Were Notosuchia (Pseudosuchia, Crocodylomorpha) warm-blooded? A palaeohistological analysis suggests ectothermy

Jorge Cubo, Mariana V A Sena, Paul Aubier, Guillaume Houee, Penelope Claisse, Mathieu G Faure-Brac, Ronan Allain, Rafael C L P Andrade, Juliana M Sayão, Gustavo R Oliveira

► To cite this version:

Jorge Cubo, Mariana V A Sena, Paul Aubier, Guillaume Houee, Penelope Claisse, et al.. Were Notosuchia (Pseudosuchia, Crocodylomorpha) warm-blooded? A palaeohistological analysis suggests ectothermy. *Biological Journal of the Linnean Society*, 2020, 131 (1), pp.154-162. 10.1093/biolinnean/blaa081 . hal-03329989

HAL Id: hal-03329989

<https://hal.sorbonne-universite.fr/hal-03329989>

Submitted on 31 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Were Notosuchia (Pseudosuchia, Crocodylomorpha) warm-blooded?

A palaeohistological analysis suggests ectothermy

JORGE CUBO¹, MARIANA V. A. SENA^{2,3}, PAUL AUBIER¹, GUILLAUME HOUÉE¹, PENELOPE CLAISSE¹, MATHIEU G. FAURE-BRAC¹, RONAN ALLAIN⁴, RAFAEL C. L. P. ANDRADE⁵, JULIANA M. SAYAO⁵, GUSTAVO R. OLIVEIRA⁶

¹ Sorbonne Université, Muséum national d'Histoire naturelle, CNRS, Centre de Recherche en Paléontologie—Paris (CR2P, UMR 7207), 4 place Jussieu - case courrier 104 - 75005 Paris, France

² Universidade Federal de Pernambuco, Departamento de Geologia, Programa de Pós-Graduação em Geociências (PPGEOC), Av. Prof. Moraes Rego, 1235, Cidade Universitária, Recife, PE, Brazil

³ Centro Universitário da Vitória de Santo Antão, Loteamento São Vicente Ferrer, 71, Cajá, Vitória de Santo Antão, PE, Brazil

⁴ Muséum national d'Histoire naturelle, CNRS, Centre de Recherche en Paléontologie—Paris (CR2P, UMR 7207), Paris, France

⁵ Universidade Federal de Pernambuco, Laboratório de Paleobiologia e Microestruturas, Rua do Alto Reservatório, s/n, Bela Vista, Vitória de Santo Antão, PE, Brazil

⁶ Universidade Federal Rural de Pernambuco, Departamento de Biologia, Laboratório de Paleontologia & Sistemática, Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, Recife, PE, Brazil

ABSTRACT

Most Notosuchia were terrestrial active predators. A few of them were semiaquatic, or were insectivorous, omnivorous or herbivorous. A question relative to their thermometabolism remains to be answered: Were Notosuchia warm-blooded? Here we use quantitative bone palaeohistology to answer this question. Two variables were used as proxies to infer the thermometabolism: resting metabolic rate and red blood cell dimensions. Resting metabolic rate was inferred using relative primary osteon area and osteocyte size, shape and density. Blood cell dimensions were inferred using harmonic mean canal diameter and minimum canal diameter. All inferences were performed using phylogenetic eigenvector maps. Both sets of analyses suggest that the seven species of Notosuchia sampled in this study were ectotherms. Considering that extant Neosuchia (their sister group) are also ectotherms, and that archosaurs were primitively endotherms, parsimony suggests that endothermy may have been lost at the node Metasuchia (Notosuchia – Neosuchia) by the Lower Jurassic. Semiaquatic taxa such as *Pepesuchus* may have had thermoregulatory strategies similar to those of recent crocodylians, whereas the terrestrial taxa (*Araripesuchus*, *Armادillosuchus*, *Iberosuchus*, *Mariliasuchus*, *Stratiotosuchus*) may have been thermoregulators similar to active predatory varanids. Thermal inertia may have contributed to maintaining a stable temperature in large notosuchians such as *Baurusuchus*.

