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Implications for the evolution of thermometabolism in
Archosauromorpha**

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1 Bone histology of *Azendohsaurus laaroussii*. Implications for the evolution of
2 thermometabolism in Archosauromorpha

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19 *Abstract.*- This paper is aimed at constraining the phylogenetic frame of the acquisition of
20 endothermy by Archosauromorpha. We analyzed the bone histology of *Azendohsaurus*
21 *laaroussii*. Stylopodial and zeugopodial bones show three tissue types: (a) avascular lamellar
22 zonal bone formed at low growth rates; (b) a scaffold of parallel fibered bone containing
23 either small primary osteons or simple vascular canals; and (c) fibrolamellar bone formed at
24 high growth rates. We used quantitative histology to infer the thermometabolic regime
25 (endothermy *versus* ectothermy) of this taxon. We define endothermy as the presence of any
26 mechanism of non-shivering thermogenesis that increases both body temperature and resting
27 metabolic rate. Thus, estimating the resting metabolic rate of an extinct organism may be a
28 good proxy to infer its thermometabolic regime (endothermy *versus* ectothermy). High resting
29 metabolic rates have been shown to be primitive for the clade *Prolacerta* – Archosauriformes.
30 Therefore, we inferred the resting metabolic rates of *Azendohsaurus laaroussii*, a sister group
31 of this clade, and of 14 extinct related taxa, using Phylogenetic Eigenvector Maps. All the
32 inferences obtained are included in the range of variation of resting metabolic rates measured
33 in mammals and birds, so we can reasonably assume that all these taxa (including
34 *Azendohsaurus*) were endotherms. A parsimony optimization of the presence of endothermy
35 on a phylogenetic tree of tetrapods shows that this derived character state was acquired by the
36 last common ancestor of the clade *Azendohsaurus* – Archosauriformes, and that there is a
37 reversion in Crocodylia.
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Introduction

The bone histology of non-archosaurian archosauromorphs has received great attention in the last decade (Ricqlès et al. 2008; Nesbitt et al. 2009; Botha-Brink and Smith 2011; Werning and Irmis 2011; Legendre et al. 2013, 2016; Ezcurra et al. 2014; Mukherjee 2015; Veiga et al. 2015; Werning and Nesbitt 2016; Jaquier and Scheyer 2017). Ricqlès et al. (2008) suggested that the capacity of reaching and maintaining very high bone growth rates is an apomorphic feature of archosauriforms. Botha-Brink and Smith (2011) showed that this capacity may have been acquired in a more inclusive node, by the last common ancestor of the clade *Prolacerta* - archosauriforms, with a reversion in *Vancleavea* (see also Nesbitt et al. 2009). Padian and Horner (2002) hypothesized that “The types of tissue deposited in the bones of extinct animals are the most direct evidence of basal metabolic rates, because they directly reflect growth rates [...]. The sustained deposition of fast-growing bone tissues, as displayed by mammals, birds and other dinosaurs, must reflect sustained high basal metabolic rates». Montes et al. (2007) provided evidence for this hypothesis by showing that the variation of bone growth rates explains significantly the variation of resting metabolic rates in a sample of extant amniotes. They argued that this is because the high rates of protein synthesis and degradation involved in the periosteal osteogenesis and endosteal osteolysis are energy consuming (Montes et al. 2007). Consistently, Legendre et al. (2016) inferred resting metabolic rates of a sample of Archosauromorpha using quantitative bone histology and Phylogenetic Eigenvector Maps. Interestingly, they inferred a resting metabolic rate of *Prolacerta* included in the range of variation of extant mammals (Legendre et al. 2016). Resting metabolic rate depends on bone growth rate (see above), but it depends also on the presence of thermogenetic mechanisms. We define endothermy as the presence of any mechanism of non-shivering thermogenesis (e.g., Lowell and Spiegelman 2000; Rowland et

