

# Phylogenetically-informed estimates of notosuchian (Archosauria, Crocodylomorpha) body size and the challenges of inferring macroevolutionary patterns in extinct groups

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**Abstract:** Notosuchian crocodylomorphs were predominantly active terrestrial predators, exhibiting a wide range of ecomorphological specializations and body sizes. Given that body size plays an important role in the life history of vertebrates, its accurate estimation for notosuchians is crucial for understanding macroevolutionary and macroecological patterns in the group. Yet, reconstructing body size of fossil species with no living representatives is challenging, as demonstrated previously for Notosuchia, as well as other taxonomic groups. Here, we estimated the total body length of 40 Cretaceous–Cenozoic notosuchian species using a phylogenetic Bayesian inference approach that accounts for non-independence of taxa, based on cranial and femoral measurements from near-complete crocodylomorph specimens. Our results reveal notable discrepancies between estimates based on crania and femora, with skull length

providing more robust estimates. We suggest that femoral length is more strongly influenced by factors such as locomotion, limb posture, and ecological habitat, all of which vary across Notosuchia (and Crocodylomorpha more broadly). Nevertheless, the sizes of both skeletal regions are significantly correlated with total body length in notosuchians. Larger body sizes are typically associated with a more semi-aquatic lifestyle, probably due to selective pressures associated with this ecology. Our findings also suggest that notosuchians from freshwater habitats and with less specialized diets were less affected by the Cretaceous–Palaeogene mass extinction event, allowing some lineages to persist and ultimately thrive in its aftermath.

**Key words:** Crocodyliformes, Notosuchia, body size evolution, ancestral states, body size selectivity, mass extinction.

BODY size influences the way organisms interact with their environment and correlates with many fundamental morphological, physiological, behavioural and ecological characteristics, making it a good proxy for various aspects of an animal's natural history (Schmidt-Nielsen 1984; Brown 1995). Hence, body size plays an important role in understanding the macroevolutionary history of animals, including their extinction vulnerability (e.g. Wilson 2013; Heim *et al.* 2015; Smith *et al.* 2016; Ripple *et al.* 2017; Monarrez *et al.* 2021; Burin *et al.* 2023; Caron & Pie 2024). The size of an animal can be captured by several measurements, with body mass and length being two of the most commonly used. Body mass relates to the weight and energy reserves of an animal, as well as to its diversity dynamics and metabolic rate (Markwick 1998; Romanach *et al.* 2007; Seymour *et al.* 2013; Grigg & Kirshner 2015; Martin 2019; Lee *et al.* 2023), whereas

body length provides insights into its total linear measurement (Bye *et al.* 2006; Önsöy *et al.* 2011; Collar *et al.* 2013; Grigg & Kirshner 2015; Gayford *et al.* 2024).

Reconstructing the body size of an extinct vertebrate is difficult, even when it is represented by the complete skeleton of an adult individual, because soft tissues are rarely preserved (e.g. Bates *et al.* 2009; see also Griffin *et al.* 2021 regarding difficulties in determining ontogenetic maturity). It becomes even more challenging when only partial skeletons are available, especially if the species belongs to a group with no living representatives. These problems are particularly exacerbated when the species has an unusual bauplan.

Numerous approaches have been developed to estimate body size of extinct vertebrates (e.g. Henderson 1999; Bates *et al.* 2009; Campione & Evans 2012; O'Brien *et al.* 2019; Gayford *et al.* 2024; Woodward *et al.* 2025).

An extensive debate over the best methods to yield robust results has led to the development of various approaches, mostly using scaling models, which range from linear regressions (e.g. Campione & Evans 2012, 2020; Gayford *et al.* 2024; Woodward *et al.* 2025) to advanced 3D reconstructions and volumetric estimates (e.g. Christiansen & Fariña 2004; Lacovara *et al.* 2014; Bates *et al.* 2015; Brassey 2016; Campione & Evans 2020; Wright *et al.* 2024; Dempsey *et al.* 2025). Many of these produce widely divergent estimates for the same species (including the same individual specimens), especially when it comes to especially large-bodied animals, with noteworthy examples including the Devonian placoderm *Dunkleosteus terrelli* (Engelman 2023a, 2023b), the Cretaceous sauropod dinosaur *Dreadnoughtus schrani* (Lacovara *et al.* 2014; Bates *et al.* 2015), the Eocene cetacean *Perucetus colossus* (Bianucci *et al.* 2023; Motani & Pyenson 2024; Paul & Larramendi 2025), and the Neogene shark *Otodus megalodon* (Cooper *et al.* 2020, 2022; Gayford *et al.* 2024; Sternes *et al.* 2024).

Crocodylomorpha comprises living crocodylians and their extinct relatives, encompassing more than 200 million years of evolutionary history (Irmis *et al.* 2013; Mannion *et al.* 2015; Lecuona *et al.* 2016; Godoy & Turner 2020; Payne *et al.* 2024). This rich past diversity includes several lineages with bauplans remarkably different from those of living forms (Godoy *et al.* 2019; Godoy 2020; Stubbs *et al.* 2021), including the fully marine thalattosuchians (Young *et al.* 2016, 2024) and the cursorial notosuchians (see below). Yet, relatively few extinct crocodylomorph species are known from complete skeletons (Mannion *et al.* 2019), such that, as with other extinct vertebrates, estimating the body size of non-crocodylian crocodylomorphs is challenging. Most estimates are based on regression equations derived from extant crocodylian specimens (e.g. Sereno *et al.* 2001; Farrow *et al.* 2005; Aureliano *et al.* 2015; Godoy *et al.* 2019; Mannion *et al.* 2019; O'Brien *et al.* 2019; Paiva *et al.* 2022). By contrast, Young *et al.* (2016) proposed the use of lineage-specific linear regressions to estimate the body length of thalattosuchians. Fortunately, many complete thalattosuchian specimens are known, which served as the basis for the equation in Young *et al.* (2016), but this is not the case for other crocodylomorph lineages. That study also highlighted the potential influence of differences in body proportions for estimating total body length of extinct crocodylomorphs (see also Stockdale & Benton 2021). More recently, O'Brien *et al.* (2019) proposed a phylogenetic approach for estimating body size, which has been applied in several studies focusing on extinct crocodylians. (e.g. Scheyer *et al.* 2019; Paiva *et al.* 2022, 2024; Conedera *et al.* 2023; Ristevski *et al.* 2023). Yet, this is still to be applied to non-crocodylian crocodylomorphs.

