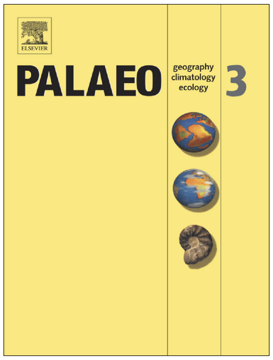

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The cost of living in Notosuchia (Crocodyliformes, Mesoeucrocodylia)

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Abstract

Limbs of terrestrial notosuchian crocodyliforms are characterized by a permanent parasagittal position that approaches that of mammals and dinosaurs. Thus, we expect high maximal rates of oxygen consumption (i.e., high aerobic capacities). To test this hypothesis, we inferred mass-independent maximal metabolic rates (MMR) in seven notosuchian species using the femur blood flow rate ($\dot{Q}$; $cm^3 s^{-}$) correlated with the maximal metabolic rate as a proxy. We employed a phylogenetic eigenvector maps (PEMs) inference model based on 20 extant tetrapod species. Generally, ectothermic amniotes have lower maximal metabolic rates than similarly sized endotherms. However, certain anatomical features of the cardiorespiratory system in varanid lizards enable them to develop a more active lifestyle than other ectothermic sauropsids. We found that the retrodicted mass-independent aerobic capacity values for Notosuchia are lower than those measured in mammals. These values are higher than those quantified in extant Crocodylia, but lower than values measured in extant lizards. Notosuchians exhibit $\dot{Q}$ values on the femoral shaft higher than *Crocodylus porosus*, suggesting greater oxygen consumption during intense exercise, but significantly lower than those measured in varanid lizards. This condition probably allowed notosuchians to engage in prolonged strenuous locomotion activities, such as hunting prey, defending themselves from predators or avoiding competitors. The evolution of Mesoeucrocodylia metabolism involves at least two phenotypes, a relatively high (Notosuchia) and a low (Neosuchia, Crocodylia) MMR.

Significance statement

We modeled three-dimensional (3D) objects from Notosuchia femora and conducted measurements on the nutrient foramina size. These values were used as a proxy to infer the blood flow rate ($\dot{Q}$) and provided insights into the maximal metabolic rate in these terrestrial crocodyliforms. Our findings suggest that Notosuchia were likely ectotherms but exhibited a more active lifestyle than extant Crocodylia. However, they had aerobic capacities significantly lower than those measured in varanid lizards.

1 Introduction

Vertebrates expend energy in diverse ways, including evading predators' attacks, foraging, growing, reproducing, homeostasis maintenance, fighting to establish a social status, etc. All these functions influence their overall fitness. The energetic cost of living can be computed using the aerobic metabolic rate measured using oxygen consumption (Clarke and Fraser, 2004; Hulbert and Else, 2000). Such measure is possible because the energy production rate of 20 kJ per liter of oxygen consumed is constant during the oxidation of nutrients in mitochondria, regardless of the intake of carbohydrates, proteins or lipids (Schmidt-Nielsen, 1997; Tieleman et al., 2009). Endotherms consume more O_2 than ectothermic vertebrates per unit of mass (Berner, 1999). This difference mainly arises from endotherms' generation of metabolic heat through non-shivering thermogenesis to maintain a body temperature higher than the ambient. Basal or standard (BMR or SMR; Hulbert and Else, 2004) and maximal (MMR) metabolic rates are respectively the lowest and the highest values of the range of aerobic metabolic activities in animals (Wiebel et al., 2004). BMR corresponds to the lowest metabolic rate in endotherms, and SMR to the metabolic rate at the thermopreference temperature in ectotherms. The driving forces governing BMR/SMR and MMR differ. Basal and standard metabolic rates appear to be primarily influenced by the metabolic activities of visceral organs and the brain (Else and Hulbert, 1985). Conversely, the maximal rate of aerobic metabolism is associated with the maximal oxygen amount that can be transported from the environment to the mitochondria (Norin and Clark, 2016). BMR is measured in adults at rest during a non-reproductive stage and a post-absorptive state under thermoneutral conditions, and is linked to the energy expenditure required for essential functions involved in tissue maintenance and homeostatic mechanisms necessary for sustaining life (Auer et al., 2015; Wiebel et al., 2004).

The aerobic MMR (VO_2 max) represents the peak rate of aerobic metabolism in an animal during strenuous activities, when the circulatory and respiratory systems are stressed to their uttermost capacities (Wang et al., 2001). It sets an upper limit to sustained vigorous locomotor capacity (Hayes et al. 2018) with more athletic species having higher MMR for their body mass (Weibel et al., 2004). This process occurs sequentially 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 (Farmer and Hicks, 2000; Wiebel et al., 2004).

