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Histology of the endothermic opah (*Lampris* sp.) suggests a new structure-function relationship in teleost fish bone

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Abstract

Endothermy, production and retention of heat by the body, appeared convergently in mammals, birds and four spiny-rayed teleost fish lineages. Of these, endothermy over most or all of the body has only appeared in two groups: tunas and the opah (*Lampris*). Hitherto, tunas have been the only spiny-rayed fishes known to have bones containing embedded osteocyte cells; others have acellular bone. We examined bone histology in *Lampris* for the first time, demonstrating the presence of cellular bone very similar to that of tunas. This contrasts with the acellular condition of its ectothermic close relatives. The distribution of this character suggests that it co-evolved with red-muscle endothermy, hinting at a common physiological

mechanism that would link bone histology to endothermy in these distantly related teleost lineages.

Keywords

Bone histology; endothermy; osteocytes; Teleostei; Lampridiformes; Scombridae

1. Introduction

Endothermy, the capacity to produce and retain metabolic heat, is a well-known trait of modern mammals and birds. In a spectacular example of convergent evolution, endothermy also evolved independently in mackerel (Lamnidae) and thresher (Alopiidae) sharks and in four separate teleost lineages [1,2], allowing them to maintain active and efficient swimming in a broad range of water temperatures [3]. Teleost endothermy is little studied relative to that in tetrapods, but may provide key insights into the physiological requirements and evolution of endothermy.

Changes in bone microstructure are thought to correlate with tetrapod endothermy. This structure-function relationship has been a valuable tool for unravelling the metabolism and thermal biology of extinct taxa, including dinosaurs [e.g., 4,5]. However, the scarcity of comparative histological and microanatomical data on teleost bone hinders our understanding of the relationship between physiology and bone microstructure in endothermic teleosts.

All known endothermic teleosts belong to the mega-diverse predominantly marine clade Acanthomorpha, or spiny-rayed fishes [6]. These groups show two distinct endothermic strategies, different from those of birds and mammals: (1) billfishes (Xiphiidae) and the butterfly kingfish *Gasterochisma melampus* (Scombridae: Gasterochismatinae), independently developed heater organs consisting of modified extraocular muscles that locally warm the brain and eyes [1,2]; (2) tunas (Scombridae: Thunnini) generate heat via the activity of red

extraocular and swimming muscles and retain it with specialised counter-current blood vessels, warming not only the head but also the axial musculature [1,2]. The opah *Lampris* sp. (Lampridiformes) has been recently shown to have both heat-generating extraocular and pectoral fin muscles, and a counter-exchange blood vessel network that heats cold oxygenated blood returning from the gills [7,8]. Thanks to this unique system, *Lampris* is the only known teleost to show endothermy over its entire body, allowing it to spend long periods of time hunting in the cold water between 50 and 400 m in depth [8].

Bone tissues in teleosts display a great variety of structures ranging from: (i) cellular bone in which osteogenic cells (osteoblasts) are enclosed by the bone matrix, and become trophic cells (osteocytes); to (ii) acellular bone that is entirely deprived of osteocytes, the osteoblasts withdrawing from the surface during deposition of the bone matrix [9–12]. Cellular bone is primitive to osteichthyans but is lost in the clade Neoteleostei, which includes acanthomorphs [11,13]. The only acanthomorphs with osteocytes reported thus far are tunas [9–11], in which bone tissues also show substantial remodelling [14]. The secondary reacquisition of osteocytes and the presence of conspicuous bone remodelling in tunas have been hypothesised to be linked with their active, endothermic metabolism [11,12,14]. Nevertheless, this assertion remains conjectural in the absence of comparative observations in lineages that independently evolved endothermy. In this context, *Lampris* provides an opportunity to test the hypothesised link between endothermy and cellular bone in teleosts. However, the bone microstructure of *Lampris* has thus far been unknown. Here we describe bone histology of this endothermic taxon and some of its ectothermic close relatives.

