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The skeleton and the mineralized tissues of the living coelacanths

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(Received August 12, 2018; accepted October 22, 2018)

ABSTRACT — The present overview of the histological studies on *Latimeria* mineralized tissues, since the discovery of the first living coelacanth in 1938, allows some anatomical and evolutionary considerations. It enlightens: i) a drastic reduction of cartilage to bone transformation processes during evolution; ii) the persistence of large volume of cartilage in the endoskeleton at adult stage; iii) the bony nature of the plates that surround the lung diverticle; iv) the presence of a developed process of spheritic mineralization in various skeletal organs: in teeth, in odontodes of the tegumentary skeleton (scales, fin rays), in scales at the interface between the external layer and the basal plate, as well as in lung bony plates.

INTRODUCTION

The first study of fossil coelacanths was done by AGASSIZ (1833–44) and was followed by a lot of papers with the discovery of new fossils (see reviews of JANVIER, 1996 and FOREY, 1998). Fossil coelacanths constitute an important monophyletic group composed of more than forty genera, eighty species, and belong to the Sarcopterygii (ANDREWS, 1973; JANVIER, 1996; FOREY, 1998; UYENO and YABUMOTO, 2007; and many others). For a century coelacanths were considered extinct since the end of the Cretaceous time (Fig. 1).

With the discovery of a living coelacanth in 1938 (SMITH, 1939) the scientific community was soon highly interested to compare the incomplete fossil sarcopterygian fishes dataset to the recent anatomical and biological organization of Latimeria chalumnae. Many authors (see THOMSON, 1969; MILLOT and ANTHONY, 1958; MILLOT et al., 1978 FOREY, 1984, 1998; JANVIER, 1996) focused their work on Latimeria as a key-taxon to test or propose various hypotheses on the origin and evolutionary history of the early tetrapods and sarcopterygii in general, and to infer their possible biological characteristics. The fossil sarcopterygian fishes are known by their fossilized mineralized tissues, essentially their bones, scales and teeth. Together with the extant lungfishes, especially Neoceratodus, Latimeria offered a unique access to the skeleton as a whole: with both mineralized and unmineralized skeletal tissues. Here, we aim to present an overview of the last eighty years (1938–2018) of histological studies of Latimeria's skeleton.

Since the discovery of the Raja Laut ("king of the sea"), off Sulawesi Island in Indonesia (ERDMANN *et al.*, 1998, 1999), the genus *Latimeria* comprises two species: *L. chalumnae* SMITH 1939 and *L. menadoensis* POUYAUD *et al.*, 1999. However our knowledge of the anatomy and biology of the living coelacanths is so far essentially based on *L. chalumnae*.

THE LATIMERIA SKELETON

The first anatomical observations on the extant coelacanth were done by SMITH (1940). The anatomy of the Latimeria skeleton has been later described in detail by MILLOT and ANTHONY (1958). The living coelacanth shows a general organization similar to that of the other actinistian fishes (THOMSON, 1969; JANVIER, 1996; FOREY, 1998). The skeleton can be divided in various parts (Fig. 2): skull, axial skeleton, paired and unpaired fins, tegumentary skeleton (scales). The skull, axial skeleton and fins are constituted of endoskeletal elements that are overlain by exoskeletal elements. In the extant Latimeria the endoskeleton of the skull shows an important regression of the bones, especially in the neurocranium, which are replaced by cartilaginous tissues, as in its Mesozoic fossil actinistian relatives (ROMER, 1937, 1942; MILLOT and ANTHONY, 1958; BJERRING, 1973; FOREY, 1998). In the same way, the endoskeleton of paired and unpaired fins is essentially constituted of four axial cartilaginous elements (Fig. 2; MILLOT and ANTHONY, 1958), with pre and post-axial



Fig. 1. Schematic phylogeny of nine fossil genera of Actinistia and the extant *Latimeria*. (modified from CASANE and LAURENTI, 2013, fig. 1).

elements and eventually minute superficial endochondral ossification (CASTANET *et al.*, 1975). The axial skeleton is composed of the notochord which is coated by an unmineralized fibrillary sheath and is totally deprived of well developed vertebrae due to the lack of ossified centra, although some discrete neural and haemal arches develop in the anterior part of the notochord (MILLOT and ANTHONY, 1958). The anterior neural and haemal spines are relatively short but they progressively increase in length posteriorly. Importantly neural and haemal spines are composed of perichondral bone surrounding a cartilaginous core (Fig. 2).

