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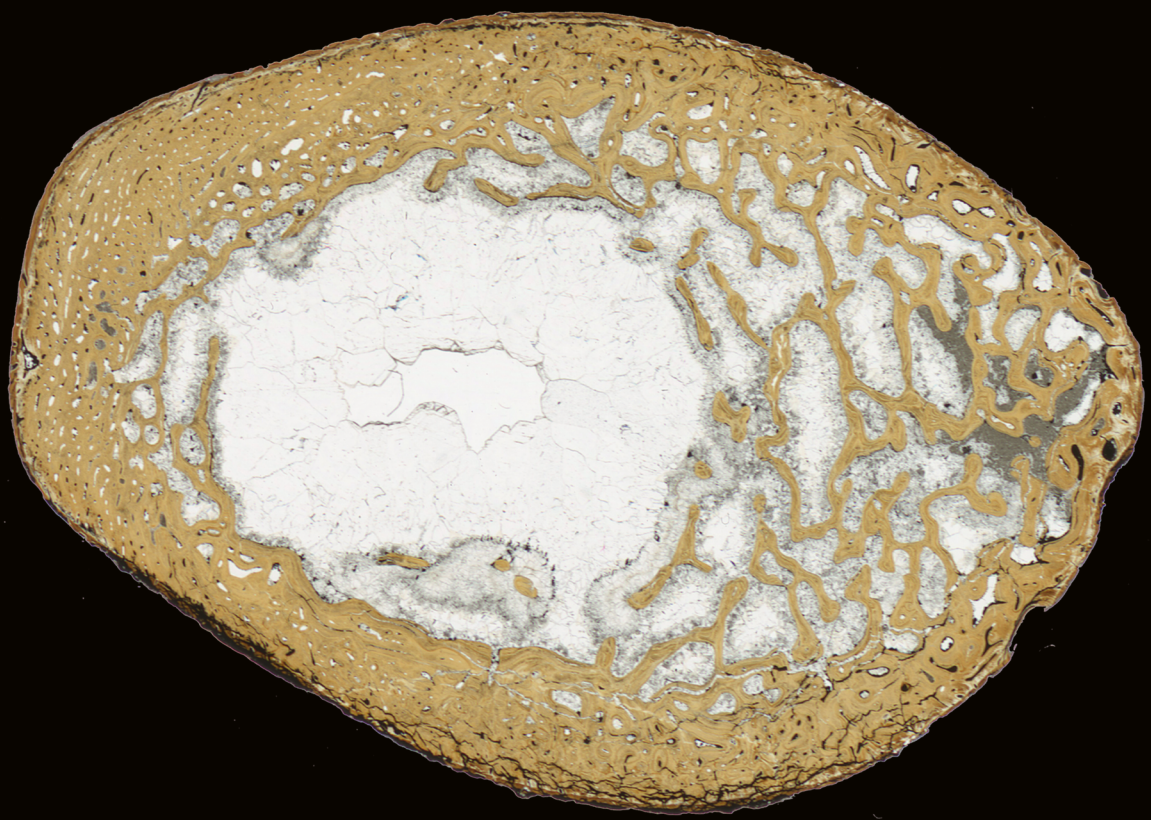
Elucidating the thermometabolism of *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 (Archosauria: Metriorhynchidae): a paleohistological study

Romain PELLARIN, Mariana SENA, François CLARAC & Jorge CUBO



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Thin section of *Thalattosuchus superciliosus* femora, mid-diaphysis (MHBR 207).

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Elucidating the thermometabolism of *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 (Archosauria: Metriorhynchidae): a paleohistological study

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ABSTRACT
Metriorhynchidae Fitzinger, 1843 is an emblematic group of crocodylomorphs whose marine and pelagic lifestyle has long aroused the interest of palaeontologists. Indeed, both their ecology and thermometabolic strategy (i.e., endotherm or ectotherm) remained debated. In order to shed light on this matter, we inferred the thermometabolism of *Thalattosuchus superciliosus* de Blainville, 1852 focusing on the femoral histology and CT-scan anatomy. Using "phylogenetic logistic regression" methods, we calculated the probability of endothermy on the basis of minimum vascular cavity diameter. Using the "phylogenetic eigenvector maps" approach, we inferred resting (based on osteocyte density) and maximum (based on minimum diameter of femoral nutrient foramina) metabolic rates. We found that *T. superciliosus* had a low probability of being endotherm and possessed a low resting metabolic rate. The study of the maximal metabolic rate allows us to suggest that *T. supercilious* was not a pursuit hunter, but perhaps rather had a sit-and-wait/opportunistic and scavenging feeding strategy, as extant crocodylians. Our study allows us to discuss the ecology of this species, but further studies relying on a wider sample of metriorhynchids are needed in order to have a better understanding of both the thermometabolism and the foraging behavior of this group.

KEY WORDS
Palaeontology, Metriorhynchidae, paleohistology, *Thalattosuchus*, thermometabolism.

RÉSUMÉ
L'élucidation du thermométabolisme de Thalattosuchus superciliosus *(de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 (Archosauria : Metriorhynchidae) : une étude paléohistologique.*
Metriorhynchidae Fitzinger, 1843 constitue un groupe emblématique de crocodylomorphes dont le mode de vie marin et pélagique a longtemps suscité l'intérêt des paléontologues. En effet, tant leur écologie que leur thermométabolisme (i.e., endotherme ou ectotherme) sont restés débattus. Afin de faire la lumière sur cette question, nous avons inféré le thermométabolisme de *Thalattosuchus superciliosus* de Blainville, 1852 en nous concentrant sur l'histologie fémorale et l'anatomie par tomographie à rayon X. En utilisant les méthodes de "régressions logistiques phylogénétiques" nous avons calculé la probabilité d'endothermie sur la base du diamètre minimal des cavités vasculaires. En utilisant l'approche des "cartes de vecteurs propres phylogénétiques" nous avons inféré les taux métaboliques au repos (sur la base de la densité ostéocytaire) et maximaux (sur la base du diamètre minimal du foramen nourricier fémoral). Nous avons constaté que *T. superciliosus* avait une faible probabilité d'être endotherme et possédait un faible taux métabolique au repos. L'étude du taux métabolique maximal nous permet de suggérer que *T. superciliosus* n'était pas un chasseur de poursuite, mais qu'il avait peut-être plutôt une stratégie de capture de proies en embuscade, opportuniste et charognarde, comme les crocodiliens actuels. Notre étude nous permet de discuter de l'écologie de cette espèce, mais d'autres études reposant sur un échantillon plus grand de métriorhynchidés sont nécessaires pour mieux comprendre le thermométabolisme et le comportement alimentaire de ce groupe.

