Journal of Morphology

RESEARCH ARTICLE OPEN ACCESS

Hyperostosis in Fishes: An Update With New Species Records

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Received: 27 July 2024 | **Revised:** 26 September 2024 | **Accepted:** 29 September 2024

Keywords: Actinopterygii | marine and fossil fishes | Tilly bones

ABSTRACT

Literature reports of hyperostosis are often misleading and have been confused with osteomas, a pathological condition. Hyperostotic bones are known to occur only in bony fishes of the class Actinopterygii, within at least 16 orders, 35 families, 89 genera, and 153 species. They are present almost exclusively in marine fishes and exceptionally in a few extinct freshwater species known from hypersaline environments and one extant cichlid. Hyperostosis is best represented in the family Carangidae where it is known to occur in 53 of approximately 181 valid species. We also provide a synthetic report on what we know and what misconceptions exist regarding hyperostosis. Patterns of hyperostosis are often species-specific but provide no useful phylogenetic information. In species known to develop hyperostosis, it is usually not apparent (non-histologically) in juveniles and typically only becomes fully developed in the largest individuals. The timing of hyperostosis on-set in different bones is often sequential rather than simultaneous across different bones. Most marine Neoteleostei have acellular skeletons but histological observations have shown that in species exhibiting hyperostosis, areas of active remodeling are composed primarily of cellular bone characterized by a rich vascular network and bone-resorbing osteoclasts.

> *As is normal in science, future researchers will build upon and improve upon what we know now.*
>
> Nelson, Grande, and Wilson (2016).

1 | Introduction

With an estimated number of 18,550 species (Fricke, Eschmeyer, and Van der Laan 2024), marine fishes exhibit an enormous diversity of anatomical features within the vertebrates. Among this anatomical complexity, accounts of fishes with unusual inflated or swollen bones have appeared irregularly in scientific and popular literature since the 17th century and generated much interest and curiosity. These bony globose or gall-like structures have generally been termed pachyostosis or fish hyperostosis (Smith-Vaniz, Kaufman, and Glowacki 1995). Isolated hyperostotic bones have been occasionally washed-up on the shore and mistaken for fossil fruits or seeds (Verdcourt 1964). An interesting description of an isolated hyperostotic anal-fin pterygiophore, with two attached fin spines (Figure 1), was given by Worm (1655, 270) who stated, “its shape as it were represents a mouse that has two movable pointed beaks ... The belly is thick, globular, almost the size of a hen's egg... It has a long tail, narrow, of the thickness of a goose feather ... From which animal, and from which part of a body, I confess myself ignorant.” There also have been newspaper articles and YouTube accounts puzzling about the identity of these isolated hyperostotic bones. Summaries (for their time) of hyperostosis are available (Gervais 1875; Köstler 1882; Korschelt 1940), and more recently by Smith-Vaniz, Kaufman,

FIGURE 1 | Hyperostotic first anal-fin pterygiophore in rotated lateral view (="Os wormianum" of Worm 1655) of Atlantic spadefish *Chaetodipterus faber*, NMW 97939, photo by H. Ahnelt; see fig. 8b for the position of the anal-fin pterygiophore (apt) in situ.

and Glowacki (1995), Aguilera et al. (2017), and Guzmán and Polaco (2002). Meunier and Herbin (2014) documented histological bone preparations, deposited in the Muséum national d'Histoire naturelle [not examined by us], of many of the species studied by Gervais (1875).

Hyperostotic bones have also been the subject of numerous papers on fossilized taxa (Klausewitz 1965; Olsen 1969; Fierstine 1968; Tiffany, Pelham, and Howell 1980; Hewitt 1983; Schlüter and Kohring, 2002; Chang et al. 2008; Aguilera et al. 2017; Schoemaker 2018; Schlüter, Kohring, and Mehl 1992; Tyler, Purdy, and Oliver 1992).

They have been found in nearly every pre-Columbian Indian mound along the Florida coast (Tiffany, Pelham, and Howell 1980) and from the Yorktown Formation, Pliocene of eastern North Carolina (Tyler, Purdy, and Oliver 1992). Aguilera et al. (2017, 1869) noted that, "an exceptional quantity of thick, swollen or hyperostotic bones occurs in all examined collections from the Rio de Janeiro shell mounds." Zooarchaeological swollen fish bones in South America were reported by Béarez (1997) from the Pacific coast of Ecuador, by Vogel and Veríssimo (1982) from southeastern Brazilian shell mounds, marine localities in Tunisia (Hewitt 1983), the Eurogeul area of the Netherlands (Schoemaker 2018), Fikirtepe, Turkey (von den Driesch 1994), and phosphate-bearing deposits along Lake Manyara, Tanzania (Schlüter, Kohring, and Mehl 1992). They are also known from marine Miocene deposits of Sharktooth Hill, Kern County, California (Fierstine 1968).

One of the earliest records of hyperostosis in extant fishes (Bell 1793) was of the longfin batfish, *Platax teira* (Fabricius), which British surgeon Bell called *Chaetodon* sp. His paper included a drawing (Figure 2) of the skeleton, clearly showing hyperostosis of some of the ribs, neural and hemal spines, first pterygiophore of the anal and dorsal fins, pelvic bone, and the supraoccipital. He commented on the spongy nature of the "tumors," which "were filled with oil" and initially believed them to be exostoses arising from disease but upon dissection correctly concluded they were natural. Bell also wondered about the advantage of these large tumors which seemed to have no evident purpose.

Given the considerable attention these globose ossifications have attracted since the 17th century and the lack of a comprehensive account on this phenomenon, we surveyed the rich history of literature accounts of hyperostotic bones in fishes. We found them to only occur in actinopterygians, within 16 orders, 35 families, 89 genera, and 153 species. The vast majority of taxa with hyperostosis are marine fishes.

We also discuss what we know and what misconceptions exist regarding hyperostosis. While this review highlights the diversity of fishes that have hyperostotic bones, the functional basis of hyperostosis, a natural phenomenon, still remains unknown (Desse et al. 1981; von den Driesch 1994; Smith-Vaniz, Kaufman, and Glowacki 1995; Meunier and Desse 1996; Meunier, Béarez, and Francillon-Vieilllot 1999; Bartosiewicz 2013; Aguilera et al. 2017; Mahmoud and Ibrahim 2021). The primary objectives of our study are to call attention to the enigmatic hyperostotic bones in fishes and to encourage others to more fully investigate their cause and function.

Hyperostotic bones have often been called "Tilly bones," (Konnerth 1966; Olsen 1966; Tiffany, Pelham, and Howell 1980; Schlüter, Kohring, and Mehl 1992; Schoemaker 2018; Schwartz 2000; Schlüter and Kohring 2002; Capasso, 2005; Chang et al. 2008), in honor of Tilly Edinger (1897–1967) who, after immigrating to the United States in 1940, spent the rest of her career at Harvard University's Museum of Comparative Zoology. Unfortunately, her extensive notes on hyperostosis are not readily available but prints of some of her photographs (Figure 3) have proved to be very useful. Dr. Edinger's busy schedule and premature death from an automobile accident in 1967 prevented her from publishing anything on fish hyperostosis.

2 | Methods

Abbreviations for all hyperostotic bones are given in Table 1. Occurrence of hyperostosis for all species is given in Table 2. Individual bones shown here on radiographs and tracings of radiographs are identified in Table 2 for those listed species, including their SL measurements. Length measurements, all rounded to centimeters (cm), are standard length (SL) measured from snout tip to anterior structural base (hypural plate) of caudal fin or, in some carangids, fork length (FL) snout tip to posterior end of shorter middle caudal-fin ray. To facilitate comparisons, all specimen images are shown as left-side views, including some originally taken on the right side and flipped horizontally using Adobe Photoshop. Unfortunately,

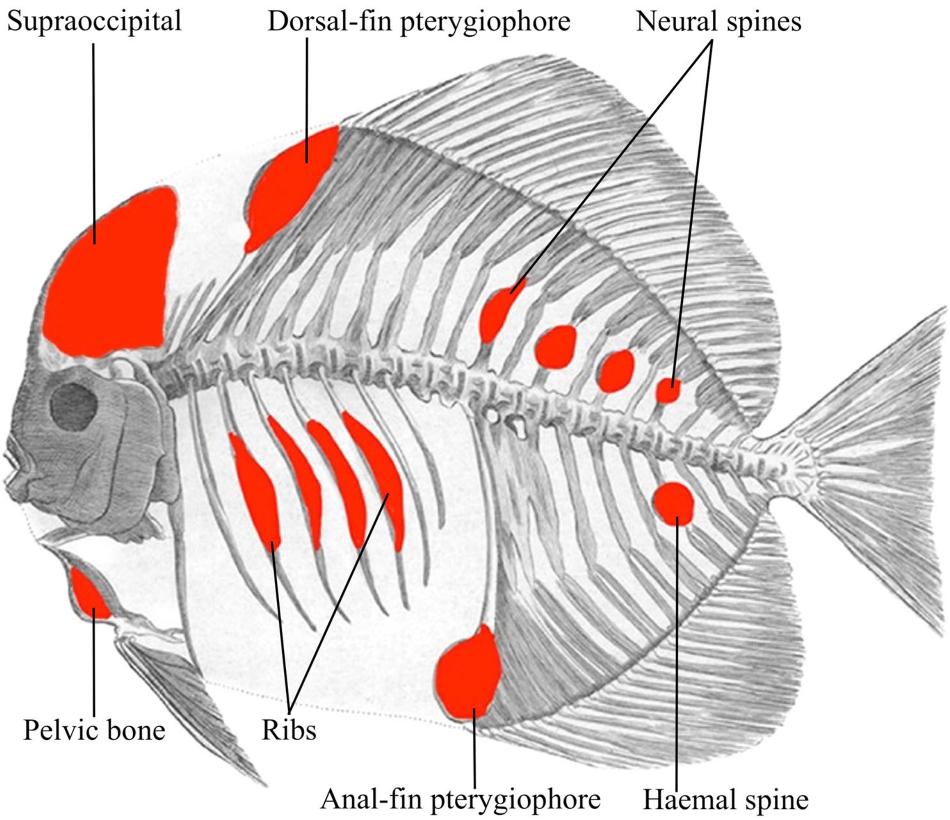


FIGURE 2 | *Platax teira* = *Chaetodon* sp. of Bell (1793), Pl. VI (Bell's original drawing with hyperostotic bones indicated in red).

measurements are not available for some of the radiographed specimens; either the specimens could not be examined by us or their length measurements were never recorded. With few exceptions only radiographs of relatively large individuals were photographed or are listed in Table 2.

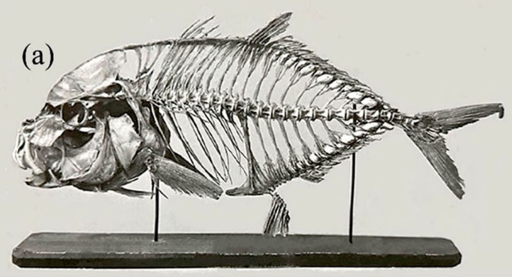
Scientific names used in this paper and the number of valid species of Carangidae are those of Eschmeyer's Catalog of Fishes (Fricke, Eschmeyer, and Van der Laan 2024). Our confirmation of hyperostotic bones (indicated in Table 2) is based on: (1) examination of radiographs or skeletons of fishes deposited in the following collections: ANSP, including the Hyrtl skeleton collection, AMNH, AMS, BMNH, CAS, FMNH, LACM, RMNH, NMNZ, NMW, SAM, SIO, SMF, TABL, USNM (specimen radiographs are indicated by RAD numbers), and ZMUC; (2) reliable publications on fish hyperostosis, especially those including photographs or illustrations; (3) examination of Edinger prints of mounted fish skeletons, see introduction; (4) emails, personal communication, and photographs provided by other ichthyologists. A few published radiographs or literature reports of hyperostosis, especially those of fossil fishes or their isolated bones, cannot be reliably identified to species, and their identifications are assumed to be correct.

2.1 | Abbreviations of Collections

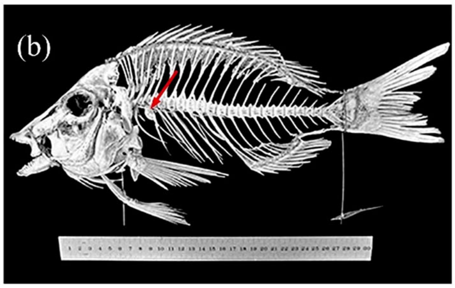
Collection abbreviations are those of Eschmeyer's Catalog of Fishes (Fricke, Eschmeyer, and Van der Laan 2024) as follows: AMS = Australia Museum, Sydney, New South Wales, Australia; ANSP = Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA; AMNH = American Museum of Natural History, New York; USA; BMNH = Natural History Museum, London, UK; CAS = California Academy of Sciences, San Francisco, USA; LACM = Natural History Museum of Los Angeles County, Los Angeles, California, USA; MTD = Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde Dresden, Germany; NMW = traditional abbreviation used here for the fish collection of the Naturhistorisches Museum Wien (NHMW) catalog numbers, Wien (Vienna), Austria; RMNH = Rijksmuseum van Natuurljike Histoire, Amsterdam, the Netherlands (current name: Naturalis Biodiversity Center); NMNZ = Museum of New Zealand Te Papa, Tongarewa, New Zealand; SAM = South African Museum, Cape Town, South Africa; SIO = Scripps Institution of Oceanography, Marine Vertebrate Collection, La Jolla, California, USA; SMF = Senckenberg Forschungsinstitut und Naturmuseum, Abteilung Marine Zoologie, Frankfurt am Main, Hessen, Germany; TABL = Tropical Atlantic Biological Laboratory, National Marine Fisheries Service, Miami, Florida, USA (specimens transferred to CAS, including some subsequently deposited at USNM or ANSP); USNM = Smithsonian Institution National Museum of Natural History, Department of Vertebrate Zoology, Division of Fishes, Washington D.C, USA; WAM = Western Australian Museum, Department of Aquatic Zoology, Ichthyology, Perth, Western Australia, Australia; ZMUC = Københavns Universitet, Zoologisk Museum, Vertebrater, Fiskesamlingen, Copenhagen, Denmark.

3 | Discussion

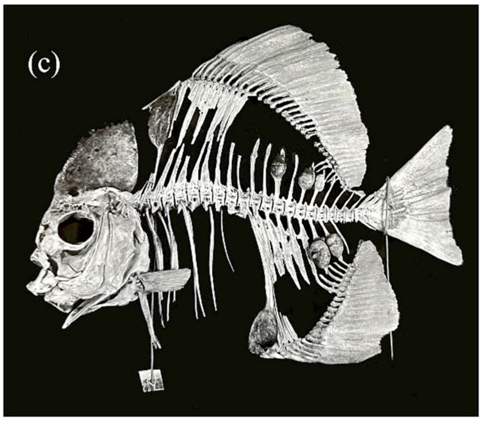
See Figures 4–13.



Gnathanodon speciosus



Lethrinus nebulosus



Platax teira

FIGURE 3 | Photographs by Tilly Edinger of skeletal mounts exhibiting hyperostosis. (a) Carangidae: *Gnathanodon speciosus* (Forsskål), RMNH 182, 40 cm SL; (b) Lethrinidae: *Lethrinus nebulosus* (Forsskål), SMF 2104, 31 cm SL (red arrow points to rib hyperostosis); (c) Ephippidae: *Platax teira* (Fabricius), SMF 7522, 33 cm SL (pelvic girdle and pterygiophores of some anal- and dorsal-fin rays missing). See Table 2 for hyperostotic bone sites for these specimens. Photos courtesy Museum of Comparative Anatomy, Harvard University.

3.1 | From Enigmatic Bones to a Natural Phenomenon

Accounts of inflated or swollen bones in fishes have appeared in the literature since the late 17th century (Bell 1793). Isolated hyperostotic bones have led to much curiosity and confusion about their identification, functional role, and affinities (Gervais 1875; Barnard 1947; von den Driesch 1994). Numerous reports of hyperostosis are erroneous and have been confused with tumors or osteomas. A good example of this confusion was Günther, (1860, 345–346) partial description of *Lepidopus caudatus*, “several of the interneural spines [dorsal-fin pterygiophores] are swollen to a globular bony mass, and are probably diseased.” For comprehensive summaries of tumors in fishes, see Schlumberger and Lucké (1948), Mawdesley-Thomas (1975) and Groff (2004). A few of the species these authors list are not included in Table 2 but their “tumors” may possibly have been cases of true hyperostosis. As noted by Brothwell (1967), “interpretation of neoplasms is one of the more … difficult aspects of paleopathology.” Although usually unavailable, histological data are important to distinguish the hyperostotic process from the occurrence of osteoid osteomas.

Below we discuss distinctions between osteomas, hyperostosis, buckler scales, and nodular excrescences. We cite literature references discussing hyperostosis in 29 families and 110 species of fishes, and independently confirm hyperostosis in 45 other species. Additional species currently unreported to have hyperostosis are to be expected. The diversity of fishes exhibiting hyperostosis and the wide range of bone cell and bone tissues involved in these fishes indicates the complexity of these functionally enigmatic structures.

3.2 | A Phenomenon of Large Fishes

For most species the full development of hyperostosis (size, shape and position) is apparent only in large specimens, and x-rays of large specimens are seldom available but are usually required for complete detection. Hyperostosis is often undetectable on radiographs of smaller individuals. As Smith-Vaniz, Kaufman and Glowacki (1995, p. 579) emphasized, “A broad size series of individuals of each species must be examined before the ontogenetic pattern of FH [fish hyperostosis] can be fully established.” von den Driesch (1994, 43) noted that one of the characteristics of tumors [=hyperostosis] is “their propensity to occur in fishes over 20 cm in length.” Hall and Witten (2019, 132) stated, “The occurrence of hyperostosis is a predictable, albeit variable, late-life history bone formation.”

The onset of hyperostosis is unknown in most species that develop hyperostotic bones as adults. A rare exception is the scabbardfish *L. caudatus*. In this species only the dorsal pterygiophores are affected by hyperostosis. First swellings of these pterygiophores appeared at a size of ~93 cm SL which became fully developed at a size of ~101 cm SL (Giarratana et al. 2012; fig. 5). For *Selene setapinnis* Tuna et al. (2023) state that “Hyperostosis was found from the length of 236 mm, and … was observed in all specimens > 260 mm.” In these two species the shift from non-hyperostotic to fully hyperostotic bones apparently occurs through an increase in size of only about 10%. However, many more ontogenetic studies are required to obtain an overview of size-dependent increase in hyperostosis.

Adults of some sharks also develop hypercalcifications (Compagno 1988, 69) that “are analogous to hyperostosis in bony fishes … and are normal rather than teratological in species where they occur.” Investigation of that subject in sharks is beyond the scope of this study.

3.3 | Distinctions of Tumors, Hyperostotic Bones, Bucklers, and Nodular Excrescences

3.3.1 | Tumors in Fishes

“Natural fish populations have been found to have tumors in almost all tissue types,” (Vijayakumar et al. 2014). Bone tumors

TABLE 1 | List of abbreviations of hyperostotic bones used in Table 2.

