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Les Ostéichthyens, du Paléozoïque aux temps actuels, au travers de l'histologie et de la paléohistologie des tissus osseux

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ABSTRACT

The aim of this short review is to emphasize the richness of the comparative histological studies on both fossil and extant Osteichthyes. Some selected examples in both Sarcopterygii (excluding tetrapods) and Actinopterygii show how it is possible to improve our knowledge on bone biology of extinct species but also to obtain new data on their palaeobiology or on their paleobiogeography. After a brief survey of the organization of bony tissues in osteichthyes, we review some examples of skeletal peculiarities in the following extinct and extant taxa: the histological structure of polypterid scales that suggests a hypothesis on the possible age and the biogeographical history of this basal actinopterygian taxon; the ossified lung of the fossil coelacanthids, with a discussion on its potential function; the histological organization of the sarcopterygian derived elasmoid scales (of *Eusthenopteron* sp., *Latimeria* sp. and *Neoceratodus* sp.). These comparative palaeohistological and histological data provide the basis of a general discussion of the evolutionary trends of bony tissues and their derivatives in Osteichthyes.

RÉSUMÉ

Le but de cette courte revue est de mettre en valeur la richesse des études histologiques comparatives de l'os des Ostéichthyens fossiles et actuels. Quelques exemples choisis chez les Sarcoptérygiens (excluant les tétrapodes) et les Actinoptérygiens, montrent qu'il est possible d'enrichir significativement les connaissances sur l'histologie osseuse des espèces disparues, mais aussi d'obtenir de nouvelles données de paléobiologie ou de paléobiogéograhie pour ces espèces. Après un rappel de l'organisation générale des tissus osseux chez les Ostéichthyens, nous présentons quelques exemples appropriés de tissus squelettiques chez des taxons fossiles et actuels suivants : une étude de la structure des écailles des Polyptères, qui permet de poser une hypothèse sur l'âge et l'histoire biogéographique de ce taxon basal d'Actinoptérygiens ; les parois ossifiées du poumon des coelacanthes fossiles, avec une discussion sur le rôle possible de cet organe ; la structure histologique des écailles élasmoïdes dérivées chez les Sarcoptérygiens (*Eusthenopteron* sp., *Latimeria* sp. et *Neoceratodus* sp.). Ces données paléohistologiques et histologiques conduisent à une présentation générale des tendances évolutives des tissus osseux et de leurs dérivés chez les Ostéichthyens.

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1. Introduction

It has long been technically difficult to analyse mineralised structures at the histological level, i.e., the cellular and extracellular structures of bony tissues and associated calcified tissues in Osteichthyes (Actinopterygii and Sarcopterygii, part of which, Tetrapoda, is not covered here), like in tetrapods. The first technical difficulty was to remove the mineral component to be able to use the classical paraffin microscopy. Studying bone after removal of mineral, which is the essential component of bone, appears as an aberration. Even if techniques for sectioning undecalcified material (adapted from petrographic techniques) are relatively old (de Ricqlès, 2006; Gervais, 1875; Stephan, 1900; Williamson, 1849), they have been infrequently used for a long time because they are technically challenging; this fact can partly explain the relative recurrent disinterest of the ichthyologist community for histological study of skeletal elements in the Osteichthyes. However, during the last four decades, sophisticated technical improvements for studying the mineralised tissues in association with advancements in the field of computing, have led to a drastic improvement in our knowledge of osteichthyan bony tissues and their biology.

As osteichthyan bones have mineral components, the skeleton can fossilize, allowing morphological and histological studies of extinct taxa (Halstead, 1963, 1969; Laurin et al., 2007; Meunier and Laurin, 2011; Ørvig, 1951, 1957; Schultze, 1966; Smith and Sansom, 1997; Smith et al., 1996; Zylberberg et al., 2010). From a technical point of view and on the basis of the skeleton history, there is no discontinuity between osteichthyan bone palaeohistology (distant past) and osteichthyan bone histology (present time); the recent past (archeozoological material) is also amenable to histo-morphological bone techniques.

