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The Osteichthyes, from the Paleozoic to the extant time, through histology and palaeohistology of bony tissues

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.

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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 paléobiogéographie 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 coelacanthés 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 (archaeozoological 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 osteichthyan 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

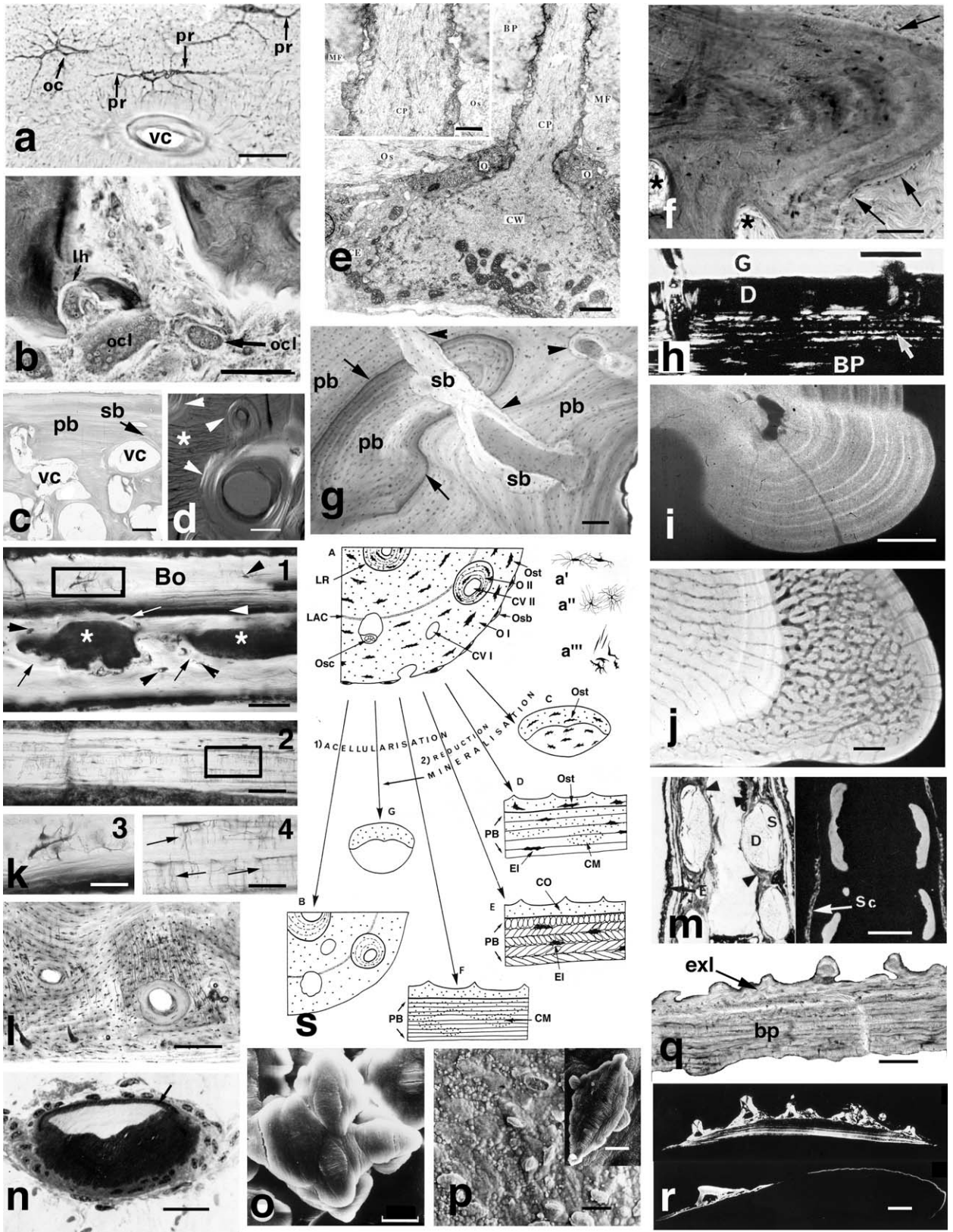
The cells that synthesize the bone substance are the osteoblasts; when they are embedded in the bone matrix, they become osteocytes that reside in an osteocytic lacuna (Francillon-Vieillot et al., 1990; Huisseune, 2000). The osteocytes are star-shaped (Fig. 1a); they show thin cytoplasmic processes laying 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 Huisseune, 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 osteichthyan 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;



- successive strata in which the fibres have the same orientation and are parallel to each other;
- successive strata whose orientation of the fibres differs between two successive strata with an angle of about 90° (Giraud-Guilles, 1988).