64 al. 2015; Nowack et al. 2017) that increases both body temperature and resting metabolic rate.
65 Thus, the resting metabolic rate of an extinct organism may be a good proxy to infer its
66 thermometabolic regime (endothermy *versus* ectothermy). Using this proxy, the results
67 obtained by Legendre et al. (2016) suggest that endothermy may have been acquired by the
68 last common ancestor of the clade *Prolacerta* - archosauriforms. The next step to better
69 constrain the phylogenetic frame of the acquisition of endothermy by Archosauromorpha
70 involves inferring the resting metabolic rate of Allokotosauria, the sister-group of the clade
71 *Prolacerta* – archosauriforms (Nesbitt et al. 2015; see also Ezcurra 2016). Therefore, we
72 analyzed the bone histology and inferred the resting metabolic rates of *Azendohsaurus*
73 *laaroussii* (Archosauromorpha, Allokotosauria; Nesbitt et al. 2015; Ezcurra 2016) using
74 Phylogenetic Eigenvector Maps.

75

76 **Material and methods**

77

78 *Material.*- We analyzed histologically skeletal remains from the non-archosauriform
79 archosauromorph *Azendohsaurus laaroussii* from the Upper Triassic (Carnian) of the Argana
80 Basin (Morocco) deposited at the Paris Muséum National d'Histoire Naturelle (MNHN).
81 *Azendohsaurus laaroussii* Dutuit, 1972 was originally described on the basis of a dental
82 fragment and two isolated teeth specialized for plants feeding (Dutuit, 1972). On the basis on
83 comparison with Ornithischian dinosaurs such as *Fabrosaurus* and *Scelidosaurus* it was
84 attributed to a new ornithischian dinosaur, becoming one of the earliest dinosaurs (Dutuit
85 1972; Thulborn, 1973, 1974; Bonaparte, 1976; Galton, 1985, 1990; Weishampel, 1990;
86 Gauffre, 1993; Hunt and Lucas, 1994; Flynn et al. 1999). In addition to the craniodental
87 remains, hundreds of disarticulated and monospecific post-cranial remains have been
88 recovered from the *locus typicus* of *Azendohsaurus laaroussii* (Dutuit, 1976). The analysis of

89 these specimens argues strongly against a phylogenetic position inside Dinosauria (Jalil and
90 Knoll, 2002). Flynn et al. (2010) named the new species *Azendohsaurus madagaskarensis*
91 from the Triassic of Madagascar and provided for the first time a comprehensive description
92 of the cranial anatomy of the genus. More recently, Nesbitt et al. (2015) provided a scrutiny
93 description the postcranial anatomy of *Azendohsaurus madagaskarensis* which is now one of
94 the best-known early archosauromorphs.

95 All the available post-cranial material in the MNHN collection attributed to
96 *Azendohsaurus laaroussii* is monotypic (Khaldoun, 2014). It was collected from the *locus*
97 *typicus* of *Azendohsaurus laaroussii* during the same initial field season (Dutuit, 1976), and
98 strongly resembles to the post-cranial skeleton of *Azendohsaurus madagaskarensis* (Fig. 1).
99 They can be confidently attributed to *A. laaroussii*. Among the diagnostic post-cranial
100 characters of the Malagasy form, only two can be checked on the available material of *A.*
101 *laaroussii* and both are present: a posteriorly expanded T-shaped interclavicle and
102 hyosphene-hypantra intervertebral articulations in anterior trunk vertebrae. This later
103 character-state was considered autapomorphic for *A. madagaskarensis* by Nesbitt et al. (2015)
104 but it may be a synapomorphy for the genus *Azendohsaurus*. The proportions of the studied
105 skeletal elements MNHN.F.ALM 435 (right humerus), MNHN.F.ALM 497 (left femur), and
106 MNHN.F.ALM 369 (right tibia), show that they are from different specimens.

