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1 **The crocodylian skull and osteoderms:**

2 **A functional exaptation to ectothermy?**

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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 poïkilothermic thermoregulation is probaly 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).

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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.

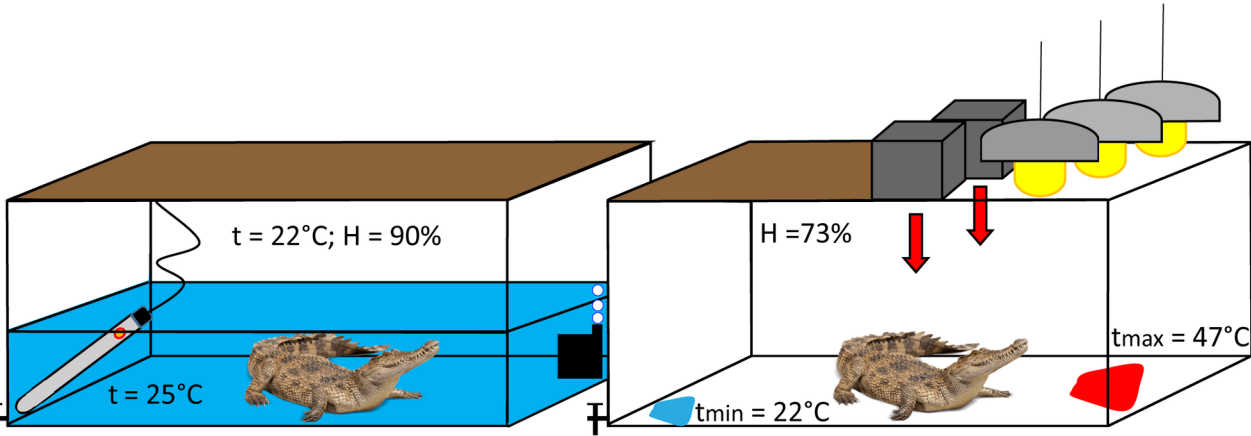
618 Figure 3: Boxplot of the recorded temperature on the fourteen regions of interest. Abbreviations: A-1:
619 Aquatic-1; HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.

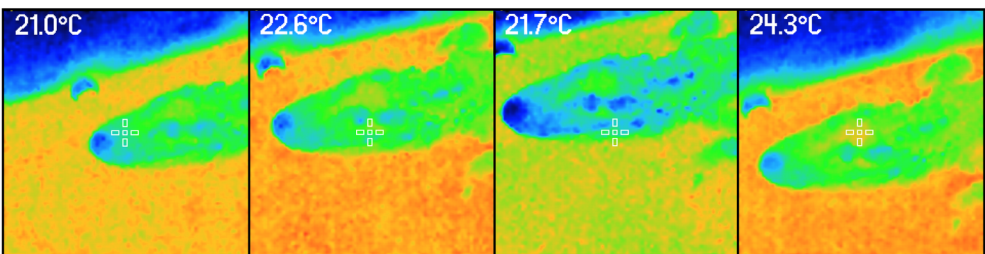
620 Figure 4A: Temperature variations above the diverse anatomical regions of interest in *Alligator*
621 *sinensis*. Abbreviations: HT-1: Heating-Terrestrial-1; A-2: Aquatic-2; HT-2: Heating-Terrestrial-2.
622 Abbreviations: S.Table: Skull Table; ost: osteoderms; Nuchal non-oss.: non-ossified part of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



