



Revisiting the aerobic capacity of Notosuchia (Crocodyliformes, Mesoeucrocodylia)

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This study examines the metabolic rates of notosuchian crocodyliforms. Although predominantly composed of terrestrial forms, the group also encompasses the putatively semi-aquatic itasuchids. The notosuchian record is particularly rich in Brazil and Argentina, which provides a basis for understanding their ecology and physiology. This research expands a previous study that investigated the aerobic capacities of these organisms, considering blood flow rate (Q) in the femoral nutrient artery as a proxy to infer their maximal aerobic metabolic rates, critical for understanding peak aerobic performance during strenuous activities. Femoral nutrient foramina act as conduits for the major blood supply to the bone and are correlated with aerobic capacity, providing insights into the physiological capabilities of the studied taxa. This study revisits and expands upon a previous dataset by including additional taxa and provides more precisely adjusted mass-independent maximal metabolic rate predictions for the sample of Notosuchia. We incorporate data from a broader spectrum of extant tetrapods and employ Phylogenetic Eigenvector Maps (PEM) to refine our analyses. PEM allow the inclusion of an auxiliary predictor related to the response variable, alongside phylogenetic eigenvectors. The results indicate notosuchians possessed higher mass-independent maximal metabolic rates (MMRs) than extant Crocodylia, and lower than those of extant varanid lizards, which suggests an elevated aerobic capacity, enabling a more active lifestyle compared to extant crocodylians. The study addresses previous miscalculations for the body mass exponent on the MMR unit. We introduce Q values based on the nutrient femoral artery lumen area instead of the total area of the nutrient foramen, and provide a corrected MMR for *Crocodylus porosus*, allowing more accurate predictions of notosuchian aerobic capacities. This research reveals metabolic flexibility within crocodyliforms, with an elevated aerobic capacity allowing notosuchians to sustain vigorous activities, possibly related to their terrestrial adaptations and active foraging strategies. □ Bone, femoral nutrient foramina, metabolic rates, Notosuchia, Phylogenetic Eigenvector Maps

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Notosuchian crocodyliforms are known for their high diversity during the Late Cretaceous, exhibiting a broad range of anatomical modifications including specialized maxillo-mandibular apparatuses with dentitions that resemble those of mammals (O'Connor *et al.* 2010; Ösi, 2013; Melstrom & Irmis 2019). Predominantly terrestrial, forms like the *Araripesuchus* and *Baurusuchus* species show adaptations to such habitats, as laterally compressed snouts and anteriorly-placed nostrils, and limb modifications indicative of cursorial locomotion, including closer radioulnar spacing and weakly sigmoidal femora with less torsion of the femoral head (Andrade & Bertini 2008; Nascimento & Zaher 2012; Godoy *et al.* 2016; Fernández Dumont *et al.* 2020). Conversely, forms like *Pepesuchus* were likely semi-aquatic (Pinheiro *et al.* 2018; Sena *et al.* 2018; Ruiz *et al.* 2024). Especially diverse in the Cretaceous of Gondwana, notosuchians are well represented in the Bauru Basin, southeastern Brazil, with over thirty described species (Ruiz *et al.* 2021; Langer *et al.* 2022; Aubier *et al.* 2023; Martins *et al.* 2024; Borsoni *et al.* 2024).

Recently published studies on crocodyliform metabolism conclude that marine lifestyles impose strong selective pressures favoring larger body sizes in crocodyliforms, compared to those living on land or in semi-aquatic forms (Gearty & Payne 2020). This was attributed to physiological constraints imposed by the marine environment, such as the need for greater diving capacity and efficient heat retention. Cubo *et al.* (2020, 2023) inferred notosuchian metabolic rates using cell and vascular densities, and the probability of endothermy using vascular canal size, in long bone thin sections. This approach allowed to infer an ectothermic thermometabolism and moderate resting metabolic rates, akin to those measured in living varanid lizards. Sena *et al.* (2023) investigated the notosuchian aerobic capacities, using femoral nutrient foramina area as a measure of the maximum rate of oxygen consumption (VO_2 max). This rate is crucial to understand an animal's capacity for sustained aerobic, high-intensity activities. Previous works by Seymour *et al.* (2012) Seymour (2013) showed that VO_2 max is a key indicator of tetrapod's peak aerobic performances. Later studies confirmed the potential links between nutrient foramina size and physiological traits (e.g. Allan *et al.* 2014; Seymour *et al.* 2024).