MOTS CLÉS
Paléontologie,
Metriorhynchidae,
paléohistologie,
Thalattosuchus,
thermométabolisme.

INTRODUCTION

Metriorhynchidae Fitzinger, 1843 is an extinct clade within Thalattosuchia Fraas, 1901 (Archosauria Cope, 1869; Crocodylomorpha Hay, 1930) whose representatives are known in the Mesozoic, from the middle Jurassic to the end of the lower Cretaceous. Mainly found in Europe (i.e., France, Germany, England, and Italy) but also in both South America (Chile and Argentina) and North America (Mexico), they are known to have returned to a pelagic marine lifestyle (Frey *et al.* 2002; Cau & Fanti 2011; Fernández *et al.* 2011; Young *et al.* 2011; Parrilla-Bel *et al.* 2013; Sachs *et al.* 2021; Le Mort *et al.* 2022). This lifestyle transition has been inferred on the basis of major morphological changes, such as the loss of osteoderms and scales, a transformation of the limbs into swimming paddles, a hypocercal caudal fin and the presence of a preorbital aperture related to a salt gland (Andrews 1913; Fernández & Gasparini 2000, 2008; Spindler *et al.* 2021; Fernández & Herrera 2022). These anatomical traits and the fossil occurrences in both coastal and pelagic sediments suggest that this return to marine life came with an adaptation to either a piscivorous or hypercarnivorous diet, depending on taxa (Young *et al.* 2010). This phenotype is convergent with those of other sauropsids such as ichthyosaurs, mosasaurs and plesiosaurs.

The ecology of an organism is especially determined by its diet, which is related to physiology (da Silva & Maia 2013). For instance, thermophysiology (i.e., the physiological and behavioral mechanisms tied to the heat production of the organism; endothermy vs ectothermy) influences feeding habits (e.g. active hunters vs sit-and-wait ambush predators; da Silva & Maia 2013). In this study, we consider endothermy as a feature linked to a high whole body resting metabolic rate (RMR), called "tachymetabolism" leading to "tachymetabolic endothermy". On the opposite, we consider ectothermy as linked to a low RMR ("bradymetabolism") (Grigg *et al.* 2022). Sometimes, a "regional endothermy" occurs within ectotherms. It is defined by a strictly local production of heat to sustain specific function or behavior (e.g. regional endothermy the skull allows to some teleosteans to keep their sensory tissue efficient in cold water; Carey 1982; Graham & Dickson 2000, 2001; Dickson & Graham 2004; Grigg *et al.* 2022). The RMR defines the energy expended by an animal at rest, measured at a specified temperature (Arnold *et al.* 2021). RMR is linked to the volume of dioxygen consumed by time unit and body-mass: mL O_2 h^{-1} for raw RMR, mL O_2 h^{-1} g^{-1} for mass-specific RMR and mL O_2 h^{-1} g^{-b} for mass-independent approach, being b the allometric scaling exponent of mass (Glazier 2005; Montes *et al.* 2007). From a general point of view, endotherms will tend to have a more active lifestyle, and a higher RMR than ectotherms. On the other hand, ectotherms tend to have lower RMRs but can exhibit a high diversity of habits (including active hunting behavior observed in monitor lizards) despite the need of external heat sources to regulate their body temperature (Clarke & Pörtner 2010).

Previous work on both the extant crocodylian heart anatomy (Seymour *et al.* 2004) and long bone paleohistology (Legendre *et al.* 2016; Cubo & Jalil 2019), supported ancestral endothermy in archosauromorphs. This assumption implies a later switch to ectothermy in Pseudosuchia von Zittel, 1890 (Faure-Brac *et al.* 2022). The morphological peculiarity of the metriorhynchids within Crocodylomorpha raises a question about whether they possessed an endothermic metabolism as it has been inferred in ichthyosaurs and plesiosaurs (with which they shared several morphological

FIG. 1. — Photography of the studied fossil material: **A**, thin section of *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 femur, mid-diaphysis (MHBR 207); **B**, **C**, photography of MPV.2010.3.611a (**B**, right femur) and MPV.2010.3.611b (**C**, left femur). Scale bars: A, 5 mm; B, C, 5 cm. Credits: B, C, photographs by Philippe Loubry (MNHN).

adaptations to the pelagic lifestyle; Massare 1988) or if they instead possessed an ectothermic thermometabolism as for the extant crocodylian (Bernard *et al.* 2010; Harrell *et al.* 2016; Fleischle *et al.* 2018; Brice & Grigg 2023).

Within crocodylomorphs, inferring the thermometabolism of Metriorhynchidae had a lot of twists and turns. Hua & de Buffrénil (1996) inferred an ectothermic regime for both Teleosauridae Geoffroy Saint-Hilaire, 1831 and Metriorhynchidae based on a qualitative description of their bone histology. Recently, Séon *et al.* (2025), using isotope geochemistry, found that metriorhynchids and plesiosaurids had a body temperature (Tb) close to their environment. This suggests inability to produce a large amount of body heat, as in bradymetabolic ectothermic organisms, contrary to ichthyosaurs for which the Tb was higher. In their study they performed a reassessment of Tb published by Séon *et al.* (2020). Recently, Cubo *et al.* (2025) performed an integrative analysis of the paleophysiology of the non-metriorhynchid metriorhynchoid *Pelagosaurus typus* Bronn, 1841. These authors concluded that *P. typus* was a semi-aquatic, ectothermic, sit-and-wait ambush predator on the basis of phylogenetic comparative methods, using femoral bone histology and CT-scan anatomy as proxies.

In order to acquire new data with a paleohistological quantitative approach, here we made an integrative study based on phylogenetic comparative methods, as it has already been done for other crocodylomorph groups (Legendre *et al.* 2016; Cubo *et al.* 2020, 2023; Faure-Brac *et al.* 2022) but not yet on metriorhynchids.

To do so, we focus on *Thalattosuchus superciliosus* de Blainville, 1852 as a case study. In a first step, here we infer the probability of endothermy using the harmonic mean diameter of vascular cavities with phylogenetic logistic regression (PLR). Huttenlocker & Farmer (2017) discovered

the correlation between the size of red blood cells and the size of vascular canals among vertebrates. Endothermic organisms tend to have smaller red blood cell diameters and so, vascular canals, than ectotherms. This adaptation led to a better oxygen diffusion to adjacent tissues because smaller cells do have higher surface to volume ratios.

