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La paléohistologie de l'ichthyosaure basal Mixosaurus Baur, 1887 (Ichthyopterygia, Mixosauridae) du Trias moyen : implications paléobiologiques

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ABSTRACT

Here, we provide the first bone histological examination of an ontogenetic series of the basal ichthyosaur *Mixosaurus* encompassing postnatal to large adult specimens. Growth marks are present in sampled humeri, a femur, a fibula, as well as in other skeletal elements (gastral ribs). Ontogenetic changes are traceable throughout stylo- and zeugopodial development, but interior remodelling and resorption deleted part of the internal growth record in the primary cortex. *Mixosaurus* humeri started as flat structures consisting of a core of endochondral woven bone and residual calcified cartilage, whereas growth continued by deposition of periosteal fibrolamellar and parallel-fibred bone. Unlike the fast-growing post-Triassic ichthyosaurs that lack growth marks, microstructural and life history data are now becoming available for a basal ichthyosaur. The high growth rate of *Mixosaurus* may indicate that higher metabolic rates characterised small, non-thunniform ichthyosaurs, as had been suggested already for post-Triassic, cruising forms.

RÉSUMÉ

Nous rapportons ici la première étude ostéohistologique d'une série ontogénétique quasi-complète (spécimens postnataux à adultes) de l'ichthyosaure basal *Mixosaurus*. Des stries de croissance sont visibles sur les humérus échantillonnés, ainsi que sur un fémur, un péroné et d'autres éléments du squelette (côtes gastriques). On peut suivre les changements ontogénétiques au cours du développement des stylo- et zeugopodes, mais le remodelage interne et la résorption ont en partie effacé l'enregistrement de la croissance interne dans le cortex primaire. Les humérus de *Mixosaurus* sont initialement des structures plates consistant en un noyau d'os endochondral en « sucre mouillé » et de cartilage calcifié rémanent. La croissance continue

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par dépôt d'os périostique fibrolamellaire et à fibres parallèles. Contrairement aux ichthyosaures post-triasiques à croissance rapide, qui ne présentent pas de stries de croissance, des données microstructurelles et d'histoire de vie sont maintenant disponibles pour un taxon basal du groupe. Le haut taux de croissance de *Mixosaurus* pourrait indiquer que les petits ichthyosaures non thunniformes étaient caractérisés par des taux métaboliques élevés, comme cela fut déjà suggéré pour les formes migrantes post-triasiques.

1. Introduction

The ichthyosaurs are a group of extinct reptiles with a strongly re-shaped body outline, showing numerous adaptations to a marine lifestyle. Because of their abundance and excellent fossil preservation, this lineage offers unique possibilities to get insights into the palaeobiology of a long extinct group of specialized marine vertebrates, which lacks any modern descendants (Sander, 2000). Ichthyosaurs are generally characterised by a fish- or dolphin-like body shape, a long snout and large eyes, but to date, the origins of ichthyosaurs within the amniote tree of life are still controversial (Motani, 1999). In more recent cladistic analyses, Ichthyopterygia have been repeatedly recovered as diapsid reptiles, possibly as sister group to Sauria, the clade which encompasses Lepidosauromorpha and Archosauromorpha (Motani et al., 1998; Müller, 2004).

Among Mixosauridae (Fig. 1), the genus *Mixosaurus,* erected by Baur (1887) based on the type species *Mixosaurus cornalianus* (Bassani, 1886), represents a particularly successful group of small to medium-sized ichthyosaurs (< 2 m body length) restricted to the Middle Triassic (Motani, 1999). McGowan and Motani (2003) recognise five species of *Mixosaurus*, including *Mixosaurus atavus* (Quenstedt, 1852), *Mixosaurus nordenskioeldii* (Hulke, 1873), *M. cornalianus* (Bassani, 1886), *Mixosaurus fraasi* (Merriam, 1910), and *Mixosaurus kuhnschnyderi* (Brinkmann, 1998), of which *M. cornalianus* and *M. kuhnschnyderi* are well known from the Middle Triassic of the Besano region, Italy, and from the Besano Formation of the Monte San Giorgio locality, Switzerland.

