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The crocodylian skull and osteoderms:

A functional exaptation to ectothermy?

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Abstract

The crocodylians are ectothermic semi-aquatic vertebrates which are assessed to have evolved from endothermic terrestrial forms during the Mesozoic. Such a physiological transition should have involved modifications in their cardio-vascular system allowing to increase the heat transfers with the surrounding environment by growing a peripheral vascularization which would be mainly located in the dermal skeleton: the dermatocranium and the osteoderms. In order to assess the implication of these anatomical regions in thermal exchanges, we have recorded the temperature above a set of representative skin areas in order to draw comparisons between the skull, the osteoderms, and the rest of the body parts which present either none or residual dermal ossification. We computed the data after the specimens were successively laid in different stereotyped environmental conditions which involved significant variations in the environmental temperature. Our results show that the osteoderms collect the external heat during the basking periods as they become significantly warmer than the surrounding skin; they further release the heat into the core of the organism as they turn out to be colder than the surrounding skin after a significant cooling period. In disregard of

the environmental temperature variations, the skull table (which encloses the braincase) remains warmer than the rest of the cranial regions and shows less temperature variations than the osteoderms; a result which has lead us to think that the braincase temperature is monitored and controlled by a thermoregulatory system. Therefore, as hypothesized by previous others regarding the skull of the crocodylians and of other ectothermic vertebrates such as the squamates, we assume that the crocodylian skull possesses shunting blood pathways which tend to maintain both the braincase and the main sensory organs at the nearest to the optimal physiological temperature depending on the external temperature variations. Concerning the skin vascularization, the study of an albino *Alligator mississippiensis* specimen permitted to observe the repartition of the superficial blood vessels by transparency through the skin. We thus testify that the skin which covers either the skull or the osteoderms is more vascularized than the skin which does not present any subjacent dermal ossification. We consequently deduce that the significant contrast in the thermal behavior between the dermal skeleton and the rest of the body is indeed correlated with a difference in the relative degree of skin vascularization. This last assessment confirms that the development of the dermal skeleton should have played a functional role in the crocodylian transition from endothermy to ectothermy through the set-up of a peripheral vessel network.

Key-words: heat-transfers, thermoregulation, basking, vascularization, dermal bones, Crocodylia.

1. Introduction

The pseudosuchians (crown and stem-crocodylians) and the avemetatarsalians (pterosaurs and dinosaurs) consist of two distinct sister lineages which evolved from one hypothetical common ancestor in the Early-Triassic (Archosauria; 250 Mya; Cope, 1869; Nesbitt, 2011). The presence of a fibrolamellar complex in the stem-archosauriform long bones lead to hypothesize that the ancestor of the archosaurs possessed a high growth rate

(Ricqlès et al., 2003, 2008). Furthermore, the high osteocyte density which has been quantified in the primary bone in both the stem-archosauriforms and the early pseudosuchians argued that these taxa had a high basal metabolic rate revealing an endothermic metabolism (Cubo et al. 2012; Legendre et al., 2016). Besides these assessments which are based on the study of bone histology in extinct species, there are anatomical features in the extant crocodylians which also suggest an endothermic origin: the existence of a four-cardiac-chambered heart separating the high systemic blood pressures from low pulmonary blood pressures like in birds and mammals (Seymour et al., 2004). Thus, unlike the rest of the ectothermic vertebrates, the crocodylians do possess a full ventricular septation (Jensen et al., 2013) though showing some specific cardiac traits: 1) the foramen of Panizza which provides communication between the right and left aorta (Franklin & Axelsson, 2000; Axelsson and Franklin, 2001); 2) the cog-tooth valve which controls the blood flow through either the pulmonary artery or the right aortic arch consequently influencing the systemic arterial blood pressure (a value which is itself correlated with the metabolic rate; Seymour et al., 2004). Even if the relation between these cardiac traits and the crocodylian ectothermic metabolism is still debated (Eme et al. 2010), the development of adaptative functions in the heat transfers between the organism and the surrounding environment must have been necessary to permit a switch from endothermy to ectothermy. As already assessed in other ectothermic vertebrates such as the squamates, these thermal exchanges shall rely on the blood flow through the vascular system (Drane et al., 1977; Sadava et al., 2009; Porter and Witmer, 2015). In this regard, several authors hypothesized that the crocodylian dermal bones consist of thermal exchange sites when basking thanks to a superficial vessel network present both in the cranial region (Porter et al., 2016; Clarac et al., 2017a) and in the osteoderms (Seidel, 1979; Farlow et al., 2010; Owerkowicz, 2016; Clarac et al., 2018). Both of these networks would be further connected to the general vascular circulation of which the flow is controlled by both the heart

beat (Seebacher and Franklin, 2004, 2007) and the cutaneous vessel vasomotion (Grigg and Alchin, 1976). Behavioral strategies such as the adoption of fully submerged to fully emerged postures (Smith, 1979; Seebacher, 1999) and the ability to gape on land (Spotila, 1977; Tattersall et al., 2006) are assumed to be associated with these physiological adaptations in parallel with the crocodylian transition to the semi-aquatic lifestyle. Indeed, despite the body heat loss when the crocodylians are in the water (Johnson, 1974; Johnson et al. 1976), the adoption of a set of variable semi-emerged postures (high float, common float; Smith, 1979) should conciliate the thermoregulatory behavior with the water to land ambush predation since it allows the animal to control its exposition to the sunrays while focusing its main neurosensory organs on potential terrestrial preys. During emerged periods, sun basking increases the global body temperature while gaping contributes to the reduction of the head temperature by water loss.