We further infer the resting metabolic rate (RMR) using the osteocyte lacunar density and phylogenetic eigenvector maps (PEM) in order to compare results. Cubo *et al.* (2012) and Legendre *et al.* (2016) showed that this variable has a good explanatory power for inferring RMR in their PEM analyses.

Finally, we quantify the peak levels of activity during strenuous activity using the blood flow through the femoral nutrient foramina and PEM. The peak level of activity of an organism defines the moment when it is most active, particularly during foraging or predation phase. During these periods, its oxygen consumption must increase, and it may reach its maximum aerobic metabolic rate (MMR). An organism's MMR is therefore a good indicator of whether it can sustain intense activity, and a number of studies have already looked at inferring this parameter in fossil organisms, using blood flow index (Qi) through the femoral nutrient foramen relative to the femur's length as a proxy (Seymour *et al.* 2012; Knaus *et al.* 2021; Sena *et al.* 2023). Qi has been proposed by Seymour *et al.* (2012) because intense activity will produce bone microfractures repaired by bone remodeling (Ponton *et al.* 2007). As a result, an organism with a high MMR will have a higher blood flow than an organism with a lower MMR, to supply oxygen to the remodeling process.

The three above-mentioned approaches will allow a new perspective through the spectrum of phylogenetic comparative methods. It will enable an integrative approach to the metabolism of metriorhynchids thanks to the findings of the previous studies and will contribute to acquire new data concerning the metabolic rates within Crocodylomorpha, with the aim to elucidate their thermometabolism evolution and paleobiology.

MATERIAL AND METHODS

FOSSIL MATERIAL

The sampled material is shown in Figure 1. The femur analyzed histologically comes from the Callovian of France and was previously studied by Hua & de Buffrénil (1996). This specimen was originally identified as *Metriorhynchus*

superciliosus de Blainville, 1852 (MHBR 207) newly renamed *Thalattosuchus superciliosus* (Young *et al.* 2021). A new thin section was prepared from the mid-diaphysis of the femur to further estimate both the resting metabolic rate (RMR) and the probability of endothermy.

The quantification of the maximum metabolic rate (MMR) has been done using two femora of *T. superciliosus* (MPV.2010.3.611a, left femur; MPV.2010.3.611b, right femur), which were provided by the Paléospace collection (Normandy, France) for CT-Scan analysis. We assume that these two femora belong to the same specimen since they are strictly symmetrical (as we checked in Geomagic Wrap), and about the same size.

The exact age of these femora is unknown, but *T. superciliosus* occurrence ranges between the base of the late/upper Callovian and the top of the Kimmeridgian *or* 164.7 to 152.1 Ma (The Paleobiology Database; Sauvage 1914; Grange & Benton 1996).

Statistical methods

As mentioned above, two phylogenetic comparative methods were used to infer the thermal physiology of *Thalattosuchus superciliosus*. Statistical analyses have been performed on R Studio software (R Development Core Team 2008). First, phylogenetic logistic regressions (PLR; Ives & Garland 2010) implemented in the package "phylolm" (Tung Ho & Ané 2014), were used to estimate the probability of endothermy (e.g. Cubo *et al.* 2023). Then, phylogenetic eigenvector maps (PEM; Guénard *et al.* 2013) implemented in the package "MPSEM", were used to infer both, resting and maximum metabolic rates (Legendre *et al.* 2016; Knaus *et al.* 2021) of the studied taxon.

Data sampling

Osteocyte density (Fig. 2A)

The protocol for measuring this variable comes from Cubo *et al.* (2012). The measurement of this variable consists of counting the number of osteocyte lacunae that are present in the bone matrix of the primary bone, in between primary osteons. *A priori* these measurements have to be performed in the deepest layers of the primary bone cortex, formed when the organism was juvenile, because the specimens that were sampled by Cubo *et al.* (2012) to construct the original dataset were juveniles. The number of lacunae is then divided by the bone area analyzed (Celldensity; number of osteocyte lacunae per µm²). Due to the extensive bone remodeling in this internal bone layer of *Thalattosuchus superciliosus* thin section, the measurements were made in outer areas of primary woven bone (approximately 2.5 mm²)

We quantified both variables on the thin section images of femur MHBR 207. Thin sections were observed using an optical microscope (Nikon Eclipse E600 POL) and photographs were taken for interpretation using a Nikon Digital Sight DS-L1 camera at Sorbonne University. The histological variables were quantified using ImageJ software (version 1.53s; Abràmoff *et al.* 2004). Thin sections of the extant specimens used to construct the dataset, and the fossil specimen MHBR 207, are curated at the Vertebrate Hard Tissue Collection of the Muséum national d'Histoire naturelle, Paris, France (MNHN).

Harmonic mean of vascular cavities (Fig. 2B)

The protocol for measuring this variable comes from Huttenlocker & Farmer (2017) and the comparative dataset has been taken from Cubo *et al.* (2023). These authors measured the minimum diameter (in µm) of approximately 50 vascular cavities in femoral mid diaphyseal transverse thin sections of 46 extant species and computed the harmonic means ($Can_{harmean}$).

Estimation of the blood flow index (Fig. 2C)

The blood flow index (Qi) calculation protocol came from Seymour *et al.* (2012). It can be computed as $Q_i = r^4/L$ (in mm^3), where r is the radius (in mm) of the minimal diameter of the nutrient foramen (NF) and L is the length of the femur (also in mm).

The fossil specimens have been scanned at the X-Ray Tomography (AST-RX) platform at the MNHN (MPV.2010.3.611a voxel size: 0.067 mm; MPV.2010.3.611b voxel size: 0.061 mm). The data were processed at the 3D imaging facilities of the UMR 7207 CR2P. The segmentation and measurement of nutrient foramina were made in Mimics® Innovation Suite v.24 (Materialise). Foramina were located manually using the scan slices in the axial view. The images were rendered in 3D using the "Multiple slice edit" tool. The segmentation as well as the estimation of the diameter of the NF have been computed on Mimics (version v.24) software. The protocol consists of measuring the diameter of the NF as close as possible to the opening in order to limit a bias of sampling between the fossil and the extant dry bones whose foramina have been measured at the surface.

