

Université de Genève

Travail de monographie du bachelor en biologie

THERMOREGULATION OF NON-AVIAN DINOSAURS

Gigantism and pulmonary capacity

par

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Année académique 2015-2016

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Abstract

The aim of this monography is to evaluate the debate around non-avian dinosaurian thermoregulation strategy. Discussions have begun with the discovery and the description of first dinosaurian fossils in the eighteenth century and they continue today. It is a very active domain where opinions and theories are disparate about their physiology and lifestyle.

This current work will approach subjects such as thermoregulation strategies, controversial theories about dinosaurs biology and compared anatomy. We will see the impact of pulmonary ventilation on metabolic activities, the growth rates signification and importance in understanding ontogenic metabolism. We will describe the interesting case of inertial homeothermy which could have led dinosaurs to gigantism and to become the biggest terrestrial animals who had ever lived.

Birds and crocodilians are the nearest relatives to non-avian dinosaurs. Studies about their similarities with dinosaurs, histology, geochemistry permit to estimate the dinosaurs biology.

The biggest debate is about to know if non-avian dinosaurs had more similarities with endothermic modern birds or with ectothermic crocodiles.

Through this work we will consider the different arguments put forward to support the two hypotheses and their counter-arguments.

Anatomically, the dinosaurs were more similar to crocodiles than to birds. This may suggest that like crocodilians, they were ectotherms. Investigations about pulmonary capacities have comparable conclusion. Nevertheless, studies about growth rates question this point of view as well as studies about body temperature whose conclusions are more uncertain about the metabolic status of non-avian dinosaurs. Discussions put non-avian dinosaurs somewhere between ecto- and endothermy.



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I. Introduction

Since their discovery, the dinosaurs have fascinated the public as well as the scientific world. The more we learn the more they amaze us. Deciphering their biology is a challenge took up every day by teams of paleontologists and biologists. Their physiology intrigues. What were their lifestyle, their metabolism and their thermoregulation strategy? Were they slow and quiet animals basking in the sun and sleeping beneath shady trees to regulate their temperature and consequently their metabolism? Or were they active and tough animals with high metabolic rates? What if... it was something in between?

Through this work we will try to present the state of the debate around the metabolism of non-avian dinosaurs. We are going to focus particularly on gigantothermy and pulmonary capacity. We will begin with an introduction about the dinosaur systematics. Then, we will approach the strategies of thermoregulations by defining important concepts and developing the advantages of endothermy. We will discuss the interesting case of heterothermy, too. We will see what clumped isotope thermometry could tell us about the body temperature of theropods. We'll move on the gigantothermy and its consequences on the metabolism. We will approach growth rates and their implication in the gigantism via two articles describing a family of theropods and a kind of extinct crocodiles. We will eventually treat the pulmonary capacity and metabolism by focusing on the case of the fossil of *Scipionyx*, a rare fossil found with soft tissues fossilized.

To reconstruct non-avian dinosaur physiology, scientists have used and still use several methods: anatomy, compared anatomy (for example, with extant and fossil birds and crocodilians), using footprints and tracks to infer speed, comparison of predator/prey ratio in paleo and today ecosystems, biophysical and behavioural modelling, bone histology, growth rates analysis, oxygen paleothermometry (Eagle et al. 2011), ...

DINOSAUR DESCRIPTION

Birds are the last living representatives of a super order of terrestrial reptiles that appeared 230 million years ago (Late Triassic Period) known as the dinosaurs. The Cretaceous–Paleogene (K-Pg) extinction event, the most important mass extinction of Phanerozoic period, eradicated the majority of life on Earth (90% of marine animal species and 70% of terrestrial vertebrate families) including non-avian Dinosaurs 66 million years ago.

Dinosaurs form a monophyletic group which shares common ancestral features, synapomorphies: *“all dinosaurs have jaw muscles that extend onto the roof of the skull, a large muscle ridge on the humerus, and well-developed processes at the hip, knee, and ankle”* (‘National Museum of Natural History - Dinosaurs’ 2016). Along with the Pterosauria (flying extinct reptiles) they form the Ornithodira clade. The Ornithodirans with the Pseudosuchians (crocodilians) form the Archosauria group. Archosauria are diapsids (possessing two temporal fossae) hence they belong to the Sauropsida group. Eventually, Sauropsida together with Synapsida (mammals) form the Amniotes (possessing “amnios”; structure enveloping the embryo).

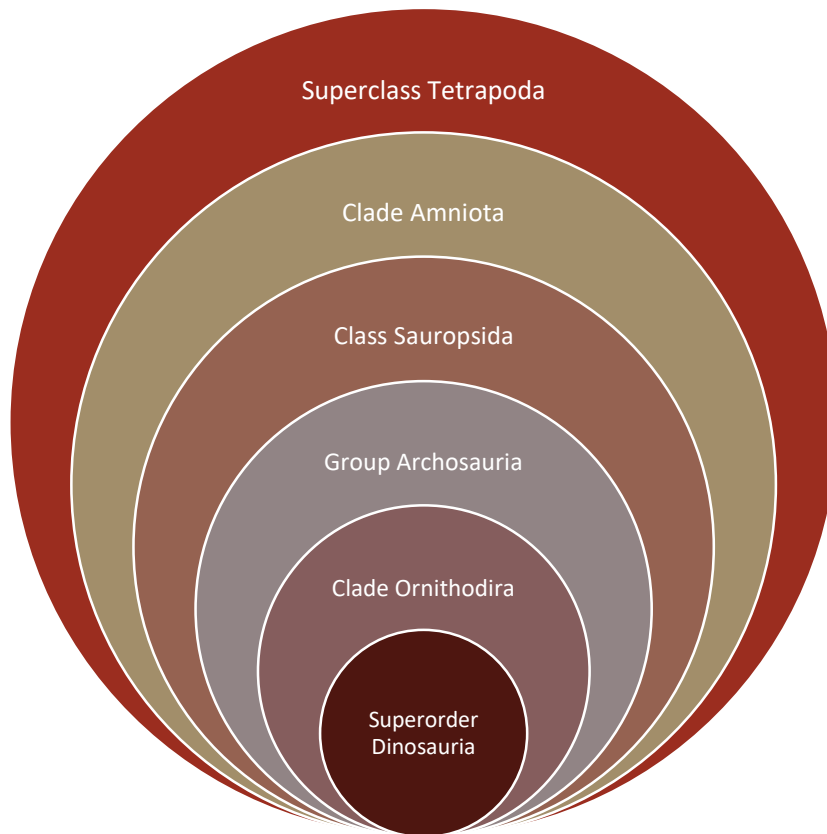


Figure 1: Dinosaurs classification

Furthermore, Dinosaurs form two orders: Saurischia and Ornithischia.