The aim of this study is to test the implication of the crocodylian dermal skeleton (the dermatocranium and the osteoderms) in the heat transfers by determining which of the body area are significantly involved in such a function. Indeed, Farlow et al. (2010) and Owerkowicz (2016) showed that the temperature straight above the osteoderms shall keep lower than the surrounding skin's regardless of the environment temperature as these bones would be permanently vascularized by the cool blood which is coming from the core of the organism in order to warm up in contact with the environmental heat. To determine the implication of both the cranial and post-cranial dermal skeleton in the heat transfers, we measured and compared the superficial temperature straight above the skull, the osteoderms and other skin areas on a sample of living crocodylians which were successively set in different stereotyped conditions (aquatic and terrestrial) themselves involving variations in the environmental temperature. We consequently assessed the thermal behavior of the

crocodylian dermal bones in contrast with the parts of skin which do not present any dermal ossification. The animal behavior was carefully reported during all the experimentation time.

2. Material and methods

2.1 Biological sample

The experimentations were performed on three farmed crocodylians at Planète Crocodiles (Route de fond d'Orveau 86320 Civaux, France). Two of these specimens both measure around one-meter length and were studied in monitored conditions involving environmental temperature changes. They belong to two different species which are representative of two different families (Crocodylidae and Alligatoridae; see Table 1 for details). The third specimen is an albino *Alligator mississippiensis* (Alligatoridae). This specimen is a sub-adult which was studied in its usual captivity enclosure without forced environmental changes. All these animals are acknowledged by Johann Doray (zoological supervisor) for the keeping of exotic reptiles, and comply with the directives of the European parliament and the council of 22 September 2010 on the protection of animals used for scientific purposes (Directive 2010/63/EU).

2.2 Experimental setting

Both the *Alligator sinensis* and the *Crocodylus niloticus* specimens were successively set in two experimental patterns which respectively simulated two different stereotyped environmental conditions for an amphibious vertebrate: an « Aquatic » phase in a flooded swamp and a « Heating-Terrestrial » phase in an emerged basking environment (Heat Lamp Dry; Franklin and Seebacher, 2003). To do so, we first let the specimens in a plastic tank (dimensions: 120 x 100 x 65 cm) which was top covered with a board and partially filled with enough water so that the animal constantly had to remain either submerged or in a semi-emerged position (at its discretion). The water temperature was set to 25 °C thanks to a

thermal probe (150 W) whereas the air temperature within the tank was equal to the room temperature (22 °C; recorded with ExoTerra Digital precision thermometer). The water temperature value has been established on the reference wet season tropical fresh water temperature (Galacatos et al., 2004; Fig. 1) and is also purposely set to a slight higher value than the air temperature as we wanted to be sure that the specimen could not warm-up if it decided to take a semi-emerged position (as detailed in Smith, 1979). Moreover, the high humidity kept within the tank also limited the temperature variations in the contained air having thus a least influence on the specimen temperature (hygrometry: 90 %; recorded with an ExoTerra Digital precision hygrometer). The water temperature was homogenized by a flow using a centrifugal pump. After one hour, we drained the water out of the tank using a tap located at its bottom. We removed the top board on one side of the tank in order to set three spotlights (50 W; 150 W; 70 W with UVB) and two warm-air blowers (1500 W) which allowed to increase and homogenize the air temperature within the tank. On the opposite side of the spotlights, the recorded temperature on the bottom of the tank still scored 22 °C whereas it reached 47 °C right under the beam light. The resulting gradient thus provided a set of values which overlapped and overshoot the crocodylian physiological inner temperature (comprised between 31-33 °C; Grigg and Alchin, 1976; Johnson et al., 1976). After one hour, we set back the first experimental setting by filling up the tank again in order to repeat the full experimentation for a second time. After each phase and for both specimens, we recorded the skin superficial temperature on fourteen different spots which are representative of the diverse anatomical regions of interest: the skull, the osteoderms, the limbs and the axial part of the body which shows no osteoderm (as presented in Fig. 2). To do so, we used an infra-red camera (C.A 1950 Diacam 2 IR Camera IP 54; Chauvin Arnoux 190, rue Championnet – 75876 Paris cedex 18 – France) which allows to record the superficial temperature of a targeted spot. The emissivity was set to 0.95 as in Farlow et al. (2010)

