# Crocodylomorph thermal paleobiophysics

Context. The field of biophysics was born in the middle of the XIXth, but it became popular by 1944 with the publication of the book “What Is Life?” by Erwin Schrödinger. This book focused on the question: "how can the events in space and time which take place within the spatial boundary of a living organism be accounted for by physics and chemistry?" Since then, this approach has been used countless times to deal with diverse problems in biology, but it has rarely been used in paleobiology.

Objectives. This project is aimed at the elucidation of the effect of thermometabolism on extinction rates and the diversification rates of Crocodyliformes over geologic time using paleobiophysics.

Biological study model. Crocodyliformes is an excellent study group because (1) it existed during a geologic period of 210 million years (from the Upper Triassic to the present); (2) it was very diversified in the past (hundreds of species) but it is restricted to 24 extant species of crocodiles, garhials and alligators in the present; and (3) it had a high disparity in terms of thermic metabolism (endothermic versus ectothermic; Cubo and Jalil 2019; Cubo et al. 2020, 2021), diet (carnivorous, piscivorous, durophagous, herbivorous; Melstrom and Irmis 2019), strategy of prey capture (sit-and-wait versus active pelagic), lifestyle (marine pelagic, marine coastal, freshwater amphibious and terrestrial; Wilberg et al. 2019), posture (sprawling versus parasagittal limbs; Hutchinson and Gatesy 2000) and body size (Godoy et al. 2019) (Figs 1-3 et Clarac et al. 2017).

Scientific question. What are the effects of thermometabolism, inferred using paleobiophysics, on the extinction rates and the diversification rates of Crocodyliformes over geologic time?

Hypotheses. We hypothesize that resting and maximum metabolic rates are decoupled, they are a function of lifestyle and diet, and they determine the probability of extinction. More precisely:

- Hypothesis 1. Terrestrial crocodyliforms like *Araripesuchus* (Fig. 1) were characterized by low resting metabolic rates (similar to those of small lizards and snakes; Cubo et al., 2020) but high maximum metabolic rates (similar to those of extant mammals of similar body size) because they are active predators.

Fig. 1. Skeleton (left) and reconstruction (right) of *Araripesuchus* (taken from Sereno and Larsson 2009).

- Hypothesis 2. Semiaquatic crocodyliforms like *Goniopholis* (Fig. 2) were characterized by low resting and low maximum metabolic rates because they are sit-and-wait ambush predators (locomotory activity is low) and the heat transfer coefficient in water is higher than in the air (0.59 versus 0.024 W/(m·K); Vogel 2005), so that to maintain a high body temperature is more expensive in the water than in the air.

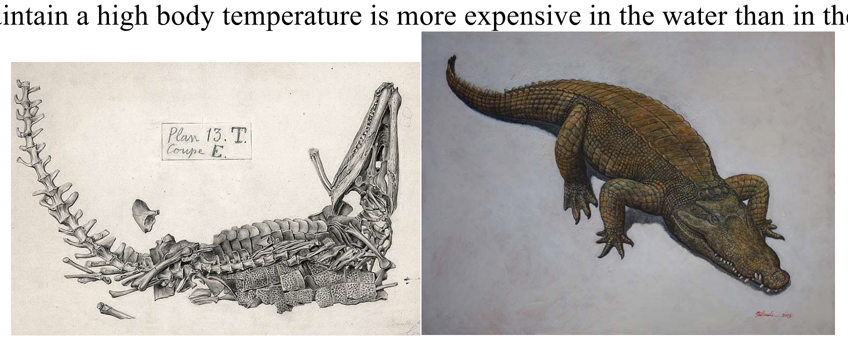


Fig. 2. Skeleton (left, by Gustave Lavalette) and reconstruction (right, by Takashi Oda) of *Goniopholis.*

- Hypothesis 3. Marine pelagic crocodyliforms like *Metriorhynchus* (Fig. 3) were active predators. As such, they had higher energy budgets than the previous organisms, and may have developed a blubber (a lipid-rich layer beneath the dermis acting as an efficient thermal insulator). According to Seon et al. (2020), “Endothermy in metriorhynchids might have been a by-product of their ecological adaptations to active pelagic hunting ». So we expect high resting metabolic rates and high maximum metabolic rates.


