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SHORT COMMUNICATION

Unexpected skeletal histology of an ichthyosaur from the Middle Jurassic of Patagonia: implications for evolution of bone microstructure among secondary aquatic tetrapods

Marianella Talevi · Marta S. Fernández

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Abstract During the Mesozoic, one of the most significant evolutionary processes was the secondary adaptation of tetrapods to life in water. Several non-related lineages invaded from the terrestrial realms and from the oceans of the entire world. Among these lineages, ichthyosaurs were particularly successful. Advance parvipelvian ichthyosaurs were the first tetrapods to evolve a fish-shaped body profile. The deep skeletal modifications of their bodies, as well as their biology, depict advance ichthyosaurs as the paradigm of secondary adaptation of reptiles to marine life. Functional inferences point to them as off-shore cruising forms, similar to a living tuna, and some of them were capable of deep diving. Bone histology of some genera such as *Temnodontosaurus*, *Stenopterygius*, *Ichthyosaurus*, and *Caypullisaurus*, characterized by overall cancellous bone, is consistent with the idea of a fish-shaped ichthyosaurs as fast and far cruisers. Here, we provide histological examination of the ribs of the Middle Jurassic parvipelvian *Mollesaurus*. Contrasting with the bone histology of other parvipelvian, *Mollesaurus* ribs are characterized by a compact and thick cortex. Our data indicate that the rib cage was heavy and suggest that not all advanced ichthyosaurs were fast cruisers. The compact and dense ribs in these parvipelvian show that advance ichthyosaurs were ecologically more diverse than previously thought and that the lightening of the skeleton reversed, as also occurred in the evolution of cetacean, at least once along the evolutionary history of ichthyosaurs.

Keywords Ichthyosaurs · *Mollesaurus* · Middle Jurassic · Bone histology

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M. Talevi (✉)
CONICET—Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro,
Isidro Lobo y Belgrano,
8332 General Roca, Río Negro, Argentina
e-mail: talevimarianela@hotmail.com

M. S. Fernández
CONICET—División Paleontología Vertebrados,
Museo de La Plata, Paseo del Bosque,
1900 La Plata, Argentina
e-mail: martafer@fcnym.unlp.edu.ar

Introduction

Ichthyosaurs and cetaceans are the only tetrapods that evolved tuna-shaped (thunniform) body plans (Motani 2002). Ichthyosaurs were one of the main predators in Mesozoic oceans, and they were traditionally considered as the paradigm of morphological modifications induced by a secondary adaptation to marine life (de Buffrénil and Mazin 1990; Massare 1988). From the terrestrial environments, basal lizard-shaped ichthyopterygians invaded the sea during the Early Triassic. By the Late Triassic, fish-shaped parvipelvian evolved and thrived soon after they emerged, becoming the only ichthyosaurs (Motani 2005). This body plan persisted since the Late Triassic until the extinction of group at the Cenomanian–Turonian boundary (Fischer et al. 2011). Functional morphological analyses depict these ichthyosaurs as far and fast cruisers (Motani 2002). The latter characteristic could have enabled them to maintain constant muscle activity efficiently during long cruising (Motani 2010). The bone histology of the parvipelvian *Temnodontosaurus*, *Stenopterygius*, *Ichthyosaurus*, *Platypterygius*, and *Caypullisaurus*, characterized by overall cancellous bone (Kolb et al. 2011; Lopuchowycz and Massare 2002; Talevi et al. 2011), is consistent with the idea of these ichthyosaurs as fast and far cruisers. On the contrary, *Mixosaurus*, a Late Triassic ichthyosaur with an intermediate body plan between the basal Early Triassic lizard-shaped and the post-Triassic fish-shaped ichthyosaurs, shows compact bones though it lacks histological specializations such as osteosclerosis or pachyostosis (Kolb et al. 2011) (Fig. 1).

Here, we provide histological examination of the ribs of the ophthalmosaurian ichthyosaur *Mollesaurus periallus* (Fernández 1999), the oldest member of the clade and a key taxon to elucidate the evolutionary history of the more advanced ichthyosaurus. Bone histology of *M. periallus* shows that advanced ichthyosaurs were ecologically more diverse than previously thought.