The concept of maximum metabolic rate is central to this discussion. It refers to the animal's capacity to sustain vigorous activities, with more athletic taxa generally maintaining higher rates (Hayes *et al.* 2018; Wang *et al.* 2001; Weibel *et al.* 2004). It is hypothesized that variation in blood perfusion reflects differences in the metabolic capacity of species, with animals exhibiting

higher levels of locomotory activity expected to have higher blood perfusion rates through larger blood vessels (Weibel *et al.* 2004). This relationship can be assessed using the nutrient foramina opening area in long bones, which suggests that more athletic animals had higher perfusion rates required for bone remodeling to repair microfractures in response to stress during locomotion (Seymour *et al.* 2012). Hence, the metabolism of extinct species has been investigated by measuring foramina periosteal opening on the shafts of their long bones and comparing them with data on extant data (e.g. Cubo *et al.* 2024; Knaus *et al.* 2021; Seymour *et al.* 2024; Varela *et al.* 2024). Ventilatory and cardiovascular processes associated with oxygen transport and delivery are augmented during activity. Oxygen transport during the peak metabolic activity involves several steps through convection of oxygen into the lungs by ventilation; oxygen diffusion from the lung air into the bloodstream, convection of oxygen-rich blood to peripheral tissues, and diffusion of oxygen to the mitochondria within cells where it is used for energy production (Bennett & John-Alder 1984; Farmer & Hicks 2000; Weibel *et al.* 2004).

Sena *et al.* (2023) concluded that notosuchians might have been more athletic than extant ambush crocodylians, possibly due to their parasagittal posture (as inferred by their postcranial anatomy) enabling more active behaviours. Building on these findings, our current study expands the analysis of maximal metabolic rates in notosuchians by incorporating nine new tetrapod taxa to the previous database (Sena *et al.* 2023) and updating the VO_2 max assessment for *Crocodylus porosus*. This aims to complement our knowledge about the physiological constraints of these crocodyliforms.

Material and methods

Dataset scope

In this investigation, we reassess previous inferences of mass-independent MMR retrodictions for seven notosuchian taxa. Our updated dataset includes 29 extant tetrapod species, including 20 species from Seymour *et al.* (2012) and nine newly added to that of Sena *et al.* (2023). This includes: two extant crocodylian species, *Alligator mississippiensis* and *Crocodylus niloticus*, three mammals (*Papio hamadryas*, *Helogale parvula*, and *Acinonyx jubatus*) and four lizards (*Tupinambis teguixin*, *Iguana iguana*, *Amphibolurus barbatus*, and *Varanus salvator*) (Supplementary Information). The additional taxa were selected based on specimens from the palaeontological collection

of the National Museum of Natural History in Paris (MNHN).

Phylogenetic framework

We derived phylogenetic relationships from the literature, employing Zurano *et al.* (2019) for Cetartiodactyla, Upham *et al.* (2019) for other mammals, Pyron *et al.* (2013) and Vidal & Hedges (2005) for squamates in general, Villa *et al.* (2018) for varanid lizards, and Pinheiro *et al.* (2021) for Mesoeucrocodylia. Branch length data for extant taxa were gathered from the Time Tree of Life (timetree.org, accessed 31 January, 2024), and those for the extinct ones from the Paleobiology Database (paleobiodb.org, accessed 31 January, 2024) and Buffrénil *et al.* (2021).

We adopted the *Notosuchia* clade definition of Leardi *et al.* (2024), encompassing *Eunotosuchia* and *Sebecia*, with their compositions as per established systematics (e.g. Larsson & Sues 2007; Pinheiro *et al.* 2018).

Morphological and physiological measurements and calculations

We focused on the area of the femoral nutrient foramina, which are responsible for more than half of the total blood flow to the bone, as an indicator of aerobic capacity, following the methodology proposed by Seymour *et al.* (2012, 2019). To calculate the blood flow rate (\dot{Q}), we determined the cross-sectional areas at the periosteal openings of the foramina by segmenting the nutrient foramina from tomographic scans of the femora of our sampled notosuchians using Mimics software at the MNHN. For specimens with multiple foramina, we added the corresponding areas and computed the radius of the resulting area assuming circularity.