Ornithischia is an extinct order. It contains 400 herbivorous species ('National Museum of Natural History - Dinosaurs' 2016). *"The name Ornithischia ("bird hip") refers to the fact that the pubis is turned backward in the pelvis. Many forms also had a basket-like mesh of bony tendons along the backbone and tail"*('National Museum of Natural History - Dinosaurs' 2016).

This order is divided in three groups:

- Thyreophorans ("shield bearers"): the armor dinosaurs, like *Stegosaurus* or *Ankylosaurus*.
- Marginocephalians ("Margin heads"): dinosaurs with a *"ridge of knobby bone around the back of the skull"* ('National Museum of Natural History - Dinosaurs' 2016), like *Pachycephalosaurus* or *Triceratops*.
- Ornithopods ("bird feet"): the most diversified group. Quadruped dinosaurs with the ability of bipedy, like *Iguanodon*.

Likewise, Saurischia order contains extincts dinosaurs and birds. *"Saurischians ("lizard hips") are so named because the bones in the pelvis are arranged in the same way as those of other reptiles. In addition, saurischians were characterized by an asymmetrical hand that had an enlarged thumb, often bearing a big claw(...) 600 species are known"* ('National Museum of Natural History - Dinosaurs' 2016).

Saurischia is formed by two major clades: Sauropods and Theropods.

- Theropods ('beast feet') were all carnivorous and contain birds. Their characteristics were *"a joint in the lower jaw to act as a shock absorber (or perhaps for increased mobility). Some theropods developed additional openings in the skull, fewer fingers, and feathers. Ranging in size from a few kilograms to several tons, and from one to 15 meters in length"* ('National Museum of Natural History - Dinosaurs' 2016).
- Sauropods ('lizard feet') were all herbivorous and the largest terrestrial beast who ever lived. Their characteristics were: *"long tails, small heads, and long necks (with extra vertebrae as well as very long vertebrae). Walking on four columnar limbs, they reached 30 meters in length, and weighed perhaps 50 tons"* ('National Museum of Natural History - Dinosaurs' 2016).



Figure 2: Dinosauria clades

DINOSAUR RENAISSANCE

In the late nineteenth and twentieth century, scientists first attributed cold bloodedness to dinosaurs and described them as slow and dimwitted ('Geotimes — January 2006 — The Three Faces of Dinosaurs' 2016).

In the late sixties of the twentieth century, the paleontologist John Ostrom questioned this assumption. Using his work on *Deinonychus*, a new species of meat-eating dinosaur he described, he argued that dinosaurs could have been dynamic animals and *Deinonychus* *"an active and agile predator"* (Ostrom 1969). He also defended that dinosaurs' metabolism should have been more similar to birds or mammals rather than to reptiles ('Geotimes — January 2006 — The Three Faces of Dinosaurs' 2016).

Moreover, Ostrom contributed to the classification of birds as dinosaurs. An idea already proposed by Thomas Huxley in 1868 ('Geotimes — January 2006 — The Three Faces of Dinosaurs' 2016). Ostrom speculated that if birds, which are descendants of dinosaurs, are warm-blooded and exhibit an active lifestyle, there are no reasons their ancestors were not ('Geotimes — January 2006 — The Three Faces of Dinosaurs' 2016).

II. Thermoregulation

Nowadays, we separate commonly vertebrates in two categories: the “warm-blooded” and the “cold-blooded”. The most wide-spread view is that only mammals and birds are warm-blooded. Others taxa such as the “reptiles” (paraphyletic group comprising all sauropsida except aves) or fishes are considered as cold-blooded. But what hides behind these archaic denominations? A warm-blooded animal would be an endothermic animal and a cold-blooded animal would be an animal ectothermic one.

“Body temperatures of vertebrates reflect the combined influences of metabolism, size, environmental temperature, and in some cases, specialized physiological strategies for heat regulation.”(Eagle et al. 2011)

DEFINITIONS

Endothermy: *“The controlled maintenance of a relatively high and more or less constant internal body temperature, where the main source of heat is a high resting (basal) metabolic rate. In living organisms this is exclusively the preserve of mammals and birds. Body temperature may exhibit circadian variability, with the amplitude typically inversely proportional to body size. Endothermy may also be suspended temporarily in periods of torpor or hibernation.”(Clarke and Pörtner 2010).*

Ectothermy: *“A physiology where the main source of heat for body temperature is environmental. Behavioural mechanisms (basking, shade-seeking) can result in a relatively high and regulated body temperature for extended periods.”(Clarke and Pörtner 2010).*

The ectothermy thus differs from the endothermy by the source of heat. The ectotherm draws the heat of its environment while the endotherm draws it of its metabolic activity.

The endothermy is often confused with homeothermy as ectothermy is confused with poikilothermy.

Poikilothermy: *“Having a variable body temperature. This characterises most terrestrial ectotherms, and also many mammals and birds when they are small.”(Clarke and Pörtner 2010).*

Homeothermy: *“The maintenance of a more or less constant body temperature. Once synonymous with what is now termed endothermy, this term refers to any organism that maintains a more or less constant internal temperature, regardless of the dominant source of heat. In some large ectotherms, the loss of metabolic heat to the environment is sufficiently slow that internal body temperature remains relatively high and constant; this is often termed inertial homeothermy (or, colloquially, gigantothermy).”(Clarke and Pörtner 2010).*

The homeotherms keep a stable body temperature contrary to the poikilotherms.

Thus an organism can be homeothermic without being endothermic.

ADVANTAGES OF ENDOTHERMY

“Hotter is better” (Clarke and Pörtner 2010)

Ectothermic lifestyle differs from an endothermic one. For example, a snake will depend on the temperature of its environment to regulate its body temperature, its locomotor activities and physiological performances (Clarke and Pörtner 2010). With the rise of body temperature, increases its metabolism; its muscle output power and the ADP phosphorylation rate to form ATP grow. In result, the locomotor performances become higher (Clarke and Pörtner 2010).

Terrestrial endotherms and ectotherms have the same sprint speed since the energy used is produced anaerobically and they have the same production rates. The endotherms like mammals have more stamina thanks to their more efficient aerobic respiratory (Clarke and Pörtner 2010). They can support much longer efforts. Therefore, an organism with a high and constant body temperature is more advantaged: *“ability to occupy thermal niches that exclude many ectothermic vertebrates, a high degree of thermal independence from environmental temperature, high muscular power output and sustained levels of activity”* (Hedrick and Hillman 2016).

Nervous system performance depends on temperature too (Clarke and Pörtner 2010). Warmer neurons, faster conduction improve communication between muscle fibres and nerves. *“Endothermy would have benefits for a predatory lifestyle in addition to more agile muscles”* (Clarke and Pörtner 2010).

