



**HAL**  
open science

# The crocodylian skull and osteoderms: A functional exaptation to ectothermy?

F. Clarac, A. Quilhac

► **To cite this version:**

F. Clarac, A. Quilhac. The crocodylian skull and osteoderms: A functional exaptation to ectothermy?. *Zoology*, 2019, 132, pp.31-40. 10.1016/j.zool.2018.12.001 . mnhn-02557596

**HAL Id: mnhn-02557596**

**<https://mnhn.hal.science/mnhn-02557596>**

Submitted on 21 Oct 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **The crocodylian skull and osteoderms:**

2 **A functional exaptation to ectothermy?**

3 F. Clarac<sup>1,2\*</sup>, A. Quilhac<sup>3</sup>

4 <sup>1</sup>Département Histoire de la Terre, Museum National d'Histoire Naturelle, UMR 7207 (CR2P), Sorbonne  
5 Universités, MNHN/CNRS/UPMC, F-75231, France

6 <sup>2</sup>Uppsala University, Department of Organismal Biology, Subdepartment of Evolution and Development,  
7 Norbyvägen 18A, SE-752 36, Uppsala, Sweden.

8 <sup>3</sup>Sorbonne Université, CNRS, Institut des Sciences de la Terre Paris (ISTeP), Paris, F-75005, France

9 \*Corresponding author: francois.clarac@mnhn.fr

10 **Abstract**

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

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

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

#### 44 **1. Introduction**

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

50 (Ricqlès et al., 2003, 2008). Furthermore, the high osteocyte density which has been  
51 quantified in the primary bone in both the stem-archosauriforms and the early pseudosuchians  
52 argued that these taxa had a high basal metabolic rate revealing an endothermic metabolism  
53 (Cubo et al. 2012; Legendre et al., 2016). Besides these assessments which are based on the  
54 study of bone histology in extinct species, there are anatomical features in the extant  
55 crocodylians which also suggest an endothermic origin: the existence of a four-cardiac-  
56 chambered heart separating the high systemic blood pressures from low pulmonary blood  
57 pressures like in birds and mammals (Seymour et al., 2004). Thus, unlike the rest of the  
58 ectothermic vertebrates, the crocodylians do possess a full ventricular septation (Jensen et al.,  
59 2013) though showing some specific cardiac traits: 1) the foramen of Panizza which provides  
60 communication between the right and left aorta (Franklin & Axelsson, 2000; Axelsson and  
61 Franklin, 2001); 2) the cog-tooth valve which controls the blood flow through either the  
62 pulmonary artery or the right aortic arch consequently influencing the systemic arterial blood  
63 pressure (a value which is itself correlated with the metabolic rate; Seymour et al., 2004).  
64 Even if the relation between these cardiac traits and the crocodylian ectothermic metabolism  
65 is still debated (Eme et al. 2010), the development of adaptative functions in the heat transfers  
66 between the organism and the surrounding environment must have been necessary to permit a  
67 switch from endothermy to ectothermy. As already assessed in other ectothermic vertebrates  
68 such as the squamates, these thermal exchanges shall rely on the blood flow through the  
69 vascular system (Drane et al., 1977; Sadava et al., 2009; Porter and Witmer, 2015). In this  
70 regard, several authors hypothesized that the crocodylian dermal bones consist of thermal  
71 exchange sites when basking thanks to a superficial vessel network present both in the cranial  
72 region (Porter et al., 2016; Clarac et al., 2017a) and in the osteoderms (Seidel, 1979; Farlow et  
73 al., 2010; Owerkowicz, 2016; Clarac et al., 2018). Both of these networks would be further  
74 connected to the general vascular circulation of which the flow is controlled by both the heart

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

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

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

## 101 **2. Material and methods**

### 102 *2.1 Biological sample*

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

### 114 *2.2 Experimental setting*

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

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

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

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

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

### 193 **3. Results**

#### 194 *3.1 General ethological observations*

195 During the « Aquatic » phases, we observed that both the *Alligator sinensis* and  
196 *Crocodylus niloticus* specimens did not always keep at the same place within the tank but  
197 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

222 similar temperature contrast is noticeable if we compare the osteoderm shield with the  
223 adjacent skin on the flanks as well as the caudal paramedian osteoderms with the lateral side  
224 of the tail (on the anterior side of the caudal crest symphysis; Figs. 2 & 4A). When comparing  
225 the skull thermal behavior with the post-cranial regions which present a dermal ossification,  
226 we notice that between two consecutive phase switches, the skull table showed lower  
227 temperature variations (up to 1 °C) than the nuchal osteoderms (up to 4.5 °C), the dorsal  
228 shield (up to 4.5 °C) and the caudal paramedian osteoderms (up to 3 °C). Although showing  
229 less intense variations, both the mean temperature of the limbs and the mean temperature of  
230 the part of the axial body which has no osteoderm (averaging the neck, the flank, the tail  
231 lateral side) negatively covary with the mean temperature value of both the skull (averaging  
232 the snout, the skull table, the jugal, the angular) and the osteoderms (averaging the nuchals,  
233 the dorsals, the caudal paramedians). Indeed, these mean temperatures vary from 22.75 °C to  
234 23.5 °C for the limbs and from 22 °C to 23.75 °C for the part of the axial body presenting no  
235 osteoderm whereas it varies from 22.25 °C to 25.25 °C for the skull and from 22.25 °C to 26  
236 °C for the osteoderms (Figs. 4A).

### 237 *3.4 The skin temperature variations between cooling and warming phases in Crocodylus* 238 *niloticus*

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

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

255         Between the consecutive phase switches within the four-hour experimentation, the  
256 skull table showed lower temperature variations (up to 2.5 °C) than the nuchal osteoderms (up  
257 to 6.5 °C), the dorsal shield (up to 4 °C) and the caudal paramedian osteoderms (up to 4 °C).  
258 The mean skull temperature covaries with both the mean temperature of the osteoderms and  
259 the mean temperature of the part of the axial body presenting no osteoderm although the skull  
260 shows much lower variations than these two other regions (especially the osteoderms; Fig.  
261 4B). Indeed, between the first « Aquatic » phase and the first « Heating-Terrestrial » phase,  
262 both the mean temperature of the skull and the mean temperature of the part of the axial body  
263 presenting no osteoderm varied within a scale of 1.5 °C whereas the mean temperature of the  
264 osteoderms varied within a scale of 3.5 °C. The mean temperature of the limbs always  
265 remained quite low and varied within a narrow scale (between 23 °C and 24 °C).

266         3.5 *The albino Alligator mississippiensis skin temperature contrast and the distribution of*  
267             *the peripheral vascularization*

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

272 recorded that the skull table was warmer than the rest of the cranial regions (up to 2.4 °C  
273 higher) and the nuchal osteoderms were colder than the surrounding skin (with a difference of  
274 0.9 °C). The dorsal shield showed a low difference with the adjacent skin on the flanks (0.3  
275 °C) and the caudal paramedian osteoderms were also only 0.5 °C warmer than the lateral side  
276 of the tail (anterior to the caudal crest symphysis; Fig. 5). If we observe the global  
277 temperature gradient on the specimen (displayed from blue to red; Fig. 5), the superficial  
278 temperature tends to be higher on the dorsal region than on the lateral sides.