Material and methods

The studied samples consist of four fragments of ribs articulated with anterior and posterior dorsal vertebrae of one specimen of the ophthalmosaurian *M. periallus*. This specimen (Museo Olsacher, Zapala, Argentina, MOZ 2282) was recovered from the Los Molles Formation (Early Bajocian) outcropping at Chacaico Sur (Neuquén Basin, Argentina) (Fernández 1999). The ribs were transversely sectioned, following standard procedures. Sections were examined under a light microscope in normal and polarized light. For comparative purposes, the ribs of *Caypullisaurus bonapartei* (Fernández 1997), an ophthalmosaurian recovered from the Tithonian (Late Jurassic) of Patagonia (Argentina), were also sectioned and analyzed. To facilitate comparisons between sections, a compactness index (CI) was calculated for all sections as the area occupied by bone multiplied by 100 and divided by the total sectional area (Houssaye and Bardet 2011). This index was calculated by means of the software ImageJ (Abramoff et al. 2004).

Results

External morphology of the ribs

Vertebral column and ribs of the specimen MOZ 2282 are partially exposed and included in the rock matrix (Fig. 2a, b). One of the dorsal ribs, articulated with an anterior dorsal vertebra, was completely removed from the matrix and showed a bizarre morphology (Fig. 2c, d). Contrasting with the slender morphology characterized by shallow furrows on the anterior and posterior surfaces of other known ichthyosaurs, the studied rib is ventrally swollen, dorso-ventrally expanded, and bears a blunt crest extending from the capitulum along the main shaft of the rib. Ventrally, the medial half of the anterior surface of the rib is grooved. The medial half of the dorsal edge bears a sharp crest. Ventral to it, the posterior surface of the rib bears a deep furrow. The same general pattern is observed in the reaming ribs, although in those ribs located in a more posterior position, the dorsal crest is less developed. The rib morphology described above is regular along the vertebral column without indications of aberrant morphology or pathological pattern.

Histological description of the ribs

All sampled rib sections of *Mollesaurus* show the same histological pattern. Macroscopically, the structure shows a compact cortical region without a free medullar cavity. This area is occupied by a cancellous tissue of secondary origin (CI=72%). A small core lumen is located in the central region of the medullar region. A compact cortical region is differentiated from the spongy core region. The cortical region exhibits a particular histology compared to the overall cancellous aspect observed in the ribs of *Caypullisaurus* (Talevi et al. 2011) (CI=34.3%) (Fig. 3). The cortex in *Mollesaurus* is composed of compact tissue of woven bone tissue where primary and secondary osteones arranged parallel to the bone surface are observed. There is no deposition of lamellar tissue in the periosteal surface. This compact tissue is better developed on the ventral part of the rib. In the innermost area of the cortical region, the secondary osteons are not arranged in any particular order; instead, they invade the tissue, suggesting a substantial remodeling of the bone tissue. Towards the medullar region, a spongy cancellous tissue is observed. The trabeculae of this tissue are formed by the remains of secondary osteons.

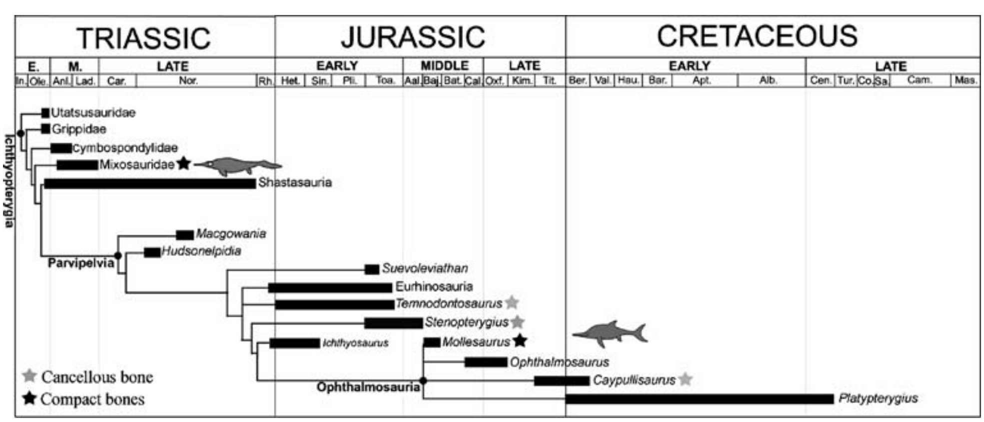

Fig. 1 Simplified phylogenetic tree of ichthyosaurs plotted against geological time (modified from Motani 2005; Fernández 1999) showing histological specializations

