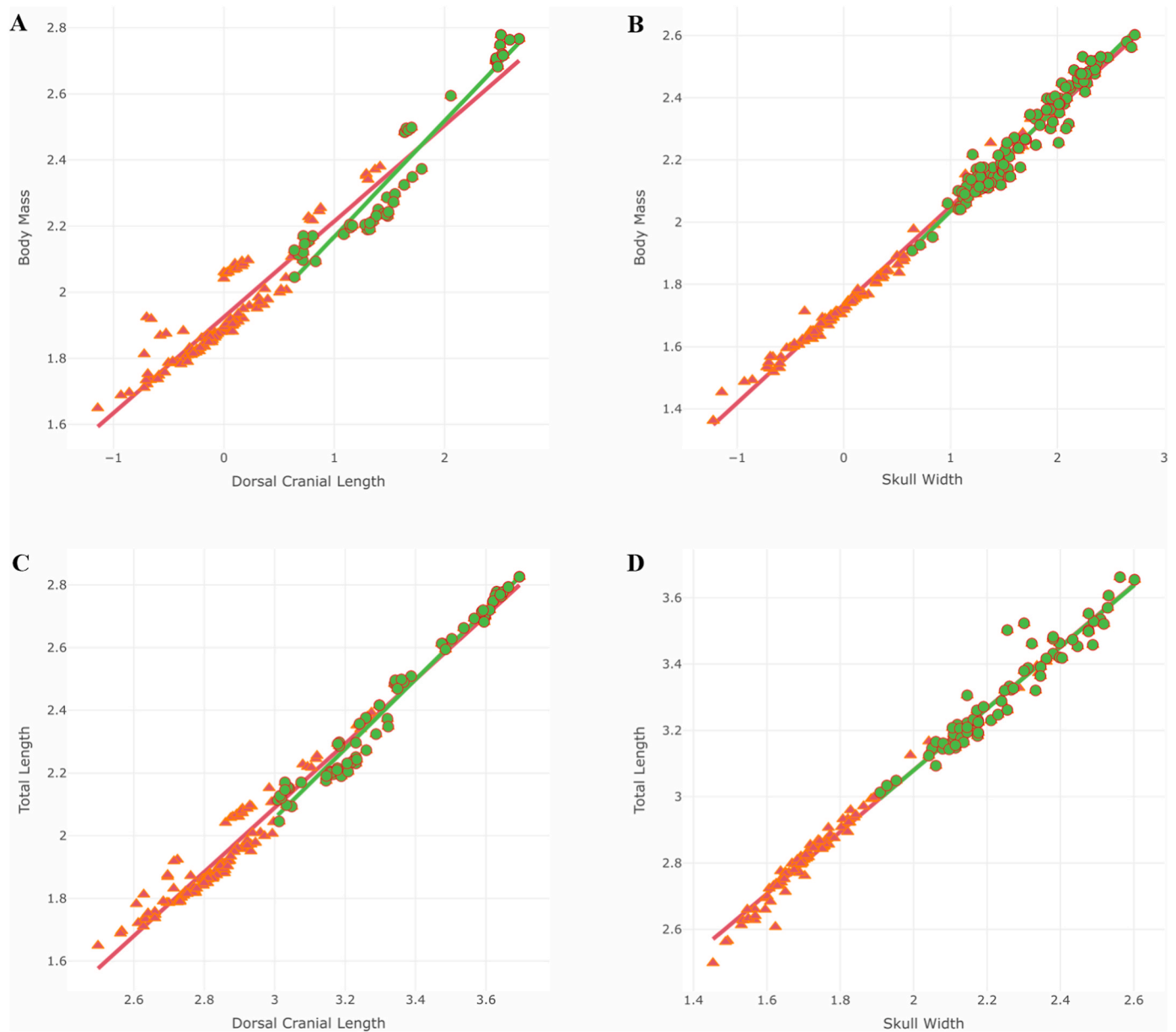
$$(2) \log_{10}(\text{TL}) = \log_{10}(\text{HW}) * 0.929 + 1.220$$

