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Ana Laura S. Paiva, Pedro L. Godoy, Ray B.B. Souza, Wilfried Klein, Annie S. Hsiou



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# 1 **Body size estimation of Caimaninae specimens from the Miocene of South** 2 **America**

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4 Ana Laura S. Paiva<sup>1</sup>, Pedro L. Godoy<sup>1,2</sup>, Ray B. B. Souza<sup>1</sup>, Wilfried Klein<sup>1</sup>, Annie S. Hsiou<sup>1</sup>

5  
6 <sup>1</sup>Department of Biology, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil

7 <sup>2</sup>Department of Anatomical Sciences, Stony Brook University, New York, United States

## 8 9 **Abstract**

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

32  
33 **Keywords:** Crocodylians; body dimensions; regression analyses; paleobiology; Pebas System.

34

35

36 **1. Introduction**

37 As with other crocodylian subgroups, Caimaninae has a currently low species richness, with  
38 only six species distributed mostly across South and Central America (Grigg & Kirshner, 2015).  
39 Most of the group displays relatively similar morphology and ecology, however the fossil  
40 record shows a much richer story, with more than 20 extinct species described. Even though  
41 most fossils are from South America, specimens from northern North America reveal a wider  
42 geographical range (Brochu 1999, 2010, 2011; Scheyer et al., 2013; Pinheiro et al., 2013;  
43 Hastings et al., 2013; 2016; Salas-Gismondi et al., 2015; Bona et al., 2018; Cossette & Brochu,  
44 2018; Cidade et al., 2019; Godoy et al., 2021; Walter et al., 2021). The group also exhibited  
45 higher morphological disparity, including variable cranial shapes, which is reflected in different  
46 ecological roles played by its members (Salas-Gismondi et al., 2015; Wilberg, 2017; Cidade et  
47 al., 2019; Godoy, 2019). In particular, Caimaninae shows remarkable body size variation,  
48 ranging from the small *Tsoabichi greenriverensis* (less than a meter long; Brochu, 2010) to the  
49 giant *Purussaurus brasiliensis* (with an estimated body length of more than 12 m; Aureliano et  
50 al., 2015).

51 The Western Amazonian region, in northern South America, is well-known for its  
52 crocodylian-rich faunas during the Miocene (Brochu, 2003; Riff et al., 2010; Hoorn et al.,  
53 2010a; Cidade et al., 2019). The Miocene deposits of Colombia (middle Miocene, Honda  
54 Group), Venezuela (late Miocene, Urumaco Formation), and northern Brazil (late Miocene,  
55 Solimões Formation) stand out for the presence of numerous caimanine specimens (Scheyer et  
56 al., 2013; Salas-Gismondi et al., 2015; Scheyer & Delfino, 2016; Souza-Filho et al., 2018),  
57 many of which inhabited a huge lake denominated as Pebas and Acre Systems. Some of these  
58 taxa are also famously known for their large sizes and peculiar morphologies (e.g.,  
59 *Purussaurus*, *Mourasuchus*, *Acreosuchus*). However, even though previous studies have  
60 estimated the body sizes of some South American Miocene caimanines (e.g., Aureliano et al.,  
61 2015; Scheyer et al., 2019; Solórzano et al., 2019; Cidade et al., 2020), some relevant specimens  
62 still lack reliable body size estimations, which precludes further investigations of the drivers  
63 behind the evolution of these large-sized caimanines.

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

79 The body size of living crocodylians is directly related to ecological and physiological  
80 aspects of these animals' biology (Grigg et al., 1998; Seebacher et al., 1999; Hurlburt et al.,  
81 2003; Seymour et al., 2012; 2013), and estimating the body size of extinct crocodylians can  
82 provide us with important clues for inferring their ancient lifestyle and further features of the  
83 associated paleoenvironments (Aureliano et al., 2015; O'Brien et al., 2019; Cidade et al., 2020;  
84 Solórzano et al., 2020). In the case of Caimaninae, body size is a particularly relevant feature  
85 if we consider that some of its taxa are among the largest known crocodyliforms (Godoy et al.,  
86 2019; Scheyer et al., 2019). Additionally, the Miocene faunas of the Western Amazonia, which  
87 supported numerous large-size caimanine taxa, offer an interesting opportunity to investigate  
88 the possible drivers of the evolution of larger sizes in the group (Hoorn et al., 2010a; Cidade et  
89 al., 2019; Scheyer et al., 2019). In this study, we estimate the body sizes (i.e., body mass and  
90 total body length) of large-sized caimanine specimens from the Miocene of South America,  
91 using multiple approaches and accounting for potential biases caused by ontogeny. For that, we  
92 constructed a comprehensive dataset of living crocodylians with cranial and body size  
93 measurements, which served as the basis for the methods applied here. Our results allowed us

94 to make comparisons between methods used, as well as to better understand and discuss the  
 95 paleobiology of these large caimanines.

96

## 97 **2. Material and Method**

### 98 *2.1 Institutional abbreviations*

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

103

### 104 *2.2 Fossils sampled and geological settings*

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

112

113 **Table 1.** Fossil caimanine specimens from the Miocene of South America included in our body  
 114 size estimation analyses. Dorsal-cranial length (DCL) and skull width (HW) measurements in  
 115 centimeters.

