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Morphological variation in the first abdominal vertebra among acanthomorph fishes – a guide for identifying fossil centra from microvertebrate sites

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Abstract: Innumerable fossil fish specimens have been recovered from microvertebrate sites – areas in which small, isolated elements of the skeleton from multiple individuals have been amassed. The accumulated skeletal remains, often the result of transportation by moving waters, provide an important window on the fauna that was present in a wider area during a broader period of time than that represented by individual articulated specimens. Although microvertebrate localities provide important records of taxa, the disarticulated condition of the fossil elements can cause difficulties for taxonomic identification. This is particularly true for fish, for which the most commonly identified elements represented in microfossil sites are vertebral centra; however, fish centra are notoriously difficult to identify at lower taxonomic levels, partly because of the vast numbers of living fish and lack of comparative collections. Arguably, the most distinctive vertebral centrum among all fish is the first abdominal centrum of Acanthomorpha. In acanthomorphs, in contrast to all other fishes, the first centrum bears two distinct (separate left and right) facets for articulation with the exoccipitals which are normally positioned more or less dorsolateral to the articular facet for the basioccipital, forming a unique tri-partite morphology. We here document the first centrum of numerous acanthomorph fishes, and assess the morphologies for taxonomic or phylogenetic consistencies that would allow us to identify isolated centra to a particular acanthomorph group. Features we document include: whether the neural arch is fused to the centrum (as in the paracanthopterygians *Lota lota* and *Percopsis omiscomaycus*) or autogenous (most acanthopterygians); whether the left and right facets for the exoccipitals meet in the midline (e.g., *Boops boops*) or are widely separated (e.g., percids and scorpaenids); appearance of bone texture on the centrum which may be an anastomosed network forming many small spaces (e.g., *Scomber* spp.) or a more solid network (e.g., Channidae), among others. From our examination of specimens, we note several unique features among the taxa examined: the first centrum of *Monopterus alba* is opisthocoelus and the first neural arch has processes extending posteriorly; the first centrum of *Leiognathus equula* has ventral processes extending from the facets for articulation with the exoccipitals; the transverse processes of *Chlorurus* sp. and *Scarus vetula* extend from the ventral area of the centrum and form long triangular processes; and the neural arch of *Siganus guttatus* has ventrolateral processes that extend to the level of the ventral surface of the centrum. We also find that the overall morphology of the first centrum is conservative within a family, indicating that, in many cases, fossil material may be identified at least to the family level.

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INTRODUCTION

Innumerable fossil fish specimens have been recovered from fossil microvertebrate sites – areas in which small, isolated elements of the skeleton from multiple individuals have been amassed. These elements are often thought to have been transported some distance from the point of origin through the action of moving water such as rivers (e.g., Peterson et al. 2011) before deposition, often in the quieter backwaters of an oxbow lake or crevasse splay. Because the fossils have been transported and accumulated, they provide an important window on the fauna that was present in a wider area during a broader period of time than that represented by individual articulated specimens. Microvertebrate accumulations provide different palaeobiodiversity and distribution data from that provided by individual articulated fossils fortuitously recovered, or from lagerstätten, which may preserve a rich diversity of taxa but generally sample calmer waters (e.g., lakes, lagoons) and narrow slices of time. In addition, vertebrate microfossil localities often document taxa that are not found in contemporaneous localities containing articulated animals (e.g., Brinkman 2019). Therefore, these localities can provide palaeoenvironmental and palaeobiodiversity data that complement data provided by articulated remains.

Although microvertebrate localities provide important records of taxa, the disarticulated condition of the fossil elements can cause difficulties for taxonomic identification. This is particularly true for many fish. Common identifiable elements preserved in microfossil sites are vertebral centra. Fish centra vary morphologically along the length of the vertebral column (e.g., Sinha et al. 2019), adding to the difficulty in identifying a single centrum as belonging to a particular taxon. Additionally, although centra morphology varies considerably among higher taxa (e.g., order), at lower taxonomic levels the variation is more subtle. Finally, identification is hampered if comparative material is lacking, or if individual elements are being compared to those of an articulated fossil in which the specimen is exposed in only one view (e.g., Brinkman 2019; Divay et al. 2020). This last issue has been partially resolved with the use of micro ct-scanning of articulated material (e.g., Brinkman et al. 2021) but ct-scanning of material is not always possible.

Among fish vertebrae, arguably the most distinctive element is the first abdominal centrum of acanthomorph fishes. Many fish have a first centrum that is similar to the rest of the abdominal centra – all centra in the column have a single anterior facet for articulation with the basioccipital. Acanthomorphs, however, have a first centrum that bears two distinct, separate left and right, facets for articulation with the exoccipitals. These facets are more or less dorsolateral to the articular facet for the basioccipital, and create a unique tri-partite morphology (e.g., Johnson and Patterson 1993). This tri-partite morphology makes acanthomorph first centra immediately recognizable in microvertebrate sites. Because there is only a single tri-partite vertebra in each fish, recognizing these first centra allows an accurate count of the minimum number of individual acanthomorph fishes that were present in the locality. Therefore, the acanthomorph first centra in a microvertebrate site provides information not otherwise available on the probable relative abundance of acanthomorphs in the assemblage.