$$(3) \log_{10}(\text{BM}) = \log_{10}(\text{TL}) * 3.003 + (-8.318)$$

These equations were then used to estimate TL and BM for the nine fossil caimanine specimens (Table 3). Overall, TL and BM estimated from DCL show higher values than those estimated from HW. The only exceptions are *Purussaurus brasiliensis* and *Purussaurus* sp., which show higher values when body size is estimated from DCL. According to these estimates, *Acrosuchus* reached up to 3.95 m and weighted up to 306.4 kg (using DCL). As for *Mourasuchus* and *Purussaurus*, if we consider their largest species (*M. amazonensis* and *P. brasiliensis*), these genera reached up to 7.67 and 10.01 m, and weighted up to 2.25 and 3.95 metric tons, respectively.

### 3.3. Phylogenetic body size estimation

In agreement with O'Brien et al. (2019), PGLS regression results demonstrated that, for our dataset of living crocodylians, HW has a strong correlation with the body size indices ( $R^2 \geq 0.87$ ; Fig. 6 and Table 4). It is worth mentioning, however, that these correlations are slightly weaker in comparison to the OLS regression results. Consequently, the phylogenetic body size estimation using BayesModelS (Table 5) shows overall lower values than those estimated with the non-phylogenetic approach. For example, the largest *Mourasuchus* (*M. amazonensis*) was estimated to be 5.27 m long (mean value) and weighting 934.3 kg (mean value). In comparison to the values estimated



**Fig. 5.** Ordinary least squares regressions (OLS) between dorsal cranial length and body size indices (body mass and the total length, A and C, respectively), and skull width against the body size indices (B and D), using both the complete dataset and the adults-only subset. Orange triangles and line represent the complete dataset (juveniles + adults), while the green circles and line represent only the adult living crocodylian specimens.

from HW using the non-phylogenetic approach, this represents a reduction of about 15% in TL and 22% in BM. For *Purussaurus brasiliensis*, a similar pattern is found, with the phylogenetic approach estimating mean values of 7.99 m and 3.5 tons (reductions of about 13% and 10% in TL and BM, respectively). According to the phylogenetic estimates, *Acerosuchus* was estimated to 3.4 m and 225.6 kg (mean values), a reduction of about 9% and 13% in comparison to the non-phylogenetic approach.

#### 4. Discussion

##### 4.1. The issue of the juveniles and the usage of the DCL as a proxy for total body size

Living crocodylians are usually regarded as juvenile throughout their first/second years after hatching, and the allometric changes during ontogeny vary across species and availability of resources (Lang, 1987;

Grigg and Kirshner, 2015). Various factors can be related to the differences in body proportions from juvenile to adult in each crocodylian species, including habitat use, food supply, and temperature (Lang, 1987). These allometric changes throughout ontogeny are reflected in our regression results (Fig. 5, Table 2), which show significantly different relationships between the cranial measurements and the body size indices when the adults-only subset is used (except for the relationship between HW and TL). This demonstrates the importance of taking the ontogeny of specimens into account when constructing the datasets used as sources for estimating the body size of extinct crocodylians.

In this context, the inclusion of juveniles in the dataset of previous studies might be problematic. For example, Aureliano et al. (2015) estimated the total body length of *Purussaurus brasiliensis* using a small dataset composed of 29 *Caiman latirostris* specimens (dataset originally from Verdade, 2000), which includes juveniles. The authors used the same *Purussaurus* specimen analyzed in our study (UFAC-1403) to

**Table 2**

Ordinary least squares (OLS) regression results between cranial measurements (DCL and HW) and body size indices (TL and BM), using both the complete dataset and the adults-only subset. The t-tests were used to assess significant differences between regression slopes of each dataset, to account for the influence of ontogeny on body proportions. DCL – dorsal-cranial length; BM – body mass; HW – skull width; TL – total length. \*Significant at alpha = 0.05.