Notosuchians are arguably the most unusual crocodylomorphs when compared to living crocodylians. Known from more than 90 species spanning the Middle Jurassic to late Neogene (e.g. Kellner *et al.* 2014; Dal Sasso *et al.* 2017; Sellés *et al.* 2020; Bravo *et al.* 2021, 2025; Leardi *et al.* 2024; Viñola López *et al.* 2025), these predominantly Gondwanan taxa (Sereno & Larsson 2009; O'Connor *et al.* 2010; Pol & Leardi 2015; Nicholl *et al.* 2021) were mostly terrestrial, displaying a wide range of ecomorphological specializations, including varying degrees of dermal shielding and cranial/dental morphologies related to distinct dietary habits (e.g. Buckley *et al.* 2000; O'Connor *et al.* 2010; Soto *et al.* 2011; Ósi 2014; Pol *et al.* 2014; Pol & Leardi 2015; Godoy *et al.* 2016; Melstrom & Irmis 2019; Godoy & Turner 2020; Montefeltro *et al.* 2020), resulting in strikingly different body proportions when compared to crocodylians (Krause *et al.* 2010; Godoy *et al.* 2014, 2016; Martinelli *et al.* 2018; dos Santos *et al.* 2025). Notosuchia includes small-bodied, mammal-like forms, such as *Pakasuchus kapilimai* (<1 m; O'Connor *et al.* 2010), to medium and large-sized hypercarnivores such as baurusuchids and sebecids (>2.5 m; Godoy *et al.* 2014; Martin *et al.* 2022).

Previous studies have attempted to estimate the body size of some notosuchians (e.g. Pol *et al.* 2014; Godoy *et al.* 2016; Molnar & Vasconcellos 2016; Aubier *et al.* 2023; Gayford *et al.* 2024; Bravo *et al.* 2025), but these did not account for their unique bauplan. Indeed, more accurately estimating the body size of notosuchians allows a better understanding of the macroevolutionary processes underlying their high disparity and ecomorphological variation. Additionally, it may also shed light on the role of body size in the group's extinction selectivity across the Cretaceous–Palaeogene mass extinction, which only a few lineages survived (Kellner *et al.* 2014; Aubier *et al.* 2023; Bravo *et al.* 2025).

In this study, we present the first attempt to estimate body sizes of notosuchians using a phylogenetic approach. Based on measurements of both cranial and appendicular bones from a newly constructed, rich dataset of the most completely preserved crocodylomorph skeletons known to date, our results improve the robusticity of notosuchian body size estimates. Furthermore, they contribute to a better understanding of the role of body size in the evolutionary history of this clade.

## MATERIAL & METHOD

### *Phylogenetic framework*

A modified version of the crocodylomorph supertree presented by Godoy (2020) was used as the phylogenetic

framework for body size predictions. Using the software Mesquite (Maddison 2017), we increased the number of tips to 467 taxa, comprising 458 crocodylomorph species and 9 outgroup species. The phylogenetic positions of the newly incorporated taxa in the supertree were based on the literature (see Paiva *et al.* (2025) for a detailed explanation). Following the approach of Godoy (2020), this supertree was used as the input (i.e. topological constraint) for time-calibration analysis under Bayesian inference, using a fossilized birth–death model (Heath *et al.* 2014; Zhang *et al.* 2016; Didier & Laurin 2020), which was carried out in MrBayes v3.2.7 (Ronquist *et al.* 2012). We used the `createMrBayesTippingNexus()` function from the `paleotree` R package (Bapst 2012), which follows the recommendations of Matzke & Wright (2016) and Gearty & Payne (2020). Uniform priors were used for the tip ages, which were obtained from the Paleobiology Database (<https://paleobiodb.org>) and the literature. The root of the tree was also estimated from a uniform prior constrained between 245 and 260 Ma, given that an older origin for Crocodylomorpha is unlikely (Irmis *et al.* 2013; Turner *et al.* 2017; Ezcurra & Butler 2018; Payne *et al.* 2024). After discarding the first 50% of trees as burn-in, 20 trees were randomly sampled from the posterior distribution for downstream analysis, in addition to the maximum clade credibility tree (MCCT), pruning taxa for which we do not have body size data.

#### *Body size data & phylogenetic regressions*

We compiled body size measurements from complete or nearly complete crocodylomorph skeletons, including both extant and fossil species, avoiding the inclusion individuals likely to be juvenile (based on the literature and/or our own assessment). We used the software ImageJ (Schindelin *et al.* 2012) to extract measurements of specimens from photographs and the literature, collecting the following measurements: dorso-cranial length (DCL; measured from the tip of the snout to the base of the skull); femoral length (FL; measured from the distal condyles to the proximal femur); and total body length (TL; measured from the tip of the snout to the tip of the tail). DCL and FL were chosen due to their strong correlation with TL in living crocodylians. Both are also easily measured and widely used as body size proxies in previous studies on crocodylomorphs (e.g. Sereno *et al.* 2001; Hurlburt *et al.* 2003; Farlow *et al.* 2005; Campione & Evans 2012; Turner & Nesbitt 2013; Aureliano *et al.* 2015; Young *et al.* 2016; Godoy *et al.* 2019; Paiva *et al.* 2022). Some otherwise mostly complete notosuchian specimens do not preserve the tail; to estimate TL for a broader array of taxa, we estimated the missing skeletal region by

proportional scaling (i.e. extrapolation) through comparisons with fully complete notosuchian skeletons. Although we anticipate some measurement errors arising from non-standardized source images and/or extrapolations of TL from specimens that lack the tail, this is arguably a minor consideration when compared to the scale of magnitude observed in crocodylomorph body size range (Godoy 2020; Stockdale & Benton 2021; Paiva *et al.* 2024). The final dataset consists of measurements for 66 complete crocodylomorph specimens, representing 48 species, 11 of which are notosuchians. DCL could be measured for 64 specimens (representing 48 species), whereas FL was measured for 45 specimens (33 species; Tables 1, S1). Apart from the predominantly Late Cretaceous notosuchians, the remaining sampled crocodylomorphs span a broad temporal scale, from Late Jurassic thalattosuchians to extant crocodylians, allowing for a broad representation of body proportions across different crocodylomorph subgroups.

We employed phylogenetic predictions based on the method proposed by O'Brien *et al.* (2019), which considers the phylogeny of the group, using information on measured body size proxies from across the crocodylomorph tree. Unlike previous studies using that method, we did not employ skull width as a proxy to estimate body size because this would drastically reduce sample size. Instead, we used DCL and FL measurements as proxies for TL, which were compiled for incomplete notosuchian specimens either directly, using a measuring tape and callipers, or from the literature, using ImageJ (Schindelin *et al.* 2012). For species with more than one specimen, we calculated mean values for the analyses (Table S1).

We used phylogenetic generalized least squares (PGLS) regressions to assess the correlation between TL and the two measurements (DCL and FL) of our sample. All measurement data were natural log-transformed prior to analysis, which was conducted in R v4.4.2 (R Core Team 2024), using scripts made available by O'Brien *et al.* (2019) and Paiva *et al.* (2022), as well as the packages `car` v3.1-2 (Fox & Weisberg 2018), `MASS` v7.3-60.2 (Venables & Ripley 2002; Ripley *et al.* 2024), `caper` v1.0.3 (Orme *et al.* 2013), `evomap` (Smaers & Mongle 2014), `rms` v6.8-1 (Harrell 2017), and `phytools` v2.1-1 (Revell 2012).