<b>Taxon</b>	<b>Specimen number</b>	<b>Formation</b>	<b>DCL</b>	<b>HW</b>
<i>Acrasuchus 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

116

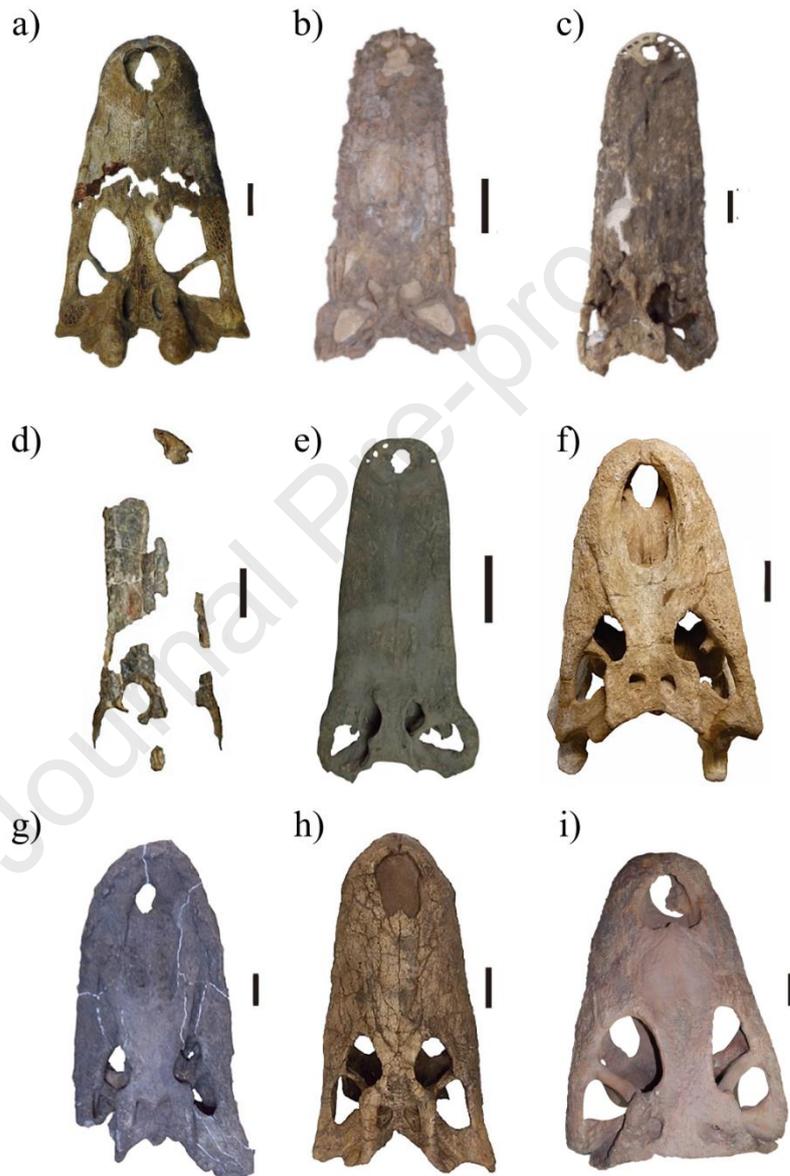
117 The Miocene Western Amazonian region shows fine fluvial-lacustrine sediments,  
 118 extensive wetlands, and flooding by mega lakes and swamps (Cozzuol, 2006; Hoorn et al.,  
 119 2010a; Muniz et al., 2021). The Solimões Formation is an extremely rich in fossils and is an  
 120 upper Miocene unit located in northwestern Brazil, recently dated to  $8.5 \pm 0.5$  Ma and  $10.89 \pm$   
 121  $0.13$  Ma (Bissaro-Júnior et al., 2019). The Urumaco Formation, in Venezuela, is also from the  
 122 upper Miocene (Díaz de Gamero & Linares, 1989) and exhibits a similarly extraordinary fauna  
 123 (Cozzuol, 2006; Sanchez-Villagra & Aguilera, 2006). Finally, the slightly older Honda Group  
 124 is middle Miocene in age (Langston & Gasparini, 1997) and located in southern Colombia.



125

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

131



132

133 **Figure 2.** Caimaninae fossil specimens measured in this present study; a) *Acresuchus*  
 134 *pachytemporalis* (UFAC 2507, scale bar = 50 mm); b) *Mourasuchus amazoensis* (DGM 526-  
 135 R, scale bar = 200 mm); c) *M. arendsi* (CIAAP-1297, scale bar = 100 mm); d) *M. atopus*  
 136 (UCMP 38012, scale bar = 100 mm); e) *M. pattersoni* (MCNC-PAL-110 72 V, scale bar = 200  
 137 mm); f) *Purussaurus brasiliensis* (UFAC 1403, scale bar = 200 mm); g) *P. mirandai* (CIAAP-

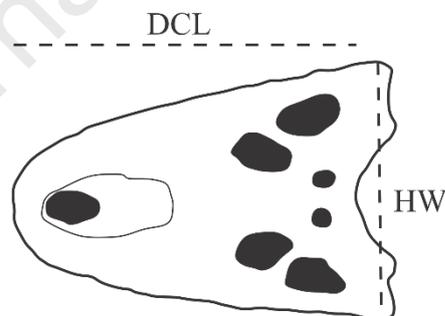
138 1369, scale bar = 100 mm); h) *P. neivensis* (UCMP 39704, scale bar = 100 mm); i) *Purussaurus*  
 139 sp. (MCNC-PAL-112 72 V, scale bar = 100 mm). Skull pictures taken from Cidade (2019).