We estimated the nutrient artery lumen area, assuming that it corresponds to 20% of the nutrient foramen area. In this, we followed Hu *et al.* (2021), who found that the lumen of a pressurized nutrient artery occupies 20% of the foramen area. In our previous work, we used the total area of the nutrient foramen, leading to an overestimation of our measurements. The femoral nutrient arterial radii were determined by the circle area equation, considering the nutrient arterial lumen areas. The blood flow rate (\dot{Q} ; mL/s), based on the arterial internal radius (r_i ; cm) of the species in our dataset was calculated using the equation proposed by Seymour *et al.* (2019):

$$\log \dot{Q} = -0.20 \log r_i^2 + 1.91 \log r_i + 1.82$$

The femoral nutrient foramina areas for notosuchians were sourced from Sena *et al.* (2023), and previously published values for extant species are provided in the Supplementary Information. The inferred body masses (BM) of the sampled notosuchians were published by Woodward *et al.* (2024) and were obtained applying the equation:

$$BM = \exp(3.6427 \cdot \ln(\text{femur length}) - 14.66296)$$

Phylogenetic comparative methods

A palaeobiological inference model for maximum metabolic rate (MMR) was developed using phylogenetic eigenvector maps (PEMs; see Guénard *et al.* 2013). The PEMs were constructed using the 'MPSEM' package (Guénard *et al.* 2013) in R (R Core Team 2023). This model enabled us to estimate the MMR of notosuchians, along with corresponding 95% confidence intervals. The normality of the residuals was checked using the Shapiro-Wilk test.

Metabolic Rate Estimations Unit

Our current methodology diverges from that of Sena *et al.* (2023), in which a weighted average of exponents was employed specifically for notosuchians. Although dividing the MMR by body mass yields a mass-specific MMR, this parameter remains influenced by body mass. A mass-independent MMR is obtained by dividing the MMR by body mass raised to an exponent determined through a regression analysis of known MMR values and body masses (White & Seymour 2005; Seymour 2013). The method applied by Sena *et al.* (2023) calculates mass-independent maximum metabolic rates using different exponents, 0.829 for sauropsids (Bennett & Dawson 1976; Seymour *et al.* 2013) and 0.87 for synapsids (White & Seymour 2005) to consider the physiological and metabolic differences between these groups. However, this approach involved using different units for different data points in a single statistical analysis and this is mathematically questionable.

Here, we employed a 0.84 exponent to body mass unit (expressed in grams) for all data points. This exponent corresponds to the phylogenetic mean computed recovered in using Mesquite (Maddison & Maddison 2014). This generates a single character matrix from distinct extant species exponents (0.829 for sauropsids 0.87 for synapsids) and a question mark for extinct taxa. Then we used the functions for extinct taxa, with the exponent recovered by using the 'Reconstruct ancestral states' function inside 'Trace' tool and 'character history source' to obtain

the phylogenetic mean of the exponent of the sample. This approach is more aligned with evolutionary principles and apparently more closely reflects the characteristics of the studied crocodyliforms. In this case, the exponent is 0.84, so mass-independent MMR data have units of $\text{mL O}_2 \text{ h}^{-1} \text{g}^{-0.84}$.

Results

For this study, the mass-independent MMR for *Crocodylus porosus* was corrected for $1.11 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-0.84}$ (Supplementary Information) and new data for two crocodylians, *Alligator mississippiensis* and *Crocodylus niloticus*, were included in our dataset. The retrodictions show a similar mass-independent values for all studied notosuchians with a mean value of approximately $1.55 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-0.84}$ using phylogeny+ \dot{Q} inference model (Table 1). Notosuchia mass-independent MMRs are higher than those measured for extant crocodylians, and lower than those of varanid lizards. The MMR lower confidence interval of notosuchians includes the sampled crocodylians and other sauropsids, such as *Iguana iguana*, the blue-tongued skink, *Tiliqua scincoides*, and the Eastern bearded dragon *Amphibolurus barbatus*.

The phylogeny+ \dot{Q} inference model has an adjusted R^2 of 0.97 and AICc of 34.43 ($p < 0.001$). We performed a leave-one-out cross-validation test to check the robustness of the model. Then, we used the

Table 1. Mass-independent maximum metabolic rate (MMR) of sampled notosuchian taxa retrodicted through phylogenetic eigenvector maps using \dot{Q} as co-predictor.

