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Is there any evidence for the presence of extensive fibrolamellar complex in *Notosuchia*? New data on *Araripesuchus wegeneri*

MATHIEU G. FAURE-BRAC AND JORGE CUBO

LETHAIA



Here we describe the bone histology of a femur of *Araripesuchus wegeneri*, using both cross and longitudinal thin sections. The parasagittal stance and high maximum metabolic rate inferred for this taxon is often linked to the capacity of formation of *sustained* fibrolamellar complex (FLC), as it occurs in extant endotherms. This paper aims to test this hypothesis. The cross section of the sampled specimen MNHN.F.GDF660 revealed it was subadult, an ideal ontogenetic stage to check the presence of FLC as this tissue is formed mainly during early ontogenetic stages and is often eroded or remodelled in the adult stage. Although localized areas of FLC have been described in other *Notosuchia*, no evidence was found here for the presence of this tissue type in *A. wegeneri*. The hypothesis of the formation of *sustained* FLC in this taxon was, thus, ruled out, even though these animals were characterized by an upright position and very high maximum metabolic rates. These organisms have, therefore, no extant equivalences. □ *Palaeohistology, fibrolamellar complex, thermophysiology, Uruguaysuchidae, palaeophysiology*

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Notosuchia is a clade of mostly terrestrial extinct crocodyliforms. It appeared during the Lower Jurassic and became extinct at the middle of the Miocene. *Nothosuchia* were characterized by an upright stance (Wu & Shu 1996; Pol 2005; Turner 2006; Nascimento & Zaher 2010; Riff & Armin 2011; Sereno & Larsson 2009; Gomani 1997; Godoy *et al.* 2016). Considering that the only extant tetrapods showing a sustained upright posture are endothermic, this morphological feature may suggest that *Notosuchia* were endothermic (Carrier 1987). However, quantitative histology suggests that *Notosuchia* were ectothermic (Cubo *et al.* 2020, 2022). Like extant crocodiles, they were able to withstand *short* peaks of high growth rate forming *localized* areas of fibrolamellar complex (FLC), especially in their limb bones (Cubo *et al.* 2017).

FLC is a bone tissue composed of a scaffold of woven bone containing primary osteons. Even when incipient (*sensu* Klein 2010, see also Woodward *et al.* 2014), FLC can be recognized using three features: 1) the presence of collagen fibres without preferent orientation detected using cross-polarized light; 2) the presence of large and globular osteocytes with radiating canaliculi forming patches of woven bone; and 3) abundant vascularity (Marotti 2010; Prondvai *et al.*

2014; Faure-Brac *et al.* 2019). Localized areas of this tissue type have been found in *Iberosuchus macrodon* Antunes, 1975 in Cubo *et al.* (2017); *Pepesuchus deiseae* Campos *et al.* 2011 in Sena *et al.* (2018); *Araripesuchus buitreaensis* Pol & Apesteguía, 2005 in Fernández-Dumont *et al.* (2021); *Neuquensuchus universitas* Fiorelli & Calvo, 2007, *Mariliasuchus amarali* Carvalho & Bertini, 1999, *Notosuchus terrestris* Woodward, 1896, *Adamantinasuchus navae* Nobre & Carvalho, 2006 in Garcia Marsà *et al.* (2022), and *Stratiotosuchus maxhechti* Campos *et al.*, 2001 in Andrade *et al.* (2023). Considering that *Notosuchia* had very high maximum metabolic rates suggesting high peaks of activity and extraordinary athletic capabilities (M. Sena, personal communication, 2023), we expect that they were able to form extensive FLC like extant endotherms.

Here we analyse the bone histology of a femur of an Uruguaysuchidae attributed to *Araripesuchus wegeneri* Buffetaut, 1981 in the search of cases of extensive FLC in *Notosuchia*. Uruguaysuchidae was a clade of small terrestrial notosuchians, that appeared at the beginning of the Cretaceous. They were inferred as omnivorous highly active species (*e.g.* Turner 2006; Ósi, 2014), and are, therefore, very good candidates to produce sustained FLC.