	HW vs TL	DCL vs TL	HW vs BM	DCL vs BM
<b>Complete dataset</b>				
Intercept	1.215	1.010	-5.419	-6.163
Slope (p-value)	0.932 (<2.2e-16*)	0.952 (<2.2e-16*)	3.130 (<2.2e-16*)	3.218 (<2.2e-16*)
R <sup>2</sup>	0.984	0.974	0.988	0.933
<b>Adults-only</b>				
Intercept	1.220	1.209	-4.669	-4.621
Slope (p-value)	0.929 (<2.2e-16*)	0.875 (<2.2e-16*)	2.804 (<2.2e-16*)	2.613 (<2.2e-16*)
R <sup>2</sup>	0.924	0.969	0.943	0.915
t-test (p-values)	0.7337475	7.03E-10*	8.22E-33*	2.28E-15*

**Table 3**

Body size estimates of the extinct caimanines based on ordinary least squares (OLS) regressions of living crocodylians. Total length (TL) was estimated from two cranial measurements (dorsal-cranial length, DCL; skull width, HW) and body mass (BM) was estimated from TL (which were in turn estimated from the two cranial measurements). TL in centimeters and BM in kilograms.

Taxon	TL from DCL	BM from DCL	TL from HW	BM from HW
<i>A. pachytemporalis</i>	395.3	306.4	374.4	260.3
<i>M. amazonensis</i>	767.7	2250.3	624.8	1212.5
<i>M. arendsi</i>	738.0	1998.7	487.8	576.3
<i>M. atopus</i>	510.2	659.8	302.2	136.7
<i>M. pattersoni</i>	735.6	1979.4	564.6	894.1
<i>P. brasiliensis</i>	926.0	3952.7	1001.3	4999
<i>P. mirandai</i>	822.5	2768.4	815.7	2700.5
<i>P. neivensis</i>	632.6	1258.3	536.7	768.2
<i>Purussaurus</i> sp.	619.2	1179.8	690.5	1637.2

estimate a mean TL of about 12.5 m for this taxon (using DCL to estimate TL). This value is significantly higher than our estimate (9.26 m) using DCL in the non-phylogenetic approach. Consequently, the body mass estimated for this specimen by Aureliano et al. (2015) was also substantially higher than ours (about 8.5 tons compared to nearly 4 tons).

Similarly, Cidade et al. (2020) also used the same dataset with juveniles (from Verdade, 2000) to estimate the TL of different *Mourasuchus* specimens, some of which are also included in our analyses. The differences are also substantial, with *M. amazonensis* (specimen DGM 526-R) estimated to 9.9 m by Cidade et al. (2020) and to 7.67 m by our non-phylogenetic approach using DCL. These conflicting results are likely at least partially due to the inclusion of juveniles and/or subadults in the living crocodylian datasets used for generating the regression equations. Therefore, we advocate for using only adult specimens in these datasets when estimating the body size of extinct crocodylians.

Another important aspect revealed by our results is the comparison between DCL and HW as proxies for body size in crocodylians. Our regression results showed that the body size indices (TL and BM) are more strongly correlated with HW than with DCL (Fig. 5, Table 2). Additionally, we found no significant difference in the relationship between HW and TL when juveniles are considered, contrasting with what was found for DCL. This might be a consequence of the plasticity of the rostral region in crocodylians, considering that DCL is a measurement that includes the rostrum. Multiple lineages convergently displaying elongated rostra (Wilberg, 2017; Godoy, 2019) and the effect of