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

## 285         **4. Discussion**

### 286         *4.1 The significancy of the experimentation*

287         As mentioned above, the thermal sensitivity of the camera imaging detector is below  
288 0.1 °C (NETD: 80 mK); this is sufficient to measure the skin temperatures and draw  
289 comparisons between the different anatomical regions within a same specimen. The  
290 minimum distance to shoot with this camera is 40 cm and the precision decreases as the  
291 distance to the target increases. In the regard, since we could shoot the *Alligator sinensis* at a  
292 distance of 50 cm we assume that the data are more precise than the one recorded from the  
293 *Crocodylus niloticus* because we had to stay at a distance comprised between 50 cm and 1 m  
294 since this specimen was more agitated and aggressive. The *Alligator mississippiensis* was  
295 targeted from an estimated distance of 1 meter but since this specimen is almost twice as large

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

298         During the « Heating-Terrestrial » phases, the specimens were able to gape as their  
299 mouth was not taped and they were able to thermoregulate at their discretion by moving from  
300 the cold spot (22 °C) to the hot spot (47 °C). For the *Alligator sinensis* specimen, the  
301 Wilcoxon test shows that the mean superficial temperature had not significantly changed  
302 between « Aquatic-1 » and « Heating-Terrestrial-1 » as well as between « Heating-Terrestrial-  
303 1 » and « Aquatic-2 » whereas this test is significant between all phase switches for the *C.*  
304 *niloticus* specimen (Table 3A; Fig. 3). Despite some disparity in the test results between the  
305 two specimens, we however argue that both the *A. sinensis* and *C. niloticus* specimens  
306 experienced two significant consecutive cooling and heating periods. Indeed, when the  
307 Wilcoxon test is not significant for *A. sinensis* between the consecutive phases (A-1 / HT-1  
308 and HT-1 / A-2; Table 3A), the skin maximum temperature value (extrema) is however  
309 successively shifted up (A-1 / HT-1) and down (HT-1 / A-2).

310         In regard of the comparison between the two specimen set of temperature, we assume  
311 that both of them reacted to the experimentation in a same manner. Indeed, even though the  
312 Wilcoxon test shows significant differences between the mean superficial temperature in the  
313 *A. sinensis* and in the *C. niloticus* after « Heating-Terrestrial-1 » and « Aquatic-2 » (Table  
314 3B), we nonetheless assume that this result is not controversial because this comparison is  
315 only based on a mean value although the contrast of temperature between the various  
316 anatomical regions always shows similar trends when the specimens are set in the same  
317 conditions (« Aquatic » or « Heating-Terrestrial » ; Fig. 4). Relying on these observations, we  
318 assume that the thermal behavior of the two experimented specimens are representative of a  
319 general pattern which resumes the heat transfer processes between the organism and the  
320 environment in Crocodylia. Nevertheless, a comparative study aiming to assess a thermal

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

#### 325 *4.2 The implication of the osteoderms in heat transfers*

326 In a previous study, Farlow et al. (2010) measured the skin temperature of a *Caiman*  
327 *latirostris* with an Infra-Red camera. These authors assessed that the temperature of the back  
328 overlying the osteoderms was cooler than that of the skin between the osteoderms when the  
329 specimen was exposed to sunrays whether in a « cold » (air temperature: 16 °C) or in a  
330 « warm » environment (air temperature: 25 °C). Consequently, they assumed that relatively  
331 cool blood from the animal's core may preferentially be flowing to the osteoderms thus  
332 exchanging heat with the surrounding environment. Within our experimental setting, our  
333 results show similar patterns after all « Aquatic » phases whereas we observed that the  
334 crocodylian osteoderms are warmer than the adjacent non-ossified skin after a « Heating-  
335 Terrestrial » phase (including a basking spot set at 47 °C; Figs. 2&4). Even if this result may  
336 appear controversial with the results published in Farlow et al. (2010), these new data lead to  
337 argue that the osteoderm blood vessels do collect the external heat during a significant  
338 warming period as assumed by these authors. Indeed, when Farlow et al. (2010) acquired the  
339 yet published data, the environmental air temperature was comprised between 16 °C and 25  
340 °C, therefore the osteoderms may not have been vascularized by a blood which was warm  
341 enough to display high temperature spots like the ones we observed after the « Heating-  
342 Terrestrial » periods during our experimentation. We base this argument on the fact that the  
343 *Caiman latirostris* physiological temperature shall be around 32 °C (estimation based on its  
344 close relative *Caiman crocodilus*; Diffenbach, 1975) so this specimen may not have been  
345 observed in a condition in which it could have been potentially exposed to overheating. In

346 order to understand the thermal behavior differences between the osteoderms and the non-  
347 ossified dermis, a previous study has shown that the presence of the osteoderms does not  
348 modify the crocodylian skin thermal conduction if we do not consider the relative presence of  
349 the blood vessels (Clarac et al., 2017b). Therefore, as a complementary approach, using the  
350 ITIS foundation database (Hasgall et al., 2015), here we have calculated that the thermal  
351 diffusivity of the blood is higher than the one of the tissues which either compose the soft skin  
352 or the osteoderms (*i.e.* the compact bone, the cancellous bone, the red and the yellow marrow;  
353 see supplementary data). Since the entire body of the crocodylians is covered with a  
354 continuous layer of keratin (Trutnau and Sommerlad, 2006), we deduce that the observed  
355 temperature contrast between the various anatomical regions must not either be due to  
356 variations in the skin reflectivity but indeed to the relative presence of blood vessels which  
357 has a main consequent influence on the global skin thermal diffusivity. In a same manner, the  
358 cutaneous water loss which is influenced by both the environmental humidity and temperature  
359 variations (Davis et al., 1980) should be homogenous along the entire skin surface since the  
360 osteoderms are always covered by a portion of dermis and by the epidermis so they can not  
361 either modify the skin surface temperature by constituting a fence to the evaporative water  
362 loss (Clarac et al., 2018; Dubansky and Dubansky, 2018). Even if the dorsal and the caudal  
363 paramedian osteoderms must partially warm up faster than both the flanks and the lateral side  
364 of the tail due to their closer position to the basking light during warming, our results clearly  
365 show that the nuchal osteoderms also warm up faster than the nuchal surrounding skin  
366 although these two neighboring anatomical regions are equidistant to the basking light (Fig.  
367 2B; Fig. 4 A&B). Therefore, the distance to the sun rays is not either the main component  
368 which explains the contrast in the temperature variations between the parts of the skin which  
369 present osteoderms and the parts of the skin which do not. A close-up on the albino *Alligator*  
370 *mississippiensis* nuchal region is presented in Figure 5 and reveals that the relative presence