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Fig. 3. Skeleton (left, taken from Benton, 2014) and reconstruction (right, by Nobu Tamura) of *Metriorhynchus*.

Hypothesis testing. The thermal balance of an organism can be modeled using the expression:

$$M = R + G + C + E + S$$

where M is the metabolic heat production, R, G, C and E are the radiant, conductive, convective and evaporative heat transfers, and S is the heat stored per second by the body (Williams 1990).

- Task 1. We will create 3D models of a pelagic marine, a terrestrial and a semiaquatic crocodyliformes to compute their thermal balance. Lateral, dorsoventral, and frontal 2D drawings modeling the outlines of the animal will be performed from fossils by one of the designers of the Centre de Recherche en Paléontologie – Paris (UMR 7207). These drawings will be used to construct 3D models in close collaboration with one of the engineers in charge of the 3D imaging service of the CR2P. These reconstructions will differ from those performed to date (e.g., figs 1-3) in that we will reconstruct 3D objects instead of 2D views.
- Task 2. We will compute the thermal balance of each organism using the 3D object created in the preceding task, and the following expressions (Williams 1990):

$$R = Radiant\ heat\ transfer = \sigma\ \varepsilon\ (T_s^4 - T_a^4)\ S$$

where σ is the Stefan-Boltzmann constant, $5.7\ 10^{-8}\ W/(m^2 \cdot K^4)$; ε is the emissivity factor for skin, 0.98 ; $T_s$ and $T_a$ are the skin and the ambient temperature (K) and S is the body surface area ($m^2$). In aquatic animals it will be near zero.

$$G = Conductive\ heat\ transfer = k\ S\ (T_s - T_f) / L$$

where k is the thermal conductivity of tissue ($0.39\ W/(m \cdot K)$); S is the body surface area ($m^2$); ($T_s$–$T_f$) are the skin and the floor temperature (K) and L the gradient length across the skin (m).

$$C = Convective\ heat\ transfer = h_c\ S\ (T_s - T_a)$$

where $h_c$ is a coefficient ($W/(m^2 \cdot K)$); S is the body surface area ($m^2$); and $T_s$ and $T_a$ are, respectively, the skin and the ambient temperature (K). In aquatic animals we will use the conductive/convective parameter.

Heat transfer by evaporation (E) will be considered as being null because it is actually null in submerged body areas and negligible in emerged body areas because of the thick keratinized epidermis. Metabolic heat production (M, W) will be computed using two methods: A) resting metabolic rates (the energy produced by an organism at rest during the post-absorptive period) will be inferred using bone histology (Cubo and Jalil 2019; Cubo et al. 2020, 2021); maximum metabolic rate (the energy produced by an organism during the periods of intense activity) will be inferred using the size of the femoral nutrient foramina (Seymour et al., 2012) measured using CT scans at the AST-RX facility of the MNHN.

To sum up, the heat stored (W) per second (s) by the body will be computed as :

$$S = M - (R + G + C).$$

S must be on average zero. For an endotherm, S must be zero constantly, whereas for an ectotherm, S is sometimes positive, sometimes negative, but, on average, it must be zero. The variable to be inferred is the body temperature. If not significantly different from the local ambient temperature, we will infer ectothermy. If significantly higher, we will infer endothermy. Finally, the above relationships will allow us to understand how heat transfers take place within organisms. To do this, they will be integrated into the Fourier heat transfer law, which is defined according to the relation :

$$\vec{j} = -\lambda . \overrightarrow{grad} . T$$

With **λ**, the thermal conductivity and T, the temperature. This law describes the heat transfer by conduction from a region with a higher temperature to a region with a lower temperature.

The 3D models produced in this thesis will have three layers of tissue. The deeper (the 'core') is the central part of the organism comprising its skeleton, viscera and muscles, the middle layer is mainly composed of lipids and the outermost layer corresponds to the skin. Each of these three layers has its own thickness ($e_n$), and thermal conductivity ($\lambda_n$).

In doing so, Fourier's Law will allow us to understand the gradient that occurs between the internal temperature of the body ($T_{core}$), the inner layer of the organism, and the outermost layer (the skin), considered to be at the same temperature as the environment ($T_a$).