according to the infra-red thermography principles by Speakman & Ward (1998). The data were plotted on colored images which were centered around a cross-hair that revealed the temperature of each targeted spot. The entire field of view of the camera was numerized so the surroundings' temperature variations were plotted by a gradient of colors from deep blue (cold) to deep red (warm). Since the value of the Noise Equivalent Thermal Difference (NETD) is 80 mK for this device when the environmental temperature is 30 °C, we deduced that the least detected temperature variations were under 0.1 °C within our experimental conditions. The obtained snapshots were then saved as an image and were further exported as numerical files (bmp format). During the entire experimentation which lasted four hours (for both specimens) including two « Aquatic » phases and two « Heating-Terrestrial » phases, the specimens were not manipulated nor taped and had the possibility to move freely within their tank. Since the tanks were not transparent and top-covered with a board, the specimens did not have any visual contact on the experimentator except when recording the data with the infra-red camera (a five-minute operation). Within the full experimentation, we testify that the pupil of the eye of neither specimen showed any inflation so that we may assume that they did not experience any stress which may have biased the data by affecting the heart beat and the resulting blood circulation. During the « Aquatic » phases, there was no forced immersion which could have influenced the heart beat and consequently the thermal exchanges. We recorded all the data (Table 2) and performed statistical analyses using Past software (PAST version 2.17c, Hammer et al., 2001) in order to compare the mean superficial temperature between the successive « Aquatic » and « Heating-Terrestrial » phases in both *Alligator sinensis* and *Crocodylus niloticus*. The purpose was to test if the successive environmental phase switches had a significant influence on the specimen mean superficial temperature (Table 3A). In a same manner, we also performed such statistical comparisons to test the difference in the mean superficial temperature between the two specimens in order to assess if

they reacted in a same way to the same experimental conditions (Table 3B). Since each temperature sampling consists of fourteen non-independant values as they belong to a same specimen (shown in Fig. 2), we analysed the data with a Wilcoxon test (non-parametric).

The same set of measures was repeated on the *Alligator mississippiensis* albino specimen directly in its enclosure after the specimen spent the full morning in its pool (several hours). The lack of melanine in the skin of the specimen allows to observe the superficial vascularization in order to notice if the blood vessel repartition matches with the superficial temperature contrasts. This specimen is kept in captivity in an enclosure including a pool in which it can dive and entirely immerge. The pool is partially surrounded by a beach on which the specimen is free to emerge at its discretion. The enclosure is located in a greenhouse which is naturally lighted and warmed-up by the daylight sunrays providing an air temperature of 20 °C at the time when the data were recorded. The water is artificially heated and set-up to a temperature of (25 °C). The measures were performed on the specimens after it voluntarily emerged on the beach under the stimulations of its animal keepers (Johann Doray and Léa Pierrefitte). As this specimen is weekly trained using classical conditioning (so called Pavlovian conditioning; Pavlov, 1927), she therefore did not experience any unusual stress during the measures. Moreover, this specimen shares its enclosure with only one other specimen (an adult *Caiman crocodilus*) which shows a very shy behavior and has therefore no dominant influence on the studied specimen (thus provoking no basal stress which may have biased the observations).

3. Results

3.1 General ethological observations

During the « Aquatic » phases, we observed that both the *Alligator sinensis* and *Crocodylus niloticus* specimens did not always keep at the same place within the tank but happened to either swim or move by bottom dwelling. Both specimens also either stayed fully

198 immersed or took semi-emerged positions (high float, common float, submerged breathing;
199 Smith, 1979). During the « Heating-Terrestrial » phases, the *Alligator sinensis* specimen spent
200 several basking periods under the light beam (especially during the second one) whereas the
201 *Crocodylus niloticus* specimen rather kept wandering between the warm spot and the cold
202 one. A mid-open mouth gaping behavior has been once observed in this specimen (Spotila,
203 1977).

204 3.2 General statistical comparisons

205 According to the Wilcoxon test, the mean superficial skin temperature in the *Alligator*
206 *sinensis* specimen was significantly different after the second « Heating-Terrestrial » phase
207 whereas it previously remained unchanged after the three first phases (Table 3A). For the
208 *Crocodylus niloticus* specimen, the mean superficial skin temperature was significantly
209 different after each phase (Table 3A). When comparing the same value after each phase
210 between the *Alligator sinensis* and the *Crocodylus niloticus*, the Wilcoxon test turned out to
211 be significant after « Heating-Terrestrial-1 » and « Aquatic-2 » whereas it was not after
212 « Aquatic-1 » and « Heating-Terrestrial-2 » which were respectively the first and the last
213 phase of the experimentation (Table 3B; Fig. 3).