371 of the superficial blood vessels (which is observable by transparency through the skin)  
372 matches with the thermal contrast between the osteoderms and the surrounding skin.  
373 Consequently, we deduce that the relative presence of the blood vessels is well the main  
374 component which explains the difference in the thermal behavior between the parts of the skin  
375 which show osteoderms and the parts of the skin which do not. In this regard, an other recent  
376 study has shown that the osteoderms (including their apical ornamentation) are more  
377 vascularized than the surrounding non-ossified dermis (Clarac et al., 2018). These data lead us  
378 to argue that the heat transfers through the osteoderms are based on the circulation of the  
379 blood in the peripheral vessels (Seidel, 1979; Farlow et al., 2010): a system which relies on  
380 both the heat conduction and the thermal convection of a fluid flow (Jiji, 2009). Concerning  
381 the role of the vascular system in heat transfers within the core organism, previous authors  
382 have proved that the crocodylian cutaneous blood flow is increased during basking periods  
383 thanks to both the acceleration of the heart beat (Robertson and Smith, 1979; Seebacher and  
384 Franklin, 2004, 2007) and the vasodilation of the peripheral vessels (Grigg and Alchin, 1976).  
385 Moreover, the same authors assessed that in absence of external heat source, the blood flow is  
386 redistributed from the dorsal surface to the core of the organism whereas its distribution to the  
387 leg skin and muscle do not significantly change with thermal variations (Seebacher and  
388 Franklin, 2007). This data would rather coincide with the fact that the axial parts of the body  
389 which lack osteoderms are relatively warmer than the osteoderms when not exposed to  
390 heating conditions; it would also explain why the stylopods and zeugopods rather remain at  
391 relatively low temperatures with a least influence of the external temperature variations (Figs.  
392 2&4). In regard of the synthesis of our results and as already assumed by several authors  
393 (Seidel, 1979; Farlow et al., 2010; Owerkowicz, 2016), we confirm the hypothesis according  
394 to which the crocodylian osteoderms play a role in the heat transfers between the organism  
395 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.

#### 421           4.4 *Evolutionary considerations*

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

#### 441           **5. Conclusion**

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

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

### 463 **Acknowledgments**

464 We thank the zoological park “Planète Crocodiles” for giving us access to their  
465 facilities and for housing all the experimentations. We address our respectful regards to  
466 Johann Doray (zoological director) and Franck Doucet (executive director) for their active  
467 participation in the set-up of an official collaboration between scientific institutions (Muséum  
468 National d’Histoire Naturelle, Sorbonne Université) and Planète Crocodiles (zoological park).  
469 We also address our thankful thoughts to Léa Pierrefitte (animal keeper) who was helpful  
470 during the experimentations as she perfectly knows the crocodylian behavior and shows

471 safety and carefulness in their handling. We also thank Joffray Fomel (director of Biotope  
472 Conception) for its technical advice in the set-up of the experimentation. Eventually, we  
473 dedicate our respectful acknowledgments to James O. Farlow and to the other anonymous  
474 referees for reviewing this article.

#### 475 **Funding sources**

476 This work was supported by a grant from the Vetenskapsrådet awarded to Sophie  
477 Sanchez (2015-04335).

#### 478 **References**

- 479 Axelsson, M., Franklin, C.E., 2001. The calibre of the foramen of Panizza in *Crocodylus*  
480 *porosus* and under adrenergic control. *J. Comp. Physiol. B.* 171, 341-346.
- 481 Cerda, I.A., Desojo, J.B., Scheyer, T.M., Schultz, C.L., 2013. Osteoderm microstructure of  
482 ‘‘rauisuchian’’ archosaurs from South America. *Geobios.* 46, 273–283.
- 483 Clarac, F., Souter, T., Cornette, R., Cubo, J., Buffrénil, Vde., 2015. A quantitative assessment  
484 of bone area increase due to ornamentation in the Crocodylia. *J. Morph.* 276, 1183–1192.
- 485 Clarac, F., Souter, T., Cubo, J., Buffrénil, Vde., Brochu, C.A., Cornette, R., 2016. Does skull  
486 morphology constrain bone ornamentation? A morphometric analysis in the Crocodylia. *J.*  
487 *Anat.* 229, 292–301.
- 488 Clarac, F., Buffrénil, Vde., Brochu, C.A., Cubo, J., 2017a. The evolution of bone  
489 ornamentation in Pseudosuchia: morphological constraints versus ecological adaptation. *Biol.*  
490 *J. Linn. Soc.* 121, 395–408.
- 491 Clarac, F., Goussard, F., Teresi, L., Buffrénil, Vde., Sansalone, V., 2017b. Do the ornamented  
492 osteoderms influence the heat conduction through the skin? A finite element analysis in  
493 Crocodylomorpha. *J. Therm. Biol.* 69, 39–53.

494 Clarac, F., Buffrénil, Vde., Cubo, J., Quilhac, A., 2018. Vascularization in ornamented  
495 osteoderms: physiological implications in ectothermy and amphibious lifestyle in the  
496 crocodylomorphs? *Anat. Rec.* 301, 175–183.

497 Cope, E.D., 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America.  
498 *Trans. Amer. Phil. Soc.* 14, 1–252.

499 Cubo, J., Le Roy, N., Martinez-Maza, C., Montes, L., 2012. Paleohistological estimation of  
500 bone growth rate in extinct archosaurs. *Paleobiology.* 38 (2), 335-349.

501 Dacke, C.G., Elsey, R.M., Trosclair, P.L., Sujiyama, T., Nevarez, J.G., Schweitzer, M.H.,  
502 2015. Alligator osteoderms as a source of labile calcium for eggshell formation. *J. Zool.*  
503 297(4), 255-264.

504 Davis, J.E., Spotila, J.R., Scheffler, W.C., 1980. Evaporative water loss from the American  
505 alligator, *Alligator mississippiensis*: the relative importance of respiratory and cutaneous  
506 components and the regulatory role of the skin. *Comp. Biochem. Physiol.* 67A, 439-446.

507 Diffenbach, C.O.C., 1975. Thermal preferences and thermoregulation in *Caiman crocodilus*.  
508 *Copeia.* 1975(3), 530-540.

509 Drane, C.R., Webb, G.J.W., Heuer, P., 1977. Patterns of heating in the body trunk and tail of  
510 *Crocodylus porosus*. *J. Therm. Biol.* 2, 127-130.

511 Dubansky, B.H., Dubansky, B.D., 2018. Natural development of dermal ectopic bone in the  
512 American Alligator (*Alligator mississippiensis*) resembles heterotopic ossification disorders in  
513 humans. *Anat. Rec.* 301, 56–76.

514 Eme, J., Gwalthney, J., Owerkowicz, T., Blank, J.M., Hicks, J.W., 2010. Turning crocodylian  
515 hearts into bird hearts: growth rates are similar for alligators with and without right-to-left  
516 cardiac shunt. *J. Exp. Biol.* 213, 2673-2680.

517 Farlow, J.O., Hayashi, S., Tattersall, G.J., 2010. Internal vascularity of the dermal plates of  
518 *Stegosaurus* (Ornithischia, Thyreophora). *Swiss. J. Geosci.* 103, 173–185.

519 Franklin, C.E., Axelsson, M., 2000. An actively controlled heart valve. *Nature.* 406, 847-848.

520 Franklin, C.E., Seebacher, F., 2003. The effect of heat transfer mode on heart rate responses  
521 and hysteresis during heating and cooling in the estuarine crocodile *Crocodylus porosus*. *J.*  
522 *Exp. Biol.* 206, 1143-1151.

523 Galacatos, K., Barriga-Salazar, R., Stewart, D.J., 2004. Seasonal and habitat influences on  
524 fish communities within the lower Yasuni river basin of the Ecuadorian Amazon. *Environ.*  
525 *Biol. Fishes.* 71 (1), 33-51.