107
108 *Histological methods.*- Skeletal elements were molded and cast prior to sectioning to
109 preserve morphological information. Casts and bone remains after histological sampling were
110 repositied at the Paleontology collection of the Paris Muséum National d’Histoire Naturelle
111 where they are available upon request to the curator. Mid-diaphyses were embedded in epoxy
112 resin and processed histologically following standard procedures (Lamm 2013). Transverse
113 sections as well as longitudinal sections (at the anterior, posterior, dorsal and ventral sides for

114 humerus and femur, and anterior, posterior, medial and lateral sides for the tibia) were
115 obtained and mounted on glass slides. They were analyzed and photographed in a Nikon
116 Eclipse E600POL microscope using normal light and cross-polarized light with lambda
117 compensator. Thin sections were repositated at the vertebrate hard tissues histological
118 collection of the Paris MNHN, where they are available upon request to the curator (thin
119 sections MNHN-F-HISTOS 2348 to 2362).

120

121 *Qualitative histology.*- The nomenclature and classification of bone tissues is based on
122 bone organization at different integration levels (Francillon-Vieillot et al. 1990). At the level
123 of bone matrix organization, three character states have been defined based on the
124 organization of collagen fibers: the presence (or absence) of woven-fibered bone matrix
125 (WB), of parallel-fibered bone matrix (PFB) and of lamellar bone matrix (LB). At the level of
126 organization of bone as a tissue, two character states have been defined based on the
127 organization of the collagen fibers, the vascular density, and the cyclicity of bone apposition:
128 the presence of lamellar-zonal bone (LZB) and the presence of the fibro-lamellar bone
129 (FLB). See Francillon-Vieillot et al. (1990) for a detailed description of these character states.
130 This pattern-oriented approach has been recently expanded towards a process-oriented view
131 based on the developmental origin of the components of bone tissue (Prondvai et al. 2014). In
132 process-oriented paleohistology, the developmental mechanisms involved in the formation of
133 bone tissue are inferred from the fine architecture of bone matrix. PFB and LB are formed by
134 the process of dynamic osteogenesis whereas WB is formed by the process of static
135 ossification (Ferretti et al. 2002; Palumbo et al. 2004; Marotti 2010; Prondvai et al. 2014;
136 Stein and Prondvai 2014; Cubo et al. 2017). Cortices can also have a composite nature
137 including (1) a scaffold of WB formed by the process of static osteogenesis and (2) centripetal
138 layers infilling primary osteons made of PFB or LB formed by the process of dynamic

139 osteogenesis. This last tissue type has been named woven-parallel complex by Prondvai et al.
140 (2014). In the context of process-oriented paleohistology, the widely used term of FLB is a
141 special case of woven-parallel complex in which there is abundant woven bone and dense
142 vascularity in the form of primary osteons (Prondvai et al. 2014).

143

144 *Quantitative histology.*- We quantified the vascular density (number of vascular canals
145 by square millimeter) in four orthogonal transects of the transverse sections of humerus,
146 femur and tibia of *Azendohsaurus laaroussii*. We used the dataset published by Legendre et
147 al. (2016) for comparative purposes. It contains the resting metabolic rates and the vascular
148 densities of humerus, femur and tibia of a sample of 13 extant species and 14 extinct species
149 of tetrapods. Data for *Mus musculus* were removed because this species was an outlier.

150

151 *Phylogenetic comparative methods.*- We tested whether vascular density explains a
152 significant fraction of the variation of resting metabolic rate using Phylogenetic Generalized
153 Least Squared regressions (PGLS, Grafen 1989), with the ‘caper’ package (Orme et al. 2013)
154 in R (R Core Team 2016). For this we used the dataset and the phylogeny published by
155 Legendre et al. (2016).

156 Moreover, we inferred the resting metabolic rates of *Azendohsaurus laaroussii* and
157 those for 14 species of extinct tetrapods using phylogenetic eigenvector maps (Guenard et al.
158 2013) with the package MPSEM package (Guenard et al. 2013) in R (R Core Team 2016).
159 For this we used our data from *Azendohsaurus laaroussii* and the dataset and the phylogeny
160 published by Legendre et al. (2016).