Phylogeny calibration

Both statistical approaches take into account the evolutionary history of the taxa that make up the dataset in order to circumvent the statistical problem of the non-independence of observations (Felsenstein 1985; Revell & Harmon 2022).

PLR on vascular harmonic-mean diameter

The phylogenetic relationships include only extant taxa that we used to construct the inference model. The latter consists of 46 species, taken from Cubo *et al.* (2023). This model will be used to infer the probability of endothermy for the studied taxa. The dataset and the topology can be found in the Supplementary data folder.

PEM on osteocyte density

The phylogenetic tree includes present-day taxa as well as the fossil taxon of interest (*T. superciliosus*; MHBR 207). This approach will allow us to infer the RMR (mL O_2 h^{-1} $g^{-0.67}$). There is no consensual value according to the mass exponent to use in metabolic rates inferences (White *et al.* 2006). Here we choose to use the scaling exponent 0.67 for the RMR, in order to fit with the original used dataset and previous studies about inferred metabolism of extinct taxa (Montes *et al.* 2007; Legendre *et al.* 2016; Cubo & Jalil 2019; Faure-Brac & Cubo 2020; Cubo *et al.* 2020, 2025). The dataset for extant taxa and the topology

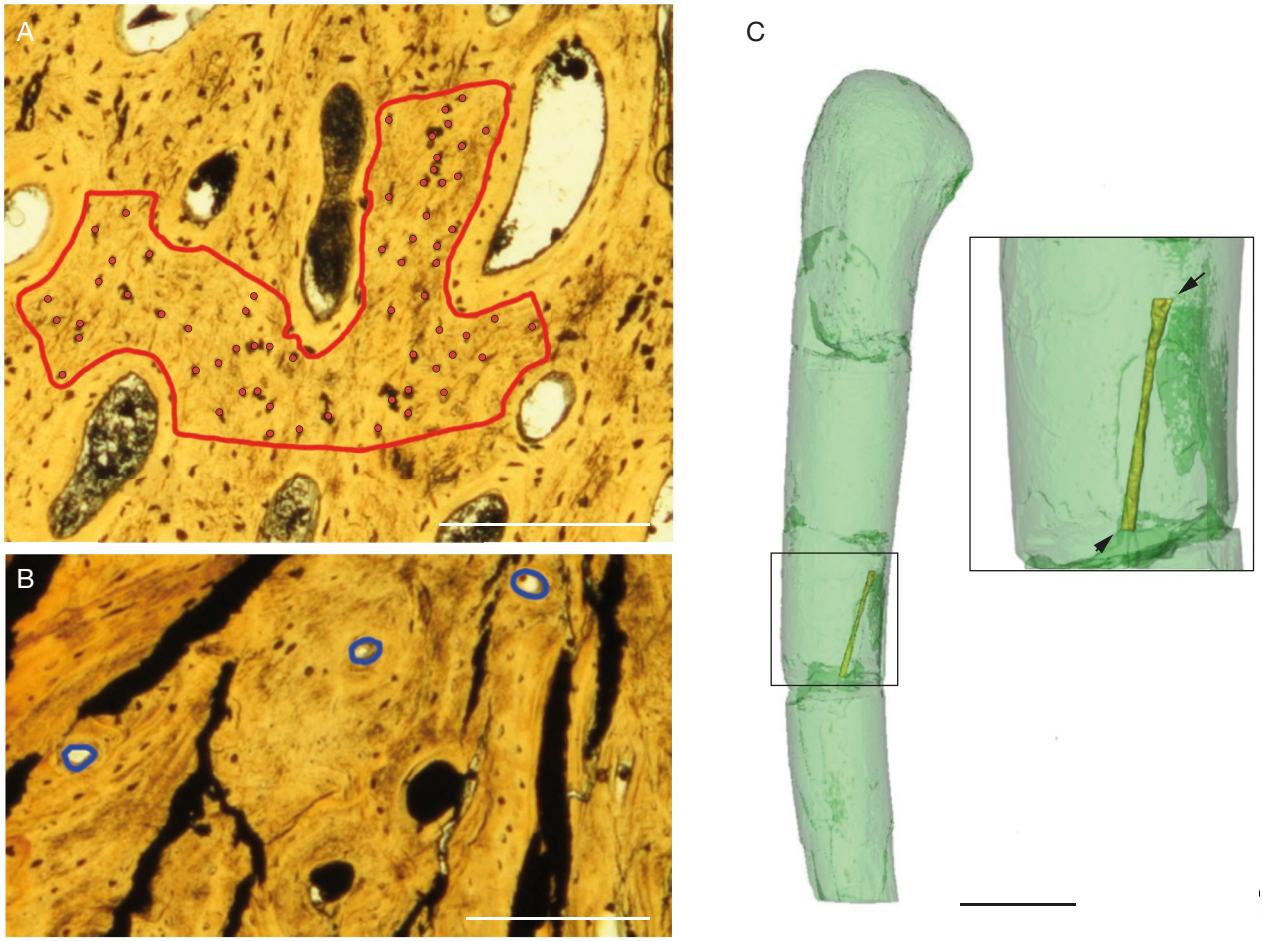

Fig. 2. — Osteological proxy used for the statistical inferences: **A**, osteocyte lacunae in primary bone (**red dots**) in a sampled area (**red line**) (MHBR 207); **B**, vascular cavities (**blue lines**) (MHBR 207); **C**, nutrient foramen (**yellow bold**) into the femur (**translucent green**), with the focus on the opening of the nutrient foramina (MPV.2010.3.611a). **Arrow**, periosteal opening; **arrow head**, medullary opening. Scale bars: A, 0.25 mm; B, 0.20 mm; C, 20 mm.

were obtained from Cubo *et al.* (2025) and modified to include *Thalattosuchus superciliosus* using Mesquite software (version 3.61; Maddison & Maddison 2019) (Supplementary data). The species was placed as the closest relative of the clade *Crocodilia* Owen, 1842. The age of this node corresponds to the dichotomy between Thalattosuchia and the other crocodylomorphs (201.4 Ma; Westphal 1962), while the tip of the branch corresponds to the last occurrence of *T. superciliosus* (152.1 Ma; Sauvage 1914).

