Life history and ossification patterns in *Miguashaia bureaui* reveal the early evolution of osteogenesis in coelacanths

Jorge Mondéjar Fernández¹,², François J. Meunier³, Richard Cloutier⁴, Gaël Clément² and Michel Laurin²

¹ Division Paleontology and Historical Geology, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany
² Centre de Recherche en Paléontologie—Paris (CR2P), UMR 7207, MNHN, CNRS, SU, Département Origines et Évolution, Muséum National d’Histoire Naturelle, Paris, France
³ Laboratoire de Biologie des Organismes et des Écosystèmes Aquatiques (BOREA), UMR 8067, MNHN, CNRS, SU, Département Adaptations du Vivant, Muséum National d’Histoire Naturelle, Paris, France
⁴ Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, Canada

ABSTRACT

The study of development is critical for revealing the evolution of major vertebrate lineages. Coelacanths have one of the longest evolutionary histories among osteichthyans, but despite access to extant representatives, the onset of their weakly ossified endoskeleton is still poorly understood. Here we present the first palaeohistological and skeletochronological study of *Miguashaia bureaui* from the Upper Devonian of Canada, pivotal for exploring the palaeobiology and early evolution of osteogenesis in coelacanths. Cross sections of the caudal fin bones show that the cortex is made of layers of primary bone separated by lines of arrested growth, indicative of a cyclical growth. The medullary cavity displays remnants of calcified cartilage associated with bony trabeculae, characteristic of endochondral ossification. A skeletochronological analysis indicates that rapid growth during a short juvenile period was followed by slower growth in adulthood. Our new analysis highlights the life history and palaeoecology of *Miguashaia bureaui* and reveals that, despite differences in size and habitat, the poor endoskeletal ossification known in the extant *Latimeria chalumnae* can be traced back at least 375 million years ago.

INTRODUCTION

The retrogressive development of the endoskeleton is among the main trends identified in the long evolutionary history of coelacanths (*Jarvik, 1980; Cloutier, 1991a, 1991b; Janvier, 1996; Forey, 1998*), and includes not only the reduction in the number of bones but also the replacement of well-ossified elements by more cartilaginous ones in the skull and postcranium. The postcranial anatomy displays a relative morphological conservatism across coelacanth evolution, as shown by the general body shape, the appendicular skeleton, and the squamation (*Schaeffer, 1948; Forey, 1998; Mondéjar-Fernández et al., 2022*).
This morphological stasis may be linked to locomotor constraints (Schaeffer, 1948; Cloutier, 1991a), while paedomorphism has been cited as the primary process responsible for reductive trends (Lund & Lund, 1985; Forey, 1998).

The braincase, axial skeleton and fins of coelacanths are composed of endoskeletal elements (e.g., neurocranium, vertebrae, mesomeres and radials) covered by dermoskeletal products (e.g., dermocranium, scales, fin rays). In the extant Latimeria chalumnae, the endoskeleton shows a reduced ossification rate, especially in the neurocranium (Millot & Anthony, 1958; Forey, 1998; Dutel et al., 2019). Similarly, the paired (pectoral and pelvic) and median (anterior and posterior dorsal, anal, and caudal) fins are essentially made of cartilage with a limited contribution of endochondral ossification (Francillon et al., 1975; Mansuit et al., 2019, 2021). Other bony tissues have been histologically surveyed, such as the mineralized plates surrounding the lung in extinct (Brito et al., 2010) and extant taxa (Cupello et al., 2017a, 2017b; Meunier et al., 2021). However, contrary to the dermoskeleton (Smith, Hobdell & Miller, 1972; Castanet et al., 1975; Giraud et al., 1978; Meunier, 1980; Meinke, 1982; Meunier & Zyberberg, 1999; Meunier et al., 2008; Mondéjar-Fernández et al., 2021), few histological studies have been carried out on the coelacanth endoskeleton (Francillon et al., 1975), thus limiting our knowledge on its microstructure and evolution.

Miguashaia bureaui from the Upper Devonian Miguasha Lagerstätte in Québec (Canada) is one of the morphologically primitive coelacanths (Schultze, 1973; Cloutier, 1991b, 1996; Forey et al., 2000; Zhu et al., 2012) and thus key to the understanding of their early evolution and lifestyle. Studies using palaeohistology as a proxy for reconstructing the palaeobiology of Devonian sarcopterygians are rare, with a few exceptions mainly focused on taxa close to the emergence of tetrapods (Laurin et al., 2007; Sanchez, Tafforeau & Ahlberg, 2014; Kamska et al., 2018). The endoskeleton of Miguashaia bureaui has never been previously histologically surveyed, although the rich and diverse material from Miguasha constitutes an extraordinary source of information (Janvier &Arsenault, 2002; Janvier, Arsenault & Desbiens, 2004; Downs & Donoghue, 2009; Zyberberg, Meunier & Laurin, 2010; Meunier & Laurin, 2012; Zyberberg, Meunier & Laurin, 2015; Chevrinais, Sire & Cloutier, 2017). Bone microstructure is informative on numerous life history traits of vertebrates, from metabolism, to growth rate, and physiology (Francillon-Vieillot et al., 1990), and these can be inferred from the density, size, and shape of the cellular bone lacunae and the intensity of vascularization, among others (Amprino, 1947). Moreover, skeletochronology provides detailed information about growth, individual age, and sexual maturity based on natural and repetitive marks on the bone (Castanet, Meunier & de Ricqles, 1977; Castanet et al., 1993; Geffen et al., 2002; Meunier et al., 2002; Morales-Nin & Panfili, 2002).