KEYWORDS: bone histology - ectothermy - endothermy – Metasuchia – Neosuchia - phylogenetic eigenvector maps - thermometabolism

INTRODUCTION

Notosuchia is a group of extinct crocodyliforms that lived from the Middle Jurassic (*Razanandrongobe sakalavae*, Dal Sasso *et al.*, 2017) to the Middle Miocene (*Sebecus*, Buffetaut & Hoffstetter, 1977; Busbey 1986). Some groups became extinct after the crisis at the end of the Cretaceous (Peirosauridae, Uruguaysuchidae), whereas others survived until the Miocene (Sebecosuchia). Notosuchians present a diverse array of body size, and inhabit different environments. Some small to medium-sized taxa (e.g., *Araripesuchus*, Sereno & Larsson, 2009), and some large ones (e.g., *Baurusuchus*, Pol *et al.*, 2014) are terrestrial, whereas other forms are semiaquatic (e.g., *Kaprosuchus*, *Mahajangasuchus*, *Stolokrosuchus*, *Pepesuchus*, Riff *et al.*, 2012; Pol *et al.*, 2014; Grigg & Kirshner, 2015; Wilberg, Turner, & Brochu, 2019). Moreover, these crocodyliforms were diversified in terms of diet: carnivorous (e.g., *Notosuchus* and baurusuchids), insectivorous or omnivorous (e.g., *Araripesuchus*, *Candidodon*, *Mariliasuchus*), omnivorous (e.g., *Armadillosuchus*), and herbivorous (e.g., *Simosuchus*, *Pakasuchus*, *Chimaerasuchus*) (Marinho & Carvalho, 2009; Godoy *et al.*, 2014; Melstrom & Irmis, 2019). A question of their palaeobiology remains unanswered: were notosuchians warm-blooded? Endotherms (e.g. birds and mammals) have high metabolic rates (tachymetabolism) and generate enough internal heat to enable physiological regulation of body temperature, while ectotherms (e.g. most other vertebrates) have low metabolic rates (bradymetabolism) and must thermoregulate behaviourally. Archosaurs are considered as being primitively endotherms. This hypothesis is based on cardiovascular (Seymour *et al.*, 2004), respiratory (Farmer & Sanders, 2010) and osteohistological (Legendre *et al.*, 2016) evidence. Considering that the outgroups *Calyptosuchus wellsi* (Aetosauria) and *Postosuchus kirkpatricki* (Rauisuchidae) were found endotherms (Cubo & Jalil, 2019), and that many notosuchians are active terrestrial predators, the null

hypothesis suggests that Notosuchia may have inherited endothermy whereas Neosuchia, their sister group, may have lost this condition when they became secondarily aquatic during the Lower Jurassic. The last hypothesis is congruent with the fact that the thermic conductivity in water is higher than in the air (0.59 versus 0.024 W/(m·K); Vogel, 2005). The heat capacity (J/K) and the density (Kg / L) of water are also higher than those of the air. Therefore, it is more costly to maintain a high body temperature in the water than in the air. Considering that most Neosuchia are sit-and-wait predators and have lower energy budgets than active aquatic endothermic predators like dolphins and penguins, natural selection may have favoured the loss of endothermy at the node Neosuchia. Qualitative histological analyses performed to date in Notosuchia are not conclusive. Cubo, Kohler, & De Buffrenil (2017) found an isolated femoral bone tissue of *Iberosuchus macrodon* that can be interpreted as either radial fibrolamellar bone tissue formed at extremely high growth rates and suggesting endothermy, or as compacted spongiosa formed at lower growth rates typical of ectotherms. Sena *et al.* (2018) found in the appendicular bones of *Pepesuchus deiseae* bone tissues formed at moderate growth rates. Here we use quantitative bone palaeohistology and the phylogenetic comparative method to elucidate what was the thermometabolic condition of these amazing archosaurs.

MATERIAL AND METHODS

MATERIAL

We included seven species of Notosuchia:

- *Araripesuchus wegeneri* Buffetaut 1981. A partial femur (MNHN.F.GDF660) from the Aptian of Gadoufaoua (Niger), Museum national d'Histoire naturelle (MNHN) (Paris, France).

- *Armadillosuchus arrudai* Marinho & Carvalho 2009. A partial femur (LPRP-USP 0774) from the Turonian–Maastrichtian of the Bauru Group (Brazil), Universidade de São Paulo (USP) (Ribeirão Preto, Brazil).

- *Baurusuchus* sp. Price 1945. A partial femur (LPRP-USP 0634 C) from the Turonian–Maastrichtian of the Bauru Group (Brazil), USP.

- *Iberosuchus macrodon* Antunes 1975. Two partial femora (IPS4930 and IPS4932) from the Palaeocene of La Boixedat (Spain). Institut Català de Paleontologia (ICP) (Sabadell, Spain). Histological descriptions of these bones can be found in Cubo *et al.* (2017).

- *Mariliasuchus amarali* Carvalho & Bertini 1999. A right humerus (UFRPE 5311) from the Turonian–Maastrichtian of the Bauru Group (Brazil), Universidade Federal Rural de Pernambuco (UFRPE) (Recife, Brazil).

- *Stratiotosuchus maxhechti* Campos *et al.* 2001. A femur (MCT1714-R) and a tibia (DGM 1477-R) from the Campanian–Maastrichtian of the Bauru Group (Brazil), Museu de Ciências da Terra (MCT), under a temporary loan to Universidade Federal de Uberlândia (UFU).