526 Grigg, G.C., Alchin, J., 1976. The role of the cardiovascular system in thermoregulation of  
527 *Crocodylus johnstoni*. *Physiol. Zool.* 49, 24– 36.

528 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software  
529 package for education and data analysis. *Palaeontol. Electron* 4: [http://palaeo-electronica.](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)  
530 [org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)

531 Hasgall, P.A., Di Gennaro, F., Baumgartner, C., Neufeld, E., Gosselin, M.C., Payne, D.,  
532 Klingenböck, A., Kuster, N., 2015. ITIS Database for thermal and electromagnetic parameters  
533 of biological tissues, Version 3.0, September 01st, [http://dx.doi.org/10.13099/VIP21000-03-](http://dx.doi.org/10.13099/VIP21000-03-0)  
534 [0](http://dx.doi.org/10.13099/VIP21000-03-0).

535 Irmis, R.B., Nesbitt, S.J., Sues, H.D., 2013. Early Crocodylomorpha. *Geo. Soc. Lon. Spec.*  
536 *Publ.* 379, 275–302.

537 Jackson, D.C., Andrade, D., Abe, A.S., 2003. Lactate sequestration by osteoderms of the  
538 broad-nose caiman, *Caiman latirostris*, following capture and forced submergence. *J. Exp.*  
539 *Biol.* 206, 3601–3606.

540 Jensen, B., Wang, T., Christoffels, V.M., Moorman, A.F.M., 2013. Evolution and  
541 development of the building plan of the vertebrate heart. *Acta Biochim. Biophys.* 1833, 783–  
542 794.

543 Jiji, L.M., 2009. *Heat Conduction*, third ed. Springer, New-York.

544 Johnson, C.R., 1974. Thermoregulation in crocodylians I. Head-body temperature control in  
545 the Papuan-New Guinean crocodiles, *Crocodylus novaeguineae* and *Crocodylus porosus*.  
546 *Comp. Physiol.* 49A, 3–28.

547 Johnson, C.R., Webb, G.J.W., Tanner, C., 1976. Thermoregulation in crocodylians II. A  
548 telemetric study of body temperature in the Australian crocodiles, *Crocodylus johnstoni* and  
549 *Crocodylus porosus*. *Comp. Physiol.* 53A, 143–146.

550 Legendre, L., Segalen, L., Cubo, J., 2013. Evidence for high bone growth rate in Euparkeria  
551 obtained using a new paleohistological inference model for the humerus. *J. Vertebr.*  
552 *Paleontol.* 33(6), 1343-1350.

553 Legendre, L., Guenard, G., Botha-Brink, J., Cubo, J., 2016. Palaeohistological evidence for  
554 ancestral high metabolic rate in archosaurs. *Syst. Biol.* 65, 989–996.

555 Martin, J.E., 2014. A sebecosuchian in a middle Eocene karst with comments on the dorsal  
556 shield in Crocodylomorpha. *Acta Palaeontol. Pol.* 60(3), 673-680.

557 Nesbitt, S.J., 2011. The early evolution of Archosaurs: Relationships and the origin of major  
558 clades. *Bull. Am. Mus. Nat. Hist.* 352, 1-292.

559 Owerkowicz, T., 2016. Heat transfer through skin with and without osteoderms in the  
560 American alligator. *FASEB J.* 30(1), 15.3.

561 Pavlov, I.P., 1927. *Conditional Reflexes: An Investigation of the Physiological Activity of the*  
562 *Cerebral Cortex*, Oxford Univ. Press, Oxford.

563 Porter, W.R., Witmer, L.M., 2015. Vascular patterns in iguanas and other squamates: blood  
564 vessels and sites of thermal exchange. PLoS ONE. 10 (10), e0139215.

565 Porter, W.R., Sedlmayr, J.C., Witmer, L.M., 2016. Vascular patterns in the heads of  
566 crocodylians: blood vessels and sites of thermal exchange. J. Anat. 229 (6), 800-824.

567 Ricqlès, Ade., Padian, K., Horner, J.R., 2003. On the bone histology of some Triassic  
568 pseudosuchian archosaurs and related taxa. Ann. Paleontol. 89, 67–101.

569 Ricqlès, Ade., Padian, K., Knoll, F., Horner, J.R., 2008. On the origin of high growth rates in  
570 archosaurs and their ancient relatives: Complementary histological studies on Triassic  
571 archosauriforms and the problem of a “phylogenetic signal” in bone histology. Ann.  
572 Paleontol. 94, 57–76.

573 Robertson, S.L., Smith, E.N., 1979. Thermal indications in the cutaneous blood flow in the  
574 American alligator. Comp. Biochem. Physiol. 62A, 569-572.

575 Sadava, D.E., Hillis, D.M., Heller, C.H., Berenbaum, M., 2009. Physiology, homeostasis, and  
576 temperature regulation, In: Gordon Orians, D.S., Heller, C. (Eds.), *Life: The Science of*  
577 *Biology 9<sup>th</sup> ed.* Sinauer Associates., Sunderland, pp. 832-851.

578 Scheyer, T.M., Desojo, J.B., 2011. Palaeohistology and external microanatomy of rauisuchian  
579 osteoderms (Archosauria: Pseudosuchia). Palaeontology. 54, 1289–1302.

580 Scheyer, T.M., Desojo, J.B., Cerda, I.A., 2014. Bone histology of phytosaur, aetosaur, and  
581 other archosauriform osteoderms (Eureptilia, Archosauromorpha). Anat. Rec. 297, 240–260.

582 Seebacher, F., 1999. Behavioural postures and the rate of body temperature change in wild  
583 freshwater crocodiles, *Crocodylus johnstoni*. Physiol. and Biochem. Zool. 72(1), 57–63.

584 Seebacher, F., Franklin, C.E., 2004. Integration of autonomic and local mechanisms in  
585 regulating cardiovascular responses to heating and cooling in a reptile (*Crocodylus porosus*).  
586 J. Comp. Physiol. B. 174, 577–585.

587 Seebacher, F., Franklin, C.E., 2007. Redistribution of blood within the body is important for  
588 thermoregulation in an ectothermic vertebrate (*Crocodylus porosus*). J. Comp. Physiol. B.  
589 177, 841–848.

590 Seidel, M.R., 1979. The osteoderms of the American Alligator and their functional  
591 significance. Herpetol. Leag. 35, 375–380.

592 Seymour, R.S., Bennett-Stamper, C.L., Johnston, S.D., Carrier, D.R., Grigg, G.C., 2004.  
593 Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. Physiol.  
594 Biochem. Zool. 77(6), 1051–1067.

595 Smith, E.N., 1979. Behavioral and physiological thermoregulation of crocodylians. Am. Zool.  
596 19, 239–247.

597 Speakman, J.R., Ward, S., 1998. Infrared thermography: principles and applications. Zoology.  
598 101, 224-232

599 Spotila, J.R., 1977. Mouth gaping as an effective thermoregulatory device in alligators.  
600 Nature. 265, 235-236.

601 Tattersall, G.J., Cadena, V., Skinner, M.C., 2006. Respiratory cooling and thermoregulatory  
602 coupling in reptiles. Resp. Physiol. Neurobiol. 154, 302-318.