The acanthomorph first centra can also provide information on the number of different taxa in the microvertebrate site. For example, Brinkman et al. (2021) recognized five acanthomorphs in the late Maastrichtian of North America based on features of the first vertebra such as the fusion of the neural arch to the centrum, contacts between the exoccipital facets, the pattern of ridges on the side of the centrum, and the presence of a ventral pit. Additionally, these unique morphologies may also be useful to identify the material to lower taxonomic levels. For example, Otero et al. (2008) reported a 'bean-shaped' facet for the exoccipital in the first centrum of a species of the fossil perciform genus *Semlikiichthys*. However, in many cases, too little is known of morphological diversity of the first centrum to make such identifications. The goal of this paper is to provide that comparative information for a variety of acanthomorph orders and families by documenting the morphology of the first centrum. We then use this information to first test our idea that the morphology of the first centrum differs significantly among higher acanthomorph groups, and then to determine if the morphology is sufficiently consistent within each of these groups to permit individual centra to be confidently attributed to the taxon.

Sept Acanthomorpha contains 43 orders with more than 260 families (Betancur-R et al. 2017; but see Nelson et al. 2016 for slightly different numbers). The Lampriformes (also spelled Lampridiformes), or the Lampriformes + Paracanthopterygii, is considered to be the sistergroup to all the rest (Nelson et al. 2016; Betancur-R et al. 2017). In addition to the tri-partite first centrum, acanthomorphs are united by numerous features (see summaries in Wiley and Johnson 2010; Nelson et al. 2016), including the one that gives them their name: the presence of true (unpaired, median) spines in the dorsal and anal fins (Johnson and Patterson 1993), although these spines are lacking in Lampriformes (Nelson et al. 2016).

Because there is a very large number of extant acanthomorphs – well over 15,000 species representing about one quarter of all vertebrates (Nelson et al., 2016; Dornberg and Near 2021) – we cannot cover all taxa here. We initiated this project because of our particular interest in identifying taxa from freshwater microvertebrate sites of Alberta, but then expanded it based on other joint projects on marine Cretaceous fishes. Overall, we consider this a preliminary start at documenting acanthomorph first centrum diversity, concentrating our attention on taxa that were readily available to us. In total, we have included representatives of 28 acanthomorph orders, with coverage of 60 families, including five that are order incertae sedis. For some families, we have multiple species, and for a few species we include multiple specimens to document variation at different taxonomic levels. We also provide brief information on the environment and distribution of each group (from Froese and Pauly 2023), to aid in narrowing the likely identity for fossil finds, although we acknowledge that environment of modern fish species is not always indicative of palaeoenvironment of their extinct relatives.

MATERIAL AND METHODS

The acanthomorph specimens we include were either legally wild-caught (particularly those from fresh waters of Canada and Africa), or were purchased from markets in Canada, Europe and Asia. The material is from the fish collections of the Canadian Museum of Nature (CMNFI), University of Alberta Museum of Zoology Fish collections (UAMZ F) and Recent material from the palaeontology collections of the Royal Ontario Museum (ROM R). The UAMZ specimens were stained with black ink to reduce translucence, dried for one day or more, then coated with ammonium chloride to enhance relief prior to being photographed with a Nikon DCM 1200 C digital camera mounted on a Zeiss Discovery V8 stereo microscope. The ROM specimens were not stained with black ink, and either coated with ammonium chloride and photographed with the same set-up, or left uncoated and photographed using a Sony nex-6 camera attached to a Wild M3C microscope. Material in the collections of the Canadian Museum of Nature was left uncoated and photographed with a portable Celestron Handheld Digital Microscope Pro. Multiple (3 to 8) photographs were taken of each specimen and photostacked using Adobe Creative Cloud Photoshop to improve focus.

We present the groups below following the scheme of relationships recovered by Betancur-R et al. (2017:fig. 2). We use the higher-level groupings as found in that paper for convenience only; use of this nomencalture is not a reflection of any analysis done by us or an endorsement of any particular classification scheme.

TERMINOLOGY

The various parts of the first vertebra have been referred to by different names in other papers, and additionally, some of the descriptive names are cumbersome. Therefore, here we provide the simplified terminology we use in the descriptions found in the results section. We have included basic terms as well, in order to make this work more accessible to researchers who may not be familiar with vertebrae or fish. Taxa given as examples in this section are described in the results section.

Anterior (articular) facet – this is the facet on the anterior face of the first centrum which articulates with the basioccipital.