Seymour et al. (2012) proposed that aerobic MMR in extinct amniotes can be estimated using the femoral blood flow rates computed from the radius of the nutrient foramen and the femoral length. In non-avian sauropsids, aerobic capacity also appears to be correlated with their lifestyle and ecology, particularly among varanids (Andrews and Pough, 1985; Christian and Conley, 1994). Nutrient foramina in long bones of tetrapods are the large openings through which the nutrient arteries enter from the external bone surface, providing blood supply to the cortical bone of the femur shaft (Hughes, 1952; Sim and Ahn, 2014). Femoral nutrient foramina were chosen because they provide a relatively consistent blood flow, as this skeletal element is primarily involved in support and terrestrial locomotion (Brookes and Revell, 1998).

Hayes and Garland (1995) suggested that more interspecific comparative studies should be performed to examine the relationship between basal/standard metabolic rate and maximal aerobic metabolic rate using phylogenetically informed statistical methods. At the time of Robert Bakker (1972) and Armand de Ricqlès (1969; 1972a, b), who were pioneers in the study of vertebrate palaeophysiology, research in this area was significantly limited compared to what palaeobiologists are capable of at this moment in time. Current studies have demonstrated that it is now possible to perform reliable inferences about the physiology of extinct tetrapods, as suggested by Hayes and Garland (1995). Phylogenetic eigenvector maps (PEMs; Guénard et al., 2013) and phylogenetic logistic regressions (PLRs; Ives and Garland, 2010) have been used to infer important traits related to the evolution of the metabolism of fossil tetrapods. Noteworthy, recent discoveries performed using these methods have revealed that Notosuchia were terrestrial ectothermic crocodyliforms (Cubo et al., 2020; 2023). In particular, PEMs have been widely employed to retrodict resting metabolic rates (RMR) in archosauromorphs (Cubo and Jalil, 2019; Cubo et al., 2020; Faure-Brac et al, 2022; Legendre et al., 2016), plesiosaurs (Fleischle et al., 2018), and synapsids (Faure-Brac and Cubo, 2020), and VO_2-max in avian dinosaurs and synapsids (Knaus et al., 2021). Here we have employed this method for the first time to retrodict VO_2-max in a series of notosuchians in order to obtain a more realistic understanding of their physiology, using the volume blood flow rate ($\dot{Q}$; cm^3 s^{-}) (Seymour et al., 2019) as a proxy to retrodict their maximal metabolic rate. From now on in this study we will consider VO_2-max as MMR for comparative purposes. These results will help elucidate the evolution of metabolism in Crocodyliformes.

2 Material and Methods

2.1 Material

Faced with different phylogenetic scenarios for the non-neosuchian Mesoeucrocodylia , here we consider the clade Notosuchia *sensu* Ruiz et al. (2021) as composed by the less inclusive clades Eunotosuchia (*sensu* Ruiz et al., 2021; composed by Uruguaysuchidae, Sphagesauria and Baurusuchidae nested within Baurusuchia) and Sebecia (composed by Itasuchidae, Peirosauridae, Mahajangasuchidae and Sebecidae; e.g., Larsson and Sues, 2007; Pinheiro et al., 2018). Nine femora of seven notosuchian taxa ranging from Cretaceous to Paleogene deposits were analyzed:

Uruguaysuchidae

Araripesuchus sp., Price, 1959. A virtually complete femur (LAPEISA-Pal- 0032), from the Late Cretaceous (Cenomanian) Kem Kem Group, Morrocco. The material is housed in the collection of the Laboratório de Paleontologia e Evolução de Ilha Solteira, FEIS, UNESP, Ilha Solteira, Brazil.

Peirosauridae

Uberabasuchus terrificus Carvalho, Ribeiro & Avilla, 2004. A complete femur (CPPLIP 501) from the Late Cretaceous (Maastrichtian [Dias-Brito et al., 2001; Menegazzo et al., 2016; Soares et al., 2021]) Serra da Galga geological unit, Bauru Group. The specimen is housed at Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”, Complexo Cultural e Científico de Peirópolis, Universidade Federal do Triângulo Mineiro (CCCP, UFTM), Uberaba, Brazil.

Itasuchidae

Itasuchus jesuinoi Price, 1955. A femur (DGM 434-R) from the Late Cretaceous (Maastrichtian [Dias-Brito et al., 2001; Menegazzo et al., 2016; Soares et al., 2020]) Serra da Galga geological unit, Bauru Group. The material is housed at Museu de Ciências da Terra, Companhia de Pesquisas de Recursos Minerais (MCTer, CPRM), Rio de Janeiro, Brazil.

Sebecidae

Sahitisuchus fluminensis Kellner, Pinheiro & Campos, 2014. Two femora (MCT 1831-R and 1835-R) from the Paleocene–Eocene of Itaboraí Basin the material is housed at Museu de Ciências da Terra, Companhia de Pesquisas de Recursos Minerais (MCTer, CPRM), Rio de Janeiro, Brazil.