As already mentioned, ectotherm metabolism is influenced by temperature. An excellent example of that is the structure of marine vertebrate communities; *“Burst speed increases with temperature in ectotherms but is independent of temperature in endotherms. If capture success depends on relative swimming speeds of predator and prey, ectothermic prey will be more vulnerable to attack by endothermic predators at low temperatures. Conversely, high temperatures should enhance the ability of ectothermic predators to prey on endotherms”*(Cairns, Gaston, and Huettmann 2008). In warm and tropical water, large ectothermic sharks dominate ecosystem. In cooler water, endothermic seabirds are more present like marine mammals who dominate ecosystems (Cairns, Gaston, and Huettmann 2008).

However, endothermy has a price. *“Ectothermic lifestyle is low-cost”*(Hedrick and Hillman 2016). Maintaining a high body temperature costs a lot of energy. At rest, for the same mass and at the same temperature, the endothermic metabolic rates are 10-15 times higher than ectothermic ones (Quick and Hillenius 2013)! The organism need more food and need tools to keep this heat inside. Mechanisms and structures like insulation and nasal turbinates help to prevent heat loss. Warm body aid to improve the digestion. *“Studies of fish, amphibians and reptiles have shown that processing food occurs faster in a warm body”*(Clarke and Pörtner 2010). Maintaining a high body temperature permits to intake energy from the meal more easily. Therefore, the better and faster an animal is able to take energy from its meal, the better will be its growth rates as observed in ectotherms living in warmer environment compared to ectotherms from cooler environment.

HETEROOTHERMY

Heterothermy: “The use of metabolic heat to produce relatively high body temperatures that are confined to certain organs or tissues, and may be constrained to limited periods of time”(Clarke and Pörtner 2010).

Heterothermy can be observed in insects, teleostean fishes and cartilaginous fishes (chondrichthyes) (Clarke and Pörtner 2010), but also in squamata as *lizards* (Tattersall et al. 2016; Farmer 2016) or *snakes* (Farmer 2016) which can raise their physical temperature of about ten degrees over the ambient temperature. In 2016 Tattersall, G. J. et al. studied heterothermy in tegu lizard *Salvator merianae* (Farmer 2016; Tattersall et al. 2016); “The team noticed that the lizards’ body temperatures remained elevated throughout the night, by up to 10°C above the burrow temperature, during the period when they were preparing to reproduce”(Farmer 2016). During the reproduction season, the body temperature of endotherms is higher. This phenomenon is also observed in species of pythons and lizards (Farmer 2016). A higher body temperature, as previously seen, boost the metabolism to face bigger energy demand during the reproduction season.

Heterothermy can also be observed in sword fishes. They enhance their optic capacity by warming their eyes and brain. These and others observations could imply that body temperature had a importance in the evolution of predatory lifestyle (Clarke and Pörtner 2010).

Ectotherms have evolved behavioural and physiological features to produce heat and increase their body temperature. Thus, through heterothermy, they can profit from endothermic advantages and minimize its energetic disadvantages.

III. Gigantism

THE TITANS

In all eras, Earth was populated with giants. The huge insects (*Meganeura*) of the Carboniferous period, the Jurassic marine reptiles several meters long like ichthyosaurs or plesiosaurs, the dinosaurs, of course, like the 20 meters long *Giraffatitan* and bordering 80 tons! As well as the Cenozoic Megafauna; Mammouth in Europe, Gigant marsupial like the hippopotamus sized *Diprotodon opatum*.

Furthermore, the oceans abound in giants. The biggest animal to ever exist is the blue whale which is on average 30 meters long for hundred tons and lives on average 80-90 years. However, dinosaur were the biggest land animals living in Earth History. There are lot of advantages of being gigantic; being less vulnerable to predation at maturity, having better success in mating, easier to maintain internal homeostasis... but giants often participate to extinction during crisis. (Vermeij 2016) Sauropod dinosaurs were the biggest of the biggest, real titans (Heeren 2011), they perish at the K-Pg extinction, smaller species survived.

Anatomy features of a giant (Heeren 2011):

- Being herbivore because carnivore life is too energy expensive (catching tons of green isn't the same that catching tons of meat)
- Having a light skull to swallow easier food without chewing
- Have limb and digits to support the huge body weight, never mind speed, think about stability
- To catch food and swallow it a long neck is needed. It's massive, light-weight vertebra (35% lighter than classic bone) help to support it.

"Sauropods seem to have somehow gotten the evolutionary Wonka ticket of all the features that they needed to grow big" (Heeren 2011).

It's important to point out that titans do not have these traits because they are big, they are big due to these characteristics.

Dinosaurs lived during the Mesozoic Era, a generally regular warm period. In this era, large predators would have developed physiological mechanisms and behaviour in order to cope with overheating. Endothermic animals have to resist to increasing temperature due to their metabolism, lifestyle and their environment. Ectotherms have to resist only to the increasing temperature due to their environment and muscular activities.

Gigantothermy, also named *inertial homeothermy* is the capacity of giant animals to attain homeothermy not because of their metabolism or behaviour but as a result of their mass (Hedrick and Hillman 2016) and a small surface area to volume ratio ('Thermoregulatory Adaptations of *Acrocantosaur Atokensis* - Evidence from Oxygen Isotopes - NCSU Digital Repository' 2016). Hence, a large body loses its temperature more slowly than a little one.

The survival of large dinosaurs in fluctuating temperature world (daily or seasonal fluctuations) should have rested on their giant body mass and low metabolic rates. Gigantothermy could have allowed them to live in cooler climates ('Thermoregulatory Adaptations of *Acrocantosaur Atokensis* - Evidence from Oxygen Isotopes - NCSU Digital Repository' 2016). The smallest dinosaurs (<10 kg) could not afford this thermoregulatory strategy because of their lowest body mass. Their thermoregulation should have rested on insulation and *"behavioural selection of microhabitats to accommodate changing daily or seasonal temperatures"* ('Thermoregulatory Adaptations of *Acrocantosaur Atokensis* - Evidence from Oxygen Isotopes - NCSU Digital Repository' 2016).

We can note other type of gigantism; *polar gigantism*. Antarctic seas are inhabited by giants like for example pycnogonids 90 cm long versus 1-10 mm tropical cousins ('Zoology: Breathing Deep' 2009). Oxygen is more dissolved in polar water than in the tropics. Consequently, it's more accessible for organism and they are easier able to increase their body mass. The only limit for the maximum potential size is the oxygen availability (Chapelle and Peck 1999). Polar gigantism is an appellation specific to species taking oxygen from water not from air.