- *Pepesuchus deiseae* Campos *et al.* 2011. A right tibia (MN 7466-V) from the Campanian–Maastrichtian of the Bauru Group (Brazil), Museu Nacional do Rio de Janeiro (Brazil).

The analyses aimed at inferring resting metabolic rates in fossils include 18 species of extant tetrapods. Resting metabolic rates were measured by Montes *et al.* (2007) using respirometry, with the exception of values for *Capreolus capreolus*, *Oryctolagus cuniculus* and *Lepus europaeus*, that were taken from Olivier *et al.* (2017). Analyses performed to infer red blood cell size in fossils include 14 species of extant tetrapods. Red blood cell sizes were taken from Huttenlocker & Farmer (2017), who measured them by imaging the stained blood smears.

OSTEOHISTOLOGICAL FEATURES

Bone histological features used to construct paleobiological inference models were: relative primary osteon area (RPOA, described by Fleischle, Wintrich, & Sander, 2018, as primary osteon density), osteocyte size, shape and density (described by Cubo *et al.*, 2012) and vascular canal diameter (Huttenlocker & Farmer, 2017). Values for the sample of *Notosuchia* were quantified in this study (supplementary file 1) and values for the sample of extant taxa were taken from Faure-Brac & Cubo (2020) for the femoral RPOA, from Legendre *et al.* (2016) and Olivier *et al.* (2016) for humeral, femoral and tibiae osteocyte size, shape and density, and from Huttenlocker & Farmer (2017) for femoral canal's harmonic mean and minimum diameter.

RPOA and osteocyte size, shape and density were used to infer resting metabolic rate (RMR in $\text{ml O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$) in *Notosuchia*. Considering that all sampled extant tetrapods were juveniles in the phase of active growth (Legendre *et al.*, 2016), these variables were quantified in the deep cortex of *Notosuchia* analysed. By deep cortex we mean in primary bone near endosteal bone. The reason is that the deep cortex of adults was formed when they were juveniles. For *Iberosuchus*, quantifications were performed on IPS4930 as it is younger than IPS4932. Harmonic mean canal diameter and minimum canal diameter were used to infer red blood cell width (μm) and area (μm^2) in *Notosuchia*. The variable “canal diameter” corresponds to the diameter of vascular spaces in bone tissue. Values for the sampled extant tetrapods were taken from Huttenlocker & Farmer (2017), who analysed adult specimens. Therefore, we quantified the vascular canal diameters in the outer cortex of the sampled *Notosuchia*, and we used *Iberosuchus* IPS4932 because it is older than IPS4930.

For extant taxa, we used phylogenies compiled by Legendre *et al.* (2016) and Faure-Brac & Cubo (2020) for figures 1, 3, and supplementary figures 1 and 2, and by Huttenlocker & Farmer (2017) for figure 2 and supplementary figure 3. Several phylogenetic analyses have been published for Notosuchia. Pol *et al.* (2014) found the following topology for the species of our sample: (*Araripesuchus* (*Marillasuchus* (*Baurusuchus* – *Stratiosuchus* – *Iberosuchus*))). Kellner *et al.* (2014) proposed the same topology for these species. In contrast, Geroto & Bertini (2019) proposed a different topology for the species of our sample: ((*Iberosuchus* – *Pepesuchus*) (*Araripesuchus* ((*Marillasuchus* – *Armادillosuchus*)(*Stratiosuchus* – *Baurusuchus*)))). We followed the more recent one (that published by Geroto & Bertini, 2019). Please note that in the topologies published by Pol *et al.* (2014) and Kellner *et al.* (2014), all seven species of our sample are included in the node Notosuchia, whereas in the topology used in this study (that published by Geroto & Bertini, 2019), *Iberosuchus* and *Pepesuchus* are not included in this node. We used phylogenetic eigenvector maps (PEMs) and the ‘MPSEM’ package (Guenard, Legendre, & Peres-Neto, 2013) in R (R Development Core Team, 2016) to infer our dependent (response) variable using a set of explanatory variables. We checked the normality of residuals of the explanatory variables (the differences between the values fitted by the PEM model and the actual values) using Shapiro-Wilk tests. If a distribution of residuals was significantly different from normality, the corresponding raw variable needs to be transformed. Finally, we performed leave-one-out cross-validation tests. For this, we estimated values of the dependent variable of extant taxa (for which these values are known) using the inference procedure of the ‘MPSEM’ package (Guenard *et al.*, 2013), and compared these inferred values to the empirical ones using a PGLS

regression and the ‘caper’ package (Orme *et al.*, 2013) in R (R Development Core Team, 2016).