**Table 4**

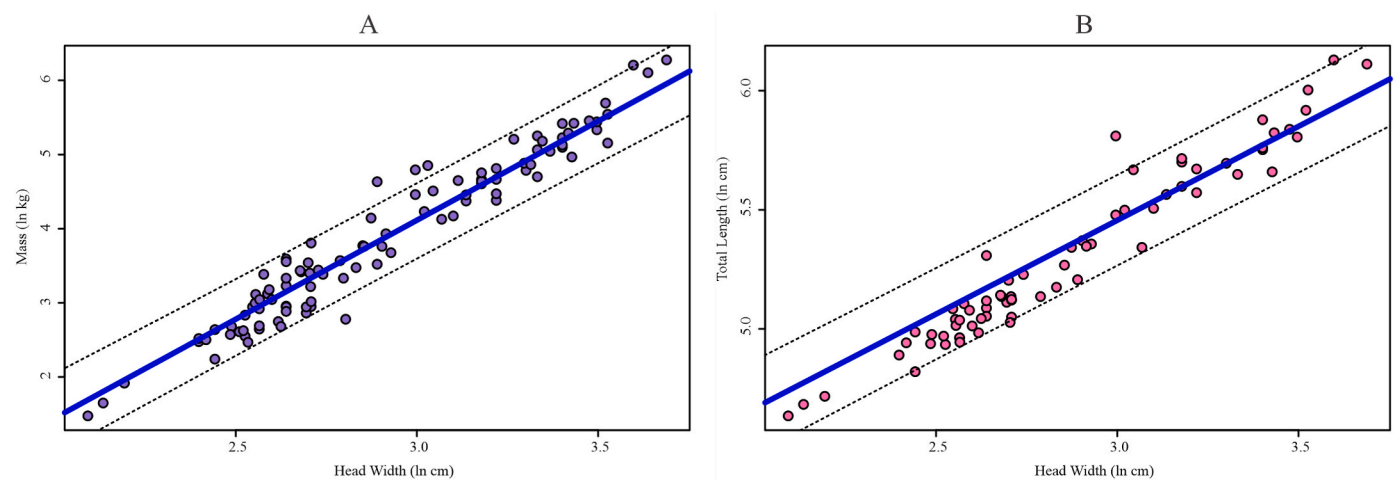
Phylogenetic generalized least squares (PGLS) regression result. BM: body mass; HW: skull width; TL: total length. \*Significant at alpha = 0.05.

	HW vs. TL	HW vs. BM
Slope (p-value)	0.7877 (<2.2e-16*)	2.6690 (<2.2e-16*)
Intercept	3.0929	-3.8928
R <sup>2</sup>	0.921	0.872

**Table 5**

Body size estimates of extinct caimanines using a phylogenetic approach. 97.5% confidence intervals are shown between parentheses. Total length (TL) in centimeters and body mass (BM) in kilograms.

Taxon	TL	BM
<i>A. pachytemporalis</i>	340.1 (304.7–378.6)	225.6 (148.0–343.8)
<i>M. amazonensis</i>	527.3 (465.4–598.6)	934.3 (585.9–1509.9)
<i>M. arendsi</i>	424.9 (376.0–479.4)	466.6 (293.7–723.6)
<i>M. atopus</i>	280.4 (251.2–313.5)	121.9 (105.9–183.2)
<i>M. pattersoni</i>	483.9 (428.7–548.9)	702.2 (441.9–1140.6)
<i>P. brasiliensis</i>	799.7 (761.6–927.5)	3520.4 (2079.8–6294.3)
<i>P. mirandai</i>	669.8 (638.8–765.6)	1977.9 (1194.1–3235.0)
<i>P. neivensis</i>	465.2 (446.8–522.5)	621.7 (387.5–996.5)
<i>Purussaurus</i> sp.	579.0 (552.4–659.0)	1285.7 (836.6–2721.0)



**Fig. 6.** Phylogenetic generalized least squares (PGLS) regressions between skull/head width against body mass (A) and total length (B), represented by the solid blue lines. The dashed lines represent the 97.5% of confidence interval. Skull width and total length are in centimeters (cm) and mass in kilograms (kg), but all into natural log-transformed.

longirostry is a known issue in the group, affecting phylogenetic analyses (e.g., Pol and Gasparini, 2009) and also body size estimations (Erickson et al., 2012; Aureliano et al., 2015; Godoy et al., 2019; Godoy and Turner, 2020). Accordingly, although DCL has been used by various studies to estimate the body size of extinct crocodylians (perhaps for being a more commonly available measurement), other measurements have been proposed as alternatives (e.g., femoral length, vertebral measurements and other cranial measurements; Hurlburt et al., 2003; Farlow et al., 2005; Iijima and Kubo, 2020). Among these, O'Brien et al. (2019) successfully demonstrated a strong correlation between skull width (HW) and body size in crocodylians, which is consistently conserved across the group. Here, we provide further support for the usage of HW for estimating the body size of extinct crocodylians, with results suggesting that it is comparatively more robust than DCL in maintaining a proportional allometry with total length along the ontogeny.