IV. Pulmonary capacity and the metabolic rates

RESPIRATORY TURBINATES

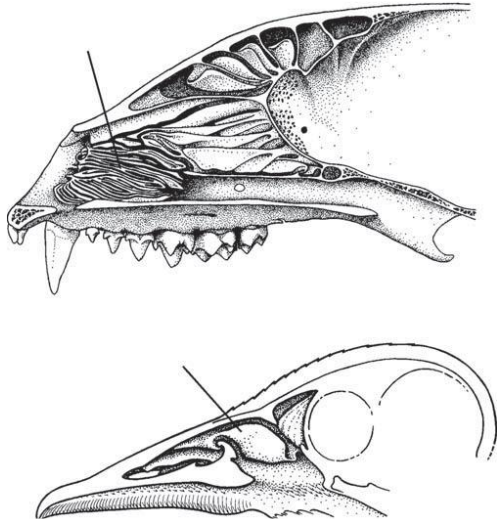


Figure 3: Nasal turbinates in mammal (top) and bird (bottom) nasal cavity (Quick and Hillenius 2013)

When we breath in, we breath in cooled air and when we breath out, we breath out heated air. Mammals and birds "nostril breathing" depends on their breathing (at rest, they have a high lung ventilation rate) to oxygenate cells to improve metabolism in order to maintain their body temperature. They are thus sensitive to losses of heat and humidity which could decrease the efficiency of their pulmonary respiration. Endotherms developed structures to decrease the losses, *nasal respiratory turbinates*. They are bony or cartilaginous complexes covered with epithelium. Nasal turbinates are situated in the nasal cavity. The air passes through them every breath.

"As the animal inhales cool outside air, the turbinate epithelia give off heat and moisture. This prevents desiccation of the lungs, but also cools the turbinates. During exhalation, therefore, as warm, moist air returns through the nose, the moisture condenses on to the cool surfaces of the turbinates, and can be recycled in the next breath" (Quick and Hillenius 2013).

So, it is about 10 % of the heat production and 30-50 % "daily water budget" that are not wasted (Lester and Costa 2006).

However, extant ectotherms do not have respiratory turbinates (Quick and Hillenius 2013). *"Their lung ventilation rates are low enough that respiratory heat and water loss are not critical problems"* (Quick and Hillenius 2013). Ectotherms have lower resting metabolic and ventilation rates than endotherms, they use less energy to maintain their body temperature, therefore they weren't afraid of water and heat loss.

Dinosaurs and basal birds didn't have nasal turbinates (Cairns, Gaston, and Huettmann 2008).

"The presence or absence of respiratory turbinates among fossil forms is thus a good indicator of their resting ventilation and metabolic rates, especially in those animals generally thought to represent the evolutionary ancestors to modern birds" (Quick and Hillenius 2013). But cartilaginous structures didn't preserve well and there are frequently absent even in endotherm fossils. Hopefully *"in extant mammals and birds a correlation exists between the presence of respiratory turbinates and a marked increase in the diameter of the nasal passage; presumably, this compensates for the increase in resistance to air flow presented by these structures"* (Quick and Hillenius 2013). Ectothermic-like nasal passage is narrow when endothermic-like passage is larger and provide space for nasal turbinates being able to support higher ventilation rates. Analysis of the cross-sectional area of fossilized theropod dinosaurs nasal passages suggest that they were more similar to those of lizards rather than those of mammals (Ruben et al. 1996).

Even *Archaeopteryx* had ectothermic-like nasal passages. *“Interestingly, in later birds the nasal cavity was drastically redesigned and enlarged. The first birds with nasal cavities large enough to accommodate respiratory turbinates were the mid-Cretaceous ornithurine birds, such as Hesperornis (Hillenius and Ruben, 2004). Thus, it appears that the most significant evolutionary change in metabolic status took place within birds, between basal forms [Archaeopteryx] and the ornithurines [Hesperornis]”* (Quick and Hillenius 2013).

DINOSAUR METABOLISM

The biggest limitation of the level of activity and its length in time is the maximal oxygen assimilation rate (Quick and Hillenius 2013). It really depends on the efficiency of the lungs. Mammals and birds lungs have the capacity of high O_2 - CO_2 exchange rates essential to sustain high activity rates.

Reptiles can achieve in the best conditions *“no more than 15–20% of the maximal performance rates of endotherms”* (Quick and Hillenius 2013) because of their less modified, and therefore less efficient, lungs.

Birds lungs are the most complex respiratory system among modern amniotes: *“they are composed of a highly specialised system of lungs and auxiliary airsacs that allow a continuous, unidirectional stream of air to pass over the respiratory exchange surfaces (...) the lung/airsac system of birds is significantly more compartmentalised and complex. Whereas in the lungs of other tetrapods the functions of gas exchange and air movement are mostly integrated into the same, single organ, in the avian respiratory system these aspects are almost completely divorced. The lungs themselves are composed of a series of narrow, parallel tubes, the parabronchi, that are the sites of gas exchange. The lungs are surprisingly compact and rigid, and their volume remains nearly constant during the ventilation cycle (unlike the closely related crocodilians, or the more distant lizards and mammals). Instead, virtually all volume change for ventilation is provided by the avascular, but highly elastic airsacs, which extend deeply into the abdomen between the visceral organs”* (Quick and Hillenius 2013).

Nevertheless, the one-way respiratory ventilation is not a feature unique to birds, it is the case of crocodilians too (Farmer 2015). Crocodilians and birds lungs could have more in common than expected; in 2012 Sanders and Farmer investigated lung embryology of alligators and birds (Farmer 2015). They affirmed that lungs of birds and crocodilians had common ontogenic origins. They also suggested that *“the less vascularised regions of alligator lungs and some of the completely avascular airsacs of birds”* (Quick and Hillenius 2013) could be homologous structures (Quick and Hillenius 2013; Farmer 2015).

They concluded: *“Although conventional wisdom is that unidirectional flow is important for the high activity and basal metabolic rates for which birds are renowned, the widespread occurrence of this pattern of flow in crocodilians indicates otherwise. Furthermore, these results show that air sacs are not requisite for unidirectional flow, and therefore raise questions about the function of avian air sacs.”*

Birds and Crocodiles have one-way respiratory ventilation (but with different functions)(Farmer 2015) we can suppose that this feature existed within their common ancestor. This characteristic could have had led dinosaurs and pterosaurs to gigantism (Vermeij 2016; Farmer 2015).

Dinosaurs, as birds and crocodiles, should had had one-way respiration ventilation (Vermeij 2016; Farmer 2015), but did they possess birds-like ventilation and lungs?

Even if exceptions exist (Dal Sasso 2003; Sasso and Signore 1998; Leonardi and Teruzzi 1993), soft tissues as lungs didn't fossilise. Hopefully *"some information about their structure and ventilation pattern can be deduced from the postcranial skeleton"* (Quick and Hillenius 2013).

Modern birds ventilation is unique and completely different from other tetrapods: *"rather than relying on lateral movements of the ribs like most tetrapods, birds use an up-and-down rocking motion of their very large sternum to expand and contract the airsacs"* (Quick and Hillenius 2013). They have a specialised sternocostal joint of their *rib cages* which it is absent in dinosaurs and also in basal birds as *Archaeopteryx* (Quick and Hillenius 2013).