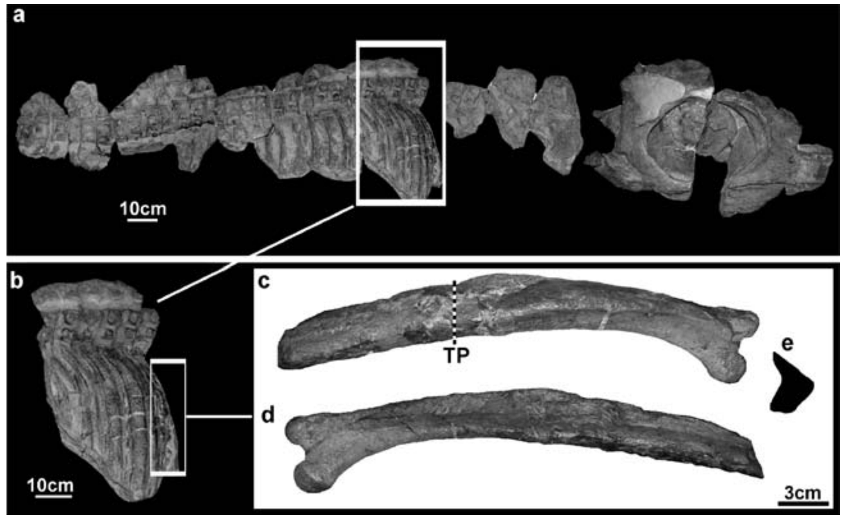

Fig. 2 *Mollesaurus periallus* MOZ 2282. **a** General view. **b** Detail of dorsal vertebrae and ribs. **c** Dorsal ribs removed from the matrix in anterior view. **d** Posterior view transverse plane (*TP*). **e** Schematic transversal section of the rib

Discussion

The histological examination of the ribs corresponding to different segments of the vertebral column of *Mollesaurus*, as well as the external morphology of the ribs, revealed an unusual pattern for an advanced parvipelvian. The compact inner and outer cortices are notably different from the cancellous bone that characterized the cortical region in *Caypullisaurus*. In *Mollesaurus*, although cancellous, the bone fills the medullar region, while in *Caypullisaurus*, there is a well-defined medullary cavity both in juveniles and adults (Talevi et al. 2011). Histological descriptions of parvipelvian ichthyosaur ribs are almost absent in the literature (e.g., Kiprijanoff 1881). However, histological condition of limb bones of the parvipelvian ichthyosaurs *Stenopterygius quadriscissus, Ichthyosaurus, Temnodontosaurus*, and *Platypterygius* (de Buffrénil and Mazin 1990; Kolb et al. 2011; Lopuchowycz and Massare 2002) is congruent with the microanatomical pattern of *Caypullisaurus* ribs (i.e., overall cancellous bones). By contrast, in the basal non-parvipelvian ichthyosaur *Mixosaurus* in which well-documented ontogenetic series have been analyzed, the compactness of bones is more pronounced than in post-Triassic ichthyosaurus and remains well developed through life (Kolb et al. 2011). Strikingly, *Mollesaurus*, a member of the advanced ophthalmosauria clade, shows a notably different histological pattern and resembles that of the Middle Triassic *Mixosaurus* in having an extensive compact cortex bone. However, deposition rates seem to be different, while the ribs and gastralia of *Mixosaurus* exclusively show parallel-fibered or lamellar–zonal tissue; the cortex of *Mollesaurus* ribs shows exclusive woven tissue, suggesting that at least the ribs had a more rapid growth in *Mollesaurus* than in *Mixosaurus*. The cortex of *Mollesaurus* ribs is not only compact but also thick, suggesting that the increase of periosteal cortex deposits has led to the alteration observed in the macromorphology of the ribs, i.e., bizarre and ventrally swollen bearing anterior and dorsal crests (Fig. 2). As the same histological pattern is observed in the anterior and posterior ribs, it is clear that a significant portion of the *Mollesaurus* skeleton was characterized by a high bone density. The increase in bone compactness, or "pachyostosis," has been considered as one of the possible strategies for adaptation to a fully aquatic life, playing a role of ballast for passive hydrostatic regulation of buoyancy and body trim (Houssaye 2009; de Ricqlès and de Buffrénil 2001; Taylor

