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

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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, Armadillosuchus, 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 wellesi* (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 repirometry, 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 ml O_2 h^{-1} $g^{-0.67}$) 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.

PHYLOGENY AND PHYLOGENETIC COMPARATIVE METHODS

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* (*Mariliasuchus* (*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* ((*Mariliasuchus* – *Armadillosuchus*)(*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 wellesi* 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, Mariliasuchus, Stratiotosuchus*) 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 *Mariliasuchus.* Nobre and Carvalho (2013) observed that *Mariliasuchus amarali* shares postcranial features with recent eusuchians, and concluded that this taxon probably had a sprawling type posture and an amphibian lifestyle. However *Mariliasuchus 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 *Mariliasuchus*' 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 *Mariliasuchus 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 *Mariliasuchus* 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

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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).

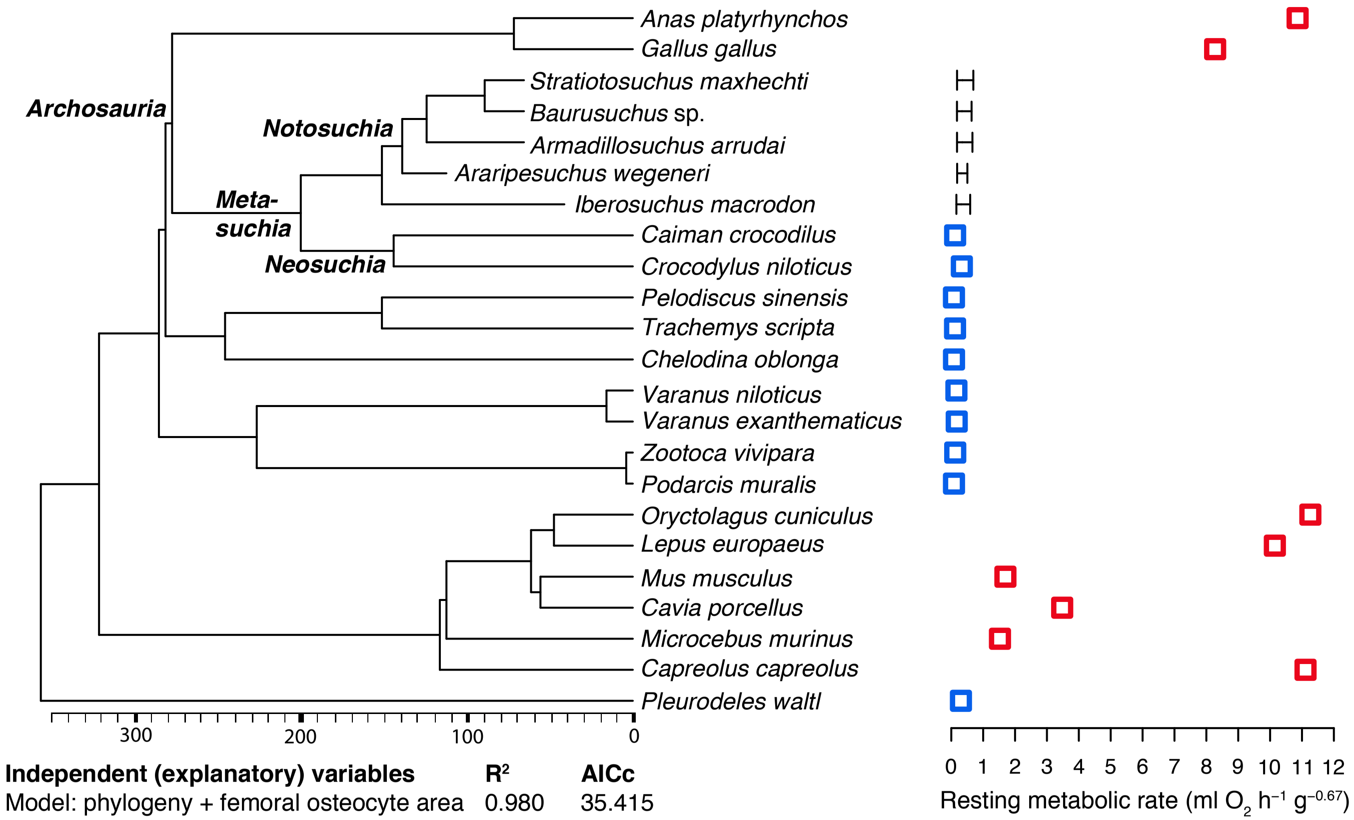
Figure 3. Optimization of the presence of endothermy onto a phylogeny of tetrapods. Inferences of extinct taxa have been performed in this study, with the exception of *Azendohsaurus laaroussii*, *Calyptosuchus wellesi* and *Postosuchus kirkpatricki*, that were performed by Cubo and Jalil (2019). Phylogeny 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 ($ml\ O2\ h^{-1}\ g^{-0.67}$)	Lower limit 95% CI	Upper limit 95% CI
Humerus	*Mariliasuchus amarali*	0.305	0.168	0.552
Femur	*Araripesuchus wegeneri*	0.304	0.183	0.504
	Armadillosuchus arrudai	0.345	0.179	0.663
	Baurusuchus sp.	0.336	0.177	0.636
	Iberosuchus macrodon	0.307	0.159	0.592
	Stratiotosuchus maxhechti	0.353	0.181	0.691
Tibia	*Pepesuchus deiseae*	0.255	0.110	0.590
	Stratiotosuchus maxhechti	0.267	0.119	0.601