Bone texture – the dorsal, lateral and ventral surfaces of the centrum may appear smooth (e.g., *Anabas testudineus*), or the bone may be formed by a network of roughly parallel ridges with small pits or cells between them (e.g., *Lates calcarifer*), or irregular ridges may anastomose and form a honeycomb texture (e.g., *Scorpaena plumieri*). The small pits or cells of the bone texture should not be confused with the large, distinct pits that may be found on dorsal, lateral and ventral surfaces of the centrum. In some taxa, large pits that cover the lateral side of the centrum (e.g., *Morone chrysops*) are part of the bone texture, and are bounded by thin ridges of bone, rather than being distinct from the rest of the bone surface.

Centrum – the body of the vertebra, separate from the exoccipital facets, neural arch, and any processes. The centrum is normally pierced by a foramen that would have accommodated the notochord.

Compressed – flattened laterally; e.g., as in the body of a flatfish or an angelfish.

Depressed – flattened dorsoventrally; e.g., as in the body of a skate or ray.

Dorsal pits – these are large, fairly deep pits found on the dorsal surface of the centrum. Paired pits may be present to accommodate the proximal tips of an autogenous (i.e., unfused) neural arch, and a medial pit may be present (e.g., *Anabas testudineus*). The pit may extend almost to anterior and posterior ends of the centrum, or may be restricted to the central area of the centrum.

Dorsal length of centrum – the distance between the anterior and posterior facets measured on the dorsal surface of the centrum.

Exoccipital facets – we use this here to refer to the paired facets found on the dorsolateral sides of the first centrum that are for articulation with the two exoccipitals.

Height of centrum – this refers to the maximal distance between dorsal and ventral edges of the centrum. If the centrum is constricted in the middle, this dimension is taken at its posterior or anterior articular facet.

Lateral pit – a large pit found on the lateral surface of the centrum below the exoccipital facet. It is distinctly larger than most pits associated with the bone texture, and is bounded by more than a single thin ridge of bone. It may be positioned relatively high on the centrum, or more ventrally, but is always on the lateral surface (e.g., *Diplodus annularis*).

Length of centrum – this measurement refers to the distance between anterior and posterior edges of the centrum.

Midpoint of the facet – the central area of the anterior or posterior facet half-way between left and right sides and halfway between dorsal and ventral edges, whether the facet is round or irregular shaped.

Neural arch – the bony bridge over the dorsal nerve cord. The arch may be unfused (autogenous) or fused to the centrum. If it is unfused, there are normally paired pits on the dorsal surface of the centrum in which the left and right sides of the neural arch insert.

Neural spine – the dorsal extension from the neural arch. This is most commonly a single median structure in acanthomorphs, but the left and right sides may remain separate (e.g., Balistidae).

Posterior accessory processes of neural arch – in some taxa, there are small processes on the neural arch which project posteriorly to articulate with the neural arch of the following vertebra (e.g., *Monopterus alba*). We do not use the term 'zygapophysis' as any homology with similarly positioned structures in tetrapods is unknown.

Posterior (articular) facet – the facet on the posterior face of the centrum which articulates with the anterior facet of the following centrum.

Transverse processes – these paired processes form on the lateral sides of the centrum and project posteriorly to reach or overlap the following centrum. They may be quite prominent or reduced in size. Normally they are positioned at midheight of the centrum, but may be located higher or lower in different species.

Ventral pit – in some taxa there is a distinct, large pit on the ventral surface of the first centrum. This may vary in shape from a round pit restricted to the middle of the bone (e.g., *Boops boops*) to narrow or slit-like pits (e.g., *Anabas testudineus*) which may extend almost to the anterior and posterior edges of the centrum.

Ventral length of centrum – the distance between the anterior and posterior facets measured on the ventral surface of the centrum.

Width of centrum – this measurement refers to the greatest distance between the two lateral edges of the centrum, measured across the anterior or posterior facet.

RESULTS

We here document several attributes of the first vertebra in acanthomorphs that vary among taxa. These include whether the neural arch is fused to the centrum or autogenous, the shape of the neural arch and fusion of the left and right sides of the neural spine. The overall shape of the centrum is based on the relative height and length and the relative lengths of the ventral and dorsal surfaces. In combination, these features cause the centrum to be rectangular, or trapezoidal in lateral view. Other features are the size, shape, and orientation of the exoccipital facets and their position relative to the anterior facet of the centrum, the shape and orientation of the anterior facet for the basioccipital, and the shape of the posterior articular facet. The bone texture on the surfaces of the centrum, and presence or absence of dorsal, lateral and ventral pits also differs among taxa. Finally, the paired transverse processes on the centrum vary in orientation, size, and vertical position. These features are noted for the taxa below. Features that are found to be unique to a single taxon among those examined are indicated.