These three specific types of arrangement are respectively called woven-fibered bone (Fig. 1f), pseudo-lamellar bone (Fig. 1g), and lamellar bone (Fig. 1h) (Francillon-Vieillot et al., 1990; Ricqlès et al., 1991). Isopedin of elasmoid scales (Meunier, 1987) can be included in the last category. Indeed, isopedin is composed of a series of strata; in each stratum, collagenous fibres are parallel to each other but their orientation changes from one stratum to the next with a given angle (Meunier and Castanet, 1982). This very specific type of lamellar network is a plywood-like structure (Giraud et al., 1978).

2.1.3. Variability of the mineral matrix

The mineral component is generally about 60% of the dry weight of the bone tissue in Osteichthyes (Casadevall

et al., 1990; Francillon-Vieillot et al., 1990) but it is heterogeneously distributed in a given bone (Fig. 1i,j). In fact, recent data have shown a relatively high variability of this parameter in osteichthyans as a whole. This mineralization rate can either decrease or increase by about 20% relatively to this mean value of 60% (Meunier, 1984a).

The progression mode of mineralization in isopedin of teleostean scales (but also in some other taxa) is noteworthy as it involves Mandl's corpuscles (Fig. 1o) (Meunier, 1997; Schönbornner et al., 1981; Zylberberg et al., 1992). These progressively grow and then merge with each other to form a rough mineralization front (Fig. 1p).

2.1.4. The vascular network

The bony tissue of Osteichthyes is a metabolically active tissue that must receive nutrients. Osteocytes take on this trophic role at the cellular level. However, when the bone is thick, especially as in cortical bone, bony tissue is, in a way, "supplied" by blood vessels that bring metabolites into the most internal areas of bone (Fig. 1j). These vessels run in specific tunnels, the vascular canals, which cross the