Sphagesauria

Coronelsuchus civali Pinheiro, Souza, Bandeira, Brum, Pereira, Castro, Ramos & Simbras, 2021. A fragmented femur (FFP PG 14), from the Late Cretaceous of the Bauru Group. The material is housed at Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro (FFP, UERJ), São Gonçalo, Brazil.

Baurusuchidae

Campinasuchus dinizi Carvalho, Teixeira, Ferraz, Ribeiro, Martinelli, Neto, Sertich, Cunha, Cunha & Ferraz, 2011. A femur (CPPLIP 1847) from the Late Cretaceous of the Bauru Group. The specimen is housed at Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price", Complexo Cultural e Científico de Peirópolis, Universidade Federal do Triângulo Mineiro (CCCP, UFTM), Uberaba, Brazil.

Pissarrachampsa sera Montefeltro, Larsson & Langer, 2011. Two femora (LPRP/USP 0019, 0019b) from the Late Cretaceous of the Bauru Group. The specimens are housed at Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo (FFCLRP, USP), Ribeirão Preto, Brazil.

Most of the taxa in our sampling are considered terrestrial crocodyliforms because of the presence of a set of cranial and post-cranial features. Cranial features related to this lifestyle include the presence of lateralized orbits, forward facing external nares and high skulls (e.g., Andrade & Bertini, 2008; Montefeltro et al., 2011; 2020). The postcranial features include robust forelimbs adapted to extensive anteroposterior movements and femoral muscle insertions more similar to those of early pseudosuchians than to those of extant crocodylians (e.g., Riff and Kellner, 2011; Godoy et al., 2016). For *Itasuchus jesuinoi*, its cranial and osteoderm morphologies are not conclusive to infer lifestyle (Marinho et al., 2006), but recent studies have considered this taxon as semiaquatic (Pinheiro et al., 2018; 2023).

2.2 Computed Microtomography (micro-CT) scan imaging and 3D reconstruction of femoral nutrient foramina

The computed microtomography (micro-CT) analyses were carried out using two systems. The smaller bone elements were scanned using the Skyscan/1273 – Bruker system, whereas the larger bone elements were scanned using the Phoenix V|tome|x M system – Waygate Technologies. For the three-dimensional reconstructions of the bones we used the software NRecon version 1.7.1.0 in scanning from Skyscan 1273 and by Datos/x 2 reconstruction software version 2.5.0 – RTM in the Laboratório de Instrumentação Nuclear of the Universidade Federal do Rio de Janeiro (LIN – UFRJ). The parameters set up for the sample scanning are listed in Table S1.

Data processing was performed at the 3D imaging facilities lab of UMR 7207 CR2P (MNHN CNRS UPMC – Paris). The segmentation analysis and measurements of nutrient foramina and additional measurements were made in Mimics® Innovation Suite v.24 (Materialise). Foramina were drawn manually in CT-scan slice views (sagittal, coronal and axial) and then imaged in 3D using the ‘Multiple slice edit’ tool. We measured the cross-sectional area of each foramen using the ‘Area’ tool surrounding the foramen in the axial view and then calculating the radius of the foramen applying the circle area equation ($A=\pi r^2$). The bone length was measured using the ‘Distance’ tool calculating the distance from the distal to the proximal extremities of the 3D object. The circumference of the midshaft of the femora was taken at three different regions drawing manually the bone outline at the midpoint on the long axis of the 3D object using the ‘Area’ tool and then calculating the average of them. We applied a new approach to infer body mass from femur volume (extracted from the 3D object of the bone) in our sampled notosuchians using a reference equation based on 61 specimens of *Alligator mississippiensis*. The ordinary least squares regression model of the relationship between femur volume and body mass is: body mass = exp(1.00729* log(femur volume) – 7.12038 (Woodward et al. 2023). The virtual reconstructions of the femora and their segmented nutrient foramina are available in the supplementary material (Figure S1).

The estimation of the blood flow index (Q_i) (mm^3) was proposed by Seymour et al. (2012): $Q_i=r^4/L$ using the radius (r; measured in mm) of the nutrient foramen and the length (L; measured in mm) of the femur, through a simplification of the Hagen–Poiseuille equation for laminar flow. The estimation of the blood flow rate $\dot{Q}$ (cm^3 s^{-s}) was proposed by Seymour et al. (2019) as $\log\dot{Q}=-0.20$

$\log r_i^2 + 1.91 \log r_i + 1.82$. $\dot{Q}$ is more appropriate to represent the blood flow in vascular canals than Q_i because the relationship in real arteries does not conform to Poiseuille's Law (Seymour et al. 2019). Consistently, in the present study we choose $\dot{Q}$ as our predictor. To compute the $\dot{Q}$ we measured the smallest cross-sectional area along the femoral nutrient foramina to obtain conservative data (Figure 1). In specimens with multiple foramina, we sum up the cross-sectional areas of its foramina and then calculate the radius from the total area to compute $\dot{Q}$.