#### *Ancestral reconstructions of body size & habitat difference*

To evaluate patterns of body size evolution in a phylogenetic context, we estimated ancestral body size values across the crocodylomorph tree using Maximum Likelihood, employing the `contMap()` function from the `phytools` v2.1-1 R package (Revell 2012), pruning taxa for

**TABLE 1.** Crocodylomorph taxa with complete skeletons included in our dataset (values in mm).

Species	DCL	FL	TL	Species	DCL	FL	TL
<i>Aeolodon priscus</i>	683	250	3470	<i>Crocodylus porosus</i>	525	–	4077
<i>Alligator mississippiensis</i> *	435	187	2867	<i>Diplocynodon darwini</i> *	149	62	790
<i>Alligator sinensis</i> *	198	145	1827	<i>Diplocynodon deponiae</i> *	105	60	635
<i>Alligatorellus bavaricus</i>	43	29	301	<i>Gavialis gangeticus</i>	598	–	4442
<i>Alligatorellus beaumonti</i>	35	26	193	<i>Hassiacosuchus haupti</i>	69	44	492
<i>Anatosuchus minor</i>	133	–	790	<i>Isisfordia duncani</i>	172	85	1046
<i>Aphaurosuchus escharafacies</i>	315	230	1241	<i>Macrospodylus bollensis</i> *	623	246	3256
<i>Apletosuchus sordidus</i>	300	–	883	<i>Melanosuchus niger</i>	524	–	3906
<i>Araripesuchus gomesii</i>	82	62	420	<i>Metriorhynchus brachyrhynchus</i>	760	320	4190
<i>Araripesuchus wegneri</i> *	119	62	661	<b><i>Montealtosuchus arrudacamposi</i></b>	210	149	1150
<i>Atoposaurus jourdani</i>	20	16	188	<i>Montsecosuchus depereti</i>	54	48	530
<i>Atoposaurus oberndorferi</i>	26	17	130	<i>Paleosuchus palpebrosus</i>	196	–	1510
<i>Baurusuchus salgadoensis</i>	420	330	2416	<i>Paleosuchus trigonatus</i>	227	–	1740
<i>Bernissartia fagesii</i>	112	55	1000	<b><i>Pakasuchus kapilimai</i></b>	74	–	487
<i>Brillianceausuchus babourensis</i>	75	45	800	<i>Pelagosaurus typus</i> *	347	143	1892
<i>Caiman crocodilus</i>	260	–	1983	<i>Plagiophthalmosuchus gracilirostris</i>	586	–	1584
<i>Caiman latirostris</i>	223	–	2100	<i>Platysuchus multiscrobiculatus</i>	455	200	2790
<i>Caiman yacare</i> *	148	26	784	<i>Rhacheosaurus gracilis</i>	290	135	1570
<b><i>Caipirasuchus mineirus</i></b>	105	95	570	<i>Shantungosuchus chuhsienensis</i>	45	35	233
<b><i>Caipirasuchus paulistanus</i></b>	142	–	780	<i>Thalattosuchus superciliosus</i> *	602	226	3220
<i>Charitomenosuchus leedsi</i>	871	321	4280	<i>Theriosuchus pusillus</i>	54	47	473
<i>Cricosaurus albersdoerferi</i>	455	118	2267	<i>Tomistoma schlegelii</i>	588	–	4368
<i>Cricosaurus bambergensis</i>	361	–	1208	<i>Tsoabichi greenriverensis</i>	67	38	572
<i>Cricosaurus suevicus</i>	328	115	2000	<b><i>Uberabasuchus terrificus</i></b>	305	–	1675

Notosuchians are highlighted in **bold**. DCL, dorso-cranial length; FL, femoral length; TL, total length. See Table S1 for the full list of complete specimens in the dataset.

\*Indicates taxa for which multiple specimens were measured (mean values are shown).

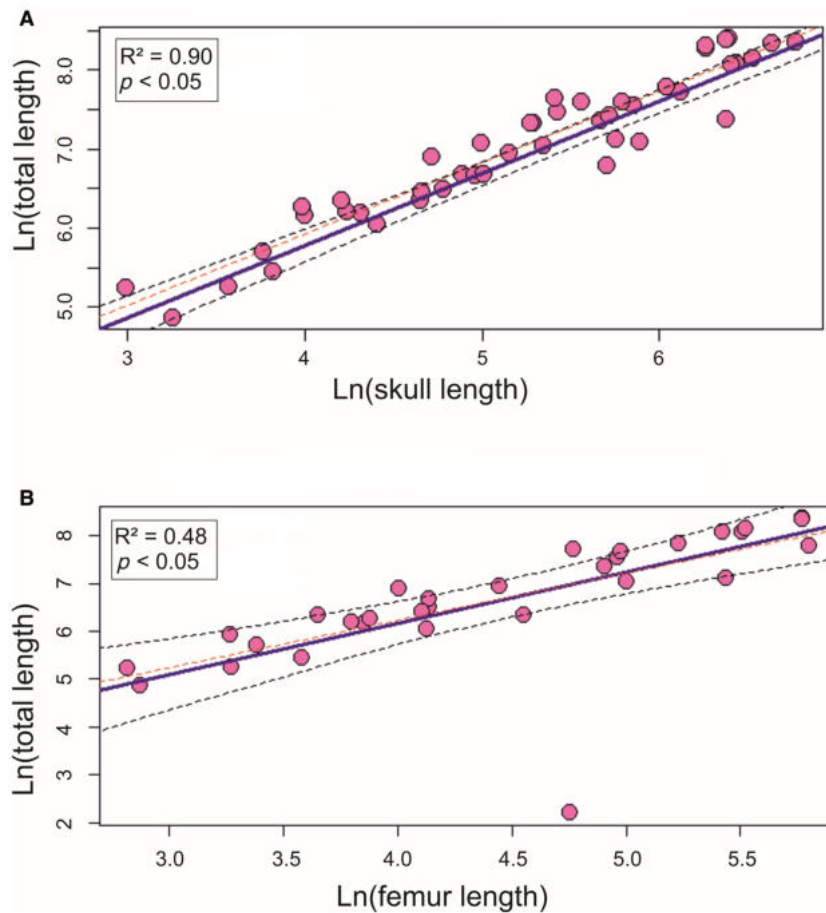
which we do not have body size data. We then mapped the body size (TL) values onto the notosuchian part of the crocodylomorph phylogeny, using both predictions (from both DCL and FL measurements) and measurements from the complete notosuchian specimens. This was done for both the MCCT and the 20 randomly sampled trees. To determine if there is a statistically significant difference between body size with respect to lifestyle (i.e. terrestrial vs semi-aquatic), we applied a Mann–Whitney–Wilcoxon test, using the `wilcox.test()` R function.

## RESULTS

The PGLS regression results show a strong, statistically significant positive correlation between TL and DCL ( $R^2 = 0.90$ ,  $p < 0.05$ ). By contrast, although significant, the positive correlation between TL and FL is only moderate ( $R^2 = 0.48$ ,  $p < 0.05$ ; Fig. 1; Paiva *et al.* 2025), suggesting that body size estimations based on cranial measurements might be more reliable and robust. Overall, body size predictions from DCL have a mean of 102 cm, whereas those estimated from FL have a mean of 149 cm

(Table 2). The results using DCL ranged from 34.5 cm (*Candidodon itapecuruense*) to 238 cm (*Stolokrosuchus lapparenti*). The smallest species estimated from FL is *Malawisuchus mwakasyungutiensis* (43.5 cm) and the largest is *Stratiotosuchus maxhechti* (335 cm).