Fig. 1. a: *Arius parkeri* (Ariidae, Siluriformes, Ostariophysi). Transverse section of a pectoral spiny ray showing lenticulate star-shaped osteocytes (oc) from which numerous cytoplasmic processes emerge (pr) (vc = vascular canal). (Bar = 50 µm); b: *Myleus ternetzi* (Serrasalmidae, Characiformes, Ostariophysi). Transverse section of the dentary showing several plurinucleated osteoclasts (ocl). On the left, there is a Howship's lacunae (lh). (Bar = 50 µm); c: *Trachurus trachurus* (Carangidae, Perciformes, Acanthopterygii). Transverse section of the supraoccipital showing acellular primary (pb) and secondary (sb) bone and several vascular cavities (vc). (Bar = 200 µm); d: *Lethrinus nebulosus* (Lethrinidae, Perciformes, Acanthopterygii). Transverse section (Transmitted polarized light) of a dorsal spiny ray showing primary canalculated bone (asterisk) and several secondary osteons (arrow heads). (Bar = 100 µm); e: *Lepisosteus oculatus* (Lepisosteidae, Holostei). Transverse section of a scale (TEM) showing a cell of Williamson (CW). (Bar = 250 µm); inset: detail of the cell process in the canalculus of Williamson; (BP = basal plate; CP = cell process; CE = lateral cell; MF = mineralisation front; O = osteoblast; Os = osteoid) (from Sire and Meunier, 1994) (Bar = 500 µm); f: *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii). Transverse section of a mandibular dentigerous bone showing fibered primary bone, osteoblasts (arrows) and two vascular cavities (asterisks). (Bar = 200 µm); g: *Cyprinus carpio* (Cyprinidae, Cypriniformes, Ostariophysi). Transverse section (Ehrlich's hematoxyline) of a dorsal spiny ray, showing one arrested growth line (arrows) in primary bone (pb) and several reversal cementing lines (arrowheads) that delimit secondary bone (sb). (Bar = 100 µm); h: *Latinopollia suarezi* (Polypteriformes, Cladistia). Transverse section (Transmitted polarized light) of a scale showing, under the dentine layer (D), eight to ten alternating faint light and dark strata of collagen fibres appearing as in orthogonal plywood (white arrow); (BP = basal plate; G = ganoin) (Meunier and Gayet, 1996). (Bar = 50 µm); i: *Cyprinus carpio* (Cyprinidae, Cypriniformes, Ostariophysi). Microradiograph of a transverse section of a dorsal spiny ray, showing the heterogeneity of mineralization rate of primary bone and the scarcity of vascular canals. (Bar = 500 µm); j: *Hoplosternum littorale* (Callichthyidae, Siluriformes, Ostariophysi). Transverse section (Microradiograph) of a pectoral spiny ray in a male fish, showing a richly vascularized bony tissue, radial canals on the left and a network of canals forming spongy bone on the right. (Bar = 250 µm); k: *Axelrodichthys araripensis*. Transverse section (Transmitted natural light) in the calcified wall of the lung; 1: enlargement of a section showing two bony laminae, separated by a very thin layer of gang (white arrowhead). The upper lamina is constituted of primary bone (Bo) only. The second shows two large vascular cavities (white asterisks), the walls of which are constituted of secondary bone (white and black arrows). The black arrowheads point to osteocytic lacunae and the inset points to Fig. k3. (Bar = 30 µm); 2: enlargement of a bony lamina constituted of primary bone, and showing numerous osteocytes (the inset points to the detail in Fig. k4). (Bar = 30 µm); 3: detail of an osteocyte from the region localized by the inset in Fig. k1. (Bar = 10 µm); 4: detail of osteocytes from the region localized by the inset in Fig. k2, showing the canaliculi that start from the osteocyte lacunae (arrows). (From Brito et al., 2010). (Bar = 10 µm); l: *Eusthenopteron foordi* (Tristichopterygidae, Sarcopterygii). Transverse section (Transmitted natural light) of a dermal plate showing a primary vascular canal on the left, and a secondary osteon on the right with its reversal cementing line. (From Zylberberg et al., 2010). (Bar = 200 µm); m: *Neoceratodus forsteri* (Ceratodidae, Dipnoi). Transverse section (Transmitted natural light on the left; microradiograph on the right) of the caudal fin showing several camptotrichia whose superficial part (S) only is mineralized contrary to the deeper one (D). The arrow heads point to a ligament between two contiguous camptotrichia; (E = epidermis; Sc = scale). (From Géraudie and Meunier, 1984). (Bar = 500 µm); n: *Protopterus annectens* (Lepidosirenidae, Dipnoi). Transverse section (TEM) of a camptotrichia showing the osteoblasts, the mineralized upper collagenous matrix and the unmineralized matrix; the arrow points to unmineralized osteoid. (From Géraudie and Meunier, 1984). (Bar = 50 µm); o: *Thunnus alalunga* (Scombridae, Perciformes, Acanthopterygii). Detail of a Mandl's corpuscle. (Bar = 2 µm); p: *Amia robusta* (Amiidae, Holostei). Mineralization front of the basal plate of a scale (SEM) (From Meunier and Poplin, 1995). (Bar = 500 µm). Inset: a detail of a Mandl's corpuscle of a scale in *Amia calva*. (Bar = 50 µm); q: *Eusthenopteron foordi* (Tristichopterygidae, Sarcopterygii). Transverse section (Transmitted natural light) of a scale showing the two main layers: the ornamented external layer (exl) and the stratified basal (bp) plate the margin of which is irregular that indicates presence of Mandl's corpuscles. (Bar = 50 µm); r: *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii). Transverse section (Transmitted polarized light on the top) and longitudinal section (Microradiograph at the bottom) of two scales showing the two main layers: the ornamented external layer with some odontodes and the unmineralized stratified basal plate. (From Castanet et al., 1975). (Bar = 2 mm); s: recapitulative scheme of the two main evolutionary trends of bony tissues in Osteichthyes: acellularisation (B, E to G) and reduction of mineralization (C to G); A: compact, cellular, vascularized and pseudo-lamellar bone with localized remodelling; a' Acipenser's osteocytes; a'' Anguilla's osteocytes; a''' *Thunnus* osteocytes; B: compact acellular, vascularized and pseudo-lamellar bone with remodelling; C: cellular osseous and cellular unmineralized permanent "proosseous" tissues: camptotrichia of *Neoceratodus forsteri* (Dipnoi, Neoceratodidae); D: cellular bone and partly unmineralized cellular isopedine: scale of *Amia calva* (Amiidae, Holostei); E: acellular bone and partly unmineralized cellular isopedine: scale of *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii) and *Neoceratodus forsteri* (Dipnoi, Neoceratodidae); F: acellular bone and partly unmineralized acellular isopedine: scale of *Hemichromis bimaculatus* (Perciformes, Acanthopterygii, Teleostei); G: acellular bone and unmineralized acellular "proosseous" tissue: camptotrichia of *Protopterus annectens* (Lepidosirenidae, Dipnoi) (CM = Mandl's corpuscle; CO = external layer; CV I = primary vascular canal; CV II = secondary vascular canal; EI = elasmocyte; LAC = arrested growth line; LR = reversal cementing line; O I = primary bone; O II = secondary bone; Osb = osteoblast; Osc = osteoclast; Ost = osteocyte; PB = basal plate).