#### 4.2. Phylogenetic and non-phylogenetic approaches

Using estimates obtained solely from HW as a reference, the non-phylogenetic approach provided consistently higher body size values (TL or BM) than the mean values estimated with the phylogenetic method. Indeed, the body sizes estimated with the non-phylogenetic approach are much closer to the upper quartile of the confidence interval calculated with the phylogenetic method (Tables 3 and 5). This pattern of lower body size values estimated by the phylogenetic method is consistent with what was reported by O'Brien et al. (2019), which also found relatively more conservative estimates of specimens previously analyzed by other studies (e.g., Sereno et al., 2001), and might be a consequence of a relatively weaker correlation between HW and body size than that found by linear regressions (e.g., OLS).

The strong phylogenetic signal reported by O'Brien et al. (2019) indicates that body size metrics are strongly phylogenetically structured in crocodylians. Consequently, the phylogenetic positions of taxa analyzed have an influence on the estimated values (O'Brien et al., 2019). Except *Melanosuchus niger*, extant caimanines are not among the largest-sized crocodylians, which might result in a rather small size estimated for their common ancestor. However, some of these taxa (in particular *Mourasuchus* and *Purussaurus*) are giant "outliers" among other caimanines, and possibly reached such large sizes as a result of faster body size evolutionary rates in that part of the tree. Given that our phylogenetic approach uses a dataset constructed solely with living taxa, this method cannot account for these potential faster rates in parts of the tree with taxa not sampled in the dataset. Given that all taxa analyzed in our study are included in relatively similar phylogenetic positions near the base of Caimaninae, perhaps the influence of a small-to medium-sized putative Caimaninae ancestor resulted in more conservative body size estimations for these specimens.

Accordingly, we might conclude that both phylogenetic and non-phylogenetic methods are potentially problematic in the case of giant Miocene caimanines. In contrast with the phylogenetic method, the non-phylogenetic approach returned possible overestimates, given that the linear regressions disregard the phylogenetic structure of the data, as well as the variation in body proportions across different taxa. Perhaps a middle ground between estimates from both approaches would be closer to the real body sizes of these Miocene caimanines.

#### 4.3. Paleobiological implications

Body size is strongly associated with many aspects of the biology of crocodylians, including ecology (e.g., specialization of diet, habitat) and physiology (Grigg et al., 1998; Seebacher et al., 1999; Seymour et al., 2012; Godoy et al., 2019; Godoy and Turner, 2020; Gearty and Payne, 2020). It is not different for extinct crocodylians, such as the Miocene Caimaninae from South America, the focus of this study. Among these is *Purussaurus brasiliensis*, which was one of the largest known

crocodyliforms and could feed on large terrestrial prey (Aureliano et al., 2015; Cidade et al., 2019). *Mourasuchus* was relatively smaller, but with a proportionally much longer skull, which is hypothesized to be associated with a "gulp-feeding" habit (Cidade et al., 2017). *Arcosuchus* was a generalist predator (Souza-Filho et al., 2018), with a *bauplan* more similar to that of living caimanines.