Subdivision TELEOSTEI Müller, 1844 (sensu Patterson and Rosen, 1977)

Sept ACANTHOMORPHA Rosen, 1973 (sensu Johnson and Patterson, 1993)

Order 1. Lampriformes – in this order, the tripartite form of the first centrum does not yet appear to be developed, as the anterior facets for the exoccipitals of the first centrum are not distinct from the facet for the basioccipital.

Family 1. Lampridae – *Lampris guttatus* (CMNFI 1983-0273.1; Plate 1, Fig. 1) is a pelagic species found globally in tropical to temperate marine waters. The neural spine is fused to the centrum. The exoccipital facets are continuous with the basioccipital facet, and all are oriented anteriorly. The exoccipital facets cover the anterior faces of the neural arch but do not meet one another medially. The anterior facet is slightly convex. The concave posterior facet is oval to rectangular, being wider than high, and the centrum lacks a notochordal foramen. The bone texture on all sides is a honeycomb of deep circular to irregular shaped spaces formed by thin anastomosing ridges with no large pits on any surface. The centrum is about half as long (anteroposteriorly) as it is wide (from side to side), and is wider than high. There are no transverse processes.

Superorder Paracanthopterygii

The composition of the Paracanthopterygii has changed over the years with different groups added and then excluded. Currently, it comprises the extant orders Polymixiiformes, Percopsiformes, Zeiformes, Stylephoriformes, and Gadiformes (e.g., Grande et al. 2013; Nelson et al. 2016; Betancur-R et al. 2017). Late Cretaceous articulated fossils from Alberta and Germany (Agassiz 1838; Wilson and Murray 1996; Newbrey et al. 2013) have been placed in the extinct order Sphenocephaliformes, which may be the sister-group to the rest of the superorder.