161 Finally, we performed an optimization of the presence of fibrolamellar bone (using our
162 data for *Azendohsaurus laaroussii* and published data for other Archosauromorpha) and an
163 optimization of the presence of endothermy (using observed resting metabolic rates for extant

164 species and inferred resting metabolic rates for extinct ones as a proxy for the
165 thermometabolic regime) onto phylogenies of Archosauromorpha and Tetrapoda respectively
166 using parsimony in Mesquite (Maddison and Maddison 2015).

167

168 **Results**

169

170 *Bone histology of Azendohsaurus laaroussii.*- Supplementary Fig. 1 shows composite
171 images of the entire diaphyseal cross sections of humerus, femur and tibia. The medial region
172 of the transverse section of the tibia is avascular (Fig. 2A). The bone matrix appears red
173 (isotropic) under cross-polarized light with lambda compensator (Fig. 2B) and black in cross-
174 polarized light without lambda compensator (not shown). This can be interpreted either as
175 woven bone or as parallel-fibered bone with fibers perpendicular to the transverse plane of
176 section (Stein and Prondvai 2014). The longitudinal section of the same (medial) region is
177 also avascular (Fig. 2C). In the longitudinal section, the bone matrix appears anisotropic (blue
178 in the picture but it can be yellow depending on the orientation to the polarizers) under cross-
179 polarized light with lambda compensator (Fig. 2D). These complementary patterns of
180 interference suggest that the cortex is composed of parallel-fibered bone, with collagen fibers
181 running parallel to the longitudinal axis of the tibia. Osteocyte lacunae have a rounded aspect
182 in the transverse section (Fig. 2A, B) and an elongate spindle shape in the longitudinal section
183 (Fig. 2C, D). Their main axis is, thus, aligned with the collagen fibers of the surrounding
184 matrix, whereas the canaliculi are perpendicular (Fig. 2C, D). We can observe erosion cavities
185 lined by a coating of endosteal lamellar tissue around the medullary cavity (Fig. 2A, B).

186 The posterior region of the transverse section of the tibia is well vascularized (Fig.
187 2E). Vascular density is higher in the deep cortex than in the outer cortex. Vascular canals are
188 longitudinal: they are rounded in transverse section (Fig. 2E, F) and elongated (with the main

189 axis parallel to the main axis of the tibia) in the longitudinal section (Fig. 2G, H). The scarce
190 vascular canals of the outer cortex are simple primary canals, whereas those of the deep
191 cortex form small primary osteons (Fig. 2F). An avascular outer circumferential layer is
192 absent. The bone matrix is isotropic (it appears red) under cross-polarized light with lambda
193 compensator in the transverse section (Fig. 2F) and anisotropic (blue) in the longitudinal
194 section (Fig. 2H). This pattern suggests that bone matrix in the posterior region of the tibia is
195 composed of parallel-fibered bone, with collagen fibers running parallel to the longitudinal
196 axis of the tibia. Osteocyte lacunae have a rounded aspect in the transverse section (Fig. 2E,
197 F) and an elongate spindle shape in the longitudinal section (Fig. 2G, H). The anterior and the
198 lateral regions of the tibia are similar to the posterior region in all respects but one: the lateral
199 region contains a line of arrested growth split into two lines.