Afs	Anal-fin spine	Na	Nasal
Apt	Anal-fin pterygiophores	Ns	Neural spine
Br	Branchiostegal ray	Op	Opercle
Boc	Basioccipital	Par	Parietal
Cl	Cleithrum (clavicle)	Pas	Parasphenoid
Cls	Cleithral spine	Pb	Pelvic bone
Co	Coracoid	Pfs	Pelvic fin spine
Cp	Caudal peduncle	Pmx	Premaxilla
Dfs	Dorsal-fin spines	Pop	Preopercle
Dpt	Dorsal-fin pterygiophores	Pro	Prootic
Epi	Epineural	Pt	Posttemporal
Epo	Epioccipital	Pto	Pterotic
Eth	Ethmoid complex	R	Rib
Exo	Exoccipital	Scl	Supracleithrum
Fr	Frontal	Sn	Supraneural (predorsal)
Hs	Hemal spine	Soc	Supraoccipital
Lac	Lacrimal (Lacrimal sabers [Smith, Everman, and Richardson 2018] or rostral projections [Yato, Nakayama, and Endo 2020])	Sop	Subopercle
Me	Mesethmoid	V	Vertebra

or osteomas are common and seldom benign (Schlumberger and Lucke 1948; Mawdesley-Thomas 1975; Capasso, 2005). Analysis of pathological bones was described in detail by Gervais (1875) and Köstler (1882). Generally, such pathological overgrowth of bone was described from single specimens and, if paired bony structures were affected, the tumor usually occurs on only one side (reviewed in Schlumberger and Lucke 1948; Rao and Lakshmi 1986; Singaravel et al. 2017). Pathological hyperossifications are known from many species of various fish families, for example, Ariidae, Cichlidae, Cyprinidae, Esocidae, Gadidae, Ictaluridae, Paralichthyidae, Sciaenidae, Sparidae, Sphyraenidae (Schlumberger and Lucke 1948; Selvaraj, Gopakumar, and Rajagopalan 1973; Rao and Lakshmi 1986; Groff 2004; Vijayakumar et al. 2014; Singaravel et al. 2017). Bertullo and Traibel (1955, fig. 1) documented tumors on the ribs of the sciaenid *Micropogon furnieri* and opined that it may have been caused by parasitism of *Tetrarhynchus* sp.

3.3.2 | Hyperostosis in Fishes

The term hyperostosis as defined here is a non-pathological condition applied to enlarged and swollen bones that are often gall-like and globose in external appearance, for example, Figures 3c and13b, resulting from the periosteal formation of excess bone. Internally these sites are spongy, highly vascularized, lack osteocytes, and have evidence of active bone remodeling. Such hyperostosis is a normal aspect of skeletal growth and development in a wide range of teleost fishes and is localized to specific bones and bone sites. Non-hyperostotic bone is acellular (anosteocytic) in neoteleosts, (Moss 1961; Parenti 1986; Meunier and Huysseune, 1991; Hall and Witten 2019), while hyperostotic bone in marine fishes has spatial juxtaposition of cellular and acellular bone tissues in adjacent and often serially homologous bone sites (Smith-Vaniz, Kaufman, and Glowacki 1995). Histological data are important to distinguish these two bone types. Schlüter and Kohring (2002, 135) also noted, "under the SEM the specimens [hyperostotic fossil bones] show a characteristic sponge-like surface pattern (their fig. 5a–d), whereas fish bones not affected by hyperostosis are smooth."

We found a surprisingly large number of hyperostotic bone sites in fishes (see Table 1). The tetraodontid *Chonerhinos naritus* (fig. 4k) is unique in having a pair of hyperostotic bones located on the caudal peduncle. If paired bones are hyperostotic, both bones are affected and to the same extent, but see discussion of an exceptional *Caranx caninus* rib (Figure 5e).

We were able to independently confirm the identifications of most of the hyperostotic species reported in the literature but for some we had to assume previous identifications were correct. We emphasize that some fishes have dense and thick bones that could easily be mistaken for hyperostosis; based on our examination of radiographs of ethanol-preserved specimens, and especially of published photographs and drawings of fossil bones, we may have occasionally made that error ourselves.

3.3.3 | Buckler scales or tabular acellular bone

Some authors refer to these large and pointed structures of zeiform fishes as being hyperostotic. We include three zeiforms in Table 2 as having hyperostosis but independently confirmed it only in *Zeus faber* Linnaeus. In addition to having bucklers, *Z. faber* also has a hyperostotic frontal, supracleithrum, cleithral spine, and preopercle (Figure 9a). Although we have not

TABLE 2 | Occurrence of hyperostosis in fishes.

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
Anguilliformes	Muraenesocidae	*Congresox talabon* (Cuvier 1829)	Khan (1983)	Dfs, Soc, V
		Congresox talabonoides (Bleeker 1852)	Khan (1983)	Dfs, Soc, V
		Cynoponticus coniceps (Jordan & Gilbert 1882)	Béarez (1997) (general observation only)	Bone not specified
		Muraenesox sp.	LACM 38119-50; identified by D. G. Smith	Op
Clupeiformes	Clupeidae	**Sardina*? *crassa* (Sauvage 1873)	Gaudant and Meunier (1996)	Eth, Fr, Hs, Ns, Pas
Cypriniformes	Cyprinidae	**Hsianwenia wui* Chang et al. (2008)	Chang et al. (2008)	Apt, Dpt, Epi, Hs, Ns, R, V
Siluriformes	Ariidae	*Bagre panamensis* (Gill 1863)	Figure 4a; USNM 28181 (RAD 116020), 9 cm SL	Eth, Fr, Soc
		Bagre pinnimaculatus (Steindachner 1876)	Guzmán & Polaco (2002)	Cl, Co, Eth, Op, Pop
Lampriformes	Veliferidae	*Metavelifer multiradiatus* Regan 1907	Figure 4b; AMS IB.2699 (RAD 119593), 34 cm SL	Apt, Dpt, (?) Pt, V
	Regalecidae	*Regalecus russellii* (Cuvier 1816)	Paig-Tran et al. (2016)	Dpt
Zeiformes	Cyttidae	*Cyttus australis* (Richardson 1848)	Tyler and Santini (2005)	Dpt, Soc
	Zeidae	*Zenopsis conchifer* (Lowe 1852)	Tyler and Santini (2005)	Dpt, Soc
		Zeus faber Linnaeus 1758	Figure 9a; NMW 60029, 35 cm SL	Cls, Fr, Pop, Scl
Gadiformes	Gadidae	*Gadus morhua* Linnaeus 1758	Radulescu, Nalbant, and Angelescu (1972)	Pop
		Melanogrammus aeglefinus (Linnaeus 1758)	Driesch (1994)	Co
			Köstler (1882) (as *Gadus aeglefinus*)	Cl
			Schoemaker (2018)	Cl, Pt, V
	Merluccidae	*Merluccius merluccius* (Linneaus 1758)	Desse et al. (1981)	Cl, Soc
			Köstler (1882) (as *Merluccius vulgaris*)	Hs
		Merluccius productus (Ayres 1855)	Guzmán and Polaco (2002)	Cl
	Trichiuridae	*Eupleurogrammus muticus* (Gray 1831)	Driesch (1994) (tab. 1, page 42; general observation only)	Bone not specified
		**Lepidopus albyi* (Sauvage 1870)	Meunier, Gaudant, and Bonelli (2010)	Dpt
		**Lepidopus proargenteus* Arambourg (1927)	Arambourg (1997) (pl. 30, fig. 1)	Dpt
		Lepidopus caudatus (Euphrasen 1788)	Chanet (2018), Cuyas Vera (2016), Gervais (1875),	Dpt

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
			Giarratana et al. (2012),Günther (1860),Korschelt (1940), Köstler (1882)	
		Trichiurus japonicus Temminck & Schlegel 1844	Starks (1911a) (footnote on page 25)	Cl
		Trichiurus lepturus Linneaus 1758	Al Nahdi, De Leaniz, and King (2016)	Hs, Ns
			Gervais (1875)	Soc
			Guzmán and Polaco (2002)	Apt, Dpt, Epo, Fr, Par, Soc
			James (1960)	Apt, Dpt, Fr, Par, Soc
			James (1967)	Apt, Dpt, Soc
			Köstler (1882)	Fr, Soc
			Meunier, Gaudant, and Bonelli (2010)	Dpt
			Olsen (1971)	Apt, Dpt
			Starks (1911a)	Cl, Epo, Fr, Par, Soc
			Tuna, Calixto, and Mesquita (2024)	Cl, Dpt, Hs, Soc,
Scombriformes	Scombridae	*Euthynnus lineatus* Kishinouye 1920	Béarez (1997), Béarez, Meunier, and Kacem (2005), Guzmán and Polaco (2002), Marrast and Béarez (2019)	V
Gobiiformes	Gobiidae	*Gobius ignotus* Gaudant 1978	Gaudant and Meunier (1996)	Hs, Ns, V
Carangiformes	Centropomidae	*Centropomus ensiferus* Poey 1860	Aguilera et al. (2017)	Exo, Pro, Soc
		Centropomus mexicanus Bocout 1868	Guzmán and Polaco (2002)	Epo, Eth, Fr, Par, Soc
		Centropomus parallelus Poey 1860	Aguilera et al. (2017)	Skull (occipital region)
			Fraser (1968)	Epo, Fr, Par, Soc
	Menidae	*Mene maculata* (Bloch & Schneider 1801)	pers. obs.; USNM 443840 (skeleton) 21 cm SL	Apt, Pb
	Carangidae	*Alectis ciliaris* (Bloch 1787)	pers. obs. CAS 16317 (radiograph), 43.5 cm SL	Eth, Soc
			Starks (1911b)	Dpt
		Atropus mentalis (Cuvier 1833)	Figure 6a; CAS 16447 (radiograph), 50 cm SL	Soc
			Driesch (1994) (as *Ulua mentalis*)	Soc
		Caranx bucculentus Alleyne & Macleay 1877	Figure 5a; USNM 173970 (RAD 116362), 36 cm SL	Dpt, Pb, Sn, Soc

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Caranx caballus Günther 1868	Figure 5b; USNM 129669 (RAD 11634), 41 cm SL	Pt
			Béarez (1997)	Apt, Dpt, Pt
		**Caranx carangopsis* Steindachner (1859)	Steindachner (1859)	Dpt, R, V
		Caranx caninus Günther 1867	Figure 5d; CAS 216871 (RAD 122051) 50 cm SL	Cl, Dpt, Pb, R [see text discussion of R]
			Figure 5e; USNM 100998 (RAD 122044), 37 cm SL	Apt, Dpt
			Fierstein (1968) (misidentified as *Caranx hippos*)	Dpt
			Guzmán & Polaco (2002)	Pb, R, Sn
			Smith-Vaniz & Carpenter (2007)	Cl, Pb, R [see text discussion of R], Sn
		Caranx crysos (Mitchill 1815)	Starks (1911b)	Pt
		Caranx fischeri Smith-Vaniz and Carpenter (2007)	Figure 5c.; ZMUC P.46362 (RAD 122076), 42 cm SL	Pt, R
			Smith-Vaniz & Carpenter (2007)	Pt, R
		Caranx hippos (Linnaeus 1758)	Figure 5f; CAS 153015 (RAD 122107), 36 cm SL	Cl, Dpt
			Figure 5g; USNM 114618 (RAD 122097), 56 cm SL	Cl, Apt, Dpt, Ns, Pb, R
			Figure 13b	Dpt
			Aguilera et al. (2017)	Cl, Ns
			Kaiser (1960) (as *Caranx carangus*)	Apt, Cl, Dpt, Hs, Ns, Pb, R, Soc
			Konnerth (1966)	Cl, Dpt, Ns, Pb, Soc
			Korschelt (1940), Starks (1911a)(as *Caranx carangus*)	Cl, Apt, Dpt, Hs, Ns, Pb, R
			Olsen (1966), Smith-Vaniz & Carpenter (2007), Starks (1911b)	Cl, Dpt, Ns, Pb
		Caranx latus Agassiz 1831	Figure 5h; CAS 258426 (RAD 116439), 63 cm SL	Cl, Scl
			Aguilera et al. (2017)	Cl, Ns
		Caranx rhonchus Geoffroy St. Hilaire 1817	We follow Fricke, Eschmeyer and Van der Laan (2024) for the generic allocation of *C. rhonchus* although it is probably incorrect Figure 6b; ANSP 159101 (RAD 118935), 37 cm SL	Cl

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Caranx senegallus Cuvier 1833	Figure 5i; ANSP 140258 (RAD 116499), 28 cm SL	Soc
		Caranx sexfasciatus Quoy & Gaimard 1825	Figure 5j; CAS 16255 (RAD 116573), 36 cm SL	Cl, Scl
			Figure 5k; CAS 16244 (RAD 116506), 71 cm SL 44	Cl, Scl
			Béarez (1997)	Cl
			Gopinath (1951)	Soc
		Caranx tille Cuvier 1833	Figure 5l; CAS 16233 (RAD 116585), 53 cm SL	Cl
		Decapterus maruadsi (Temminck& Schlegel 1843)	Figure 6c; ANSP 139120 (RAD 116720), 29 cm SL	Soc
		Decapterus russelli (Rüppell 1830)	Driesch (1994) (tab 1, page 42; general observation only)	Bone not specified
		Euprepocaranx dorsalis (Gill 1863)	pers. obs.; LACM 33797-70, 27 cm SL	Sn, Soc
			Fig. 6d; SIO 61-247 (RAD 116317), 40.5 cm SL	Sn, Soc
			Béarez (1997) (as *Caranx otrynter*)	Soc
			Guzmán & Polaco (2002) (as *Carangoides dorsalis*)	Sn, Soc
			Starks (1911a) (as *Citula dorsalis*)	Sn, Soc
		Gnathanodon speciosus (Forsskål 1775)	Fig. 3a; RMNH 182 (Skeletal mount, Edginer photo.), 40 cm SL	Apt, Dpt
			Starks (1911b)	Apt, Dpt
		Kaiwarinus equula (Temminck & Schlegel 1844)	Barnard (1947)	Scl, Soc
		Oligoplites altus (Günther 1868)	Pers. obs.; SIO 80-49 (RAD 117316), 37 cm SL	Cl, Fr
			Béarez (1997)	Apt, Cl, Dpt
			Starks (1911b) (as *Oligoplites mundus*)	Fr, Soc
		Oligoplites palometa (Cuvier 1932)	pers. observation; CAS 27069 (skeleton), 47 cm SL	Apt, Cl, Dpt, Fr, Soc
			Pers. obs.; USNM 121805 (RAD 117323), 28 cm SL	Cl, Dpt
		Oligoplites saliens (Bloch 1793)	Figure 6e, CAS-SU 53065 (RAD 117327), 42 cm SL	Cl, Dpt, Fr, Hs, Ns, Soc
		Paraselene orstedii (Lütken 1880)	Figuree 6f; USNM 79971 (RAD 117428), 21 cm SL	Apt, Dpt, Soc
			Starks (1911a) (as *Selene oerstedii*)	Soc

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Platycaranx chrysophrys (Cuvier 1833)	pers. observation; LACM 38119-19, 47 SL	Soc
			Fig. 6h; ANSP 149396 (RAD 1167225), 60.5 cm SL	Soc
			Driesch (1994) (as *Caranx chrysophrys*)	Soc
			Lidour et al. (2020)	Exo, Soc
		Pseudocaranx georgianus (Cuvier 1833)	Figure 6g; NMNZ P.30775 (CS195), 77 cm SL	Dpt, Sn, Soc
			Smith-Vaniz & Jelks (2006)	Soc
		Scomberoides commersonnianus Lacepède 1801	Figure 6i; CAS uncatalogued (RAD 117397), 89 cm SL	Cl, Hs, Ns, Pt
			Driesch (1994)	Cl, Hs, Ns, Pt
			Jawad & Ibrahim (2017) (misidentified as *Alepes vari*), 46 cm SL	Hs, Ns
			Korschelt (1940) (misidentified as *Chorinemus lysan*)	Cl, R
			Mahmoud & Ibrahim (2021) (misidentified as *Scomberoides lysan*)	Hs, Ns
		Selar crumenophthalmus (Bloch 1793)	Aleve (1966)	Soc
		Scyris alexandrina (Geoffroy St. Hilaire 1817)	Pers. obs.; AMNH 88901 (Skeleton), 38 cm SL	Apt, Cl, Dpt, Soc
			Driesch (1994)	Ns
			Smith-Vaniz, Kaufman, and Glowacki (1995),fig. 1b	Apt, Cl, Dpt, Hs, Ns, Soc
		Scyris indica (Rüppell 1830)	Figure 6j; CAS 16306(RAD 116166-003), 46 cm SL	R, Sn, Soc
			Cantor (1849)	Sn, Soc
			Desse et al. (1981) (as *Alectis indica*)	Soc
		Selene brevoortii (Gill 1863)	Béarez (1997)	Soc
			Guzmán & Polaco (2002)	Soc
			Starks (1911b) (as *Selene vomer*)	Cl, Co
		Selene dorsalis (Gill 1863)	Driesch (1994) tab. 1, page 42; General observation only)	Bone not specified
		Selene setapinnis (Mitchill 1815)	Pers. obs.; AMNH 57884 (skeleton), 33 cm SL	Co, Dpt
			Starks (1911b) (as *Vomer setipinnis*)	Co, Dpt
			Tuna et al. (2023)	Apt, Co, Dpt

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
			Tuna et al. (2021	Cl, Dpt
		Selene vomer (Linnaeus 1758)	Guzmán & Polaco (2002)	Cl, Co, Fr, Ns, Sn, Soc
			Starks (1911b)	Cl, Co, Soc
		Seriola dumerili (Risso 1810)	Rapisarda et al. (2008)	Hs
		Trachinotus africanus Smith 1967	Figure 11a; ANSP 73240, 31 cm SL	Dpt, Lac, Na,
		Trachinotus anak Ogilby 1909	Figure 11b; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3C), FMNH 55290, 55 cm SL	Lac, Na, R
			Wada, Itou, and Motomura (2019)	Lac, Na, R
		Trachinotus blochii (Lacepède 1801)	Figure 11c; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3A), ANSP 148773, 43 cm SL	Sn
			Figure 11i; ANSP 144395 (RAD 117594), 21 cm SL	Sn
			Smith-Vaniz & Walsh (2019)	Sn
		Trachinotus falcatus (Linnaeus 1758)	Figure 11d; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3F), ANSP 148731, 43 cm SL	Lac, Na, Sn, R
		Trachinotus kennedyi Steindachner (1875)	Figure 11e; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3E), ANSP 148767, 64 cm SL	Lac, Na, Sn, R
			Figure 12; CAS-SU 12076, 43.5 cm SL	Lac, Na, Sn, R
			Béarez (1997)	R
		Trachinotus maxillosus Cuvier 1832	Figure 6k; ANSP 140837 (RAD 117698), 51 cm SL	Apt, Dpt, Lac, R
			Figure11f; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3D), TABL 107667, 51 cm SL	Apt, Dpt, Lac, R
		Trachinotus mookalee Cuvier 1832	Figure 11g; 76, after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 3B), ANSP 138879, 45 cm SL	Sn, Soc
			Figure 11h; ANSP 148755 (RAD 117700), 34 cm SL	Sn, Soc
			Smith-Vaniz and Walsh (2019)	Soc
		Trachurus capensis Castelnau 1861	Pers. obs.; SAM 11947 (RAD 117826), 34 cm SL	Cl
		Trachurus declivis (Jenyns 1841)	Pers. obs.; AMS I.15110 (RAD 119458)	Soc