603 Trutnau, L., Sommerlad, R., 2006. Crocodylians their Natural History and Captive Husbandry,  
604 ed. Chimaira, Franckfurt am Main.

605

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.

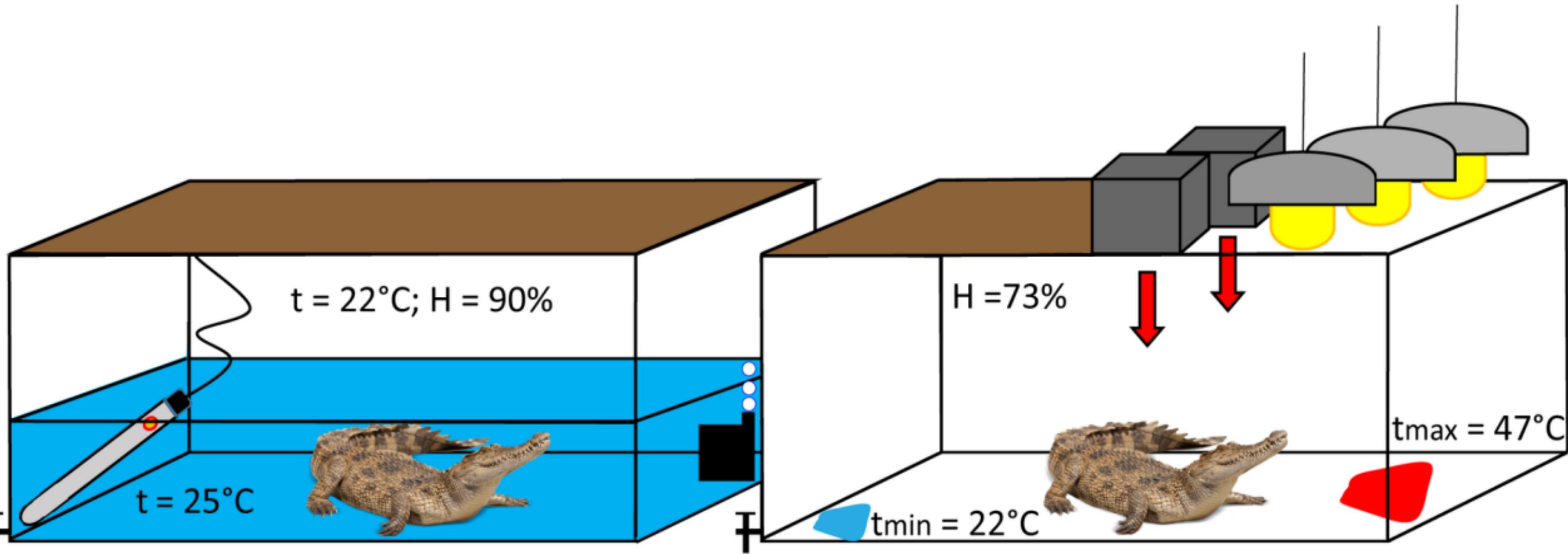
618 Figure 3: Boxplot of the recorded temperature on the fourteen regions of interest. Abbreviations: A-1:  
619 Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.

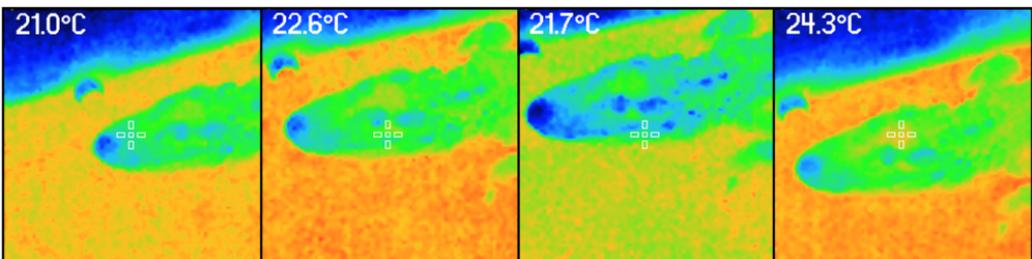
620 Figure 4A: Temperature variations above the diverse anatomical regions of interest in *Alligator*  
621 *sinensis*. Abbreviations: HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.  
622 Abbreviations: S.Table: Skull Table; ost: osteoderms; Nuchal non-oss.: non-ossified part 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.



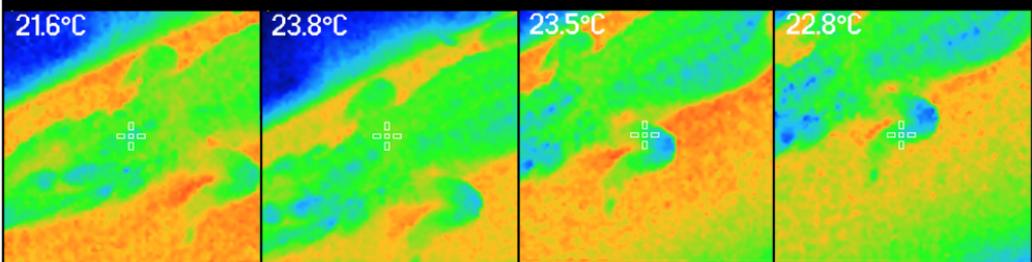


Snout

Jugal

Angular

Skull table

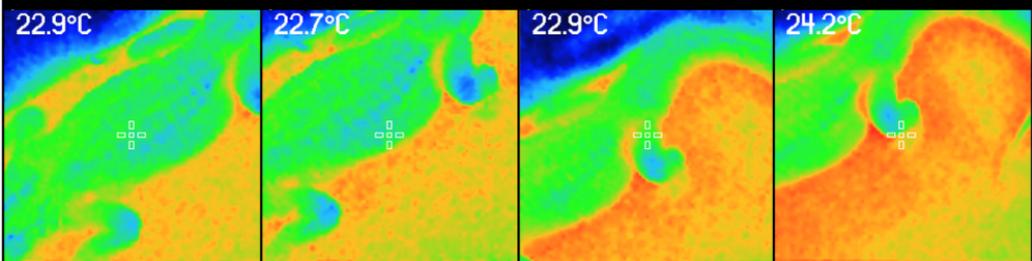


Nuchal ost.

Nuchal non-oss.

Arm

Forearm

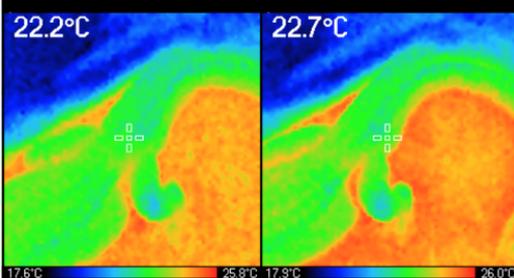


Dorsal ost.