An hypothesis proposes that gastralia (belly ribs) could have been used by dinosaurs to *"ventilate an avian-like abdominal airsac system"* (Quick and Hillenius 2013). Even if gastralia is common throughout amniotes, it can't be an argument for bird-like ventilation for a simple reason, birds do not have gastralia. More than that, *"in those extant forms that retain them (crocodilians and Sphenodon), gastralia are not known to contribute to inhalation as proposed (...) Negative pressures generated in the abdominal airsacs by the action of gastralia in this manner would likely have resulted in a paradoxical, inward movement of this unreinforced region, and cause significant loss of ventilatory efficiency"* (Quick and Hillenius 2013).

SQUELETAL PNEUMATICITY

"the phenomenon of having air filled bones" (Wedel 2006).

"The presence of pneumatised vertebrae in sauropods, nonavian theropods, pterosaurs and Archaeopteryx has been frequently cited as evidence for a bird-like lung/airsac system" (Quick and Hillenius 2013). But there is no evidence that it has a role in modern birds respiration or ventilation. As proof, pneumatised bones are not present in all birds (Quick and Hillenius 2013) and skeletal pneumaticity isn't restricted to birds. Mammals and crocodilians have sinuses in their skull, even fish have postcranial pneumatised bones (Farmer 2006). Even if birds are the only extant amniotic taxon owning post-cranial pneumaticity.

"Because it plays no role in lung function, skeletal pneumaticity, whether cranial or postcranial, cannot be considered reliably diagnostic for the advanced lung design of modern birds" (Quick and Hillenius 2013).

Skeletal pneumaticity is mostly described as weight reduction; lighter neck for giant sauropod and light bones for birds (Quick and Hillenius 2013; Heeren 2011)

Today, there are no convincing evidences for avian-like ventilation within dinosaurs (Quick and Hillenius 2013).

V. Focus on few aspects, on few articles

After the exploration of thermoregulation aspects such as physiological implications, pulmonary capacity, gigantothermy or metabolic rates, we will focus on a selection of articles.

We will examine the controversy over the Grady et al. article published in 2014 in the journal *Science*. The authors had proposed a new strategy of thermoregulation for dinosaurs; mesothermy.

Then, we will approach the Clumped isotope thermometry technology. Eagle et al. used it to predict the body temperature of dinosaurs and refute older models.

Thus, we will compare the growth rates of two giants; the Tyrannosauridae family and the terrible crocodile, *Deinosuchus*. They both reached titanic dimensions through different strategies with distinct implications for their metabolism.

Finally, we will consider the contribution of *Sciopynx samniticus* for the understanding of dinosaur anatomy.

CONTROVERSIAL SUBJECT

Research on the physiology of non-avian dinosaurs is an active and controversial domain. Very different opinions fuse, oppose, debate.

Recently, there was a controversy around the article “*Evidence for Mesothermy in dinosaurs*” of Grady et al. published in *Science* in June, 2014 (Grady et al. 2014). Based on a comparative analysis of the growth rates (calculations based on skeletochronology, a technique using bone growth rings called *annuli* or *LAG; lines of arrested growth* (Hall 1992; D’Emic 2015)) of vertebrates with known physiological profiles, the authors concluded that dinosaurs would have had an intermediate metabolic rate, between ectotherms and endotherms. Dinosaurs going, according to them, into none of the two categories, they would belong to an intermediate category; *mesotherms*.

“*Our results suggest that the modern dichotomy of endothermic versus ectothermic is overly simplistic*”(Grady et al. 2014)

In May, 2015, appear two comments of the article in *Science*. One of Myhrvold (Myhrvold 2015) and other one of D’Emic (D’Emic 2015).

Mr. Myhrvold, a *patent troll* and theoretical and mathematical physics doctor criticised the presence of statistical and methodical errors (Myhrvold 2015). He blamed them for deviation from accepted statistical practices. Having corrected their errors and having redone their calculations, he established that non-avian dinosaurs group overlaps the ectothermic and endothermic groups. He concluded that “*growth rate does not predict metabolism*” (Myhrvold 2015).

Mr. D’Emic, University palaeontologist, focused on another point: The growth rate. Grady and al. used annual growth rates to estimate daily growth rates. At first, D’Emic mentioned the difference of the number of days and their duration in one year during the Era of dinosaurs, then he underlined that a daily estimation of the growth rate mean that the authors support that it is continuous in time. Nevertheless, in climates with contrasted seasons, it is not the case. Large number of animals does not grow up during the dry season. D’Emic declared that the *growth ring* would not represent years but shorter periods. It would lead to an underestimation of the real growth rate. By doubling the rate of growth, D’Emic obtained that the regression of dinosaurs approaches the placental mammals one, what would mean that dinosaurs could be endothermic animals.

Moreover, D'Emic revealed that all the dinosaurs did not have to share exactly the same physiology.

“Grady et al. suggest that “the modern dichotomy of endothermic versus ectothermic is overly simplistic.” Indeed, any typology—including the proposed concept of mesothermy—imposed upon the continuum of organismal physiology bears the risk of oversimplifying life history to the degree that apparent patterns are not linked to the processes that they are hypothesized to represent” (D’Emic 2015).

In the same issue of *Science*, was published the response of the group of Grady et al (Grady et al. 2015). They did agree with Myhrvold but they completely denigrated D’Emic. They accepted the proposed corrections but did not change their minds, dinosaurs were still *mesothermic*.

CLUMPED ISOTOPE THERMOMETRY

Clumped isotope thermometry was used by Eagle et al. in their study about body temperature of non-avian dinosaurs wrote in the article “Dinosaur Body Temperature determined from isotopic ordering in fossil biominerals” published in *Science* in 2011.

As they explained: *“This technique is founded on the thermodynamic preference of rare heavy isotopes of carbon (^{13}C) and oxygen (^{18}O) to bond with each other (^{13}C - ^{18}O), or “clump,” in carbonate-containing minerals. Unlike the well-established oxygen isotope thermometer, application of clumped isotope thermometry is not dependent on knowing or assuming the oxygen isotope composition of the water from which a mineral grew” (Eagle et al. 2011).*

They focused their study on *“tooth enamel [of large Jurassic sauropod ; *Brachiosaurus brancai* and *Camarasaurus sp.*] as the most desirable record of primary growth temperature on the basis of multiple lines of evidence suggesting that the large and closely packed apatite crystals in enamel, as well as its organic-poor nature, can permit the preservation of geochemical signatures even over long time scales” (Eagle et al. 2011).*

They assumed that *“this approach is capable of reconstructing the expected body temperatures of modern and fossil mammals and ectotherms with an accuracy of $\sim 1^\circ\text{C}$ and a precision (1 SE) of 1° to 2°C ” (Eagle et al. 2011).*

In 2006, Gillooly et al. proposed a biophysical model to predict dinosaur body temperature. It's based on allometric scaling laws and dinosaur growth rate analysis (Eagle et al. 2011). According to this model, there would be a positive correlation between body temperature and body mass. The largest sauropods body temperature should have reached over 40°C (Gillooly, Allen, and Charnov 2006). There could be an example of *gigantothermy* (reaching high body temperature because of large body mass) and could involve that dinosaurs were ectotherms.