Here we investigate the palaeohistology of the median fin bones (radials) of the Devonian coelacanth Miguashaia bureaui and compare it with the extant Latimeria chalumnae. Our main objectives are: 1. to describe bone microstructure with respect to life history traits in Miguashaia bureaui; 2. to evaluate the importance of endoskeletal ossification in the coelacanth postcranium and retrace its evolution; and 3. to elucidate the palaeoecology of one of the earliest coelacanths.
Miguashaia bureaui occurs in the 375 Myr-old (middle Frasnian, Upper Devonian) Escuminac Formation, Miguasha, Québec, Canada. Fossil material used for the histological investigation is housed at the Musée d’Histoire naturelle de Miguasha (MHNM) and consists of a block (MHNM 06-1238, Fig. 1) containing scales and disarticulated elements (Mondéjar-Fernández et al., 2021) associated with radial bones, most likely from the caudal fin of a single individual given the partial articulation and similar relative size of the osseous remains. Based on scale diameter (ca. 25 mm), our studied specimen (MHNM 06-1238) has an estimated total length (TL) of approximately 400 mm.

The fossil material was embedded in a polyester resin and sectioned after 48 h of drying in an incubator at 40 °C. The selected sections were cut with a diamond saw, ground on a diamond plate, polished with a suspension of alumina powder to a thickness of 60–80 μm, glued on a glass slide with 20/20 araldite, and observed under transmitted light.
natural light with an Olympus BX51 microscope. Pictures were taken with a digital camera Olympus Camedia C-5060.

Comparative data on *Latimeria chalumnae* come from microradiographies (X-ray beam power: 10 to 15 KV at 7 to 8 mA; distance between the X-ray source and the specimens: 10 cm) of MNHN-ZA-AC-2012-26 (CCC79, adult female, 78 kg, 163 cm TL) (*Francillon et al., 1975*), housed in the Collection of Comparative Anatomy of the Muséum national d’Histoire naturelle (MNHN) of Paris, France.

All the fossil material of *Miguashaia bureaui* is housed at the Musée d’Histoire naturelle de Miguasha (MHNM) (32 specimens; updated count from *Cloutier, Proust & Tessier (2011)*), parc national de Miguasha, Québec (Canada) with the exception of the three specimens (including the holotype ULQ Esc 120) at Université Laval (Québec City, Québec, Canada), six specimens at The Natural History Museum (BMNH) (London, UK), and one specimen at the American Museum of Natural History (New York, USA).

**RESULTS**

**Morphology**

The radials are cylindrical bones (between 1–2 cm in length and 2–3 mm in width) composed of a slightly narrowing median shaft (diaphysis) and two small, somewhat enlarged dorsal and ventral extremities (epiphyses) (ra, Fig. 1) (*Cloutier, 1996*). The bones are roughly circular in cross section and may present a lateral expansion (Figs. 2, 3). The epiphyses articulate with the ossified dermal fin rays (lp, Fig. 1A) and are open-ended in fossil specimens (Fig. 1B) (*Cloutier, 1996*), suggesting the occurrence of distal cartilaginous pads in the living animal.

**Histology**

**Diaphyseal bone histology**

Transversal (Figs. 2–4) and longitudinal (Figs. 5A, 5C, 5E–5H) sections reveal that the radials are composed of a relatively thick cortex surrounding a central medullary cavity (or medulla) that measures from 50 µm to 1 mm in diameter, depending on the location of the section across the diaphysis (Figs. 4A, 4D). The osseous tissue consists of primary periostic bone with superimposed layers of parallel-fibered or pseudo-lamellar bone. The enclosed star-shaped cell lacunae (*i.e.*, osteocyte lacunae) (30–40 µm in length and 2, 5–5 µm in width) send ramified cytoplasmic processes (*i.e.*, canaliculi) in a heterogenous extracellular matrix (Figs. 3, 4C, 4E, 4F, 5G, 5H). Their orientation is variable, from roughly radial close to the medulla (Figs. 3A, 3B, 3D, 3E, 4C) to parallel to the external surface approaching the periphery (Figs. 3C, 3F, 4F–4E). The bony layers are crossed by radial (Fig. 3A) or axial (Figs. 3B, 3D, 3E) vascular canals, the majority of which are narrow simple primary canals, but some of the axial ones are surrounded by concentric layers of bone lamellae (*i.e.*, primary osteons) (Figs. 3B, 3E, 4D). The cortex shows substantial cyclicity (Figs. 2–4) evidenced by concentric lines of arrested growth (*i.e.*, LAGs) separating the bone layers (*i.e.*, zones). In the areas close to the medulla, the zones are thicker, display larger vascular canals, larger osteocyte lacunae, and are crossed by Sharpey’s fibres (Fig. 5H) whereas the zones close to the periphery are thinner, the number
of vascular canals decreases drastically, and the osteocyte lacunae are fewer and smaller (Figs. 3C, 3E, 3F, 4B, 4E, 4F). Growth was highly asymmetrical, as shown by the eccentric location of the medullary cavity and the variable thickness of the zones (Fig. 2). The regular profile of the inner walls of the medulla indicates that little resorption of the cortex occurred, if any.