214 3.3 The skin temperature variations between cooling and warming phases in *Alligator* 215 *sinensis*

216 All along the four-hour experimentation which included the double succession of two
217 « Aquatic » and « Heating-Terrestrial » phases, the temperature of the skull table was higher
218 than on the other cranial regions (with an exception for the angular temperature which
219 increased after the second « Heating-Terrestrial » phase; Figs. 2 & 4A). The temperature of
220 the nuchal osteoderms was higher than on the non-ossified part of the nuchal region after each
221 « Heating-Terrestrial » phase whereas it was oppositely lower after each « Aquatic » phase. A

similar temperature contrast is noticeable if we compare the osteoderm shield with the adjacent skin on the flanks as well as the caudal paramedian osteoderms with the lateral side of the tail (on the anterior side of the caudal crest symphysis; Figs. 2 & 4A). When comparing the skull thermal behavior with the post-cranial regions which present a dermal ossification, we notice that between two consecutive phase switches, the skull table showed lower temperature variations (up to 1 °C) than the nuchal osteoderms (up to 4.5 °C), the dorsal shield (up to 4.5 °C) and the caudal paramedian osteoderms (up to 3 °C). Although showing less intense variations, both the mean temperature of the limbs and the mean temperature of the part of the axial body which has no osteoderm (averaging the neck, the flank, the tail lateral side) negatively covary with the mean temperature value of both the skull (averaging the snout, the skull table, the jugal, the angular) and the osteoderms (averaging the nuchals, the dorsals, the caudal paramedians). Indeed, these mean temperatures vary from 22.75 °C to 23.5 °C for the limbs and from 22 °C to 23.75 °C for the part of the axial body presenting no osteoderm whereas it varies from 22.25 °C to 25.25 °C for the skull and from 22.25 °C to 26 °C for the osteoderms (Figs. 4A).

3.4 The skin temperature variations between cooling and warming phases in Crocodylus niloticus

Like previously observed on the *Alligator sinensis* specimen, the superficial temperature on the skull table of the *Crocodylus niloticus* specimen was always higher than on the other cranial regions (the snout, the jugal, the angular) though there was an exception after « Heating-Terrestrial-1 » (Fig. 4B). As also previously observed on the *Alligator sinensis*, the temperature of the nuchal osteoderms was lower than on the non-ossified part of the nuchal region after each « Aquatic » phase whereas the contrary was observed after each « Heating-Terrestrial » phase. The temperature of the osteoderm shield was up to 2.5 °C higher than the adjacent skin on the flanks after the « Heating-Terrestrial » phases whereas

these two anatomical regions shared the same values after the « Aquatic » phases. The caudal paramedian osteoderms were always warmer than the lateral side of the tail (anterior to the caudal crest symphysis) although it showed a more pronounced difference after the « Heating-Terrestrial » phases. Indeed, the temperature on the caudal paramedian osteoderms varied between 23.5 °C and 28.5 °C whereas it was scaled between 23 °C and 24.5 °C on the lateral side of the tail. The temperature of the arm was higher or equal to the forearm's during the whole experimentation. In a same manner, the temperature of the leg was always higher than the temperature of the foreleg while showing a pattern of covariation.

Between the consecutive phase switches within the four-hour experimentation, the skull table showed lower temperature variations (up to 2.5 °C) than the nuchal osteoderms (up to 6.5 °C), the dorsal shield (up to 4 °C) and the caudal paramedian osteoderms (up to 4 °C). The mean skull temperature covaries with both the mean temperature of the osteoderms and the mean temperature of the part of the axial body presenting no osteoderm although the skull shows much lower variations than these two other regions (especially the osteoderms; Fig. 4B). Indeed, between the first « Aquatic » phase and the first « Heating-Terrestrial » phase, both the mean temperature of the skull and the mean temperature of the part of the axial body presenting no osteoderm varied within a scale of 1.5 °C whereas the mean temperature of the osteoderms varied within a scale of 3.5 °C. The mean temperature of the limbs always remained quite low and varied within a narrow scale (between 23 °C and 24 °C).

3.5 The albino Alligator mississippiensis skin temperature contrast and the distribution of the peripheral vascularization

The specimen spent several hours in a 25 °C water while recurrently exposing herself to the sunrays by adopting semi-emerged postures (mainly the common float which allows to emerge the head and the nuchal region; Smith, 1979). Right after the specimen was called to emerge on the beach by its animal keepers (as detailed above in *Material and Methods*), we

recorded that the skull table was warmer than the rest of the cranial regions (up to 2.4 °C higher) and the nuchal osteoderms were colder than the surrounding skin (with a difference of 0.9 °C). The dorsal shield showed a low difference with the adjacent skin on the flanks (0.3 °C) and the caudal paramedian osteoderms were also only 0.5 °C warmer than the lateral side of the tail (anterior to the caudal crest symphysis; Fig. 5). If we observe the global temperature gradient on the specimen (displayed from blue to red; Fig. 5), the superficial temperature tends to be higher on the dorsal region than on the lateral sides.

Since the studied *Alligator mississippiensis* is an albino specimen, the lack of melanine allows to observe the superficial blood vessels by transparency through the skin. Our photographs show that the skin vascularization is higher straight above both the dermatocranium and the osteoderms than on the rest of the organism which shows either none or residual dermal ossification (*i.e.* the non-ossified nuchal region, the flanks, the lateral sides of the tail and the limbs; Fig.5).