2. Material and methods

Histological sections were cut from bones of two extant lampridiforms (electronic supplementary material, Table S1): *Lampris* sp. (MNHN-ZA-AC-A-7506, Muséum national

d'Histoire naturelle, Paris, France) and *Velifer hypselopterus* (MNHN-ICOS-01117), along with six Late Cretaceous neoteleosts including the stem-lampridiform [15] †*Aipichthys velifer* (MNHN.F.HAK1991). These fossils were included to document the trait in some of the earliest representatives of the clade (Table S1). Each sample was embedded in epoxy resin. The sections were sawn and ground to obtain 50-60 µm thickness, and examined with an Axiovert microscope in transmitted natural light.

3. Results

Primary bone in the rib of *Lampris* includes numerous elongate osteocyte lacunae (Fig. 1a,b), with their main axis perpendicular to the direction of growth. The canaliculi that housed the cytoplasmic extensions of the cells are fewer than in typical teleost bone [12]; they are relatively short, few are ramified (Fig. 1e), and they all point toward the periosteum (Fig. 1d). Primary bone shows a parallel-fibered structure, with layers of aligned osteocytes alternating with lines of arrested growth (Fig. 1c,d). The rib is spongy, with numerous cavities (Fig. 1a) surrounded by secondary bone limited by cementing lines (Fig. 1g). The secondary bone incorporates fewer osteocytes than areas of primary bone (Fig. 1f,g).

The scapula of *Velifer* is composed of acellular bone: no osteocytes are incorporated in the bone tissue. However, it is perforated by numerous canals that are winding and bifurcated, indicating that they probably housed cytoplasmic extensions from surface osteoblasts (Fig. 1h). The rib of every Late Cretaceous taxon sampled (including the stem-lampridiform †*Aipichthys*) also consists of acellular bone, without any identifiable features.

4. Discussion

Prior to this study, lampridiform osteohistology was only reported from an unknown bone of *Trachipterus* [9] and from the dorsal-fin pterygiophores of *Regalecus* [16], two elongate-

bodied lampridiforms that collectively are the sister-group of *Lampris* [15]. Both have acellular non-hyperostotic bones (hyperostotic bones occasionally contain a few embedded osteocytes in bones of species that otherwise have acellular bones [16]). Therefore, *Lampris* is the only known lampridiform with cellular bone in normal conditions (Table S2). Furthermore, the red muscles and counter-exchange vascular networks indicative of endothermy are absent among other lampridiforms, suggesting the absence of endothermy in all lampridiforms other than *Lampris* [8] (Fig. 2).

In scombrids, cellular bone is described in *Auxis*, *Euthynnus*, *Katsuwonus* and *Thunnus* [9,11,12], i.e. "true" tunas (Thunnini), which are all red-muscle endotherms [1,2]. Conversely, ectothermic scombrids such as the mackerels *Scomber* and *Scomberomorus* [1] have acellular bone [9,10] (Fig. 2, Table S2). Amongst the acanthomorphs that show cranial-only endothermy [1,2], billfishes also have acellular bone (Table S2) with histological features indicative of extensive remodelling, such as secondary osteons [17,18]. The absence of osteocytes in billfishes and ecologically comparable large-bodied fast-swimming pelagic predators (e.g., *Coryphaena*, *Seriola*) [9,10] excludes the possibility of a size-related distribution of osteocytes in acanthomorphs. Among teleosts virtually all taxa show either cellular or acellular bone consistently throughout all bones of the skeleton [10–12]. Therefore, we do not expect the presence of osteocytes to be affected by proximity with warmer regions of the body.

The widespread distribution of acellular bone among lampridiforms and other acanthomorphs (including some of the stratigraphically oldest fossils) indicates that cellular bone evolved independently from acellular ancestors in the *Lampris* and tuna lineages (Fig. 2, Table S2). Our survey of endothermic acanthomorphs and their immediate ectothermic relatives then suggests that osteocytes are found only in red-muscle endotherms amidst the

whole diversity of the clade, this physiology correlating perfectly with the occurrence of secondarily cellular bone in the acanthomorph clade (Fig. 2).

This is reinforced by the observation that, despite their independent evolutionary origins, bone tissues of *Lampris* and tunas share peculiar histological features: conspicuous remodelled bone [12,14] and similar-looking osteocytes with an elongate cell body and very few cytoplasmic projections, differing from the 'star-shaped' lacunae of other teleosts that are typically more rounded with numerous cytoplasmic projections [12,19]. These similarities, and their difference from the primitive condition of cellular bone in non-acanthomorph teleosts, may reflect either functional similarity of osteocytes in *Lampris* and tuna, and/or constraints on their morphology resulting from evolutionary reacquisition. This remains uncertain.