[Insert figure 1 here]

2.3 Phylogenetic relationships

Phylogenetic relationships among taxa were taken from published literature: Zurano et al. (2019) for Cetartiodactyla, Upham et al. (2019) for other mammalian groups, Pyron et al. (2013) for squamates and Villa et al. (2018) for varanid lizards. The phylogenetic relationship between Mesoeucrocodylia was taken from Pinheiro et al. (2021). The topology and branch lengths information for deeply nested clades in the phylogeny were obtained using Time Tree of Life (http:/www.timetree.org; data downloaded on May 14 2022) to extant taxa and Paleobiology Database (paleobiodb.org; data downloaded on May 14 2022) to extinct taxa. When the ages of two successive nodes collapsed, we arbitrarily added 1 Ma in between the more and less inclusive nodes to facilitate graphic visualization.

2.4 Predictive Modeling

We used phylogenetic eigenvector maps (PEMs; Guénard et al., 2013) and the package MPSEM (Guénard and Legendre, 2018) in R v.4.0.2 (R Core Team 2013) to estimate our response variable, mass-independent maximum metabolic rate (ml O_2 h^{-1} $g^{-0.85}$), for the sampled notosuchians. We built PEMs using the blood flow rate ($\dot{Q}$) as the explanatory variable. The values of absolute MMR and body mass of extant species were compiled by Seymour et al. (2012) from the published literature in which the oxygen consumption rate (VO_2; ml O_2 h^{-1}) was measured using a flow-through respirometry system. The absolute MMR value of a *Crocodylus porosus* specimen weighing 470 kilograms in Seymour et al. (2012) was converted assuming that 164 ml O_2 min^{-1} corresponds to 9847 ml O_2 h^{-1}. Birds were not included in our analysis because of uncertainties associated with additional blood flow through pneumatic foramina and the biomechanical discrepancy in hindlimbs between cursorial and volant birds (Allan et al., 2014).

Considering that MMR is correlated with the body mass, we use the power of 0.83 in sauropsids (Bennett and Dawson, 1976) and 0.87 in synapsids (White and Seymour, 2005). The units of the mass-independent maximal metabolic rates for our retrodictions were computed from the weighted average of the exponents used in the sample extant species containing twelve mammals and eight reptiles. Then the MMR unit of our inferences was ml O_2 h^{-1} $g^{-0.85}$.

To test the robustness of this model we performed a leave-one-out cross-validation test and the non-parametric Wilcoxon signed-rank test to compare the inferred and the measured MMR values in extant taxa. Finally, the resulting inference model was used to infer the MMR in our sample of Notosuchia. PEMs aim to infer the trait variation using the shared phylogenetic history and an explanatory variable (here the volume blood flow rate, $\dot{Q}$). The extent of variation of the response variable (here MMR) differs from (is lower than) that of the explanatory variable (here $\dot{Q}$). This is because the extent of variation depends on the units and the intrinsic nature of each variable.

3 Results

Mean values of femora measurements, body mass, foramina areas and the explanatory variables (Q_i and $\dot{Q}$) are shown in Table S2. *Pissarachampsa sera* presents the highest femora $\dot{Q}$

values, but according to the body mass estimation *Itasuchus jesuinoi* individual was the largest individual in our sample.

The MMR values retrodicted by our analysis for the notosuchian species are similar among them. Notosuchia mass-independent MMRs are significantly higher than those measured in *Crocodylus porosus*, and lower than those measured in other ectotherms, such as varanid lizards and blue-tongued skinks, *Tiliqua scincoides* and *T. rugosa*. The retrodictions of the mass-independent MMR in Notosuchia range from ~0.70 to 0.71 ml O_2 $h^{-1}g^{-0.85}$ using $\dot{Q}$. These estimations show that the analyzed Notosuchia species had higher mass-independent maximal aerobic levels than their closest extant relatives like *Crocodylus porosus* (~ 0.20 ml O_2 $h^{-1}g^{-0.83}$) (Table 1).

[Insert Table 1]

The phylogeny+$\dot{Q}$ inference model has an adjusted R^2 of 0.9361 ($p<0.001$). We performed a leave-one-out cross-validation test to check the robustness of the model. Then, we used the non-parametric Wilcoxon signed-rank test to compare the MMR values measured in extant species and compiled by Seymour et al. (2012) (white squares in Figure 2) with the values predicted by our inference model for these extant species (crosses in Figure 2). Knaus et al. (2021) excluded *Chelonia mydas* from their dataset because it was an outlier, but we keep it in our sample. We did not find significant differences between the observed (white squares in Figure 2) and predicted (crosses in Figure 2) values (p-value = 0.9563). Thus, we used the model to infer maximum metabolic rates and the corresponding 95% confidence intervals in our notosuchian sampled species. Retrodicted values for Notosuchia using these models are shown in Figure 2.