Species	Collection number	Mass-independent MMR ($\text{mL O}_2 \text{ h}^{-1} \text{g}^{-0.84}$)
<i>Campinasuchus_dinizi</i>	CPPLIP 1847	1.5809
<i>Araripesuchus_sp</i>	LAPEISA-Pal- 0032	1.5737
<i>Sahitisuchus_fluminensis</i>	MCT 1835-R	1.5441
<i>Sahitisuchus_fluminensis</i>	MCT 1831-R	1.5834
<i>Itasuchus_jesuinoi</i>	DGM 434-R	1.5156
<i>Pissarrachampsa_sera</i>	LPRP USP 0019	1.5134
<i>Pissarrachampsa_sera</i>	LPRP USP 0019b	1.4869
<i>Coronelsuchus_civali</i>	FFP PG 14	1.5869
<i>Uberabasuchus_terrificus</i>	CPPLIP 501	1.5631

non-parametric Wilcoxon signed-rank test to compare the MMR values measured in extant species and compiled by Seymour *et al.* (2012) (red, purple and orange squares in Fig. 1). We did not find significant differences between the observed and the predicted values (p -value = 0.3579). Thus the retrodictions for Notosuchia made by our model are robust.

Discussion

In this study, we found that the mass-independent Metabolic Rate (MMR) values ($1.55 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-0.84}$) are higher than those ($0.7 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-0.85}$) previously reported by Sena *et al.* (2023). Our analysis, based on Phylogenetic Eigenvector Maps (PEM), suggests that the phylogeny+ \dot{Q} model is effective for predicting mass-independent MMR. These more precise retrodictions reveal that Notosuchia likely possessed a more elevated aerobic capacity compared to what was previously retrodicted by Sena *et al.* (2023).

This study corrects the mass-independent MMR of *Crocodylus porosus* using a value ($0.137 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-1}$) higher than the previous miscalculations ($0.021 \text{ mL O}_2 \text{ h}^{-1} \text{g}^{-1}$). Recovering the phylogenetic mean of 0.84 from our dataset as the exponent for body mass simplifies our analysis and offers a broader overview of metabolic scaling from an evolutionary perspective. This approach, however, may not adequately account for the inherent physiological and metabolic adaptations distinguishing endotherms from ectotherms within our sample (Seymour 2013). Such disparities can influence metabolic rates, suggesting that a singular exponent may fall short of capturing the complexity in these variations.

Among the sauropsids, the mass independent MMR range for notosuchians encompass those measured for blue-tongued skinks, *Tiliqua* spp. In scincid and agamid lizards, such as *Tiliqua* and *Amphibolurus*, the unicameral lungs are relatively large and highly expandable (Daniels *et al.* 1994). The absence of a muscular diaphragm allows these lungs to expand freely into a substantial portion of the body cavity. Additionally, the shape and volume of the lungs exhibit a certain degree of plasticity due to the abdominal organs, which can compress the caudal and ventral regions of the lungs (Munns & Daniels 2007). This anatomical flexibility may contribute to the unexpectedly relative high MMR values observed in the sampled blue-tongue skinks and agamid lizards.

As ectothermic tetrapods, notosuchians' physiological functions, including resting and maximal oxygen consumption rates, significantly rely on ambient temperatures (Bennett & John-Alder 1984; Cubo *et al.*