Whether the correspondence documented here is due to a physiological advantage of reacquiring osteocytes in red-muscle endotherms, or to a passive consequence of elevated metabolism, it provides strong evidence for a structure-function correlation between bone microstructure and endothermy in acanthomorph teleosts. Unlike in tetrapods, histological indicators of metabolism have rarely been addressed by studies of teleost bone [20]. To overcome this limitation, more comparative structural studies incorporating physiological considerations, at the inter- and intraspecific scale would be needed. Applying such findings to fossil taxa may permit breakthrough investigation into fish palaeophysiology (for instance, in potentially endothermic fossil acanthomorphs), a field that is currently poorly developed but is promising considering the advances in tetrapod palaeophysiology that were enabled by palaeohistology [e.g., 4,5]. This would allow a better understanding of bone biology and evolution in a group representing half of modern vertebrate diversity.

Data accessibility. Data are available as the electronic supplementary material.

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Author contributions. D.D., F.J.M. and O.O. conceived the project. F.J.M. supervised specimen acquisition and preparation, and realised histological observations and photographs. D.D., F.J.M., M.F., R.B.J.B. and O.O. analysed and interpreted the data. D.D. and F.J.M. drafted the original manuscript and figures. All authors revised and edited the manuscript, approved the final version and agree to be accountable for all aspects of the work.

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Competing interests. We have no competing interests.

Ethical statement. This research is based exclusively on specimens from natural history collections.

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Figures:

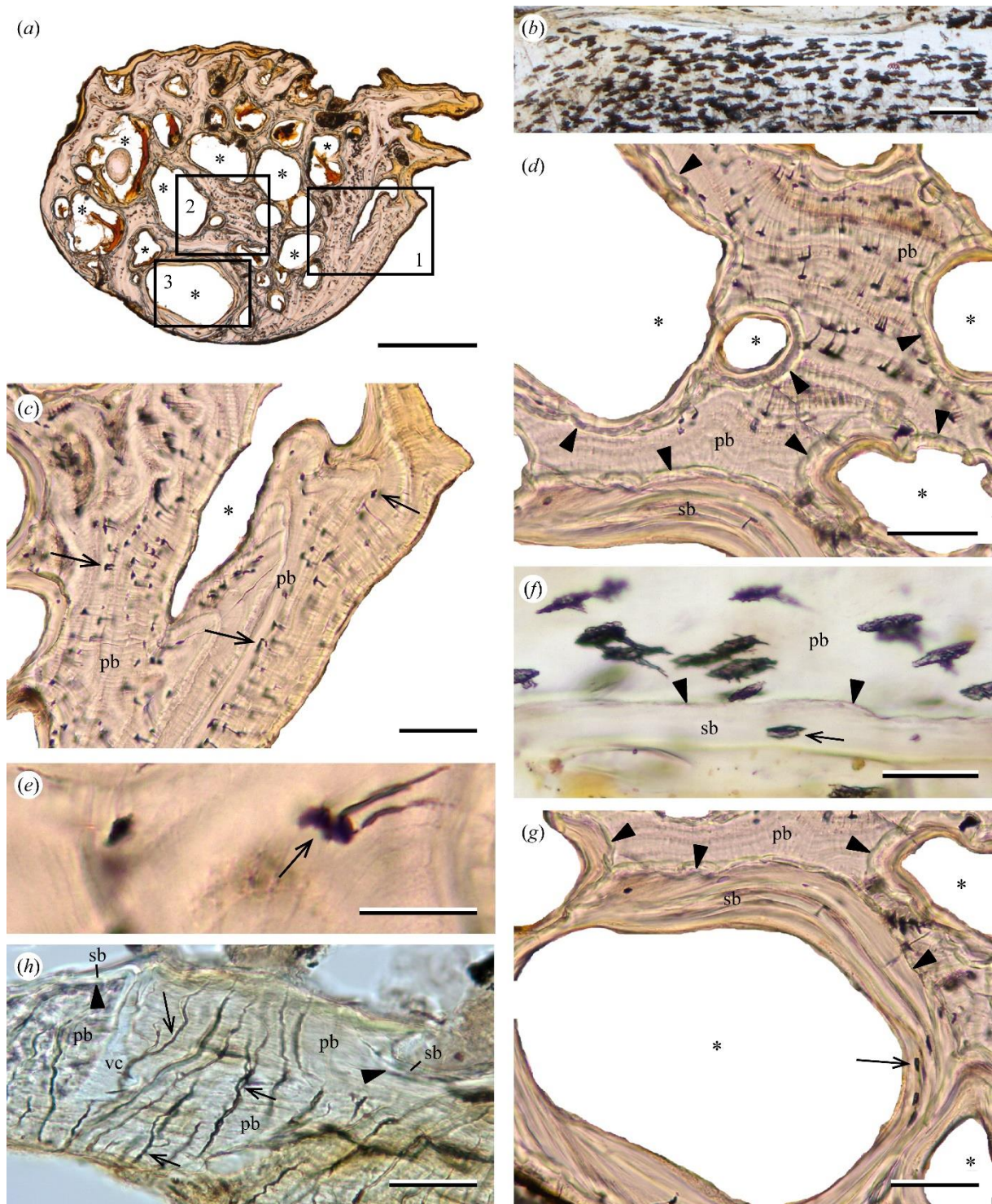


Figure 1. (a-g) *Lampris* sp. (MNHN-ZA-AC-A-7506). Sections of the rib (natural transmitted light). (a) Entire cross section showing numerous vascular cavities (asterisks). (b)

Longitudinal section showing numerous osteocyte lacunae. (c) Detail of inset 1, showing

osteocyte lacunae (arrows) in primary bone. (d) Detail of inset 2 showing an area of primary bone with circularly-oriented osteocytes, and vascular cavities fringed by secondary bone. (e) Detail of an osteocyte (arrow) in primary bone with its radially-oriented canaliculi. (f) Longitudinal section showing osteocytes in primary bone. An osteocyte lacuna is seen in secondary bone (arrow). (g) Detail of inset 3 showing remodelled secondary bone including osteocytes without canaliculi (arrow). (h) *Velifer hypselopterus* (MNHN-ICOS-01117). Cross section of the scapula (transmitted natural light) showing the lack of osteocytes, but the presence of bifurcated (arrows) osteoblastic canaliculi inside the primary bony tissues. Some areas of secondary bone are visible.

pb, primary bone; sb, secondary bone; *, marrow cavities. Arrowheads point to reversal lines between primary and secondary bone. Scale bars, (a) 500 μm , (b-d,g) 100 μm , (e-f,h) 50 μm .