bone matrix. Depending on the presence/absence of vascular canals, their abundance and their spatial arrangement, various bony tissue types can be defined: e.g., avascular bone that lacks vascularization, vascular bone with radial (Fig. 1i) or longitudinal canals (Fig. 1j) (Francillon-Vieillot et al., 1990; Ricqlès et al., 1991).

2.1.5. The cementing lines

Osteichtyan bony tissue can occasionally show very thin linear chromophilic structures (about 1 µm thick) (Castanet, 1979, 1981). They contain more proteoglycans and less collagenous microfibrils than the surrounding bone; moreover, they are generally weakly hypermineralised (Castanet, 1981). These lines mark temporal disruptions of the osteogenic sequences and they have a

true function of a cement between two phases of bone matrix deposition; they are called cementing lines. These disruptions of the bone-depositing activity are of two types (Fig. 1g,i). First, a complete interruption of the osteogenic processes during the growth phases of the animal, often due to bad climatic conditions: lines of arrested growth (or LAG) (Castanet, 1981), proven to be very useful for sclerochronological applications (Panfili et al., 2002). Second, the start of a local new osteogenic phase in an area where bony tissue has been previously resorbed: reversal cementing lines (RCL). The LAG are observed in primary bone only, resulting from periostic activity, whereas the RCL delimit an area of secondary bone and thus indicate an erosion-reconstruction process responsible for bone remodelling. When bone remodelling affects a vascular canal, the new