Flank

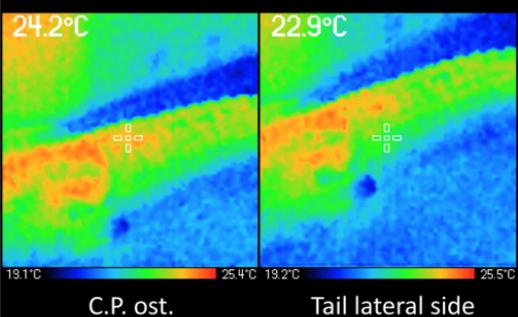
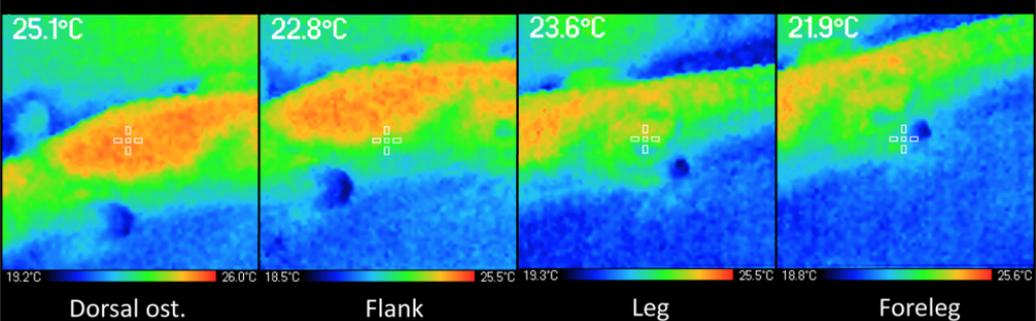
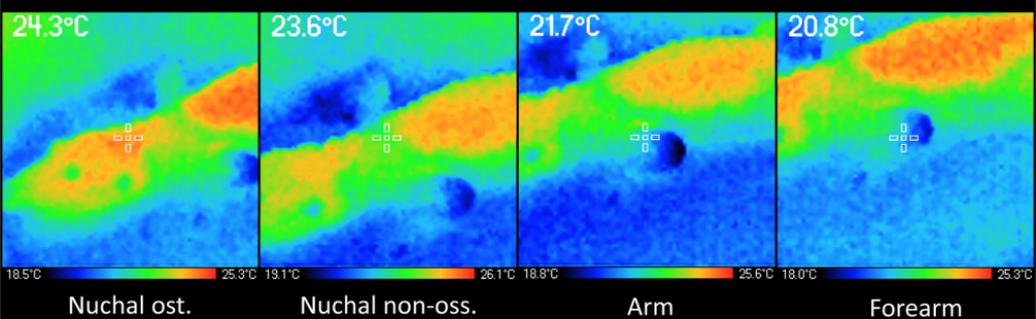
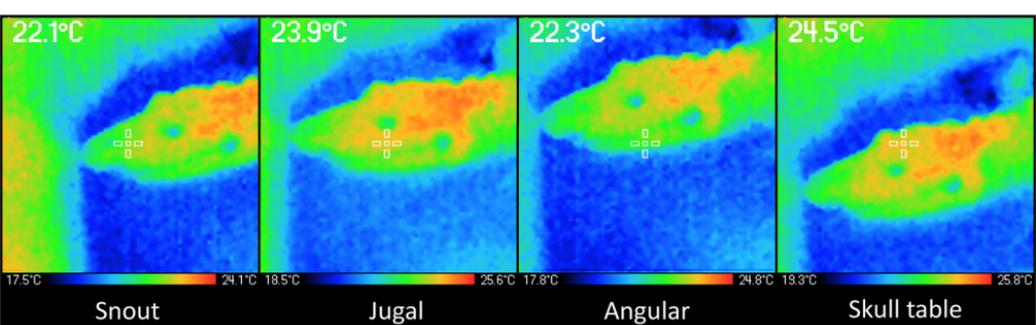
Leg

Foreleg

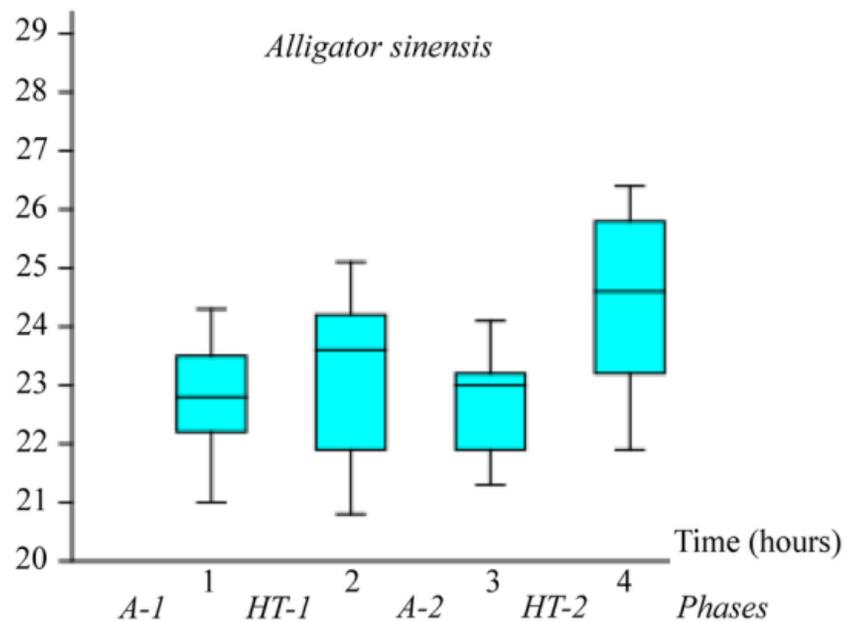


C.P. ost.

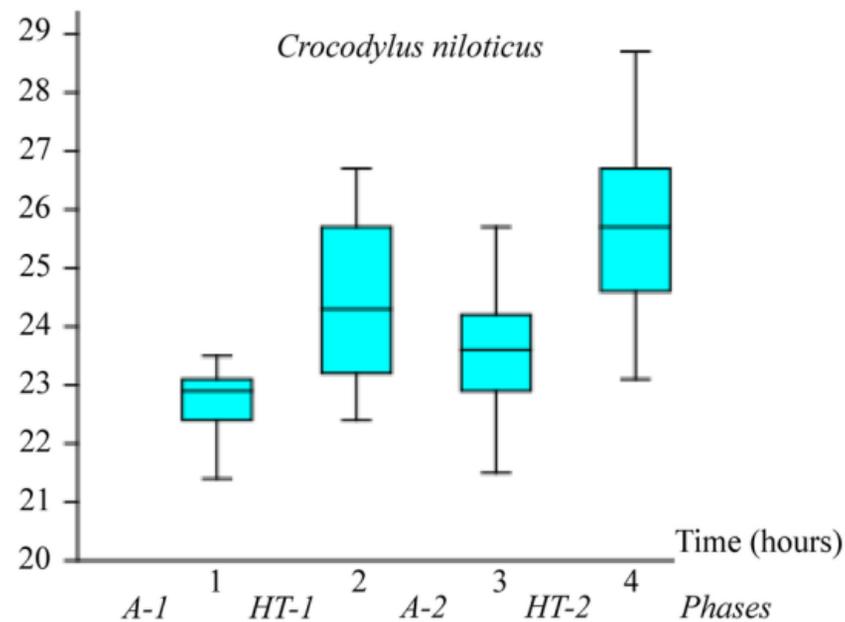
Tail lateral side



Skin temperature (°C)