**Mineralized cartilage and endochondral ossification**

The medulla was probably filled up, at least partially, by unmineralized cartilaginous tissue in the living animal, but most of it has not been fossilized. However, patches of mineralized cartilage can still be seen (Figs. 5A–5F). The mineralized structures are spheritic, with the crystals and the organic matrix showing a radial arrangement, and display thin increment lines (i.e., Liesegang rings), which separate the successive layers formed during calcification. Spherical chondrocyte lacunae reveal the location of the chondrocytes (Fig. 5F). The mineralized cartilage shows marks of erosion and has been

---

**Figure 2** Median fin bone palaeohistology of *Miguashaia bureaui* (MHNM 06-1238). (A and B). Transversal cross sections of two radials. Black arrowheads indicate the lateral expansions of the bones. White arrowheads indicate LAGs (lines of arrested growth). Insets are detailed in Fig. 3.

Full-size DOI: 10.7717/peerj.13175/fig-2
Figure 3  Median fin bone palaeohistology of *Miguashaia bureaui* (MHNM 06-1238). (A) Large zone with radial vascular canals (vc) and large osteocyte lacunae. (B) Axial vascular canals (vc) (i.e., primary osteons). (C) Detail of a wide (left) and several narrow (right) zones. (D) Inset of a zone with axial vascular canals (vc) and large osteocyte lacunae. (E) Detail of a wide zone (left) with axial vascular canals (vc) and large osteocyte lacunae and one of the first avascular narrow zones (right) with small osteocyte lacunae. (F) Detail of several tightening narrow zones. White arrow heads indicate the presumed course of the LAGs represented in Fig. 2. Black arrows with white heads indicate osteocyte lacunae. Abbreviations: vc, vascular canal.

Figure 4  Median fin bone palaeohistology of *Miguashaia bureaui* (MHNM 06-1238). (A, D) Transversal cross section of two radials and detailed insets (B and C, E and F, respectively). Note the difference in width of the medullary cavity (mc) between the mid-diaphysis (A) and near the epiphyses (D). (B) Peripheral layers of compact bone from the specimen in (A). Note the lack of vascularization and the reduction in the number of osteocyte lacunae. (C) Deeper layers of compact primary bone. Note the larger size of the osteocyte lacunae in comparison with more peripheral layers. (E and F) Peripheral layers illustrating a drastic reduction in the number of osteocyte lacunae and highlighting the putative location of the periosteal membrane or peristeme (dark brown). Black arrows with white heads indicate osteocyte lacunae. Abbreviations: mc, medullary cavity.
Figure 5 Comparative histology of extinct (*Miguashaia bureaui*) and extant (*Latimeria chalumnae*) coelacanths. (A–H) Thin sections of *Miguashaia bureaui* (MHNM 06-1238) in transmitted light. Longitudinal (A, C) and transversal (B) cross section of three radials. (D–F) Remnants of calcified cartilage with mineralized cartilaginous spheritic structures (black arrowheads) and bony trabeculae (black arrows) around a bony cortex (white asterisks) with vascular canals (vc) evidencing localized remodeling processes of the primary bone (white arrowhead). (G) Detail of osteocyte lacunae with long cytoplasmic prolongations (*canaliculi*) (black arrows with white heads). (H) Detail of Sharpey’s fibres (white arrows with black
replaced by thin bony trabeculae (Figs. 5D–5F), a phenomenon characteristic of endochondral ossification (Francillon-Vieillot et al., 1990). The occurrence of these patches of calcified cartilage also confirms the lack of medullary erosion of the cortex.

**Skeletochronological analysis**

The serial organization of thick vascularized bony layers followed by thin avascular layers is indicative of growth processes, with the wide zones representing areas of fast growth typical of the juvenile period, and the narrow zones corresponding to the slower growth of adulthood (Castanet, Meunier & de Ricqles, 1977; Castanet et al., 1993; Geffen et al., 2002; Meunier et al., 2002; Morales-Nin & Panfilii, 2002; Schucht, Klein & Lambertz, 2021) (Fig. 2). Lines of arrested growth (LAGs) are structures expressing a pause of the osteogenesis during annual estivation and/or hibernation in poikilothermic vertebrates (Castanet, Meunier & de Ricqles, 1977; Castanet, 1985; de Ricqlès et al., 1991).

One growth mark (i.e., one LAG and the immediately neighbouring layer), represents a seasonal and biological cycle. All the studied bones express simple LAGs, suggesting a single period of torpor with a likely annual frequency. Four wide zones followed by three thinner zones can be identified (Fig. 2). The absence of bone resorption accurately preserves the integrity of the growth marks and allows to confidently infer an age of seven years to the animal at the time of its death. A decrease in the growth-mark width towards the periphery indicates a possible acquisition of sexual maturity in its fifth year of life (Fig. 6A, Table 1).

**DISCUSSION**

Our data confirm that in *Miguashaia bureaui* the increment in thickness of the radials resulted from the activity of an external osteogenic membrane (i.e., periosteum), which centrifugally deposited layers of primary bone across the diaphysis. These layers, separated by cementing LAGs, indicate a cyclical growth (Fig. 2). The distal elongation of the radials was likely due to the activity of chondroblasts as suggested by the combined occurrence of calcified cartilage and endochondral bony trabeculae in the medulla and close to the epiphyses (Figs. 5A–5F) (Meunier & Laurin, 2012). The calcification of cartilage took place in the form of hypertrophic cartilage (Haines, 1942) of spheritic type as observed in extant actinopterygians (e.g., the carp *Cyprinus*) (Zylberberg & Meunier, 2008). Remnants of calcified cartilage have also been found in other Devonian sarcopterygians like *Eusthenopteron forodii* (Laurin et al., 2007; Meunier & Laurin, 2012; Sanchez, Tafforeau & Ahlberg, 2014) and juveniles of *Acanthostega gunnari* (Sanchez et al., 2016). The retention of calcified cartilage in adult individuals of *Miguashaia bureaui* suggests a relatively modest endochondral ossification and slow epiphyseal growth. A poor
Figure 6 Skeletochronology and size range of *Miguashaia bureaui*. (A) Growth curves showing bone deposition rate in the cortex of two radials (a, b correspond to the bones illustrated in Figs. 2A, 2B and measured in Table 1) (MHNM 06-1238). The arrow points to the presumed acquisition of sexual maturity. (B) Histogram of the estimated total length of all the *Miguashaia bureaui* specimens and their frequency of occurrence in the Escuminac Formation (see Table 2). Profiles correspond to the juvenile morphotype (based on ULQ120; 197 mm TL) in grey and the adult morphotype (based on BMNH P.58691, BMNH P.62794, MHNM 06-41, MHNM 06-494; ca. 375 mm TL) in black (modified after Cloutier, 1996).