(Continues)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Trachurus indicus Nekrasov 1966	Figure 6l; ANSP 140349 (RAD 117767), 27 cm SL	Cl, Soc
		Trachurus japonicus (Temminck& Schlegel 1844)	Pers. obs.; USNM 44896 (RAD 117769), 28 cm SL	Cl, Soc
			Aleve (1966)	Cl, Soc
			Hotta (1958)	Soc
			Suda (1996)	Cl
		Trachurus mediterraneus (Steindachner 1868)	Laroche, Peron, and Galy (1982)	Cl, Soc
		Trachurus murphyi Nichols 1920	Pers. obs.; SIO 65-674 (RAD 117788)	Soc
			Béarez (1997)	Soc
		Trachurus novaezelandie Richardson 1842	Pers. observation; NMNZ P.28770 (radiograph)	Cl, Soc
		Trachurus ponticus Aleev 1956	Aleve (1966)	Cl, Soc
		Trachurus symmetricus Ayres 1855	Pers. obs; CAS 26779 (skeleton), 52 cm SL	V
		Trachurus trachurus (Linnaeus 1758)	Aleve (1966), Desse et al. (1981), Laroche, Peron, and Le Galy (1982)	Cl, Soc
		Trachurus trecae Cadenat 1950	Aleve (1966)	Cl, Soc
		Turrum coeruleopinnatum (Rüppell 1830)	Pers. obs.; CAS 16483 (RAD 116236)	Pt
Cichliformes	Cichlidae	*Tilapia guinasana* Trewavas 1936	Greenwood (1992)	Epo, Fr
Cyprinodontiformes	Cyprinodontidae	**Aphanius crassicaudus* (Agassiz 1832)	Bedosti (1999), Gaudant (1979)	Co, Epi, Hs, Ns, Cl, R, Scl, V
			Chang et al. (2008)	Epi, Hs, Ns, R, V
			Meunier and Gaudant (1987)	V
Perciformes	Serranidae	*Centropristis striata* (Linnaeus 1758)	Bortone (1977)	Fr
	Platycephalidae	*Platycephalus fuscus* Cuvier 1829	Johnson (1973) (ethmoid complex misidentified as "prefrontal")	Eth, Fr, Lac, Me, Na
		Platycephalus indicus (Linnaeus 1758)	Johnson (1973) (ethmoid complex misidentified as "prefrontal")	Eth, Fr, Lac, Me, Na
	Triglidae	*Prionotus stephanophrys* Lockington 1881	Figure 4c; LACM31987-1 (RAD 119751), 29 cm SL	Eth, Fr, V
		Pterygotrigla cajorarori Richards and Yato (2012)	Richards and Yato (2012)	Cl, Cls, Dfs, Lac, Fr, Par
			Yato, Nakayama, and Endo (2020)	Cl, Dfs, Lac, Fr, Par

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Pterygotrigla hemisticta (Temmincki & Schlegel 1843)	Yao, Nakayama, and Endo (2020)	Cls, Fr, Lac, Op
	Scorpaenidae	**Scorpaenopterus siluridens* (Steindachner 1859)	Leighton Kesteven (1928)	Op
Acropomatiformes	Acropomatidae	*Verilus pacificus* (Mochizuki 1979)	Yamanoue (2016)	Apt
	Pentacerotidae	*Paristiopterus gallipavo* Whitley 1944	Figure 4d; AMNH 219441 (skeleton photo), 38 cm SL	Hs
		Paristiopterus labiosus (Günther 1872)	Pers. obs.; AMNH 89746 (skeleton photo), 45 cm SL	Hs
		Zanclistius elevatus (Ramsay & Ogilby 1888)	Figure 4e; USNM 17697 (RAD 127155), 19 cm SL	Soc
Acanthuriformes	Lutjanidae	*Lutjanus guttatus* (Steindachner 1869)	Béarez (1997	Soc
		Lutjanus mahogoni (Cuvier 1828)	Pers. obs.; AMNH 56616 (skeleton)	Dpt, Soc
	Haemulidae	*Conodon nobilis* (Linnaeus 1758)	Guzmán and Poloaco (2002)	Fr, Par, Soc
		Pomadasys argenteus (Forsskål 1775)	Pers. obs.; SMF 7283 (skeletal mount, Edinger Photo)	Fr, Par, R, Soc
			Nammalwar (1976) (as *Pomadasys hasta*)	FR, Par, Soc
			Klausewitz (1965), Meunier and Desse (1994) (as *Pomadasys hasta*)	Fr, Par, Soc
		Pomadasys argyreus (Valenciennes 1833)	Driesch (1994)	Fr, Soc
		Pomadasys commersonnii (Lacepède 1801)	Pers. obs.; LACM 38122-25	Soc
		Pomadasys stridens (Forsskål 1775)	Jawad (2013)	Ns
	Sparidae	*Acanthopagrus australis* Günther 1859	Figure 4f; USNM 59873 (RAD 119620), 54 cm SL, after Smith-Vaniz, Kaufman, and Glowacki (1995, Fig. 1C) (misidentified as *Pagrus pagrus*)	Fr, Sn, Soc
		Argyrops filamentosus (Valenciennes 1830)	Driesch (1994) (Table 1, page 42; General observation only)	Bone not specified
		Argyrops spinifer (Forsskål 1775)	Driesch (1994)	Fr, Soc
		Calamus brachysomus (Lockington 1880)	Guzmán and Polaco (2002)	Epo, Eth, Soc
		Calamus nodosus Randall & Caldwell 1966	Guzmán adn Polaco (2002)	Scl
		Calamus taurinus Jenyns 1840	Pers. obs.; CAS 66690	Exo, Soc

(Continues)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Chrysoblephus gibbiceps (Valenciennes 1830)	Barnard (1947)	Soc
		Chrysophrys auratus (Foster 1801)	We follow Fricke, Eschmeyer and Van der Laan (2024) in treating *Chrysophrys* and *Pagrus* as different genera but they can be distinguished solely on different hyperostosis patterns, and we believe only *Pagrus* Linneaus 1816 should be recognized. Figure 4g; ANSP 153836 (RAD 119588), 52 cm SL	Fr, Hs, Sn, Soc
			Gauldie and Czochanska (1990)	Hs
			Giarratana et al. (2012) (identified as *Pagrus unicolor*)	Soc
			Jawad, Wallace, and Dyck (2015) (misidentified as *Pagrus pagrus*)	Hs
			Leighton Kesteven (1928) (identified as *Pagrosomus auratus*)	Fr, Soc
			Köstler (1882)	Fr, Soc
			Yasuda and Mizuguchi (1969a), Yasuda and Mzuguchi (1969b)	Fr, Hs, Soc
		Dentex dentex (Linnaeus 1758)	Matić-Skoko and Ferri (2009)	Hs
		Evynnis cardinalis (Lacepède 1802)	Ebina (1936)	Fr, Soc
		Lagodon rhomboides (Linnaeus 1766)	Guzmán and Polaco (2002)	Fr, Soc
		Lithognathus lithognathus (Cuvier 1829)	Köstler (1882) (as *Pagellus lithognatus*)	Fr, Soc
		Pagrus major (Temminck & Schlegel 1848)	pers. obs.; USNM 216639 (RAD 119619), 25 cm SL	Fr, Sn, Soc
			Schlumberger and Lucké (1948) (as *Pagrosomus major*)	Hs
			Yasuda and Mizuguchi (1969a), Yasuda and Mizuguchi (1969b) (as *Chrysophrys major*)	Fr, Soc
		Stenotomus caprinus Jordan & Gilbert 1882	Figure 4h (RAD 114361), 13 cm SL	Pt
	Lethrinidae	*Lethrinus nebulosus* (Forsskål 1775)	Figure 3b; SMF 21204 (skeletal mount, Edinger photo), 31 cm SL	R
	Sciaenidae	*Callaus delicosa* (Tschudi 1846)	Sasaki (1989) (as *Sciaena delicosa*)	Apt, Dpt, Epo

(Continues)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
		Johnius belangerii (Cuvier 1830)	Pers. com., LACM 38290-28	V
		Micropogonias furnieri (Desmarest 1823)	Vazzoler (1971)	Dpt, V
		Nibea squamosa Sasaki (1992)	Sasaki (1992)	Afs, Apt, Dfs, Dpt, Fr, Soc, Op, V
		Otolithoides biauritus (Cantor 1849)	Figure 7d; after Chabanaud (1927, pl. I, fig. 5)	Br
			Chabanaud (1926), 17 (as *Sciaenoides biauritus*)	Br
		Panna perarmata (Chabanaud 1926)	Figure 7b,c; after Chabanaud (1927, pl. II, fig. 1)	Afs, Dfs, Pfs
			Chabanaud (1926), Chabanaud (1927) (as *Sciaenoides perarmatus*)	Afs, Pfs
		Paralonchurus peruanus (Steindacher 1875)	Figure 7f; NMW 84795 (RAD 122439), 32 cm SL	Cl, Fr, Na, R, Sn, V
			Cuyas Vera (2016)	Fr, V
			Steindachner (1875) (as *Gemyanemus peruanus*)	Sn, R, V
		Pogonias coubinas (Lacepède 1803)	Azpelicueta et al. (2019)	Apt, Dfs, Dpt
		Pogonias cromis (Linnaeus 1766)	Figure 7g, USNM 127238, 41 cm SL	Dpt, Ns
			Tuna et al. (2021)	Dpt, V
		Pseudotolithus elongatus (Bowdich 1825)	Figure 7a; after Chabanaud (1927, pl. I, fig. 1)	Afs, Apt, Dfs
			Chabanaud (1926), Chabanaud (1927) (as *Corvina nigrita*)	Afs, Apt, Dfs
		Sciaena callaensis Hildebrand 1946	Figure 7h; USNM 219420 (RAD 122505), 31 cm SL	Apt, Co, Dpt, Ns
			Sasaki (1989)	Epi
	Drepaneidae	*Drepane africana* Osório 1892	Pers. obs.; USNM 202727 (RAD 112284), 20 cm SL	Apt, Dpt, Fr, Soc
		Drepane longimana (Bloch & Schneider 1801)	Pers. obs.; LACM 38294-29 (skull)	Fr, Soc
			Pers. obs.; NMW 90900 (radiograph)	Fr, Soc
			Driesch (1994)	bone not specified
			Heemstra (2001)	Fr
			Jawad (2013)	Hs, Ns
			Murty (1967) (Footnote on page 325.)	Fr, Hs, Soc
		Drepane punctata (Linnaeus 1758)	Figure 4i; USNM 206154 (RAD 112271), 27 cm SL	Fr, Hs, Ns, Soc
			Pers. obs.; NMW 93893	Apt, Dpt, Fr, Soc

(Continues)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
			Al Abri et al. (2023)	Dfs, Fr, Hs, Ns, Soc
			Cantor (1849)	Fr
			Driesch (1994)	Fr, Hs, Ns, Soc
			Murty (1967)	Fr, Hs, Lac, Ns, R, Soc
	Ephippidae	*Chaetodipterus faber* (Broussonet 1782)	Figure 8; USNM 80900 (RAD 112252), 23.5 cm SL	Cl, Fr, Soc
			Figure 8b; NMW 93686, 41 cm SL	Apt, Cl, Hs, Os, Pb, R, Soc
			Pers. obs.; USNM 80900 (RAD 112252), 24 cm SL	Soc
			Aguilera et al. (2017)	Soc
			Cavalluzzi (2000)	Apt, Dpt, Hs, Ns
			Gervais (1875)	Soc
			Gregory (1933)	Eth, Fr, Soc
			Guzmá nand Polaco (2002)	Apt, Cl, Par, Soc
			Kaiser (1960)	Apt, Cl, Dpt, Hs, Ns, Pb, R, Soc
			Konnerth (1966)	Apt, Soc
			Korschelt (1940) (as *Platax arthriticus*)	Apt, Dpt, Hs, Ns, Soc
			Köstler (1882)	Apt, Cl, Dpt, Hs, Ns, R, Soc
			Schlumberger and Lucké (1948)	Apt, Cl
			Tuna (2015)	Apt, Cl, Hs, R, Soc
		Chaetodipterus zonatus (Girard 1858)	Pers. obs.; USNM 94600 (RAD 112265), 17 cm SL	Dpt
		Ephippus goreensis Cuvier 1831	Figure 8c; USNM 279579 (RAD 119617), 18 cm SL	Fr
		Platax batavianus Cuvier 1831	Figure 8d; USNM 174067 (RAD 112297), 29 cm SL	Apt, Fr, Hs, R, Soc
			Figure 8e; CAS 248423 (RAD 119613), 41.5 cm SL	Apt, Fr, Hs, Ns, R, Soc
		Platax orbicularis (Forsskål 1775)	Pers. obs.; USNM 58006 (RAD 112306), 26 cm SL	Fr
		Platax pinnatus (Linnaeus 1758)	Jawad (2013)	Apt, Fr, Cl, Pb, Sn, Soc
		Platax teira (Fabricius 1775)	Figure 3c; SMF 7522 (skeletal mount, Edinger photo), 33 SL	Apt, Fr, Hs, Ns, Sn, Soc
			Figure 8f; USNM 195059 (RAD 112342), 35 cm SL	Dpt, Hs, Ns, Pb, R, Soc
			Figure 8g; USNM 195057 (RAD 112340), 35 cm SL	Dpt, Hs, Ns, Pb, R, Soc
			Bell (1793) (as *Chaetodon* sp.)	Dpt, Hs, Ns, Pb, R, Soc

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
			Cavalluzzi (2000)	Soc
			Driesch (1994) (after Bell 1793)	Dpt, Hs, Ns, Pb, R, Soc
			Jawad (2013)	Dpt, Hs, Ns
			Jawad and Bannai (2014)	Ns
			Korschelt (1940) (as *Platax arthriticus*)	Apt, Dpt, Hs, Ns, Soc
			Köstler (1882)	Apt, Dpt, Fr, Hs, Ns, R, Soc
			Mahmoud and Ibrahim (2021) (misidentified as adult *Pomacanthus sexstriatus)*	Apt, Dpt, Fr, Hs, Ns, R, Soc
		Proteracanthus sarissophorus (Cantor 1849)	Figure 8h; CAS-SU 14270 (RAD 11922-003), 25 cm SL	Afs, Apt, Dfs, Dpt, Lac
			Cavalluzzi (2000)	Lac
		Zabidius novemaculeatus (McCulloch 1916)	Figure 8i; USNM 173519 (RAD 112351), 25 cm SL	Apt, Dpt, Fr
	Scatophagidae	*Scatophagus argus* (Linnaeus 1766)	Korschelt (1940)	Dpt
		Selenotoca multifasciata (Richardson 1846)	Figure 4j; USNM 59870 (RAD 103842), 29 cm SL	Apt, Hs, Ns, R, Sn
			Smith-Vaniz et al. (1995), after Smith-Vaniz, Kaufman and Glowacki (1995, fig. 1D)	Apt, Hs, Ns, Sn
Tetradontiformes	Tetradontidae	*Chonerhinos naritus* (Richardson 1848)	Figure 4k; BMNH 2013.4.21.1, 17 cm SL	Apt, Cp, Epo, Fr, Soc, Sn
			Tyler (1980) (as *Xenopterus naritus*)	Cp, Hs, Ns
		Lagocephalus gloveri Abe & Tabeta 1983	Tyler, Purdy, and Oliver (1992)	Eth, Cl, Hs, Ns
		Lagocephalus inermis (Temminck & Schlegel 1850)	Figure 4l; USNM 207052 (RAD 119768), 32 cm SL	Fr, Hs, Ns
			Tyler, Purdy, and Oliver (1992)	Eth, Hs, Ns
		Lagocephalus laevigatus (Linnaeus 1766)	Tyler (1980)	Eth, Hs, Ns, Cl, Pop
		Lagocephalus lunaris (Bloch & Schneider 1801)	Abe (1960)	Eth, Hs
			Tyler, Purdy, and Oliver (1992)	Co, Eth, Hs, Ns, Pop
		Lagocephalus spadiceus (Richardson 1845)	Abe (1960)	Hs, Ns
			Tyler, Purdy, and Oliver (1992)	Hs, Ns
		**Sphoeroides hyperostosis* (Tyler, Purdy, and Oliver 1992)	Tyler, Purdy, and Oliver (1992)	Cl, Op, Pop, Sop

(Continues)

TABLE 2 | (Continued)

Order	Family	Species	Occurrence basis	Hyperostotic bone sites
	Monacanthidae	*Aluterus schoepfi* (Walbaum 1792)	Schlumberger anbd Lucké (1948)	Dpt
		Aluterus monocerus (Linnaeus 1758)	Figure 4m; AMS I.15757-002 (RAD 119756), 40 cm SL	Cl, Dpt, V
			Driesch (1994)	Cl, V
		Nelusetta ayraud (Quoy & Gaimard 1824)	Figure 4n; WAM P.28392-001 (RAD 119765), 48 cm SL	Dpt, Hs, Ns
	Balistidae	*Abalistes stellatus* (Anonymous 1798) [ex Lacepède]	Figgure 4o; WAM P.25838-002 (RAD 119767), 28 cm SL	Dpt

Note: Classification follows Eschmeyer's Catalog of Fishes (Fricke, Eschmeyer, and Van der Laan 2024). (*). Occurrence basis is justified in numbered references or listed specimens; see Methods for museum abbreviations and Table 1 for bone abbreviations. Measurements in centimeters (cm) are standard length (SL).

confirmed their observations, according to Tyler and Santini (2005, Table 1) *Cyttus australis* (Richardson) and *Zenopsis conchifer* have hyperostotic dorsal-fin pterygiophores and supraoccipital bones.

The only investigation of buckler scale histology (Meunier and Béarez 2019) is based on *Z. faber*. These authors believed buckler scales were "neoformations" but with the caveat (p. 198), "ontogenetic studies were necessary to validate and strengthen our hypothesis." Meunier and Béarez (2019, 198) also stated that the bony scutes "are made of acellular tubular bone … [with] secondary bone on the walls of central vascular cavities … deprived of osteoblastic canaliculi." Also present were vascular canals and localized bone remodeling. Although this bony tissue type has osteoblastic canaliculi, no osteocytes are present (Hughes, Bassett, and Moffat 1994; Sire and Meunier 2017). The later authors also acknowledged (p. 198) that "The biological significance of this peculiar acellular secondary bone associated with acellular 'tubular' primary bone is unknown."

Our study of buckler scales is very limited but we note their occurrence as follows: The zeids *Zenopsis nebulosa* (Temminck and Schlegel), *Z. conchifer* (Lowe), and *Z. faber* (Figure 9a) have large bucklers along the bases of the dorsal- and anal-fins. The paranoid species *Cyttopsis roses* (Lowe) and *Stethopristes eos* Gilbert have a single row of large bucklers along the ventral midline. The oreosomatid, *Oreosoma atlanticum* Cuvier has a double row of bucklers near the ventral midline (Figure 9c), and in *Allocyttus verrucosus* (Gilchrist) there are two rows of enlarged cones or wart-like scales on the abdomen.

3.3.4 | *Nodular excrescences* (Figure 10)

These nodules are pathological structures; they sit on top of the bone or skin, and the bone itself is not affected by hyperostosis. The external surface of hyperostotic bones is hard, in contrast to the skin-covered soft surface of nodular excrescences. Rao and Lakshmi (1986, 123) suggested that "the formation of nodules is… due to an impairment of the ultimobranchial glands which control calcium metabolism in fishes." They also stated (p. 124), "sporadic occurrence of nodular excrescences in [the marine catfish] *Arius tenuispinis* … is explained as an idiosyncratic response to a proximate contaminant in the aquatic environment."

Radiographs of two species we examined, *Drepane punctata* (Figure 4i) and *Caranx bucculentus* (Figure 5a), each have a pair of nodular excrescences positioned on the caudal fin. We found these nodules present in four specimens of *D. punctata* and in two *C. bucculentus*. Al Abri, Jawad and Al-Nahdi (2023, fig. 4) presented photographs of *D. punctata*, including an excellent radiograph of a 430 mm TL hyperostotic specimen with conspicuous nodules on the caudal fin.