4. Discussion

4.1 The significancy of the experimentation

As mentioned above, the thermal sensitivity of the camera imaging detector is below 0.1 °C (NETD: 80 mK); this is sufficient to measure the skin temperatures and draw comparisons between the different anatomical regions within a same specimen. The minimum distance to shoot with this camera is 40 cm and the precision decreases as the distance to the target increases. In the regard, since we could shoot the *Alligator sinensis* at a distance of 50 cm we assume that the data are more precise than the one recorded from the *Crocodylus niloticus* because we had to stay at a distance comprised between 50 cm and 1 m since this specimen was more agitated and aggressive. The *Alligator mississippiensis* was targeted from an estimated distance of 1 meter but since this specimen is almost twice as large

as the two others (Table 1) we assume that it compensates the loss of accuracy due to the distance.

During the « Heating-Terrestrial » phases, the specimens were able to gape as their mouth was not taped and they were able to thermoregulate at their discretion by moving from the cold spot (22 °C) to the hot spot (47 °C). For the *Alligator sinensis* specimen, the Wilcoxon test shows that the mean superficial temperature had not significantly changed between « Aquatic-1 » and « Heating-Terrestrial-1 » as well as between « Heating-Terrestrial-1 » and « Aquatic-2 » whereas this test is significant between all phase switches for the *C. niloticus* specimen (Table 3A; Fig. 3). Despite some disparity in the test results between the two specimens, we however argue that both the *A. sinensis* and *C. niloticus* specimens experienced two significant consecutive cooling and heating periods. Indeed, when the Wilcoxon test is not significant for *A. sinensis* between the consecutive phases (A-1 / HT-1 and HT-1 / A-2; Table 3A), the skin maximum temperature value (extrema) is however successively shifted up (A-1 / HT-1) and down (HT-1 / A-2).

In regard of the comparison between the two specimen set of temperature, we assume that both of them reacted to the experimentation in a same manner. Indeed, even though the Wilcoxon test shows significant differences between the mean superficial temperature in the *A. sinensis* and in the *C. niloticus* after « Heating-Terrestrial-1 » and « Aquatic-2 » (Table 3B), we nonetheless assume that this result is not controversial because this comparison is only based on a mean value although the contrast of temperature between the various anatomical regions always shows similar trends when the specimens are set in the same conditions (« Aquatic » or « Heating-Terrestrial » ; Fig. 4). Relying on these observations, we assume that the thermal behavior of the two experimented specimens are representative of a general pattern which resumes the heat transfer processes between the organism and the environment in Crocodylia. Nevertheless, a comparative study aiming to assess a thermal

behavior variability between alligatorids, crocodylids and gavialids shall be further tested on a larger sample which would include a diversity of specimens that would be representative of various species while nonetheless sharing a comparable size which would correspond to a similar volumetric heat capacity.

4.2 The implication of the osteoderms in heat transfers

In a previous study, Farlow et al. (2010) measured the skin temperature of a *Caiman latirostris* with an Infra-Red camera. These authors assessed that the temperature of the back overlying the osteoderms was cooler than that of the skin between the osteoderms when the specimen was exposed to sunrays whether in a « cold » (air temperature: 16 °C) or in a « warm » environment (air temperature: 25 °C). Consequently, they assumed that relatively cool blood from the animal's core may preferentially be flowing to the osteoderms thus exchanging heat with the surrounding environment. Within our experimental setting, our results show similar patterns after all « Aquatic » phases whereas we observed that the crocodylian osteoderms are warmer than the adjacent non-ossified skin after a « Heating-Terrestrial » phase (including a basking spot set at 47 °C; Figs. 2&4). Even if this result may appear controversial with the results published in Farlow et al. (2010), these new data lead to argue that the osteoderm blood vessels do collect the external heat during a significant warming period as assumed by these authors. Indeed, when Farlow et al. (2010) acquired the yet published data, the environmental air temperature was comprised between 16 °C and 25 °C, therefore the osteoderms may not have been vascularized by a blood which was warm enough to display high temperature spots like the ones we observed after the « Heating-Terrestrial » periods during our experimentation. We base this argument on the fact that the *Caiman latirostris* physiological temperature shall be around 32 °C (estimation based on its close relative *Caiman crocodilus*; Diffenbach, 1975) so this specimen may not have been observed in a condition in which it could have been potentially exposed to overheating. In

order to understand the thermal behavior differences between the osteoderms and the non-ossified dermis, a previous study has shown that the presence of the osteoderms does not modify the crocodylian skin thermal conduction if we do not consider the relative presence of the blood vessels (Clarac et al., 2017b). Therefore, as a complementary approach, using the ITIS foundation database (Hasgall et al., 2015), here we have calculated that the thermal diffusivity of the blood is higher than the one of the tissues which either compose the soft skin or the osteoderms (*i.e.* the compact bone, the cancellous bone, the red and the yellow marrow; see supplementary data). Since the entire body of the crocodylians is covered with a continuous layer of keratin (Trutnau and Sommerlad, 2006), we deduce that the observed temperature contrast between the various anatomical regions must not either be due to variations in the skin reflectivity but indeed to the relative presence of blood vessels which has a main consequent influence on the global skin thermal diffusivity. In a same manner, the cutaneous water loss which is influenced by both the environmental humidity and temperature variations (Davis et al., 1980) should be homogenous along the entire skin surface since the osteoderms are always covered by a portion of dermis and by the epidermis so they can not either modify the skin surface temperature by constituting a fence to the evaporative water loss (Clarac et al., 2018; Dubansky and Dubansky, 2018). Even if the dorsal and the caudal paramedian osteoderms must partially warm up faster than both the flanks and the lateral side of the tail due to their closer position to the basking light during warming, our results clearly show that the nuchal osteoderms also warm up faster than the nuchal surrounding skin although these two neighboring anatomical regions are equidistant to the basking light (Fig. 2B; Fig. 4 A&B). Therefore, the distance to the sun rays is not either the main component which explains the contrast in the temperature variations between the parts of the skin which present osteoderms and the parts of the skin which do not. A close-up on the albino *Alligator mississippiensis* nuchal region is presented in Figure 5 and reveals that the relative presence