RESULTS

RESTING METABOLIC RATE INFERENCES

PERFORMED USING RPOA AND OSTEOCYTE DENSITY, AREA AND SHAPE

The datasets used to perform analyses are available in supplementary file 1. We used PEMs to infer the mass-independent resting metabolic rates (RMRs) of *Notosuchia* using RMRs values quantified in a sample of extant tetrapods, histological features quantified in both *Notosuchia* and extant tetrapods, and the phylogeny. The dependent (response) variable is RMR, and the explanatory variables are the phylogeny and osteohistological features: RPOA and osteocyte density, area and shape. The response variable (RMR) was transformed using natural logarithms because raw values are skewed. With a single exception, the distributions of residuals of the explanatory variables (the differences between the values fitted by the PEM models and the actual values) were not significantly different from normality (supplementary file 2). Therefore, no transformation of explanatory variables was needed. For each bone we chose the model that maximizes the R^2 value and, in case of tie, the model that minimizes the AIC value. The selected models were (supplementary file 2): phylogeny + osteocyte shape for the humerus (supplementary figure 1), phylogeny + osteocyte area for the femur (Fig. 1), and phylogeny + osteocyte shape for the tibia (supplementary figure 2). Inferences and 95% confidence intervals are shown in Table 1. Additionally, we inferred values of the dependent variable of extant taxa (for which these values are known) using leave-one-out cross-validation tests. For the sample of extant taxa, regressions of inferred values to empirical values performed using PGLS were highly significant: $R^2=0.994$, p-value =

2.2e-16 for the humerus; $R^2=0.990$, p-value = 2.2e-16 for the femur; $R^2=0.977$, p-value = 1.521e-10 for the tibia.

RED BLOOD CELL SIZE INFERENCES

PERFORMED USING VASCULAR CANAL DIAMETER

The datasets used to perform analyses is available in supplementary file 1. We used PEMs to infer red blood cell (RBC) dimensions of Notosuchia using RBC values quantified in a sample of extant tetrapods, vascular canal diameters quantified in both Notosuchia and extant tetrapods, and the phylogeny. The dependent (response) variables were RBC_{width} and RBC_{area} , and the explanatory variables are femoral harmonic mean canal diameter and femoral minimum canal diameter. The distributions of residuals of the explanatory variables (the differences between the values fitted by the PEM model and the actual values) were not significantly different from normality (supplementary file 2). Therefore, no transformation of explanatory variables was needed. For each dependent variable we chose the model that maximizes the R^2 value and, in case of tie, the model that minimizes the AIC value. The selected models are (supplementary file 2): phylogeny + harmonic mean canal diameter to infer red blood cells width (Fig. 2); and phylogeny + minimum canal diameter to infer red blood cells area (supplementary figure 3). Inferences and 95% confidence intervals are shown in Table 2. Additionally, we inferred values of the dependent variable of extant taxon (for which these values are known) using leave-one-out cross-validation tests. For the sample of extant taxa, regressions of inferred values to empirical values performed using PGLS were significant: $R^2=0.891$, p-value=3.981e-07 for red blood cell width and $R^2=0.425$, p-value=0.01154 for red blood cell area.

DISCUSSION

METHODOLOGICAL CONSIDERATIONS

We used two variables as proxies to infer endothermy: resting metabolic rate (White, Phillips, & Seymour, 2006; Clarke & Portner, 2010) and red blood cell dimensions (Snyder & Sheafor, 1999; Huttenlocker & Farmer, 2017). For a range of body masses from 50 to 1000g, the resting metabolic rate of birds and mammals exceed those of ectotherms by a factor of, respectively, 15 and 12 (Clarke & Portner, 2010).

Furthermore, birds and mammals are characterized by smaller vascular canal minimum sizes than ectotherms (Huttenlocker & Farmer, 2017). It has been shown that smaller capillaries produce higher diffusive gas exchange and higher resistance to blood flow (Snyder & Sheafor, 1999). In endotherms, red blood cells undergo cell deformation during capillary flow (Snyder & Sheafor, 1999). Therefore, in these organisms, the presence of small capillaries increases resistance even if there are more capillaries in a given volume of tissue. The presence of smaller vascular canal minimum sizes in endotherms (birds and mammals) can thus be associated with their high oxygen uptake and their four chambered heart, allowing high systemic blood pressures (Snyder & Sheafor, 1999; Huttenlocker & Farmer, 2017). Resting metabolic rate, red blood cell dimensions, and the thermometabolism (endothermy or ectothermy), are known in our sample of extant tetrapods. They are inferred in the sample of *Notosuchia* using a model that includes osteohistological features and the phylogeny. The interesting point is that we performed two separate sets of analyses, using two independent samples of extant tetrapods, to infer two variables used as proxies of endothermy (resting metabolic rate, red blood cell dimensions), and we obtained the same inferences in *Notosuchia* (see below).