3.4 | Specific Observations of Hyperostosis in Carangid Fishes

Smith-Vaniz and Carpenter (2007) reported the inconsistent occurrence of hyperostosis of the third rib in *Caranx caninus* Günther and speculated (erroneously) that this variability might be a case of sexual dimorphism. Based on our examination of radiographs of 35 adults (35–67 cm FL), six had hyperostotic third ribs (see Smith-Vaniz and Carpenter 2007, fig. 14a) and all the others had normal ribs. Our radiograph of *C. caninus* (Figure 5e) is also interesting because while the right third rib is clearly hyperostotic, its counterpart on the left side is normal. Large individuals of several different families, including at least two carangids, have the distal ends of some of the ribs hyperostotically paddle-shaped (e.g., *Selenotoca multifasciata*, Figure 4j; *Caranx fischeri*, Figure 5c; *Paralonchurus peruanus*, Figure 7f; and *Platax batvianus*, Figure 8e). Like most other aspects of hyperostosis, why this distinctive shape-change in rib morphology seems to occur only in a few individuals of certain species and families is a mystery. At least three hyperostotic ribs are usually present in adults of four of the seven species of *Trachinotus* that develop hyperostosis (Figures 11 and 12); depending on the species, hyperostotic ribs begin on vertebra 3 to 5 and their position is usually species-specific. In what we consider to be geographic variation in *Caranx hippos*, relative development of hyperostosis of the first dorsal-fin pterygiophore is noticeably different in all adults on opposite sides of the Atlantic Ocean. In specimens from the western Atlantic, this bone is very robust (Figure 13b) but it is relatively slender

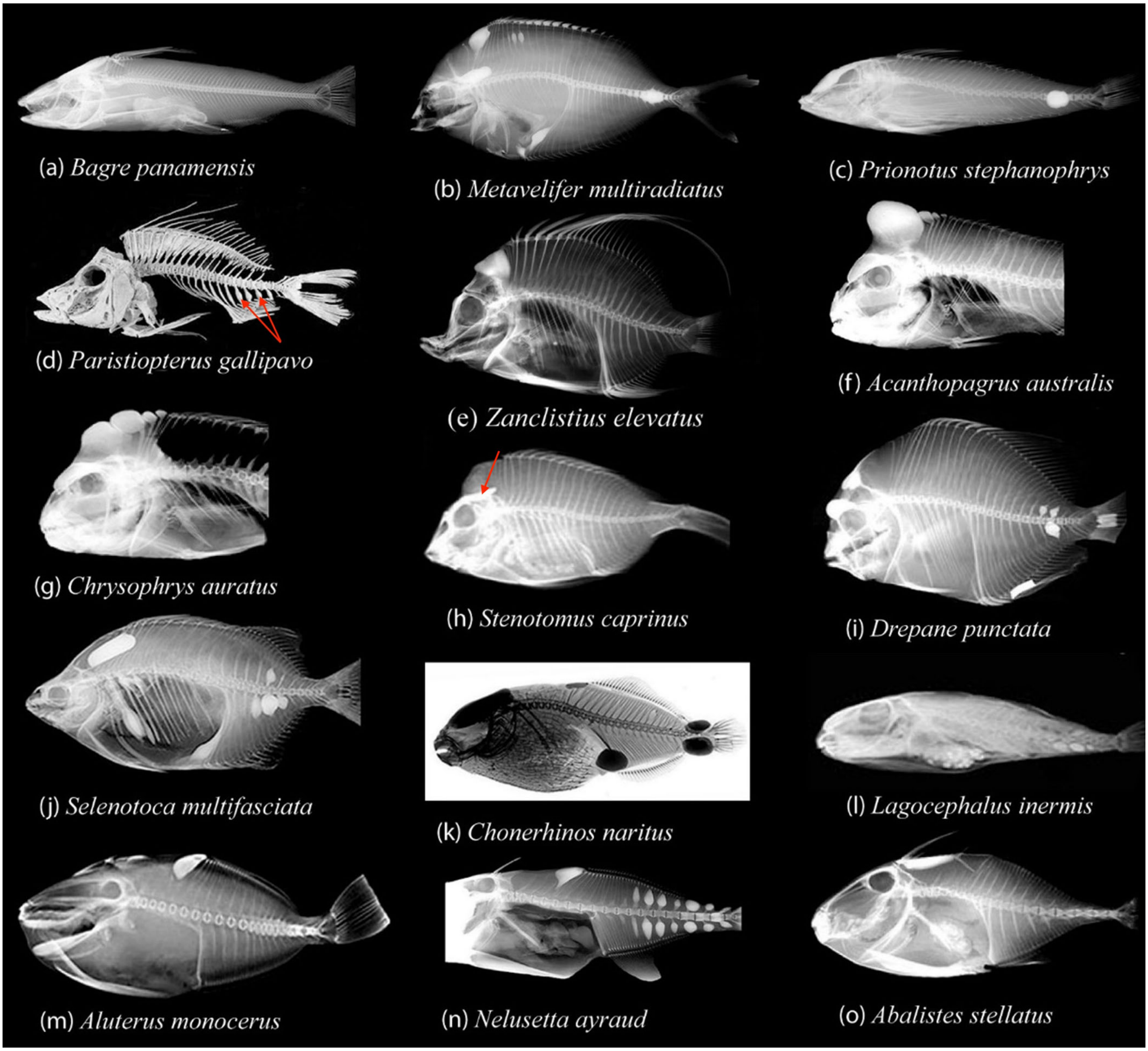


FIGURE 4 | Selected hyperostotic species. Ariidae: (a) *Bagre panamensis* (Gill), USNM 28181, 9 cm SL; Veliferidae: (b) *Metavelifer multiradiatus* Regan, AMS IB.2699, 34 cm SL; Triglidae: (c) *Prionotus stephanophrys* Lockington, LACM 31987-1, 29 cm SL; Pentacerotidae: (d) *Paristiopterus gallipavo* Whitley, AMNH 219441, 38 cm SL (red arrows point to hyperostotic hemal spines), photo courtesy S. Schaefer; (e) *Zanclistius elevatus* Ramsay & Ogilby, USNM 176976, 19 cm SL (red arrow points to hyperostotic supraoccipital); Sparidae: (f) *Acanthopagrus australis* Günther, USNM 59873, 54 cm SL; (g) *Chrysophrys auratus* (Foster), ANSP 153836, 52 cm SL; (h) *Stenotomus caprinus* Jordan & Gilbert, USNM 158390, 13 cm SL (red arrow points to hyperostotic posttemporal); Drepaneidae: (i) *Drepane punctata* (Linnaeus), USNM 206154, 27 cm SL (pale structures on caudal fin are nodular excrescences); Scatophagidae: (j) *Selenotoca multifasciata* (Richardson), USNM 59870, 29 cm SL; Tetraodontidae: (k) *Chonerhinos naritus* (Richardson), BMNH 2013.4.21.1, 17 cm SL, photo by K. Webb; (l) *Lagocephalus inermis* (Temminck & Schlegel), USNM 207052, 32 cm SL; Monacanthidae: (m) *Aluterus monocerus* (Linnaeus), AMS I.15757-002, 40 cm SL; (n) *Nelusetta ayraud* (Quoy & Gaimard), WAM P.28392-001, 48 cm SL; Balistidae: (o) *Abalistes stellatus* (Anonymous) [ex Lacepède], WAM P.25838-002, 28 cm SL. See Table 2 for hyperostotic bone sites for these specimens. Figure (d) courtesy of American Museum of Natural History, British Museum of Natural History, and all other figures courtesy Smithsonian Institution, used with permission.

in eastern Atlantic adults (Smith-Vaniz and Carpenter 2007, figs. 11 and 12).

In carangids with multiple hyperostotic bones, the supraoccipital is usually the first bone to develop hyperostosis and this occurs in at least 23 species. The cleithrum or coracoid is hyperostotic in 19 of such species. See Table 2.

3.5 | Erroneous Records of Species Reported to Have Hyperostosis

1. In his important paper on swollen dorsal-fin elements in living and fossil *Caranx*, Fierstine (1968), identified specimens from the Gulf of California as *Caranx hippos*. However, Smith-Vaniz and Carpenter (2007) determined

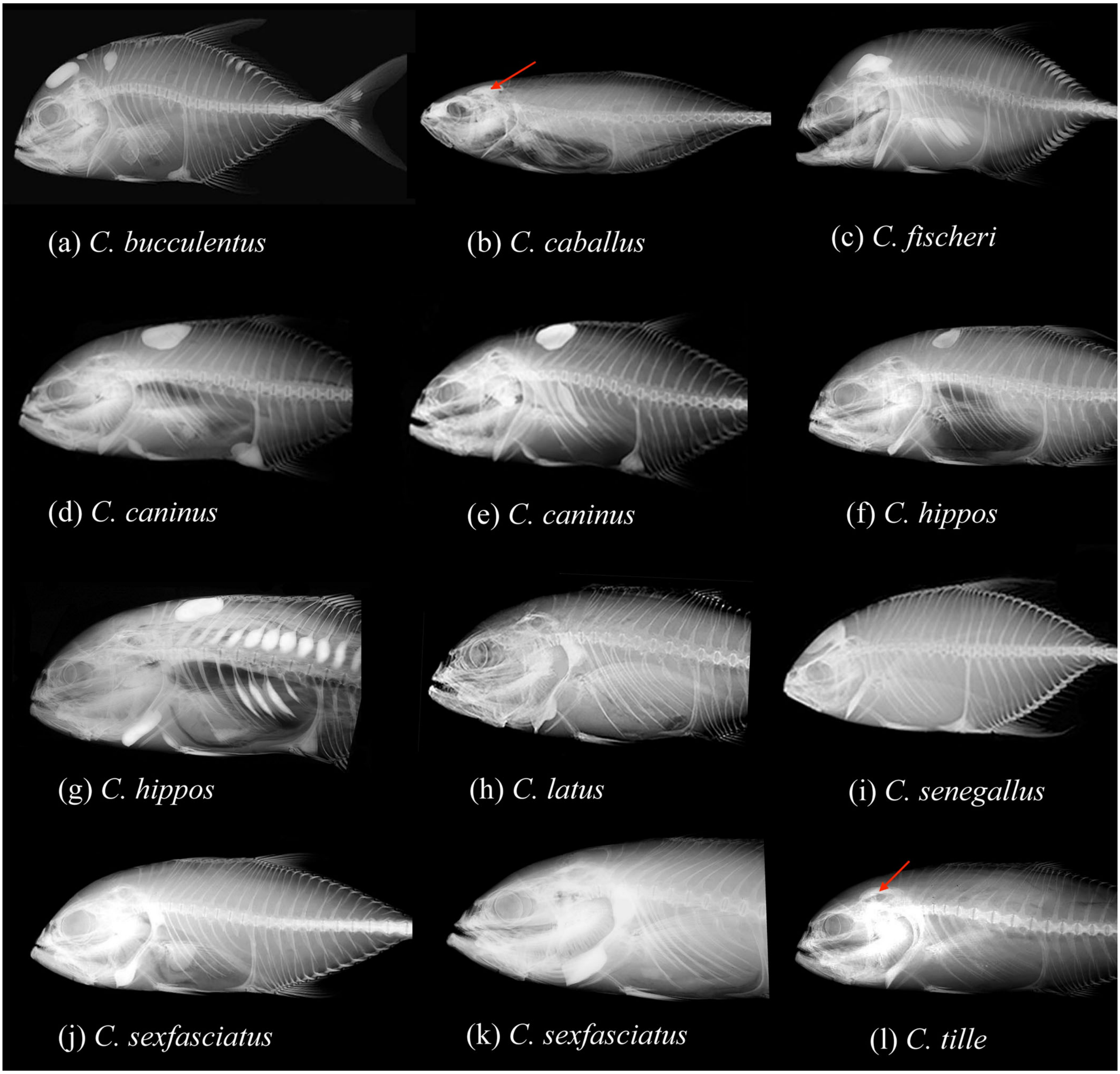


FIGURE 5 | Radiographs of selected species of carangid genus *Caranx* exhibiting hyperostosis. (a) *C. bucculentus* Alleyne & Macleay, USNM 173970, 36 cm SL (Pale structures on caudal fin are nodular excrescences); (b) *C. caballus* Günther, USNM 128669, 41 cm SL (red arrow points to hyperostotic posttemporal); (c) *C. fischeri* Smith-Vaniz & Carpenter, ZMUC P.46362, 42 cm SL; (d) *caninus* Günther, CAS 216871, 50 cm SL; (e) C. *caninus*, USNM 100998, 37 cm SL; (f) *C. hippos* (Linnaeus), CAS 153015, 36 cm FL; (g) C. *Caranx hippos*, USNM 114618, 56 cm FL); (h) *C. latus* Agassiz, CAS 258426, 63 cm SL.; (i) *C. senegallus* Cuvier, ANSP 140258, 28 cm SL; (j) *C. sexfasciatus* Quoy & Gaimard, CAS 16255, 36 cm SL; (k) *C. sexfasciatus*, CAS 16244, 71 cm SL; (l) *C. tille* Cuvier, CAS 16233, 53 cm SL (red arrow points to hyperostotic posttemporal). See Table 2 for hyperostotic bone sites for these specimens. All figures courtesy of Smithsonian Institution, used with permission.

that *Caranx hippos* is restricted to the Atlantic Ocean and replaced in the eastern Pacific by the superficially similar *C. caninus*.

2. Selvaraj, Gopakumar, and Rajagopalan (1973) described skin, bone, and fin tumors on different regions of the body in the catfish *Arius jella* Day. They stated (p. 574) "The true tumors which are present in both sexes of *T. jella*, probably represent hyperostosis." Some of the skin tumors they documented contained ossified small "stones" (plate I, fig. F) "of unknown origin." Their descriptions of these structures agree best with true tumors and others with nodular excrescences.
3. Jawad and Ibrahim (2017, figs. 6 and 7) reported hyperostosis in *Alepes vari* Cuvier, but this was actually a large (46 cm SL) specimen of *Scomberoides commersonnianus* Lacepède.
4. Jawad and Akyol (2018, fig. 3) reported, and included a photograph, of a single specimen of *Mullus barbatus* with a deformed and compacted vertebral column and

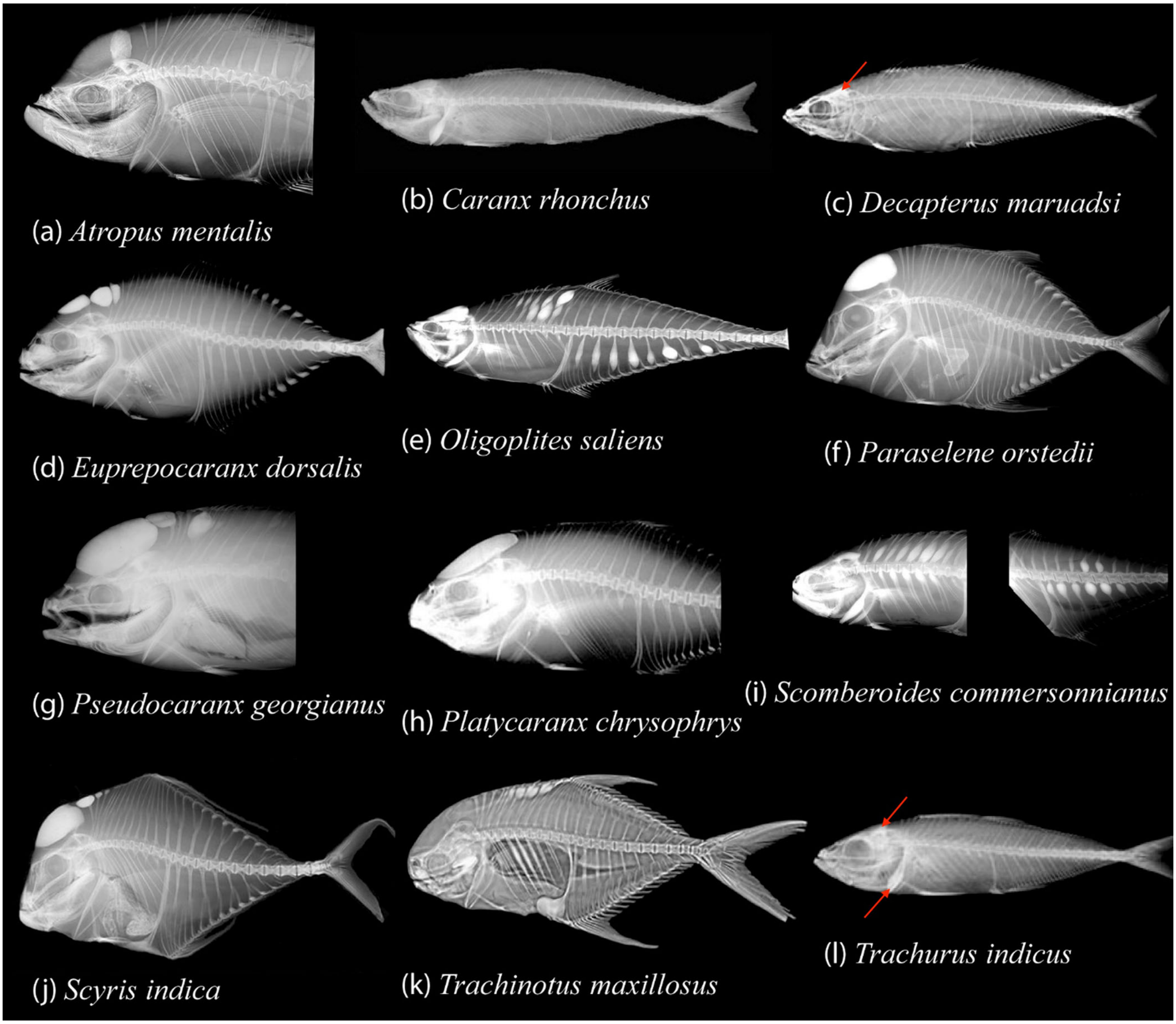


FIGURE 6 | Radiographs of selected hyperostotic species of Carangidae. (a) *Atropus mentalis* (Cuvier), CAS 16447 50 cm SL); (b) *Caranx rhonchus* Geoffroy St. Hilaire, ANSP 159101, 37 cm SL; (c) *Decapterus maruadsi* (Temminck & Schlegel), ANSP 139120, 29 cm SL (red arrow points to hyperostotic supraoccipital); (d) *Euprepocaranx dorsalis* (Gill), SIO 61-247, 40.5 cm SL; (e) *Oligoplites saliens* (Bloch), CAS-SU 53065, 41 cm SL; (f) *Paraselene orstedii* (Lütken), USNM 79971, 21 cm SL; (h) *Platycaranx chrysophrys* (Cuvier), ANSP 149396, 60.5 cm SL; (g) *Pseudocaranx georgianus* (Cuvier) NMNZ P.30775, 77 cm SL, image by C. Struthers; *Scomberoides commersonnianus* Lacepède, CAS uncat. (GVF 60-113), 89 cm SL; (j) *Scyris indica* (Rüppell, CAS 16306, 46 cm SL; (k) *Trachinotus maxillosus* Cuvier, ANSP 140837, 51 cm SL; (l) *Trachurus indicus* Nekrasov, ANSP 140349, 27 cm SL (red arrows point to hyperostotic supraoccipital and cleithrum). See Table 2 for hyperostotic bone sites for these specimens. Figure (h) courtesy of Museum of New Zealand Te Papa; all others courtesy of Smithsonian Institution, used with permission.

two small calluses on the neural and hemal spines (described as hyperostosis). They stated (p. 62) "further studies and monitoring are necessary to elucidate the occurrence of the phenomenon, and suggested genetics, pollution, parasites, etc. could be the cause." We consider it premature to attribute this single occurrence to hyperostosis, at least to fish hyperostosis.