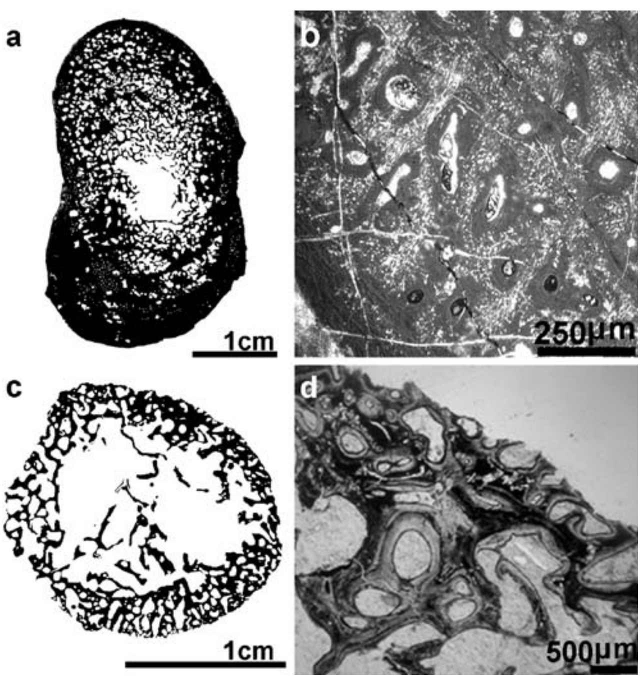

Fig. 3 *Mollesaurus periallus* MOZ 2282. **a** General view of the transverse section of the rib. **b** Peripheral region of the compact cortex. *Caypullisaurus bonapartei* MLP 85-I-15-1. **c** General view of the transverse section of the rib. **d** Peripheral region of the cancellous cortex

2000; Street and O'Keefe 2010). The association between compact and dense ribs and particular life strategies among fully aquatic tetrapods is still unclear. In sirenians, skeletal ballast in their thoracic region has been associated with life in shallow coastal environments (de Buffrénil et al. 1990). In *Mixosaurus*, the presence of compact cortical bone, associated with other morphological traits, has been related with their lifestyle as near-shore or shelf dweller with frequent access to open or deep-marine environments (Kolb et al. 2011). In *Mollesaurus*, as well as in all other parvipelvians, morphological traits, such as fish-shaped and dark-adapted eyes, indicate the ability to cruise and to dive more deeply than the basal forms (Motani 2009). This is not necessarily contradictory with the bone histology of *Mollesaurus*; however, it introduces an interesting topic: *Mollesaurus* could have been pelagic and inhabit deeper waters, and also far cruiser but not necessarily fast cruiser. In any case, bone histology of *Mollesaurus* indicates that the lifestyle of the more derived clade of parvipelvian, i.e., the ophthalmosaurians, was more diverse than previously thought. The presence of compact and dense cortical bone in *Mollesaurus* ribs is also significant in reconstructing the evolutionary history of such specialization within the highly adapted marine lineage of ichthyopterygians. As it occurs in other secondary aquatic tetrapods, there are two general patterns of inner bone architecture: overall cancellous bone versus higher compactness of bone; the latter was the first to occur in the fossil record as documented by the bone histology of the Early Triassic *Utatsusaurus* and the Late Triassic *Mixosaurus* (Nakajima 2008; Kolb et al. 2011). The acquisition of a lighter skeleton followed this stage and occurred at the present state of the knowledge least in the Early Jurassic, as documented by the parvipelvian *Ichthyosaurus, S. quadriscissus*, and *Caypullisaurus*. Bone histology in the Bajocian (Middle Jurassic) *Mollesaurus* clearly illustrates a reversion process in bone architecture during the history of the parvipelvian ichthyosaurs. Notably, in the evolutionary history of sirenians and cetaceans, fully aquatic tetrapod lineages, reversion processes affecting skeletal inner structure also occurred (Gray et al. 2007; de Buffrénil et al. 2010).