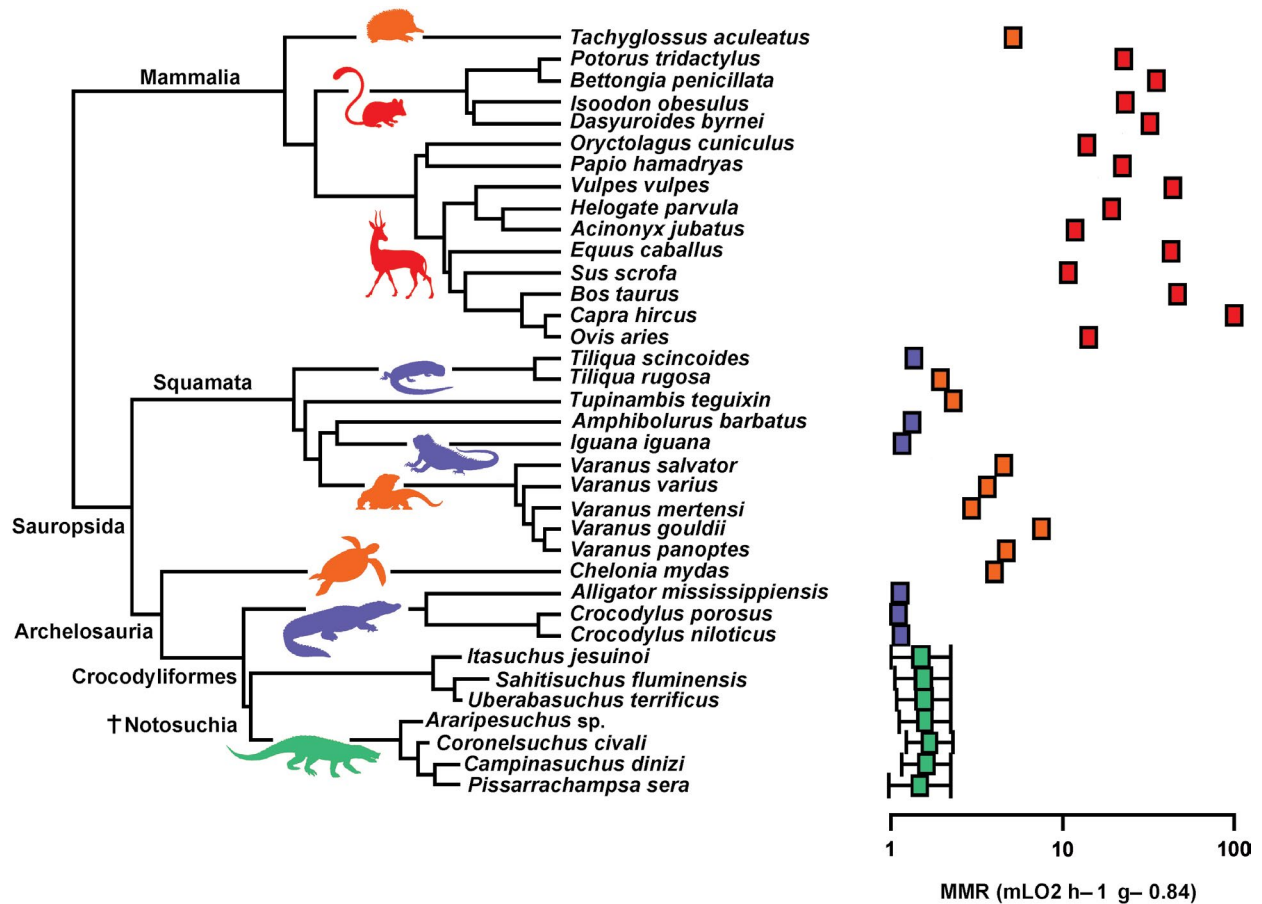


Fig. 1. Phylogenetic relationships among extant taxa used to construct the mass-independent maximum metabolic rates inference model and the extinct *Notosuchia* for which we performed retrodictions using \hat{Q} as co-predictor. Branches are proportional to time. The tetrapod silhouettes have been modified and adapted from copyright-free images provided by Freepik (<http://www.freepik.com>).

2020, 2023). This thermal dependence likely shaped their daily activity patterns, enabling periods of intense locomotion and exploration, similar to patterns observed in other ectothermic species such as varanid lizards. Such behavioural flexibility would have been crucial for large notosuchians, such as baurusuchids (e.g. *Pissarrachampsia sera*), to confront predators or actively pursuing prey, as suggested for the group (Montefeltro *et al.* 2020), whereas smaller species (e.g. *Araripesuchus*) might have relied on agility to evade threats.

A burrowing habit has been suggested for a few notosuchians. Vasconcellos & Carvalho (2006) suggest that the holotype of the peirosaurid *Uberabasuchus terrificus* might have been preserved articulated within a burrow. Martinelli *et al.* (2019) described the first Late Cretaceous burrow attributed to a notosuchian, found in sediments of the Serra da Galga Formation in Uberaba, Minas Gerais state, southeastern Brazil. Considering this habit, notosuchians could

remain active throughout the day to reenter their burrows during the late afternoon, with the body temperature falling throughout the evening and night. This behaviour is described for tegu lizards by Milsom *et al.* (2008). Difficulties still arise from the unknown disposition of maintenance processes during activity in determining how long these crocodyliforms could maintain strenuous exercise. This consideration should include anaerobic glycolysis with progressive acidosis and lactate accumulation (Bennett 1978). For now, we can say they have greater endurance than extant crocodylians but likely less than teiid lizards. Nevertheless, the studied notosuchians still display mass-independent MMRs almost half of those values measured in varanid lizards. Carrier (1987) showed that the presence of large vertebral processes supporting the locomotor muscles and unloading of the respiratory systems and the presence of parasagittal members indicate the possession of diaphragmatic muscles and the lateral stability of the vertebral

column, allowing and efficient breathing that is associated with endothermy.