The scales belong to the exoskeleton. In both extant coelacanth species they are of elasmoid type, composed of an upper external layer also called "external ornamented layer", and of a lower thicker layer, called the basal plate, which is stratified and almost totally unmineralized (Fig. 3). The upper external layer is ornamented with radial crests. In the posterior area of the scale these radial reliefs are overlain by numerous denticulations, the odontodes, which can be superposed (Fig. 3). The anterior area of the external layer, which is covered by the anterior scales, shows crests with irregularities that have been interpreted as growth marks and tentatively used for ageing coelacanths (HUREAU and OZOUF, 1977; MILLER, 1979).

The tooth plates of the buccal cavity support series of teeth of various sizes (Fig. 4). They range in three morphotypes: the fangs (7–10 mm in height), middle-sized teeth (3–4 mm in height) and rounded tubercles (MILLOT and ANTHONY, 1958). The teeth of the two first categories are conical and sharp whereas those of the third category have an obtuse tip (Fig. 5). Fangs of *Latimeria* are inserted into a socket (MILLOT and ANTHONY, 1958; HOBDELL and MILER, 1969; CASTANET *et al.*, 1975) and they have a smooth external surface (MILLOT *et al.*, 1978; MEUNIER *et al.*, 2015).

A particularity of the exoskeleton of *Latimeria* is the abundance of odontodes at the surface of various skull bones



Fig. 2. *Latimeria chalumnae*. Skeleton (bones, cartilages and fin rays) of entire fish based on MILLOT and ANTHONY (1958) and after FOREY (1998). Note *i*) the monobasal insertion of pectoral, pelvic, anal and second dorsal fins on their respective girdle; *ii*) the presence of minute neural and haemal arches (respectively arrow-heads and arrows). (Scale = 100 mm).



Fig. 3. *Latimeria chalumnae* and *L. menadoensis*. Details of the posterior field of scales (SEM). A, *L. chalumnae*. General view of the odontodes. The posterior margin of the scale is on the upper left. (scale = $500 \mu m$). B, *L. menadoensis*. General view of the odontodes. The posterior margin of the scale is on the upper right. (scale = $500 \mu m$). C, *L. menadoensis*. Closed-up view of the odontodes positioned on the radial crests of the external layer. (scale = $100 \mu m$). D, *L. chalumnae*. Closed-up view of the odontodes positioned on the radial crests of the external layer, and two superimposed odontodes are seen on the right (*). (scale = $100 \mu m$). E, *L. chalumnae*. Closed-up view of two superimposed odontodes with the apical part of the lower one being eroded (arrow). (scale = $100 \mu m$). (After MEUNIER *et al.*, 2008).



Fig. 4. *Latimeria chalumnae*. Buccal roof showing the different tooth types: fangs (black arrow-heads), small caniniform teeth (white arrow-heads) and patches of round shaped teeth (black arrows), especially on the parasphenoid tooth plate (t.par) and the medial side of the pterygoid (t.pt). The front side is on the top of the figure. (After MILLOT and ANTHONY, 1958). (scale = 10 mm).



Fig. 5. Latimeria chalumnae. Coronoid and coronoid tooth structure. A, Tomographic imaging of a coronoid element. Three-dimensional reconstruction of the dental plate showing a fang, one mid-sized caniniform tooth (*) and numerous small round-shaped teeth (arrow-heads). The virtual section shows i) the plies of the dentine in the lower half of the pulp cavity (pc); ii) the bone of attachment (ba) between the tooth and the coronoid bony tissue. On the right of the figure, the coronoid shows a network of vascular cavities and canals (vc). (de = dentine; en = enamel) (scale = 1 mm). (After MEUNIER *et al.*, 2015, Fig. 9-10). B, Microradiography of a cross section at the base of a fang showing several plies of the dentine wall (white arrow-heads). (bo = bone; pc = pulp cavity; de = dentine). (scale = 1 mm). (from CASTANET *et al.*, 1975). C, Scanning Electron Microscopy of the spheritic dentine. The white and black asterisks point respectively to the external surface of the tooth and to the wall of the pulp cavity. (scale = 25 μm).

(MILLOT and ANTHONY, 1958; BERNHAUSER, 1961), on the fin rays (CASTANET *et al.*, 1975) and on the posterior (free) area of scales (Fig. 3) (MILLOT and ANTHONY, 1958; CASTANET *et al.*, 1975; HADIATY and RACHNATIKA, 2003; MEUNIER *et al.*, 2008).