Material and methods

Here we describe the bone histology of a cross section and associated longitudinal sections (MNHN-Histos 3171, 3172, 3173, 3176 and 3179) made from femur MNHN.F.GDF660 attributed to *Araripesuchus wegneri* (although the diagnosis doesn't exclude *Anatosuchus minor* Sereno *et al.* 2003) found in the Aptian of Gadoufaoua (Niger). A sample of the femur was cut close to midshaft of the diaphysis, and it was embedded in epoxy resin before being cut and polished, following the protocol described by Lamm (2013). These sections were already used in previous publications focusing on quantitative histology (Cubo *et al.* 2020, 2022), but never formally described. They are stored in the histological collection of the National Museum of Natural History of Paris and are available upon request to its curator.

Bone sections were studied using a Nikon Eclipse E600 Pol microscope with its integrated camera and an Axioskop Zeiss microscope equipped with a Canon PowerShot A640 camera, under both linear (LPL) and cross (XPL) polarized light, and for some of them, using a lambda wave plate (when using the first microscope) for an easier visualization of the different fibre orientations. Fibres without any preferential direction, i.e. running in all spatial dimensions, or parallel-fibred bone cut transversely to the main axis of its fibres, will display isotropy and therefore appear black (without lambda wave plate) or magenta (with lambda wave plate) (Bromage *et al.* 2003; Faure-Brac *et al.* 2019). Parallel-fibred bone, when cut in a plane parallel to the main axis of its fibres, will display anisotropy and therefore appear white (without lambda wave plate) or cyan / yellow (with lambda wave plate) (Bromage *et al.* 2003; Faure-Brac *et al.* 2019). While not necessary, the longitudinal sections are useful to ascertain the identification of bone tissues (Faure-Brac *et al.* 2019). The adding of longitudinal counterparts of the studied cross section will allow us to be as confident as possible in our interpretations.

To identify areas composed of FLC, we followed the diagnosis key presented in Prondvai *et al.* (2014) with addenda of criteria proposed by Faure-Brac *et al.* (2019). The identification of FLC is based on four criteria: 1) the presence of a tissue showing general isotropy at low magnification in areas of woven bone in between primary osteons; 2) patches of anisotropic tissues forming primary osteons; 3) the absence of alignment between the lacunae in the scaffold of woven bone; and 4) the presence of radiating canaliculi from large and irregular lacunae, without any preferential direction in the woven bone areas. When those four criteria are met,

then FLC can be unambiguously identified. All referred nomenclature is from de Buffr enil & Quilhac (2021).

Results

All images given here are available in the supplementary files without any marks.

Cross section

The cross section has an overall elliptical shape, with its medial part being thicker than the others. A disorganized region is visible in the lateral area but seems to have been partially broken (Figs 1, 2). The presence of Sharpey's fibres identifies it as a muscular attachment (Fig. 2, black arrowheads). The cortex is mostly constituted of a typical lamellar zonal bone (LZB) pattern, with a succession of five larger zones (i.e. regions of higher growth rate, mostly isotropic and well vascularized; Fig. 3z1–z5) and of five smaller annuli (i.e. regions formed at low growth rate, heavily anisotropic and almost avascular; Fig. 3a1–a5), while the whole section is not homogeneous and displays regional peculiarities. Sometimes, annuli display stops of growth as shown by the presence of intern lines of arrested growth (Fig. 4, asterisks). While this global pattern is very well marked in the anterior (Fig. 3), lateral (Supplementary Fig. 1), and posterior