of the superficial blood vessels (which is observable by transparency through the skin) matches with the thermal contrast between the osteoderms and the surrounding skin. Consequently, we deduce that the relative presence of the blood vessels is well the main component which explains the difference in the thermal behavior between the parts of the skin which show osteoderms and the parts of the skin which do not. In this regard, an other recent study has shown that the osteoderms (including their apical ornamentation) are more vascularized than the surrounding non-ossified dermis (Clarac et al., 2018). These data lead us to argue that the heat transfers through the osteoderms are based on the circulation of the blood in the peripheral vessels (Seidel, 1979; Farlow et al., 2010): a system which relies on both the heat conduction and the thermal convection of a fluid flow (Jiji, 2009). Concerning the role of the vascular system in heat transfers within the core organism, previous authors have proved that the crocodylian cutaneous blood flow is increased during basking periods thanks to both the acceleration of the heart beat (Robertson and Smith, 1979; Seebacher and Franklin, 2004, 2007) and the vasodilation of the peripheral vessels (Grigg and Alchin, 1976). Moreover, the same authors assessed that in absence of external heat source, the blood flow is redistributed from the dorsal surface to the core of the organism whereas its distribution to the leg skin and muscle do not significantly change with thermal variations (Seebacher and Franklin, 2007). This data would rather coincide with the fact that the axial parts of the body which lack osteoderms are relatively warmer than the osteoderms when not exposed to heating conditions; it would also explain why the stylopods and zeugopods rather remain at relatively low temperatures with a least influence of the external temperature variations (Figs. 2&4). In regard of the synthesis of our results and as already assumed by several authors (Seidel, 1979; Farlow et al., 2010; Owerkowicz, 2016), we confirm the hypothesis according to which the crocodylian osteoderms play a role in the heat transfers between the organism and the environment through the set-up of a peripheral blood vessel network.

396 4.3 *The skull implication in thermoregulation*

397 A recent study by Porter et al. (2016) has shown that the skull of the crocodylians
398 presents a vascular system which consists of several anastomosed dense plexuses which
399 potentially work as sites of thermal exchange. The blood vessel network is especially well
400 reticulated in the nasal region and further communicates with the braincase through the
401 median and lateral nasal veins which thus consist of a pathway passing by the neurosensory
402 tissues. All our results show that the snout is always colder than the skull table in disregard of
403 the environmental variations; this assessment suggests that the nose would systematically
404 behave as a site in which the heat would be capted and further driven to the braincase by the
405 nasal veins (Figs. 2, 4 & 5). Moreover, the superficial vessels of both the skull table and the
406 frontal could as well drive the warm blood to the braincase and further to the heart through the
407 dorsal longitudinal sinus. Our results show that the temperature of the skull (and noticeably
408 the skull table; Fig. 4) covaries with the osteoderms' temperature though showing less intense
409 variations. Since both of these anatomical regions are equally exposed to the heating beam
410 when basking in a terrestrial position, we assume that there may be a control of the blood flow
411 in the skull which should differ from the osteoderms in order to avoid major temperature
412 variations in the most vital sensory organs (the eyes, the ears, the brain). In this regard, Porter
413 et al. (2016) have evidenced that the nasal vein bifurcates along two routes thus allowing to
414 shunt the blood flow. The first one is the medial route which forms a tributary of the olfactory
415 veins and dorsal longitudinal sinus (as already mentioned above) whereas the second one (the
416 lateral route) drains into the orbit via the supraorbital and ophthalmotemporal vein
417 anastomosis therefore joining the heart while avoiding the braincase sensory organs.
418 Consequently, we assume that the blood flow in the crocodylian skull may be shunted from
419 one pathway to the other depending on the external temperature in order to keep the brain and
420 the main sensory organs at a temperature which tends to reach the physiological optimum.