Fig. 1 *Lampris guttatus*

Fig. 2 *Percopsis omiscomaycus*

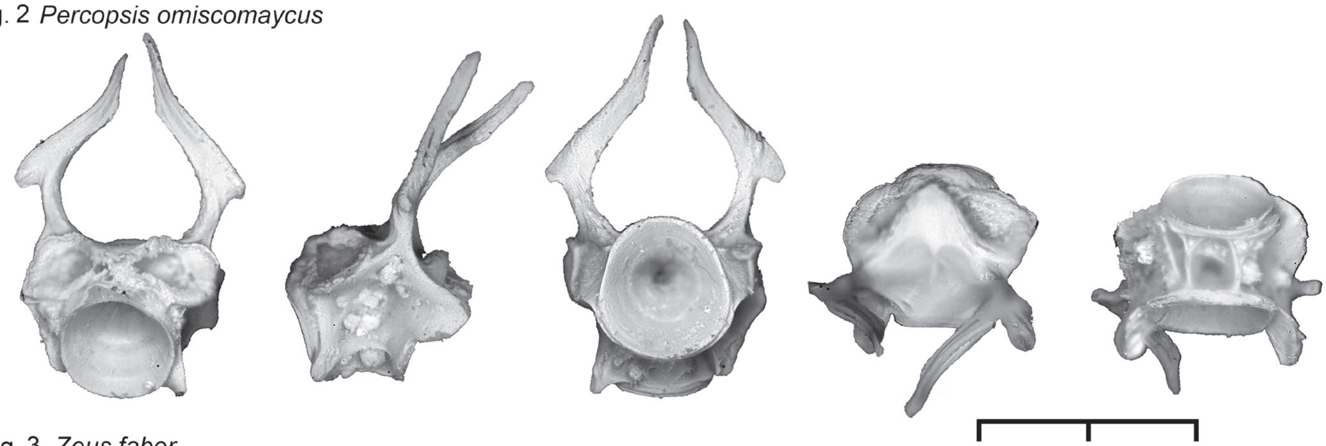


Fig. 3 *Zeus faber*

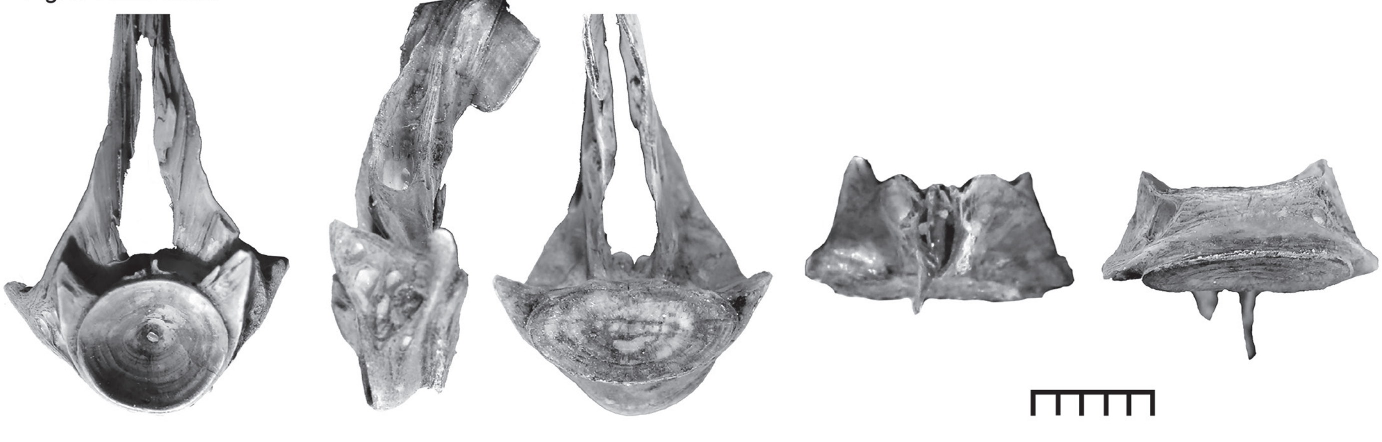


Plate 1. First centrum of Lampriformes and Paracanthopterygii – Percopsiformes and Zeiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 1. Lampriformes, Lampridae, *Lampris guttatus*, CMNFI 83-0273.
Figure 2. Percopsiformes, Percopsidae, *Percopsis omiscomaycus,* ROM R6494.
Figure 3. Zeiformes, Zeidae, *Zeus faber*, UAMZ F8899.

Order 2. Percopsiformes – this order groups three families of small, freshwater fishes from North America: Percopsidae, Aphredoderidae, and Amblyopsidae. Articulated fossils described as extinct species are known from Alberta and Montana (Grande, L. 1988; Murray 1996; Murray and Wilson 1996). The amblyopsid *Amblyopsis spelaea*, from southeastern USA, has a distinctive first vertebra, with the facets for articulation with the exoccipitals widely spaced, not contacting one another in the midline, and positioned low on the centrum so that the dorsal edges of the facets align with the dorsal edge of the exoccipital facet (Murray 1994:fig. V-8A). A similar morphology was found in a first centrum from the Cypress Hills Formation of Saskatchewan, which lead to it being identified as aff. Amblyopsidae (Divay et al. 2015:fig. 6F).

Family 2. Percopsidae – *Percopsis omiscomaycus* (ROM R6494; Plate 1, Fig. 2) is found throughout North America. The neural arch is fused with the centrum. The left and right facets for the exoccipitals are tear drop-shaped with the points almost meeting in the midline dorsally, and the facet for the basioccipital is oriented slightly ventrally. In lateral view, the antero-posterior length of the centrum is slightly greater dorsally than ventrally, and the length of the centrum is slightly less than its height. There are only a few pits on the lateral surface. The transverse process is on the dorsal half of the centrum and projects posteriorly. The posterior articular facet is sub-round, wider dorsally than ventrally. There are two pits on the dorsal surface and a single, large ventral pit.

Order 3. Zeiformes – The zeiformes have been characterize in part by having the exoccipital facets narrowly spaced (Nelson et al. 2016); however, in comparison to some other taxa, these facets are not that close together and do not meet each other in the midline in our exemplar specimen. Most zeiform species are deep sea inhabitants, and none are found in fresh waters (Nelson et al. 2016). Two zeiforms have been named for fossils from Europe (Italy and Portugal; see Murray 2016).

Family 3. Zeidae – *Zeus faber* (UAMZ F8899, Plate 1, Fig. 3) is a marine, sometimes brackish fish with a worldwide distribution; our specimen is from the Mediterranean Sea. The neural arch is fused to the centrum. The exoccipital facets are small, well-separated, and located to either side of, and projecting above, the dorsal surface of the anterior articular facet. They are oriented dorsally. The centrum is much narrower anteroposteriorly than high. The circular anterior facet is inclined slightly ventrally. The posterior articular facet is depressed, forming a wide oval and is flat (acoelus). The notochordal foramen is in the centre of both facets. There are a few enlarged pits on the lateral side of the centrum, although the bone texture is otherwise fairly smooth and there are no pits on the ventral surface. The transverse processes are oriented dorsally, extending above the dorsal surface of the centrum to articulate with the processes of the neural arch on the following centrum. In dorsal view, the centrum tapers posteriorly from the wider anterior facet to the posterior facet.

Order 4. Gadiformes – the majority of the species in this order are marine, but two species are found in fresh waters: the burbot, *Lota lota*, is confined to fresh waters, and the tomcod, *Microgadus tomcod*, normally a marine fish, has populations that are landlocked in some freshwater environments in eastern North America. The neural arch on the first vertebra is fused to the centrum and the relatively small exoccipital facets are positioned dorsally on the centrum, at the base of the neural arch in all of our examined material.