Using both the MCCT and 20 randomly sampled trees (Fig. 2 and see Paiva *et al.* 2025), small to medium body sizes (<100 cm) are estimated as the ancestral condition for most notosuchian lineages, particularly when using DCL as a proxy for body size reconstruction (Fig. 2A). Uruguaysuchids, candidodontids, *Comahuesuchus brachybuccalis*, most sphagesaurians and *Gondwanasuchus scabrosus*, were small-bodied, as well as their most recent common ancestor (<70 cm). Medium to large body sizes are observed among sebecids, highly nested baurusuchids, and some peirosaurids, but their most recent common ancestors exhibited medium sizes (c. 131 cm). The results using FL as a proxy (Fig. 2B) reveal different body size ancestral patterns. Whereas the most recent common ancestor of baurusuchids remains medium-to-large-sized, and uruguaysuchids and sphagesaurians small, that of sebecids was estimated as larger sized (>250 cm). Notably, the most recent common ancestor of peirosaurids is estimated as medium to large-sized using DCL (c. 180 cm),



**FIG. 1.** Phylogenetic generalized least squares (PGLS) regression analyses of skull (A) and femur (B) lengths in relation to total body length in our crocodylomorph dataset. Each pink circle represents an individual. The solid line indicates the PGLS regression, the red dashed line represents the simple linear regression, and the black dashed lines are the confidence intervals. All variables were log-transformed prior to the analysis.

but small-sized using FL (<100 cm). See Paiva *et al.* (2025) for specific results for the 20 randomly sampled trees and body size estimated for the ancestral reconstructions.

A Mann–Whitney–Wilcoxon test resulted in a statistically significant difference ( $p = 0.01$ ) between the body sizes of terrestrial and semi-aquatic taxa, with semi-aquatic species exhibiting larger sizes than their terrestrial counterparts (Fig. 3).

## DISCUSSION

### *Challenges in estimating body size of notosuchians*

As noted above, notosuchians comprise a clade of primarily terrestrial crocodylomorphs (Soto *et al.* 2011; Pol *et al.* 2014; Pol & Leardi 2015; Wilberg *et al.* 2019; Klock *et al.* 2022; Cubo *et al.* 2023; Sena *et al.* 2023), with high

levels of ecological disparity (Buckley *et al.* 2000; O'Connor *et al.* 2010; Soto *et al.* 2011; Ösi 2014; Pol *et al.* 2014; Pol & Leardi 2015; Godoy *et al.* 2016; Godoy & Turner 2020; Montefeltro *et al.* 2020). Their morphology differs substantially from that of extant crocodylians, from which they diverged *c.* 180–200 Ma (e.g. Godoy *et al.* 2019; Payne *et al.* 2024), with most notosuchians characterized by shorter and higher skulls, laterally positioned orbits (Godoy 2020; Leardi *et al.* 2024), straighter femora and inferred erect postures (Buckley *et al.* 2000; Godoy *et al.* 2016; Tavares *et al.* 2017; Montefeltro 2019; Klock *et al.* 2022), among many other characteristics. Determining body proportions in notosuchians is therefore challenging, as the group has no living representatives (Gayford *et al.* 2024).

Although the employed phylogenetic approach seeks to reduce issues arising from different body proportions within Crocodylomorpha, our results still indicate some notable discrepancies between body size estimates derived

**TABLE 2.** Notosuchian taxa for which mean total length (in mm) was estimated based on dorsocranial length (DCL) and femoral length (FL), using our phylogenetic predictions with their respective 75% confidence intervals.

Species	DCL	Total length (75% CI)	FL	Total length
<i>Microsuchus schilleri</i>	–	–	53	453 (360–575)
<i>Araripesuchus tsangatsangana*</i>	69	400 (290–559)	91	826 (649–1053)
<i>Araripesuchus buitreaensis*</i>	125.4	686 (533–881)	–	–
<i>Uruguaysuchus aznarezi</i>	61.5	348 (289–422)	–	–
<i>Mahajangasuchus insignis</i>	–	–	290	2923 (2285–3798)
<i>Kaprosuchus saharicus*</i>	474	2329 (1764–3064)	–	–
<i>Itasuchus jesuinoi</i>	–	–	225.9	2261 (1746–2903)
<i>Uberabasuchus terrificus</i>	–	–	161.8	1509 (1183–1948)
<i>Hamadasuchus rebouli*</i>	163.5	900 (730–1099)	–	–
<i>Stolokrosuchus lapparenti</i>	490	2387 (1905–2981)	–	–
<i>Pepesuchus deiseae</i>	346	1769 (1271–2479)	–	–
<i>Barrosasuchus neuquenianus</i>	315.5	1652 (1293–2110)	–	–
<i>Lomasuchus palpebrosus</i>	276	1471 (1159–1847)	–	–
<i>Gasparinisuchus peirosauroides</i>	326	1688 (1358–2112)	–	–
<i>Libycosuchus brevirostris</i>	177	954 (718–1274)	–	–
<i>Simosuchus clarki</i>	120	645 (448–965)	106.5	957 (746–1234)
<i>Neuquensuchus universitas</i>	–	–	88.5	773 (623–963)
<i>Malawisuchus mwakasyungutiensis*</i>	67	399 (339–468)	53	435 (359–531)
<i>Candidodon itapecuruense</i>	56.4	345 (280–427)	–	–
<i>Morrinhosuchus luziae</i>	109.9	595 (457–775)	–	–
<i>Notosuchus terrestris*</i>	142.7	764 (603–963)	93	794 (630–990)
<i>Coronelsuchus civali</i>	–	–	129	1130 (906–1401)
<i>Mariliasuchus amarali*</i>	100.7	546 (432–700)	99.6	852 (674–1094)