Among the various components of the whole skeleton, and apart the SMITH's pioneer work (SMITH, 1940), numerous studies have been carried out on the histological organization of scales (ROUX, 1942; SMITH *et al.*, 1972; CASTANET *et al.*, 1975; GIRAUD *et al.*, 1978a; MILLER, 1979; SMITH, 1979; MEUNIER, 1980; MEUNIER and ZYLBERBERG, 1999; HADIATY and RACHMATIKA, 2003; MEUNIER *et al.*, 2008) and teeth (MILLER and HOBDELL, 1968; GRADY, 1970; HOBDELL and MILLER, 1969; CASTANET *et al.*, 1975; SHELLIS and POOLE, 1978; SMITH, 1978; SASAGAWA *et al.*, 1984; MEUNIER *et al.*, 2015). Contrary to the superficial skeleton, there are clearly less histological studies of the skeletal bony elements (FRANCILLON *et al.*, 1975). Meanwhile, in addition to the usual skeletal elements, specific bony tissues have been described in fossil (BRITO *et al.*, 2010) and extant coelacanths (CUPELLO *et al.*, 2015, 2017), such as the mineralized plates surrounding the lung. These bony plates in actinistians do not belong to the skeleton *sensu stricto*. They are specific bony specializations in relation to the lung (see below), as is the "rocker bone" in relation to the gas bladder of some ophidiiform teleosts (PARMENTIER *et al.*, 2008). Despite the name, the rocker bone is not true bony tissue (PARMENTIER *et al.*, 2008), contrary to



Fig. 6. Latimeria chalumnae. Bone histology. A, Thin section in a coronoid bone (Basic fuchsin staining) showing primary bone (pb) with osteocytes, secondary bone (sb), a cementing line (arrow-heads) and a vascular cavity (vc). (scale = $50 \mu m$). Inset: detail of osteocytes (arrow-heads) and their osteocytic canalicles. (scale = $25 \mu m$). B. Thin section in a coronoid bone (Hemalun-PIC staining) showing cellular primary bone (pb) and its periostic membrane (white arrows). On the right, numerous collagenous fibres (cf) enter the bony matrix where they form SHARPEY's fibres. The asterisks points to secondary vascular cavities limited by cementing lines (white arrow-heads); a primary vascular canal (vc) is seen. (scale = 100 μ m). C, X-ray ground section in the cortical region of the angular showing primary bone with regular alternative of heterogeneous mineralized bony tissue. The black arrow-heads point to primary vascular canals, the white arrows to cementing lines, and the white arrow-heads to erosive bays. The asterisks point to two confluent secondary vascular cavities). (scale = $200 \ \mu m$). D, Ground section of the angular, in a deeper region than C. Several bulks of secondary bone (sb) are limited by cementing lines (black arrow-heads). Primary bone (pb) persists in different areas. The white asterisks point to secondary vascular cavities. (scale = $200 \ \mu m$). (C, D: After FRANCILLON et al., 1975).

the bony plates of fossil and extant coelacanths (BRITO *et al.*, 2010; CUPELLO *et al.*, 2017).

ADULT LATIMERIA SKELETAL TISSUES

Bony tissues

Cortical areas of the dermal skeleton are constituted of primary periosteal bony tissue. Its mineralization is heterogeneous and generally marked by series of growth lines, probably due to alternative physiological cycles linked to seasonal variations (Fig. 6). The cortical primary bone shows vascular canals and numerous SHARPEY's fibres (Fig. 6B). The centre of these bones is frequently made of a spongiosa with vascular cavities surrounded by secondary bony deposits that result from remodelling processes (Fig. 6). This secondary bone is separated from the primary one by reversal cementing lines that are hypermineralized.

Bone remodelling in adult specimens can be more or less developed according to a bone and within a given bone. Primary bone is destroyed by osteoclasts and the deposition process of the secondary bone results from the activity of osteoblasts that have replaced the osteoclasts. The secondary bone does generally not replaced the whole primary bone areas, which can still be recognizable by the presence of