Alas, a Amiot et al. study published the same year using enamel phosphate oxygen isotopes on smaller dinosaur taxa refuted the modelling result. According to it, Cretaceous dinosaurs (weighting from 10 to 9000 kg), would had body temperature of 33° to 38°C (Eagle et al. 2011).

Eagle et al. estimated the temperature of teeth formation of two species; *Brachiosaurus brancai* and *Camarasaurus sp.* Their results were lower than those predicted by Gillooly's model (Eagle et al. 2011). The estimated temperatures were situated between temperatures of extant and extinct crocodiles and modern birds.

The authors discussed their results and raised a few questions: Did dinosaurs have developed “heat dissipating adaptations and a low basal metabolism” (Eagle et al. 2011) or did they have features to compensate the internal heat production due to endothermic metabolism to maintain body temperatures as predicted by their results?

They concluded: “our data are most consistent with the hypothesis that sauropods sustained high metabolic rates during ontogeny to reach their gigantic size so rapidly, but that in maturity a combination of physiological and behavioral adaptations and/or a slowing of metabolic rate prevented problems with overheating and avoided excessively high body temperatures” (Eagle et al. 2011).

The authors did not have clear opinion on the temperature regulation strategy used by sauropods. A lot of questions remained open.

GROWTH RATES

1. “GIGANTISM AND COMPARATIVE LIFE-HISTORY PARAMETERS OF TYRANNOSAURID DINOSAURS”

The first article is “Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs” published in *Nature* by Erickson et al. (2004). In this *letter to Nature* the authors worked on Tyrannosauridae - a well known family of apex predators – to study their growth patterns and the mechanism which leads these large carnivorous animals to titans.

To determine growth rates, the team determined the size, weight and the age of a 20 specimens sample; adolescent, juvenile, sub-adult and adult representatives of the North American Late Cretaceous tyrannosaurids *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Daspletosaurus torosus* and *T. rex*.

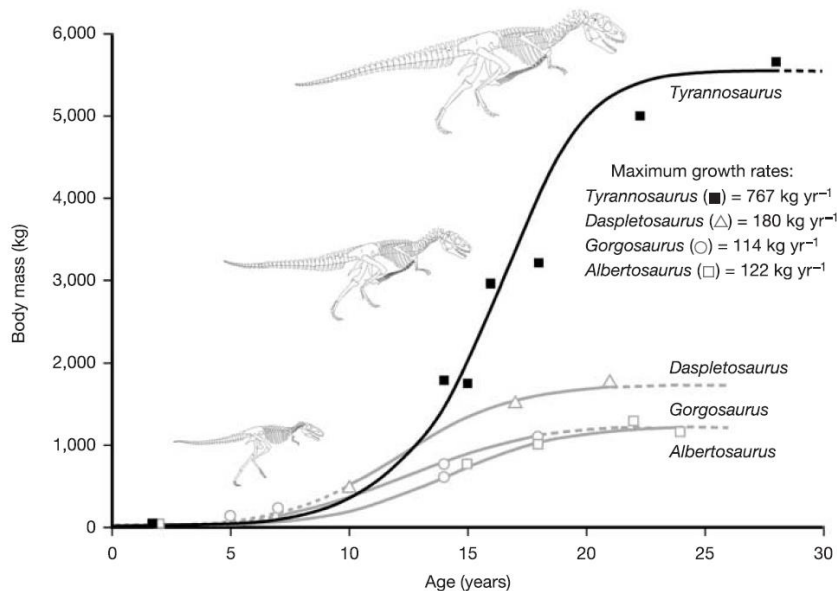


Figure 2 Logistic growth curves for *Tyrannosaurus* and three related tyrannosaurids. Note that the exponential stages (the regions of maximal slope) are similar in duration but differ in slope (that is, growth rates). Regression equations (mass in kg, age in years) are as follows: *T. rex*, mass = $\{5,551/[1 + e^{-0.57(\text{age} - 16.1)}]\} + 5$, $r^2 = 0.953$; *D. torosus*,

mass = $\{1,728/[1 + e^{-0.44(\text{age} - 12.1)}]\} + 5$, $r^2 = 0.992$; *G. libratus*, mass = $\{1,234/[1 + e^{-0.38(\text{age} - 12.4)}]\} + 5$, $r^2 = 0.950$; *A. sarcophagus*, mass = $\{1,218/[1 + e^{-0.43(\text{age} - 14.1)}]\} + 5$; $r^2 = 0.985$.

Figure 4: Logistic growth curves for four tyrannosaurids (Erickson et al. 2004)

To do that, the authors used several methods. *“Conservative estimates of body mass (...) were made by using femoral circumference measures. Longevity and size data were plotted and least-squares regression was used to determine the first empirical growth curves for tyrannosaurids. The length and timing of the various developmental stages and the maximal growth rates for each taxon were compared”* (Erickson et al. 2004).

They estimated growth rate of *T. rex* from 2 to 28 years old and from 29.9 to 5'654 kilograms of body mass. The somatic maturity had been estimated to begin on average at 18.5 years of age. The exponential stage rates were maintained for four years for all the 4 species.

T. rex outgroups specimens had been estimated having from 2 to 24 years of age and having from 50.3 to 1791 kg of body mass.

“T. rex had a maximal growth rate of 2.1 kg/day, reached skeletal maturity in two decades and lived for up to 28 years. T. rex's great stature was primarily attained by accelerating growth rates beyond that of its closest relatives. (...) The maximal growth rates for the three smaller tyrannosaurid taxa ranged from 0.31 to 0.48 kg/day” (Erickson et al. 2004)

The figure 4 represents the logistic growth curves for the four tyrannosaurids: *Tyrannosaurus*, *Daspletosaurus*, *Gorgosaurus* and *Albertosaurus*. We can see that the growth rate (slope of the exponential state of the growth) depends on the body mass but also that the growth rate of the *Tyrannosaurus rex* surpasses those of other much smaller species.

Erickson et al. concluded that *“The key developmental modification that propelled T. rex to giant proportions was primarily through evolutionary acceleration in the exponential stage growth rate and the transition zones bounding it”* (Erickson et al. 2004).