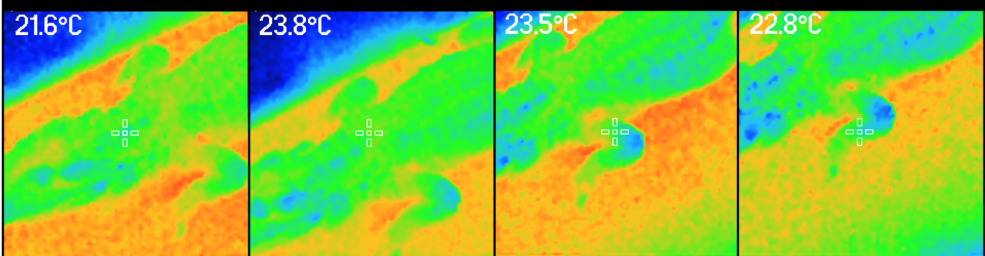


Snout

Jugal

Angular

Skull table

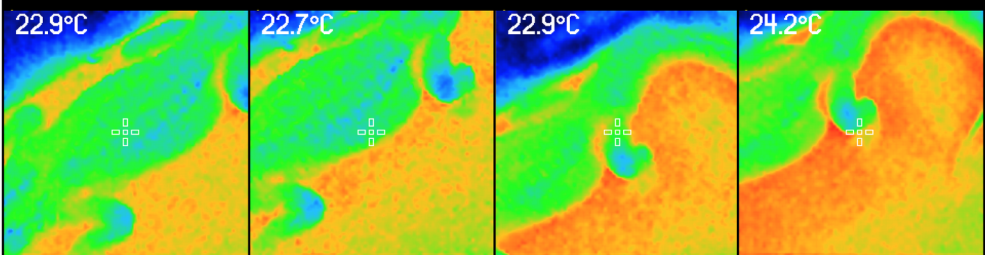


Nuchal ost.

Nuchal non-oss.

Arm

Forearm

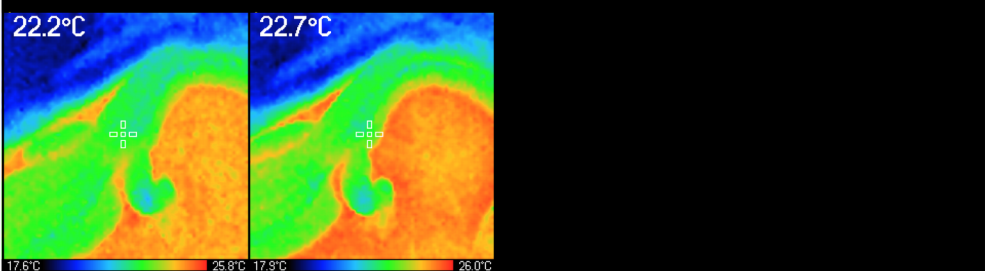


Dorsal ost.

Flank

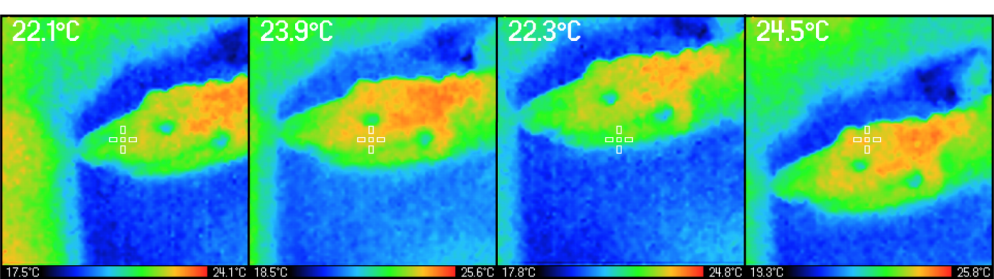
Leg

Foreleg



C.P. ost.