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References

Abramoff MD, Magelhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophoton Int 11:36–42

de Buffrénil V, Mazin JM (1990) Bone histology of the ichthyosaurs: comparative data and functional interpretation. Paleobiology 16:435–447

de Buffrénil V, de Ricqlès A, Ray C, Domning D (1990) Bone histology of the ribs of the archaeocetes (Mammalia: Cetacea). J Vertebr Paleontol 10:455–466

de Buffrénil V, Canoville A, D'Anastasio R, Domning P (2010) Evolution of sirenian pachyosteosclerosis, a model-case for the study of bone structure in aquatic tetrapods. J Mamm Evol 17:101–120

de Ricqlès A, de Buffrénil V (2001) Bone histology, heterochronies and the return of tetrapods to life in water: where are we? In: Mazin J-M, de Buffrénil V (eds) Secondary adaptation to life in water. Verlag Dr. F. Pfeil, München, pp 289–306

Fernández M (1997) A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, northwestern Patagonia, Argentina. J Paleontol 71:479–484

Fernández M (1999) A new ichthyosaur from the Los Molles Formation (Early Bajocian), Neuquén Basin, Argentina. J Paleontol 73:677–681

Fischer V, Clément A, Guiomar M, Godefroit P (2011) The first definite record of a Valanginian ichthyosaur and its implications on the evolution of post-Liassic Ichthyosauria. Cretac Res 32:155–163

Gray M, Kainec K, Mandar S, Tomko L, Wolfe S (2007) Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans. Anat Rec 290:638–653

Houssaye A (2009) “Pachyostosis” in aquatic amniotes: a review. Integr Zool 4:325–340

Houssaye A, Bardet N (2011) Rib and vertebral microanatomical characteristics of hydropelvic mosasauroids. Lethaia. doi:10.1111/j.1502-3931.2011.00273.x

Kiprijanoff W (1881) Studien über die fossilen Reptilien Russlands. Theil 1. Gattung Ichthyosaurus König aus dem Sewerischen Sandstein oder Osteolith der Kreide-Gruppe. Mém Acad Imp des Sci Saint-Pétersbourg 28:1–103

Kolb C, Sánchez-Villagra M, Scheyer T (2011) The palaeohistology of the basal ichthyosaur *Mixosaurus* Baur, 1887 (Ichthyopterygia, Mixosauridae) from the Middle Triassic: palaeobiological implications. C R Palevol 10:403–411

Lopuchowycz VB, Massare JA (2002) Bone microstructure of a cretaceous ichthyosaur. Paludicola 3:139–147

Massare J (1988) Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. Paleobiology 14:187–205

Motani R (2002) Scaling effects in caudal fin kinematics: implication for ichthyosaurian speed. Nature 415:309–312

Motani R (2005) Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. Annu Rev Earth Planet Sci 33:395–420

Motani R (2009) The evolution of marine reptiles. Evo Edu Outreach 2:224–235

Motani R (2010) Warm-blooded “sea dragons?”. Science 328:1361–1362

Nakajima Y (2008) Growth strategies in early ichtchyosaurs: an osteohistological study. J Vertebr Paleontol 28(3 suppl):44A

Street H, O'Keefe F (2010) Evidence of pachyostosis in the cryptocleidoid plesiosaur *Tatenectes laramiensis* from the Sundance Formation of Wyoming. J Vertebr Paleontol 30:1279–1282

Talevi M, Fernández M, Salgado L (2011) Variación ontogenética en la histología ósea de *Caypullisaurus bonapartei* Fernández, 1997 (Ichthyosauria: Ophthalmosauridae). Ameghiniana, 48: in press

Taylor M (2000) Functional significance of bone ballast in the evolution of buoyancy control strategies by aquatic tetrapods. Hist Biol 14:15–31