[Insert Figure 2 here]

Regarding the position and number of femoral nutrient foramina recognized among these notosuchians, although as a rule femora present only a single nutrient foramen, in our sample *Sahitisuchus fluminensis* (MCT 1835-R), *Itasuchus jesuinoi, Pissarachampsa sera* (LPRP/USP 0019b) and *Araripesuchus* sp. have two foramina. They are usually located distal to the fourth trochanter as its path were virtually reconstructed (supplementary material, plates S1–S4).

4 Discussion

Results obtained in this study, in conjunction with those from Cubo et al. (2020; 2023) offer comprehensive insights to our understanding of the aerobic metabolic scopes of Notosuchia. Notosuchian maximal metabolic rates are higher than those quantified in living crocodylians. These extinct crocodyliforms show resting metabolic rates similar to varanid lizards (Cubo et al. 2020; 2023), but their mass-independent MMRs are significantly lower. To give an outline, our retrodictions combined with the lower RMR estimations by Cubo et al. (2020; 2023), suggest that notosuchians were ectotherms that possessed a higher aerobic capacity than their closest extant relatives.

The bone microstructural features of amniotes reflect their lifestyle, growth patterns and life history traits (Padian and de Ricqlès, 2020). Both extinct and extant crocodyliforms and other non-avian sauropsids exhibit a similar histological pattern in their long bones, characterized by zones of woven bone containing primary osteons and simple vascular canals, and annuli composed of parallel-fibered bone tissue containing growth marks (Buffrénil et al., 2008; Sena et al., 2018; 2022; Woodward et al., 2014). These similarities are evident in their resting metabolic rate (Cubo et al. 2020; 2023). In contrast, mammals typically possess long bones formed by fibro-lamellar complex and dense Haversian bone (Mayer et al., 2020; Straehl et al., 2013). The amount of bone remodeling reflects the activity level of organisms. MMR of non-avian sauropsids is lower than that of endothermic amniotes (birds and mammals) due to their shorter capacities of strenuous exercise. As a consequence, their athletic performances are reduced compared to birds and mammals (Weibel et al., 2004). Non-avian sauropsids retain more primary bones, requiring less oxygen consumption and smaller nutrient foramina reducing blood flow rate ($\dot{Q}$) compared to endotherms. Conversely, active endotherms usually demand high $\dot{Q}$ to repair damage, such as microfractures caused by intense exercise, especially in large individuals, where high loading forces lead to extensive secondary remodeling (Allan et al., 2014; Straehl et al., 2013).

The maximal capacity for oxygen uptake during exercise in an organism is represented by the MMR. The relatively high oxidative metabolism in notosuchians may be associated with their active cursorial habit. Active predators, such as *Varanus* have much higher levels of oxygen transport compared to herbivorous iguanid and agamid lizards of similar body mass (Bartholomew and Tucker, 1964; Wilson, 1974). Active predators have significantly higher metabolic rates than ambush or fossorial predators. For instance, day-active lizards generally have greater energy requirements than do fossorial lizards of similar body mass (Andrews and Pough, 1985).

This pattern parallels what is observed in mammals, where species using active defense mechanisms such as running and fighting (e.g., horses, goats, cows) exhibit elevated MMRs, whereas more sluggish mammals relying on passive defenses like armor have low MMRs (Seymour, 2013). There are exceptions among sauropsids like *Chelonia mydas*, which has a high activity level involving long-distance migration, swimming and foraging. This species is capable of a significant oxygen uptake during swimming compared with resting (Enstipp et al., 2011). These metabolic differences arise from the higher costs of cardiovascular and muscle work associated with differences in the athletic performance (Zimmerman and Hubold, 1998). With a higher MMR compared to sit-and-wait crocodylians, notosuchians likely utilized more active defense and hunting mechanisms.

The studied notosuchians display mass-independent MMRs lower than those measured in large and mid-sized monitor lizards and blue-tongued skinks but higher than those quantified in extant semiaquatic crocodiles. They have larger femoral $\dot{Q}$, indicative of higher levels of activity, compared to those of their modern relatives suggesting that notosuchians had an elevated oxygen consumption and were engaged in more intense exercise. Terrestrial notosuchians were likely more athletic and probably spent more time in vigorous exercise, such as hunting prey or fighting against predators and competitors, compared to their modern crocodylian counterparts. Most lizards inflate their lungs using some muscles they use for walking so they cannot run and breathe effectively at the same time (Carrier, 1987; Wang et al., 1997). However, terrestrial varanids have large muscular throats used like bellows to pump air into their lungs even when they are running (Frappell et al., 2002). Varanid lizards tend to have a higher VO_2 and endurance levels than non-varanid lepidosaurs (Bartholomew and Tucker, 1964; Clemente et al., 2009). This could have been a strategy employed by notosuchians.