200 The stylopodial bones (femur and humerus) show a well developed vascularization in
201 the deep cortex mainly formed by vascular canals parallel to the bone periphery (circular
202 canals) connected through abundant radial anastomoses (Fig. 3A-D). This pattern of vascular
203 orientation is more regular in the femur (Fig. 3A, B) than in the humerus (Fig. 3C, D) but
204 vascular density decreases from the inner to the outer cortex in both cases. The bone matrix is
205 made of either a scaffold of woven bone containing primary osteons (fibro-lamellar bone;
206 e.g., Fig. 3E, F) or a scaffold of parallel fibered bone containing both simple vascular canals
207 and primary osteons (e.g. Fig. 3G, H). We can observe the anisotropic (blue in the picture)
208 aspect of the scaffold of bone matrix in a longitudinal section of the humerus under polarized
209 light suggesting that it is made of parallel fibered bone with collagen fibers oriented parallel
210 to the main axis of the bone (Fig. 3H). Please note that the matrix around vascular canals
211 appears isotropic (red) in this longitudinal section (Fig. 3H) whereas it appears anisotropic
212 (blue in the picture) in the transverse section (Fig. 3G), suggesting that it is made of parallel
213 fibered bone forming primary osteons with collagen fibers perpendicular to the main axis of

214 the humerus. Avascular outer circumferential layers or lines of arrested growth are absent in
215 both femur and humerus (Fig. 3A-D).

216 In summary, vascular canals are more abundant in the deep cortex than in the outer
217 cortex in all three bones suggesting an ontogenetic decrease of bone growth rates (e.g., Fig.
218 2E). Considering that the avascular outer circumferential layer of parallel fibered bone is
219 absent (we observed vascular canals near the bone periphery in many regions, e.g., Fig. 2E),
220 and that lines of arrested growth are absent in all analyzed regions but one (the lateral region
221 of the tibia), we conclude that the analyzed specimens were subadults. The two lines of
222 arrested growth observed in the lateral region of the tibia probably correspond to the split of a
223 single line formed during bone cortical drift because they are absent in the anterior, posterior
224 and medial sides of the same section.

225

226 *Inferring the resting metabolic rate of Azendohsaurus laaroussii.*- First we tested
227 whether vascular density explains a significant fraction of the variation of resting metabolic
228 rate using the sample of extant tetrapods published by Legendre et al. (2016). For this we used
229 Phylogenetic Generalized Least Squared regressions (Grafen 1989). In all three cases
230 (humerus, femur and tibia), vascular density explained highly significant portions of the
231 variation of resting metabolic rate (85%, 73.3% and 78.9% respectively). Thus *a priori* we
232 can infer the resting metabolic rate of *Azendohsaurus laaroussii* confidently using the
233 vascular density values measured in the humerus, the femur and the tibia (65.56; 34.83 and
234 47.19 vascular canals by squared millimeter respectively) and the comparative data published
235 by Legendre et al. (2016).

236 Phylogenetic Eigenvector Maps (Guenard et al. 2013) includes an AIC procedure to
237 select the explanatory variables (here vascular density and/or the phylogeny) to be used to
238 infer the response variable (here the resting metabolic rate) of extinct taxa (here

239 *Azendohsaurus laaroussii* and the sample of extinct Archosauromorpha published by
240 Legendre et al. 2016). According to the AIC procedure, the variable that maximizes the R
241 squared and minimizes the AIC value should be selected. In the case of the humerus we
242 obtained the same R squared when using vascular density and the phylogeny and when using
243 only the phylogeny, but the AIC value was lower when using both vascular density and the
244 phylogeny (Fig. 4). We inferred a resting metabolic rate of $3.11 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ and a
245 confidence interval of $2.87 - 3.36 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ for *Azendohsaurus laaroussii* using the
246 phylogeny and vascular density of the humerus (Fig. 4). In the case of the femur we found a
247 slightly higher R squared and a lower AIC value when using the phylogeny only (Fig. 5). We
248 inferred a resting metabolic rate of $2.20 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ and a confidence interval of $1.55 -$
249 $2.85 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ for *Azendohsaurus laaroussii* using only the phylogeny (this is
250 equivalent to an optimization; Fig. 5). Finally, in the case of the tibia we obtained again the
251 same R squared when using vascular density and the phylogeny and when using only the
252 phylogeny, but the AIC value was lower when using both vascular density and the phylogeny
253 (Fig. 6). We inferred a resting metabolic rate of $2.53 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ and a confidence interval
254 of $2.25 - 2.82 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-0.67}$ for *Azendohsaurus laaroussii* using the phylogeny and the
255 vascular density of the tibia (Fig. 6).