140

### 141 2.3 Dataset of living crocodylians

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

153



154

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

157

### 158 2.4 The influence of ontogeny

159 As our dataset includes juvenile individuals, we accounted for a possible impact of  
 160 ontogeny on the body proportions of crocodylians by creating two subsets: one with all  
 161 specimens and another one excluding the juveniles. We used body size as a proxy for sexual  
 162 maturity, depending on the species for selecting the adult specimens, following the literature  
 163 (Verdade, 2000; Thorbjarnarson et al., 2001; Antelo, 2008; Da Silva & Lenin, 2010; Bazuijen

164 et al., 2010; Cox, 2010; Fergusson, 2010; Platt et al., 2010; Targarona et al., 2010;  
165 Thorbjarnarson, 2010; Van Weerd, 2010; Webb et al., 2010; Gignac & Erickson, 2015; Shirley  
166 et al., 2016; Briggs-Gonzales et al., 2017; Bashyal et al., 2021; Deem et al., 2021). Hatchlings  
167 have about 50 grams of mass, approximately 30 cm in length, growing about “a foot a year”  
168 until reaching sexual maturity (7 to 15 years, depending on the species and sex; Grigg &  
169 Kirshner, 2015). This demonstrates the different body proportions at different ontogenetic  
170 stages. The resulting adults-only subset includes 206 specimens. We then accounted for the  
171 influence of ontogeny on the body proportions by comparing the regression coefficients of both  
172 the complete dataset and the adults-only subset (using t-tests). These regressions were used to  
173 investigate the relationships between the cranial measurement, DCL and HW, and the body size  
174 indices, TL and BM.

175

### 176 *2.5 Body size estimation methods*

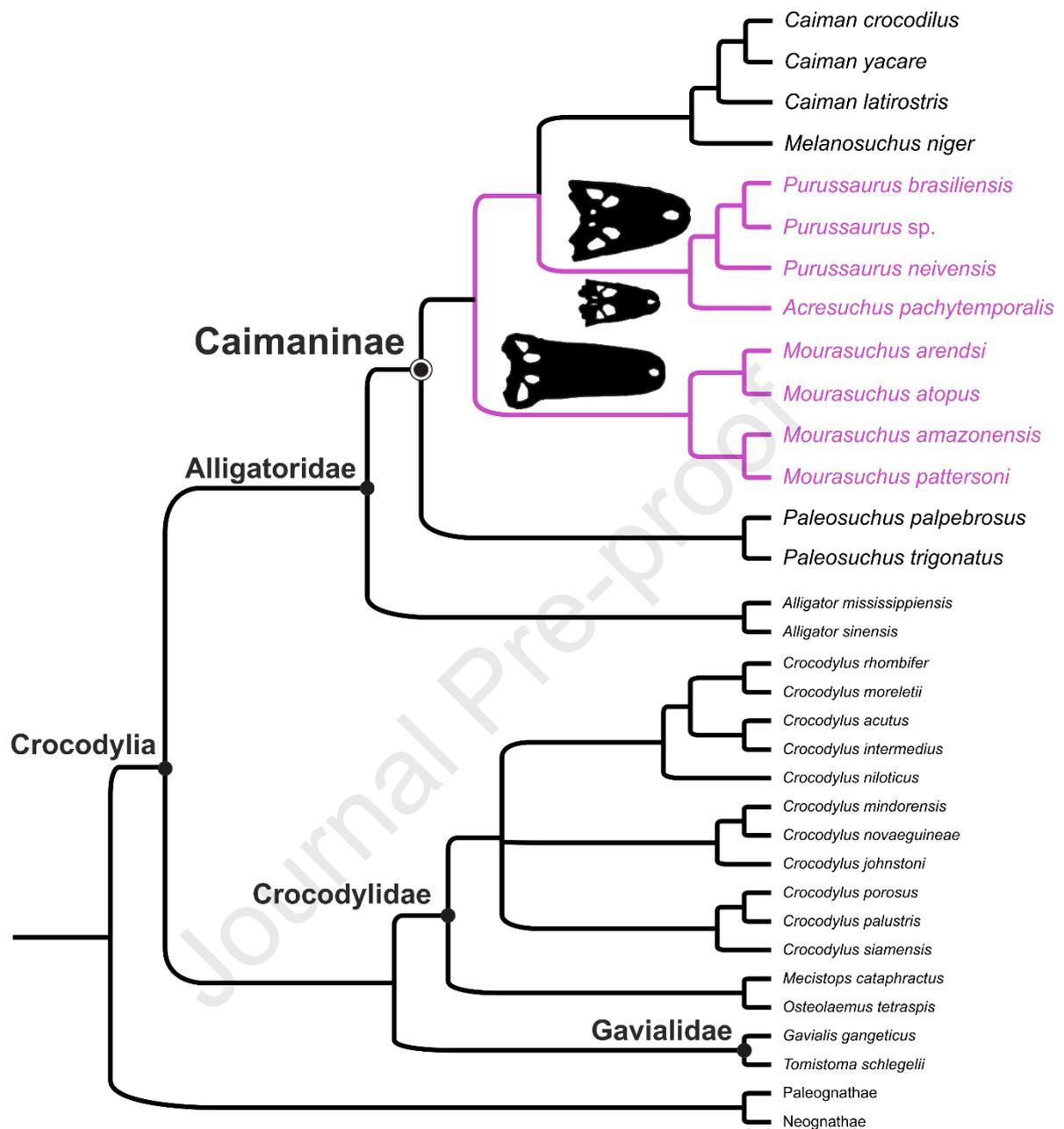
177 All collected measurements were log-transformed prior to the regression and body size  
178 estimation analyses (Gingerich, 2000). Two different approaches, a non-phylogenetic and a  
179 phylogenetic one, were applied to estimate the TL and BM of extinct Caimaninae. The non-  
180 phylogenetic method was solely based on linear regressions (ordinary least square; OLS), using  
181 the data collected from the living crocodylians included in our dataset, which were log<sub>10</sub>-  
182 transformed. We regressed both cranial measurements (DCL and HW) against both body size  
183 indices (TL and BM), using both the complete dataset and the adults-only subset. The regression  
184 results were used to obtain the equations which were then applied to estimate TL and BM of  
185 the fossil specimens. The regressions were performed in R (version 4.1.3; R Core Team, 2022).