Several notosuchian taxa, including the *Sebecus icaeorhinus*, *Notosuchus terrestris*, *Mariliasuchus amarali*, and *Pakasuchus kapilimai* bear postcranial modifications that suggest an upright stance and possible cursorial abilities. These features hint at a more efficient terrestrial movement strategy and are reminiscent of those found in certain land-dwelling mammals (Pol 2005; Nascimento & Zaher 2010; Pol et al., 2012; Cotts et al. 2016; Godoy et al. 2016; Montefeltro 2019). Additionally, the evolution of a mammal-like heterodont dentition occurred independently across several groups, including sphagesaurids, *Araripesuchus* spp., *Malawisuchus mwakasyungutiensis*, and *Chimaerasuchus paradoxus*. This suggests dietary diversity within the groups (Ósi 2013; Pol et al. 2014; Melstrom & Irmis 2019).

Whereas baurusuchids, itasuchids, and sebecids are characterized by their large size, other notosuchians are smaller, comparable to medium-sized mammals. This similarity in size implies that these notosuchians might have occupied similar ecological roles in the Gondwanan landmasses as mammals did in the northern continents, indicating a convergent evolutionary path towards filling ecological niches across different geographical regions (O'Connor et al. 2010).

Varanid lizards and crocodylians exhibit significant differences in their cardiopulmonary systems, which underlie their distinct aerobic capabilities and responses to exercise. Varanids, known for their exceptional aerobic abilities among non-crocodylian sauropsids, can consume oxygen at rates twice as high as other similar-sized lizards (Thompson & Withers 1997; Farmer 2015a). This high level of aerobic activity is supported by their specialized heart structure, which includes thicker walls and a muscular ridge that effectively separates the chambers during heartbeat (Webb et al. 1971). The gular pump likely assists with ventilation in these lizards, supporting their capacity for high aerobic activity by ensuring balanced and compensated circulatory convection (Frappell et al. 2002). Moreover, unidirectional airflow without extrapulmonary air sacs has been identified in non-avian sauropsids such as crocodylians, varanids and iguanas (Farmer 2015b; Farmer & Sanders 2010; Schachner et al. 2014; Cieri et al. 2014). Crocodylians shares some cardiac features with the highly active birds like the complete septation between the atria and ventricles and the persistence of the right aortic arch as the parent vessel of the carotid arteries. However, unlike birds, both aortic arches persist in adult crocodylians. Although these animals are capable of sustained locomotion, they have a low gas transport capacity and require from 2 to 4 hours to recover after intense exercise (Bennett et al.

1985). The findings that notosuchians possessed slightly higher maximal metabolic rates than their extant crocodylian relatives show that a broader metabolic flexibility was present within crocodyliforms evolutionary history. This variation in the metabolic rates of notosuchians is in line with the countless studies that deal with the morphological and dental variation of this group, reinforcing the notion of an evolutionary capacity to occupy different ecological roles.

Conclusions

This investigation into the metabolic rates of notosuchian crocodyliforms, which expands a previous dataset with nine additional tetrapod taxa, provided new and better insights into their physiological constraints. These findings confirm that notosuchians possessed a mass-independent maximal aerobic capacity that, although lower than that of varanid lizards, exceeded that of extant crocodylians. Comparatively, this elevated aerobic capacity likely facilitated a more active lifestyle, supported by their anatomical adaptations for terrestrial mobility, such as a parasagittal stance. The corrected MMR values for *Crocodylus porosus*, along with the inclusion of additional crocodylian species (i.e. *A. mississippiensis* and *C. niloticus*) and an adjustment in the mass-independent MMR, have refined our understanding of notosuchian metabolic rates. This provides a clearer scenario of notosuchian ecological roles and adaptive strategies within the Cretaceous ecosystems.

Supplementary Material

File 1. Dataset

File 2. Mass-independent_MMRdata1_0.84a

File 3. Mass-independent_MMRdata1_0.84b

File 4. Script_PEM_Notosuchia_2

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