Fig. 7. Latimeria menadoensis and L. chalumnae. Ground sections of scales. A, L. menadoensis. Longitudinal section; X-ray. The superficial bony layer (bo) and the odontodes (arrow-heads) are mineralized whereas the basal plate (BP) totally lacks mineralization (asterisks). Vascular canals are present within the superficial bony layer. The arrow on the upper right indicates the direction of the head. B–C, L. chalumnae. Transversal sections; respectively polarized light and X-ray. B, The basal plate is made of stratified layers of collagenous fibres (arrow). The arrow-heads point to the superficial odontodes. C, The superficial bony layer and the odontodes (arrow-heads) are mineralized whereas the basal plate (BP) totally lacks mineralization (asterisks). D, L. chalumnae. Longitudinal section; X-ray. The superficial bony layer (bo) and the odontodes (arrow-heads) are mineralized whereas the basal plate (BP) totally lacks mineralization (asterisks). D, L. chalumnae. Longitudinal section; X-ray. The superficial bony layer (bo) and the odontodes (arrow-heads) are mineralization (asterisks). (af = anterior field; pf = posterior field). E, L. menadoensis. Broken frozen scale showing the different fibres directions in the successive layers of the basal plate. The rotation of the fibres directions from one layer to another characterizes a plywood-like organization. The arrow points to the crests of the superficial layer. (A, B, C: scale = 1 mm; D: scale = 2 mm; E: scale = 200 μm). (B, C, D after CASTANET et al., 1975; A, E after MEUNIER et al., 2008).

SHARPEY's fibres and/or growth marks (Fig. 6).

The dermal fin rays that sustain paired and unpaired fins in Latimeria are true lepidotrichia (CASTANET et al., 1975). They are made of two parallel opposite gutter-shaped hemirays, each of which being a series of hemisegments articulated by a collagenous ligament. Each hemisegment is made of a mineralized collagenous fibrillary matrix with embedded osteocytes. The hemisegments are sometimes fused at the basal part of the rays due to centrifugal deposition of bony laminae around the primary articulation, and eventually to the mineralization of the ligament (see figs. 19, 20 in CASTANET et al., 1975). Odontodes observed on the external convex surface of the rays are similar to those present on the dermal bones of the skull and scales. The distal extremity of the lepidotrichia is overlapped by actinotrichia (GÉRAUDIE and MEUNIER, 1980) that are long tapered rods of elastoidin, a fibrous protein of collagenous nature (FAURÉ-FREMIET, 1936; GARRAULT, 1936). The presence of lepidotrichia with distal actinotrichia in Latimeria, as in the fins of Actinopterygii, is

regarded as a plesiomorphic character for Osteichthyes (GéRAUDIE and MEUNIER, 1980, 1984).

The upper layer of the Latimeria scale is relatively thin and it is constituted of bony tissue with embedded osteocytes, whereas the basal plate is much thicker and composed of numerous strata made of thick collagenous fibres (Fig. 7). Between two collagenous layers there are star-shaped cells (SMITH et al., 1972, pl. VI; CASTANET et al., 1975, fig. 12), the elasmocytes, which cytoplasmic processes insert between the collagenous fibres. These fibres are set in a very specific network. In each layer, the fibres are parallel to each other and the direction of the fibres change from a layer to another one. This regular organization results in a spatial arrangement termed "twisted plywood" (GIRAUD et al., 1978a,b). The rotation of fibres direction from one layer to the next has a mean angle of 27° (GIRAUD et al., 1978a). This organization is found in each scale of L. chalumnae. In L. menadoensis, the basal plate of the scales is also a twisted plywood but its rotation angle seems to be slightly less regular (MEUNIER et al.,



Fig. 8. Latimeria chalumnae. Cartilage histology (after FRANCILLON et al., 1975). A, MECKEL's cartilage (thin histological section; Hemalun-PIC staining). An erosive vascular cavity (black asterisk) is separated from the medullary cavity (mc) by a layer of enchondral bone (eb). Elongate chondrocytes (arrow-heads) are seen in the cartilage. (scale = $50 \mu m$). B, Scapulocoracoid (ground section 3 mm thick; x-ray). The cartilage (ca) is invaded by resorption canals (white asterisks), their wall is covered by thin bony layers, here clearly visible in white colour. The white arrow-heads point to the erosion front of the cartilage. (scale = 1 mm). C, Scapulocoracoid (thin histological section; Stoelzner staining). In the cartilage (ca), the vascular cavities (vc), resulting from a chondroclastic activity, are bordered by thin bony lamellae here visible in black colour (arrow-heads). (scale = $250 \mu m$).