Table 1 Bone deposition in *Miguashaia bureaui* (MHNM 06-1238).

|   | 0 | 1 | 2  | 3  | 4  | 5  | 6  | 7  |
|---|---|---|----|----|----|----|----|----|
| 1 (Fig. 2A) | 0  | 459| 903|1,418|1,856|2,064|2,124|2,265|
| 2 (Fig. 2B) | 0  | 162| 366| 582| 913|1,033|1,150|1,247|

Note: Measurements of cumulative radial bone deposition (μm) between the medullary margin and the various LAGs numbered from the inner part of the cortex to the periphery (i.e., from the first year of development (0) to the last year of life (7)).
endochondral ossification also occurs in the mainly cartilaginous paired fins of *Latimeria chalumnae* (*Francillon et al., 1975; Mansuit et al., 2019, 2021*), where the thin bony trabeculae show evidence of spheritic mineralized cartilage as well (Figs. 5I–5K).

Moreover, in both *Miguashaia bureaui* and *Latimeria chalumnae*, bone remodelling is also limited to the inner walls of a few vascular canals and some endosteal bone deposition (Fig. 5).

The presence of fast and slow-growing osseous layers is characteristic of ectothermic vertebrates (*de Ricqlès et al., 1991; Castanet, Francillon-Vieillot & de Ricqlès, 2003; Legendre et al., 2016; Legendre & Davesne, 2020*). Their distribution in *Miguashaia bureaui* suggests that growth may have been indefinite but submitted to a pronounced cyclicity (such as seasonality), hinting at a poikilothermic metabolism. Moreover, a substantial reduction in thickness of the zones towards the periphery is generally explained by the acquisition of sexual maturity (*Castanet et al., 1993; Meunier et al., 2002*), which, despite that the reduction in deposition rate is not very drastic, points to the occurrence of the first reproduction in *Miguashaia bureaui* in the course of its fifth year (Fig. 6A). A short pre-reproductive period matches the range of some extant predatory osteichthyans of similar size to *Miguashaia bureaui* like bichirs (*e.g.*, *Polypterus senegalus*) (*Daget, Bauchot & Arnoult, 1965*), sturgeons (*e.g.*, *Acipenser brevirostrum*) (*Kynard, 1997*), gars (*e.g.*, *Lepisosteus osseus*) (*Smylie, Shervette & McDonough, 2016*), dipnoans (*e.g.*, *Lepidosiren paradoxa*) (*Flower, 1935*), as well as extant Batrachia (*e.g.*, urodeles and anurans) (*Castanet, Francillon-Vieillot & de Ricqlès, 2003; Amat & Meiri, 2018*). A rapid growth and acquisition of maturity in *Miguashaia bureaui* are likely associated with the production of numerous offspring via external fertilization (*Bone & Moore, 2008*) and may also have enabled to quickly outgrow the larval and juvenile stages, more vulnerable to predation. However, it contrasts with the extremely late maturity revealed in *Latimeria chalumnae* (*Mahé, Ernande & Herbin, 2021*), which has been suggested to be related to internal fertilization and the production of a fully-developed offspring by viviparity after a long gestation period. The life history differences between *Miguashaia bureaui* and *Latimeria chalumnae* may reflect the more than 375 million years of evolution that separates both taxa but may also be due to their different sizes and habitats, with *Miguashaia* being a relatively small predator (Table 2, Fig. 6B) dwelling in moderately deep to shallow waters, while *Latimeria* is characterized by its large body size and is adapted to life in the deep waters of the mesopelagic zone where resources are less abundant (*Forey, 1998; Cupello et al., 2017a; Mahé, Ernande & Herbin, 2021*).
The differences in bone-growth rate identified in *Miguashaia bureaui* may also reveal differences in overall living conditions and changes in habitat across ontogeny. The Escuminac Formation represents a tropical, brackish, estuarine paleoenvironment (*Schultze & Cloutier, 1996; Cloutier, Proust & Tessier, 2011*) and most specimens come from laminated facies associated with tidal deposits. *Miguashaia bureaui* was suggested to be a predator within the Escuminac fauna (*Chevrinais, Jacquet & Cloutier, 2017*) but only a single specimen (MHNM 06-1237) preserves digestive content composed of a few of the spinicaudatan (conchostracan) *Asmusia membranacea* while six other specimens show solely amorphous organic matter. *Miguashaia bureaui* is only a minor component of the fossil assemblage representing 0.19% of the total abundance of vertebrate specimens (42 individuals out of 21,446 Escuminac vertebrate specimens). Of the 42 specimens, two could be considered juveniles measuring between 70 and 80 mm in length (*Schultze, 1973; Cloutier, 1996*), while rare specimens reached approximately 180 mm, and most other specimens are ca. 400–465 mm in total length (Table 2; Fig. 6B). One of the two juvenile specimens (MHNM 06-1633) was found in a nursery (or effective juvenile habitat) in association with hundreds of embryonic, larval, and juvenile individuals of the “placoderm” *Bothriolepis canadensis*, and the sarcopterygians *Scaumenacia curta*, *Fleurantia denticulata* and *Eusthenopteron foordi*. Although MHNM 06-1633 is relatively small for the species, it is one of the largest individuals found in the nursery. Juvenile specimens have not been found in association with larger adults. The Escuminac nursery may thus have been used by coelacanths, but most likely *Miguashaia bureaui* was not a permanent resident of the palaeoestuary, which suggests that the larger adult individuals inhabited and probably reproduced in more open and deeper marine waters, and only sporadically visited the Escuminac palaeoestuary.