We can wonder about the effect of the number of extinct taxa (for which we performed inferences), relative to the number of extant ones used to construct the inference models. Results are the same irrespective of the relative number of extinct taxa included in the model: as an example, *Stratiotosuchus maxhechti* was inferred as being ectotherm using a model based on the bone histology of the femur (five extinct taxa) and using a model based on the bone histology of the tibia (two extinct taxa).

Finally, we checked the reliability of our inferences performing leave-one-out cross-validation tests: we estimated values of the dependent variable of extant taxa (for which these values are known) using the inference procedure, and performed regressions of the inferred values to the measured (actual) values. All regressions were significant, suggesting that the inferences performed for Notosuchia are reliable.

PALEOBIOLOGICAL INFERENCES

The question to be answered is: were Notosuchia warm-blooded? Considering that archosaurs were primitively endotherms (Seymour *et al.*, 2004; Farmer & Sanders, 2010; Legendre *et al.*, 2016), that the outgroups of Notosuchia analysed to date (*Calyptosuchus wellsi* and *Postosuchus kirkpatricki*) were found endotherms (Cubo & Jalil, 2019), and that Notosuchia includes a wide range of active terrestrial predator species (Carvalho *et al.*, 2004; 2007; Carvalho, Campos & Nobre, 2005; Nascimento & Zaher, 2010 ; Godoy *et al.*, 2014), the null hypothesis suggests that Notosuchia were endotherms. This hypothesis has been refuted by our results. Both sets of analyses, those aimed at inferring resting metabolic rates and those performed to estimate red blood cell dimensions, show that the seven species of Notosuchia sampled in this study may have been ectotherms. Considering that extant Neosuchia (their sister group) are also ectotherms, parsimony suggests that endothermy may have been lost at the node

Metasuchia (Notosuchia – Neosuchia) by the Lower Jurassic (Fig. 3). Among Notosuchia, semiaquatic taxa such as *Pepesuchus* may have had thermoregulatory strategies akin to those of recent crocodylians (e.g., control of heat flow through the skin by basking, and opening the mouth to promote cooling by evaporation; Grigg & Kirshner, 2015), whereas the terrestrial species (*Araripesuchus*, *Armadillosuchus*, *Iberosuchus*, *Marillasuchus*, *Stratiosuchus*) may have been thermoregulators similar to active predatory varanids. Varanid lizards have high aerobic capacities and can sustain higher activity levels than other lizards (Pough, 1980; Mendyk *et al.*, 2014). These terrestrial notosuchians may have occupied sunlit areas for basking or while foraging, and they possibly entered into burrows (Marinho & Carvalho, 2009, Carvalho *et al.*, 2010) for lowering body temperature when necessary. Clarac & Quilhac (2019) showed that, in crocodylians, «osteoderms collect the external heat during the basking periods as they become significantly warmer than the surrounding skin. The presence of osteoderms in terrestrial Notosuchia (e.g., *Iberosuchus*) probably involved in heat intake during basking suggests that these organisms relied on external heat to perform high levels of activity inferred by functional morphology analyses. In the large sebecosuchians (e.g., *Baurusuchus*; Pol *et al.*, 2014) the body temperature should have been more or less stable throughout the day because of thermic inertia. This feature made them more independent from external heating, which may have allowed extra time for hunting. The lifestyle of a few taxa is still debated. This is the case of *Marillasuchus*. Nobre and Carvalho (2013) observed that *Marillasuchus amarali* shares postcranial features with recent eusuchians, and concluded that this taxon probably had a sprawling type posture and an amphibian lifestyle. However *Marillasuchus amarali* also presents cranial features which corresponds to a terrestrial habit, like a short and high skull, lateral orbits, frontal external nares, and long and robust limbs, indicating a quadrupedal

posture (Vasconcellos and Carvalho, 2005; Andrade and Bertini, 2008). Besides some histological and microanatomic features were found in *Marillasuchus*' thin sections (unpublished data) which corroborates its terrestrial habit, such as the absence of bone specializations, tubular ribs and long bones showing a compact cortical bone and a free marrow cavity or a loose spongiosa filling in medullary region (Houssaye et al., 2016). Moreover *Marillasuchus amarali* is found in deposits of the Adamantina Formation from Bauru group which are interpreted as semi-arid environments with sand sheets crossed by ephemeral river systems surrounding an interior desert inside Paraná basin during Late Cretaceous from the Gondwana (Fernandes and Ribeiro, 2015). For all these reasons we considered that *Marillasuchus* had a terrestrial lifestyle. Future research on the palaeophysiology, the lifestyle, the diet and on the general paleobiology of Notosuchia are necessary to fully understand their ecological role and the causes of their extinction