Tail lateral side

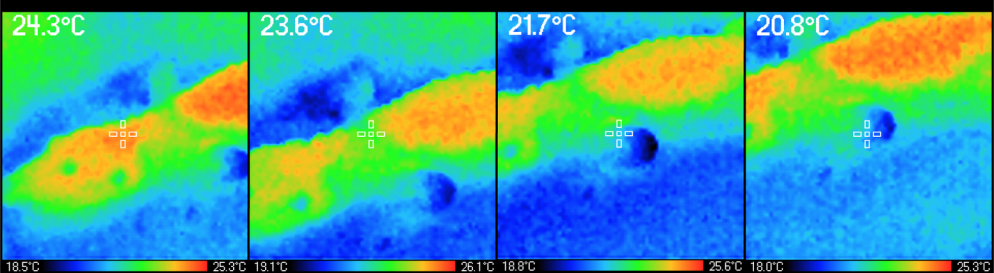


Snout

Jugal

Angular

Skull table

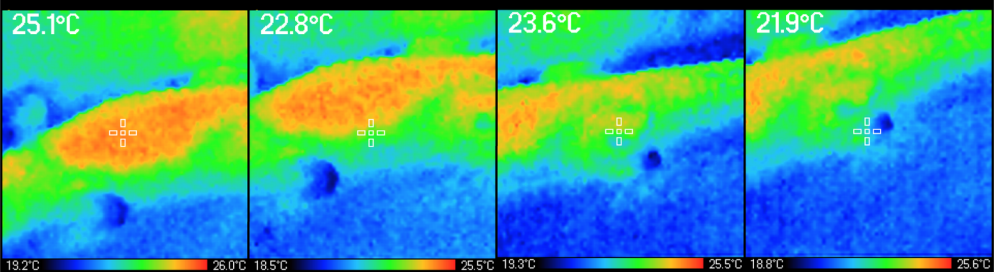


Nuchal ost.

Nuchal non-oss.

Arm

Forearm

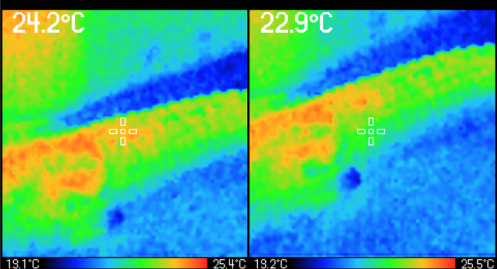


Dorsal ost.

Flank

Leg

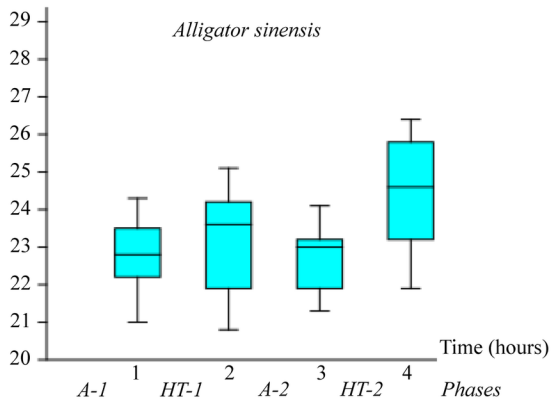
Foreleg



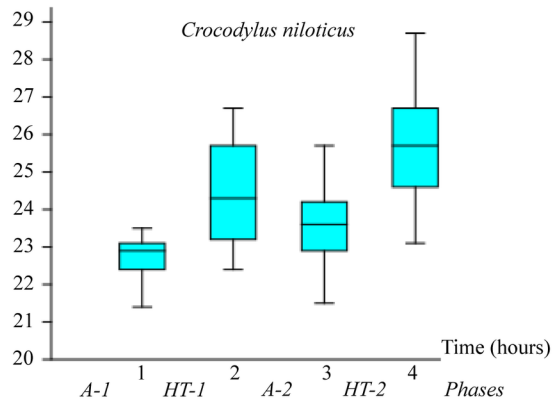
C.P. ost.

Tail lateral side

Skin temperature (°C)

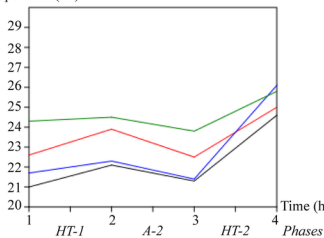


Skin temperature (°C)



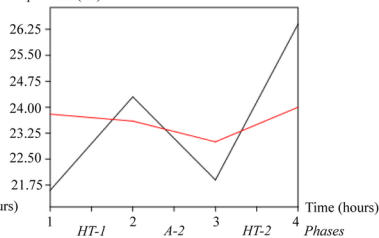
Temperature (°C)

— S.Table — Jugal
— Snout — Angular



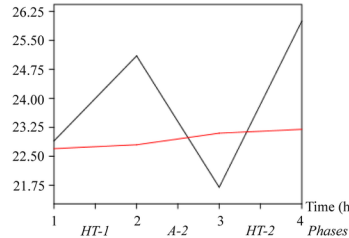
Temperature (°C)

— Nuchal ost.
— Nuchal non-oss.