5. Jawad, Fjelldal, and Hansen (2018a, fig. 2b) included photographs of a pea-sized "hyperostotic" bone on one hemal spine in *Ciliata mustela* (Linnaeus), Lotidae. The same specimen had a "severe deformity," in which some of the vertebra were compacted. They also stated (p. 959) "The type of vertebral abnormalities observed in the present specimen is usually caused by either pollution or parasitic infections." The co-occurrence of both a deformed (teratological) vertebra and one pea-size swelling on a single bone is likely not a case of fish hyperostosis but instead the result of pollution or parasitism.

6. Jawad et al. (2018) reported, and included photographs of vertebral deformities and minute, pea-size swellings (Figure 3) on the hemal spines of two, mature, wild haddock,

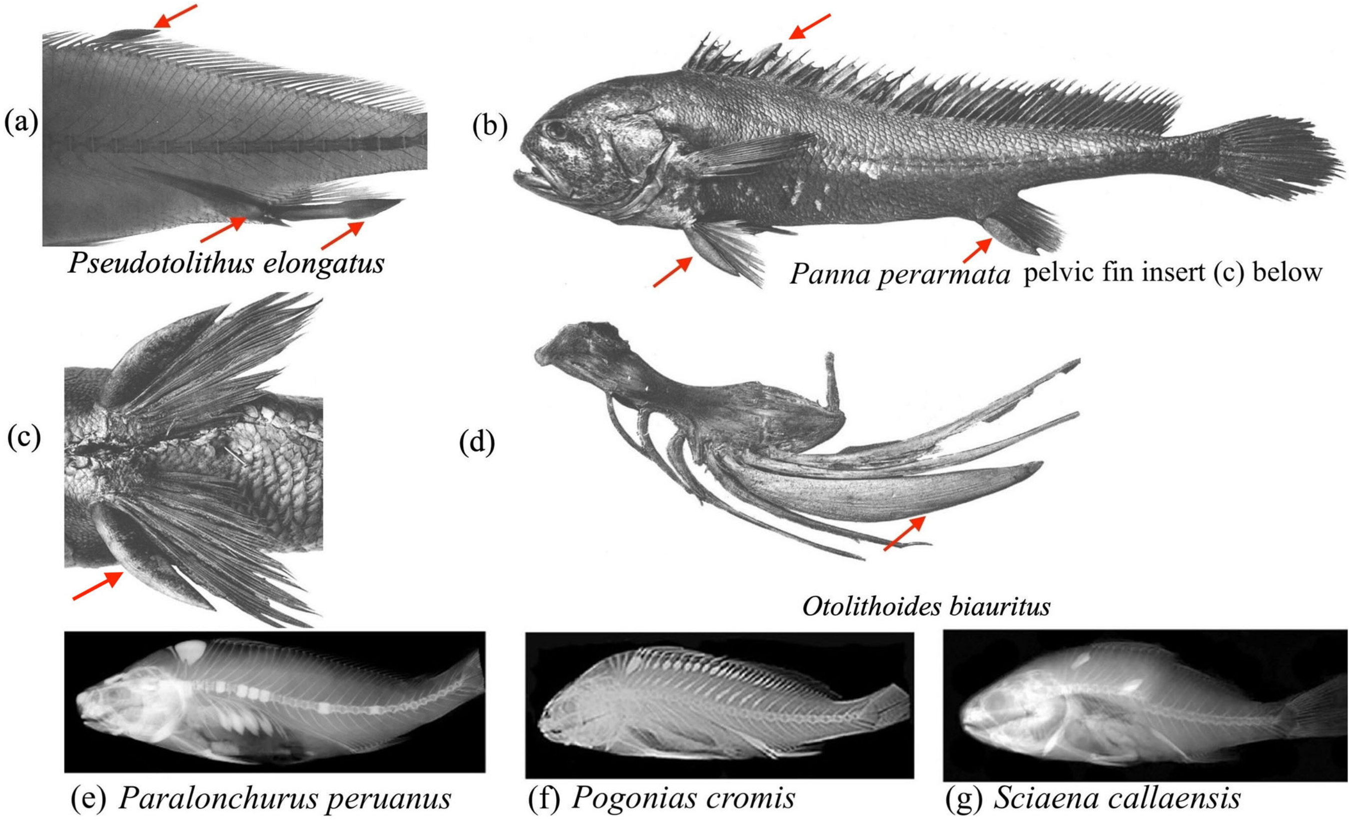


FIGURE 7 | Selected hyperostotic species of Sciaenidae. (a) *Pseudotolithus elongatus* (Bowdich); (b, c) *Panna perarmata* (Chabanaud); (d) *Otolithoides biauritus* (Cantor); (e) *Paralonchurus peruanus* (Steindachner), NMW 84795, 320 cm SL, photo by N. Bogutskaya; (f) *Pogonias cromis* (Linnaeus), USNM 127238, 41 cm SL; (g) *Sciaena callaensis* Hildebrand, USNM 219420, 31 cm SL. Red arrows point to hyperostotic structures. Figures (a, d) after Chabanaud (1927), pl. I; Figures (b, c) after Chabanaud (1927), pl. II. See Table 2 for hyperostotic bone sites for these specimens. Figure (e) courtesy of Naturhistorisches Museum Wien, Figures (f, g) courtesy of Smithsonian Institution, used with permission.

Melanogrammus aeglefinus (Linnaeus) from Masfjorden in western Norway. They stated that a fracture may have induced the "hyperostosis" which, in this case, is a callus formation induced by a healing process rather than hyperostosis in the sense of fish hyperostosis. In their study of axial skeleton fracture repair mechanisms in Atlantic cod, *Gadus morhua* Linnaeus, Fjelldal et al. (2018) reinforced the probability suggested by Jawad et al. (2018) when they observed two of four fish with fractures or small calluses on their neural (fig. 1d) or hemal spines, and that 1 year later the calluses either remained or developed into normal morphology.

7. Unsubstantiated reports of hyperostosis in *Caranx* (or *Carangoides*) *bartholomaei* Cuvier by Olsen (1969) are apparently erroneous. A digital radiograph of a large (35 cm FL) specimen, ANSP 17787 from Bermuda, courtesy of Lyle Luckenbill, exhibited no hyperostosis.

3.6 | What We Know About Hyperostosis

1. *Hyperostosis is under genetic control* (Gauldie and Czochanska 1990; Smith-Vaniz, Kaufman, and Glowacki 1995). Over a century ago, Köstler (1882, 430) mentioned that "these thickenings [hyperostosis] … have become hereditary … were passed on to the offspring and have now become a permanent characteristic of the species." Breder CM (1952, 196) stated, "that such growths [hyperostosis] are under genetic control need hardly be labored … they appear at regular times in the ontogeny of the individual." Evidence of the predictable nature of hyperostosis in fishes is our observation that hyperostotic skeletal growth typically follows a consistent and species-specific pattern in most species once a certain minimum size has been reached (e.g., Smith-Vaniz and Carpenter 2007, fig. 11; Smith-Vaniz and Walsh 2019, fig. 20). Another indication of genetic influence is sexual dimorphism of the hyperostotic supraoccipital and frontal bones in the sparid *Chrysophrys auratus* (see Moran, Burton, and Caputi 1999).
2. *It has something to do with environmental conditions and calcium regulation*. Hyperostosis occurs almost exclusively in marine fishes. The five exceptions are four fossil species: a cyprinodontid, †*Aphanius crassicaudus* (Agassiz), known from Miocene hypersaline habitats along the northern margins of the Mediterranean Sea (Gaudant 1979; Meunier and Gaudant 1987; Bedosti 1999; Chang et al. 2008), a clupeid, †*Sardina*? *crassa* (Sauvage), from the Miocene of western Algeria, and a goby, †*Gobius ignotus* Gaudant, from Messinian evaporates of Cherasco,

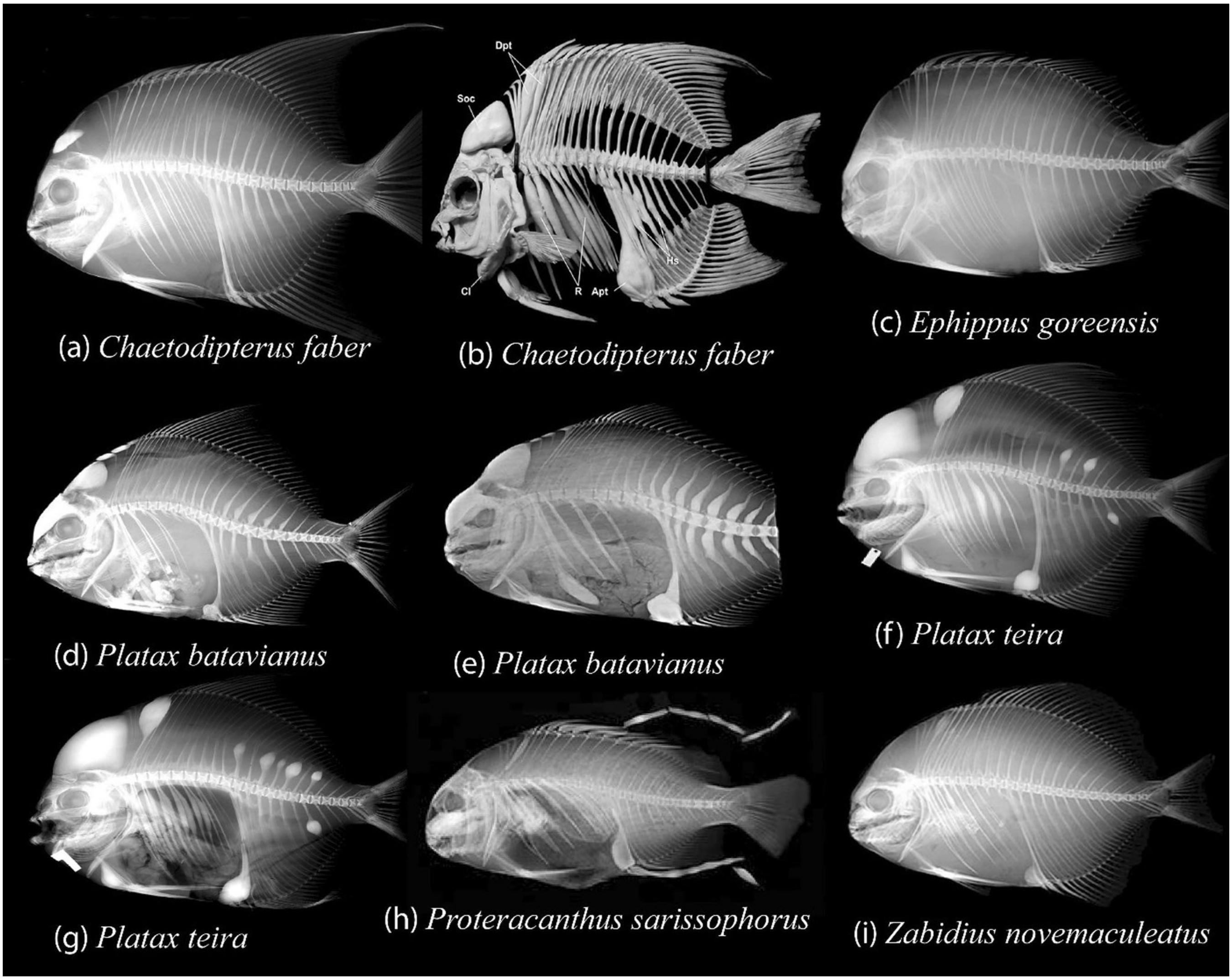


FIGURE 8 | Selected hyperostotic species of Ephippidae. (a) *Chaetodipterus faber* (Broussonet), USNM 80900, 23.5 cm SL; (b) *Chaetodipterus faber*, NMW 93686, 41 cm SL (Note the shape of the first anal-fin pterygiophore = 'Os wormianum', photo by K. Schiller & H. Ahnelt); (c) *Ephippus goreensis* Cuvier, USNM 279579, 18 cm SL; (d) *Platax batavianus* Cuvier, USNM 174067, 29 cm SL; (e) *Platax batavianus*, CAS 248423, 41.5 cm SL; (f) *Platax teira* (Fabricius, USNM 195059, 35 cm SL; (g) *Platax teira* USNM 195057, 35.5 cm SL; (h) *Proteracanthus sarissophorus* (Cantor), CAS-SU 14270, 25 cm SL; (i) *Zabidius novemaculeatus* (McCulloch), USNM 173519, 25 cm SL. See Table 2 for hyperostotic bone sites for these specimens. Figure (b), courtesy of Naturhistorisches Museum Wien, and all others courtesy of Smithsonian Institution, used with permission. Apt, anal-fin pterygiophore; Cl, cleithrum; Dpt dorsal-fin pterygiophore; Hs, hemal spine; R, rib; Soc, supraoccipital.

Italy (Gaudant and Meunier 1996), and a fossil cyprinid, †*Hsianwenia wui* Chang et al. (2008) known from Pliocene lake deposits in the Qaidam Basin of the Tibetan Plateau.

According to Chang et al. (2008:13248), the fossil cyprinodontid and cyprinid are "pachyostotic" species that occurred "in similar deposits rich in carbonates ($CaCO_3$) and sulfates ($CaSO_4$), showing that both were adapted to the extreme conditions resulting from aridification of the two areas. The overall skeletal thickening was most likely through deposition of the oversaturated calcium …".

The only known extant hyperostotic freshwater species is the cichlid, *Tilapia guinasana* Trewavas, originally endemic to a sink hole (Lake Guinas) in northern Namibia, and subsequently successfully introduced in nearby Lake Otjikoto. According to Greenwood (1992:35), "Lake Guinas has a very high calcium carbonate content ($CaCO_3$, 185 ppm), an environmental factor to which [the species] … might have responded, physiologically, by increasing the volume and calcification of certain bones."

Referring to fossil hyperostotic fish bones from phosphate-bearing deposits, Schlüter, Kohring and Mehl (1992:129) stated, "The origin of the pathological alteration is probably related to extreme hydrochemical conditions … especially its high content of fluorine." Chang et al. (2008) concluded that the extraordinary skeletal bone thickening of *Hsianwenia wui*, represents an adaptive mode due to aridification resulting in hydrochemical conditions high in calcium content. *Aphanius crassicaudus*, with nearly identical thickened

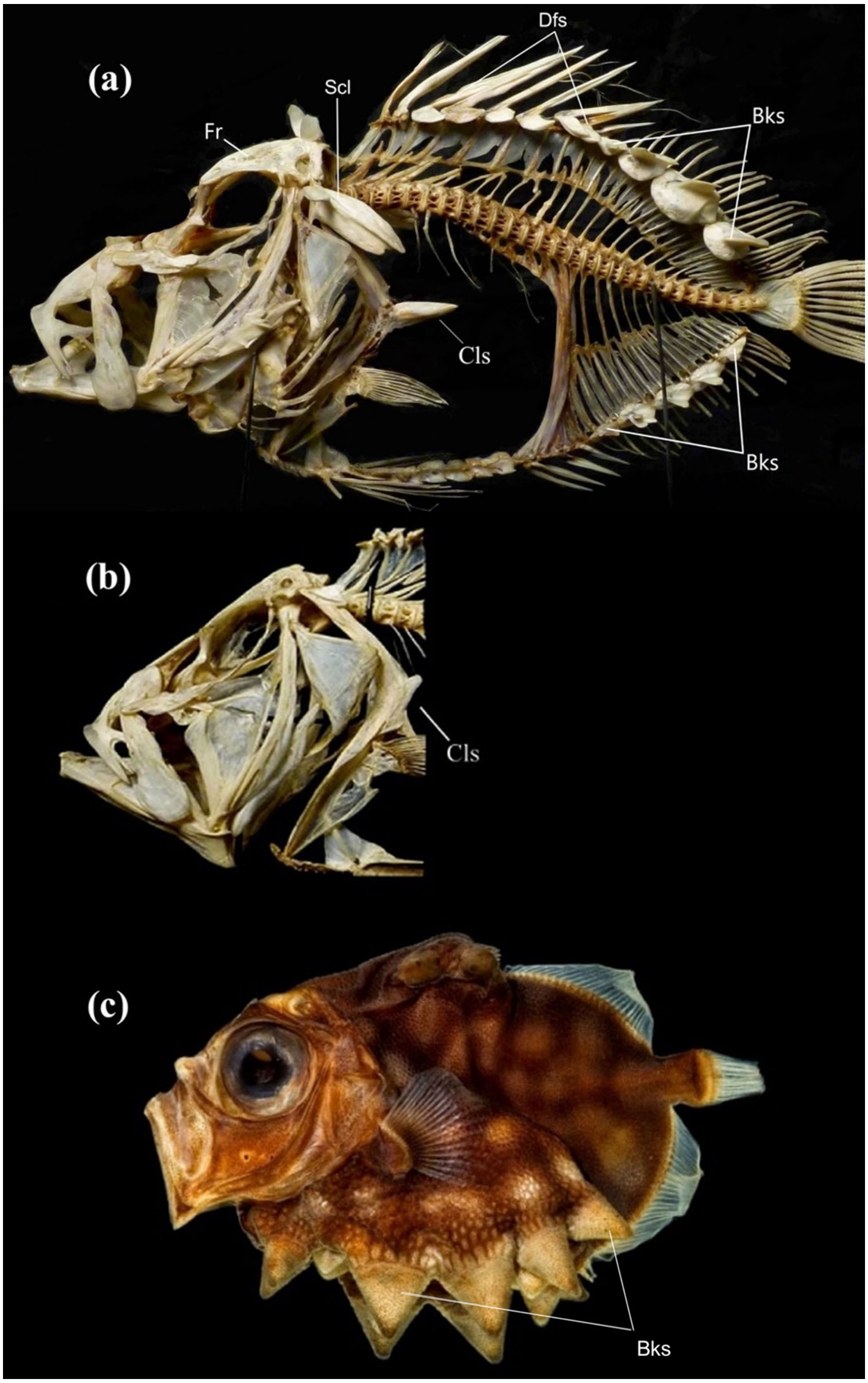


FIGURE 9 | Selected Zeiform species. (a) Zeidae: *Zeus faber* Linnaeus (hyperostotic), NMW 60029, 35 cm SL, photo by K. Schiller & H. Ahnelt; (b) *Z. faber* (non-hyperostotic), NMW 60033, 35 cm SL, photo by K. Schiller & H. Ahnelt, (c) Oreosomatidae: *Oreosoma atlanticum* Cuvier, USNM 385874, 8.5 cm SL, photo by S.J. Raredon, courtesy of Smithsonian Institution, used with permission. Figures (a, b), courtesy of Naturhistorisches Museum, Wien. Bks, buckler scales; Cl, cleithrum; Cls, cleithral spine; Dfs, spines of dorsal fin; Fr, frontal; Scl, supracleithrum.

bones (Gaudant 1979), was subjected to essentially the same environmental conditions. Schoemaker (2018:44) stated that fossil Haddock, *Melanogrammus aeglefinus*, had hyperostotic vertebrae, cleithra and posttemporal bones, "perhaps in response to hydrochemical conditions," but based on limited observations, he erroneously concluded these bones were normal in all modern haddocks. Tuna (2015:108) noted that "hyperostotic and non-hyperostotic species occur sympatrically" [and are] "not explained, exclusively, by an environmental factor."

3. The functional significance of hyperostosis is unknown but at the cellular level there is evidence of a high degree of remodeling activity. Future experimental studies with live fishes combined with histology will be necessary to understand the functional significance of hyperostosis.