ACKNOWLEDGEMENTS

We thank Roger Seymour (The University of Adelaide), Holly Woodward (Oklahoma State University) and an anonymous reviewer for helpful comments that improved the quality of the manuscript. We gratefully thank Dr. Max Langer (Universidade de São Paulo), Dr. Douglas Riff (Universidade Federal de Uberlândia), and Dr. Felipe Chinaglia Montefeltro (Universidade Estadual Paulista) and Alexander W. A. Kellner (Museu Nacional – UFRJ) for making available the thin-sections images of *Baurusuchus* sp., *Armadillosuchus arrudai* and *Stratiotosuchus maxhecthi*. We thank the curator of the archosaur collection of the Muséum national d'Histoire naturelle (Paris, France) for allowing us to perform thin sections of a partial femur (GDF660) of *Araripesuchus wegneri*, and to Hayat Lamrous (Sorbonne Université) for performing these sections.

We thank the curators of the Paleovertebrate Sector of the Museu Nacional (MN/UFRJ) which provides the *Pepesuchus deiseae* and *Mariliasuchus amarali* and *Stratiotosuchus maxhecthi*'s fossils. Some of the specimens used here were prepared in the Paleohistology lab at Des Moines University (Medical and Health Sciences Institution). The authors sincerely thank Des Moines University and, especially, Dr. Sarah Werning for having Dr. Rafael Andrade as an exchange student, and the opportunity to use their facilities

REFERENCES

- Andrade MB & Bertini RJ. 2008.** Morphological and anatomical observations about *Mariliasuchus amarali* and *Notosuchus terrestris* (Mesoeucrocodylia) and their relationships with other South American notosuchians. *Arquivos do Museu Nacional* (Rio de Janeiro). **66**: 5–62.
- Buffetaut E & Hoffstetter R. 1977.** Discovery of crocodilian *Sebecus* in Miocene of eastern Peru. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences Serie D* **284**: 1663–1666.
- Busbey A.B. 1986.** "New material of *Sebecus* cf. *huilensis* (Crocodilia: Sebecosuchidae) from the Miocene La Venta Formation of Colombia". *Journal of Vertebrate Paleontology* **6**: 20–27.
- Campos DA, Oliveira GR, Figueiredo RG, Riff D, Azevedo SAK, Carvalho LB & Kellner AWA. 2011.** On a new peirosaurid crocodyliform from the Upper Cretaceous, Bauru Group, southeastern Brazil. *Anais da Academia Brasileira de Ciências* **83**: 317–327.
- Carvalho IS, Ribeiro LCB & Avilla LS. 2004.** *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* **7**: 975–1002.

- Carvalho IS, Campos ACA & Nobre PH. 2005.** *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* **8**: 11–30.
- Carvalho IS, Vasconcellos FM & Tavares SAS. 2007.** *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* **1607**: 36–46.
- Carvalho IS, Brandoni de Gasparini Z, Salgado L, de Vasconcellos FM & Marinho TS. 2010.** Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography Palaeoclimatology Palaeoecology* **297**: 252–262.
- Clarac F & Quilhac A. 2019.** The crocodylian skull and osteoderms: A functional exaptation to ectothermy? *Zoology* **132**: 31–40.
- Clarke A & Portner HO. 2010.** Temperature, metabolic power and the evolution of endothermy. *Biological Reviews* **85**: 703–727.
- Cubo J, Le Roy N, Martinez-Maza C & Montes L. 2012.** Paleohistological estimation of bone growth rate in extinct archosaurs. *Paleobiology* **38**: 335–349.
- Cubo J & Jalil NE. 2019.** Bone histology of *Azendohsaurus laaroussii*: Implications for the evolution of thermometabolism in Archosauromorpha. *Paleobiology* **45**: 317–330.
- Cubo J, Kohler M & De Buffrenil V. 2017.** Bone histology of *Iberosuchus macrodon* (Sebecosuchia, Crocodylomorpha). *Lethaia* **50**: 495–503.
- Dal Sasso C, Pasini G, Fleury G & Maganuco S. 2017.** *Razanandrongobe sakalavae*, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is the oldest known notosuchian. *PeerJ* **5**: e3481.
- Farmer CG & Sanders K. 2010.** Unidirectional airflow in the lungs of alligators. *Science* **327**: 338–340.