In the middle Miocene, the Pebas System formed a cluster of lakes, rivers, and swamps with a degree of marine influence, which extended from the Acre region, part of the Brazilian Amazon, Peru, Venezuela, Colombia, and Bolivia (Wesselingh and Salo, 2006; Hoorn et al., 2010a, b; Alvim et al., 2021). This mega-wetland system originated about 23 Ma (Hoorn et al., 2010a; Wesselingh et al., 2006) as a result of the Andean uplift, making all hydrodynamics flow from the mountains to the central portion of northwestern South America, promoting the diversification of invertebrate and vertebrate faunas (Wesselingh and Salo, 2006), and high availability of resources (Hoorn et al., 2010a, b). This uplift created a barrier in the atmospheric circulation that consequently resulted in drastic climate changes (Hoorn et al., 2010a). The middle Miocene was known as the Miocene Climatic Optimum, due to its significantly increasing temperatures (Buchardt, 1978; Böhme, 2003; Kaandorp et al., 2005; Super et al., 2018; Methner et al., 2020; Steinhorsdottir et al., 2021). In contrast, the lake in the early late Miocene, approximately 10 Ma, went from a lacustrine to a fluvial system, known as Acre System (Hoorn et al., 2010a; Latrubesse et al., 2010), in which the vertebrate fauna, especially the crocodylians, reached its peak in body size. These simultaneous factors allowed the evolution and diversification of these peculiar crocodylians who shared this ecosystem.

In living crocodylians, diet varies according to the size of the individual (Brochu, 2001; Aureliano et al., 2015; Grigg and Kirshner, 2015), with cranial shape also influencing dietary specialization (Gignac et al., 2019). Caimaninae has a high cranial disparity, which is reflected in a variable diet across and within species. Taxa with broader skulls maximize the amount of food ingested (Piras et al., 2014), whereas those with short rostra usually feed on terrestrial mammals and reptiles, and those with long snouts, have a more piscivorous or invertebrate diet (Webb et al., 1978; Cidade et al., 2019). Regarding body size, we can hypothesize that larger taxa were relatively slower, suggesting less active predatory strategies. The decrease in swimming performance in *Crocodylus porosus* specimens was observed as the body length increase, which influences on prey capture (Elsworth et al., 2003). Additionally, large body sizes hinder the locomotion in a terrestrial environment (Blanckenhorn, 2000), which is consistent with the semiaquatic lifestyle proposed for these large caimanines of the Pebas and Acre Systems. The time spent in water could also be associated with thermoregulation (i.e., to avoid overheating), given that large organisms dissipate heat at much lower rates due to their relatively surface/volume ratio (Grigg et al., 1998; Markwick, 1998; Seebacher et al., 1999, 2003).

## 5. Conclusions

We constructed a large dataset with body size data from living crocodylian specimens for estimating the total length (TL) and body masses (BM) of extinct caimanines from the Miocene of South America. In doing so, we also investigated the influence of ontogeny on the relationship between cranial measurements and body size indices. We found that these relationships change during ontogeny, with dorsal cranial length (DCL) being relatively more susceptible to variation than skull width (HW). Therefore, we strongly advocate against the inclusion of juvenile and/or subadult specimens in datasets used for estimating the body sizes of extinct crocodylians.

Using a subset with only adult specimens, we estimated the body sizes of nine extinct caimanine specimens from the Miocene of South America, using a phylogenetic and a non-phylogenetic approach. Overall, the phylogenetic approach provided more conservative estimates, possibly a result of the phylogenetic placement of the specimens within Caimaninae, a group of comparatively small-to medium-sized



extant species. As our phylogenetic method cannot account for potential increased body size evolutionary rates in parts of the tree, we hypothesize that a possible small-sized Caimaninae ancestor had a significant influence on estimating lower body size values for the extinct specimens. On the other hand, the non-phylogenetic approach cannot account for the non-independency of the data (and the variation of body proportions in different crocodylian taxa), possibly extrapolating the estimates. We therefore conclude a middle ground between the values estimated by both methods might be closer to the real body sizes of these specimens.

### CRediT authorship contribution statement

**Ana Laura S. Paiva:** Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Pedro L. Godoy:** Writing – review & editing, Supervision, Investigation. **Ray B.B. Souza:** Writing – review & editing, Investigation. **Wilfried Klein:** 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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### Supplementary Material

All data and code used in the analyses can be found in a dedicated Zenodo repository (<https://zenodo.org/record/6788500#.Yr9IEbnMLr>), <https://doi.org/10.5281/zenodo.6788500>.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2022.103970>.

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