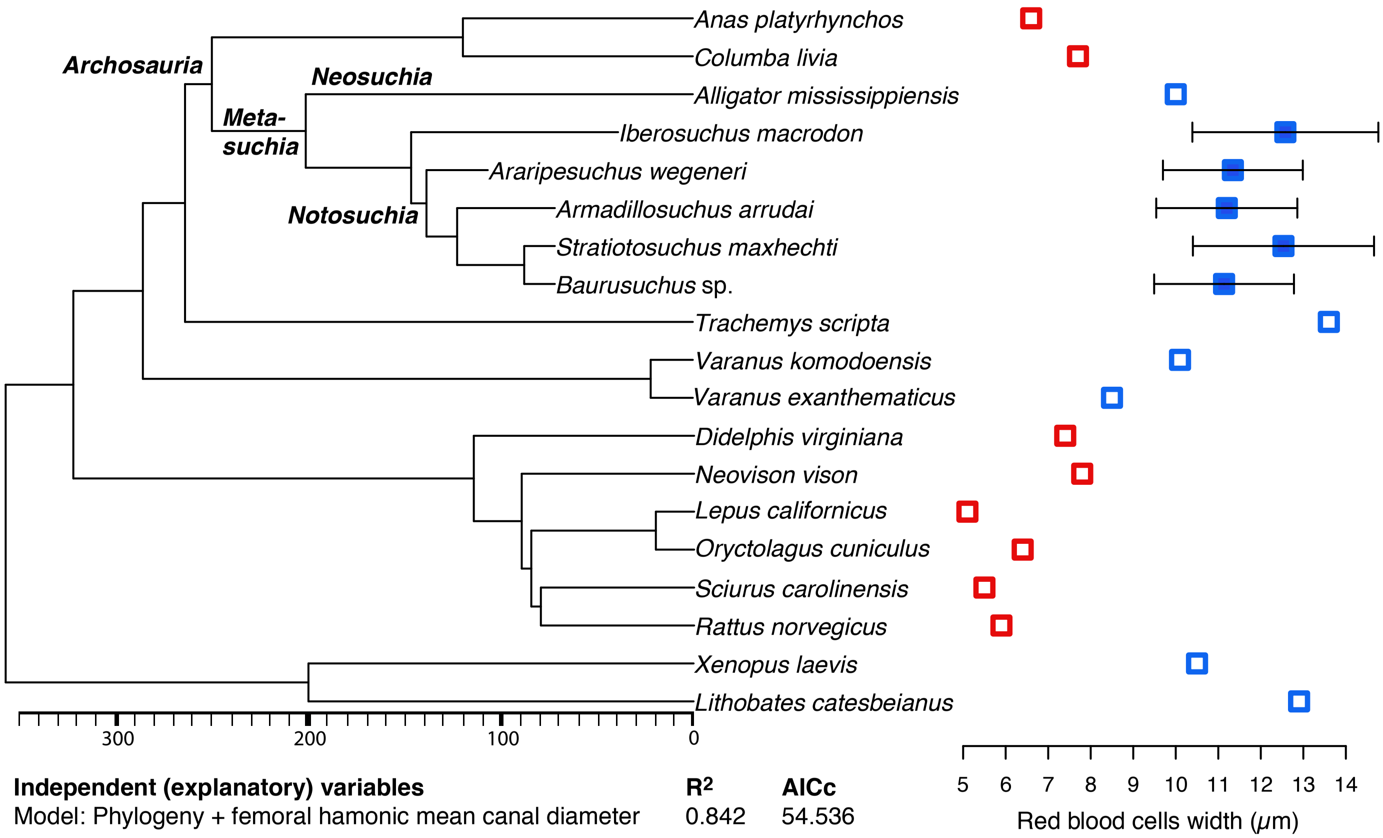
Table 1. Inferences of resting metabolic rate ($ml\ O2\ h^{-1}\ g^{-0.67}$) of the sample of Notosuchia analysed in this study using phylogenetic eigenvector maps models that included the following predictors: phylogeny + osteocyte shape for the humerus, phylogeny + osteocyte area for the femur, and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