Fig. 1. **a:** *Arius parkeri* (Ariidae, Siluriformes, Ostariophysii). Section transversale d'un rayon épineux pectoral montrant des ostéocytes étoilés lenticulaires (**oc**) desquels partent de nombreux prolongements cytoplasmiques (**pr**) (**vc**= canal vasculaire). (Échelle = 50 µm); **b:** *Myleus ternetzi* (Serrasalmidae, Characiformes, Ostariophysii). Section transversale d'un dentaire montrant des ostéoclastes plurinucléés (**ocl**). Sur la gauche, on remarque une lacune de Howship (**lh**). (Échelle = 50 µm); **c:** *Trachurus trachurus* (Carangidae, Perciformes, Acanthopterygii). Section transversale d'un supraoccipital montrant de l'os acellulaire primaire (**pb**) et secondaire (**sb**), ainsi que plusieurs cavités vasculaires (**vc**). (Échelle = 200 µm); **d:** *Lethrinus nebulosus* (Lethrinidae, Perciformes, Acanthopterygii). Section transversale (Lumière transmise polarisée) d'un rayon épineux dorsal montrant de l'os primaire riche en canalicules cytoplasmiques (astérisque) et plusieurs ostéones secondaires (têtes de flèches). (Échelle = 100 µm); **e:** *Lepisosteus oculatus* (Lepisosteidae, Holostei). Section transversale d'une écaille (MET) montrant une cellule de Williamson (**CW**) (échelle = 250 µm); encadré : détail d'un prolongement cytoplasmique dans la canalicule de Williamson; (**BP**= plaque basale; **CP**= prolongement cellulaire; **CE**= cellule latérale; **MF**= front de minéralisation; **O**= ostéoblaste; **Os**= ostéoïde) (d'après Sire et Meunier, 1994) (échelle = 500 µm); **f:** *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii). Section transversale d'un os dentigère mandibulaire montrant de l'os fibreux primaire, des ostéoblastes (flèches) et deux cavités vasculaires (astérisques). (Échelle = 200 µm); **g:** *Cyprinus carpio* (Cyprinidae, Cypriniformes, Ostariophysii). Section transversale (Hématoxyline d'Ehrlich) d'un rayon épineux dorsal, montrant une ligne d'arrêt de croissance (flèches) dans l'os primaire (**pb**) et plusieurs lignes cimentantes de réversion (têtes de flèches) qui délimitent l'os secondaire (**sb**). (Échelle = 100 µm); **h:** *Latinopollia suarezi* (Polypteriformes, Cladistia). Section transversale (Lumière polarisée transmise) d'une écaille, montrant sous la couche de dentine (D), huit à dix strates alternativement sombres et claires et indiquant une organisation des fibres de collagène en un « contre-plaqué » orthogonal (flèche blanche); (**BP**= plaque basale; **G**= ganoïne) (Meunier et Gayet, 1996). (Échelle = 50 µm); **i:** *Cyprinus carpio* (Cyprinidae, Cypriniformes, Ostariophysii). Microradiographie d'une section transversale dans un rayon épineux dorsal, montrant un taux de minéralisation hétérogène de l'os primaire et le petit nombre de canaux vasculaires. (Échelle = 500 µm); **j:** *Hoplosternum littorale* (Callichthyidae, Siluriforme, Ostariophysii). Section transversale (Microradiographie) d'un rayon épineux pectoral d'un individu mâle, montrant un tissu osseux richement vascularisé, avec des canaux radiaires sur la gauche et un réseau complexe de canaux formant de l'os spongieux sur la droite. (Échelle = 250 µm); **k:** *Axelrodichthys araripensis*. Section transversale (Lumière naturelle transmise) dans la paroi calcifiée d'un poulmon; **1:** agrandissement d'une section montrant deux laminae osseuses, séparées par une très fine couche de gangue (tête de flèche blanche). La lamina supérieure est constituée seulement d'os primaire (**Bo**). La seconde montre deux grandes cavités vasculaires (astérisques blancs) dont les parois sont constituées d'os secondaire (flèches blanches et noires). Les têtes de flèches noires pointent les lacunes ostéocytaires et l'encadré renvoie à la Fig. k3. (Échelle = 30 µm); **2:** agrandissement d'une lamina constituée d'os primaire, et montrant de nombreux ostéocytes (l'encadré renvoie à la Fig. k4). (Échelle = 30 µm); **3:** détail d'un ostéocyte de la région localisée dans l'encadré de la Fig. k1. (Échelle = 10 µm); **4:** détail des ostéocytes de la région localisée dans l'encadré de la Fig. k2, montrant les canalicules qui partent des lacunes ostéocytaires (flèches) (d'après Brito et al., 2010) (échelle = 10 µm); **l:** *Eusthenopteron foordi* (Tristichopteridae, Sarcopterygii). Section transversale (Lumière naturelle transmise) d'une plaque dermique, montrant un canal vasculaire primaire à gauche, et un canal vasculaire secondaire, à droite, limité par une ligne cimentante de réversion (d'après Zylberberg et al., 2010) (échelle = 200 µm); **m:** *Neoceratodus forsteri* (Ceratodidae, Dipnoi). Section transversale (Lumière naturelle transmise à gauche; microradiographie à droite) de la nageoire caudale montrant plusieurs camptotriches dont seule la partie superficielle (**S**) est minéralisée, contrairement à la zone profonde (**D**). Les têtes de flèches montrent des structures ligamentaires entre deux camptotriches adjacents; (**E**=épiderme; **Sc**=écaille). (d'après Géraudie et Meunier, 1984). (Échelle = 500 µm); **n:** *Protopterus annectens* (Lepidosirenidae, Dipnoi). Section transversale (TEM) d'un camptotriche montrant des ostéoblastes, la matrice collagénique superficielle minéralisée (claire) et la partie profonde non minéralisée (sombre); la flèche indique la substance ostéoïde superficielle avant sa minéralisation (d'après Géraudie et Meunier, 1984). (Échelle = 50 µm); **o:** *Thunnus alalunga* (Scombridae, Perciforme, Acanthopterygii). Détail d'un corpuscule de Mandl. (Échelle = 2 µm); **p:** *Amia robusta* (Amiidae, Holostei). Front de minéralisation de la plaque basale d'une écaille (MEB) (d'après Meunier et Poplin, 1995). (Échelle = 500 µm). Encadré : détail d'un corpuscule de Mandl d'une écaille d'*Amia calva*. (Échelle = 50 µm); **q:** *Eusthenopteron foordi* (Tristichopteridae, Sarcopterygii). Section transversale (Lumière naturelle transmise) d'une écaille montrant les deux couches principales : la couche externe ornementée (**ex1**) et la plaque basale stratifiée (**bp**) dont la limite inférieure est irrégulière, ce qui indique la présence de corpuscules de Mandl. (Échelle = 50 µm); **r:** *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii). Section transversale (Lumière transmise polarisée en haut) et section longitudinale (Microradiographie en bas) de deux écailles montrant deux couches : la couche externe ornementée qui supporte quelques odontodes et la plaque basale stratifiée non minéralisée (d'après Castanet et al., 1975). (Échelle supérieure ou égale à 2 mm); **s:** schéma récapitulatif des deux tendances évolutives des tissus osseux chez les Ostéichtyens : acellularisation (B, E–G) et réduction de la minéralisation (C–G); **A:** os compact, cellulaire, vascularisé et pseudo-lamellaire, avec un remaniement localisé; **a'** ostéocytes d'Acipenser; **a''** ostéocytes d'Anguilla; **a'''** ostéocytes de *Thunnus*; **B:** os compact acellulaire, vascularisé et pseudo-lamellaire, avec remaniement; **C:** tissu osseux cellulaire minéralisé et tissu « pré-osseux » cellulaire non minéralisé permanent : camptotriches de *Neoceratodus forsteri* (Dipnoi, Neoceratodidae); **D:** os cellulaire et isopédine cellulaire incomplètement minéralisée : écaille d'*Amia calva* (Amiidae, Holostei); **E:** os acellulaire et isopédine cellulaire non minéralisée : écaille de *Latimeria chalumnae* (Coelacanthidae, Actinistia, Sarcopterygii) et de *Neoceratodus forsteri* (Dipnoi, Neoceratodidae); **F:** os acellulaire et isopédine acellulaire incomplètement minéralisée : écaille d'*Hemichromis bimaculatus* (Perciforme, Acanthopterygii, Teleostei); **G:** os acellulaire et tissu « pré-osseux » acellulaire non minéralisée : camptotriches de *Protopterus annectens* (Lepidosirenidae, Dipnoi) (**CM**= corpuscule de Mandl; **CO**= couche externe; **CV I**= canal vasculaire primaire; **CV II**= canal vasculaire secondaire; **El**= élastomocyte; **LAC**= ligne d'arrêt de croissance; **LR**= ligne cimentante de réversion; **O I**= os primaire; **O II**= os secondaire; **Os b**= ostéoblaste; **Os c**= ostéoclaste; **Os t**= ostéocyte; **PB**= plaque basale).