186 For the phylogenetic approach, we followed the protocol made available by O’Brien et  
187 al. (2019), which uses phylogenetically-informed Bayesian analyses to predict body size (TL  
188 and BM) from HW. O’Brien et al. (2019) reported high phylogenetic signals of body size  
189 metrics in Crocodylia, including HW, TL, and BM, therefore the usage of a phylogenetic  
190 approach to account for the non-independence of allometric data in the group is justified.  
191 Phylogenetic generalized least squares (PGLS) regressions were used to analyze the  
192 relationship between HW and body size (TL and BM) in a phylogenetic context. Also, taking  
193 HW as the dependent variable, we used the BayesModelS method (Nunn & Zhu, 2014) to

194 estimate TL and BM, together with confidence and prediction intervals. This method assumes  
195 a Brownian motion model of evolutionary change and uses Monte-Carlo Markov-Chain  
196 (MCMC) to estimate an unknown variable of a specimen in a given phylogenetic framework  
197 and from a dataset of measured variables (Garland & Ives 2000; Nunn & Zhu, 2014; O'Brien  
198 et al., 2019).

199 We replaced the dataset used by O'Brien et al. (2019) with our own dataset of living  
200 specimens, which were transformed into natural logarithms. O'Brien et al. (2019) also  
201 estimated the BM of fossils using a 25% mass reduction, considering that their dataset contains  
202 only captive animals (given that the mass of captive crocodylians is, on average, 25% lower;  
203 Erickson et al., 2003; 2004). However, as our dataset contains both captive and wild crocodylian  
204 specimens and preliminary analyses did not demonstrate a significant difference when a 25%  
205 mass reduction was applied to the dataset, we decided not to reduce the mass of captive animals  
206 in our dataset. As the phylogenetic framework, we updated the extant crocodylian tree used by  
207 O'Brien et al. (2019), which in turn is a modified version of the molecular phylogeny (i.e., with  
208 sequences of nuclear genes and portions of mitochondrial genes) constructed by Erickson et al.  
209 (2012). Based on the phylogenetic hypothesis of Godoy et al. (2020), we manually included  
210 *Caiman yacare* to the tree using Mesquite (version 3.70; Maddison & Maddison, 2021), as well  
211 as the nine extinct caimanine taxa sampled in our study (Table 1). The final tree topology  
212 includes 31 crocodylian taxa (Figure 4). As done by O'Brien et al. (2019), we added near-zero  
213 (0.0001) branch lengths to the added extinct species. The BayesModelS predictions use  
214 phylogenetic signals (both Pagel's  $\lambda$  and Blomberg's  $K$ ; Pagel, 1999; Blomberg et al., 2003),  
215 which were calculated prior to the analyses. We implemented a MCMC run for 2,000,000  
216 generations, with the first 500,000 generations discarded as burn-in and a thin of 1,000 to  
217 estimate the TL and BM of fossil caimanines. BayesModelS and PGLS analyses were  
218 implemented in R, using an adapted version of the scripts made available by O'Brien et al.  
219 (2019), which includes functions from R packages *car* (Fox & Weisberg, 2019), MASS  
220 (Venables & Ripley, 2002), *caper* (Orme et al., 2018), *evomap* (Smaers & Mongle, 2014), and  
221 *rms* (Harrell, 2021). The R codes used in our analyses are available as Supplementary Material.