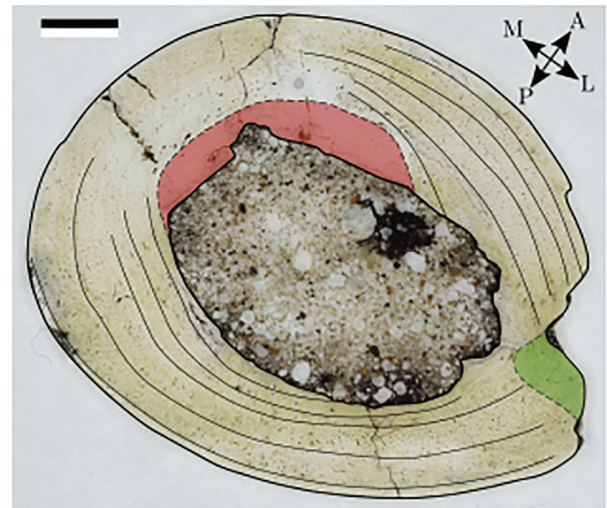


Fig. 1. Interpretation of the femoral cross section of *A. wegneri* (MNHN.Histos 3171). This picture was obtained using the digital microscope Hirox RH-2000, equipped with an optic Hirox MXB-2016Z, and its associated software. Solid and thick lines: internal and external edges of the section. Solid and thin lines: LAGs. Dotted line: delineation of specific area. Green area: lateral broken muscular attachment. Red area: secondary remodelling. A: anterior; P: posterior; M: medial and L: lateral. Scale bar: 2.5 mm.

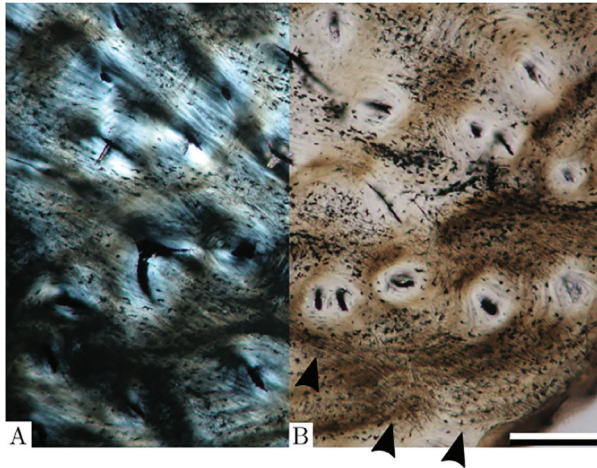


Fig. 2. Lateral muscular attachment, seen in A) LPL and B) XPL (MNHN.Histos 3171). Black arrowheads – examples of Sharpey's fibres. The centre of the bone is at the top and the external edge at the bottom. Scale bars: 200 μ m.

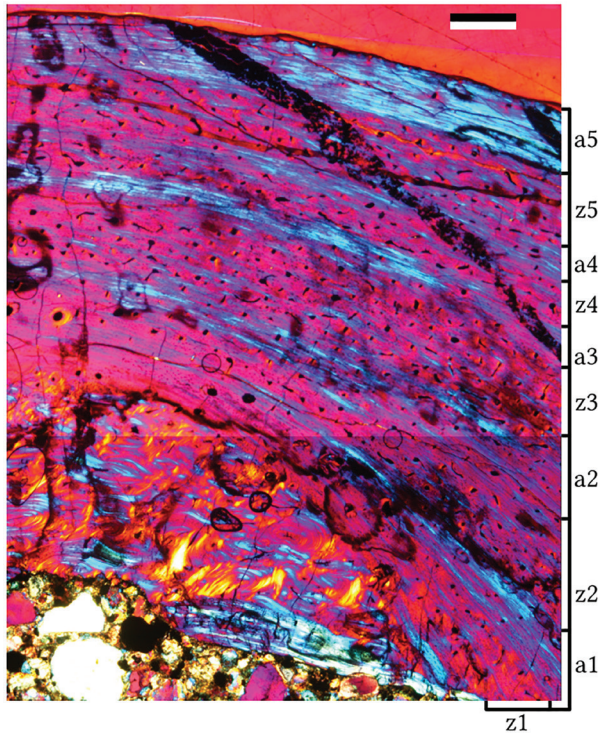


Fig. 3. Composite picture of the anterior part of the section, seen in XPL. Layers z1 to z5: zones; a1 to a5: annuli. Scale bar: 500 μ m.

(Supplementary Fig. 2) regions, it becomes almost indistinguishable in the medial one (Supplementary Fig. 3). The area of the muscular attachment loses the LZB pattern and presents a vascularization equivalent to zones, but on its whole thickness (Fig. 2).