2008). The basal plate in both species is unmineralized (Fig. 7) excepted at the contact between the superficial layer and the basal plate, where spheritic mineralized granules are seen in the very first layers of the basal plate (MEUNIER, 1980; MEUNIER and ZYLBERBERG, 1999; MEUNIER *et al.*, 2008). There is no pore-canal system so *Latimeria*'s scales are not cosmoid, contrary to most of palaeozoic sarcopterygian fishes. Due to the presence of an unmineralized stratified basal plate, the scales of *Latimeria* are defined as elasmoid-like scales. However the plywood-like organization is considered to be homologous with the bony basal plate of cosmoid scales of extinct sarcopterygian fishes (MEUNIER, 1980; SIRE and HUYSSEUNE, 2003; MONDEJAR, 2018; SCHULTZE, 2018). **Cartilages**

The cartilaginous tissues in Latimeria are characterized by long chondrocytes (Fig. 8) contrary to those of teleostean fishes that are relatively spherical in shape (MEUNIER, 1979; Zylberberg and Meunier, 2008). Cartilage tissues can show an endochondral ossification process. This phenomenon has been studied respectively on the urohyal (PEGUETA, 1968), the MECKEL's cartilage and the proximal piece of the pectoral girdle (FRANCILLON et al., 1975). The endochondral ossification is relatively limited when it occurs and the volume of enchondral bone remains reduced to thin bony layers (Fig. 8). The cartilage is destroyed by chondroclasts in areas where endochondral ossification occurs. Serial chondrocytes, known at the origin of the calcified cartilage, seem to be lacking in the endochondral ossification process in Latimeria (FRANCILLON et al., 1975). This constitutes a true difference with teleostean endochondral ossifications (MEUNIER, 1979; ZYLBERBERG and MEUNIER, 2008). **Tooth tissues**

The three tooth morphotypes described in *Latimeria* are fangs (7–10 mm in height), middle-sized teeth (3–4 mm in height) and rounded tubercles (MILLOT and ANTHONY, 1958). These teeth and tubercles are constituted of a cone of orthodentine set around a large pulp cavity and overlain by an external hypermineralized layer considered as true enamel (GRADY, 1970; CASTANET *et al.*, 1975; SHELLIS and POOLE, 1978; SMITH, 1978; SASAGAWA *et al.*, 1984). Various studies have revealed the presence of globular dentine (Fig. 5) at the periphery of the first third of the tooth (MILLER and HOBDELL, 1968; HOBDELL and MILLER, 1969; SHELLIS and POOLE, 1978; SASAGAWA *et al.*, 1984). This typical histological organization characterizes the various teeth of the bucco-pharyngeal cavity as well as the various odontodes of the dermal bony plates, the fin rays and the scales (CASTANET *et al.*, 1975).

In the fang the inner wall of the pulp cavity displays a series of plies (Fig. 5; MEUNIER *et al.*, 2015). These plies start at the base of the tooth and reach at least the first third to the half of the tooth towards its tip (Fig. 5). Such plies are also present but less developed in the small caniniform teeth (MEUNIER *et al.*, 2015). These dentine plies in the pulp cavity characterizes a plicidentine organization of orthodentine type. These primary plies correspond to a simplexodont plicidentine



Fig. 9. *Latimeria chalumnae*. Lung plates. A, Isolated lung plate of an adult specimen (CCC24). (scale = 500 μm). B, Cross section (azocarmin staining) in the anterior part of the vestigial lung showing its lumen (lu), two thin lung diverticles (arrows) and four surrounding plates (1–4) (oe = ventral wall of the oesophagous). (scale = 1 mm). C, Detail of the lung plate n°3 of B, showing the central weakness zone (*) and SHARPEY's fibres (s) that enter the plate. (scale = 50 μm). D, Detail of a section (hematoxylin-Eosin staining) in a lung plate showing an osteocyte lacuna (*) and the Liesegang lines (arrow-heads) that characterize a spheritic mineralization. (scale = 20 μm). E, Detail (hematoxylin-Eosin staining) of two osteocyte lacuna (*) with their osteocytic processes (arrow-heads) that penetrate the extracellular collagenous matrix. (scale = 20 μm). (B after MILLOT and ANTHONY, 1978; C, D after CUPELLO *et al.*, 2017).

type according to the definition of MEUNIER *et al.* (2013). This organization is less complex than the three other plicidentine types (polyplocodont, eusthenodont and dendrodont), which are described in most of extinct and extant Sarcopterygii (SCHULTZE, 1969, 1970).