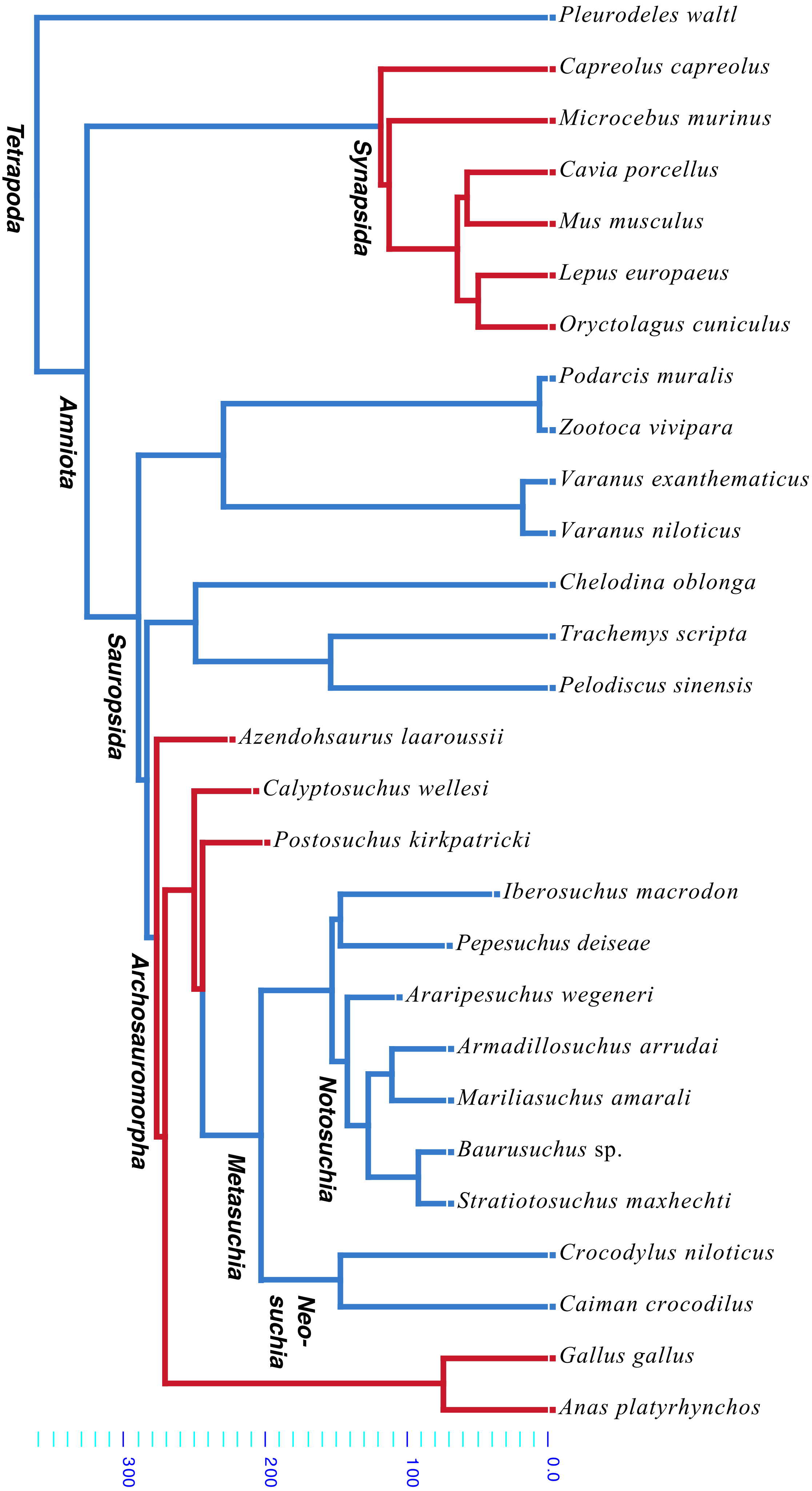
Taxa	Inferred RBC variables	Inferred values	Lower limit 95% CI	Upper limit 95% CI
Araripesuchus wegeneri	RBC_{width} (µm)	11.343	9.699	12.988
	RBC_{area} ($µm^2$)	149.990	131.047	168.934
Armadillosuchus arrudai	RBC_{width} (µm)	11.200	9.541	12.859
	RBC_{area} ($µm^2$)	152.124	130.900	173.348
Baurusuchus sp.	RBC_{width} (µm)	11.136	9.492	12.780
	RBC_{area} ($µm^2$)	148.022	127.322	168.722
Iberosuchus macrodon	RBC_{width} (µm)	12.577	10.391	14.764
	RBC_{area} ($µm^2$)	155.884	132.297	179.470
Stratiotosuchus maxhechti	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 ($µm^2$) included phylogeny + minimum canal diameter. Abbreviations: CI, confidence interval; RBC, red blood cells.