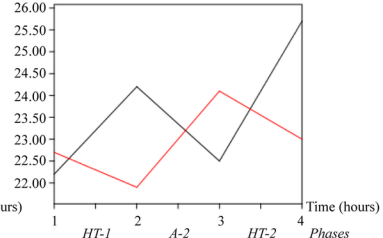
Temperature (°C)

— Dorsal ost.
— Flank



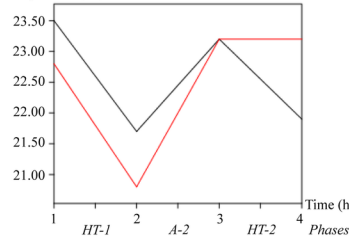
Temperature (°C)

— C.P. ost.
— Tail lateral side



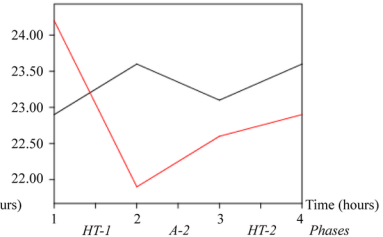
Temperature (°C)

— Arm
— Forearm



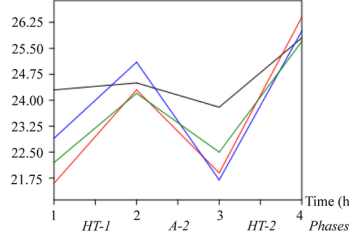
Temperature (°C)

— Leg
— Foreleg



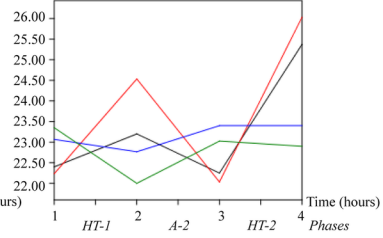
Temperature (°C)

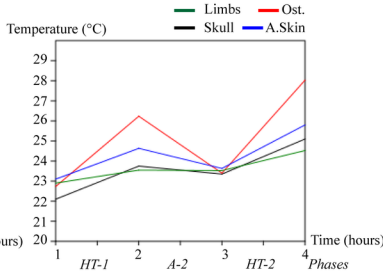
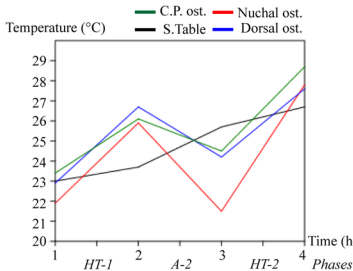
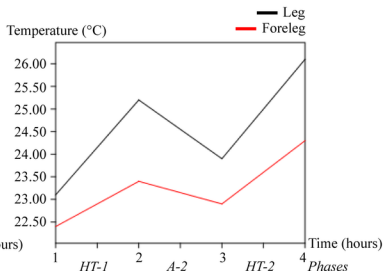
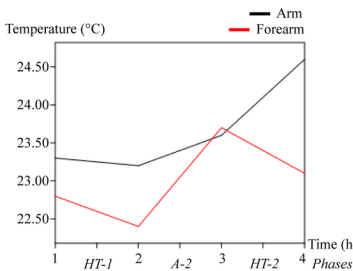
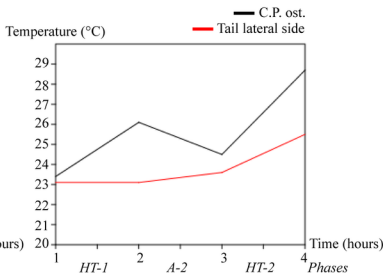
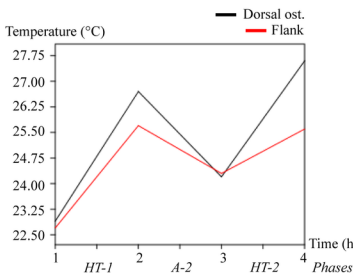
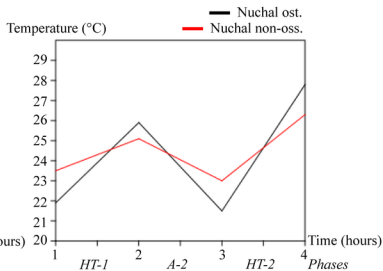
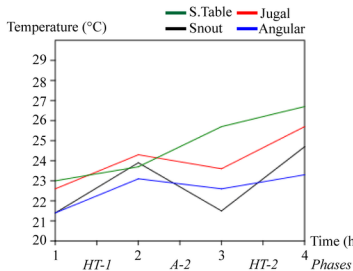
— C.P. ost. — Nuchal ost.
— S.Table — Dorsal ost.