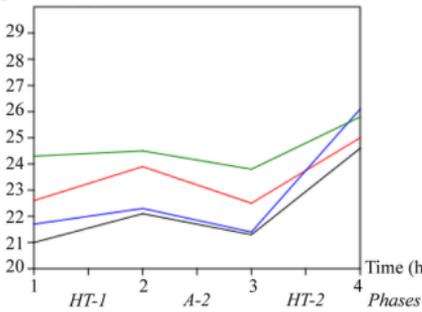


Skin temperature (°C)



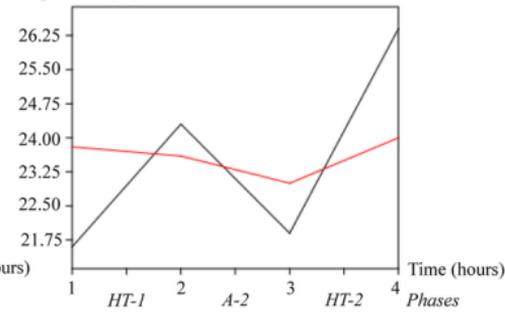
Temperature (°C)

— S.Table — Jugal  
— Snout — Angular



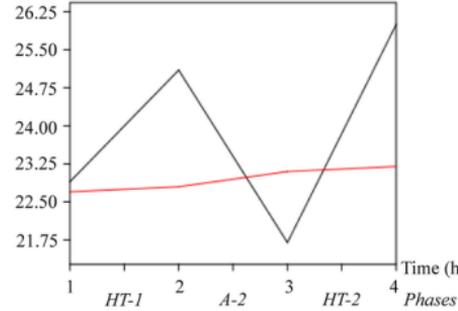
Temperature (°C)

— Nuchal ost.  
— Nuchal non-oss.



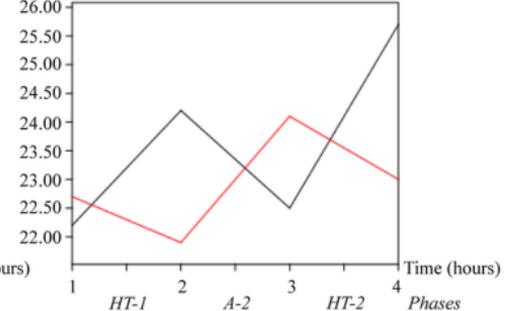
Temperature (°C)

— Dorsal ost.  
— Flank



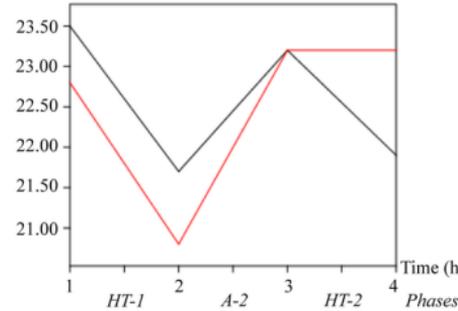
Temperature (°C)

— C.P. ost.  
— Tail lateral side



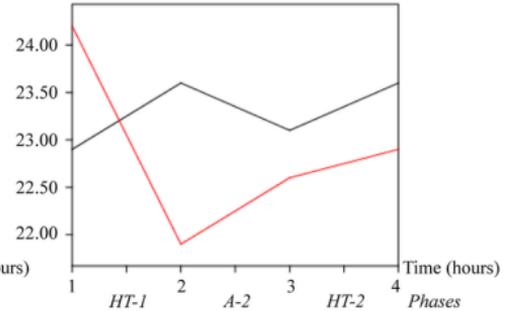
Temperature (°C)

— Arm  
— Forearm



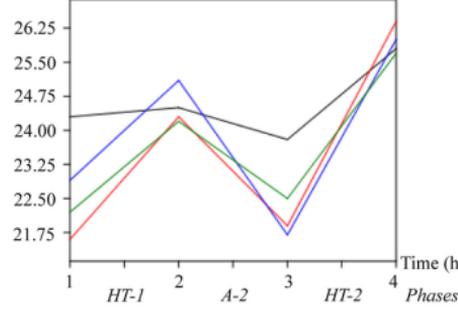
Temperature (°C)

— Leg  
— Foreleg



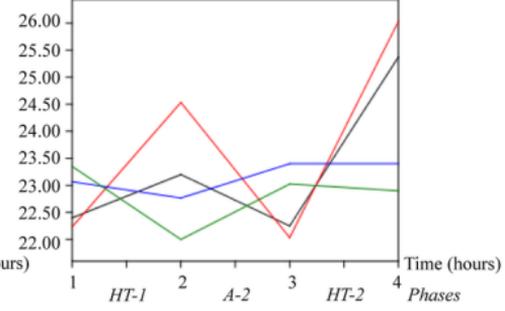
Temperature (°C)

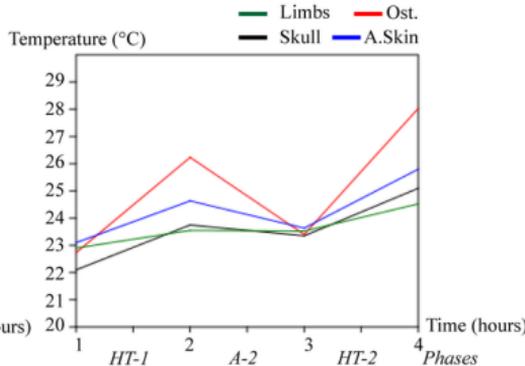
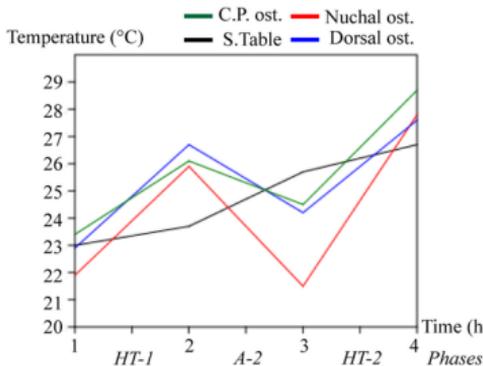
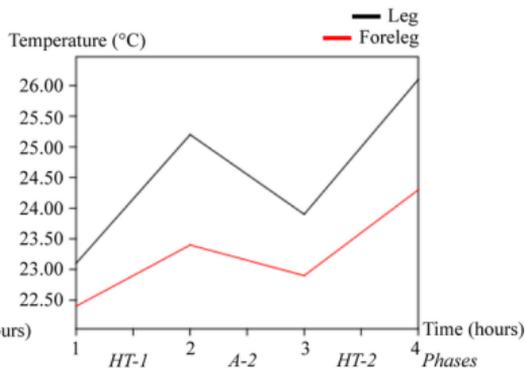
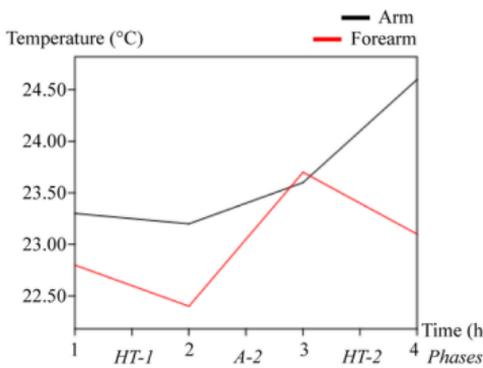
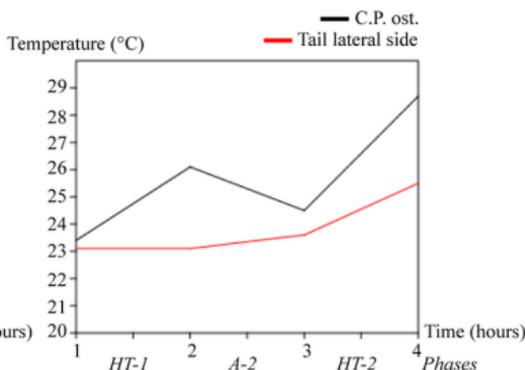
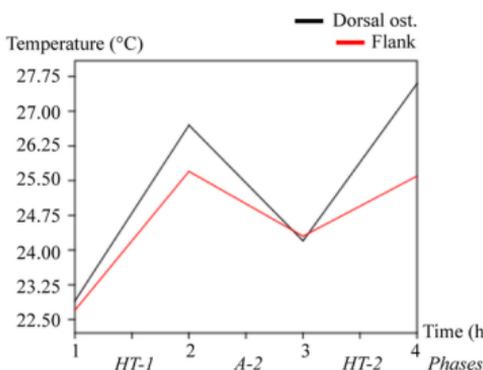
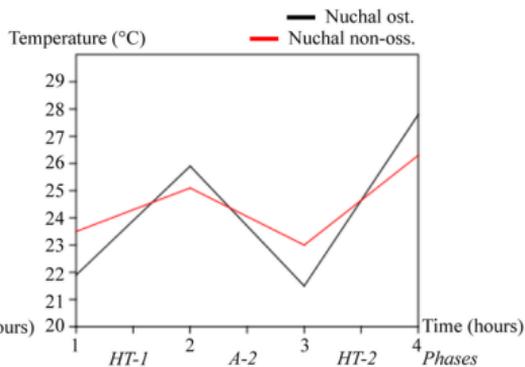
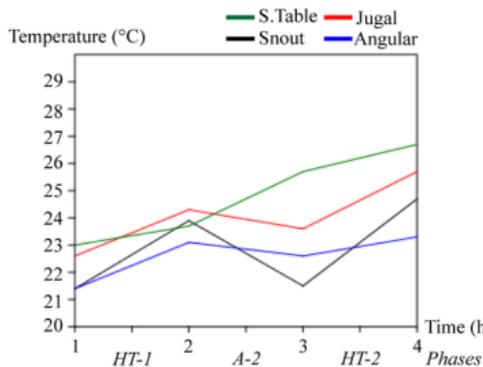
— C.P. ost. — Nuchal ost.  
— S.Table — Dorsal ost.