Family 4. Gadidae – *Gadus microcephalus* (CMNFI 1976-0274.1; Plate 2, Fig. 4) is a coastal marine fish that also enters brackish waters. It is found across the Canadian Arctic and reaches south to the Gulf of Saint Lawrence in the Atlantic Ocean and to California in the Pacific Ocean. The exoccipital facets extend anteriorly well in front of the anterior facet; they are oriented anteriorly. Anterior and posterior facets are almost circular, and the notochordal foramen is slightly dorsal to the midpoint. The broad, rounded, transverse processes are positioned at midheight and angle posterolaterally. The bone texture is an open network of ridges defining oval spaces of varying sizes.

Family 5. Lotidae – the two species of lotids we figure are fairly similar. They differ in the size and orientation of the exoccipital facets, with those of *Lota lota* being oriented more laterally, and those of *Brosme brosme* being larger and extending farther anteriorly.

a. Lotidae – *Brosme brosme* (CMNFI 1987-0335.1; Plate 2, Fig. 5), the cusk, a marine fish, is found in coastal waters of the northern Atlantic Ocean and the North Sea, reaching south to Newfoundland in Canada. The neural arch, although broken in the figured specimen, is fused to the centrum as in other members of the family. The exoccipital facets are positioned dorsally on the centrum, at the base of the arch. They are oriented anterodorsally, and project farther anteriorly past the anterior facet than in *Lota lota*. The anterior facet is circular and the posterior facet is oval, being wider than high. The centrum is rectangular in lateral view, and almost as long antero-posteriorly as it is tall. The transverse processes are broadly rounded and extend posterolaterally from the midheight of the centrum. The bone texture is formed by thin ridges of bone forming a network of irregularly shaped spaces, with no large pits on any surfaces.

b. Lotidae – *Lota lota* (UAMZ F4831, Plate 2, Fig. 6). The burbot is found in circum-Arctic fresh waters; our specimen is from the North Saskatchewan River, Alberta. The exoccipital facets are much smaller than the circular anterior facet, and extend above the dorsal surface of the centrum, but are restricted to the lateral edges. The centrum is almost as long as it is high. The broad transverse processes are positioned at the dorsal edge of the centrum and directed posterolaterally ending in a point. The posterior articular facet is depressed and more oval compared to the anterior facet. The notochordal foramen is slightly above the midpoint on both facets, but lower than that of *Brosme brosme*. The ventral surface is ornamented with a network of thin bone ridges that are not parallel. These ridges delineate oval, elongate or irregular shaped cells. There are no large pits on the ventral or dorsal surfaces of the centrum. A single, deep, large pit is present on the lateral surface.

Family 6. Merluccidae – *Merluccius* cf. *M. bilinearis* (CMNFI Z000404; Plate 2, Fig. 7). This species is found