PEM on minimal diameter of nutrient foramina

The phylogenetic tree includes extant taxa as well as fossil taxa. This approach will allow to infer the mass-specific MMR (mL O_2 h^{-1} g^{-1}). It is important to note that some authors have shown that the MMR is corrected with different mass exponents depending on the clade. Mammals have a mass exponent of 0.870, higher than that of sauropsids at 0.829 (mass-independent maximum metabolic rate; White & Seymour 2005; Seymour *et al.* 2013). By using a mass exponent of 1 (mass-specific metabolic rate), we ensure that we can use a larger dataset including both Synapsida Osborn, 1903 and Sauropsida Huxley, 1864, to infer the MMR of *T. superciliosus*. The dataset for extant taxa and the topology were taken from Cubo *et al.* (2025) (Supplementary data). *Thalattosuchus superciliosus* has been added manually thanks to Mesquite software (version 3.61; Maddison & Maddison 2019), branched as the closest relative of the clade *Crocodilia* Owen, 1842. The age of this node corresponds to the dichotomy between Thalattosuchia and the other crocodylomorphs (201.4 Ma; Westphal 1962), while the tip of the branch corresponds to the last occurrence of *T. superciliosus* (152.1 Ma; Sauvage 1914).

Abreviations

Insitutions

CR2P	Centre de recherche en Paléontologie – Paris;
MHBR	Muséum d'histoire naturelle du Havre;
MNHN	Muséum national d'Histoire Naturelle, Paris;
MPV	Paléospace, Villers-sur-Mer.

Facilities

AST-RX	Accès Scientifique à la Tomographie à Rayons X.

Methodology

PEM	phylogenetics eigenvector maps;
PLR	phylogenetic logistic regressions.

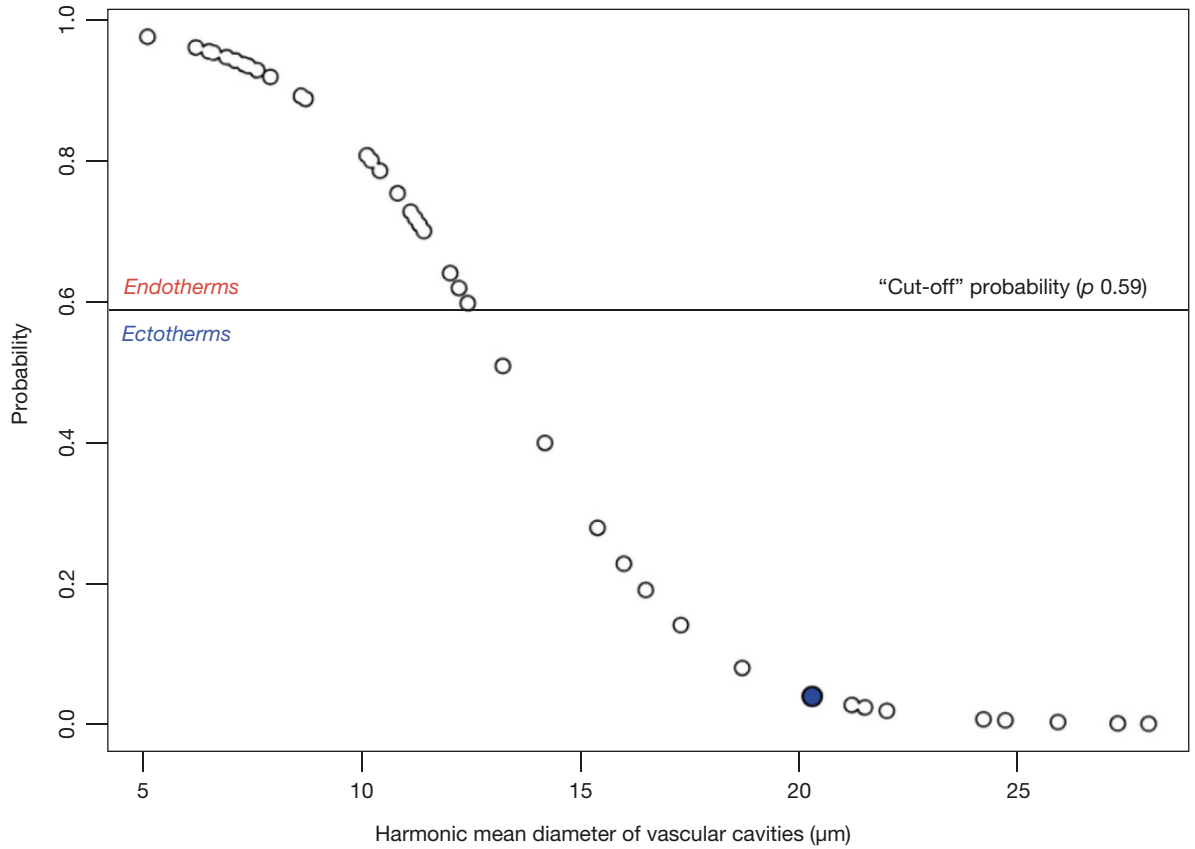

FIG. 3. — Distribution of probability of being endothermic inferred for *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 within the sample of extant tetrapods, using a phylogenetic logistic regression model that includes femoral vascular canal diameter (computed as Canharmean) as the explanatory variable. The **blue dot** indicates the position of *Thalattosuchus superciliosus* (MHBR 207) among the sampled extant taxa (**white dots**).

TABLE 1. — Quantified variable for estimating the RMR with PEM, and results for analysis computed with the better option (*Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021). Unit: mL O_2/h/g$^{0.67}$. Abbreviations: **PEM**, phylogenetics eigenvectors maps; **RMR**, resting metabolic rate.

Quantified response variable	**PEM (MHBR 207)**		
Celldensity (cell per µm²)	**Lower limit**	**RMR**	**Upper limit**
0.0005 (sd = 0.0001)	0.07	0.13	0.23

Biological traits
MMR maximum metabolic rate;
RMR resting metabolic rate.

R packages
MPSEM modelling phylogenetic signals using eigenvector maps;
phylolm phylogenetic linear regression.

RESULTS

ESTIMATION OF THE PROBABILITY OF ENDOTHERMY

PLR using $Can_{harmean}$ as an explanatory variable allowed to estimate the probability of endothermy for *T. superciliosus*. The harmonic mean of the diameter of *T. superciliosus* vascular cavities is 20.1 (Sd = 7.5) µm. We used this value to infer the probability of endothermy of *T. superciliosus* using the predictive model published by Cubo *et al.* (2023): $p(\text{endothermy}) = \exp(-0.45\ Can_{harmean} + 6.04)/[1 + \exp(-0.45\ Can_{harmean} + 6.04)]$. Replacing $Can_{harmean}$ by the value measured in *T. superciliosus* (20.1 µm) we obtained a $p(\text{endothermy}) = 0.04$. This probability is far lower than the cut-off probability of 0.59 separating endotherms from ectotherms (Cubo *et al.* 2023), suggesting that *T. superciliosus* was most likely an ectotherm (Fig. 3).