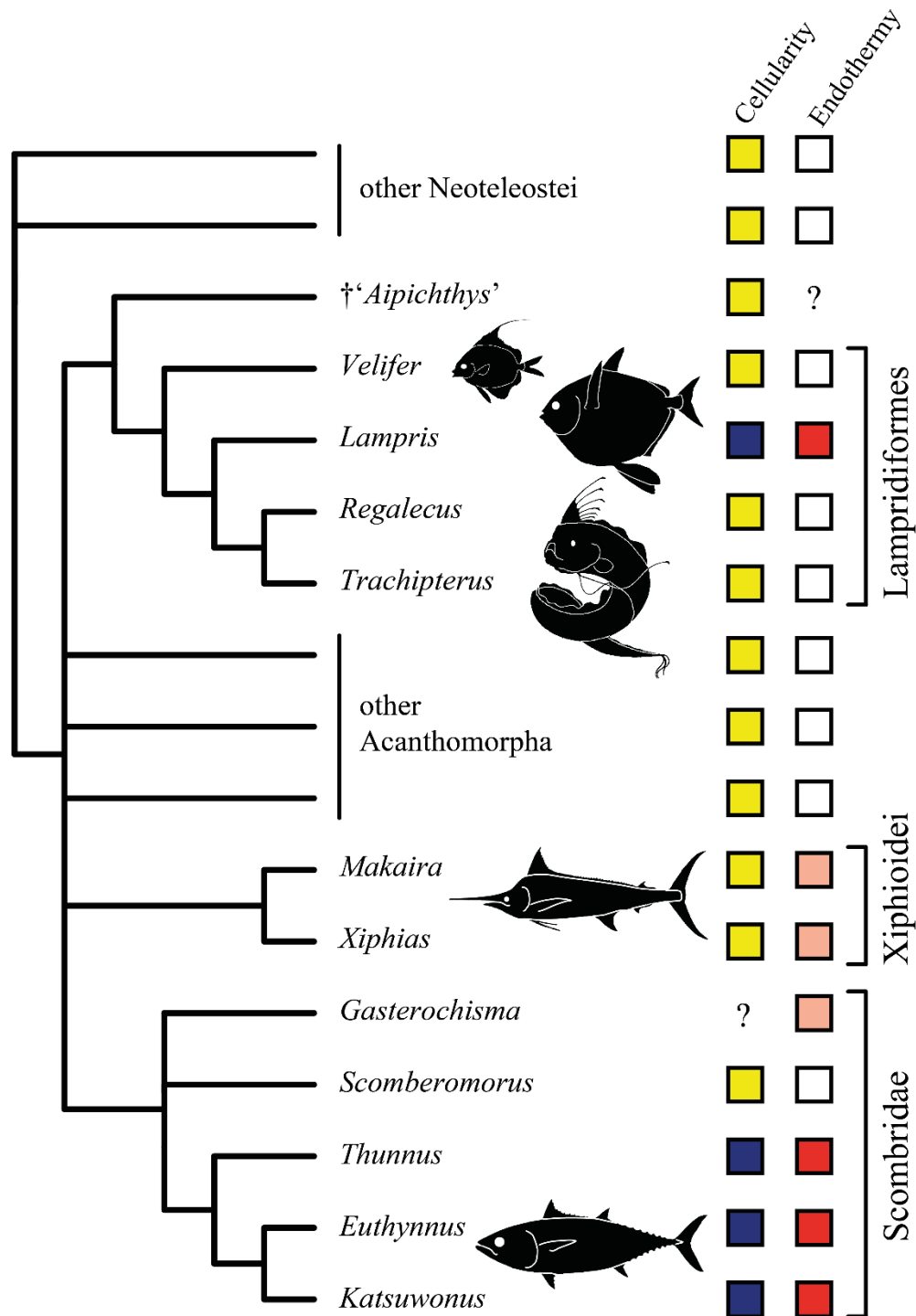


Figure 2. Phylogenetic distribution of the osteohistological and metabolic parameters considered in this study among Neoteleostei. Acellular bone is in yellow, cellular bone in dark blue. Ectothermic taxa are in white, taxa with brain heaters (cranial-only endothermy) in light pink, with red-muscle endothermy in red. Tree topology is adapted from [1,15,21].

Electronic Supplementary Material (ESM)

Histology of the endothermic opah (*Lampris guttatus*) suggests a new structure-function relationship in teleost fish bone

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2 ESM tables

Comment on the renewed taxonomy of *Lampris* species

The individual of *Lampris* sp. studied here (MNHN-ZA-AC-A-7506) is a historical specimen previously referred to the species *Lampris guttatus*. The original publications in which endothermy was initially reported were also based on individuals referred to *L. guttatus* [1,2]. Shortly after completion of our histological work, the once circumglobal *L. guttatus* was divided in five species, each having a more limited geographical range [3]. As a consequence, the specimens in which whole-body endothermy has been detected [1] would belong to the North Pacific species *L. incognitus* (N. Wegner, pers. comm.), and our specimen might not pertain to the same species. There is no available information on where MNHN-ZA-AC-A-7506 was collected, and since the specimen consists only in a portion of vertebral column and associated ribs, it is impossible to confirm its identity based on comparative anatomy. On the other hand, the six extant species of *Lampris* are all very similar in terms of ecology, external morphology and behaviour [3], and all seem to share similar pectoral muscle anatomy (N. Wegner, pers. comm., D.D. and F.J.M. pers. obs.). It is then reasonably likely that they are all capable of endothermy, which would not change the conclusions of the present paper.

ESM table S1. List of specimens used for the histological observations.

Only one bone was sampled for each extant taxon, due to their rarity in osteological collections. Only non-pathological and non-hyperostotic bones were used. When possible, only ribs were sampled, with one exception (*Velifer hypselopterus*) that we do not expect to affect the results since cellular or acellular bone has been shown to be consistent over the whole skeleton in virtually all teleosts [4,5].