The radials, neural and haemal spines of *Miguashaia bureaui* are among the sole endoskeletal postcranial elements retrieved so far, despite the good preservation of ontogenetic series from Miguasha (*Cloutier, 1996, 2010*), suggesting a truly low perichondral and endochondral ossification rate of the vertebral column and associated elements (Fig. 1A). A poorly ossified postcranium is common among early osteichthysans (*Janvier, 1996*), including coelacanths (*Forey, 1998*) such as *Diplocercides kayseri* from the Devonian of Germany, in which the radials appear to be only perichondrally ossified (*Stensiö, 1937*). The neural arches and spines of *Laugia groenlandica* from the Triassic of Greenland (*Stensiö, 1932*) also display a wide medullary cavity, possibly filled by cartilage, but the endoskeleton of the paired fins is surprisingly well ossified, as in *Shoshonia arctopteryx* from the Devonian of the USA (*Friedman, Coates & Anderson, 2007*). Many other extinct coelacanths are known from endoskeletal postcranial material (*e.g.*, *Forey, 1998; Long, 1999*) but, to our knowledge, the ossification rate of the endoskeleton has not been palaeohistologically evaluated in these taxa.

**CONCLUSIONS**

Our data on the caudal fin radial bones of *Miguashaia bureaui* provide the first evidence of the potential of both perichondral and endochondral ossification in the postcranium of early coelacanths, with perichondral ossification being the main source of bone deposition.
and endochondral ossification having a minor contribution (Figs. 2, 5D–5F). This condition, also present in *Latimeria chalumnae* (*Francillon et al., 1975; Meunier, Cupello & Clément, 2019*) (Figs. 5I–5K), likely represents a retention of the primitive state for osteichthyans (*Janvier, 1996*), as suggested by the poorly ossified endoskeleton of close relatives of coelacanths, like onychodonts (*Andrews et al., 2005; Mondéjar-Fernández, 2020*). Miguashaia bureaui illustrates that, despite a different life history from that of *Latimeria chalumnae*, a postcranial osteogenetic pattern with reduced endochondral ossification and secondary bone remodelling has been maintained for the last 375 million years, showcasing a remarkable case of histological stasis in coelacanth evolution.

**ACKNOWLEDGEMENTS**

We warmly thank Severin Morel (MNHN) for the thin-sections, Philippe Loubry (MNHN) for the photographs, and Marc Herbin (MNHN) for granting access to the *Latimeria* collections under his care. Johanne Kerr (parc national de Miguasha) prepared the loan of specimens and Nathaniel Bertrand Maltais and Laurianne Richard (UQAR) helped with the photographs.

**ADDITIONAL INFORMATION AND DECLARATIONS**

**Funding**

Jorge Mondéjar Fernández was supported by the Louis Gentil-Jacques Bourcart prize of the French Academy of Sciences. Richard Cloutier was funded by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Grant Disclosures**

The following grant information was disclosed by the authors:
Louis Gentil-Jacques Bourcart prize of the French Academy of Sciences.
Natural Sciences and Engineering Research Council of Canada.

**Competing Interests**

The authors declare that they have no competing interests.

**Author Contributions**

- Jorge Mondéjar Fernández conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- François J. Meunier conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Richard Cloutier conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
Gaël Clément conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Michel Laurin analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability
The following information was supplied regarding data availability:

The raw data is available in Tables 1, 2 (measurements), Fig. 6 (graphs obtained from these measurements), Fig. 1 (a modified drawing with original information and fossil material), and Figs. 2–5 (histological photographs).

REFERENCES

Amat F, Meiri S. 2018. Geographical, climatic and biological constraints on age at sexual maturity in amphibians. Biological Journal of the Linnean Society 123:34–42 DOI 10.1093/biolinnean/blx127.

Amprino R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l’accroissement. Archives de Biologie 58:315–330.

Andreas M, Long J, Ahlberg P, Barwick R, Campbell K. 2005. The structure of the sarcopterygian Onychodus jandemarrai n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. Earth and Environmental Science Transactions of The Royal Society of Edinburgh 96(3):197–307 DOI 10.1017/S0263593300001309.

Bone Q, Moore R. 2008. Biology of fishes. England: Taylor & Francis.

Brito PM, Meunier FJ, Clément G, Geffard-Kuriyama D. 2010. The histological structure of the calcified lung of the fossil coelacanth Axelrodichthys araripensis (Actinistia: Mawsoniidae). Palaeontology 53:1281–1290 DOI 10.1111/j.1475-4983.2010.01015.x.

Castanet J. 1985. La squelettochronologie chez les reptiles I. Résultats expérimentaux sur la signification des marques de croissance squelettiques chez les lézards et les tortues. Annales des Sciences Naturelles 13:23–40.