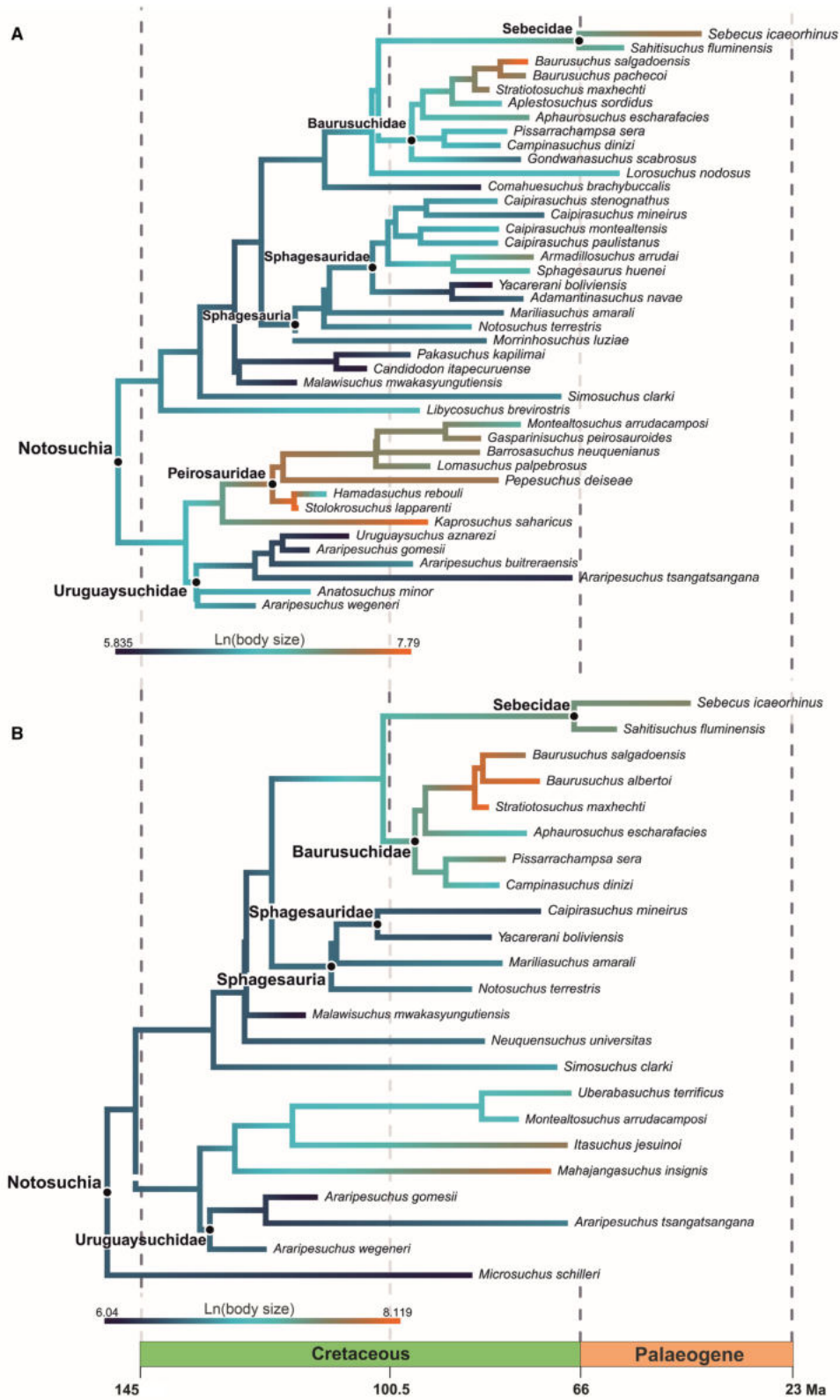
(continued)

**TABLE 2.** (Continued)

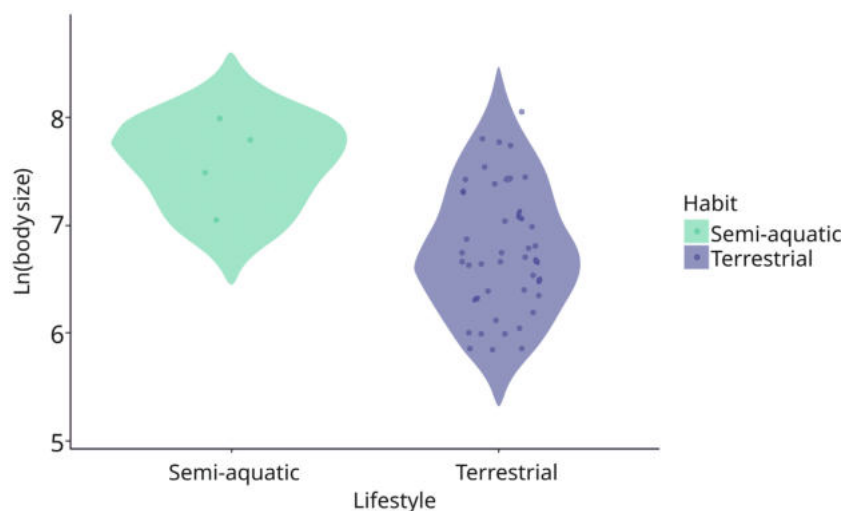
Species	DCL	Total length (75% CI)	FL	Total length
<i>Adamantinasuchus navae</i>	60	559 (439–713)	–	–
<i>Yacararani boliviensis*</i>	100.9	350 (276–453)	71.6	590 (458–755)
<i>Sphagesaurus huenei</i>	209	1069 (841–1335)	–	–
<i>Armadillosuchus arrudai</i>	296	1487 (1180–1885)	–	–
<i>Caipirasuchus montealtensis*</i>	152.7	809 (667–976)	–	–
<i>Caipirasuchus catanduensis</i>	161.2	847 (708–1013)	–	–
<i>Caipirasuchus stenognathus</i>	142	755 (609–925)	–	–
<i>Comahuesuchus brachybuccalis*</i>	81.5	404 (309–530)	–	–
<i>Gondwanasuchus scabrosus</i>	133.9	599 (487–737)	–	–
<i>Campinasuchus dinizi</i>	177.6	763 (628–918)	129.2	1104 (876–1397)
<i>Pissarrachampsia sera</i>	200	842 (686–1026)	221	1995 (1584–2527)
<i>Stratiosuchus maxhechti</i>	454	1867 (1545–2264)	354	3356 (2642–4281)
<i>Baurusuchus albertoi</i>	–	–	328	3090 (2443–3894)
<i>Baurusuchus pachecoi</i>	343	1593 (1330–1899)	–	–
<i>Lorosuchus nodosus</i>	254.8	1136 (821–1576)	–	–
<i>Sahitisuchus fluminensis</i>	261	1171 (849–1637)	201.5	1849 (1409–2384)
<i>Sebecus icaeorhinus</i>	386	1655 (1136–2396)	220	2010 (1514–2682)

\*Taxa for which multiple specimens were included in the analysis (using mean values of measurements).

from DCL and FL measurements. For instance, the estimated total body length of *Araripesuchus tsangatsangana* is 40 cm when using DCL, but twice as long (c. 80 cm) when using FL. Similarly, the estimate for *Pissarrachampsia sera* based on DCL (84 cm) is considerably lower than the FL-based estimate (almost 200 cm). A comparable pattern is observed in *Stratiosuchus maxhechti*, with a medium size of 187 cm estimated from DCL, but 336 cm when based on FL. These substantial differences



**FIG. 2.** Ancestral reconstructions of body size of complete notosuchians and estimated body sizes using different proxies: A, dorsal-cranial length; B, femoral length. The body size values are natural log-transformed. The tree used for this reconstruction is the maximum clade credibility tree. See Paiva *et al.* (2025) for the results using 20 randomly sampled trees.