From Meunier, 1987; Meunier and Huysseune, 1992.

layers of bone matrix form a secondary vascular cavity (Fig. C, k1) or secondary osteon (Fig. 1d,l).

2.2. Bony tissue typology

Generally, in one individual, bony tissue differs from one bone to another or, even, between several areas of the same bone. It can also change all along the life of the animal, as in tetrapods. Bony tissue characteristics can also vary from one species to the next. Because of these numerous bony-tissue characteristics, histologists have constructed typological classifications of bone. Subsequently, they have realized that these typologies may have a functional significance; therefore, it is now possible to establish a functional classification of bony tissue essentially based on the components of bone and on the modalities of bone vascularization (Francillon-Vieillot et al., 1990; Ricqlès et al., 1991).

3. Some steps of this history

3.1. Origin and palaeobiogeography of the Polypterids

The ganoid scale of Polypterids is composed of the three layers typical for scales of Palaeonisciforms: a superficial layer of ganoine covering a layer of lacunar and vascular dentine, and a deeper layer, the basal plate, made of bony tissue (Daget et al., 2001). However, a fourth layer located between the dentine layer and the bony basal plate has been described (Sire, 1989, 1990; Sire et al., 2009); it consists of a series of collagenous strata organised in an orthogonal plywood-like structure. This fourth layer is true isopedine (or elasmidine; Schultze, 1996) and it is regarded as a specificity of Polypterids. Even though polypterid fossil remains were known only from the Upper Cenozoic times till the eighties, palaeohistological studies of isolated scales from Cenomanian-Santonian localities of Africa revealed that they had an isopedine layer between dentine and basal plate. These scales therefore belonged to a polypterid and as a consequence the geological age of Polypteridae was seriously increased (Gayet and Meunier, 1996; Gayet et al., 1988). Moreover, similar studies performed on Maastrichtian and early Late Palaeocene isolated scales from Bolivia (Gayet and Meunier, 1992; Meunier and Gayet, 1996) and East Brazil revealed also the presence of an isopedine layer (Fig. 1h). This identification proves that polypterids must have lived in South America. Because this taxon is a strictly primary freshwater inhabitant, e.g. a primary fish strictly intolerant to salt water (Banarescu, 1990, 1995; Myers, 1949), polypterids must have been older than the opening of the South Atlantic Ocean during the Lower Cretaceous. A second conclusion can be inferred from these palaeohistological studies: the polypterids already had a very recognizable morphology in the Cretaceous, as confirmed by the presence of dorsal finlet spines and vertebrae (both being morphological characters of extant polypterids) in the various Cretaceous fossil beds in Africa (Daget et al., 2001) and South America (Dutra and Malabarba, 2001). Moreover, an articulated fossil cladistian, which has been described from the Cretaceous of Morocco (Dutheil, 1996), indicates the great

diversification of this group during the Upper Cretaceous (Daget et al., 2001).