The bony plates of the lung

The lung of *Latimeria* is reduced to a short oesophagus diverticulum (CUPELLO *et al.*, 2015) surrounded by scattered small and thin ovoid plates (Fig. 9A, B). These plates cover the surface of the vestigial lung, and are composed of a fibrous matrix with fibrocytes: it is a cellular bony tissue (CUPELLO *et al.*, 2017). Each plate is enclosed in a membranous bag. These plates look fragile in their middle plane since a central weakness zone opened on the microtome knife, creating an artefactual lumen (Fig. 9C) (CUPELLO *et al.*, 2017). The fibres are collagenous and organized in superposed layers. The cells are true osteocytes (Fig. 9E) with a more or less star-shaped outline, and send cytoplasmic extensions in the thickness of the plate (Fig. 9D, E). Rare lining cells (osteoblasts) are

present on the surface of the plates, and conjunctive fibres (SHARPEY's fibres) penetrate within the plate (Fig. 9C). The extracellular matrix shows various staining intensities with concentric and parallel (Fig. 9D) or globular shaped lines. These lines are considered to be Liesegang lines that characterize an active spheritic mineralizing process. The lung plates of Latimeria are thus true bony plates, and are homologous with the large bony plates known in the abdominal cavity of fossil actinistians (BRITO et al., 2010; CUPELLO et al., 2017). The calcified walls that surrounded the lung of the Cretaceous coelacanth Axelrodichthys are made of large osseous plates of various thickness (BRITO et al., 2010), as those of other fossil coelacanths (CLEMENT, 1999, 2005). The bony tissue of these plates is a vascularized cellular bone with more or less large vascular cavities and some internal remodelling (BRITO et al., 2010). Moreover the mineralization of the lung ossified plates in Axelrodichthys is spheritic as in Latimeria's plates (CUPELLO et al., 2017). So there is a continuity of the histological structure of the lung plates in the coelacanths during their



Fig. 10. *Latimeria chalumnae*. Various odontodes. Ground sections in A) the posterior field (= free ornamented area) of a scale and B, C) a dermal bone. A, Odontode lying on the external layer. Spheritic mineralized granules are seen (arrow-heads) at the frontier of the external layer and the first layers of the basal plate. B, Odontode lying at the surface of a dermal bone. C, Dermal bone overlaid by the dermis (white asterisks). Two odontodes are visible: one at the surface of the bone with its tip eroded (arrow-heads), and an older one (*) covered by more recent bony layers. (scale for A, B, C = 100 μ m). (bp = basal plate; bo = bone; de = dentine; pc = pulp cavity; vc = vascular cavity).

evolution, but with an important reduction of the bony plates in *Latimeria* linked to the vestigial state of its lung (CUPELLO *et al.*, 2015, 2019).

CONCLUSION

This overview of eighty years (1938–2018) of histological work on *Latimeria* skeletal tissues allows some anatomical and evolutionary considerations. It can be enlightened a drastic reduction of endochondral ossification during the long evolutionary history of coelacanths. The persistence of large volume of cartilage in the endoskeleton at adult stage can be compared to the "little bone and considerable cartilage" that characterize the skeleton of a number of demersal notothenioid telostean fishes (EASTMAN *et al.*, 2014).

A processus of spheritic mineralization has been recently highlighted in various skeletal elements of Latimeria, by the presence of globular dentine in teeth, in odontodes of the tegumentary skeleton (scales, fin rays), in scales at the interface between the external layer and the basal plate, as well as in lung bony plates. The spheritic mineralization (i.e., a radiating arrangement of hydroxyapatite crystals and of the organic matrix) in vertebrate skeletal tissues is considered as a precursor of inotropic mineralization (specific interactions between collagen fibrils and the mineral phase) that possibly represents a derived evolutionary stage of calcification mechanisms (ØRVIG, 1951, 1968; FRANCILLON-VIEILLOT et al., 1990; ZylberBerg et al., 1992). The simultaneous presence of both mineralization processes (spheritic and inotropic) in the mineralized tissues of Latimeria and in other osteichthyans such as teleosteans (Zylberberg and Meunier, 2008) is however questionable. The mineralized spherules present at the limit between the external layer and the basal plate of Latimeria scales are considered to be the product of an inotropic mineralization (MEUNIER and ZYLBERBERG, 1999). It thus appears that the state of the mineralized spherules observed in the various skeletal tissues of Latimeria, including the lung bony plates, must be studied with adapted ultrastructural techniques in order to test their true origin: spheritic or inotropic mineralization?

ACKNOWLEDGEMENTS

This contribution is linked to an international roundtable on coelacanths evolution held at the Kitakyushu Museum and at the Aquamarine Fukushima in August 2017. We would like to thank the anonymous reviewers for their constructive comments and valuable suggestions. C.C. was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001 (Programa Nacional de Pós Doutorado-PNPD).

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