The impact of the general adaptation to the marine environment is clearly observable in the bone histology of ichthyosaurs. Whilst studies on bone histology of fossil reptiles have been done by many researchers in the past (Scheyer et al., 2010), the bone histology of marine reptiles, and especially of ichthyosaurs, is not well examined. Among others, Gross (1934), Kiprijanoff (1881) and Seitz (1907) already made useful detailed observations on the bone histology of post-Triassic ichthyosaurs (Fig. 1), such as *Ichthyosaurus, Ophthalmosaurus* and *Platypterygius*. In these works, the peculiar spongy nature of the bones was already noted. Especially Seitz (1907), who because of preservational restrictions analysed only thin-sections of ribs (and also restudied Kiprijanoff's original sections), mentioned that the primary bone tissue houses not only primary vascular canals and osteons but is also subject to secondary remodelling. Gross (1934) further encountered primary and secondary osteons and larger resorption bays in a section of a lower jaw of *Ichthyosaurus* sp. and in the rib of *Ophthalmosaurus icenicus*. More recently, de Buffrénil and Mazin (1990) gave a comparative account on the bone histology of the ichthyosaurs *Stenopterygius* and *Ichthyosaurus*, as well as the Early Triassic *Omphalosaurus*, an enigmatic taxon whose systematic position is still under debate (Motani, 2000; Sander and Faber, 2003). de

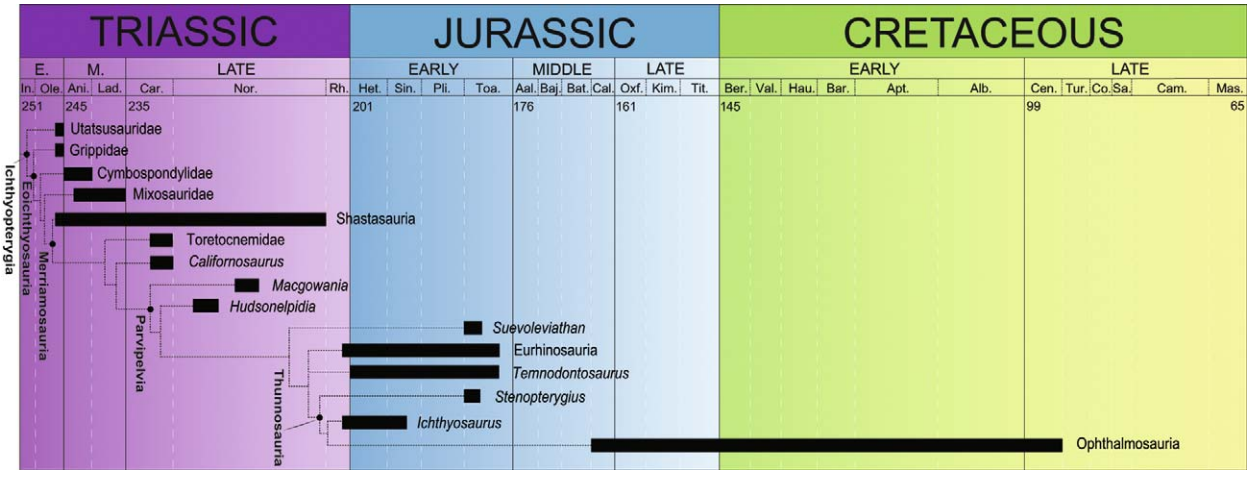

Fig. 1. Simplified time-calibrated cladogram (modified from McGowan and Motani, 2003; Motani, 2005; Walker and Geissman, 2009 [GSA 2009 Geologic Time Scale]) showing the interrelationships of the Ichthyopterygia and the position of the Mixosauridae within the clade.
Fig. 1. Cladogramme simplifié (d'après McGowan et Motani, 2003 ; Motani, 2005 ; Walker and Geissman, 2009 [GSA 2009 Geologic Time Scale]) montrant les relations entre les Ichthyopterygia et position des Mixosauridae au sein du clade.