INFERENCE OF METABOLIC RATES

Resting metabolic rate

The data were log-transformed before the analysis. Figure 4 shows the results of PEM for RMR. The values of RMR that were inferred for *T. superciliosus* can be found in Table 1 (p-value <0.01), as for the measurements of osteocyte lacunar density. As for the variable Celldensity, the RMR that we inferred for *T. superciliosus* was not significantly different from those measured in extant ectotherms including other crocodylians (Fig. 4).

Maximum metabolic rate

The minimal radius for the nutrient foramen of MPV.2010.3.611a is 0.76 mm and it is 0.625 mm for MPV.2010.3.611b. These measurements, and the length

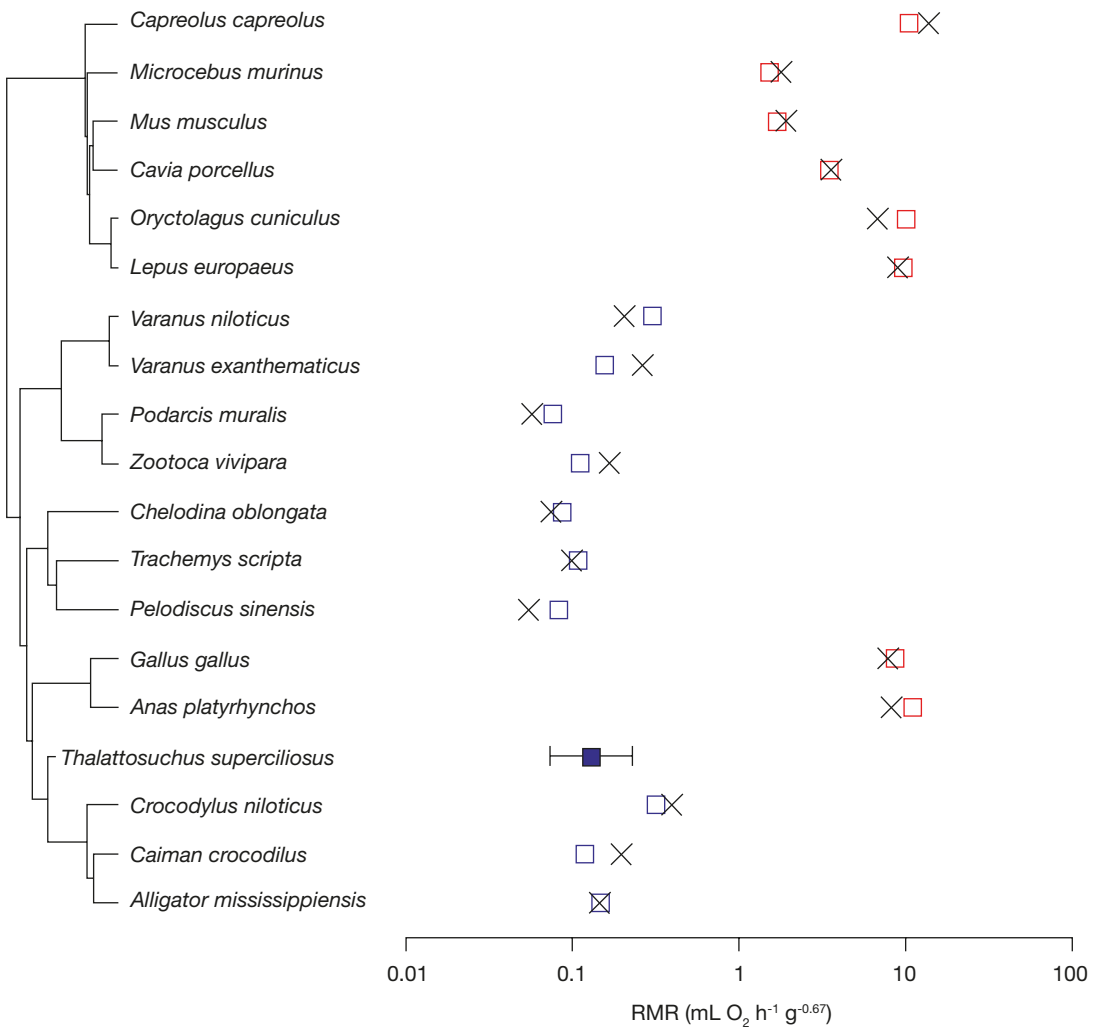

Fig. 4. — Results of the PEM analysis aimed at inferring the RMR of *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 (specimen MHBR 207). Empty squares are empirical data of extant tetrapods, whereas crosses are fitted values. Filled square is the inferred value for *Thalattosuchus superciliosus* (MHBR 207). Logarithmic scale. Abbreviations: **PEM**, phylogenetics eigenvectors maps; **RMR**, resting metabolic rate.

size of the whole femurs (MPV.2010.3.611a: 28.1 cm long; MPV.2010.3.611b: 27.8 cm long) allowed us to compute the Qi estimation (Table 2). Data were log transformed before the analysis. Figure 5 shows the results of PEM for MMR only for MPV.2010.3.611a because of the similarity of the results for the two femurs. The values of MMR that we inferred on both femora of *T. superciliosus* can be found in Table 2 (p-value <0.01). The MMR inferred for *T. superciliosus* is clearly in the range of ectotherms (Fig. 5).