256

257 **Discussion**

258

259 *Evolution of fibrolamellar bone in Archosauromorpha.*- The formation of
260 fibrolamellar bone is very energy consuming because it involves the combined action of static
261 osteogenesis (to form a scaffold of woven bone at high growth rates involving high rates of
262 protein synthesis) and dynamic osteogenesis (osteonal infilling with lamellar or non-lamellar
263 parallel fibered bone) (Prondvai et al. 2014). Therefore the capacity of reaching and

264 maintaining very high bone growth rates during ontogeny, recorded by the presence of
265 fibrolamellar bone in the bone cortex, may be a reliable proxy to infer the metabolic rate of
266 extinct animals (see the introduction). Four previous studies have analyzed the evolution of
267 the presence of fibrolamellar bone in Archosauromorpha in a phylogenetic context (Botha-
268 Brink and Smith 2011; Mukherjee 2015; Veiga et al. 2015; Jaquier and Scheyer 2017). Here
269 we performed parsimony optimizations of this character state (Fig. 7 and Supplementary Figs.
270 2 and 3) using our observations on the bone histology of *Azendohsaurus laaroussii*, and the
271 observations on other Archosauromorpha published previously (summarized in Table 1).

272 We observed three bone tissue types in the humerus, femur and tibia of
273 *Azendohsaurus laaroussii*: (i) avascular lamellar zonal bone (e.g., Fig. 2A-D); (ii) a cortex
274 formed by a scaffold of parallel fibered bone (with collagen fibers parallel to the longitudinal
275 axis of the bone) containing either small primary osteons infilled by lamellar parallel fibered
276 bone (inner part of the cortex, Fig. 2F) or simple vascular canals (outer part of the cortex, Fig.
277 2F) and (iii) fibrolamellar bone (e.g., Fig. 3E-F). Therefore we coded presence of FLB for
278 *Azendohsaurus* (Fig. 7 and Supplementary Figs. 2 and 3).

279 We coded presence of FLB for Archosauria because this character state has been
280 reported both in Pseudosuchia (e.g., Ricqlès et al. 2003; Padian et al. 2004; Nesbitt 2007;
281 Tumarkin-Deratzian 2007) and in Ornithodira (Ricqlès et al. 2000; Padian et al. 2004; Cubo et
282 al. 2015). Consistently, Cubo et al. (2012) inferred a high bone growth rate for the last
283 common ancestor of archosaurs. Lepidosauromorpha has been chosen as an outgroup and is
284 characterized by the absence of this character state (Fig. 7 and Supplementary Figs. 2 and 3).

285 We performed an optimization of the presence of FLB onto the phylogeny of
286 Archosauromorpha published by Nesbitt et al. (2015) (Fig. 7). Moreover, we carried out two
287 supplementary optimizations of the presence of FLB using the phylogenies of
288 Archosauromorpha published by Pritchard et al. (2015) (Supplementary Fig. 2) and Ezcurra

289 (2016) (Supplementary Fig. 3). All three analyses showed a flickering on and off pattern that
290 prevents inferring the primitive condition for this clade. Moreover, the parsimony method
291 fails to find the condition for the three more inclusive (basal) nodes of the clade. The only
292 robust conclusion obtained in the three analyses is congruent with that published by Botha-
293 Brink and Smith (2011): the fibrolamellar bone was acquired by the last common ancestor of
294 *Prolacerta* - archosauriforms, with a reversion in *Vancleavea* (Fig. 7 and Supplementary
295 Figs. 2 and 3).