They also assumed that in the Tyrannosauridae family, the growth rate could be different from species to species which is the first evidence of this kind of patterns in non-avian dinosaurs taxon. Such phenomenon occur within other groups like primates within Eutheria (Erickson et al. 2004).

2. “HOW THE “TERROR CROCODILE” GREW SO BIG”

In contrast, crocodylians and lizard attained gigantism by an other way, *“their growth rates were retained and the exponential stages lengthened”*(Erickson et al. 2003).

The second article is “How the “terror crocodile” grew so big” by Erickson and Brochu, 1999 likewise published in *Nature* (1999). The authors defined the way *Deinosuchus* got giant. *“Deinosuchus is a giant crocodylian from the Late Cretaceous period of North America. It was 8 to 10 metres long and weighed between 2,500 and 5,000 kg, three to five times more than the largest crocodiles alive today”* (Erickson and Brochu 1999).

Did the gigantic crocodylians grow with the same mechanism as dinosaur ? We know that crocodylians are ectothermic and they are the birds closest relatives among sauropsida. Did *Deinosuchus* have a accelerated growth rate? Or did he have typically reptilian rates, understand *“rapid linear increases early in development, with rates typically declining by the first decade after hatching”* (Erickson and Brochu 1999). Extant crocodiles grow 30cm a year in the first years after hatching ('Crocodile | Reptile | Britannica.com' 2016; Erickson and Brochu 1999) and afterwards, their grow with lower rates until they die ('Crocodile | Reptile | Britannica.com' 2016).



Figure 5: *Deinosuchus* skull compared to alligator skull. (dinopedia.wikia.com)

As in the first article (Erickson et al. 2004), the authors combined size and body estimations throughout development. They “counting growth rings in dorsal osteoderms from several individuals from the Campanian Judith River Formation of Montana and the Aguja Formation of Texas” to estimate the longevity and “based estimates of total length for adult *Deinosuchus* on a large mandibular ramus from Texas and regression curves for the American alligator (*Alligator mississippiensis*) and saltwater crocodile (*Crocodylus porosus*)” (Erickson and Brochu 1999).

They found that “plots of length against age for *Deinosuchus* outgroups show that the primitive character state for growth in non-gavialoid crocodylians was characterized by rapid linear increases early in development, with rates typically declining by the first decade after hatching. *Deinosuchus* showed similar rates (about 0.3 metres per year) to other crocodylians from the phylogenetic bracket during the first five to ten years of life, but maintained these juvenile growth rates for several decades” (Erickson and Brochu 1999).

Analysis of primary histological structure of bones and specially the deposited lamellar-zonal bone tissue supported hypothesis that *Deinosuchus* growth rate did not go through an acceleration like dinosaur rates.

Erickson and Brochu concluded “the evolution of increased metabolic rates in dinosaurs is believed to have facilitated the evolution of gigantism by enabling them to build their skeletons swiftly using fibro-lamellar bone. *Deinosuchus* achieved the same outcome, but it took much longer.

Dinosaurs of similar size to Deinosuchus, such as hadrosaurs (‘duck-billed dinosaurs’), reached adult size in only seven to eight years, whereas the giant crocodylian required more than 35 years. We believe that the retention of an ectothermal physiology constrained Deinosuchus to the deposition of slow-forming somatic tissues (such as lamellar bone) throughout development, necessitating a greater developmental time to reach dinosaurian proportions” (Erickson and Brochu 1999).

SCIOPONYX SAMNITICUS



Figure 6: Fossilized soft tissues. *Sinosauropteryx* on the left. *Scioponyx* on the right. The bottom image is an image of *Scioponyx* preserved soft tissues under ultraviolet illumination. (Quick and Hillenius 2013)

In 1980, Giovanni Todesco a fossil collector found a fossilized *Scioponyx samniticus* at Pietraroia, a “small village nestled in the Matese mountains, about 80 km northeast of Naples (...) The Pietraroia Plattenkalk, known since the 18th century for its beautiful fossil fishes, is a Lower-Cretaceous formation of Albian age, dated to about 110 Myr.” (Dal Sasso 2003).

During thirteen years, the specimen had waited in the house basements until Todesco presented him to “Museo di Storia Naturale di Milano” palaeontologists, Leonardi and Teruzzi. He appeared for the first time in an article in 1993 (Dal Sasso 2003; Sasso and Signore 1998; Leonardi and Teruzzi 1993). In 1998 he was baptized “*Scioponyx samniticus*” by Dal Sasso and Signore (Dal Sasso and Signore 1998).

The fossil was the juvenile (Dal Sasso 2003) of a new species resembling to a baby *Sinosauropteryx* and could not be affiliate to any coelurosaurian family. “*Scioponyx* is more puzzling than a *compsognathid* [Compsognathidae, a family of little carnivorous theropods, basal group of coelurosaurs (‘GEOL 104 Lecture 23: Theropoda II, Coelurosauria: Tyrant Kings and Lesser Royals’ 2016)]. The Italian baby theropod shows a true mosaic of characters that does not allow attribution to any known coelurosaurian family [clade of modern birds and theropods “closer to Neornithes [modern birds] than to Carnosauria”(Padian, Hutchinson, and Jr 1999)]” (Dal Sasso and Signore 1998).

Scipionyx was the first dinosaur discovered in Italy, more than that, it was a juvenile (it was very rare) and most of all, *Scipionyx samniticus* was the first dinosaur fossil with fossilized soft tissues!(Dal Sasso 2003; Sasso and Signore 1998; Leonardi and Teruzzi 1993).

In 1999, Ruben et al. published an article in *Science* "Pulmonary function and metabolic physiology of theropods dinosaurs" (Ruben et al. 1999) where they analysed the fossil of *Scipionyx samniticus* with ultraviolet light. The soft tissues fossilized were "portions of the intestines, liver, trachea, and skeletal muscles"(Ruben et al. 1999) The purpose of the study was to "describe these soft tissues and discuss their implications for pulmonary structure and function in *Scipionyx*"(Ruben et al. 1999).

a) *The colon*

The posterior colon position in abdomen of *Scipionyx samniticus* had more similarity with mammals of crocodilians anatomy and clearly opposed to birds; "The posterior colon, or colorectal intestine, is situated far dorsally, at about the same level as the vertebrae in the lumbar-sacral region. This condition is comparable to the position of the colon in living taxa such as crocodilians and mammals (...) In contrast, the colon (or rectum) of birds is invariably suspended by the dorsal mesentery (mesocolon) so that it is situated in the mid-abdominal cavity, some distance from the roof of the cavity. This mid-abdominal suspension of avian large (and small) intestines provides a distinct segregation of the colon from the dorsally and medially attached abdominal air sacs (which extend caudally from the dorsally attached parabronchi)." (Ruben et al. 1999).