3.2. The ossified lung of the Coelacanthids

The extant osteichthyan diversity is illustrated by the teleosts, which have colonized a multitude of available biotopes. Looking back into geological times, osteichthyan diversity is essentially represented by the Sarcopterygii and the actinopterygian predecessors of teleosteans. Palaeohistological studies can tackle interesting biological topics such as the so-called “calcified lung” (Williamson, 1849) of most of the fossil coelacanthids. Histological studies of the lung of the Aptian-Albian coelacanthid *Axelrodichthys araripensis* (Brazil) have shown that the walls of the lung were composed of osseous sheets (Fig. 1k) (Brito et al., 2010). These sheets show all the characteristics of true bone: lamellar matrix with osteocytes (Fig. 1k2–4), primary and secondary vascular canals or cavities (Fig. 1k1). One question arises: what can be the real function of such an, a priori, “rigid lung”?

In living individuals, the pulmonary walls were reinforced by ossified plates, probably separated by connective tissue; therefore, each plate may have moved independently from the others. This calcified organ present in *Axelrodichthys* is in a ventral position and its single anterior opening is located under the opercule, suggesting a direct connection with the pharynx or the oesophagus. The calcified organ of *Axelrodichthys*, like that of other fossil coelacanthids, is here regarded as an ossified lung. The reinforcement of the pulmonary walls by the overlying osseous sheets is interpreted as a means of adapting volumetric changes in the manner of bellows, a necessary function for air ventilation in pulmonary respiration. Other functional hypotheses such as hydrostatic and/or acoustic functions have also been discussed (Brito et al., 2010).

3.3. Organisation of elasmoid scales in the Sarcopterygii

Within the actinopterygian clade, the so-called ganoid scales are thick juxtaposed rhomboid scales observed in “basal” taxa. These scales have evolved into imbricated thin and flexible elasmoid scales in various more recent taxa (Meunier, 1981, 1984b; Meunier and Brito, 2004; Schultze, 1966, 1977; Sire et al., 2009). This evolutionary process has contributed to a lightening of the dermal skeleton (Zylberberg et al., 1992), and has improved the efficiency of swimming (Burdak, 1979). Similar specializations can be pointed out in the sarcopterygian clade, e.g. the thick cosmoid scales of extinct osteolepids (Ørving, 1957; Sire et al., 2009; Thomson, 1975) and the elasmoid scales of extant dipnoids and coelacanthids (Meunier and François, 1980; Meunier and Zylberberg, 1997; Meunier et al., 2008). In *Neoceratodus* and *Latimeria* (Fig. 1r), elasmoid scales present an extreme specialization, because the basal plate is composed of an unmineralized network of collagenous fibres that are organized into a double twisted plywood (Giraud et al., 1978). Palaeohistological studies of various sarcopterygian taxa show intermediate states of differentiation (Ørving, 1957; Schultze, 1977), with scales where the basal plate is partly mineralised as, for example,

the scales of the Late Devonian (Frasnian) tetrapodomorph *Eusthenopteron foordi* (Fig. 1q) (Zylberberg et al., 2010). In this species, we can observe a true plywood organization of the basal plate, which shows an obvious mineralisation front characterized by Mandl's corpuscles (Zylberberg et al., 2010).

3.4. Evolution of bony tissues in Osteichthyes

The bony tissues in the Osteichthyes have been subjected to few evolutionary trends across geological times (Denison, 1963; Francillon-Vieillot et al., 1990; Ørvig, 1968; Ricqlès et al., 1991). There are only new arrangements of the constituents that already exist when the mineralised osseous tissues appear. These arrangements reveal various adaptive trends (Ørvig, 1968).

However, three main trends can be mentioned when we examine the bony skeleton of Osteichthyes over geological times, i.e. from the Palaeozoic to the present. The first one is obvious at the morpho-anatomical level: it is the progressive reduction of the skeleton, especially the dermal skeleton. This reduction of the dermal skeleton is obvious when looking at the Palaeozoic armoured Heterostraci, Osteostraci and Placodermi compared to the extant Teleostei (Janvier, 1996), and even occurred within Osteostraci (Otto and Laurin, 2001). The two other trends are revealed at the micro-anatomical level: acellularisation of bone and reduction of its mineralization. These two processes are summarized and illustrated in Fig. 1s.