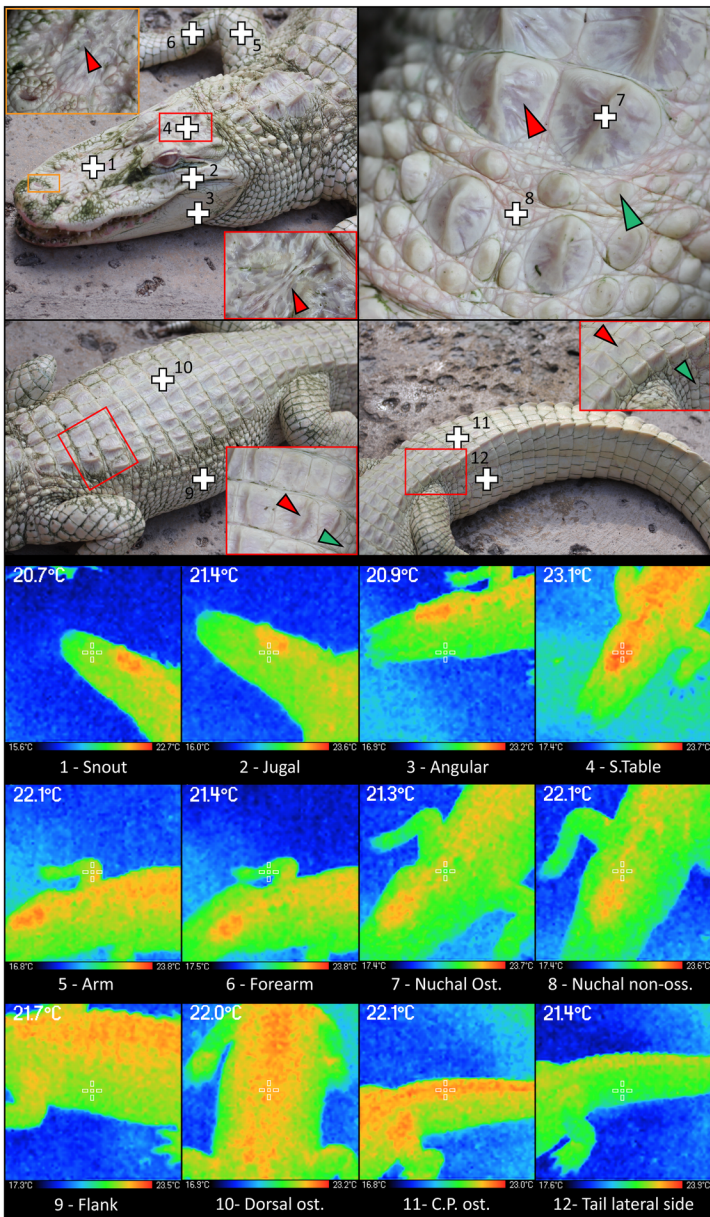


Temperature (°C)

— 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
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.