4. Hyperostosis occurs in a diverse range of marine fishes (Figures 3–9a, 11 and Table 2). It is most common in the Carangidae (Jacks and Pompanos) occurring in 19 genera and at least 53 of 181 species, followed by the Sparidae

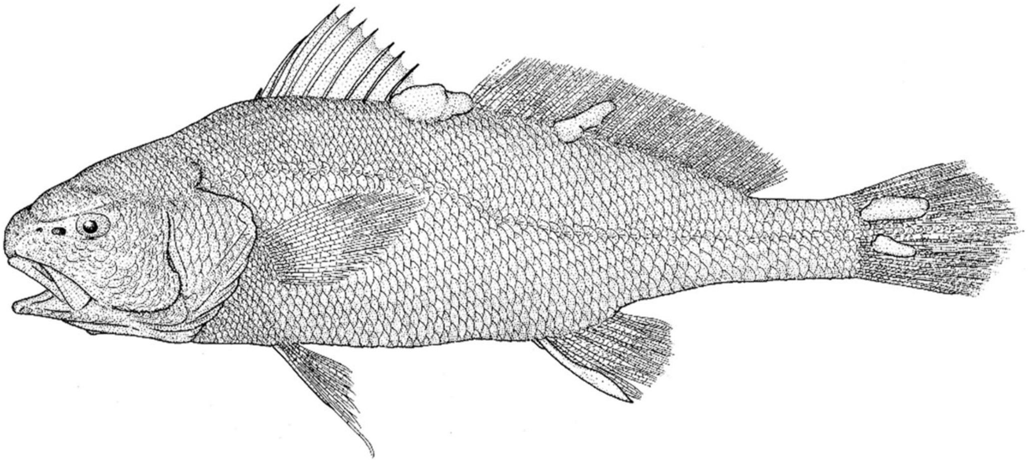


FIGURE 10 | Sciaenidae, *Nibea sqamosa* Sasaki, 53 cm SL, showing nodular excrescences; after Sasaki (1992), fig. 1; courtesy of *Japanese Journal of Ichthyology*, used with permission.

(Porgies) and Sciaenidae (Drums and Croakers) and with 14 and 11 species, respectively.

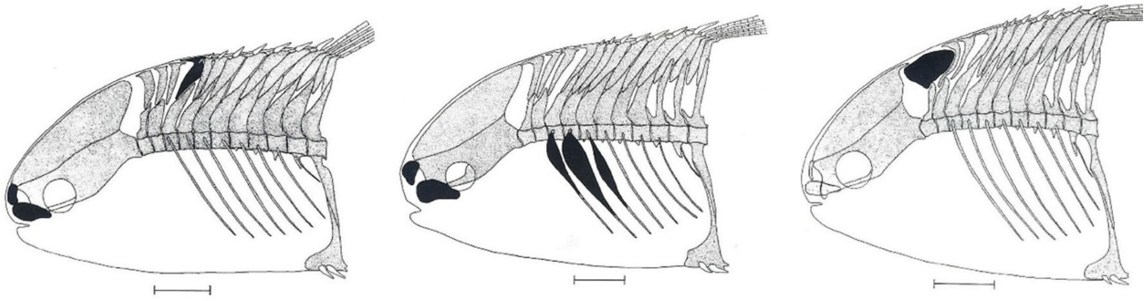
5. Hyperostosis has no apparent phylogenetic significance as it occurs in many unrelated taxa at all levels. (see Table 2). Also relevant is our observation that patterns of hyperostosis in presumably closely related species seldom, if ever, are in close agreement.
6. It is useful as an aid to species identifications. Many externally similar species can easily be misidentified (e.g., Trachinotus spp., Figure 11), and patterns of hyperostosis in adults of congeneric species co-occurring in the same habitat are often very different. The allopatric species *Caranx hippos* (Atlantic) and *C. caninus* (Eastern Pacific) are virtually identical externally and were recognized as conspecific in much of the older literature until Smith-Vaniz and Carpenter (2007) showed that their patterns of hyperostosis are consistently different.

Accurate identification of isolated bones is also essential for evaluation of zooarchaeological research. Hyperostotic bones from kitchen middens and shell mounds can be useful, "particularly for radiocarbon dating, and isotopes … [and] for paleoenvironment interpretation," Aguilera et al. (2017).

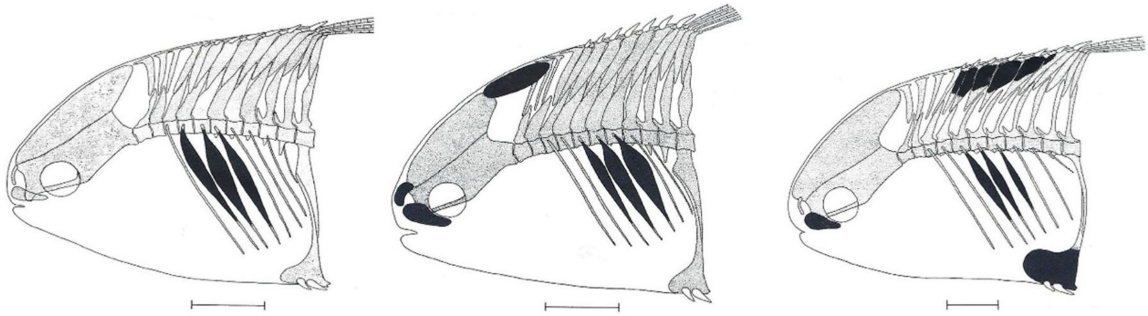
7. Most teleost marine fishes have acellular bones except in hyperostotic species where areas of active remodeling are composed primarily of cellular bone (Smith-Vaniz, Kaufman, and Glowacki 1995). These areas of remodeling activity are a predictable manifestation of bone growth and development in many taxa (Smith-Vaniz, Kaufman, and Glowacki 1995). The fossil cyprinodontid, †Aphanius crassicaudus, apparently is an exception in having swollen avascular bones (Meunier and Gaudant 1987).

3.7 | Unsubstantiated Statements About Hyperostosis

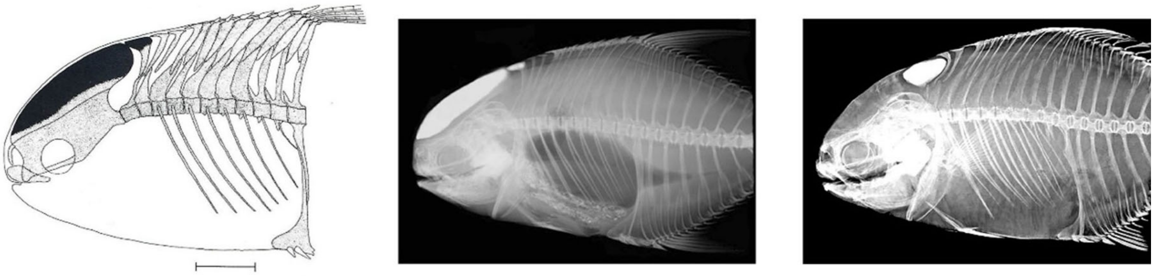
1. *Hyperostosis is sporadic and irregular in occurrence*. This statement is common because some authors seem to be unaware that in many species hyperostosis is first apparent only in relatively large specimens. The pattern of bones that exhibit hyperostosis is also a progression that is usually complete only in the largest and presumably older individuals.
2. *Hyperostosis has a pathological origin*. Schlumberger and Lucke (1948); Capasso, (2005); Köstler (1882); Cantor (1849, 114), and others used the scientific names "*Chaetodon arthriticus*" or *Platax arthriticus* Jordan and Starks in reference to Bell (1793) description and drawing of *Chaetodon* sp. because they incorrectly believed its hyperostotic bones were pathological in origin. However, most authors now agree that hyperostosis is not a pathological formation, including Bell (1960, 1793), Olsen (1971), Desse et al. (1981), Gauldie and Czochanska (1990), Smith-Vaniz, Kaufman, and Glowacki (1995).
3. *Fishes exhibiting hyperostosis are diseased and unsafe to eat*. A good account of this erroneous belief is the graphic account from the 1841 to 1843 logbook of the U.S. sloop-of war "Dale" of the aversion of to eating hyperostotic fishes from Paita, a port in northern Peru: "Fish are abundant in this Bay… but there is a peculiarity in the shape of their bones, which may be set down as a *phenomenon*: The *rib, spinal*, and some others of their bones, are remarkably enlarged *in spots*, as to have the appearance of being *swollen by disease*… Some of our Officers, conceiving that this anomaly in the bones indicated *disease* in the Fish, - a kind *of piscatorial rheumatism,* - would not eat of them; and as diarhea [sic] prevailed in the ship at the time, the fish had to bear the blame of it" (White 1841, cited in Camp 1965). Even today this belief is still common among some fishers and consumers.
4. Hyperostosis *aids in buoyancy or equilibrium* (Gopinath 1951, 274; Desse et al. 1981; Rao and Lakshmi 1986; Meunier and Desse 1996; Capasso 2005). Breder CM (1952, 193) noted that hyperostotic fish bones are "packed with fat and have little difference in specific gravity from that of other muscle which they may replace." However, according to Gauldie and Czochanska (1990, 204) "There was no significant difference in fatty-acid composition"



(a) *T. africanus* (b) *T. anak* (c) *T. blochii*



(d) *T. falcatus* (e) *T. kennedyi* (f) *T. maxillosus*



(g) *T. mookalee* (h) *T. mookalee* (i) *T. blochii*

FIGURE 11 | Species of carangid genus *Trachinotus* exhibiting hyperostosis (shown in black). (a) *T. africanus* Smith, ANSP 73240, 31 cm SL; (b) *T. anak* Ogilby, FMNH 55290, 55 cm SL; (c) *T. blochii* (Lacepède), ANSP 148735 45 cm SL; (d) *T. falcatus* (Linnaeus), ANSP 148765, 51 cm SL; (e) *T. kennedyi* Steindachner, ANSP 148767, 64 cm SL; (f) *T. maxillosus* Cuvier, ANSP 140837, 51 cm SL; (g) *T. mookalee* Cuvier, ANSP 148769, 67 cm SL. Outline drawings based on tracings of radiographs by W.S-V. Figures (a–g) after Smith-Vaniz, Kaufman, and Glowacki (1995). Radiographs (h) *T. mookalee*, ANSP 148755, 34 cm SL; (i) *T. blochii*, ANSP 148733, 43 cm SL. See Table 2 for hyperostotic bone sites for these specimens. Images (h) and (i) courtesy of the Smithsonian Institution, used with permission, and all others courtesy of Marine Biology, used with permission.

between a vertebra and enlarged hyperostotic hemal spine in the snapper, *Chrysophrys auratus* (Forster). Breder CM (1952, 193) also stated, "while every structure and its position has an effect on flotation of a fish it by no means can be assumed that bony growths are *ever* added to a fish as a response to needs of equilibrium." Hewitt (1983, 63) stated "The hypothesis of Gopinath (1951, 274) that dense carangid supraoccipital 'ossification must, in all probability, be attributed to demand for hydrostatic balance and stability,' is difficult to accept." Congeneric species living in the same habitat and with essentially the same morphology (e.g., species of *Trachinotus*) may have quite different patterns of hyperostosis or none at all. It is also doubtful that the hyperostotic nasal and lacrimal bones of *Trachinotus africanus* (Figure 11a), T. *anak* (Figure 11b), and T. *kennedyi* (Figure 11e) would aid in bottom feeding. In addition, most fishes also have swim bladders to help regulate buoyancy. Many species with hyperostotic bones are large fast-swimming piscivores (e.g., *Caranx*) where lighter or heavier bones would be unnecessary as an equilibrium aid. Capasso (2005, 11) believed that the fossil cyprinodontid, *Aphanius crassicaudus*, adopted hyperostosis "to facilitate immersion and swimming in the highly dense water by increasing the weight of their skeletons". This hypothesis contradicts Breder's and others opinion that hyperostotic bones are essentially neutrally buoyant.

5. *Hyperostosis aids in fin erection*. Many others have repeated this belief following Fierstine (1968:6) who stated, "The supracarinales muscle forms a thin anterior layer which originates on the posterior most free basal and inserts on the anterior midborder of the hyperostosis. The

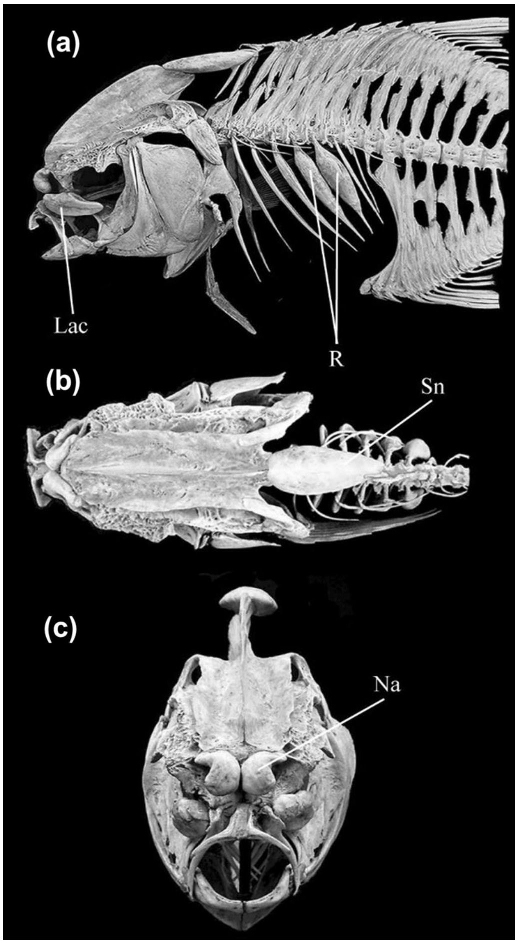


FIGURE 12 | Hyperostosis in *Trachinotus kennedyi*, CAS-SU 12076, 43.5 cm SL, in (a) lateral, (b) dorsal and (c) frontal views. Courtesy of California Academy of Sciences, used with permission. Lac, lacrimal; Na, nasal; R, rib; Sn, supraneural.

dorsal surface of the swollen basal [=pterygiophore of first dorsal-fin spine] serves as the point of origin for the inclinator muscles of the first and second spines of the dorsal fin. The inclinator muscles are unusual in two ways: (1) in most fishes they originate from the surface of the great lateral muscles rather than from a bony surface and (2) they normally take a lateral-medial orientation rather than an anterior-posterior direction. These two differences suggest that the enlarged basal *may* [our italics] function to erect the dorsal fin by increasing the surface area for the origin of the inclinator muscles of the first and second dorsal spines." He further stated, "If the growth [of this pterygiophore] has a selective advantage (such as surface area for muscle origin), it could not increase linearly with the length of the fish unless it could increase its volume without increasing in weight. This problem could be solved by increasing the cancellous tissue and filling the spaces with buoyant fat, so that an increase in volume would not change the center of gravity for the fish."

These surmises are only untested hypotheses, and there are no studies showing that an enlarged pterygiophore next to the first dorsal-fin spine facilitates fin erection.

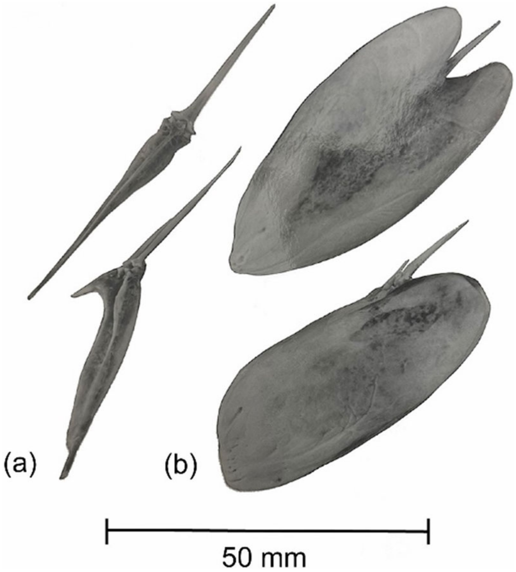


FIGURE 13 | First dorsal-fin pterygiophore of *Caranx latus* and *C. hippos*, both 36.5 cm FL, in dorsal (above) and lateral (below) views; (a) *C. latus* (non-hyperostotic) and (b) *C. hippos* (hyperostotic). After Smith-Vaniz, Kaufman, and Glowacki (1995), fig. 2. Courtesy of Marine Biology, used with permission.

6. *Teratological vertebrae have been frequently and erroneously reported as hyperostosis*. As discussed previously, we consider several literature reports attributed to hyperostosis (Jawad and Akyol 2018; Jawad, Fjelldal, and Hansen 2018; Jawad, Hansen et al. 2018) involving vertebral deformities to have been based on misinterpretations. Several authors have cited the report by McCrimmon and Bidgood (1965) of abnormal vertebrae in the rainbow trout, *Oncorhynchus mykiss* (Walbaum), as "*Salmo gairdneri* Richardson," as a case of hyperostosis, which it clearly is not. Couch et al. (1979, 39) discussed "an extreme dysplasia of vertebrae: the dominant feature was hyperostosis … primarily involving acellular bone" in sheephead minnow, *Cyprinodon variegatus* Lacepède, that had been exposed to the herbicide trifluralin. Cerón-Carrasco (2013, 2) reported a singular globular deformity in a vertebra of a large European ling, *Molva molva* (Linnaeus), which she stated, "is known as hyperostosis, a bone tumor." Schoemaker (2018) described and photographed a large series of isolated and deformed fossil vertebrae from beaches of the Eurogeul area, which he identified as Tilly bones (hyperostotic bones) of haddock, *Melanogrammus aeglefinus* Linnaeus, suggesting that the vertebrae may have been exposed to some extreme environmental condition. Fjelldal et al. (2021, 1049) documented vertebral deformities and slight calluses of neural spines, anal-fin pterygiophores, caudal-fin rays, and rib fractures in wild and cultured wrasse, *Labrus bergylta* Ascanius, as "possible … fish hyperostosis" and suggested that it occurred in early development and was induced by chronic mechanical stress. Jawad and Akyol (2023, 82) documented vertebral deformities in one specimen each of *Sphyraena sphyraena* Linnaeus and *Trachinus radiatus* Cuvier, latter as "mild case of … hyperostsis," and stated, "it is likely… [they] were exposed to unfavorable environmental impacts."

7. H*yperostosis is a nonmalignant neoplastic disease such as a virus* (Günther 1860; Chabanaud 1926; Korschelt 1940; Groff 2004). The fact that it occurs in all individuals of some species makes this hypothesis highly improbable.

3.8 | Conclusions

The primary objectives of our study are to call attention to the enigmatic hyperostotic bones in fishes and to encourage others to more fully investigate their cause and function. We document the occurrence of hyperostosis in 16 orders, 35 families, 89 genera, and 153 species of fishes, establishing that it is often species-specific, a valuable identification aid, but provides no useful phylogenetic information. We also discuss unsubstantiated statements regarding hyperostosis etiology, reiterating that it is a natural phenomenon under genetic control and is involved with calcium metabolism. Hyperostosis has potential for research on calcium metabolism in marine fishes, especially experimental studies of bone growth and development. We agree with Meunier and Huysseune (1992, 456) who stated in reference to hyperostosis, "We only regret the great scarcity of physiological studies in relation to these bone and bone-derived tissues. Such knowledge would undoubtedly contribute to better understanding of their physiological function and of the evolutionary history of their development."

Author Contributions

Julia Klein provided impetus for the research with a database and literature search on hyperostosis as part of her master's thesis. Harald Ahnelt encouraged and supervised her research. William F. Smith-Vani conceived the idea of the publication, added additional references, made many specimen radiographs, examined most of the others, and produced Table 2. Julia Klein and Harald Ahnelt translated and interpreted German references. All of the authors participated in writing the manuscript.