296

297 *Constraining the phylogenetic frame of the acquisition of endothermy by*
298 *Archosauromorpha*. - The resting metabolic rate may be a good proxy to infer the
299 thermometabolic regime (endothermy *versus* ectothermy) of extinct organisms because
300 thermogenesis is very energy consuming (see the introduction). Legendre et al. (2016) used
301 this proxy in Archosauromorpha and concluded that endothermy may have been acquired by
302 the last common ancestor of the clade *Prolacerta* - archosauriforms. We inferred the resting
303 metabolic rate of a member of the sister group of this clade (*Azendohsaurus laaroussii* :
304 Allokotosauria) as the next step to better constrain the phylogenetic frame of the acquisition
305 of endothermy by Archosauromorpha. Moreover, we inferred resting metabolic rate values for
306 the sample of 14 extinct Archosauromorpha analyzed by Legendre et al. (2016). The values
307 inferred for all these taxa are included in the range of variation measured in the sample of
308 extant endotherms (mammals and birds) (Fig. 4-6). Considering that thermogenesis is very
309 energy consuming, we can reasonably assume that all these taxa were endotherms. A
310 parsimony optimization of the presence of endothermy in the whole sample (including extant
311 taxa of known thermometabolism and extinct taxa of inferred thermometabolism) shows that
312 endothermy was acquired twice, by mammals and by the last common ancestor of the clade
313 *Azendohsaurus* – archosauriforms, and that within this last clade there is a reversion in

314 Crocodylia (Fig. 8). Considering that many archosauriforms have been found in the Permian
315 and that endothermy may have been acquired in a more inclusive clade (*Azendohsaurus* –
316 archosauriforms), this key evolutionary event took place probably in the Permian. Bernard et
317 al. (2010) inferred fully developed endothermy for ichthyosaurs and plesiosaurs and incipient
318 endothermy for mosasaurs using a geochemical approach. These conclusions are congruent
319 with those obtained using a paleohistological approach (Buffrénil and Mazin 1990 for
320 ichthyosaurs; Fleischle et al. 2018 for plesiosaurs; and Houssaye et al. 2013 for mosasaurs).
321 Thermogenetic mechanisms have also been described in Actinopterygii: at the extraocular
322 muscles that warm the eyes and brain in billfishes (Xiphoidei) and in the butterfly kingfish
323 *Gasterochisma melampus* (Scombridae: Gasterochismatinae) (Davesne et al. 2018). Future
324 research on the biochemical basis of thermogenesis in extant taxa and on paleobiological
325 inference of resting metabolic rates in extinct taxa are needed to elucidate the origin and the
326 evolutionary patterns of endothermy in Osteichthyes.

327

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329

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507

508

Figure captions

509

510 FIGURE 1. *Azendohsaurus laaroussii* Dutuit 1972, (Argana Basin, Irohalène Member,
511 Carnian) : 1 & 2: MNHN.F.ALM 586 left humerus (1) and mould of MNHN.F. 435 right
512 humerus (2) in dorsal (a), ventral (b), anterior (c), proximal (e) and distal (f) views; 3 & 4:
513 MNHN.F. ALM 498 and 502, two ends of the same left femur (3) and mould of
514 MNHN.F.ALM 497 left femur (4) in ventral (a), dorsal (b) and posterior (c) views; 5 & 6:
515 MNHN.F. ALM 398 right tibia (5) and MNHN.F. 369 mould of left tibia (6) in medial (a) and
516 lateral (b) views. The arrow-heads show the level of the thin sections. Abbreviations : a.fi,
517 articulation for fibula; cap, capitellum; cc, cnemial crest; dp, deltopectoral crest; ect,
518 ectepicondyle; gr, groove; int, internal trochanter; tro, trochlea.

519

520 FIGURE 2. Transverse (A, B, E, F) and longitudinal (C, D, G, H) sections of the medial (A-D)
521 and the posterior (E-H) regions of the right tibia MNHN.F ALM369 of *Azendohsaurus*
522 *laaroussii* under normal light (A, C, E, G) and cross-polarized light with lambda compensator
523 (B, D, F, H). Periosteum is on the left. Arrows: primary osteons. Arrowheads: erosion cavities
524 lined along its periphery by a coating of endosteal lamellar tissue. Scale bars: 300 µm.