Castanet J, Francillon-Vieillot H, de Ricqlès A. 2003. The skeletal histology of the Amphibia. In: Heatwole H, Davies M, eds. Amphibia Biology. Chipping Norton, UK: Surrey Beatty & Sons, 1598–1683.

Castanet J, Francillon-Vieillot H, Meunier F-J, de Ricqlès A. 1993. Bone and individual aging. In: Hall BK, ed. Bone: Bone Growth-B. Vol. 7. Boca Raton, FL: CRC Press, 245–283.

Castanet J, Meunier F, Bergot C, François Y. 1975. Données préliminaires sur les structures histologiques du squelette de Latimeria chalumnae. 1- Dents, écailles, rayons de nageoires. In: Coll. Inter. CNRS, “Problèmes actuels de Paléontologie. Evolution des Vertébrés”, Paris159–168 4-9 Juin 1973.

Castanet J, Meunier F-J, de Ricqlès A. 1977. L’enregistrement de la croissance cyclique par le tissu osseux chez les vertébrés poikilothermes. Comptes Rendus de l’Académie des Sciences 270:2853–2856.

Chevrinais M, Jacquet C, Cloutier R. 2017. Early establishment of vertebrate trophic interactions: food web structure in Middle to Late Devonian fish assemblages with exceptional fossilization. Bulletin of Geosciences 92(4):491–510 DOI 10.3140/bull.geosci.1651.

Chevrinais M, Sire JY, Cloutier R. 2017. From body scale ontogeny to species ontogeny: histological and morphological assessment of the Late Devonian acanthodian Triazeugacanthus affinis from Miguasha, Canada. PLOS ONE 12(4):e0174655 DOI 10.1371/journal.pone.0174655.
Cloutier R. 1991a. Patterns, trends, and rates of evolution within the Actinistia. *Environmental Biology of Fishes* 32:23–58 DOI 10.1007/BF00007444.

Cloutier R. 1991b. Intereelationships of Palaeozoic actinistians: patterns and trends. In: Chang MM, Liu YH, Zhang GR, eds. *Early Vertebrates and Related Problems of Evolutionary Biology*. Beijing: Science Press, 379–428.

Cloutier R. 1996. The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). In: Schultze H-P, Cloutier R, eds. *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. München, Germany: Verlag Dr. Friedrich Pfeil, 227–247.

Cloutier R. 2010. The fossil record of fish ontogenies: insights into developmental patterns and processes. *Seminars in Cell & Developmental Biology* 21:400–413 DOI 10.1016/j.semcdb.2009.11.004.

Cloutier R, Proust JN, Tessier B. 2011. The Miguasha Fossil-Fish-Lagerstätte: a consequence of the Devonian land-sea interactions. *Palaeobiodiversity and Palaeoenvironments* 91(4):293–323 DOI 10.1007/s12549-011-0058-0.

Cupello C, Meunier F-J, Herbin M, Clément G, Brito PM. 2017a. Lung anatomy and histology of the extant coelacanth shed light on the loss of air-breathing during deep-water adaptation in actinistians. *Royal Society Open Science* 4(3):161030 DOI 10.1098/rsos.161030.

Cupello C, Meunier F-J, Herbin M, Janvier P, Clément G, Brito PM. 2017b. The homology and function of the lung plates in extant and fossil coelacanths. *Scientific Reports* 7(1):1–8 DOI 10.1038/s41598-017-09327-6.

Daget J, Bauchot ML, Arnould J. 1965. Étude de la croissance chez *Polypterus senegalus* Cuvier. *Acta Zoologica Stockh* 46:297–309 DOI 10.1111/j.1463-6395.1965.tb00736.x.

de Ricqlès A, Meunier FJ, Castanet J, Francillon-Vieillot H. 1991. Comparative microstructure of bone. In: Hall BK, ed. *Bone*. Vol. 3. Boca Raton: CRC Press, 1–78.

Downs JP, Donoghue PC. 2009. Skeletal histology of *Bothriolepis canadensis* (Placodermi, Antiarchi) and evolution of the skeleton at the origin of jawed vertebrates. *Journal of Morphology* 270(11):1364–1380 DOI 10.1002/jmor.10765.

Dutel H, Galland M, Tafforeau P, Long JA, Fagan MJ, Janvier P, Herrel A, Santini MD, Clément G, Herbin M. 2019. Neurocranial development of the coelacanth and the evolution of the sarcopterygian head. *Nature* 569(7757):556–559 DOI 10.1038/s41586-019-1117-3.

Flower SS. 1935. Further notes on the duration of life in animals.—I. Fishes: as determined by otolith and scale-readings and direct observations on living individuals. *Proceedings of the Zoological Society of London* 105(2):265–304 DOI 10.1111/j.1469-7998.1935.tb06249.x.

Forey PL. 1998. *History of the coelacanth fishes*. London: Chapman & Hall.

Forey PL, Ahlberg PE, Lušťević E, Zupinš I. 2000. A new coelacanth from the Middle Devonian of Latvia. *Journal of Vertebrate Paleontology* 20(2):243–252 DOI 10.1671/0272-4634(2000)020[0243:ANCFTM]2.0.CO;2.

Francillon H, Meunier F-J, Phong NT, de Ricqlès A. 1975. Données préliminaires sur les structures histologiques du squelette de *Latimeria chalumnae*. II. In: *Tissus Osseux et Cartilages. Problèmes Actuels de Paléontologie, Évolution des Vertébrés*, Colloque International, CNRS, 169–174.