Acknowledgments

The following ichthyologists called our attention to hyperostotic species that might have otherwise been overlooked, or provided supporting documentation and other assistance: K. Bemis and B.B. Collette (USNM), E. Dondorp and W. Renema (RMNH), J. Fong (CAS); B. Frable (SIO), K. Hartel (MCZ), A. Hay (AMS), B. Hutchins, G. Moore and J. Ritchie (WAM), M. Arce, K. Luckenbill and M. Sabaj (ANSP), J. Mclaine (BMNH), G. Nelson (formerly AMNH), W.J. Richards (University of Miami), C.D. Roberts and C. Struthers (NMNZ), K. Sasaki (Kochi University), S.A. Schaefer and R.J. Thoni (AMNH), D.G. Smith (USNM), C. Swift (formerly LACM), and M. Westneat (formerly FMNH). Curators and staff at the following major ichthyological collections: AMNH, AMS, ANSP, BMNH, CAS, LACM, NHMW, NMNZ, SIO, USNM, generously facilitated this study by providing specimen data and examination at their respective institutions, and their cooperation is gratefully appreciated. While an undergraduate student, W.L. Smith (University of Kansas) also helped locate and remove for examination large tank carangids at SIO. K. Luckenbill (ANSP) provided a PDF of an important reference, and radiographs of several large carangids at our request. We are also grateful for the cooperation of A. Reft (National Systematics Laboratory, National Oceanic and Atmospheric Administration) and D. Pitassy (USNM) for providing radiographs of selected specimens when this study was nearing completion. Specimen support and access to specimens in their care was provided by K. Murphy and D. Pitassy (USNM). We also thank N. Bogutskaya (NHMW), J. Maclaine (BMNH), S.J. Raredon (USNM), K. Schiller (NHMW), and R.J. Thoni (AMNH) for providing photographs of hyperostotic fishes, and K. Sasaki for permission to reproduce Figure 10. Librarian B. Hardwick of the Bancroft Library is thanked for granting permission to use the logbook quote from the U.S. sloop-of-war "Dale." Smithsonian librarian S. Zwicker and Laith Jawad (Auckland, New Zealand) were also helpful in finding PDFs of hard to obtain references. We thank M.K. Dolack for an English translation of a large German publication. We also thank M. G. Girard for providing SL measurements of selected specimens and G. D. Johnson for calling our attention to hyperostosis in *Mene maculatus*. Additionally, W.F.S.-V. thanks Howard Jelks for formatting and labeling several figures. The manuscript benefited from reviews and constructive comments of R. Britz (MTD**)**, M.G. Girard (USNM), G.D. Johnson (USNM), and W. Knight (Martha Jefferson Hospital, Charlottesville, Virginia). We also thank two anonymous reviewers for their thorough reviews that improved the manuscript.

Finally, we are grateful for Eschmeyer's Catalog of Fishes (Fricke, Eschmeyer, and Van der Laan 2024). Without that on-line resource we would have spent much effort determining which scientific names used in many of the older publications on hyperostosis were junior synonyms. The Biodiversity Heritage Library (http://www.biodiversitylibrary.org/) has also served as an important source for hard-to-find references. We also benefited greatly from examination of radiographs of fishes that can be viewed and downloaded using the online Smithsonian fish collection search, which was called to our attention by L. Palmer (USNM).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

References

Abe, T. 1960. "Taxonomic Studies on the Puffers from Japan and Adjacent Regions—Corrigenda and Addenda. Part II." *Japanese Journal of Ichthyology* 8, no. 1–2: 3–6.

Aguilera, O., I. Rocha, M. S. Lopes, et al. 2017. "The Bone Degenerative Processes in Senile Fishes from Holocene Brazilian Shell Mounds." *Journal of Fish Diseases* 40, no. 12: 1869–1881. https://doi.org/10.1111/jfd.12662.

Al Abri, N. M., L. A. Jawad, and A. Al-Nahdi. 2023. "Hyperostotic Bones Observed in the First Record Specimen of Spotted Sicklefish, *Drepane Punctata* (Linnaeus, 1788), from the Gulf of Oman." *The Anatomical Record* 306: 665–671. https://doi.org/10.1002/ar.25101.

Al Nahdi, A., C. G. De Leaniz, and A. J. King. 2016. "Two Distinct Hyperostosis Shapes in Ribbonfish, *Trichuris lepturus* Linnaeus 1758." *Bulletin of the European Association of Fish Pathologists* 36: 132–136.

Aleve, Y. G. 1966. "On Thickness of Bones in the Carangoid Fishes (Pisces, Perciformes)." *Zoologicheskii Zhurnal* 45, no. 6: 944–947 [English translation by Bureau of Commercial Fisheries, UDC 597.583.1.591.471.4].

Arambourg, C. 1927. "Les poissons fossils d'Oran." *Matériaux pour la Carte Géologique de l'Algérie, sér. 1. Paléontologie* 6: 1–298.

Azpelicueta, M. M., S. M. Delpiani, A. L. Cione, C. Oliveira, A. P. Marceniuk, and J. M. Díaz de Astarloa. 2019. "Morphology and Molecular Evidence Support the Validity of *Pogonias Courbina* (Lacepède, 1803) (Teleostei: Sciaenidae), with a Redescription and Neotype Designation." *PloS ONE* 14: e0216280. https://doi.org/10.1371/journal.pone.0216280.

Barnard, K. H. 1947. “Further Notes on South African Marine Fishes.” *Annals of the South African Museum* 36: 341–406.

Bartosiewicz, L. 2013. *Shuffling Nags, Lame Ducks: The Archaeology of Animal Disease; With a Contribution on Avian Palaeopathology by Erika Gál*. Oxford, UK: Oxbow Books.

Béarez, P. 1997. “Las piezas esqueléticas diagnósticas en arqueoictiología del litoral ecuatoriano.” *Bulletin de l'Institut français d'études andines* 26, no. 1: 11–20.

Béarez, P., F. J. Meunier, and A. Kacem. 2005. “Description Morphologique Et Histologique De I'hyperostose Vertebrale Chez La Thonine Noire, *Euthynnus lineatus* (Teleostei: Perciformes: Scombridae).” *Cahiers de Biologie Marine* 46: 21–28.

Bedosti, N. 1999. “Pachyostosis in *Aphanius crassicaudus* (Agassiz) (Teleostei, Cyprinodontidae) from the Upper Miocene of Monte Castellano, Italy.” *Miscellaneous Paleontologica del Museo Civico di Storia Naturale di Verona* 8: 143–158.

Bell, W. 1793. “Description of a species of *Chaetodon*, Called, By the Malays, Ecan Bonna.” *Philosophical Transactions of The Royal Society of London* 83: 7–9.

Bertullo, V. H., and R. M. Traibel. 1955. “Neoplasma de los peces de las costas Uruguayas 1. Osteoma de la costilla pleural de la corvina (*Micropogon opercularis*).” *Anales de la facultad de Veterinaria* 1955: 55–59.

Bhatt, Y. M., and N. N. Murti. 1960. “Hyperotosis in *Trichiurus haumeal* (Forskal).” *Journal of the University of Bombay* 28: 84–89.

Bortone, S. A. 1977. “Osteological notes on the Genus *Centropristis* (Pisces: Serranidae).” *Gulf of Mexico Science* 1, no. 1: 1–11.

Breder, Jr., C. M. 1952. “The Problem of Directives to Cellular Proliferation As Illustrated By Ontogenetic Processes in Certain Fishes.” *Growth* 16: 189–198.

Brothwell, D. 1967. “The Evidence of Neoplasms.” In *Diseases in Antiquity*, edited by D. Brothwell, and T. Sandison, 320–345. Springfield: CC Thomas.

Camp, C. L. 1965. *Philo White's Narrative of a Cruise in the Pacific to South America and California on the U.S. Sloop-of-war “Dale” 1841–1843*. Denver: Old West Publishing Co.

Cantor, T. 1849. “Catalog of Malayan Fishes.” *Journal of the Asiatic Society of Bengal* 18, no. 2: 983–1443.

Capasso, L. L. 2005. “Antiquity of Cancer.” *International Journal of Cancer* 113, no. 1: 2–13. https://doi.org/10.1002/ijc.20610.

Cavalluzzi, M. R. 2000. “Osteology, Phylogeny, and Biogeography of the Marine Fish Family Ephippidae (Perciformes, Acanthuroidei), With Comments on Sister Group Relationships.” Dissertation, College of William and Mary, Virginia Institute of Marine Science, 1–213. https://doi.org/10.25773/v5-pm7s-3q12.

Cerón-Carrasco, R. (2013). “The Fish Remains From the Excavations at Castle Hill, Banff.” Unpublished report for Headland Archaeology Ltd, NMRS, 1–7.

Chabanaud, M. P. 1926. “Fréquence, symétrie et constance spécifique d'hyperostoses externs chez divers poissons de la famille Sciénidés.” *Comptes Rendus des séances de l'Académie des Sciences* 182: 1647–1649.

Chabanaud, M. P. (1927. “Hyperostoses externes poissons de la famille des “Sciaenidae”.” *Archives du Muséum d'Histoire Naturelle Ser. 6* 2: 35–47 + pls. 1-2.

Chanet, B. 2018. “Swollen Bones in Jacks and Relatives (Teleostei: Acanthomorphata: Carangidae).” *Cybium* 42, no. 1: 99–103. https://doi.org/10.26028/cybium/2018-421-010.

Chang, M., X. Wang, H. Liu, et al. (2008). “Extraordinarily Thick-boned Fish Linked to the Aridification of the Qaidam Basin (Northern Tibetan Plateau).” Proceedings of the National Academy of Science, 105 (36), 13246–13251. https://doi.org/10.1073/pnas.0805982105.

Compagno, L. J. V. 1988. *Sharks of the Order Carcharhiniformes*, 486. Princeton University Press.

Couch, J. A., J. T. Winstead, D. J. Hansen, and L. R. Goodman. 1979. “Vertebral Dysplasia in Young Fish Exposed to the Herbicide Trifluralin.” *Journal of Fish Diseases* 2: 35–42.

Cuyas Vera, O. D. 2016. “Osteología de *Paralonchurus peruanus* “suco” proveniente de la caleta de Huanchaco, La Libertad.” *Tesis* para optar el titulo professional de biólogo pesquero. Biblioteca Digital, 1–45. Peru: Universidad Nacional de Trujillo.

Desse, G., F. J. Meunier, M. Peron, and J. Laroche. 1981. “Hyperostose vertebrale chez l'animal.” *Rhumatologie* 33, no. 2: 105–119.

von den Driesch, A. 1994. Hyperostosis in Fish.” In W. Van Neer (Ed.), *Fish Exploitation in the Past. Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques, Tervuren*, vol. 274, 37–46.

Ebina, K. 1936. “On the Growth of *Evynnis cardinalis* (LACÉPÈDE).” *Journal of the Imperial Fisheries Institute* 31, no. 2: 69–78.

Fierstine, H. L. 1968. “Swollen Dorsal Fin Elements in Living and Fossil *Caranx* (Teleostei: Carangidae).” *Contributions in science* 137: 1–10.

Fjelldal, P. G., A. Madaro, M. Hvas, L. H. Stien, F. Oppedal, and T. W. Fraser. 2021. “Skeletal Deformities in Wild and Farmed Cleaner Fish Species Used in Atlantic Salmon *Salmo salar* Aquaculture.” *Journal of Fish Biology* 98: 1049–1058. https://doi.org/10.1111/jfb.14337.

Fjelldal, P. G., T. van der Meeren, T. W. K. Fraser, F. Sambraus, L. Jawad, and T. J. Hansen. 2018. “Radiological Changes during Fracture and Repair in Neural and Haemal Spines of Atlantic Cod (*Gadus morhua*).” *Journal of Fish Diseases* 41: 1871–1875. https://doi.org/10.1111/jfd.12899.

Fraser, T. H. 1968. “Comparative Osteology of the Atlantic Snooks (Pisces, *Centropomus*).” *Copeia* 1968, no. 3: 433.

Fricke, R., Eschmeyer, W. N., and Van der Laan, R. (Eds.) (2024). “Eschmeyer's Catalog of Fishes: Genera, Species, References.” http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp.

Gaudant, J. 1979. “Pachylebias crassicaudus (Agassiz) (Poisson téléostéen, cyprinodontiforme), un constituant majeur de l'ichthyofaune du Messinien continental du bassin méditerranéen.” *Geobios* 12, no. 1: 47–73.

Gaudant, J., and F. J. Meunier. 1996. “Observation d'un cas de pachyostose chez un Clupeidae fossile du miocene terminal de l'ouest Algérien, *Sardina?crassa* (Sauvage, 1873).” *Cybium* 20, no. 2: 169–183.

Gauldie, R. W., and Z. Czochanska. 1990. “Hyperostotic Bones from the New Zealand Snapper *Chrysophys auratus* (Sparidae).” *Fishery Bulletin* 88: 201–206.

Gervais, P. 1875. “De l'hyperostose chez l'homme et chez les animaux (2: poissons).” *Journal de Zoologie* 4: 445–462.

Giarratana, F., A. Ruolo, D. Muscolino, F. Marino, M. Gallo, and A. Panebianco. 2012. “Occurrence of Hyperostotic Pterygiophores in the Silver Scabbardfish, *Lepidopus caudatus* (Actinopterygii: Perciformes: Trichiuridae).” *Acta Ichthyologica et Piscatoria* 42, no. 3: 233–237. https://doi.org/10.3750/AIP2011.42.3.07.

Gopinath, K. 1951. “On a Peculiar Bone Formation in the Supra-Occipital Crest of Some Carangid Fishes.” *Journal of the Zoological Society of India* 3, no. 2: 267–276.

Grabda, E. 1982. “Fungi-Related Outgrowths on Pterygophores of Single Fins of *Lepidopus caudatus* (Euphrasen, 1788) (Pisces: Trichiuridae).” *Acta Ichthyologica et Piscatoria* 12: 87–105.

Greenwood, P. H. 1992. “A Redescription of the Uniquely Polychromatic African Cichlid Fish *Tilapia guinasana* Trewavas, 1936.” *Bulletin of the British Museum of Natural History (Zoololgy)* 58, no. 1: 21–36.

Gregory, W. K. 1933. “Fish Skulls, A Study of the Evolution of Natural Mechanisms.” *Transactions of the American Philosophical Society* 23, no. 2: vii+75-481 [Reissued 1959, Erick Lundberg, Laurel, Maryland].

Groff, J. M. 2004. “Neoplasia in Fishes.” *Veterinary Clinics of North America: Exotic Animal Practice* 7: 705–756. https://doi.org/10.1016/j.cvex.2004.04.012.

Günther, A. 1860. “Catalogue of the Fishes in the British Museum. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae.” *British Museum London* 21: 1–548.

Guzmán, A. F., and O. J. Polaco. 2002. “Hiperostosis en Peces Mexicanos.” *Archaeofauna* 11: 45–62.

Hall, B. K., and P. E. Witten. 2019. “Plasticity and Variation of Skeletal Cells and Tissues and the Evolutionary Development of Actinopterygian Fishes.” In *Evolution and Development of Fishes*, edited by Z. Johanson, C. Underwood and M. Richter, Chapter 7, 126–143. Cambridge University Press.

Heemstra, P. C. 2001. “Drepanidae. Sicklefishes.” In *Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Bony Fishes, Part 3 (Menidae to Pomacentridae)*, edited by K. E. Carpenter and V. H. Niem, 3221. –3223. Rome: FAO.

Hewitt, R. A. 1983. “Teleost Hyperostoses: A Case of Miocene Problematica from Tunisia.” *Tertiary Research* 5, no. 2: 63–70.

Hotta, H. 1958. “Abnormal Development of the Cranial Bones of “Jack Mackerel” *Trachurus Japonicus* Temminck & Schlegel with Growth.” *Japanese Journal of Ichthyology* 7, no. 2/3/4: 115–117.

Hughes, D. R., J. R. Bassett, and L. A. Moffat. 1994. “Histological Identification of Osteocytes in the Allegretto Acellular Bone of the Sea Breams *Acanthopagus australis*, *Pagrus auratus* and *Rhabdosarg sarba* (Sparidae, Perciformes, Teleostei).” *Anatomy and Embryology* 190: 163–179.

James, P. S. B. R. 1960. “Instances of Excessive Thickening of Certain Bones in the Ribbon Fish *Trichiurus lepturus* Linnaeus.” *Marine Biological Association of India* 2, no. 2: 253–258.

James, P. S. B. R. 1967. “The Ribbon-Fishes of the Family Trichiuridae of India.” *Marine Biological Association of India Memoir* 1: 1–226.

Jawad, L., A. Wallace, and W. Dyck. 2015. “Documentation of the Case of Hyperostosis in the Silver Bream, *Pagrus auratus* (Forster, 1801) Sampled from Waters Around New Zealand.” *Boletim do Instituto de Pesca, São Paulo* 41: 1043–1047.

Jawad, L. A. 2013. “Hyperostosis in Three Fish Species Collected from the Sea of Oman.” *The Anatomical Record* 296, no. 8: 1145–1147. https://doi.org/10.1002/ar.22564.

Jawad, L. A., and O. Akyol. 2018. “Vertebral Anomalies in *Mullus barbatus* (Actinopterygiidae: Osteichthyes: Mullidae), Collected from Izmir Bay, North-Eastern Aegean Sea, Turkey.” *International Journal of Marine Science* 8, no. 7: 59–65. https://doi.org/10.5376/ijms.2018.08.0007.

Jawad, L. A., and O. Akyol. 2023. “Skeletal Abnormalities in *Sphyraena sphyraena* (Linnaeus, 1758) and a *Trachinus radiatus* Cuvier, 1829 Collected from the North-Eastern Agean Sea, Izmir, Turkey.” *Annales, Series Historia Naturalis* 33: 11–22. https://doi.org/10.19233/ASHN.2023.12.

Jawad, L. A., and M. Bannai. 2014. “Characterization of Hyperostosis in *Platax teira* (Forsskål, 1775) Collected from Marine Water of Iraq, Northwest Arabian Gulf.” *Sky Journal of Agricultural Research* 3, no. 6: 109–111.

Jawad, L. A., P. G. Fjelldal, and T. J. Hansen. 2018. “First Report on Vertebral Abnormality in the Fivebeard Rockling *Ciliata mustela* (Linnaeus, 1758) (Osteichthyes: Lotidae) from Masfjorden, Western Norway.” *Marine Biodiversity* 48: 957–961. https://doi.org/10.1007/s12526-016-0545-7.

Jawad, L. A., T. J. Hansen, S. Meier, J. E. Skjæraasen, and P. G. Fjelldal. 2018. “Vertebral Column Deformity in Adult Wild Haddock (*Melanogrammus aeglefinus*).” *Journal of Fish Diseases* 41: 1909–1915. https://doi.org/10.1111/jfd.12903.

Jawad, L. A., and M. Ibrahim. 2017. “On Some Cases of Fish Anomalies in Fishes from the Port of Jubail, Saudi Arabia, Arabian Gulf.” *International Journal of Marine Science* 7: 188–199. https://doi.org/10.53776/ijms.2017.07.0020.

Johnson, C. R. 1973. “Hyperostosis in Fishes of the Genus *Platycephalus* (Platycephalidae).” *Japanese Journal of Ichthyology* 20, no. 3: 178.

Kaiser, H. E. 1960. “Untersuchungen zur vergleichenden Osteologie der fossilen und rezenten Pachyostosen.” *Paleontographica (A)* 114: 113–196.

Khan, M. Z. 1983. “Hyperostosis in *Muraenesox talabonoides* (Bleeker).” *Indian Journal of Fisheries* 30: 333–334.

Klausewitz, W. 1965. “Über die ungewöhnliche Ausbildung des Schädeldaches von *Pomadasys hasta*.” *Senckenbergiana Lethaea* 46a: 161–175.

