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Microstructural features of the femur in early ophiacodontids: A reappraisal of ancestral habitat use and lifestyle of amniotes

Caractères microstructuraux du fémur chez les premiers ophiacodontes : réexamen du mode de vie ancestral des amniotes

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ABSTRACT

Ophiacodontids have long been considered the basalmost synapsids, and to have retained a fairly aquatic, piscivorous lifestyle typical of stem-amniotes. A restudy of their bone histology and microanatomy shows that *Clepsydrops collettii*, a Late Carboniferous ophiacodontid, has a thin, compact cortex and lacks a medullary spongiosa, two features that suggest a truly terrestrial lifestyle. The Early Permian *Ophiacodon uniformis* has a thicker cortex with a few resorption cavities and bone trabeculae surrounding the free medullary cavity. An inference model yields a terrestrial lifestyle for both taxa, though *O. uniformis* may have been slightly more aquatic (possibly amphibious) than *C. collettii*. However, an optimization of inferred lifestyle of other early stegocephalians (based on bone microanatomy) suggests that the first amniotes were terrestrial. The potentially amphibious lifestyle of *O. uniformis*, though not supported by our inference model, would thus be secondary. Histological features of femoral cortices in these two taxa closely resemble those previously described in extant species of large varanids and teids. This similarity, along with other comparative elements, is discussed in reference to the possible growth patterns and life history traits of *Clepsydrops* and *O. uniformis*.

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Mots clés :
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RÉSUMÉ

Les ophiacodontidés ont longtemps été considérés comme les synapsidés les plus basaux et on leur a longtemps attribué le mode de vie aquatique et le régime piscivore typique des premiers amniotes-souches. Cette étude de micro-anatomie et d'histologie osseuse montre que le fémur de *Clepsydrops collettii*, un taxon du Carbonifère supérieur, possède un cortex compact peu épais et est dépourvu de spongieuse médullaire, deux caractères indicatifs d'un mode de vie franchement terrestre. *Ophiacodon uniformis*, du Permien inférieur, a un cortex plus épais avec quelques lacunes de résorption, ainsi que des travées osseuses autour de la cavité médullaire. L'usage d'un modèle d'inférence conduit à attribuer un mode de vie terrestre à ces deux taxons, encore que *O. uniformis* ait pu être un peu plus aquatique (peut-être

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amphibie) que *C. collettii*. Cependant, l'optimisation des inférences de mode de vie effectuées chez d'autres stégocéphales en référence à la micro-anatomie de leurs os suggère que les premiers amniotes étaient terrestres. D'éventuelles mœurs amphibies chez *Ophiacodon* (bien qu'elles ne soient pas confirmées par l'emploi de nos modèles d'inférence) seraient donc secondaires. Les caractères histologiques du fémur dans les deux taxons étudiés ici rappellent fortement ceux attribués dans la littérature aux grands varanidés et téidés. Cette similitude, ainsi que d'autres éléments comparatifs, est discutée en référence aux modèles de croissance et aux traits d'histoire de vie qui pourraient être attribués à *Clepsydrops* et à *O. uniformis*.

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1. Introduction

Extant amniotes include mostly terrestrial taxa, but does this reflect the initial amniotic condition? The amniotic egg is usually viewed as a useful, though not necessary adaptation to a terrestrial lifestyle (Skulan, 2000). However, even if we provisionally accept the current wisdom that the amniotic egg is a terrestrial adaptation, this does not necessarily imply that the first amniotes were terrestrial for their entire life cycle. Indeed, Romer (1957, 1958) thought that the first amniotes were still amphibious, perhaps even mostly aquatic taxa, and that they laid their eggs on land because it was a safer environment, with less predator pressure, than the aquatic environment. Even today, in at least some environments, there are apparently advantages in laying eggs outside water because some amphibians have adapted to lay eggs in this way (Martin and Carter, 2013). The benefit of laying eggs on land would have increased the farther we go back in time because there were fewer terrestrial predators back then (Laurin, 2010; Romer, 1957, 1958). Laying terrestrial eggs is also advantageous in alpine environments, in which eggs risk being swept away by the fast current, and this has led to the suggestion that this hazard may have been the selective pressure that led to the appearance of the amniotic egg (Goin and Goin, 1962). Although these considerations suggest that the amniotic egg is obviously optimized for terrestrial reproduction, they do not necessarily imply that the first amniotes were terrestrial animals.