Despite possessing a highly specialized and very efficient ventilatory system, living crocodiles are semiaquatic ambush predators (Farmer and Carrier, 2000), not requiring a high aerobic capacity for locomotion. The ability for bounding and galloping gaits is observed in certain crocodylids and gharials, but it is likely absent in the alligator and caiman groups (Zug, 1974; Allen et al., 2015). Small species employ these extreme locomotion types for short bursts of speed, whereas larger animals exhibit relatively less extreme gait kinematics (Hutchinson et al., 2019). These features are not congruent with their lifestyle as semiaquatic sit-and-wait predators (Farmer and Carrier, 2000) and instead represent the possibility of a legacy from their more athletically performant ancestral archosaurs (Sereno and Larsson, 2009; Seymour et al., 2004). These features are possibly reversionary adaptations from an endothermic ancestral state to an ectothermic strategy in living non-avian sauropsids (Grigg et al., 2022), as evidenced by the archosauromorph *Azendohsaurus laaroussii* (Cubo and Jalil, 2019). The thermometabolic strategy shift in crocodyliforms would have preserved a higher aerobic capacity in certain groups, such as Notosuchia.

In terms of the number of femoral nutrient foramina, the presence of variation between right and left femora in *Sahitissuchus fluminensis* and *Pissarachampsa sera* suggests a potential intraskeletal plasticity for femoral perfusions. This variability has also been observed in extant chickens, in which paired femora exhibit distinct numbers of nutrient foramina (Hu et al., 2022). However, even with varying number of nutrient foramina, the blood flow rates between both femora should remain similar. In this study, the paired femora of *Sahitissuchus fluminensis* and *Pissarachampsa sera* demonstrated a similar mass-independent metabolic rate.

Through a comprehensive analysis of metabolic data reported in previous studies, we assessed potential differences in the aerobic metabolic profiles of crocodyliforms. When the RMR of extinct notosuchians are compared with extant crocodylians as reported in Cubo et al. (2020; 2023), there was no significant difference between them, suggesting that RMR of crocodyliforms does not significantly differ among terrestrial Notosuchia and semiaquatic Crocodylia. However, our findings indicate significant differences when comparing the MMRs. Using this metric, notosuchians exhibit higher mass-independent MMR.

Considering that MMR is positively correlated with endurance (Garland, 1984), our results suggest that notosuchians were able to sustain higher activity levels than *Crocodylus porosus*. The higher endurance of notosuchians may offer ecological advantages in terms of extended travel distances, as previously proposed for Australian varanids by Clemente et al. (2009). Conversely, the lower endurance in extant crocodylians is congruent with their sit-and-wait predation strategy. Our study contributes to the understanding of the metabolic characteristics of notosuchians, shedding light on their ecological adaptations and activity patterns.

5 Conclusions

Cubo et al. (2020; 2023) discovered that the ectothermic condition for Notosuchia may have been acquired at the beginning of the Cretaceous or earlier. In this study, we demonstrate that notosuchians had a higher oxygen consumption than modern crocodilians during periods of intensive activity. Extant crocodylians are ectotherms characterized by low activity levels but certain anatomical features suggest that they had a more athletic lifestyle in the past. These features include unidirectional air-flow through the lungs, completely septated ventricle, and galloping gait for some species, as *Crocodylus johnsoni* Krefft, 1873 (Jensen et al., 2014; Wang et al., 2001). These remnants of their athletic ancestors allow small Crocodylia being able of running short distances during sudden dangerous situations. As for Notosuchia, the mass-independent aerobic capacities are lower than those quantified in varanid lizards but surpass those observed in extant Crocodylia. Our findings suggest that these notosuchians were active hunters able to intake high levels of oxygen that enhanced their endurance capabilities allowing them to engage prolonged running periods, a behavior similar to that exhibited nowadays by the large terrestrial varanids, such as *Varanus giganteus*, in the Australian desert.

In conclusion, there has been an increasing interest in recent years to estimate metabolic rates of extinct archosaurs using phylogenetic comparative methods (Cubo et al., 2020; 2023; Wiemann et al., 2022). The discoveries made in the present study may encourage new and similar investigations into the energetic aerobic costs of locomotion in closely related taxa, such as marine crocodiles (Thalattosuchia).

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Supplementary information

R-scripts, phylogeny files and databases for running the MMR in Notosuchia are available on: https://github.com/MAVAAS/MMR-Notosuchia/tree/d5fa8446a8c0a75ac78184721 7e97b20091c90a5

Dataset. Measurements of the sampled notosuchian femora and maximal metabolic rate information estimations in the present study.

Table S1. Micro CT scanning parameters.

Table S2. Means and standard deviations (SD) of sampled notosuchian femora.