Fig. 4 *Gadus macrocephalus*

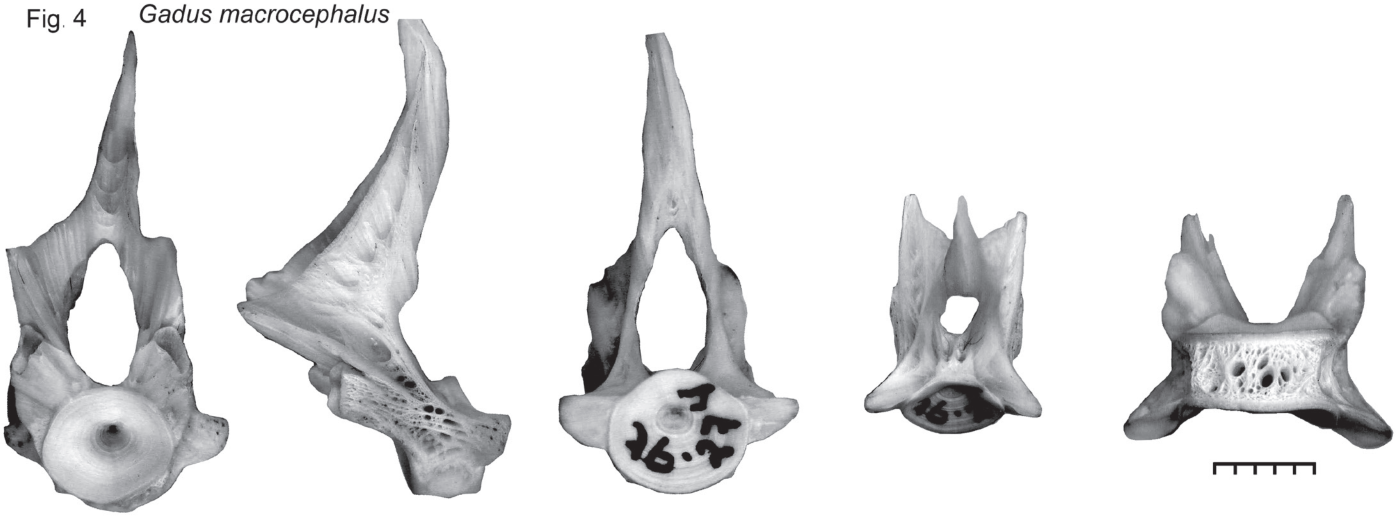


Fig. 5 *Brosme brosme*

Fig. 6 *Lota lota*

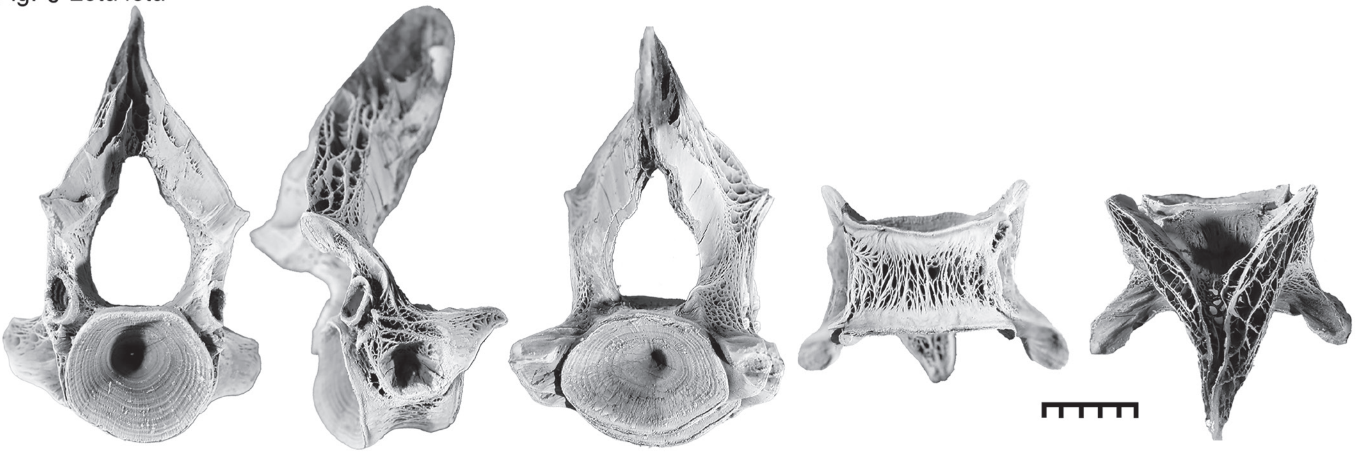


Fig. 7 *Merluccius* cf. *M. bilinearis*

in the near-shore coastal waters of the Atlantic off Canada and the United States, south to the Bahamas. In common with other gadiforms, the neural arch is fused to the centrum. The exoccipital facets are located higher on the centrum than the other examined taxa, extend farther anteriorly than the centrum and are oriented anterodorsally.

(Opposite page) Plate 2. First centrum of Paracanthopterygii – Gadiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 4. Gadiformes, Gadidae, *Gadus microcephalus* CMNFI 1976-0274.1. The dorsal view is tipped up posteriorly to show the bone under the arch.
Figure 5. Gadiformes, Lotidae, *Brosme brosme,* CMNFI 1987-0335.1.
Figure 6. Gadiformes, Lotidae, *Lota lota*, UAMZ F4831.
Figure 7. Gadiformes: Merluccidae: *Merluccius* cf. *M. bilinearis,* CMNFI Z000404.

The posterior facet is larger and slightly more oval than the circular anterior facet. The notochordal foramen is located more centrally than in the lotids. The posterolaterally projecting transverse processes are narrower than those of the other gadiforms examined. The bone texture is more open, with larger spaces formed by the thin ridges, and ventrolaterally there is a pair of large pits.

Unnamed Superorder

The Polymixiiformes, Trachichthyiformes and Beryciformes are not included in either Paracanthopterygii or Acanthopterygii by Betancur-R et al. (2017). They instead form successive sister groups (Polymixiiformes, then Trachichthyiformes + Beryciformes) to the Acanthopterygii.

Order 5. Beryciformes – this order contains the Stephanoberycoidei (pricklefishes, gibberfishes, and whalefishes) and the Berycoidei (bigscales and alfonsinos). All taxa are found in marine waters.

Family 7. Berycidae – *Beryx decadactylus* (CMNFI 1966-0459.8; Plate 3, Fig. 8) is found in tropical to temperate coastal waters worldwide. The neural arch is autogenous. The circular anterior facet is slightly convex. It is about the same size as the almost circular, slightly concave exoccipital facets, which are positioned dorsal to the centrum, and oriented anterodorsally. These facets do not meet in the midline (our figured specimen retains some flesh between the facets). The anterior and posterior facets are both inclined such than the centrum is wedge-shaped in lateral view; in ventral view, the centrum tapers from the smaller anterior facet to the larger posterior facet. The notochordal opening is visible in the posterior facet, but it does not extend through the centrum and there is no foramen on the anterior facet. The small, hooked, transverse processes are located dorsal to midheight and extend posteriorly well past the centrum. The bone texture is smooth, with only a few small pits formed by ridges of bone on the ventral surface. The dorsal surface bears a pair of deep, circular neural arch pits close to the midline.