**FIG. 3.** Body size distribution of terrestrial (44 taxa; in purple) and semi-aquatic (6 taxa; in green) notosuchians. Values are natural log transformed (originally in mm).

are especially apparent within baurusuchids, a group of terrestrial hypercarnivores that possibly occupied similar ecological niches to theropod dinosaurs (Godoy *et al.* 2014; Montefeltro *et al.* 2020). A notable discrepancy is also observed in the sebecid *Sahitisuchus fluminensis* (117 and 185 cm based on DCL and FL, respectively), although it is less pronounced than in baurusuchids. Notably, the species exhibiting the greatest differences in body size estimates tend to be associated with larger forms from the Cretaceous and Paleocene. One possibility is that these discrepancies reflect methodological limitations in body size estimations; for example, a poorly sampled tree might prevent the phylogenetic approach from capturing these changes in body proportions. Alternatively, these discrepancies might be more related to different cranial and femoral proportions in these taxa. Although DCL might seem to be counterintuitive as a more suitable proxy of body size due to the high cranial disparity amongst notosuchians, the skull in crocodylomorphs scales allometrically with body size, producing a strong correlation (Dodson 1975; McHenry *et al.* 2006; O'Brien *et al.* 2019; Godoy *et al.* 2019; Godoy 2020; Bestwick *et al.* 2022; Srinivas *et al.* 2025). By contrast, the femur is likely to be more strongly influenced by locomotion, limb posture and ecological habitat (Farlow *et al.* 2005; Campione & Evans 2012; Godoy *et al.* 2016; Iijima *et al.* 2018; Pochat-Cottilloux 2025), all of which vary across Notosuchia (and across Crocodylomorpha more broadly). Whereas femoral circumference is widely used to predict body mass, femoral length has weaker support (Campione & Evans 2012; Campione *et al.* 2014; Woodward *et al.* 2025). Consequently, the higher  $R^2$  values from DCL support its use as a more reliable predictor of body size. Nevertheless, further fossil

discoveries are needed to determine whether such inconsistencies arise from variation in ontogenetic allometry or potential biases in the datasets used to derive these proxies. The incorporation of additional cranial measurements and postcranial bones could also help determine whether this dissimilarity is exclusively attributable to differences in the employed elements.

Given that distinct skeletal elements scale differently to body size (Iijima & Kubo 2019), it is expected that divergent TL estimates will be obtained from DCL and FL. The crocodylomorph skull is characterized by substantial morphological variation, even within subclades, with notosuchians exhibiting notably high morphological disparity (e.g. Brochu 2001; Wilberg 2017; Godoy *et al.* 2019; Godoy 2020; Felice *et al.* 2021; Bravo *et al.* 2021; Melstrom *et al.* 2025). By contrast, the femur is not typically highly variable among species of the same subclade (Young *et al.* 2016) and has been extensively used in studies of crocodylomorphs and other terrestrial vertebrates (e.g. Christiansen & Fariña 2004; Farlow *et al.* 2005; Benson *et al.* 2014; Young *et al.* 2016; Iijima & Kubo 2019; Campione & Evans 2020; Nelson *et al.* 2023; Woodward *et al.* 2025). We can further assess this using the peirosaurid *Uberabasuchus terrificus*, which is represented in our dataset by two individuals, a semi-complete (CPPLIP 630) and an incomplete specimen (CPPLIP 501) (Table S1). The results show that the body size estimate (150 cm) based on the FL of the latter specimen is similar to the TL measured from the complete skeleton (167 cm), suggesting greater robustness for TL estimates from FL. However, this example contrasts with our PGLS results, with the coefficient of determination ( $R^2$ ) indicating a stronger correlation between DCL and TL than between FL and TL. Even though the femur is less

variable than the skull, it is important to be cautious when using this measurement to estimate notosuchian body size due to the moderate  $R^2$  value found in our regressions. The use of skull measurements as proxies for total body length is widespread in studies of crocodylomorphs (e.g. Sereno *et al.* 2001; Aureliano *et al.* 2015; Young *et al.* 2016; Godoy *et al.* 2019; O'Brien *et al.* 2019; Scheyer *et al.* 2019; Godoy 2020; Cidade *et al.* 2021; Bestwick *et al.* 2022; Paiva *et al.* 2022, 2024; Aubier *et al.* 2023) and our results confirm consistent and robust estimates of total body length of notosuchians using DCL as a proxy.

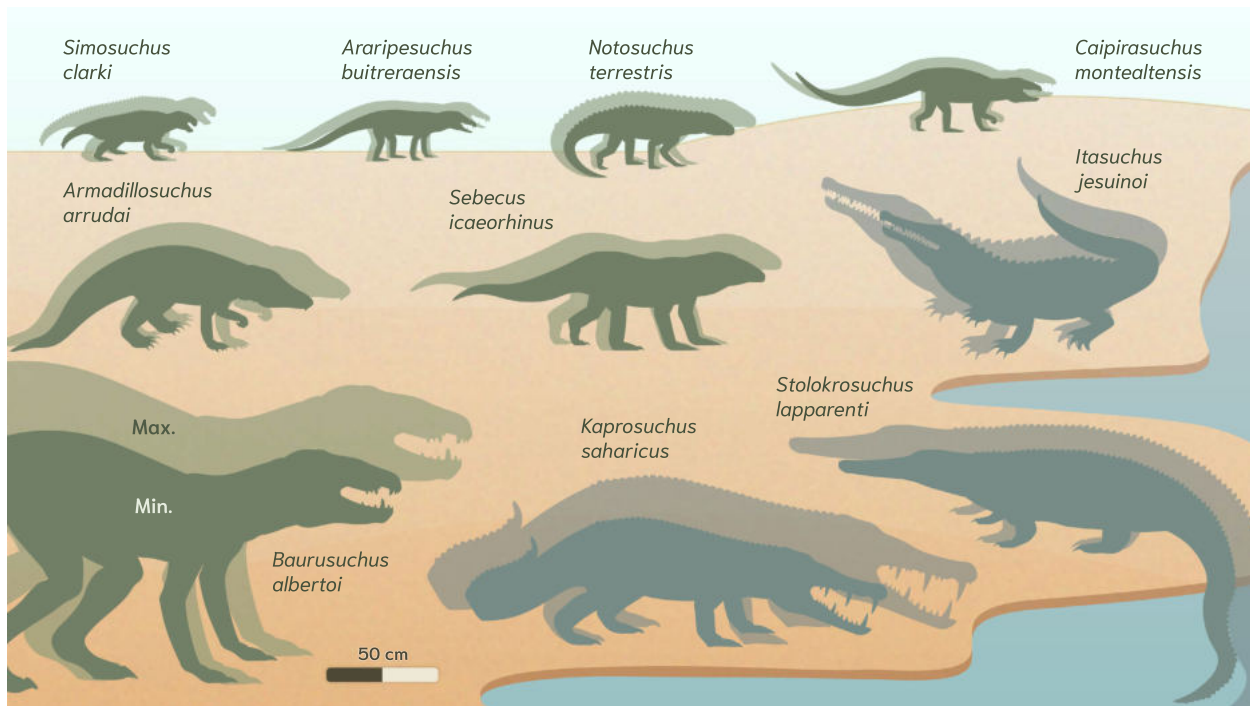
Some of our estimates also differ substantially from those of previous studies. A notable example is *Mahajangasuchus insignis*, which was originally estimated to be 400 cm long (Krause *et al.* 2006), but is here inferred to be much shorter (292 cm). This species is known from a nearly complete skeleton (Buckley *et al.* 2000; Krause *et al.* 2006; Turner & Buckley 2008), lacking most of the skull and tail, and no previous analytical methods were used to infer its size. Our estimate for this species is FL-based, which suggests caution given the moderate  $R^2$  value found by our PGLS analyses. The body size estimated here for *Pissarrachampsia sera* (84 cm using DCL) is very different to that reported by Godoy *et al.* (2016) (2.7–3.5 m), which is based on the equations of Farlow *et al.* (2005), established from measurements of extant crocodylians. But perhaps the most surprising result is the body size estimated for *Stratiosuchus maxhetchi*, which was previously proposed to be 400 cm (Riff & Kellner 2011), approximating our FL-based (335 cm), whereas our estimate based on DCL is only 186 cm. By contrast, our estimates of some notosuchians are close to previously published body size reconstructions (e.g. *Kaprosuchus saharicus*, *Sebecus icaeorhinus*, *Simosuchus clarki*; see Table S2 for more comparisons). The stratigraphically earliest known probable sebecoid, *Ogresuchus furatus*, was not included in our database due to its incomplete preservation; however, based on our FL-based regression equation, its estimated total length is 101 cm, which is very close to the previously published estimate (98 cm; Sellés *et al.* 2020). We suggest that the main reason for the differences with some previous studies is that our body size estimates are based on Bayesian phylogenetic analyses that consider the non-independence of the data (i.e. taking into account the evolutionary history of the group; O'Brien *et al.* 2019; Paiva *et al.* 2022, 2024).