Francillon-Vieillot H, de Buffrenil V, Castanet J, Géraudie J, Meunier F-J, Sire J-Y, Zylberberg L, de Ricqlès A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: JG Carter, ed. *Skeletal Biominalization: Patterns, Processes and Evolutionary Trends*. Vol. I. New York, NY: Van Nostrand Reinhold, 471–530.
Friedman M, Coates MI, Anderson P. 2007. First discovery of a primitive coelacanth fin fills a major gap in the evolution of lobed fins and limbs. *Evolution & Development* **9**(4):329–337 DOI 10.1111/j.1525-142X.2007.00169.x.

Geffen AJ, de Pontual H, Wright PJ, Mosegaard H. 2002. Life history events. In: Panfilii J, de Pontual H, Troade H, Wright PJ, eds. *Manual of Fish Sclerochronology*. Brest, France: Ifremer-Ird coedition, 99–104.

Giraud MM, Castanet J, Meunier FJ, Bouligand Y. 1978. The fibrous structure of coelacanth scales: a twisted plywood. *Tissue and Cell* **10**(4):671–686 DOI 10.1016/0040-8166(78)90054-X.

Haines RW. 1942. The evolution of epiphyses and of endochondral bone. *Biological Reviews* **17**(4):267–292 DOI 10.1111/j.1469-185X.1942.tb00440.x.

Janvier P. 1996. *Early vertebrates*. Oxford, UK: Clarendon Press.

Janvier P, Arsenault M. 2002. Calcification of early vertebrate cartilage. *Nature* **417**(6889):609 DOI 10.1038/417609a.

Janvier P, Arsenault M, Desbiens S. 2004. Calcified cartilage in the paired fins of the osteostracan *Eusthenopteron foordi* (Traquair 1880), from the Late Devonian of Miguasha (Québec, Canada), with a consideration of the early evolution of the pectoral fin endoskeleton in vertebrates. *Journal of Vertebrate Paleontology* **24**(4):773–779 DOI 10.1671/0272-4634(2004)024[0773:CCITPF]2.0.CO;2.

Jarvik E. 1980. *Basic structure and evolution of vertebrates*. Vol. I. London: Academic Press.

Kamska V, Daeschler EB, Downs JP, Ahlberg PE, Tafforeau P, Sanchez S. 2018. Long-bone development and life-history traits of the Devonian tristichopterid *Hyneria lindae*. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **109**(1–2):75–86 DOI 10.1017/S175569101800083X.

Kynard B. 1997. Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes* **48**:319–334 DOI 10.1023/A:1007372913578.

Laurin M, Meunier FJ, Germain D, Lemoine M. 2007. A microanatomical and histological study of the paired fin skeleton of the Devonian sarcopterygian *Eusthenopteron foordi*. *Journal of Paleontology* **81**(1):143–153 DOI 10.1666/0022-3360(2007)81[143:AMAHSO]2.0.CO;2.

Legendre LJ, Davesne D. 2020. The evolution of mechanisms involved in vertebrate endothermy. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**(1793):20190136 DOI 10.1098/rstb.2019.0136.

Legendre LJ, Guénard G, Botha-Brink J, Cubo J. 2016. Palaeohistological evidence for ancestral high metabolic rate in archosaurs. *Systematic Biology* **65**(6):989–996 DOI 10.1093/sysbio/syw033.

Long JA. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Records of the Western Australian Museum, Supplement* **57**:37–53.

Lund R, Lund WL. 1985. Coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bulletin of Carnegie Museum of Natural History* **25**(1–74).

Mahé K, Ernande B, Herbin M. 2021. New scale analyses reveal centenarian African coelacanths. *Current Biology* **31**(16):3621–3628.e4 DOI 10.1016/j.cub.2021.05.054.

Mansuit R, Clément G, Herrel A, Dutel H, Tafforeau P, Santin MD, Herbin M. 2019. Development and growth of the pectoral girdle and fin skeleton in the extant coelacanth *Latimeria chalumnae*. *Journal of Anatomy* **236**(3):493–509 DOI 10.1111/joa.13115.
Mansuit R, Clément G, Herrel A, Dutel H, Tafforeau P, Santin MD, Herbin M. 2021. Development and growth of the pelvic fin in the extant coelacanth *Latimeria chalumnae*. *Anatomical Record* 304(3):541–558 DOI 10.1002/ar.24452.

Meinke DK. 1982. A light and scanning electron microscope study on the dermal skeleton of *Spermatodus* (Pisces: Coelacanthini) and the evolution of the dermal skeleton in coelacanths. *Journal of Paleontology* 56:620–630.

Meunier FJ. 1980. Les relations isopédine-tissu osseux dans le post-temporal et les écailles de la ligne latérale de *Latimeria chalumnae* (Smith). *Zoologica Scripta* 9:307–317 DOI 10.1111/j.1463-6409.1980.tb00669.x.

Meunier FJ, Cupello C, Clément G. 2019. The skeleton and the mineralized tissues of the living coelacanths. *Bulletin of Kitakyushu Museum of Natural History and Human History* 17:37–48 DOI 10.34522/kmnh.17.0_37.

Meunier FJ, Cupello C, Herbin M, Clement G, Brito PM. 2021. The lungs of extinct and extant coelacanths: a morphological and histological review. *Cybium* 45(1):21–30 DOI 10.26028/cybium/2021-451-002.

Meunier FJ, Erdmann MV, Fermon Y, Caldwell RL. 2008. Can the comparative study of the morphology and histology of the scales of *Latimeria menadoensis* and *L. chalumnae* (Sarcopterygii: Actinistia, Coelacanthidae) bring new insight on the taxonomy and the biogeography of recent coelacanths? In: Cavin L, Longbottom A, Richter M, eds. *Fishes and the Break-up of Pangaea*. Special Publications, 295. London: Geological Society, 295–360.