222



223

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

227

### 228 3. Results

#### 229 3.1 The influence of ontogeny on crocodylian body proportions

230 We statistically assessed the influence of ontogeny on the relationship between the  
 231 cranial measurements (DCL and HW) and body size (TL and BM) of living crocodylians by

232 comparing the regression coefficients when using the complete dataset or the adults-only  
 233 subset. Overall, OLS results showed strong relationships between the two cranial measurements  
 234 (HW and DCL) and both TL and BM, in agreement with previous works (e.g., Sereno et al.  
 235 2001; Hurlburt et al 2003; O'Brien et al. 2019). Also, the results with the complete dataset show  
 236 that the body size indices are slightly more strongly correlated with HW than with DCL.

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

244

245 **Table 2.** Ordinary least squares (OLS) regression results between cranial measurements (DCL  
 246 and HW) and body size indices (TL and BM), using both the complete dataset and the adults-  
 247 only subset. The t-tests were used to assess significant differences between regression slopes of  
 248 each dataset, to account for the influence of ontogeny on body proportions. DCL – dorsal-  
 249 cranial length; BM – body mass; HW – skull width; TL – total length. \*Significant at  $\alpha =$   
 250 0.05.

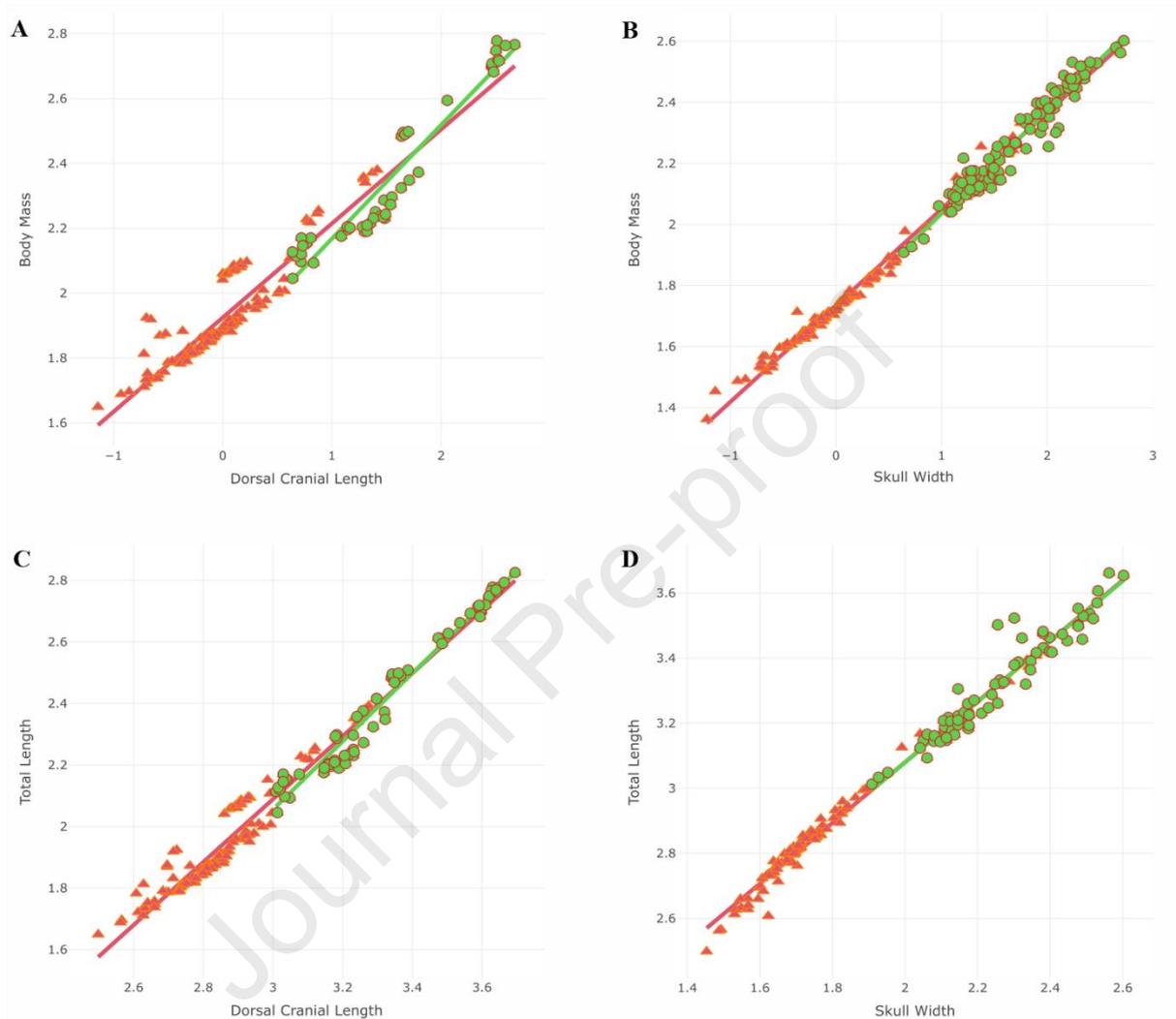
	HW vs TL	DCL vs TL	HW vs BM	DCL vs BM
<b>Complete dataset</b>				
Intercept	1.215	1.010	-5.419	-6.163
Slope (p-value)	0.932 (<2.2e-16*)	0.952 (<2.2e-16*)	3.130 (<2.2e-16*)	3.218 (<2.2e-16*)
R <sup>2</sup>	0.984	0.974	0.988	0.933
<b>Adults-only</b>				
Intercept	1.220	1.209	-4.669	-4.621
Slope (p-value)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