- Task 3. Predictions deduced from our hypotheses will be tested using inferences obtained in task 2. Results obtained will be mapped onto a phylogeny containing the relationships among the organisms included in our sample (a tree similar to that of figure 1, but including all organisms analyzed as terminals). The pattern obtained will be discussed in the light of knowledge about internal biotic factors other than the thermic metabolism (diet, strategy of prey capture, lifestyle, posture and body size) and external abiotic factors (local paleotemperature, local pluviometry, global sea-level and global oxygen concentration). Results and conclusions will be published in high level scientific journals.

Timetable. The tentative schedule is:

| Tasks | Actions | Semester | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1st | 2nd | 3rd | 4th | 5th | 6th |
| 1 | A. Elaboration of lateral, dorsoventral, and frontal 2D drawings from fossils | XX | | | | | |
| | B. Construction of 3D models using 2D drawings | | XX | | | | |
| 2 | A. Inferences of resting metabolic rates using bone paleohistology | XX | XX | | | | |
| | B. Inferences of maximum metabolic rates using femoral nutrient foramina measured fro CT scans at AST-RX facility of the MNHN | | XX | XX | | | |
| | C. Computation of thermal balances using 3D models and metabolic rates | | | XX | | | |
| | D. Presentation of results at the International Congress of Vertebrate Morphol. | | | XX | | | |
| 3 | A. Hypotheses testing using results obtained in task 2 | | | XX | | | |
| | B. Evolutionary analyses mapping results obtained in task 2 onto a phylogeny | | | | XX | | |
| | C. Presentation of results at the International Symposium on Paleohistology | | | | | | XX |
| | D. Writing the PhD thesis and 3 papers (with results of actions 2.A., 3.A. 3.B.) | | | XX | XX | XX | XX |

Feasibility. The sample of extinct organisms are ready for analysis because they are available in the collections of the National Museum of Natural History of Paris (MNHN), or the skeletal reconstruction has been published. At UMR 7207, the designers and the engineers in charge of the 3D imaging service have the know-how necessary to perform the 3D reconstructions of sampled extinct organisms (e.g., they will take into account muscle insertions and muscle volumes to elaborate the drawings). Bone thin sections necessary to perform inferences of resting metabolic rate are available in the Hard Tissues Collection of the MNHN. Femora necessary to infer maximum metabolic rates using nutrient foramina size measured from CT scans at AST-RX facility of the MNHN are also available. Moreover, the know-how necessary to construct the inference models is available. One of the supervisors (Jorge Cubo) is a biologist that performs routinely inferences of thermometabolism in extinct organisms. He supervised 6 PhD theses and published tens of papers on this subject. The challenge here is to develop and use a new, more complex and reliable, methodology based on paleobiophysics. The other supervisor (Eric Brunet) is a physicist. He will supervise the development of the procedure to compute the thermal balance and to infer the body temperature of the sample of extinct organisms.

Innovation: Beyond the understanding of the evolution of the amazing group of Crocodyliformes, one of the main contributions of this PhD thesis involves the development of a methodology allowing to infer the thermal balance of extinct organisms. Thermometabolism is a key feature because it determines the relationships among organisms and their environment. The methodology developed in this project could be used to solve other problems such as the function of the dorsal sail of *Dimetrodon* or of *Spinosaurus*, or the gigantothermy of sauropod dinosaurs.

Risks and scientific obstacles to overcome : the quantification of femoral nutrient foramina (to infer maximum metabolic rates) using CT scans will be difficult because these foramina are filled with sediment in fossils. We will overcome this obstacle thanks to the experience of engineers of the AST-RX facility of the MNHN.

Societal interest: Crocodyliformes showed a great diversity in the past, with more than 500 species that lived during the last 252 million years (Mannion et al. 2019), but an extremely reduced diversity in the present : there are only 24 extant species, of which 10 face a high extinction risk (http://www.iucncsg.org/; 2015). The increase of extinction rates linked to anthropic activities is a subject of high interest for human societies. To apply efficient tools aimed at slowing down the biodiversity decline, politicians have to be informed by scientists, who have to understand the causes of extinction increase. This project can contribute to understand causes of biodiversity decline in the past, and this may be useful to cope with the current biodiversity crisis.