Acellularisation of bone is a heterochronic process that has appeared several times in the history of agnathans and gnathostomes. The aspidine of heterostracans, an extinct agnathan group from the Palaeozoic, is a true acellular bony tissue (Halstead, 1963, 1969) and the most ancient (Denison, 1963; Ørvig, 1951, 1968). In osteichthyans, acellular bone is known from the sarcopterygian Lepidosirenidae, more precisely from their fin rays, the camptotrichia (Fig. 1s G) (Géraudie and Meunier, 1984) and from some teleostean taxa (Meunier, 1987). Among extant teleosteans, more than half of the species have acellular bone (Fig. 1s B, F–G), including a part of the Salmoniforms and Acanthomorpha (Kölliker, 1859; Meunier, 1987; Moss, 1961, 1965; Stephan, 1900) except for some Thunninae (Amprino and Godina, 1956).

The progressive reduction of mineralization had developed in the dermal skeleton and is especially noticeable in the scales (Fig. 1s D–F and Fig. 1o–r), but also in a variety of dermatotrichia, such as the camptotrichia (Fig. 1s C, G and Fig. 1m–n). Therefore, the evolutionary trends within the Osteichthyes consist of the acquisition of a cellular bone within the various lineages or the loss of mineralization e.g. in the camptotrichia of *Neoceratodus*; but these two trends can also co-occur, as in the basal plate of the eslamoid scales of the majority of Teleostei (Meunier, 1987; Meunier and Huysseune, 1992; Sire and Meunier, 1981).

Another example of the difficulty of classifying skeletal tissues within Osteichthyes is provided by chondroid bone (not reviewed in the present paper; Benjamin, 1989; Huysseune and Sire, 1990), a tissue with characteristics intermediate between cartilage and bone and found mostly

in articular areas in the head of Teleostei (Huysseune and Verraes, 1986; Meunier and Huysseune, 1992).

4. Conclusions

Cartilages, bones and teeth have long been considered as inert in Osteichthyes. In fact, this is not true, as shown by the extensive remodelling process observed for example in the vertebrae of Tuna (Amprino and Godina, 1956), even though remodelling can be relatively modest in certain other species. Bone in the osteichthyan skeleton is a living tissue that has various physiological functions (Meunier and François, 1992), and as such, it maintains close relationships with the other tissues of the organism. Thus, remodelling in osteichthyan bony tissues ensures exchanges between bone and the inner medium and thus, participates in various homeostatic activities that are under hormonal control (Kacem et al., 1998; Persson et al., 1998; Kacem and Meunier, 2003, 2009; Lopez, 1973; Sbahi et al., 2007, 2009; Witten and Hall, 2003). Examples of very active mineralised tissue remodelling are known from Palaeozoic sarcopterygians (Thomson, 1975) and from the Mesozoic semionotid *Lepidotyle* (Meunier and Gayet, 1992); a migratory behaviour between rivers and seas, perhaps because of reproductive necessities, has been hypothesized to explain these erosion-reconstruction processes that allow a release of mineral ions trapped into the bone (Meunier and Gayet, 1992; Thomson, 1975, 1977).

From a physiological point of view, the osteichthyan skeleton is under the control of various factors: mineral (Ca, P) supply, hormones, vitamins... (Lall and Lewis-McCrea, 2007). Moreover, skeletal growth leads to changes in bone morphology and proportion (Ricqlès et al., 1991) while maintaining the mechanical functions of bone, such as the transmission of thrust by the vertebral axis during swimming (Meunier and Ramzu, 2006). The osteichthyan skeleton is a morpho-functional complex that has been neglected for a long time by physiologists who focused on other anatomical systems playing other functions like swimming, feeding, blood circulation, homeostasy, reproduction, excepted for the cellular bone of teleosts such as eels, some cyprinids, and the salmonids. Fortunately, in the last two decades, the situation has progressed, especially with acellular bone of some species, particularly on the medaka, a cyprinodontid, and on various cichlids (Witten and Huysseune, 2009). However, it would be useful to study larger, commercially important species, such as the sea bream, the turbot, and the bass. In general, comparative histophysiological studies constitute a promising field of scientific research that will significantly improve our understanding of bone biology, especially in fossil Osteichthyes, but also in Teleostei that represent 95% of the extant Osteichthyes.

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