251

252

253

254



255

256 **Figure 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 head width against the body  
 257 size indices (B and D), using both the complete dataset and the adults-only subset. Orange  
 258 triangles and line represent the complete dataset (juveniles + adults), while the green circles  
 259 and line represent only the adult living crocodylian specimens.  
 260

261

### 262 3.2 Non-phylogenetic body size estimation

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

266

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

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

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

270

271 These equations were then used to estimate TL and BM for the nine fossil caimanine  
 272 specimens (Table 3). Overall, TL and BM estimated from DCL show higher values than those  
 273 estimated from HW. The only exceptions are *Purussaurus brasiliensis* and *Purussaurus* sp.,  
 274 which show higher values when body size is estimated from DCL. According to these estimates,  
 275 *Acrasuchus* reached up to 3.95 m and weighted up to 306.4 kg (using DCL). As for  
 276 *Mourasuchus* and *Purussaurus*, if we consider their largest species (*M. amazonensis* and *P.*  
 277 *brasiliensis*), these genera reached up to 7.67 and 10.01 meters, and weighted up to 2.25 and  
 278 3.95 metric tons, respectively.

279

280 **Table 3.** Body size estimates of the extinct caimanines based on ordinary least squares (OLS)  
 281 regressions of living crocodylians. Total length (TL) was estimated from two cranial  
 282 measurements (dorsal-cranial length, DCL; skull width, HW) and body mass (BM) was  
 283 estimated from TL (which were in turn estimated from the two cranial measurements). TL in  
 284 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	2,250.3	624.8	1,212.5
<i>M. arendsi</i>	738.0	1,998.7	487.8	576.3
<i>M. atopus</i>	510.2	659.8	302.2	136.7
<i>M. pattersoni</i>	735.6	1,979.4	564.6	894.1
<i>P. brasiliensis</i>	926.0	3,952.7	1,001.3	4,999
<i>P. mirandai</i>	822.5	2,768.4	815.7	2,700.5
<i>P. neivensis</i>	632.6	1,258.3	536.7	768.2
<i>Purussaurus</i> sp.	619.2	1,179.8	690.5	1,637.2

285

### 286 3.3 Phylogenetic body size estimation

287 In agreement with O'Brien et al. (2019), PGLS regression results demonstrated that, for  
 288 our dataset of living crocodylians, HW has a strong correlation with the body size indices ( $R^2$

289  $\geq 0.87$ ; Figure 6 and Table 4). It is worth mentioning, however, that these correlations are  
 290 slightly weaker in comparison to the OLS regression results. Consequently, the phylogenetic  
 291 body size estimation using BayesModelS (Table 5) shows overall lower values than those  
 292 estimated with the non-phylogenetic approach. For example, the largest *Mourasuchus* (*M.*  
 293 *amazonensis*) was estimated to be 5.27 m long (mean value) and weighting 934.3 kg (mean  
 294 value). In comparison to the values estimated from HW using the non-phylogenetic approach,  
 295 this represents a reduction of about 15% in TL and 22% in BM. For *Purussaurus brasiliensis*,  
 296 a similar pattern is found, with the phylogenetic approach estimating mean values of 7.99 m  
 297 and 3.5 tons (reductions of about 13% and 10% in TL and BM, respectively). According to the  
 298 phylogenetic estimates, *Acrasuchus* was estimated to 3.4 m and 225.6 kg (mean values), a  
 299 reduction of about 9% and 13% in comparison to the non-phylogenetic approach.

300

301 **Table 4.** Phylogenetic generalized least squares (PGLS) regression result. BM: body mass;  
 302 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