Independent (explanatory) variables	**R^2**	**AICc**
Model: phylogeny + femoral osteocyte area	0.980	35.415


Archosauria
Neosuchia
Meta-
suchia
Notosuchia
Anas platyrhynchos
Columba livia
Alligator mississippiensis
Iberosuchus macrodon
Araripesuchus wegeneri
Armadillosuchus arrudai
Stratiotosuchus maxhechti
Baurusuchus sp.
Trachemys scripta
Varanus komodoensis
Varanus exanthematicus
Didelphis virginiana
Neovison vison
Lepus californicus
Oryctolagus cuniculus
Sciurus carolinensis
Rattus norvegicus
Xenopus laevis
Lithobates catesbeianus
300
200
100
0
5
6
7
8
9
10
11
12
13
14
Red blood cells width (μm)
Independent (explanatory) variables
Model: Phylogeny + femoral hamonic mean canal diameter
R²
0.842
AICc
54.536


Pleurodeles waltl
Capreolus capreolus
Microcebus murinus
Cavia porcellus
Mus musculus
Lepus europaeus
Oryctolagus cuniculus
Podarcis muralis
Zootoca vivipara
Varanus exanthematicus
Varanus niloticus
Chelodina oblonga
Trachemys scripta
Pelodiscus sinensis
Azendohsaurus laaroussii
Calyptosuchus wellesi
Postosuchus kirkpatricki
Iberosuchus macrodon
Pepesuchus deiseae
Araripesuchus wegeneri
Armadillosuchus arrudai
Mariliasuchus amarali
Baurusuchus sp.
Stratiotosuchus maxhechti
Crocodylus niloticus
Caiman crocodilus
Gallus gallus
Anas platyrhynchos
Tetrapoda
Amniota
Synapsida
Sauropsida
Archosauromorpha
Metasuchia
Notosuchia
Neo-suchia
300
200
100
0.0