4.4 Evolutionary considerations

As mentioned in the introduction, the crown-crocodylians are ecto-poikilothermic vertebrates which evolved from ancestral Triassic forms which are assessed to be endothermic (Riquelès et al., 2003, 2008; Cubo et al. 2012; Legendre et al., 2013, 2016). The early terrestrial pseudosuchians (but also later forms such as sebesuchians) only possessed two rows of compact thus poorly vascularized osteoderms (Scheyer and Desojo, 2011; Cerda et al., 2013; Irmis et al., 2013; Martin, 2014; Scheyer et al., 2014). At the Triassic-Jurassic transition, the number of rows increased and formed a dorsal shield (sometimes also ventral) in both the crocodyliforms and teleosaurids while they showed a higher degree of bone ornamentation (apical sculpture; Clarac et al., 2015). In parallel with the osteoderms, the degree of ornamentation of the skull also increased when the crocodyliforms and teleosaurids transitioned to the semi-aquatic lifestyle (Clarac et al., 2017a). A recent study on extant crocodylians has proved that the osteoderm apical ornamental pits increase the skin vascularization by providing a superficial cluster of blood vessels (Clarac et al., 2018). Based on a similar process, we hypothesize that the development of the skull ornamentation supplies a peripheral vessel network which is involved in the basking heat capture like in the osteoderms. Consequently, we assume that both the skull and the osteoderm vascularization have played a functional role in the adaptation to the ectothermic amphibious lifestyle through the set-up of a peripheral vascular network of which the blood flow is controlled by the cardiac beat, the vasomotion and the shunt and of peripheral vessel pathways.

5. Conclusion

As previously hypothesized by several authors (Seidel, 1979; Farlow et al., 2010; Owerkowicz, 2016; Porter et al., 2016; Clarac et al., 2017a; Clarac et al., 2018), both the skull and the osteoderms are involved in the crocodylian ecto-poikilothermic thermoregulation through the set-up of a peripheral vascular network. Whether cranial or post-cranial, the

crocodylian dermal skeleton captures the external heat during basking thanks to the increase of the blood flow which is controlled by both the cardiac activity (heart beat) and the vasomotion. The warm blood is afterward redistributed to the core organism thus allowing the vital organs to remain at an optimal physiological temperature when no longer exposed to a heating source. As the skull temperature contrast remains constant between the anatomical regions in disregard of the external temperature variations, we assume that there are shunting blood pathways which help to maintain the braincase and the main sensory organs at an optimal physiological temperature depending on the environmental variations. Nevertheless, our results do not signify that the vascular system which is set-up through and straight above the crocodylian dermal skeleton is exclusively involved in thermoregulation. Indeed, this system may implicate other adaptative and/ or ontogenetic functions which rely on exchanges between the plasma and the bone matrix such as egg shelling in females (Dacke et al., 2015) and respiratory acidosis buffering during prolonged apnea (Jackson et al., 2003). Consequently, the role of the crocodylian dermal skeleton vascular system in the ecto-poikilothermic thermoregulation is probably not exclusive and could therefore consist of an exaptation which allowed a secondary transition from endothermy to ectothermy in Pseudosuchia (Legendre et al., 2016).

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606

607 **Figure captions**

608 Figure 1: Experimental setting. On the left side: the « Aquatic » configuration; on the right side: the
609 « Heating-Terrestrial » configuration. Abbreviations: t: temperature; H: hygrometry (see text for
610 details).

611 Figure 2A: Skin temperature above the fourteen diverse anatomical regions of interest in *Alligator*
612 *sinensis* after the first « Aquatic » phase (A-1). Abbreviations: S.Table: Skull Table; ost: osteoderms;
613 Nuchal non-oss.: non-ossified part of the Nuchal region; C.P. ost.: Caudal Paramedian osteoderms.

614 Figure 2B: Skin temperature above the fourteen diverse anatomical regions of interest in *Alligator*
615 *sinensis* after the first « Heating-Terrestrial » phase (HT-1). Abbreviations: S.Table: Skull Table; ost:
616 osteoderms; Nuchal non-oss.: non-ossified part of the Nuchal region; C.P. ost.: Caudal Paramedian
617 osteoderms.

618 Figure 3: Boxplot of the recorded temperature on the fourteen regions of interest. Abbreviations: A-1:
619 Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.

620 Figure 4A: Temperature variations above the diverse anatomical regions of interest in *Alligator*
621 *sinensis*. Abbreviations: HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.
622 Abbreviations: S.Table: Skull Table; ost: osteoderms; Nuchal non-oss.: non-ossified part of the nuchal
623 region; C.P. ost.: Caudal Paramedian osteoderms; A.Skin: Part of the Axial body presenting no
624 osteoderm (resuming the nuchal region, the flanks, the lateral side on the tail). NB: The graph lines
625 between the different plotted values simply indicate the sense of variation of the temperatue between
626 two phases but do not mean that this type of variation is linear.

627 Figure 4B: Temperature variations above the diverse anatomical regions of interest in *Crocodylus*
628 *niloticus*. Abbreviations: HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.
629 Abbreviations: S.Table: Skull Table; ost: osteoderms; Nuchal non-oss.: non-ossified part of the Nuchal
630 region; C.P. ost.: Caudal Paramedian osteoderms; A.Skin: Part of the Axial body presenting no
631 osteoderm (resuming the nuchal region, the flanks, the lateral side on the tail). NB: The graph lines

632 between the different plotted values simply indicate the sense of variation of the temperature between
633 two phases but do not mean that this type of variation is linear.