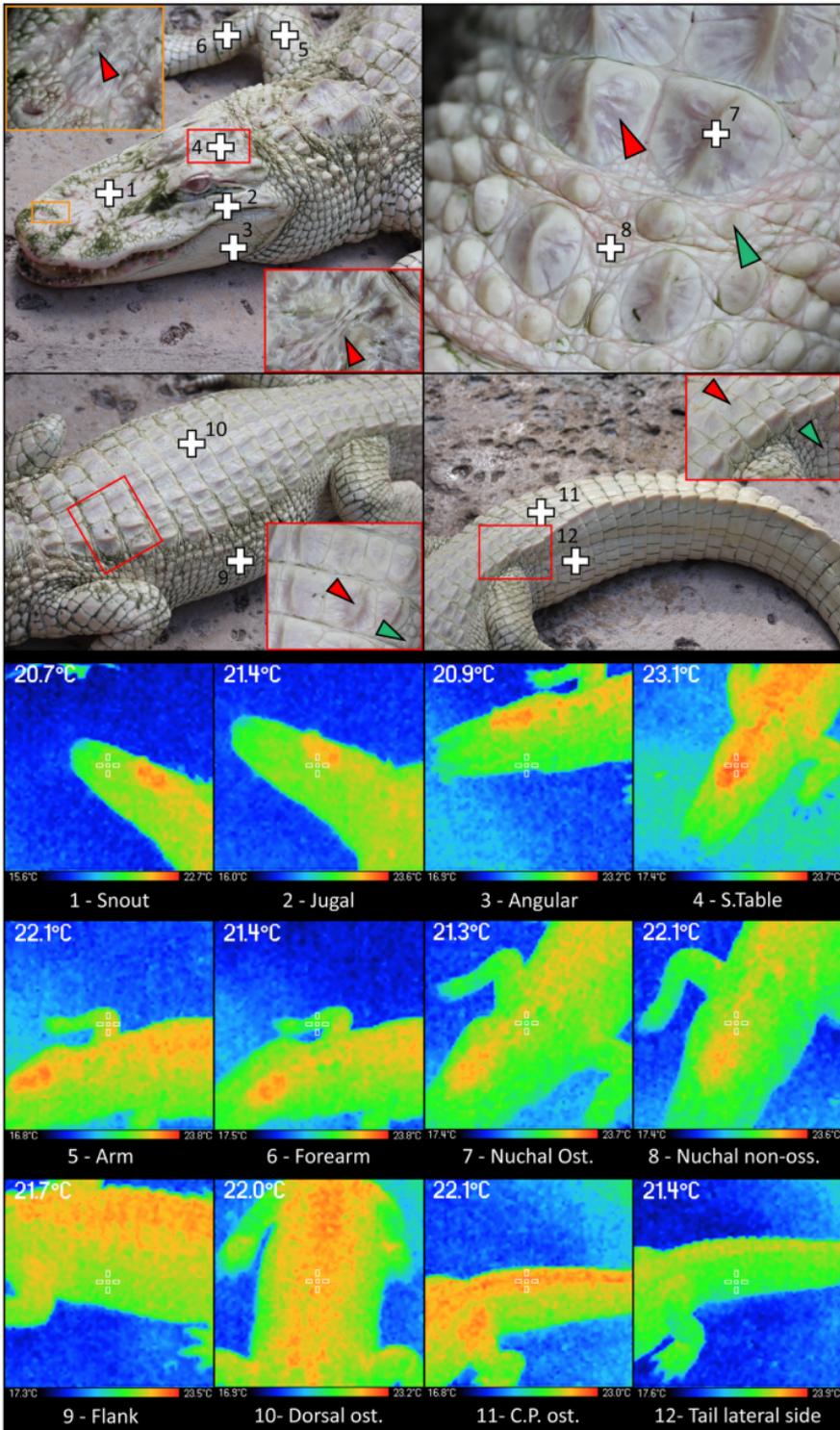


Temperature (°C)

— 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
<b>Anatomical regions</b>	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
<b>Statistical values</b>	Mean	22.8	23.1	22.7	24.4	22.7	24.4	23.5	25.7	21.7
	Median	22.8	23.2	22.8	24.3	22.9	24.3	23.6	25.7	21.5
	Std dev.	0.7	1.1	0.7	1.3	0.5	1.2	0.8	1.3	0.5
	Max	24.3	25.1	24.1	26.4	23.5	26.7	25.7	28.7	23.1
	Min	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	<b>0.01</b>
<i>C. niloticus</i>	<i>p-value</i>	<b>0.01</b>	<b>0.04</b>	<b>0.01</b>

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	<b>0.02</b>	<b>0.04</b>	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.