In addition to the two extant lampridiforms, six fossil acanthomorphs and close neoteleost relatives from the Cenomanian (Late Cretaceous) of Lebanon were sampled as well.

For *Lampris* sp. (MNHN-ZA-AC-A-7506) the 7th abdominal rib was sectioned transversally and longitudinally ~5 mm from the articular head. For fossil taxa, we took samples where ribs were already fragmented or broken. The thin section photographs of Fig. 1 were modified to edit out background noise and remaining soft tissues in bone cavities.

All thin sections are kept in the palaeohistological collections of the Muséum national d'Histoire naturelle (MNHN, Paris, France).

Taxon	Dry skeleton specimen number	Bone sampled
<i>Lampris</i> sp.	MNHN-ZA-AC-A-7506	7 th abdominal rib
<i>Velifer hypselopterus</i>	MNHN-ICOS-01117	scapula
† <i>'Aipichthys' velifer</i>	MNHN.F.HAK1991	1 st and 6 th abdominal rib
† <i>Omosoma</i> sp.	MNHN.F.SHA2563d	7 th abdominal rib
† <i>Acrogaster heckeli</i>	MNHN.F.SHA38g	posteriormost abdominal rib
† <i>Eurypholis</i> sp.	MNHN.F.HAK1550	3 rd abdominal rib
† <i>Ctenothrissa vexillifer</i>	MNHN.F.HAK246d	6 th abdominal rib
† <i>Pycnosteroides levispinosus</i>	MNHN.F.HDJ55	posteriormost abdominal rib

ESM table S2. Selected list of acanthomorph and neoteleost taxa for which the type of bone (cellular or acellular) is known.

Systematic position	Taxon	Bone type	References
Other Neoteleostei			
Neoteleostei <i>incertae sedis</i>	† <i>Ctenothrissa vexillifer</i>	acellular	this study
Aulopiformes	† <i>Eurypholis</i> sp.	acellular	this study
Acanthomorpha			
Acanthomorpha <i>incertae sedis</i>	† <i>Pycnosteroides levispinosus</i>	acellular	this study
stem-Lampridiformes	† <i>Aipichthys</i> ' <i>velifer</i>	acellular	this study
Lampridiformes, Veliferidae	<i>Velifer hypselopterus</i>	acellular	this study
Lampridiformes, Lampridae	<i>Lampris</i> sp.	cellular	this study
Lampridiformes, Trachipteridae	<i>Trachipterus trachipterus</i>	acellular	[6]
	<i>Zu cristatus</i>	acellular	[6]
Lampridiformes, Regalecidae	<i>Regalecus russelii</i>	acellular (except in hyperostotic pterygiophores)	[7]
Polymixiiformes	† <i>Omosoma</i> sp.	acellular	this study
Trachichthyiformes	† <i>Acrogaster heckeli</i>	acellular	this study
Xiphioidae, Xiphiidae	<i>Xiphias gladius</i>	acellular	[6,8]
Xiphioidae, Istiophoridae	<i>Istiophorus albicans</i>	acellular	[4,8]
	<i>Kajikia albida</i>	acellular	[8]
	<i>Makaira nigricans</i>	acellular	[4,8]
	<i>Tetrapturus angustirostris</i>	acellular	[8]
	<i>Tetrapturus belone</i>	acellular	[6]
Scombridae, Scombrini	<i>Scomber scombrus</i>	acellular	[6]
Scombridae, Scomberomorini	<i>Scomberomorus cavalla</i>	acellular	[4]
	<i>Scomberomorus maculatus</i>	acellular	[4,9]
Scombridae, Thunnini	<i>Auxis rochei</i>	cellular	[6]
	<i>Euthynnus affinis</i>	cellular	[10]
	<i>Euthynnus alletteratus</i>	cellular	[11]
	<i>Euthynnus lineatus</i>	cellular	[12]
	<i>Katsuwonus pelamis</i>	cellular	[4,5,10,13]
	<i>Thunnus alalunga</i>	cellular	[6,10,13–15]
	<i>Thunnus albacares</i>	cellular	[10]
	<i>Thunnus obesus</i>	cellular (scales)	[16]
	<i>Thunnus thynnus</i>	cellular	[6,11,17]

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