634 Figure 5: Temperature variations above the diverse anatomical regions of interest in *Alligator*
635 *mississippiensis* (see text for details). High vascular density areas are pointed with red arrows whereas
636 low vascular density areas are pointed with green arrows. Abbreviations: S.Table: Skull Table; ost:
637 osteoderms; Nuchal non-oss.: non-ossified part of the Nuchal region; C.P. ost.: Caudal Paramedian
638 osteoderms.

C.P. ost.

Tail lateral side

Skin temperature (°C)

Skin temperature (°C)

Temperature (°C)

— S.Table — Jugal
— Snout — Angular

Temperature (°C)

— Nuchal ost.
— Nuchal non-oss.

Temperature (°C)

— Dorsal ost.
— Flank

Temperature (°C)

— C.P. ost.
— Tail lateral side

Temperature (°C)

— Arm
— Forearm

Temperature (°C)

— Leg
— Foreleg

Temperature (°C)

— C.P. ost. — Nuchal ost.
— S.Table — Dorsal ost.

Temperature (°C)

— Limbs — Ost.
— Skull — A.Skin

Family	Genus	Species	SVL (cm)	Full length (cm)	Weight (kg)	Sex	CITES number
Alligatoridae	<i>Alligator</i>	<i>sinensis</i>	50	107	4	Male	208 246 000 135 135
Alligatoridae	<i>Alligator</i>	<i>mississippiensis</i>	NA	180	NA	Female	ES-DE-00047/111
Crocodylidae	<i>Crocodylus</i>	<i>niloticus</i>	48	96	6	Female	FRA250 228 500 026 372

Table 1: Sampled specimens with taxonomic references. Abbreviations: SVL: Snout Ventral Length; NA: Non-Attributed.

	<i>A.sinensis</i> Temperature (°C)					<i>C.niloticus</i> Temperature (°C)				<i>A.mississippiensis</i> Temperature (°C)
	Phase	A-1	HT-1	A-2	HT-2	A-1	HT-1	A-2	HT-2	NA
Anatomical regions	Snout	21	22.1	21.3	24.6	21.4	23.9	21.5	24.7	20.7
	Jugal	22.6	23.9	22.5	25	22.6	24.3	23.6	25.7	21.4
	Angular	21.7	22.3	21.4	26.1	21.4	23.1	22.6	23.3	20.9
	S.table	24.3	24.5	23.8	25.8	23	23.7	25.7	26.7	23.1
	Nuchal ost.	21.6	24.3	21.9	26.4	21.9	25.9	21.5	27.8	21.3
	Nuchal	23.8	23.6	23	24	23.5	25.1	23	26.3	22.1
	Arm	23.5	21.7	23.2	21.9	23.3	23.2	23.6	24.6	22.1
	Forearm	22.8	20.8	23.2	23.2	22.8	22.4	23.7	23.1	21.4
	Dorsal ost.	22.9	25.1	21.7	26	22.9	26.7	24.2	27.6	22
	Lateral side	22.7	22.8	23.1	23.2	22.7	25.7	24.3	25.6	21.7
	Leg	22.9	23.6	23.1	23.6	23.1	25.2	23.9	26.1	21.5
	Foreleg	24.2	21.9	22.6	22.9	22.4	23.4	22.9	24.3	21
	C.P. ost.	22.2	24.2	22.5	25.7	23.4	26.1	24.5	28.7	22.1
	L.side.tail	22.7	21.9	24.1	23	23.1	23.1	23.6	25.5	21.4
Statistical values	<i>Mean</i>	22.8	23.1	22.7	24.4	22.7	24.4	23.5	25.7	21.7
	<i>Median</i>	22.8	23.2	22.8	24.3	22.9	24.3	23.6	25.7	21.5
	<i>Std dev.</i>	0.7	1.1	0.7	1.3	0.5	1.2	0.8	1.3	0.5
	<i>Max</i>	24.3	25.1	24.1	26.4	23.5	26.7	25.7	28.7	23.1
	<i>Min</i>	21	20.8	21.3	21.9	21.4	22.4	21.5	23.1	20.7

Table 2: Dataset. Abbreviations: A-1: Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2; NA: Non-Attributed; S.table: Skull table; ost: osteoderms; C.P.: Caudal Paramedian; L.side.tail: the Lateral side of the tail (on the anterior side of the caudal crest symphysis; see text for details); Std dev.: Standard deviation; Max: Maximum value; Min: Minimum value.

Inter-phase analysis	Wilcoxon-test	A-1 / HT-1	HT-1 / A-2	A-2 / HT-2
<i>A. sinensis</i>	<i>p-value</i>	0.47	0.39	0.01
<i>C. niloticus</i>	<i>p-value</i>	0.01	0.04	0.01

Table 3A: Inter-phase statistical comparisons. Abbreviations: A-1: Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2; see text for details.

Inter-specimen analysis	Wilcoxon-test	A-1	HT-1	A-2	HT-2
<i>A. sinensis</i> - <i>C. niloticus</i>	<i>p-value</i>	0.95	0.02	0.04	0.06

Table 3B: Inter-specimen statistical comparisons. Abbreviations: A-1: Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2; see text for details.