They raised the idea of the absence of "avian-style, abdominal air sacs (...) [which] are of fundamental importance to the function of both neo- and paleopulmo portions of the lung in extant birds "(Ruben et al. 1999). They argued that without these air-sacs (or simply without the place for), an avian style air-sac breathing system could not exist in *Scipionyx* (Ruben et al. 1999).

b) *The trachea*

Ruben et al. described the *Scipionyx* trachea similar to trachea of crocodilians and having an anatomy opposed to bird trachea; "Like the trachea of crocodilians, *Scipionyx's* trachea in this region is situated well ventral to the vertebral column. In contrast, except in specialized, long-necked birds, the avian posterior cervical trachea is usually positioned dorsally and adjacent to the vertebral column, thereby facilitating entry of the trachea into the dorsally attached parabronchi" (Ruben et al. 1999).

c) *The liver*

Once again, the liver was compared to crocodilians liver with whom it had more common characteristic than with birds one; "As in crocodilians, *Scipionyx's* liver is situated ahead of the large intestine and fills the anterior most portion of the abdominal cavity. Furthermore, as in crocodilians and the theropod *Sinosauroptryx*, the anterior border of the liver in *Scipionyx* is vertically oriented and completely subdivides the visceral cavity into anterior pleuropericardial and posterior abdominal regions" (Ruben et al. 1999).

d) *Hepatic piston*

“Hepatic piston, diaphragm-assisted breathing in crocodilians is powered by the diaphragmatic muscles that originate on the gastralia and distinctly shaped pubes and insert on the lateral surfaces of the liver”(Ruben et al. 1999). Hepatic piston permits to enhance the respiratory ventilation, improve the O_2 - CO_2 exchange rates and increase the aerobic activity of muscle.

The *Scipionyx* triradiate pelvis was comparable to crocodilians pelvis which is important to *“accommodate diaphragmatic muscle function”* linked to the diaphragm-assisted breathing (Ruben et al. 1999).

Scipionyx had a liver, a trachea, a colon and a pelvis described as crocodilian-like despite of bird-like. The possibility for him to breath like birds is very weak. *Sinosauroptryx* and *Scipionyx* were very different, but, in the two cases, data indicated diaphragm-assisted breathing; according to the authors, that *“reinforce the hypothesis that diaphragm-assisted lung ventilation was widespread in theropod dinosaurs”* (Ruben et al. 1999).

The absence of nasal turbinates involved that *Scipionyx* as other theropods dinosaurs had ectothermic-like ventilation. Ruben et al. proposed that costal breathing (as seen in varanus) could support ectothermic activity rates. With a diaphragm-assisted respiration, dinosaurs could increase their lung ventilator to approached the O_2 - CO_2 exchange rates of extant mammals (Ruben et al. 1999).

In conclusion: *“although these dinosaurs maintained ectotherm-like routine metabolic rates, they were, nevertheless, capable of sustaining active oxygen consumption rates and activity levels well beyond those of even the most active living reptiles”*(Ruben et al. 1999).

VI. Conclusion

The non-avian dinosaur physiology has always been a debated subject. To understand their biology, scientists have many technical and material obstacles to overcome. These dinosaurs are extinct, it's impossible to directly test hypothesis in a laboratory. It's impossible to dissect or observe a breathing or eating non-avian dinosaur. The solution is to study histology, geochemistry and their nearest cousins, birds and crocodylians and infer information about their physiology.

Moreover, understanding their thermoregulation would allow to know more about their physiology due to the fact that the metabolic processes depend on the body temperature. We saw the influence of the temperature on the breathing, the digestion and the muscular activities. It also influences the lifestyle by its constraints and advantages. The vision that we have of dinosaurs change according to the strategy which we attribute to them: if endothermic, they were lively, strength and led an active lifestyle, if ectothermic, they were lazy, moved slowly and basked in the sun half of the day.

In 2006, Gillooly et al. proposed a biophysical model to predict dinosaur body temperature. It's suggested that the bigger the body mass was, the higher the body temperature was. This could be explained with gigantothermy.

However, the same year this hypothesis was rejected by a group working on smaller dinosaurs(Eagle et al. 2011). In 2011, the model was one more time refuted by Eagle et al. study using clumped isotopic thermometry to estimate the temperature of teeth formation of two giant sauropods(Eagle et al. 2011). Eagle's team didn't give an opinion on the strategy allowing the giants to raise a body temperature of 36-38°C: they would have been ectotherms which have mechanisms (physiological and/or behavioural) to evacuate the surplus of heat, or endotherms which managed to develop barriers from an overheating due to their metabolism.

In this debate two fronts are in confrontation: those who argue that dinosaurs were by their physiology closer to modern birds and those who argue that they were closer to the crocodylians physiology. The arguments of both camps base themselves among others on the anatomy, the respiratory system, the growth rates, and the comparison with birds and Crocodylia.

The arguments put forward by the endothermy hypothesis are endothermy ecological advantages, dinosaur accelerated growth rates, high metabolic rates, presence of avian-like ventilation, skeletal pneumaticity, etc.

On the other side, the arguments advanced by the ectothermy hypothesis are the disadvantages of endothermy and the advantages of ectothermy in the Mesozoic era, especially its "low-cost" side, absence of nasal turbinates, the anatomy of nasal passage, gigantothermy, *Scipionyx* fossil (crocodylian-like anatomy of colon and liver), possibility of diaphragm assisted breathing, etc.

In between these two sides, there are teams like Grady et al.'s(Grady et al. 2014) which propose that dinosaurs would had been a part of none of the two groups. Basing themselves only on dinosaur growth rates estimations and comparisons with those of extant animals, they assert that dinosaurs would had had metabolic rates between those of ectotherms and endotherms, classifying them as mesotherms. They triggered a debate in *Science* in 2014-2015(Grady et al. 2014; Myhrvold 2015; D'Emic 2015; Grady et al. 2015). Two other teams who defy this hypothesis. Grady et al. defended themselves and did not change their mind on the question.

Furthermore, there is a particular thermoregulation strategy called heterothermy; it's an elevation of the body temperature over the environmental temperature limited to a period of time or to certain organs. This phenomenon is observed within swordfishes but also within snakes and lizards during the reproduction season.

Eventually, this debate is not closed yet and as a matter of fact, it is almost impossible that it will be definitely closed one day. Non-avian dinosaurs died out 66 million years ago and the only hints of their biology we have, are fossil. The arguments from both fronts are of the same nature, but are completely opposed. Our knowledge of the physiology of birds and crocodiles is far from being completed. The first step in better understanding dinosaur biology will be to improve our knowledge of thermoregulation itself and physiology of Sauropsida, specially birds. The preserved soft tissues are very rare but provide considerable data which advance the research. Technologies such as thermometry or skeletochronology will provide many important information about their lifestyle too.

The physiology of dinosaurs remains a puzzle in which there are still lacking pieces.

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