Plate S1. High-resolution 3D femoral reconstructions of *Sahitisuchus fluminensis* MCT 1831-R (A) and 1835-R (B) in medial view, featuring highlighted nutrient foramina in yellow and blue in the details. The bone structures are visualized in green, with the color gradient indicating bone density.

Plate S2. High-resolution 3D femoral reconstructions of *Uberabasuchus terrificus* CPPLIP 501 (A) and *Itasuchus jesuinoi* DGM 434-R (B) in medial view, featuring highlighted nutrient foramina in yellow and blue in the details. The bone structures are visualized in green, with the color gradient indicating bone density.

Plate S3. High-resolution 3D femoral reconstructions of the baurusuchids, *Pissarachampsa sera* LPRP USP 0019b (A) and *Campinasuchus dinizi* CPPLIP 1847 (B) in medial view, featuring highlighted nutrient foramina in yellow and blue in the details. The bone structures are visualized in green, with the color gradient indicating bone density.

Plate S4. High-resolution 3D femoral reconstructions of *Araripesuchus* sp. LAPEISA-Pal-0032 (A) and *Coronelsuchus civali* FF PG 14 (B) in medial view, featuring highlighted nutrient foramina in yellow and blue in the details. The bone structures are visualized in green, with the color gradient indicating bone density.

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Figures Captions

Figure 1. A, Photograph of the entire left femur in medial view the white arrow indicates a nutrient foramen located distal to the fourth trochanter in *Pissarrachampsa sera* (LPRP/USP 0019). B, 3D reconstruction of *Pissarrachampsa sera* femur with the nutrient foramen segmented and highlighted in yellow. (2-column fitting image)

Figure 2. 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 $\dot{Q}$ as co-predictor. Timescale on the right in millions of years (Ma). (2-column fitting image)

Table 1. Mass-independent maximum metabolic rate (MMR) of sampled notosuchian taxa calculated through phylogenetic eigenvector maps with Q̇ as co-predictor. (1.5-column fitting image)

Species	**Lower limit** (**ml O_2 $h^{-1}g^{-0.85}$**)	**Maximum metabolic rate** (**ml O_2 $h^{-1}g^{-0.85}$**)	**Upper limit** (**ml O_2 $h^{-1}g^{-0.85}$**)
Itasuchus jesuinoi	0.34	0.70	1.44
Uberabasuchus terrificus	0.35	0.71	1.42
Sahitisuchus fluminensis	0.34	0.71	1.45
Araripesuchus sp.	0.37	0.71	1.37
Coronelsuchus civali	0.36	0.71	1.38
Campinasuchus dinizi	0.36	0.71	1.41
Pissarrachampsa sera	0.34	0.70	1.45

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:

Highlights

- Notosuchia were ectotherms with a high aerobic capacity compared to extant crocodylians;
- They likely were more athletic crocodyliforms when compared to *Crocodylus porosus*;
- The evolutionary history of Crocodyliformes shows a shift from a high to a low aerobic MMR reducing their energetic budget.