525

526 FIGURE 3. Transverse sections of the left femur MNHN.F ALM497 (A, anterior region; B,
527 posterior region; E, F, postero-dorsal region), and the right humerus MNHN.F ALM435 (C,
528 anterior region; D, posterior region; G, posterior region with higher magnification), and a
529 longitudinal section of the same humerus (H, posterior region) of *Azendohsaurus laaroussii*
530 under normal light (A-E) and cross-polarized light with lambda compensator (F-H).
531 Periosteum is on the left in A and C, on the right in B and D and in the bottom in G.

532 Endosteum is in the bottom in E, F, H. Arrow: primary osteon. Arrowhead: woven bone.

533 Scale bars: 1 mm in A-D; 300 μ m in E-H.

534

535 FIGURE 4. Resting metabolic rates quantified in a sample of extant tetrapods and inferred in a
536 sample of extinct Archosauromorpha using the phylogeny and the vascular density of the
537 humerus. Data for *Azendohsaurus laaroussii* were obtained in this study and data for other
538 taxa as well as the phylogeny were taken from Legendre et al (2016). Resting metabolic rate
539 inferred for *Azendohsaurus*, *Prolacerta*, *Garjainia* and *Euparkeria* are in the range of
540 variation of extant mammals, whereas the value inferred for *Postosuchus* is in the range of
541 variation of extant birds.

542

543 FIGURE 5. Resting metabolic rates quantified in a sample of extant tetrapods and inferred in a
544 sample of extinct Archosauromorpha using the phylogeny only. Data for *Azendohsaurus*
545 *laaroussii* were obtained in this study and data for other taxa as well as the phylogeny were
546 taken from Legendre et al (2016). Resting metabolic rate inferred for *Azendohsaurus*,
547 *Proterosuchus* and *Maiasaura* are in the range of variation of extant mammals, values
548 inferred for *Calyptosuchus*, *Lesothosaurus*, *Allosaurus* and *Troodon* are in the range of
549 variation of extant birds, whereas value inferred for *Rutiodon* is intermediate.

550

551 FIGURE 6. Resting metabolic rates quantified in a sample of extant tetrapods and inferred in a
552 sample of extinct Archosauromorpha using the phylogeny and the vascular density of the tibia.
553 Data for *Azendohsaurus laaroussii* were obtained in this study and data for other taxa as well
554 as the phylogeny were taken from Legendre et al (2016). Resting metabolic rate inferred for
555 *Azendohsaurus*, *Prolacerta*, *Proterosuchus*, *Garjainia*, *Lesothosaurus*, *Maiasaura* and
556 *Thecodontosaurus* are in the range of variation of extant mammals, the value inferred for

557 *Allosaurus* is in the range of variation of extant birds, whereas value inferred for

558 *Lourinhanosaurus* is intermediate.

559

560 FIGURE 7. Optimization using parsimony of the presence of fibrolamellar bone in the
561 stylopodial and zeugopodial bones of the Archosauromorpha analyzed to date (data
562 summarized in Table 1). The topology is based on Nesbitt et al (2009) for Archosauriformes,
563 and on Nesbitt et al (2015) for non-archosauriform Archosauromorpha with the exception of
564 the phylogenetic position of *Aenigmastropheus parringtoni* that has been taken from Ezcurra
565 et al (2014). The minimum age of taxa has been taken from the Paleobiology Database. Black
566 branches indicate presence of fibrolamellar bone, white branches indicate absence and black
567 and white branches indicate uncertain character state.

568

569 FIGURE 8. Optimization using parsimony of the presence of endothermy in a sample of
570 tetrapods. The presence of endothermy was inferred in extinct tetrapods using resting
571 metabolic rates estimated through phylogenetic eigenvector maps. Red corresponds to the
572 presence of endothermy and blue to the presence of ectothermy. The phylogeny has been
573 taken from Legendre et al (2016).