Meunier FJ, Journiac N, Lavoué S, Rabet N. 2002. Caractéristiques histologiques des marques de croissance squelettique chez l’*Atipa*, *Hoplosternum littorale* (Hancock, 1828) (Teleostei, Siluriformes), dans le marais de Kaw (Guyane française). *Bulletin Français de la Pêche et de la Pisciculture* 364:49–69.

Meunier FJ, Laurin M. 2012. A microanatomical and histological study of the fin long bones of the Devonian sarcopterygian *Eusthenopteron foordi*. *Acta Zoologica* 93(1):88–97 DOI 10.1111/j.1463-6395.2010.00489.x.

Meunier FJ, Zylberberg L. 1999. The structure of the external layer and of the odontodes of scales in *Latimeria chalumnae* (Sarcopterygii, Actinistia, Coelacanthidae) revisited using scanning and transmission electron microscopy. In: Séré B, Sire J-Y, eds. *Proceedings of the 5th Indo-Pacific Fish conference, Nouméa*. Paris: Fr. Ichtyol, 109–116.

Millot J, Anthony J. 1958. *Anatomie de Latimeria chalumnae. T.I. Squelette, muscles et formations de soutien*. Paris: CNRS Edr.

Mondéjar-Fernández J. 2020. A new onychodont (Osteichthyes; Sarcopterygii) from the Middle Devonian of Morocco and its bearing on early osteichthyian evolution. *Journal of Systematic Palaeontology* 18(7):573–606 DOI 10.1080/14772019.2019.1655495.

Mondéjar-Fernández J, Meunier FJ, Cloutier R, Clément G, Laurin M. 2021. A microanatomical and histological study of the scales of the Devonian sarcopterygian *Miguashaia bureaui* and the evolution of the squamation in coelacanths. *Journal of Anatomy* 2021(2):1–28 DOI 10.1111/joa.13428.

Morales-Nin B, Panfili J. 2002. Age estimation. In: Panfili J, de Pontual H, Troadec H, Wright PJ, eds. *Manual of Fish Sclerochronology*. Brest, France: Ifremer-Ird coedition, 91–98.

Sanchez S, Tafforeau P, Ahlberg PE. 2014. The humerus of *Eusthenopteron*: a puzzling organization presaging the establishment of tetrapod limb bone marrow. *Proceedings of the Royal Society B: Biological Sciences* 281(1782):20140299 DOI 10.1098/rspb.2014.0299.
Sanchez S, Tafforeau P, Clack JA, Ahlberg PE. 2016. Life history of the stem tetrapod *Acanthostega* revealed by synchrotron microtomography. *Nature* 537(7620):408–411 DOI 10.1038/nature19354.

Schaeffer B. 1948. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the coelacanthine. *American Museum Novitates* 1378:1–32.

Schultze PJ, Klein N, Lambertz M. 2021. What’s my age again? On the ambiguity of histology-based skeletochronology. *Proceedings of the Royal Society B: Biological Sciences* 288(1955):20211166 DOI 10.1098/rspb.2021.1166.

Schultze H-P. 1973. Crossopterygier mit heterozerker Schwanzflosse aus dem Oberdevon Kanadas, nebst einer Beschreibung von Onychodontida-Resten aus dem Mitteldevon Spaniens und aus dem Karbon der USA. *Palaeontographica Abteilung* 143:188–208.

Schultze H-P, Cloutier R. 1996. Comparison of the Escuminac Formation ichthyofauna with other late Givetian/early Frasnian ichthyofaunas. In: Schultze H-P, Cloutier R, eds. *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. München, Germany: Verlag Dr. Friedrich Pfeil, 348–368.

Smith MM, Hobdell MH, Miller WA. 1972. The structure of the scales of *Latimeria chalumnae*. *Journal of Zoology* 167:501–509 DOI 10.1111/j.1469-7998.1972.tb01741.x.

Smylie M, Shervette V, McDonough C. 2016. Age, growth, and reproduction in two coastal populations of longnose gars. *Transactions of the American Fisheries Society* 145(1):120–135 DOI 10.1080/00028487.2015.1111256.

Stensiö EA. 1932. Triassic fishes from East Greenland. *Meddelelser om Groenland* 83:1–305.

Stensiö EA. 1937. On the Devonian coelacanths of Germany with special reference to the dermal skeleton. *Kungliga Svenska Vetenskapsakademiens Handlingar* 3(16):1–56.

Zhu M, Yu X, Lu J, Qiao T, Zhao W, Jia L. 2012. Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. *Nature Communications* 3:772 DOI 10.1038/ncomms1764.

Zylberberg L, Meunier F-J. 2008. New data on the structure and the chondrocyte populations of the haemal cartilage of abdominal vertebrae in the adult carp *Cyprinus carpio* (Teleostei, Ostariophysi, Cyprinidae). *Cybium* 32(3):225–239 DOI 10.26028/cybium/2008-323-005.

Zylberberg L, Meunier F-J, Laurin M. 2010. A microanatomical and histological study of the postcranial dermal skeleton in the Devonian sarcopterygian *Eusthenopteron foordi*. *Acta Palaeontologica Polonica* 55(3):459–470 DOI 10.4202/app.2009.1109.

Zylberberg L, Meunier F-J, Laurin M. 2015. A microanatomical and histological study of the postcranial dermal skeleton of the Devonian actinopterygian *Cheirolepis canadensis*. *Acta Palaeontologica Polonica* 61(2):363–376 DOI 10.4202/app.00161.2015.