What does the fossil record tell us about the lifestyle of the earliest amniotes? Ichnological evidence suggests that some Carboniferous stegocephalians ventured onto land (Keighley et al., 2008), even though this does not rule out the possibility that these taxa were still largely amphibious, if not mostly aquatic. Furthermore, trackways can be deposited underwater (Brand, 1992; Brand and Tang, 1991), so it is not obvious how reliable such ichnological data are to infer habitat use in long-extinct taxa. This interpretation is supported by the recent discovery of Middle Devonian stegocephalian trackways, probably produced by a taxon that was still largely aquatic (Niedzwiedzki et al., 2010). The oldest known unequivocal amniote skeletal remains are from Joggins, Nova Scotia (Carroll, 1964), and date back to the Early Pennsylvanian, about 315–316 Ma (Calder et al., 2005), Late Bashkirian to Early Moscovian (Gradstein et al., 2012). Most stegocephalians found in Joggins may have been terrestrial, based on their morphology, but the fact that most fossils were preserved in tree stumps raises the possibility that the Joggins thanatocoenosis is a biased sample of the biocoenosis that it represents.

The scant skeletal remains found in Joggins, combined with unfavorable preservation (appendicular long bones are strongly flattened; ML, personal observation) has so far prevented the use of other types of data, such as bone microanatomy, to corroborate previous interpretations about the lifestyle of the stegocephalians found in Joggins. However, long bone microanatomy of slightly more recent, Permo-Carboniferous stegocephalians, including amniotes, has started yielding clues about the lifestyle of the first amniotes (Canoville and Laurin, 2010; Germain and Laurin, 2005; Huttenlocker and Rega, 2012; Kriloff et al., 2008; Laurin et al., 2004; Quémeneur et al., 2013). Among Permo-Carboniferous amniotes, ophiacodontids are especially relevant to assess the primitive amniotic condition, for two reasons. First, Romer (1961) viewed ophiacodontids as aquatic to amphibious, piscivorous taxa. Second, ophiacodontids are historically important: following Romer (1961), they have indeed been supposed to be the basalmost synapsids (in fact, Romer considered them to be the ancestral stock of other synapsids), a viewpoint that was upheld much more recently by Carroll (1988). Several more recent explicit phylogenetic analyses (Laurin, 1993; Reisz, 1986; Reisz et al., 1992) have not supported this conclusion, and placed ophiacodontids among eupelycosaurs, though Benson (2012: fig. 2C) found some support for a very basal position of this taxon. Ophiacodontids thus formed a cornerstone of Romer's scenario about the origin of amniotes, along with the apparently amphibious to aquatic diadectomorph *Limnoscelis paludis* (Romer, 1946), and they remain important to assess the primitive lifestyle of amniotes and synapsids even under recent phylogenies.

The question, however, proves to be complex and a recent morphometric study of the *Ophiacodon* spine (Felice and Angielczyk, 2014) failed to reach a clear-cut, unambiguous conclusion on this topic. Below, we test Romer's (1957, 1958), and Felice and Angielczyk's (2014) ideas about the lifestyle of ophiacodontids, through a microanatomical study of two taxa of different geological ages: the Late Carboniferous *Clepsydrops collettii* and the Early Permian *Ophiacodon uniformis*. We hypothesize, because of the difference in geological age between both taxa (at least 15 Ma; see below), that *C. collettii* retains a lifestyle closer to that of the earliest ophiacodontids and probably of the earliest amniotes as well, than *O. uniformis*. We also take this opportunity to further describe their histology, in complement to previous descriptions by Enlow

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