There is presence of secondary bone remodelling, especially in the anterior and medial sections (Fig. 1

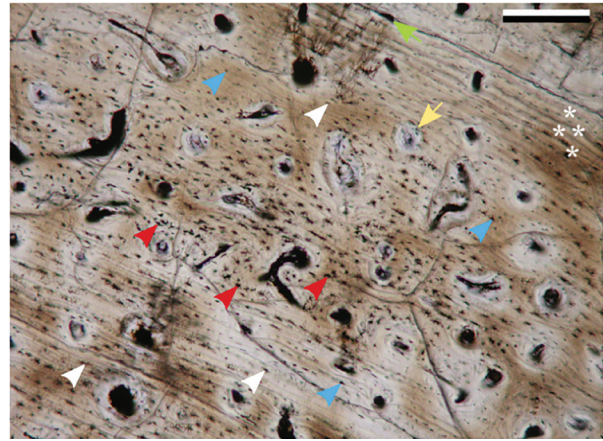


Fig. 4. Medial cortical area seen in LPL (MNHN.Histos 3171). Arrows: green – vascular canal; yellow – primary osteon. Arrowheads: white – elongated lacunae; blue – pin-head lacunae; red – globular and dense lacunae. White asterisks: line of arrested growth. Scale bars: 200 μ m.

and Supplementary Fig. 4). This remodelling is almost absent in other areas of the bone, suggesting it never occurred or has been eroded by perimedullary resorption, as clear evidence of erosion of the inner cavity has been observed (Fig. 1 and Supplementary Fig. 1). The section is lightly fractured, especially in the posterior area (Supplementary Fig. 2), which is probably due to taphonomic mechanical constraints. The general aspect of the osteohistology allows us to draw several general interpretations. First, the presence of bone remodelling indicates that the specimen was at least a subadult. The outermost layer of PFB displays some vascular canals and is rather thick. Therefore, it seems improbable it is an external fundamental system (EFS), so the specimen probably did not reach somatic maturity. This specimen is, therefore, ideal to investigate the potential presence of sustained FLC: it is almost at the end of its juvenile growth, the fastest, but is not aged enough for it to be erased by perimedullary erosion or secondary remodelling.

The vascularization of the cortex is associated with the cyclicity of the LZB: it is denser in zones than in annuli. It consists of a majority of small osteons and primary vascular canals, oriented longitudinally (parallel to the main axis of the bone), with the presence of reticulation (easily visible in Fig. 3). Both kinds of canals can be found in the same layer (Fig. 4, yellow and green arrows). Huge secondary osteons can be observed in the inner part of the anterior area, being evidence of a strong remodelling (Supplementary Fig. 4). Secondary osteons share the same orientations as the simple vascular canals.

At first sight bone tissue of the medial area looks like FLC but a closer observation shows that the bone matrix surrounding primary osteons is mainly formed by parallel fibred bone with an orientation parallel to the main axis of the bone (Supplementary Fig. 6). Therefore these fibres appear red or black in the transverse section (isotropic) but they appear white or orange/blue in longitudinal section (anisotropic). In conclusion, the scaffold containing primary osteons is composed of parallel-fibred bone, so we are not facing FLC. When we used the criteria proposed by Faure-Brac *et al.* (2019) we failed again to identify FLC: the cells of the bone tissue in between primary osteons are typically elongated or pin-shaped in both cross and longitudinal sections (Figs 4, 5).

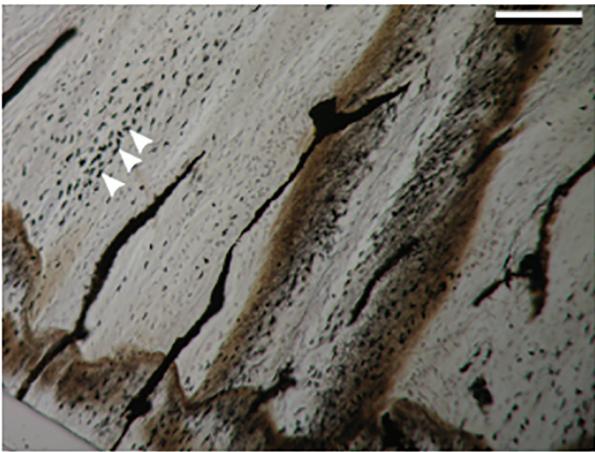


Fig. 5. Medial area of the femoral longitudinal section seen in LPL (MNHN.Histos 3179). The diaphysis is at the bottom. White arrows – patch of dense globular lacunae. Scale bars: 200 μm .