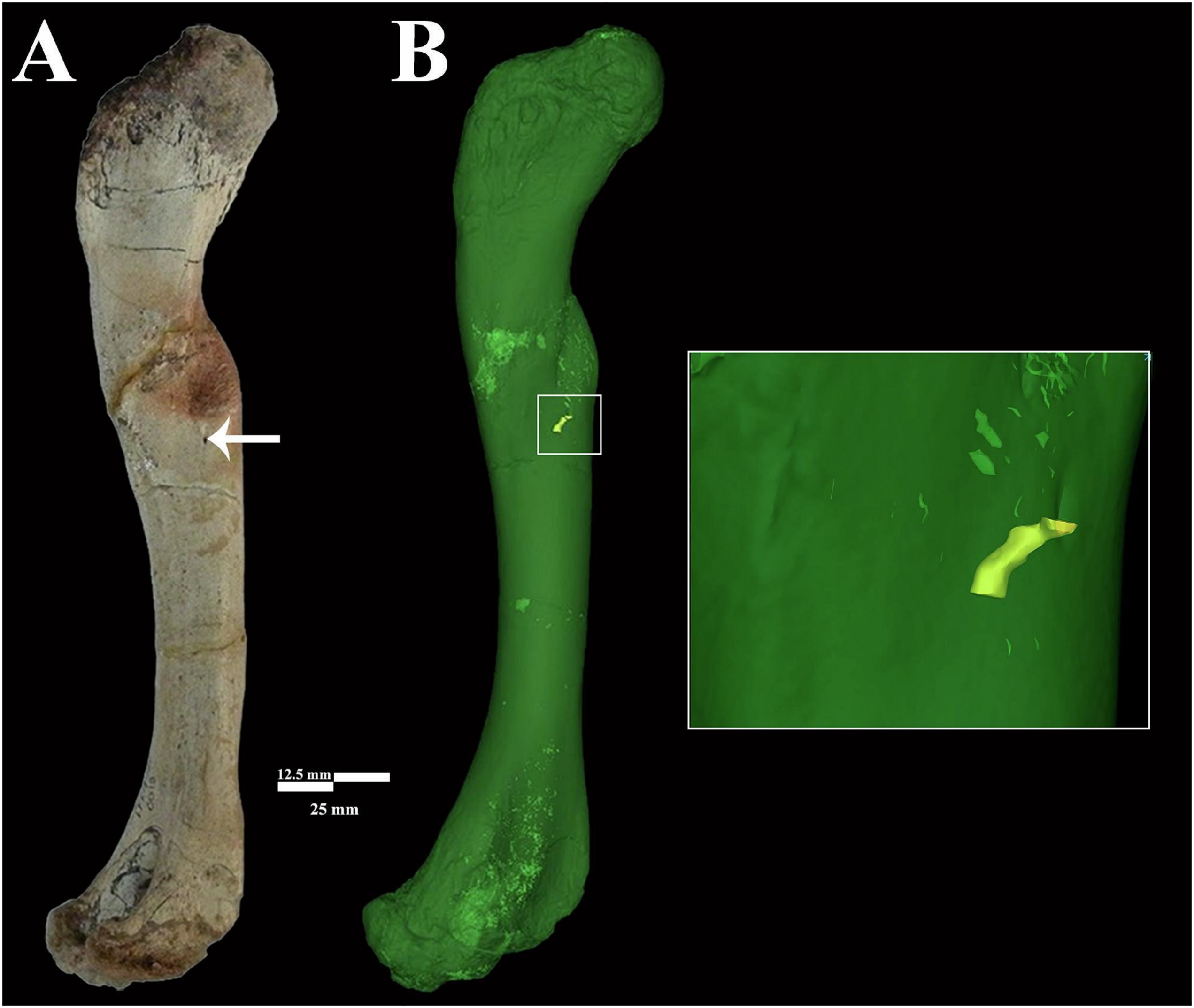

Figure 1

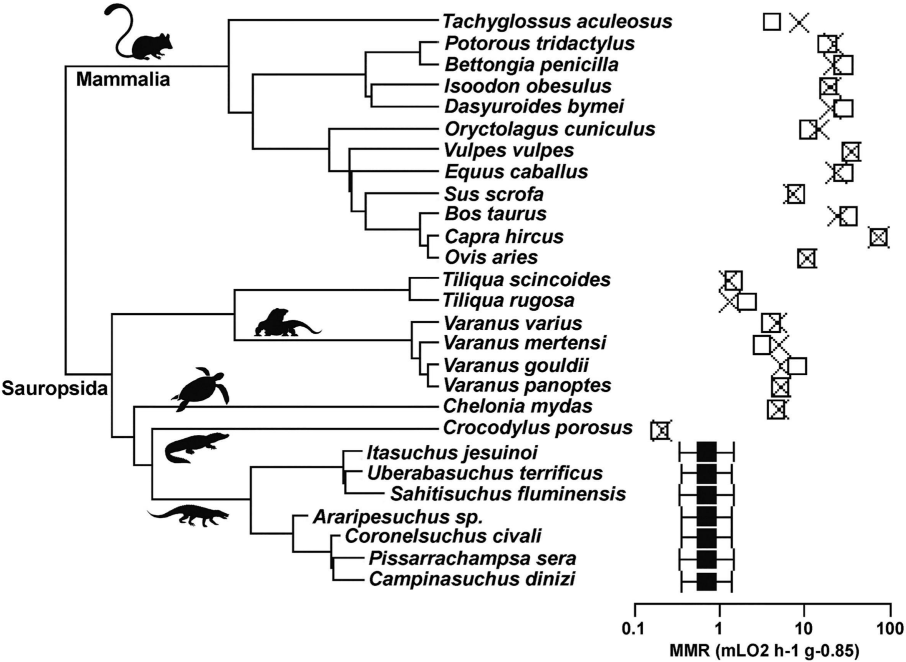
Mammalia
Sauropsida
Tachyglossus aculeosus
Potorous tridactylus
Bettongia penicilla
Isoodon obesulus
Dasyuroides bymei
Oryctolagus cuniculus
Vulpes vulpes
Equus caballus
Sus scrofa
Bos taurus
Capra hircus
Ovis aries
Tiliqua scincoides
Tiliqua rugosa
Varanus varius
Varanus mertensi
Varanus gouldii
Varanus panoptes
Chelonia mydas
Crocodylus porosus
Itasuchus jesuinoi
Uberabasuchus terrificus
Sahitisuchus fluminensis
Araripesuchus sp.
Coronelsuchus civali
Pissarrachampsa sera
Campinasuchus dinizi
0.1
1
10
100
MMR (mLO2 h-1 g-0.85)

Figure 2