- Faure-Brac MG & Cubo J. 2020.** Were the synapsids primitively endotherms? A palaeohistological approach using phylogenetic eigenvector maps. *Philosophical Transactions of the Royal Society B-Biological Sciences* **375**: 20190138.
- Fernandes LA & Ribeiro CM. 2015.** Evolution and palaeoenvironment of the Bauru Basin (Upper Cretaceous, Brazil). *Journal of South American Earth Science*. **61**: 71–90.
- Fleischle C, Wintrich T & Sander PM. 2018.** Quantitative histological models suggest endothermy in plesiosaurs. *Peerj* **6**: e4955.
- Geroto CF & Bertini RJ. 2019.** New material of *Pepesuchus* (Crocodyliformes; Mesoeucrocodylia) from the Bauru Group: implications about its phylogeny and the age of the Adamantina Formation. *Zoological Journal of the Linnean Society* **185**: 312–334.
- Godoy PL, Montefeltro FC, Norell MA & Langer MC. 2014.** An additional baurusuchid from the cretaceous of Brazil with evidence of interspecific predation among Crocodyliformes. *PLoS ONE* **9**: e97138.
- Guenard G, Legendre P & Peres-Neto P. 2013.** Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution* **4**: 1120–1131.
- Grigg G & Kirshner D. 2015.** Biology and evolution of crocodylians. Nova York: Cornell University Press.
- Houssaye A, Sander PM & Klein N. 2016.** Adaptive Patterns in Aquatic Amniote Bone Microanatomy—More Complex than Previously Thought. *Integrative and Comparative Biology*, **56**: 1349–1369.
- Huttenlocker AK & Farmer CG. 2017.** Bone microvasculature tracks red blood cell size diminution in Triassic mammal and dinosaur forerunners. *Current Biology* **27**: 48–54.
- Kellner AWA, Pinheiro AEP & Campos DA. 2014.** A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K-Pg boundary. *PloS ONE* **9**: e81386.

- Legendre LJ, Guenard G, Botha-Brink J & Cubo J. 2016.** Palaeohistological evidence for ancestral high metabolic rate in archosaurs. *Systematic Biology* **65**: 989–996.
- Marinho TS & Carvalho IS. 2009.** An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. *Journal of South American Earth Sciences* **27**: 36–41.
- Melstrom KM & Irmis RB. 2019.** Repeated evolution of herbivorous crocodyliforms during the age of dinosaurs. *Current Biology* **29**: 2389.
- Mendyk RW, Augustine L & Baumer M. 2014.** On the thermal husbandry of monitor lizards. *Herpetological Review* **45**: 619–632.
- Montes L, Le Roy N, Perret M, De Buffrenil V, Castanet J & Cubo J. 2007.** Relationships between bone growth rate, body mass and resting metabolic rate in growing amniotes: a phylogenetic approach. *Biological Journal of the Linnean Society* **92**: 63–76.
- Nascimento PM & Zaher H. 2010.** A new Baurusuchidae from the Upper Cretaceous of Brazil. *Papéis Avulsos de Zoologia* **50**: 323–361.
- Nobre PH & Carvalho I de S. 2013.** Postcranial skeleton of *Mariliasuchus amarali* Carvalho and Bertini, 1999 (Mesoeucrocodylia) from the Bauru Basin, Upper Cretaceous of Brazil. *Ameghiniana* **50**: 98–113.
- Olivier C, Houssaye A, Jalil NE & Cubo J. 2017.** First palaeohistological inference of resting metabolic rate in an extinct synapsid, *Moghreberia nmachouensis* (Therapsida: Anomodontia). *Biological Journal of the Linnean Society* **121**: 409–419.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N & Pearse W. 2013.** *Caper: Comparative Analyses of Phylogenetics and Evolution in R*.
- Pol D, Nascimento PM, Carvalho AB, Riccomini C, Pires-Domingues RA & Zaher H. 2014.** A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE* **9**: e93105.

Pough FH. 1980. The Advantages of ectothermy for tetrapods. *The American Naturalist* **115**: 92–112.

Riff D, Souza RG, Cidade GM, Martinelli AG & Souza-Filho JP. 2012. Crocodilomorfos: a maior diversidade de répteis fósseis do Brasil. *Terræ* **9**: 12–40.

Sena MVA, Andrade RCLP, Sayao JM & Oliveira GR. 2018. Bone microanatomy of *Pepesuchus deiseae* (Mesoeucrocodylia, Peirosauridae) reveals a mature individual from the Upper Cretaceous of Brazil. *Cretaceous Research* **90**: 335–348.

Sereno PC & Larsson HCE. 2009. Cretaceous Crocodyliforms from the Sahara. *Zookeys*: 1–143.

Seymour RS, Bennett-Stamper CL, Johnston SD, Carrier DR & Grigg GC. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. *Physiological and Biochemical Zoology* **77**: 1051–1067.

Snyder GK & Sheafor BA. 1999. Red blood cells: Centerpiece in the evolution of the vertebrate circulatory system. *American Zoologist* **39**: 189–198.

Vasconcellos FM & Carvalho IS. 2005. Estágios de desenvolvimento de *Mariliasuchus amarali*, Crocodyliformes Mesoeucrocodylia da Formação Adamantina, Cretáceo Superior da Bacia Bauru, Brasil. *Anuário do Instituto de Geociências*. **28**: 49–69.