Longitudinal section

The fibres are, in their vast majority, anisotropic, while isolated isotropic patches can be found in different regions (Supplementary Fig. 6). A few patches constituted of dense and globular lacunae can be located in the cortex in various places (Fig. 5). There are always associated with strongly anisotropic tissue. On the contrary to what was observed in the cross-section, the LZB pattern is hardly visible in the longitudinal sections, whichever studied area.

Discussion

The growth of *A. wegneri* MNHN.F.GDF600 seems to be similar to those of typical crocodylians: an

alternation of annuli formed at low growth rates and zones formed at higher growth rates. The exception of the medial area of the analysed femur could be explained by a morphogenetic mechanism (e.g. generating bone curvature), a biomechanical mechanism (e.g. the influence of load and posture) and / or the need to reach a higher thickness quickly. It could be the same phenomenon as proposed by Cubo *et al.* (2017) in *Iberosuchus macrodon*, although, in the latter, the tissue was restrained to a smaller portion of the cortex. A similar explanation could be proposed for the lateral muscular attachment.

However, no sustained FLC was found in *A. wegneri*, like as it occurs in extant crocodylians and other crocodylomorphs including notosuchians, even in the earliest stage of growth (de Buffrénil *et al.* 2021). The possibility of formation of extensive areas of FLC cannot be ruled out because these areas could have been eroded by perimedullary erosion or/and replaced by the secondary remodelling. We would need an ontogenetic series to test this hypothesis. The addition of longitudinal sections allow us to confirm this interpretation, as no extensive areas of woven bone were found either. The growth rates of *A. wegneri* are similar to those of its extant relatives, crocodylians, or even lower (Enlow 1969; Padian *et al.* 2004; Tumarkin-Deratzian 2007; Woodward *et al.* 2014; Faure-Brac *et al.* 2019). As for them, the growth rate in zones is not high enough to produce FLC, or this FLC is restricted to small areas. The smaller rates could be explained by the difference in size. *A. wegneri* was a small crocodylomorph whose adult skull size was estimated near to 1m long (Pol 2005). Extant crocodylians are far bigger, therefore the presence of FLC in the latter (e.g. Tumarkin-Deratzian 2007) could be an adaptation to reach a bigger size quicker. The comparison with the bone microstructure of another *Araripesuchus*, *A. buitrensensis* described recently by Fernández-Dumont *et al.* (2021) shows that the femur, particularly, does not exhibit a clear alternation of zones and annuli, but only a homogenous annulus-like tissue, while the overall shape and some specificities (such as the presence of Sharpey's fibres in the postero-lateral area, whose shape is close to the broken part of our section displaying the same fibres) are very close to our specimen. The absence of alternation can be the result of an older ontogenetic stage for *A. buitrensensis* and, therefore, the loss of a younger stage with higher growth rates, or simply differences between the two species. More specimens are needed to investigate more deeply this question. Nevertheless, none species were able to form sustained FLC.

The lack of extensive FLC is in total accordance with the ectothermic regime as inferred recently by Cubo *et al.* (2020, 2022) for Notosuchians but is not congruent with the finding of very high maximum metabolic rates suggesting high peaks of activity and extraordinary athletic capabilities (M. Sena, personal communication, 2023). *A. wegneri* had a phenotype with no equivalent in the extant fauna: an ectothermic terrestrial species with an upright parasagittal stance and high maximum metabolic rates (M. Sena, personal communication, 2023). Extant crocodylians are still able to sustain a parasagittal-like gallop but only for a limited period.

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