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Long bone histology of *Ophiacodon* reveals the geologically earliest occurrence of fibrolamellar bone in the mammalian stem lineage

*L'histologie d'os longs d'*Ophiacodon *révèle l'occurrence la plus précoce d'os fibro-lamellaire dans la lignée souche mammalienne*

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ABSTRACT

Shared histological characteristics have been observed in the bone matrix and vascularity between Ophiacodontidae and the later therapsids (Synapsida). Historically, this coincidence has been explained as simply a reflection of the presumed aquatic lifestyle of *Ophiacodon* or even a sign of immaturity. Here we show, by histologically sampling an ontogenetic series of *Ophiacodon* humeri, as well as additional material, the existence of fibrolamellar bone (FLB) in the postcranial bones of a pelycosaur. Our findings have reaffirmed what previous studies first described as fast growing tissue, and by proxy, have disproven that the highly vascularized cortex is simply a reflection of young age. This tissue demonstrates the classic histological characteristics of true FLB. The cortex consists of primary osteons in a woven bone matrix and remains highly vascularized throughout ontogeny, providing evidence for fast skeletal growth. Overall, the FLB tissue we have described in *Ophiacodon* is more advanced or "mammal-like" in terms of the osteonal development, bone matrix, and skeletal growth than what has been described thus far for any other pelycosaur taxon. With regards to the histological record, our results remain inconclusive as to the preferred ecology of *Ophiacodon* due to a similar cortical vascularity pattern exhibited by other carnivorous pelycosaurs. Our findings have set the

Abbreviations: BCBB, Briar Creek Bonebed; C, circumference; EC, erosional cavity; EFS, external fundamental system; Fm, formation; FLB, fibrolamellar bone; HL, hatching line; L, length; LAG, line of arrested growth; LB, lamellar bone; MC, medullary cavity; MR, medullary region; MOS, morphological ontogenetic stage; OL, osteocyte lacunae; PFB, parallel-fibered bone; RCBB, Rattlesnake Canyon Bonebed; RSC, Rattlesnake Canyon; SF, Sharpey's fibers; WB, woven bone; WPC, woven parallel-fibered complex.

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evolutionary origins of FLB and high skeletal growth rates back approximately 20 million years to the Early Permian, and by phylogenetic extension perhaps the Late Carboniferous.

Mots clés :
Pélycosauriens
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Os fibro-lamellaire

RÉSUMÉ

Il a été observé des caractéristiques histologiques partagées, dans la matrice et la vascularisation de l'os, entre les Ophiacodontidae et les thérapsidés (Synapsida) plus tardifs. Historiquement, cette coïncidence a été expliquée comme simplement un reflet du style présumé de vie aquatique d'*Ophiacodon*, ou même comme un signe d'immaturité. Ici est montrée histologiquement par l'échantillonnage des humérus d'une série ontogénétique d'*Ophiacodon*, ainsi que de matériel additionnel, l'existence d'os fibro-lamellaire dans les os post-crâniens d'un pélycosaure. Nos découvertes ont réaffirmé ce que des études antérieures avaient d'abord décrit comme tissu de croissance rapide ou par proxy, ont réfuté le fait que le cortex très vascularisé soit simplement un reflet du jeune âge. Ce tissu démontre les caractéristiques histologiques classiques d'un vrai os fibro-lamellaire (FLB). Le cortex est constitué d'ostéones primaires dans une matrice osseuse tramée et reste très vascularisé tout au long de l'ontogénie, fournissant la preuve d'une croissance osseuse rapide. Dans l'ensemble, le tissu FLB décrit chez *Ophiacodon* est plus avancé – ou de « type mammalien » – en termes de développement des ostéones, matrice osseuse et croissance du squelette, que ce qui avait été décrit, et de loin, pour tout autre taxon de pélycosaures. À propos de l'enregistrement histologique, nos résultats restent peu concluants en ce qui concerne l'écologie préférée d'*Ophiacodon*, en raison d'un *pattern* de vascularisation corticale similaire à celui d'autres pélycosaures. Nos découvertes placent les origines évolutives du FLB et les forts taux de croissance du squelette, à 20 Ma près, au Permien inférieur et, par extension phylogénétique, peut-être au Carbonifère.

1. Introduction

1.1. Background

Ophiacodon (Marsh, 1878) is a basal synapsid that belongs to the clade Ophiacodontidae (Nopcsa, 1923) that existed between the Late Carboniferous and the Early Permian (Romer and Price, 1940). *Ophiacodon* is considered a more derived member of the clade, compared to, e.g., *Clepsydrops* (Laurin and de Buffrénil, 2016). Note that we use the term "pelycosaur" (paraphyletic) throughout this paper in an informal way and not as a clade name, to avoid using the cumbersome "non-therapsid synapsid".

Using a putative growth series of *Ophiacodon retroversus* (Fig. 1), Brinkman (1988) suggested that morphological ontogenetic stages (MOS) in pelycosaurs can be defined on the basis of degree of ossification of the limb bones. Size alone cannot be used as a proxy for reconstructing ontogenetic age in pelycosaur taxa because individuals of the same size may represent different stages of development. However, because of the delayed ossification observed in the epiphyses of *Ophiacodon* (Romer and Price, 1940), Brinkman was restricted as to what elements to use to test his hypothesis that the ossification of the limb bones is a better means of interpreting relative age of an individual than size. He chose the humerus because the complex articulations in the epiphyses exhibited more than two stages of ontogeny. We hypothesize that if the MOS of limb bones can be defined by degrees of ossification, then we should be able to relate MOS to bone histology.

Early histologic studies of *Ophiacodon* long bones, albeit based on scanty material, all concur that the histology contrasts in vascularity, matrix organization, and presence of growth marks from that observed in other pelycosaurs (Enlow, 1969; Enlow and Brown, 1957, 1958; de Ricqlès, 1974a,b). One explanation for these differences was an aquatic or amphibious lifestyle (Romer and Price, 1940) in *Ophiacodon*. Germain and Laurin (2005) tested this hypothesis by quantifying the global compactness of a complete transverse section and comparing it to that of extant animals. These authors advised caution when interpreting their results. Enlow (1969), however, noted that the characteristics of *Ophiacodon* bone tissue reflected fast skeletal growth, but he suggested this could just be the juvenile condition of his sample as adequate detailed ontogenetic comparisons were lacking for pelycosaurs.

Most recently, Laurin and de Buffrénil (2016) described the bone histology of the more basal ophiacodontid *Clepsydrops collettii* from a femur measuring 56.8 mm in length. This is one of the smallest femora on record for this species (Romer and Price, 1940; Shelton, 2015), but its small size may not necessarily indicate a juvenile (see above). Laurin and de Buffrénil (2016) compared the histology of the specimen to that of a femur of *O. uniformis* and noted that the cortex of *C. collettii* is much thinner, suggesting more of a terrestrial life style for the geologically earlier species. Additionally, Laurin and de Buffrénil (2016) found that *Ophiacodon* grew fast relative to extant squamates, and then found evidence of determinate growth in the form of an external fundamental system. Laurin and de Buffrénil