DISCUSSION

The lifestyle of *Thalattosuchus superciliosus*

Hua & de Buffrénil (1996) hypothesized that *T. superciliosus* was ectothermic on the basis of a qualitative osteohistological description: both the presence of lines of arrest growth (LAGs) and the type of bone microstructure, are similar to those of extant crocodylians'. They especially noticed the presence of conspicuous growth marks in the whole skeleton, which were recognized as typical of an ecto-poikilothermic organism, because the growth of ectothermic organisms is affected by the seasonality of the environment (Hua & de Buffrénil 1996; Angilletta *et al.* 2002; Hjernquist *et al.* 2012). However, some studies reported LAGs in endothermic both extinct and extant taxa, such as dinosaurs and mammals (Farlow *et al.* 1995; Köhler *et al.* 2012). These LAGs are the evidence of torpor, hibernation or harsh conditions in endothermic species and so, it should not be considered as the most suitable proxy to infer either ectothermy or endothermy in extinct vertebrates. Nevertheless, our results based on both the cellular density of primary bone and the minimal diameter of vascular cavities, tend to confirm this previous assumption, based on: 1) the probability of endothermy in *T. superciliosus* (p = 0.04), which is far lower than the cutoff probability (p = 0.59) that separates endotherms from ectotherms (Fig. 3; Cubo *et al.* 2023); and 2) the resting metabolic rate of *T. superciliosus* which does not differ in order of magnitude from that of the extant crocodylians while also being far lower than those of both mammals and birds (Fig. 4).

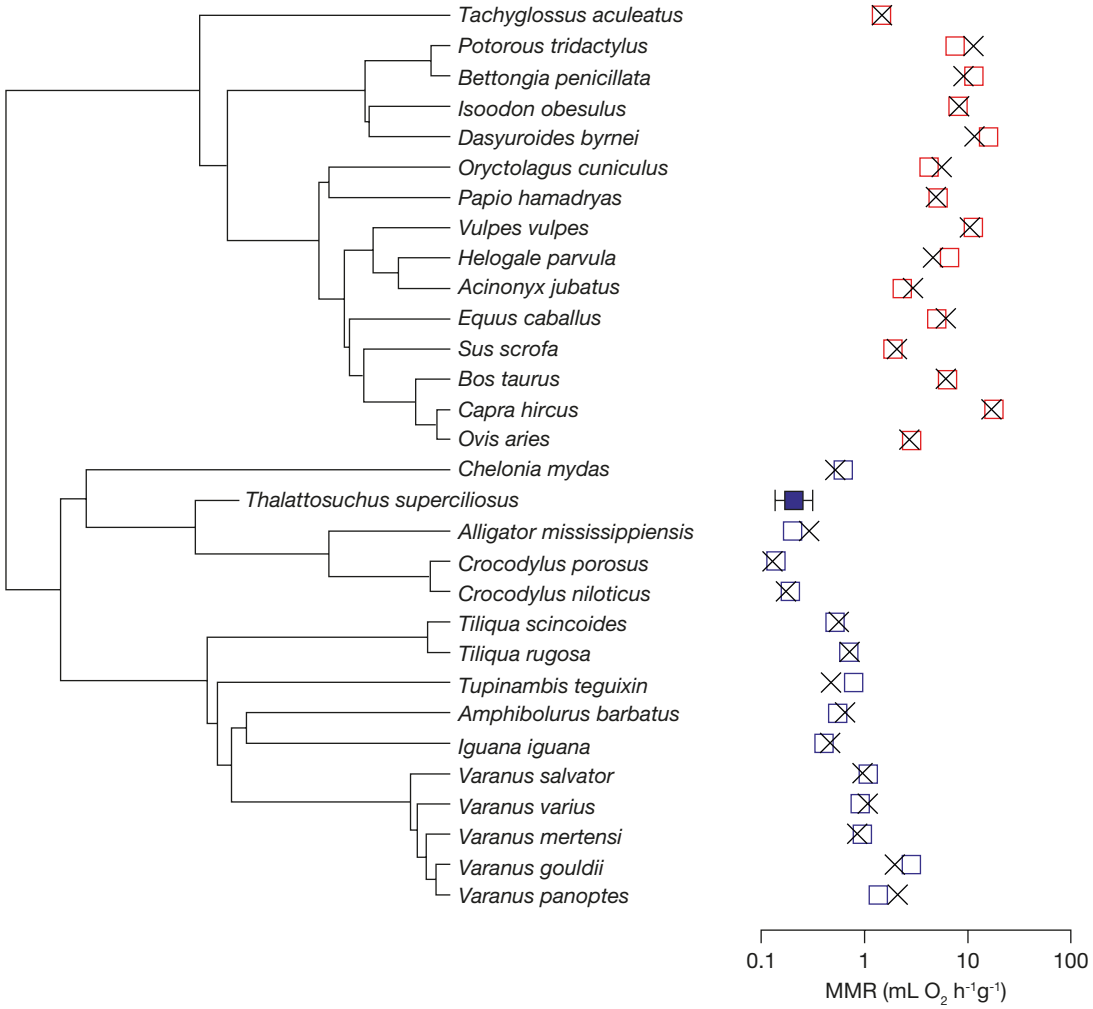

Fig. 5. — Results of the PEM analysis aimed at inferring the MMR of *Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021 (specimen MPV.2010.3.611a). Empty squares are empirical data from extant tetrapods, whereas crosses are fitted values. Filled square is the inferred value for *Thalattosuchus superciliosus* (MPV.2010.3.611a). Logarithmic scale. Abbreviations: **MMR**, maximum metabolic rate; **PEM**, phylogenetics eigenvectors maps.

Our results also agree with a more recent study by Séon *et al.* (2025), which revealed that the body temperature of *T. superciliosus* was close to that of seawater. Other previous studies based on thermal measurements in extant crocodylians (i.e., *Crocodylus johnstoni* Krefft, 1873 and *Crocodylus porosus* Schneider, 1801) have shown that the body temperature equalizes the water temperature when individuals stay immersed for several hours (Seebacher & Grigg 1997; Barham *et al.* 2024)

The congruence of the results between extant species (i.e., *Crocodylus johnstoni*, *Crocodylus porosus*) and *Thalattosuchus superciliosus*, suggests that they share similar resting and maximal metabolic rates despite living in different environments (fresh and brackish waters vs open seas).

These results suggest that *T. superciliosus* was not an "endothermic active-swimmer" unlike the contemporaneous ichthyosaurs, pliosaurs and plesiosaurs (Bardet *et al.* 2014) which are assessed to be endothermic according to both paleohistological and isotopic data (Bernard *et al.* 2010; Fleischle *et al.* 2018). On the basis of a theoretical approach, Massare (1988) compared plesiosaurs, pliosaurs, metriorhynchids and ichthyosaurs on their swimming capabilities. Massare (1988) suggested an undulating mode of swimming with the trunk and the tail (axial-undulatory) for Metriorhynchidae, more or less like the extant crocodylians. For their part, plesiosaurs and pliosaurs practiced an underwater flight like marine turtles, less efficient than the powerful caudal swim of an ichthyosaur (axial oscillatory or axial suboscillatory, analogous to extant dolphins) but more efficient than metriorhynchid ones. Massare (1988) indicated that crocodiles possessed many adaptations for optimal transient swimming, they were good at fast starts and turns for lunging at prey, making them even more likely to be ambush predators.