Konnerth, A. 1966. “Curious Swollen Bones Found in Fossil Deposits and in Kitchen Middens Appear in the Skeleton of Some Fishes.” *Oceanus* 12, no. 2: 6–9.

Korschelt, E. 1940. “Über die Konstanz im Auftreten von Knochenverdickungen am Fischskelett.” *Marburger Sitzungsbericht* 73, no. 2: 2–14.

Köstler, M. 1882. “Über Knochenverdickungen am Skelette von Knochenfischen.” *Zeitschrift für wissenschaftliche Zoologie* 37: 430–456.

Laroche, J., M. Peron, and Y. Le Galy. 1982. “Ètude de l'hyperostose vertébrale et crânienne chez deux téléostéens *Trachurus trachurus* et *Trachurus mediterraneus*, par la diffraction des rayons X et l'incorporation de. 45° Ca.” *Comptes Rendus des séances de l'Académie des Sciences* 294: 1045–1050.

Leighton Kesteven, H. 1928. “Contributions to the Cranial Osteology of the Fishes. No. VI.” *Records of the Australian Museum* 16, no. 2: 316–346.

Lidour, K., P. Béarez, V. Charpentier, and S. Méry. 2020. “The Prehistoric Fisheries of Akab Island (United Arab Emirates): New Insights into Coastal Subsistence during Neolithic in Eastern Arabia.” *The Journal of Island and Coastal Archaeology* 15, no. 1: 80–103. https://doi.org/10.1080/1556489.2018.1531330.

Lima, F. C., A. P. M. Souza, E. F. M. Mesquita, G. N. Souza, and V. C. J. Chinelli. 2002. “Osteomas in Cutlass Fish, *Trichiurus lepturus* L., from Niteroi, Rio de Janeiro State, Brazil.” *Journal of Fish Diseases* 25, no. 1: 57–61. https://doi.org/10.1046/j.1365-2761.2002.00336.x.

Mahmoud, M. A., and M. Ibrahim. 2021. “Overview on Pathogenesis and Histopathological Observations of Hyperostosis in Two Fish Species; *Scomberoides lysan* (Forsskal, 1775) and *Pomacanthus sextriatus* (Cuvier, 1831) Collected from El-Jubail Province, Saudi Arabia.” *Bulletin of the European Association of Fish Pathologists* 41, no. 3: 111–117. https://doi.org/10.48045/001c.31528.

Marrast, A., and P. Béarez. 2019. “Osteometry and Size Reconstruction of the Indian and Pacific Oceans'*Euthynnus* Species, *E. affinis* and *E. lineatus* (Scombridae).” *Cybium* 43: 187–198. https://doi.org/10.26028/cybium/2019-423-007.

Matić-Skoko, S., and J. Ferri. 2009. “First Record of Hyperostotic Bones in a Common Dentex, *Dentex dentex* (Sparidae) from the Adriatic.” *Cybium* 33: 341–342.

Mawdesley-Thomas, L. E. 1975. “Some Aspects of Neoplasia in Marine Animals.” *Advances in Marine Biology* 12: 151–231.

McCrimmon, H. R., and B. Bidgood. 1965. “Abnormal Vertebrae in the Rainbow Trout with Particular Reference to Electrofishing.” *Transactions of the American Fisheries Society* 94, no. 1: 84–88.

Meunier, F. J., and P. Béarez. 2019. “Histological Study of the Cutaneous Bony Scutes in the John dory, *Zeus faber* Linnaeus, 1758 (Teleostei: Zeiformes: Zeidae).” *Cahiers de Biologie Marine* 60, no. 2: 195–199. https://doi.org/10.21411/CBM.A.260F6487.

Meunier, F. J., P. Béarez, and H. Francillon-Vieilllot. 1999. “Some Morphological and Histological Aspects of Hyperostosis in the Eastern Pacific Marine Fish *Prionotus stephanophrys* Lockington, 1880 (Trigilidae).” Proceedings of Fifth Indo-Pacif Fish Conference, Nouméa, 1997, Paris Society of France Ichthyology, 125–133, 1999.

Meunier, F. J., and J. Desse. 1994. “Histological Structure of Hyperostotic Cranial Remains of *Pomadasys hasta* (Osteichthyes, Perciformes, Haemulidae) from Archaeological Sites of the Arabian Gulf and the Indian Ocean.” In *Fish Exploitation in the Past. Proceedings of the Seventh Meeting of the ICAZ Fish Remains Working Group.Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques*, edited by W. Van Neer, Vol. 274, 47–53.

Meunier, F. J., and J. Desse. 1996. “Les hyperostoses chez les Téléostéens: description, histologie et problèmes étiologiques.” *Ichtyophysiologica Acta* 10: 130–141.

Meunier, F. J., and J. Gaudant. 1987. “Sur un cas de pachyostose chez un poisson due Miocéne terminal du basin méditerranéen, *Aphanius Crassicaudus* (Agassiz) (Teleostei, Cyprinodontidae).” *Comptes rendus de l'Académie des Sciences, 305 Ser* 2: 925–928.

Meunier, F. J., J. Gaudant, and E. Bonelli. 2010. “Morphological and Histological Study of Hyperostosis of *Lepidopus albyi* (Sauvage, 1870), a Fossil Trichiuridae from Tortonian (Upper Miocene) of Piedmont (Italy).” *Cybium* 34, no. 3: 293–301. https://doi.org/10.26028/CYBIUM/2014-381-004.

Meunier, F. J., and M. Herbin. 2014. “La collection de preparations histologiques effectuée par Paul Gervias (1816-1879) sur le squelette des “poissons.”.” *Cybium* 38, no. 1: 23–42.

Meunier, F. J., and A. Huysseune. 1991. “The Concept of Bone Tissue in Osteichthyes.” *Netherlands Journal of Zoology* 42: 445–458.

Moran, M., C. Burton, and N. Caputi. 1999. “Sexual and Local Variation in Head Morphology of Snapper, *Pagrus auratus*, Sparidae, in the Shark Bay Region of Western Australia.” *Marine and Freshwater Research* 50, no. 1: 27–34. https://doi.org/10.1071/MF98031.

Moss, M. L. 1961. “Studies of the Acellular Bone of Teleost Fish.” *Cells Tissues Organs* 46: 343–362.

Murty, V. S. 1967. “Notes on Hyperostosis in the Fish *Drepane punctata* (Linnaeus).” *Journal of the Marine Biological Association of India* 9, no. 2 [issued 1969]: 323–326.

Nammalwar, P. 1976. “A Note on Hyperostosis in the Perch *Pomadasys hasta* (Bloch).” *Indian Journal of Fisheries* 23, no. 1–2: 247–248.

Nelson, J. S., T. C. Grande, and M. V. H. Wilson. 2016. *Fishes of the World* (5th edition, Vol. 707. Hoboken, New Jersey: John Wiley & Sons).

Olsen, S. J. 1966. “Peculiar Swollen Fish Bones.” *Florida Wildlife* 20, no. 3: 22–23.

Olsen, S. J. 1969. “Hyperostotic Fish Bones from Archaeological Sites.” *Archeological Society of New Jersey Bulletin* 24: 17–18.

Olsen, S. J. 1971. “Swollen Bones in the Atlantic Cutlassfish, *Trichiurus lepturus* Linnaeus.” *Copeia* 1971, no. 1: 174–175. https://doi.org/10.2307/144162.

Paig-Tran, E. W. M., A. S. Barrios, and L. A. Ferry. 2016. “Presence of Repeating Hyperostotic Bones in Dorsal Pterygiophores of the Oarfish, *Regalecus russellii*.” *Journal of Anatomy* 229: 560–567. https://doi.org/10.1111/joa.12503.

Parenti, L. R. 1986. “The Phylogenetic Significance of Bone Types in Euteleost Fishes.” *Zoological Journal of the Linnean Society* 87: 37–51.

Radulescu, I., T. Nalbant, and N. Angelescu. 1972. “Neoformatii osoase la *Gadus morhua* (L) si *Cyprinus carpio* (L).” *Bulletinul de Cercetări Piscicole* 31, no. 3–4: 67–70.

Rao, K. S., and K. Lakshmi. 1986. “Case-Study of Nodular Excrescences in *Arius tenuispinis*, Hitherto Considered As Osteoma.” *Diseases of Aquatic Organisms* 1: 123–130.

Rapisarda, G., F. Macrí, M. Manganaro, F. Mariona, G. Mazzullo, and F. Quaglio. 2008. “Iperostosi in Ricciola (*Seriola dumerilii*) e pagro (*Pagrus pagrus*).” *Ittiopatologia* 5: 195–200.

Richards, W. J., and T. Yato. 2012. “The Tropical Species of the Subgenus *Pterygotrigla* (Pisces: Triglidae: *Pterygotrigla*) with Description of a New Species.” *Zootaxa* 3484: 53–64. https://doi.org/1011646/zootaxa.3484.1.3.

Richards, W. J., T. Yato, and P. R. Last. 2003. “Revision of the Gurnard Fish Genus *Otohine* (Triglidae: *Pterygotriga*).” *Smithiana, Publications in Biodiversity, Bulletin* 2, no. 1: 1–18.

Sasaki, K. 1989. “Phylogeny of the Family Sciaenidae, with Notes on Its Zoogeography (Teleostei, Perciformens).” *Memoires of the Faculty of Fisheries Hokkaido University* 36, no. 1–2: 1–137.

Sasaki, K. 1992. “Two New Species of *Nibea* (Sciaenidae) from Northern Australia and Papua New Guinea.” *Japanese Journal of Ichthyology* 39, no. 1: 1–7. https://doi.org/10.11369/jji1950.39.1.

Schlumberger, H. G., and B. H. Lucke. 1948. “Tumors of Fishes, Amphibians, and Reptiles.” *Cancer Research* 8: 657–753.

Schlüter, T., and R. Kohring. 2002. “Palaeopathological Fish Bones from Phosphorites of the Lake Manyara Area, Northern Tanzania—Fossil Evidence of a Physiological Response to Survival in an Extreme Biocenosis.” *Environmental Geochemistry and Health* 24, no. 2: 131–140.

Schlüter, T., R. Kohring, and J. Mehl. 1992. “Hyperostotic Fish Bones (“Tilly Bones”) from Presumably Pliocene Phosphorites of the Lake Manyara Area, Northern Tanzania.” *Paläontologische Zeitschrift* 66, no. 1–2: 129–136.

Schoemaker, M. 2018. “De Tilly Bones Van Het Eurogeulgebied. Door Hyperostose Vervormde Wervels Van *Melanogrammus aeglefinus* (Linnaeus, 1758).” *Afzettingen* 39: 40–45.

Schwartz, F. J. 2000. “Odyssey of a Whitemouth Croaker (*Micropogonias furneiri*; Family Sciaenidae) Possessing Hyperostotic Bones, Uruguay to North Carolina.” *Journal of the Elisha Mitchell Scientific Society* 116: 262–264.

Selvaraj, G. S. D., K. Gopakumar, and M. Rajagopalan. 1973. “On the Occurrence of Osteochondroma and Osteoma in the Marine Cat-Fish *Tachysurus jella* (Day).” *Journal of the Marine Biological Association of India* 15, no. 2: 571–576.

Singaravel, V., A. Gopalakrishnan, K. Raja, M. Rajkumar, and H. W. Ferguson. 2017. “Neoplasia in Goldlined Seabream, *Rhabdosargus sarba* (Forsskål, 1775).” *Journal of Fish Diseases* 41: 405–411. https://doi.org/10.1111/jfd.12737.

Sire, J. Y., and F. J. Meunier. 2017. “Typical Tubules in the Acellular Bone of Gilthead Sea Bream *Sparus aurata* (Teleostei: Perciformes: Sparidae).” *Cahiers de Biologie Marine* 58: 467–474. https://doi.org/10.21411/CBM.A.1F4F35D7.

Smith, W. L., E. Everman, and C. Richardson. 2018. “Phylogeny and Taxonomy of Flatheads, Scorpionfishes, Sea Robins, and Stonefishes (Percomorpha: Scorpaeniformes) and the Evolution of the Lachrymal Saber.” *Copeia* 106, no. 1: 94–119. https://doi.org/10.1643/CG-17-669.

Smith-Vaniz, W. F., and K. E. Carpenter. 2007. “Review of the Crevalle Jacks, *Caranx hippos* Complex (Teleostei: Carangidae), with a Description of a New Species from West Africa.” *Fishery Bulletin* 105: 207–233.

Smith-Vaniz, W. F., and H. L. Jelks. 2006. “Australian Trevallies of the Genus *Pseudocaranx* (Teleostei: Carangidae), with Description of a New Species from Western Australia.” *Memoirs of Museum Victoria* 63: 97–106.

Smith-Vaniz, W. F., L. S. Kaufman, and J. Glowacki. 1995. “Species-Specific Patterns of Hyperostosis in Marine Teleost Fishes.” *Marine Biology* 121: 573–580. https://doi.org/10.1007/bf00349291.

Smith-Vaniz, W. F., and S. J. Walsh. 2019. "Indo-West Pacific Species of *Trachinotus* With Spots on Their Sides As Adults, With Description of a New Species Endemic to the Marquesas Islands (Teleostei: Carangidae)." *Zootaxa* 4651: 1–37.

Starks, E. C. 1911a. "Osteology of Certain Scombroid Fishes. The Osteological Characters of the Scombroid Fishes of the Families Gempylidae, Lepidopidae and Trichiuridae." *Leland Stanford Junior University Publication Series* 5: 17–26.

Starks, E. C. 1911b. "Osteology of Certain Scombroid Fishes. the Osteology and Relationships of the Fishes Belonging to the Family Carangidae." *Leland Stanford Junior University Publication Series* 5: 27–49.

Steindachner, F. 1859. "Beiträge zur Kenntnis der fossilen Fischfauna Österreichs." *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe Wien* 37: 673–703.

Steindachner, F. 1875. "Ichthyologische Beiträge (II) I. Die Fische von Juan Fernandez in den Sammlungen des Wiener Museums." *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe* 71: 443–480.

Suda, Y. 1996. "Osteology and Muscular Attachments of the Japanese Jack Mackerel, *Trachurus japonicus*." *Bulletin of Marine Science* 58: 438–493.

Tiffany, III, W. J., R. E. Pelham, and F. W. Howell. 1980. "Hyperostosis in Florida Fossil Fishes." *Florida Scientist* 43, no. 1: 44–49.

Tuna, F. A. P. 2015. "Comparative Characterization of Hyperostosis in Two Different Species of Family Ephippidae Bleeker, 1859." *Sky Journal of Agricultural Research* 4: 109–113.

Tuna, F. A. P., F. A. A. Calixto, M. Luz, and E. F. M. Mesquita. 2023. "Patterns Description of Hyperostosis Observed in Atlantic Moonfish *Selene setapinnis* and Lookdown *Selene vomer*." *Journal of Morphology* 284: e21640. https://doi.org/10.1002/j40mor.21640.

Tuna, F. A. P., F. A. A. Calixto, and E. F. M. Mesquita. 2024. "Description of Hyperostotic Bones Pattern in Largehead Hairtail *Trichiurus lepturus*." *Zoomorphology* 143: 151–157. https://doi.org/10.1007/s00435-023-00633-4.

Tuna, F. A. P., F. A. A. Calixto, M. C. Salomão, C. E. R. Coutinho, K. R. Estanek, and E. F. M. Mesquita. 2021. "The Presence of Hyperostosis in Atlantic Moonfish, *Selene setapinnis* (Mitchill, 1815) in the Brazilian Coast - Case Report." *Arquivo Brasileiro de Medicina Veterinária e Zootecnia* 73, no. 1: 179–183. https://doi.org/10.1590/1678-4162-12131.

Tyler, J. C. 1980. "Osteology, Phylogeny, and Higher Classification of the Fishes of the Order Plectognathi (Tetraodontiformes)." National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular 434: 1–422.

Tyler, J. C., R. W. E. Purdy, and K. H. Oliver. 1992. "A New Species of *Sphoeroides* Pufferfish (Teleostei: Tetraodontidae) with Extensive Hyperostosis from the Pliocene of North Carolina." *Proceedings of the Biological Society of Washington* 105: 462–482.

Tyler, J. C., and F. Santini. 2005. "A Phylogeny of the Fossil and Extant Zeiform-Like Fishes, Upper Cretaceous to Recent, with Comments on the Putative Zeomorph Clade (Acanthomorpha)." *Zoologica Scripta* 34, no. 2: 157–175. https://doi.org/10.1111/j.1463-6409.2005.00180.x.

Vazzoler, A. E. A.M. 1971. "Diversificação fisiológica e morfológica de *Micopogon furnieri* (Desmarest, 1822) ao Sul de Cabo Frio, Brasil." *Boletim do Instituto Oceanográfico Sao Paulo* 20, no. 2: 1–70.

Verdcourt, B. 1964. "Fossil Seeds and Parrot Fish Bones." *Journal of the East African Natural History Society and Coryndon-Museum* 24, no. 5: 92–93.

Vijayakumar, R., A. Gopalakrishnan, K. Raja, and K. Sinduja. 2014. "Occurrence of Tumour (Odontoma) in Marine Fish *Sphyraena jello* from the Southeast Coast of India." *Diseases of Aquatic Organisms* 108: 53–60. https://doi.org/10.3354/dao02691.

Vogel, M. A. C., and S. G. Veríssimo (1982). "Sobre a Natureza e o possível significado das "amêndoas" encontradas no Sambaqui de Camboinhas." In: K. Suguio (Ed.), Atas do IV Simpósio do Quaternário do Brasil, Rio de Janeiro, pp. 443–452.

Wada, H., M. Itou, and H. Motomura. 2019. "First Japanese Record of *Trachinotus anak* (Perciformes: Carangidae) from Kagoshima Prefecture, Japan." *Japanese Journal of Ichthyology* 66, no. 2: 181–186. https://doi.org/10.11369/jji.19-009.

White, P. 1841. "The Fish of Paya: Logbook entry for 7 October 1841." In *United States Ship "Dale" Cruize [sic] in the Pacific in the years 1841–1843*. Berkeley: Bancroft Library, University of California.

Worm, O. 1655. *Museum Wormianum. Seu Historia rerum rariorum, tam naturalium, quam artificialium, tam domesticarum, quam exoticarum, quae Hafniae Danorum in aedibus authoris servantur: Variis et accuratis iconibus illustrata*, Amsterdam: Ludovicum & Danielem Elzevirios, 389.

Yamanoue, Y. 2016. "Revision of the Genus *Verilus* (Perciformes: Acropomatidae) with a Description of a New Species." *Journal of Fish Biology* 89, no. 5: 2375–2398. https://doi.org/10.1111/jfb.13124.

Yasuda, F., and K. Mizuguchi. 1969a. "Specific Characters of Three Sparid Fishes Referred to the Genus *Chrysophrys* in the Indo-Pacific." *Japanese Journal of Ichthyology* 16, no. 1: 24–30.

Yasuda, F., and K. Mizuguchi. 1969b. "A Study of the Osteological Characters of Six Sparid Fishes Referred to the Genera *Chrysophrys* and *Pagrus*." *Japanese Journal of Ichthyology* 16, no. 1: 31–34.

Yato, T., P. R. Last, and W. J. Richards. 2003. "Revision of the Gurnard Fish Subgenus *Otohime* (Triglidae: *Pterygotrigla*)." *South African Institute for Aquatic Biodiversity* 2: 1–18.

Yato, T., N. Nakayama, and H. Endo. 2020. "Fresh Coloration and Hyperostotic Variations in *Pterygotrigla cajorarori* Richards and Yato." *Japanese Journal of Ichthyology* 67, no. 1: 129–135.