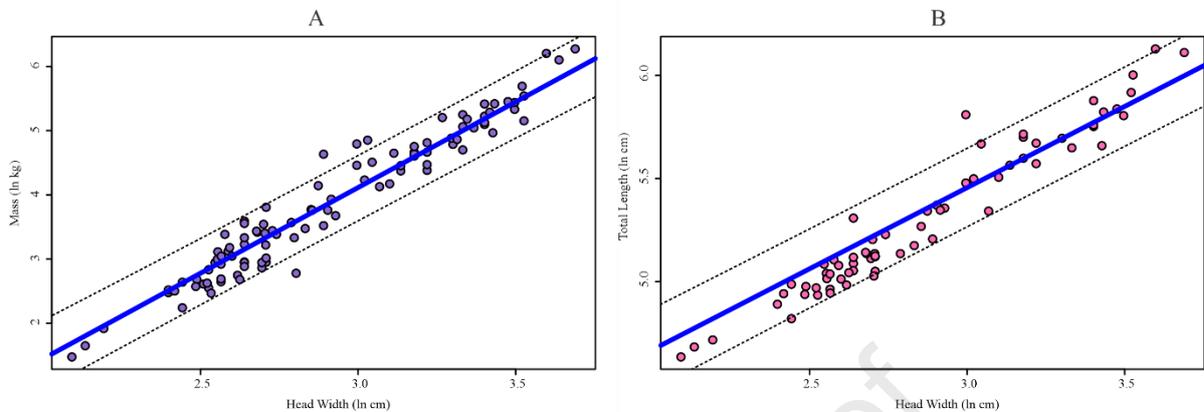
303

304 **Table 5.** Body size estimates of extinct caimanines using a phylogenetic approach. 97.5%  
 305 confidence intervals are shown between parentheses. Total length (TL) in centimeters and body  
 306 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 - 1,509.9)
<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 - 1,140.6)
<i>P. brasiliensis</i>	799.7 (761.6 - 927.5)	3,520.4 (2,079.8 - 6,294.3)
<i>P. mirandai</i>	669.8 (638.8 - 765.6)	1,977.9 (1,194.1 - 3,235.0)
<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)	1,285.7 (836.6 - 2,721.0)

307

308



309

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

314

#### 315 4. Discussion

##### 316 4.1 The issue of the juveniles and the usage of the DCL as a proxy for total body size

317 Living crocodylians are usually regarded as juvenile throughout their first/second years  
 318 after hatching, and the allometric changes during ontogeny vary across species and availability  
 319 of resources (Lang, 1987; Grigg & Kirshner, 2015). Various factors can be related to the  
 320 differences in body proportions from juvenile to adult in each crocodylian species, including  
 321 habitat use, food supply, and temperature (Lang, 1987). These allometric changes throughout  
 322 ontogeny are reflected in our regression results (Figure 5, Table 2), which show significantly  
 323 different relationships between the cranial measurements and the body size indices when the  
 324 adults-only subset is used (except for the relationship between HW and TL). This demonstrates  
 325 the importance of taking the ontogeny of specimens into account when constructing the datasets  
 326 used as sources for estimating the body size of extinct crocodylians.

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

332 12.5 m for this taxon (using DCL to estimate TL). This value is significantly higher than our  
333 estimate (9.26 m) using DCL in the non-phylogenetic approach. Consequently, the body mass  
334 estimated for this specimen by Aureliano et al. (2015) was also substantially higher than ours  
335 (about 8.5 tons compared to nearly 4 tons). Similarly, Cidade et al. (2020) also used the same  
336 dataset with juveniles (from Verdade, 2000) to estimate the TL of different *Mourasuchus*  
337 specimens, some of which are also included in our analyses. The differences are also  
338 substantial, with *M. amazonensis* (specimen DGM 526-R) estimated to 9.9 m by Cidade et al.  
339 (2020) and to 7.67 m by our non-phylogenetic approach using DCL. These conflicting results  
340 are likely at least partially due to the inclusion of juveniles and/or subadults in the living  
341 crocodylian datasets used for generating the regression equations. Therefore, we advocate for  
342 using only adult specimens in these datasets when estimating the body size of extinct  
343 crocodylians.

344 Another important aspect revealed by our results is the comparison between DCL and  
345 HW as proxies for body size in crocodylians. Our regression results showed that the body size  
346 indices (TL and BM) are more strongly correlated with HW than with DCL (Figure 5, Table  
347 2). Additionally, we found no significant difference in the relationship between HW and TL  
348 when juveniles are considered, contrasting with what was found for DCL. This might be a  
349 consequence of the plasticity of the rostral region in crocodylians, considering that DCL is a  
350 measurement that includes the rostrum. Multiple lineages convergently displaying elongated  
351 rostra (Wilberg, 2017; Godoy, 2019) and the effect of longirostry is a known issue in the group,  
352 affecting phylogenetic analyses (e.g., Pol & Gasparini, 2009) and also body size estimations  
353 (Erickson et al., 2012; Aureliano et al., 2015; Godoy et al., 2019; Godoy & Turner, 2020).  
354 Accordingly, although DCL has been used by various studies to estimate the body size of extinct  
355 crocodylians (perhaps for being a more commonly available measurement), other  
356 measurements have been proposed as alternatives (e.g., femoral length, vertebral measurements  
357 and other cranial measurements; Hurlburt et al., 2003; Farlow et al., 2005; Iijima & Kubo,  
358 2020). Among these, O'Brien et al. (2019) successfully demonstrated a strong correlation  
359 between skull width (HW) and body size in crocodylians, which is consistently conserved  
360 across the group. Here, we provide further support for the usage of HW for estimating the body  
361 size of extinct crocodylians, with results suggesting that it is comparatively more robust than  
362 DCL in maintaining a proportional allometry with total length along the ontogeny.

