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

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

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

Material and methods

Material.- We analyzed histologically skeletal remains from the non-archosaurifom archosauromorph *Azendohsaurus laaroussii* from the Upper Triassic (Carnian) of the Argana Basin (Morocco) deposited at the Paris Muséum National d'Histoire Naturelle (MNHN). *Azendohsaurus laaroussii* Dutuit, 1972 was originally described on the basis of a dental fragment and two isolated teeth specialized for plants feeding (Dutuit, 1972). On the basis on comparison with Ornithischian dinosaurs such as *Fabrosaurus* and *Scelidosaurus* it was attributed to a new ornithischian dinosaur, becoming one of the earliest dinosaurs (Dutuit 1972; Thulborn, 1973, 1974; Bonaparte, 1976; Galton, 1985, 1990; Weishampel, 1990; Gauffre, 1993; Hunt and Lucas, 1994; Flynn et al. 1999). In addition to the craniodental remains, hundreds of disarticulated and monospecific post-cranial remains have been recovered from the *locus typicus* of *Azendohsaurus laaroussii* (Dutuit, 1976). The analysis of these specimens argues strongly against a phylogenetic position inside Dinosauria (Jalil and Knoll, 2002). Flynn et al. (2010) named the new species *Azendohsaurus madagaskarensis* from the Triassic of Madagascar and provided for the first time a comprehensive description of the cranial anatomy of the genus. More recently, Nesbitt et al. (2015) provided a scrutiny description the postcranial anatomy of *Azendohsaurus madagaskarensis* which is now one of the best-known early archosauromorphs.

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

Histological methods.- Skeletal elements were molded and cast prior to sectioning to preserve morphological information. Casts and bone remains after histological sampling were reposited at the Paleontology collection of the Paris Muséum National d'Histoire Naturelle where they are available upon request to the curator. Mid-diaphyses were embedded in epoxy resin and processed histologically following standard procedures (Lamm 2013). Transverse sections as well as longitudinal sections (at the anterior, posterior, dorsal and ventral sides for humerus and femur, and anterior, posterior, medial and lateral sides for the tibia) were obtained and mounted on glass slides. They were analyzed and photographed in a Nikon Eclipse E600POL microscope using normal light and cross-polarized light with lambda compensator. Thin sections were reposited at the vertebrate hard tissues histological collection of the Paris MNHN, where they are available upon request to the curator (thin sections MNHN-F-HISTOS 2348 to 2362).

Qualitative histology.- The nomenclature and classification of bone tissues is based on bone organization at different integration levels (Francillon-Vieillot et al. 1990). At the level of bone matrix organization, three character states have been defined based on the organization of collagen fibers: the presence (or absence) of woven-fibered bone matrix (WB), of parallel-fibered bone matrix (PFB) and of lamellar bone matrix (LB). At the level of organization of bone as a tissue, two character states have been defined based on the organization of the collagen fibers, the vascular density, and the cyclicity of bone apposition: the presence of lamellar-zonal bone (LZB) and the presence of the fibro-lamellar bone (FLB). See Francillon-Vieillot et al. (1990) for a detailed description of these character states. This pattern-oriented approach has been recently expanded towards a process-oriented view based on the developmental origin of the components of bone tissue (Prondvai et al. 2014). In process-oriented paleohistology, the developmental mechanisms involved in the formation of bone tissue are inferred from the fine architecture of bone matrix. PFB and LB are formed by the process of dynamic osteogenesis whereas WB is formed by the process of static ossification (Ferretti et al. 2002; Palumbo et al. 2004; Marotti 2010; Prondvai et al. 2014; Stein and Prondvai 2014; Cubo et al. 2017). Cortices can also have a composite nature including (1) a scaffold of WB formed by the process of static osteogenesis and (2) centripetal layers infilling primary osteons made of PFB or LB formed by the process of dynamic osteogenesis. This last tissue type has been named woven-parallel complex by Prondvai et al. (2014). In the context of process-oriented paleohistology, the widely used term of FLB is a special case of woven-parallel complex in which there is abundant woven bone and dense vascularity in the form of primary osteons (Prondvai et al. 2014).

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

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

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

Finally, we performed an optimization of the presence of fibrolamellar bone (using our data for *Azendohsaurus laaroussii* and published data for other Archosauromorpha) and an optimization of the presence of endothermy (using observed resting metabolic rates for extant species and inferred resting metabolic rates for extinct ones as a proxy for the thermometabolic regime) onto phylogenies of Archosauromorpha and Tetrapoda respectively using parsimony in Mesquite (Maddison and Maddison 2015).

Results

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

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

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

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

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

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

Azendohsaurus laaroussii and the sample of extinct Archosauromorpha published by Legendre et al. 2016). According to the AIC procedure, the variable that maximizes the R squared and minimizes the AIC value should be selected. In the case of the humerus we obtained the same R squared when using vascular density and the phylogeny and when using only the phylogeny, but the AIC value was lower when using both vascular density and the phylogeny (Fig. 4). We inferred a resting metabolic rate of 3.11 mL O_2 h^{-1} $g^{-0.67}$ and a confidence interval of 2.87 – 3.36 mL O_2 h^{-1} $g^{-0.67}$ for *Azendohsaurus laaroussii* using the phylogeny and vascular density of the humeurs (Fig. 4). In the case of the femur we found a slightly higher R squared and a lower AIC value when using the phylogeny only (Fig. 5). We inferred a resting metabolic rate of 2.20 mL O_2 h^{-1} $g^{-0.67}$ and a confidence interval of 1.55 – 2.85 mL O_2 h^{-1} $g^{-0.67}$ for *Azendohsaurus laaroussii* using only the phylogeny (this is equivalent to an optimization; Fig. 5). Finally, in the case of the tibia we obtained again the same R squared when using vascular density and the phylogeny and when using only the phylogeny, but the AIC value was lower when using both vascular density and the phylogeny (Fig. 6). We inferred a resting metabolic rate of 2.53 mL O_2 h^{-1} $g^{-0.67}$ and a confidence interval of 2.25 – 2.82 mL O_2 h^{-1} $g^{-0.67}$ for *Azendohsaurus laaroussii* using the phylogeny and the vascular density of the tibia (Fig. 6).

Discussion

Evolution of fibrolamellar bone in Archosauromorpha.- The formation of fibrolamellar bone is very energy consuming because it involves the combined action of static osteogenesis (to form a scaffold of woven bone at high growth rates involving high rates of protein synthesis) and dynamic osteogenesis (osteonal infilling with lamellar or non-lamellar parallel fibered bone) (Prondvai et al. 2014). Therefore the capacity of reaching and maintaining very high bone growth rates during ontogeny, recorded by the presence of fibrolamellar bone in the bone cortex, may be a reliable proxy to infer the metabolic rate of extinct animals (see the introduction). Four previous studies have analyzed the evolution of the presence of fibrolamellar bone in Archosauromorpha in a phylogenetic context (Botha-Brink and Smith 2011; Mukherjee 2015; Veiga et al. 2015; Jaquier and Scheyer 2017). Here we performed parsimony optimizations of this character state (Fig. 7 and Supplementary Figs. 2 and 3) using our observations on the bone histology of *Azendohsaurus laaroussii*, and the observations on other Archosauromorpha published previously (summarized in Table 1).

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

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

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

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

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

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

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Figure captions

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

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

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

Endosteum is in the bottom in E, F, H. Arrow: primary osteon. Arrowhead: woven bone. Scale bars: 1 mm in A-D; 300 µm in E-H.

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

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

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

Allosaurus is in the range of variation of extant birds, whereas value inferred for *Lourinhanosaurus* is intermediate.

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

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