#### Notosuchian body size evolution

During the Cretaceous, notosuchians exhibited remarkable diversity, characterized by different ecomorphotypes, body sizes, and lifestyles (Buckley *et al.* 2000;

Krause *et al.* 2010; O'Connor *et al.* 2010; Soto *et al.* 2011; Godoy *et al.* 2014, 2016; Ósi 2014; Pol *et al.* 2014; Pol & Lardi 2015; Martinelli *et al.* 2018; Godoy & Turner 2020; Montefeltro *et al.* 2020; dos Santos *et al.* 2025; Pochat-Cottilloux 2025). In general, the group exhibited small to medium sizes (Fig. 2). Early notosuchians (e.g. some *Araripesuchus* species, *Anatosuchus minor*, *Candidodon itapecuruense*, *Malawisuchus mwakasyungutiensis*, *Ogresuchus furatus*) were generally small, except for *Stolokrosuchus lapparenti*, which reached c. 238 cm. However, by the Late Cretaceous, the group had evolved into larger-bodied forms (Godoy *et al.* 2019), including baurusuchids and peirosaurids. Simultaneously, their environment was also changing. Notosuchians primarily inhabited semi-arid regions (Carvalho *et al.* 2010), which gradually increased in aridity throughout the Cretaceous (Price *et al.* 1998; Garcia *et al.* 1999; Goldberg & Garcia 2000; Hay & Floegel 2012). During this period, terrestrial forms displayed a range of body sizes, whereas semi-aquatic taxa tended to develop larger sizes (Figs 3, 4). Living in an environment with alternating periods of extreme drought and heavy rainfall (Carvalho *et al.* 2010) may have favoured semi-aquatic forms, allowing the evolution of larger-bodied species (Fig. 4).

Large-bodied extant crocodylians exhibit minimal thermal fluctuations due to their relatively low surface to volume ratio, which helps to minimize heat loss (Smith 1976; Markwick 1998; Seebacher *et al.* 1999; Gearty & Payne 2020). As is the case with living species, palaeohistological data seems to support an ectothermic physiology for notosuchians (Cubo *et al.* 2020, 2023; Faure-Brac 2025), possibly requiring behavioural strategies to regulate body temperature during the day, such as burrowing or basking (Marinho & Carvalho 2009; Carvalho *et al.* 2010). Some of the largest known crocodylomorphs include thalattosuchians, tethysuchians and caimanines, which all had a semi-aquatic to fully-aquatic lifestyle and were also probably ectotherms (Sereno *et al.* 2001; Young *et al.* 2014; Wilberg *et al.* 2019; Jouve 2021; Faure-Brac *et al.* 2022; Paiva *et al.* 2022; Forêt *et al.* 2024; Faure-Brac 2025), though this assessment is more controversial for thalattosuchians, especially metriorhynchids (Séon *et al.* 2020). Despite notosuchians being predominantly terrestrial, some taxa possibly frequented freshwater environments, with a few forms even inferred to have been secondarily semi-aquatic ambush predators (e.g. *Lorosuchus nodosus*, *Pepesuchus deiseae* and *Stolokrosuchus lapparenti*; Gasparini *et al.* 1991; Larsson & Gado 2000; Turner & Buckley 2008; Sereno & Larsson 2009; Pol & Powell 2011; Kellner *et al.* 2014; Pinheiro *et al.* 2018), and thus they are likely to have exhibited similar thermoregulatory behaviours to other crocodylomorphs with similar ecologies.



**FIG. 4.** Notosuchian maximum and minimum body sizes in terrestrial (green) and freshwater (blue) ecosystems. Maximum and minimum sizes of each individual are provided in Table 2, represented by their respective confidence of interval. Scale bar represents 50 cm. Illustration created by Science Graphic Design.

Although the pattern of larger body sizes associated with semi-aquatic notosuchians matches that of other crocodylomorphs (Godoy *et al.* 2019; Gearty & Payne 2020; Godoy & Turner 2020), the mode of evolution that gave rise to this condition might be different. Godoy *et al.* (2019) examined which evolutionary model best explains the observed distribution of body size among crocodylomorphs and reported that a multi-regime Ornstein–Uhlenbeck model received the greatest support among the tested models. This suggests that crocodylomorph body size evolution is consistent with an adaptive landscape scenario, in which taxa in each macroevolutionary regime would have constrained upper and lower body size values. According to Godoy *et al.* (2019), the regime shifts would be associated with multiple factors, such as the origin of diverse subclades, but also with ecological transitions, such as from terrestrial to more aquatic habitats. Nevertheless, when exploring the fit of the same evolutionary models to body size data focused specifically on Notosuchia, the authors found a different result, with no clear distinction between tested evolutionary models, including models associated with stochastic evolution (e.g. Brownian motion-based models). Godoy *et al.* (2019) interpreted this as evidence of a more relaxed mode of evolution within Notosuchia, which could help explain the high body size disparity seen in the group. Therefore, although notosuchian body

size evolution might indeed be driven by a different mode of evolution than other crocodylomorphs, our body size estimates indicate that ecological transitions also played an important role. Aquatic adaptations may have imposed constraints on the body size of more aquatic notosuchians, as seen in other crocodylomorph clades (Gearty & Payne 2020).