In the present study, I want to give some results acquired from palaeohistological studies but with reference to extant ostechthyan material. Effectively, going back and forth between the fossil material and the extant species is a necessity to improve the interpretation of the observations on the histological organization of extinct species. It is also required to gain an evolutionary perspective on bone biology and, maybe, more generally on osteichthyan palaeobiology, considering that mineralised bony tissues record the influences of biological and/or external events that have accompanied the animals during their lives.

2. Histological characteristics of bony tissues in Osteichthyes

To understand the nature and the function of the skeleton in extant as well as in extinct Osteichthyes, including the Teleostei that include more than half of the extant vertebrate species, it is necessary to give some fundamental explanations about bony tissues and their derivatives.

2.1. Bony tissue components

The osteichthyan bony tissue is a connective tissue enriched with type I collagenous fibres that mineralise. The mineral component of bone is a calcium phosphate that crystallizes as hydroxyapatite.

2.1.1. Cellular components

The cells that synthesize the bone substance are the osteoblasts; when they are embedded in the bone matrix, they become osteocytes that reside in an osteocytic lacuna (Francillon-Vieillot et al., 1990; Huysseune, 2000). The osteocytes are star-shaped (Fig. 1a); they show thin cytoplasmic processes laying in the *canaliculi*. These canaliculi form a variably developed network that participates in bone nutrition; they are abundant in basal actinopterygians (Fig. 1sa',a") and reduce in the Thunini (Fig. 1sa"'). The number and the shape of the osteocytes vary according to the taxa, as already described by Stephan (1900). Moreover, in a number of teleostean species, bone is wholly deprived of osteocytes (Fig. 1c); in this case, bone is named "acellular bone" (Kölliker, 1859; Moss, 1961, 1965) or "anosteocytic bone" (Weiss and Watabe, 1979). In acellular bone, it seems that the osteoblasts retreat from the front of bone synthesis instead of being taken up in the bone matrix to become osteocytes (Moss, 1961, 1965). In certain cases, they remain at the surface and send cytoplasmic processes of variable length and degree of ramification into the bony tissue (Fig. 1d). This last type of bone, deprived of true osteocytes but with incorporated cytoplasmic processes, can be called primary canaliculated bone or tubular acellular bone (Hughes et al., 1994). Bone is destroyed by specialized cells, the osteoclasts, which are generally multinucleated (Fig. 1b) (Sire et al., 1990), although much teleosteans have mononucleated osteoclasts, particularly in taxa deprived of osteocytes (Witten and Huysseune, 2009). Bone growth implies a peripheral accretion due to the activity of a periost that overlays the bone (Francillon-Vieillot et al., 1990; Ricqlès et al., 1991).

Let us take a look at the extant Holostei. Indeed, these osteichthyans have a cellular bone with well-differentiated osteocytes; but they also show special cells, the cells of Williamson that rest at the surface of the bone and send a cytoplasmic extension housed in a specific canalicule into the osseous tissue (Fig. 1e). These canaliculi of Williamson have been described in fossil Subholostei and Holostei (Aldinger, 1937; Meunier and Gayet, 1992; Ørvig, 1951; Schultze, 1966; Sire and Meunier, 1994) and they represent a very useful diagnostic character but unfortunately, they are rarely taken into account in the phylogenetic studies (Grande, 2010).

2.1.2. Organization of the fibrillar matrix

The collagen is deposited by the osteoblasts as thin microfibrils that are packed to form fibres that are clearly recognizable with a transmission electron microscope, even in some very well preserved fossil material (Zylberberg and Laurin, 2011). Three modes of arrangement have been defined for the collagenous fibres in the bony matrix (Francillon-Vieillot et al., 1990; Ricqlès et al., 1991):

- an unordered intermingled network;