Vogel S. 2005. Living in a physical world V. Maintaining temperature. *Journal of Biosciences* **30**: 581–590.

White CR, Phillips NF & Seymour RS. 2006. The scaling and temperature dependence of vertebrate metabolism. *Biology Letters* **2**: 125–127.

Wilberg EW, Turner AH & Brochu CA. 2019. Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports* **9**: 514.

FIGURE CAPTIONS

Figure 1. Resting metabolic rate inferred for a sample of *Notosuchia* using palaeohistology and phylogenetic eigenvector maps. We used a model that included phylogeny + osteocyte area for the femur as explanatory factors. Blue squares indicate ectothermy and red squares endothermy. For fossil taxa, segments represent the 95% confidence interval of the inferences. Abbreviations: AIC, Akaike information criterion. Phylogeny for extant taxa has been compiled by Legendre *et al.* (2016) and Olivier *et al.* (2017), and for extinct one has been taken from Geroto & Bertini (2019).

Figure 2. Red blood cell width inferred for a sample of *Notosuchia* using palaeohistology and phylogenetic eigenvector maps. We used a model that included phylogeny + harmonic mean canal diameter for the femur as explanatory factors. Blue squares indicate ectothermy and red squares endothermy. For fossil taxa, segments represent the 95% confidence interval of the inferences. Abbreviations: AIC, Akaike information criterion. Phylogeny for extant taxa has been compiled by Huttenlocker & Farmer (2017), and for extinct one has been taken from Geroto & Bertini (2019).

Figure 3. Optimization of the presence of endothermy onto a phylogeny of tetrapods. Inferences of extinct taxa have been performed in this study, with the exception of *Azendohsaurus laaroussii*, *Calyptosuchus welllesi* and *Postosuchus kirkpatricki*, that were performed by Cubo and Jalil (2019). Phylogeny for extant taxa has been compiled by Legendre *et al.* (2016) and Olivier *et al.* (2017), and for extinct one has been taken from Geroto & Bertini (2019). Red branches: endothermy. Blue branches: ectothermy.

Bones	Taxa	Inferred RMR (ml O ₂ h ⁻¹ g ^{-0.67})	Lower limit 95% CI	Upper limit 95% CI
Humerus	<i>Mariliasuchus amarali</i>	0.305	0.168	0.552
Femur	<i>Araripesuchus wegneri</i>	0.304	0.183	0.504
	<i>Armادillosuchus arrudai</i>	0.345	0.179	0.663
	<i>Baurusuchus</i> sp.	0.336	0.177	0.636
	<i>Iberosuchus macrodon</i>	0.307	0.159	0.592
	<i>Stratiotosuchus maxhecti</i>	0.353	0.181	0.691
Tibia	<i>Pepesuchus deiseae</i>	0.255	0.110	0.590
	<i>Stratiotosuchus maxhecti</i>	0.267	0.119	0.601

Table 1. Inferences of resting metabolic rate (ml O₂ h⁻¹ g^{-0.67}) of the sample of Notosuchia analysed in this study using phylogenetic eigenvector maps models that included the following predictors: phylogeny + osteocyte shape for the humerus, phylogeny + osteocyte area for the femur, and phylogeny + osteocyte shape for the tibia. Abbreviations: CI, confidence interval.

Taxa	Inferred RBC variables	Inferred values	Lower limit 95% CI	Upper limit 95% CI
<i>Araripesuchus wegeneri</i>	RBC _{width} (μm)	11.343	9.699	12.988
	RBC _{area} (μm ²)	149.990	131.047	168.934
<i>Armadosuchus arrudai</i>	RBC _{width} (μm)	11.200	9.541	12.859
	RBC _{area} (μm ²)	152.124	130.900	173.348
<i>Baurusuchus</i> sp.	RBC _{width} (μm)	11.136	9.492	12.780
	RBC _{area} (μm ²)	148.022	127.322	168.722
<i>Iberosuchus macrodon</i>	RBC _{width} (μm)	12.577	10.391	14.764
	RBC _{area} (μm ²)	155.884	132.297	179.470
<i>Stratiotosuchus maxhechti</i>	RBC _{width} (μm)	12.533	10.403	14.663
	RBC _{area} (μm ²)	161.011	137.690	184.332

Table 2. Inferences of red blood cells dimensions of the sample of Notosuchia analyzed in this study using a PEM model. The model to infer red blood cells width (μm) included phylogeny + harmonic mean canal diameter as predictors. The model to infer red blood cells area (μm²) included phylogeny + minimum canal diameter. Abbreviations: CI, confidence interval; RBC, red blood cells.