#### *The influence of body size on the diversity & extinction of notosuchians*

Body size is a critical factor for many biological aspects of organisms, including extant crocodylians (Grigg *et al.* 1998; Grigg & Kirshner 2015; Godoy & Turner 2020; Stockdale & Benton 2021; Benson *et al.* 2022), and it might also be one of the primary determinants of extinction selectivity during biotic crises in many vertebrates (Liow *et al.* 2008; Codron *et al.* 2012; Wilson 2013; Smith *et al.* 2018; Monarrez *et al.* 2021; Aubier *et al.* 2023; Boscaini *et al.* 2025). Since their origin, crocodylomorphs have survived numerous extinction events (Bronzati *et al.* 2015; Mannion *et al.* 2015; Tennant *et al.* 2016; de Celis *et al.* 2020; Aubier *et al.* 2023; Forêt *et al.* 2024; Payne *et al.* 2024), including the Cretaceous–Palaeogene (K–Pg) mass extinction, 66 Ma, which eradicated many vertebrate groups, such as non-avian dinosaurs,

pterosaurs, and most marine reptiles, especially large-bodied taxa (e.g. Bardet 1995; Barrett *et al.* 2008; Benson *et al.* 2010; Benson 2018; Brusatte *et al.* 2015). Several crocodylomorph groups survived the K–Pg extinction, including crocodylians, dyrosaurids and sebecoids (Brochu 2003; Martin *et al.* 2014; Mannion *et al.* 2015; Pol & Lardi 2015; Cidade *et al.* 2019; Godoy *et al.* 2019; Godoy & Turner 2020; Bravo *et al.* 2021, 2025; Jouve 2021; Aubier *et al.* 2023; Forêt *et al.* 2024). Crocodylians underwent considerable diversification after the crisis (Brochu 2003; Cidade *et al.* 2019; Rio & Mannion 2021), with an increase in morphological disparity and body sizes (Godoy *et al.* 2019), linked to climatic and environmental changes throughout the Cenozoic (Mannion *et al.* 2015; Solórzano *et al.* 2020; Paiva *et al.* 2024; Payne *et al.* 2024). Similarly, tethysuchians also diversified considerably, possibly as a result of the availability of vacant ecological niches, notably in the marine realm, as well as high temperature conditions, which potentially facilitated the evolution of large-bodied taxa (Martin *et al.* 2014; Cidade *et al.* 2019; Godoy *et al.* 2019; Jouve 2021; Forêt *et al.* 2024). Moreover, members of boundary-crossing lineages of both crocodylians and tethysuchians were primarily semi-aquatic (Cidade *et al.* 2019; Jouve 2021).

Freshwater environments were possibly less affected by the K–Pg extinction event (Sheehan & Fastovsky 1992; Robertson *et al.* 2013), and this factor might also have influenced the survival of sebecoids, the only known members of Notosuchia to persist into the Cenozoic (Brochu 2003; Pol & Lardi 2015; Cidade *et al.* 2019; Godoy *et al.* 2019; Bravo *et al.* 2021, 2025; Aubier *et al.* 2023). Sebecoids were already present before the extinction event. The stratigraphically earliest known probable member of the group, *Ogresuchus furatus*, from the latest Cretaceous of Spain, exhibited a terrestrial lifestyle (Sellés *et al.* 2020; though see Ruiz *et al.* (2025) for a baurusuchian placement of *Ogresuchus*). Following the K–Pg extinction, the earliest recorded sebecoids include the semi-aquatic *Tewkensuchus salamanquensis* from the early Paleocene (Bravo *et al.* 2025), followed by the first terrestrial sebecids of the Paleocene, *Sebecus querejazus* and *Sebecus ayrampu* (Buffetaut & Marshall 1991; Bravo *et al.* 2021). Subsequently, *Lorosuchus nodosus* (though see Bravo *et al.* (2021) for a position outside Sebecidea), from the middle Paleocene to early Eocene, probably occupied a semi-aquatic habitat (Pol & Powell 2011), whereas the early Eocene species *Bretesuchus bonapartei* and *Sahitisuchus fluminensis* had a terrestrial lifestyle (Gasparini *et al.* 1993; Kellner *et al.* 2014).

Although most phylogenetic analyses support a close relation between sebecoids and baurusuchids (Pol *et al.* 2014; Bravo *et al.* 2021; Nicholl *et al.* 2021; Marinho *et al.* 2022), others recover sebecoids as more closely

related to peirosaurians, resulting in the Sebecia clade (Larsson & Sues 2007; Ruiz *et al.* 2021, 2025). Some peirosaurians, such as *Barreirosuchus franciscoi*, *Pepesuchus deiseae* and *Stolokrosuchus lapparenti*, were likely to have been semi-aquatic (Gasparini *et al.* 1991; Larsson & Gado 2000; Iori & Garcia 2012; Pinheiro *et al.* 2018; Sena *et al.* 2018; Ruiz *et al.* 2025). If the latter phylogenetic hypothesis is correct, it is therefore plausible that some early sebecoids might also have been semi-aquatic. However, considering that peirosaurians were semi-aquatic animals, it raises the question of why that group did not survive the K–Pg extinction event.

It is likely that small-bodied notosuchians were less affected by the K–Pg extinction, whereas large-bodied members were more susceptible, as seen in many other terrestrial vertebrate groups (Longrich *et al.* 2012, 2016; Benson 2018; Smith *et al.* 2018; Boscaini *et al.* 2025). Small-bodied species tend to have a diverse diet, whereas specialists might be at higher risk of extinction in abiotic crises, as specialization increases vulnerability over time and generalism fosters persistence, ecological fitting, and opportunities for speciation (Colles *et al.* 2009; Dennis *et al.* 2011). Small notosuchians (e.g. early sebecoids) are likely to have exhibited less dietary specialization in the early Cenozoic (Kellner *et al.* 2014) and a more diverse diet (Ösi 2014; Montefeltro *et al.* 2020; Aubier *et al.* 2023; Melstrom *et al.* 2025), which allowed them to adapt to the fluctuating resource availability in the aftermath of the K–Pg transition. As inferred for ectothermic animals, notosuchians are most likely to have relied on environmental temperature: a moderate resting (Cubo *et al.* 2020, 2023) and high aerobic capacity (Sena *et al.* 2023, 2025) has been reconstructed for the group. This suggests that the K–Pg extinction might have disproportionately impacted highly active terrestrial predators with greater hunting capabilities, such as large-bodied notosuchians. Therefore, small, semi-aquatic notosuchians with less specialized diets might have been more likely to survive. Different responses to environmental changes may have occurred, potentially shaped by variations in ecological strategies and, consequently, different body sizes. Studies investigating and exploring the relation between diverse diets, metabolic plasticity, and extinction resilience across different notosuchian body sizes could provide deeper insights into how the group adapted to the environmental challenges of the K–Pg transition and early Cenozoic.

## CONCLUSION

Notosuchians exhibit a diverse bauplan, ranging from small to large body sizes. Their skull length is demonstrated to be a reliable proxy for estimating body size, yielding values between 34.5 and 238 cm. In the

evolutionary history of the group, the earliest notosuchians were relatively small (<100 cm), but as arid climatic conditions became more prevalent, their body sizes increased. Larger body sizes are primarily associated with semi-aquatic habits, as observed in some peirosaurids and sebecoids, a pattern already found in other crocodylomorphs (Godoy *et al.* 2019; Gearty & Payne 2020; Godoy & Turner 2020). However, small-bodied forms may have been favoured due to their habits and enhanced survivability following the K–Pg extinction event, particularly in less-specialized species. Environmental changes played a crucial role in shaping variations in ecomorphotypes and body size among notosuchians. Future fossil discoveries, incorporating additional skeletal elements, will provide more accurate and precise body size estimations and offer deeper insights into ecological adaptations of these crocodylomorphs to changing environmental conditions.

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## DATA ARCHIVING STATEMENT

Data and code for this study are available in Zenodo: <https://zenodo.org/records/20208106>.

*Editor.* Gabriel Ferreira

## SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.70061>):

**Table S1.** Measurements of all complete crocodylomorph specimens and incomplete notosuchian specimens not included in the main text.

**Table S2.** Comparisons of notosuchian body sizes from the literature and the current study.

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