363

364 *4.2 Phylogenetic and non-phylogenetic approaches*

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

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

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

393

394 *4.3 Paleobiological implications*

395           Body size is strongly associated with many aspects of the biology of crocodylians,  
396 including ecology (e.g., specialization of diet, habitat) and physiology (Grigg et al., 1998;  
397 Seebacher et al., 1999; Seymour et al., 2012; Godoy et al., 2019; Godoy & Turner, 2020; Gearty  
398 & Payne, 2020). It is not different for extinct crocodylians, such as the Miocene Caimaninae  
399 from South America, the focus of this study. Among these is *Purussaurus brasiliensis*, which  
400 was one of the largest known crocodyliforms and could feed on large terrestrial prey (Aureliano  
401 et al., 2015; Cidade et al., 2019). *Mourasuchus* was relatively smaller, but with a proportionally  
402 much longer skull, which is hypothesized to be associated with a “gulp-feeding” habit (Cidade  
403 et al., 2017). *Acrasuchus* was a generalist predator (Souza-Filho et al., 2018), with a *bauplan*  
404 more similar to that of living caimanines.

405           In the middle Miocene, the Pebas System formed a cluster of lakes, rivers, and swamps  
406 with a degree of marine influence, which extended from the Acre region, part of the Brazilian  
407 Amazon, Peru, Venezuela, Colombia, and Bolivia (Wesselingh & Salo, 2006; Hoorn et al.,  
408 2010a, b; Alvim et al., 2021). This mega-wetland system originated about 23 Ma (Hoorn et al.,  
409 2010a; Wesselingh et al., 2006) as a result of the Andean uplift, making all hydrodynamics flow  
410 from the mountains to the central portion of northwestern South America, promoting the  
411 diversification of invertebrate and vertebrate faunas (Wesselingh & Salo, 2006), and high  
412 availability of resources (Hoorn et al., 2010a, b). This uplift created a barrier in the atmospheric  
413 circulation that consequently resulted in drastic climate changes (Hoorn et al., 2010a). The  
414 middle Miocene was known as the Miocene Climatic Optimum, due to its significantly  
415 increasing temperatures (Buchardt, 1978; Böhme, 2003; Kaandorp et al., 2005; Super et al.,  
416 2018; Methner et al., 2020; Steinthorsdottir et al., 2020). In contrast, the lake in the early late  
417 Miocene, approximately 10 Ma, went from a lacustrine to a fluvial system, known as Acre  
418 System (Hoorn et al., 2010a; Latrubesse et al., 2010), in which the vertebrate fauna, especially  
419 the crocodylians, reached its peak in body size. These simultaneous factors allowed the  
420 evolution and diversification of these peculiar crocodylians who shared this ecosystem.

421           In living crocodylians, diet varies according to the size of the individual (Brochu, 2001;  
422 Aureliano et al., 2015; Grigg & Kirshner, 2015), with cranial shape also influencing dietary

423 specialization (Gignac et al., 2019). Caimaninae has a high cranial disparity, which is reflected  
424 in a variable diet across and within species. Taxa with broader skulls maximize the amount of  
425 food ingested (Piras et al., 2014), whereas those with short rostra usually feed on terrestrial  
426 mammals and reptiles, and those with long snouts, have a more piscivorous or invertebrate diet  
427 (Webb et al., 1978; Cidade et al., 2019). Regarding body size, we can hypothesize that larger  
428 taxa were relatively slower, suggesting less active predatory strategies. The decrease in  
429 swimming performance in *Crocodylus porosus* specimens was observed as the body length  
430 increase, which influences on prey capture (Elsworth et al., 2003). Additionally, large body  
431 sizes hinder the locomotion in a terrestrial environment (Blanckenhorn, 2000), which is  
432 consistent with the semiaquatic lifestyle proposed for these large caimanines of the Pebas and  
433 Acre Systems. The time spent in water could also be associated with thermoregulation (i.e., to  
434 avoid overheating), given that large organisms dissipate heat at much lower rates due to their  
435 relatively surface/volume ratio (Grigg et al., 1998; Markwick, 1998; Seebacher et al., 1999,  
436 2003).

437

## 438 5. Conclusions

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

447 Using a subset with only adult specimens, we estimated the body sizes of nine extinct  
448 caimanine specimens from the Miocene of South America, using a phylogenetic and a non-  
449 phylogenetic approach. Overall, the phylogenetic approach provided more conservative  
450 estimates, possibly a result of the phylogenetic placement of the specimens within Caimaninae,  
451 a group of comparatively small- to medium-sized extant species. As our phylogenetic method  
452 cannot account for potential increased body size evolutionary rates in parts of the tree, we

453 hypothesize that a possible small-sized Caimaninae ancestor had a significant influence on  
454 estimating lower body size values for the extinct specimens. On the other hand, the non-  
455 phylogenetic approach cannot account for the non-independency of the data (and the variation  
456 of body proportions in different crocodylian taxa), possibly extrapolating the estimates. We  
457 therefore conclude a middle ground between the values estimated by both methods might be  
458 closer to the real body sizes of these specimens.

459

#### 460 **Supplementary Material**

461 All data and code used in the analyses can be found in a dedicated Zenodo repository  
462 (<https://zenodo.org/record/6788500#.Yr9IEnbMLrc>), doi: 10.5281/zenodo.6788500.

463

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476

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- 759

Highlights:

- Body proportions of crocodylians vary during ontogeny;
- Juveniles should not be used to estimate the body size of extinct crocodylians;
- Phylogenetic approach provides more conservative body size estimates;
- Dorsal cranial length is less robust than skull width as a proxy for body size.

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**Declaration of interests**

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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