Even though *Thalattosuchus superciliosus* and extant crocodylians have inhabited drastically different ecosystems, they might have shared the feeding behavior of a slow swimmer, either scavenger or ambush predator. A recent study published by Hua *et al.* (2024) indeed revealed the scavenging behavior of "*Metriorhynchus* cf. *superciliosus*", based on the description of stomach contents ("invertebrate" shells, incomplete gills of *Leedsichthys* Woodward, 1889).

TABLE 2. — Quantified variable for estimating the MMR with PEM, and results for analysis computed with the better option (*Thalattosuchus superciliosus* (de Blainville) Young, Brignon, Sachs, Hornung, Foffa, Kitson, Johnson & Steel, 2021). Unit: mL O_2/h/g. Abbreviations: **MMR**, maximum metabolic rate; **PEM**, phylogenetics eigenvectors maps.

	PEM			Quantified variable		
	Lower limit	**MMR**	**Upper limit**	**Foramen radius (mm)**	**Femoral length (mm)**	**Qi (mm³)**
MPV.2010.3.611a	0.18	0.31	0.54	0.76	281.47	0.0012
MPV.2010.3.611b	0.18	0.30	0.50	0.625	277.84	0.0005

This type of opportunistic behavior is common in extant *C. porosus* in the open sea, which reinforces the hypothesis that *T. superciliosus* did not differ much from extant semi-aquatic crocodiles in terms of behavior (Hua *et al.* 2024). In this regard, Massare (1987), and more recently, Foffa *et al.* (2024), investigated the morphology of teeth and jaw shapes in marine reptiles; they classified the metriorhynchids as predominantly generalist and/or piscivorous, on the basis of dental and cranial morphology.

The evolution of ectothermy in Crocodylomorpha

From an evolutionary perspective, previous paleohistological studies that were conducted on extinct archosauriforms led to assess that the early Triassic archosaur common ancestor was probably endothermic (Seymour *et al.* 2004; Legendre *et al.* 2016; Cubo & Jalil 2019). Since the early Jurassic, the crocodylomorphs have colonized a variety of environments (Wilberg *et al.* 2019) such as both fresh and brackish waters (i.e., Dyrosauridae Stefano, 1903 and Goniopholididae Cope, 1875) (Andrade & Sayão 2014; Faure-Brac *et al.* 2022), open seas (i.e., Metriorhynchidae; Hua & de Buffrénil, 1996) and emerged lands (i.e., Notosuchia Gasparini, 1971) (Sereno & Larsson 2009; Pol *et al.* 2014). In contrast to this ecological diversity, all recent studies on post-Triassic crocodylomorph taxa (i.e., Dyrosauridae, Goniopholididae, Notosuchia, non-metriorhynchid metriorhynchoids) revealed a common ectothermic metabolism (Cubo *et al.* 2020, 2023, 2025; Faure-Brac *et al.* 2022). In this regard, our results emphasize that the crocodylomorph ectothermy is not an adaptive trait that would be specific to the extant crocodylian semi-aquatic ambush predator lifestyle; it would instead consist of a historical constraint that was inherited from the last common ancestor of Thalattosuchia and Neosuchia (Botha *et al.* 2023). Nevertheless, regarding thalattosuchians, further investigations remain necessary in order to understand the evolution of thermometabolism in other taxa of the group.

Limits and perspectives.

We limited our sampling to a single specimen for our RMR analysis because paleohistology is a destructive practice that usually prevents the access to a large sample. Therefore, here we studied a single species within Metriorhynchidae, assuming that it is a good representative of a clade containing more than thirty species (Young *et al.* 2013).

As for the MMR, the two femora of *T. superciliosus* (i.e., MPV.2010.3.611a and MPV.2010.3.611b) probably belong to the same individual (because they are symmetric and of similar size) and show very similar values in the diameter of nutrient foramina. Nevertheless, these two values give a major difference (of an order of magnitude) after the computation of the Qi, which questions the use of the formula published in Seymour *et al.* 2012 (Table 2). The variation of Qi seems however not to bring a lot of difference in the estimated MMR, which also strongly suggests that use of phylogeny as an explanatory variable has a huge influence on the result of a PEM analysis. In order to have a critical view of the effectiveness of the nutrient foramina Qi as a proxy for MMR inferences within aquatic (both extant and extinct) taxa, new studies must therefore be carried out.

Beyond the methodological approach itself, MMR had never been inferred in aquatic fossil organisms before this study (as far as we know). It would therefore be relevant to use this approach on both ichthyosaurs and plesiosaurs in order to compare the level of activity in extinct marine sauropsids. The nutrient foramina bring blood into the bone to repair the micro-damages caused by intense activity (Allan *et al.* 2014). Since fully aquatic amniotes do not withstand the same gravitational constraints as terrestrial ones due to the buoyancy, applying this proxy for marine organisms using extant terrestrial relatives could potentially lead to an underestimated MMR inference in *T. superciliosus*.

CONCLUSION

Osteohistological analyses suggest that *T. superciliosus* had a bradymetabolic ectothermic metabolism, like extant crocodylians and, presumably, notosuchians, goniopholidids, dyrosaurids and non-metriorhynchid metriorhynchoids (Legendre *et al.* 2016; Cubo *et al.* 2020, 2023, 2025; Faure-Brac *et al.* 2022). This result is consistent with the assessment of estimated body temperature by Séon *et al.* (2025) of *Metriorhynchus* aff. *superciliosus*, and suggests that ectothermy characterizes at least some metriorhynchids. However, only larger sample within this group could rigorously support this hypothesis. The study of the maximum metabolic rate shows that *T. superciliosus* fits within the range of extant ectothermic crocodylians, which suggests that they were more likely scavengers or ambush hunters than active predators like endothermic marine "reptiles". However, new studies are needed to overcome the caveats cited above, in order to deepen this first attempt at inferring MMR in metriorhynchids.

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Declaration of interest
The authors declare that they have no conflict of interest.

Data availability
Supplementary data to this article can be found online at: https://doi.org/10.5852/cr-palevol2025v24a17_s1

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