Superorder Acanthopterygii

The rest of the acanthomorph orders are grouped in the Acanthopterygii. Although numerous authors have proposed higher-level groups for some of these orders, there is still significant disagreement among the phylogenetic analyses (see Dornberg and Near 2021).

Order 6. Holocentriformes – encompasses the tropical, marine squirrelfishes which are placed in a single family.

Family 8. Holocentridae – *Holocentrus ascensionis* (CMNFI 1987-0334.1; Plate 3, Fig. 9) is associated with reefs in the Western Atlantic from the southern USA to Brazil and in the Gulf of Mexico and Caribbean. Our figured specimen is quite small and details are not that clear. The neural arch on the first centrum is autogenous. The oval exoccipital facets are oriented almost dorsally, and do not meet one another in the midline. The anterior facet is triangular, with the narrow point oriented dorsally, and is oriented anteroventrally such that the centrum is much shorter along the ventral edge than the dorsal edge. The posterior facet is more circular, with the notochordal foramen dorsal to the midpoint. The small, pointed transverse processes are positioned above midheight on the centrum, and hook medially. The bone texture is quite smooth, with only a few small, shallow depressions on the surfaces. The neural arch pits are circular.

Order 7. Batrachoidiformes – the marine toadfishes have large, depressed heads with tapered bodies. There are about 100 species all in a single family.

Family 9. Batrachoididae – *Opsanus* cf. *O. tau* (CMNFI 1976-0099.1; Plate 3, Fig. 10) is found in United States coastal waters of the Western Atlantic. The neural arch is fused to the centrum, although it is broken in the figured specimen. The exoccipital facet is located dorsolaterally on the centrum, at the base of the neural arch, and oriented almost dorsally. The anterior facet is triangular, and the posterior facet is circular to oval, being slightly wider than high; both are oriented vertically. The notochordal foramen is positioned just dorsal to midheight. The broad, rounded transverse processes project posterolaterally. The bone texture is an open network of thick and thin ridges delimiting irregularly shaped spaces; it covers the lateral, ventral and dorsal surfaces. The centrum is about the same measurement in all dimensions (height, width and length).

Order 8. Scombriformes – the mackerels are split into two suborders, Scombroidei and Stromateioidei according to Nelson et al. (2016); however, Betancur-R et al. (2017)

Fig. 8 *Beryx decadactylus*

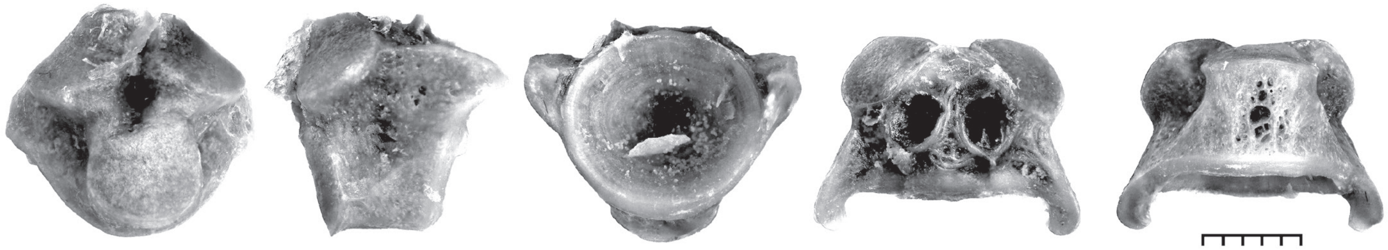


Fig. 9 *Holocentrus ascensionis*

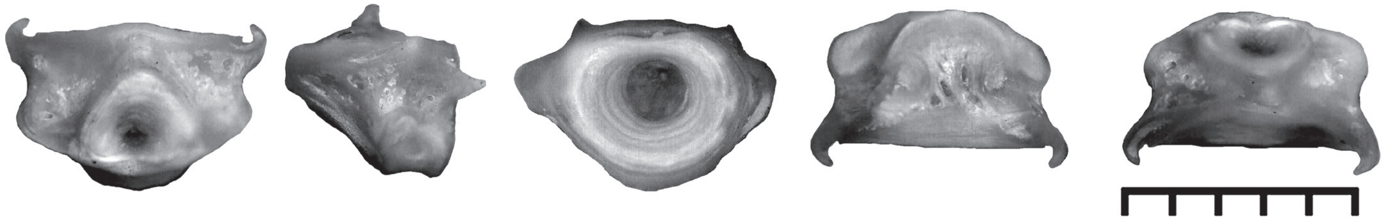


Fig. 10 *Opsanus* cf. *O. tau*

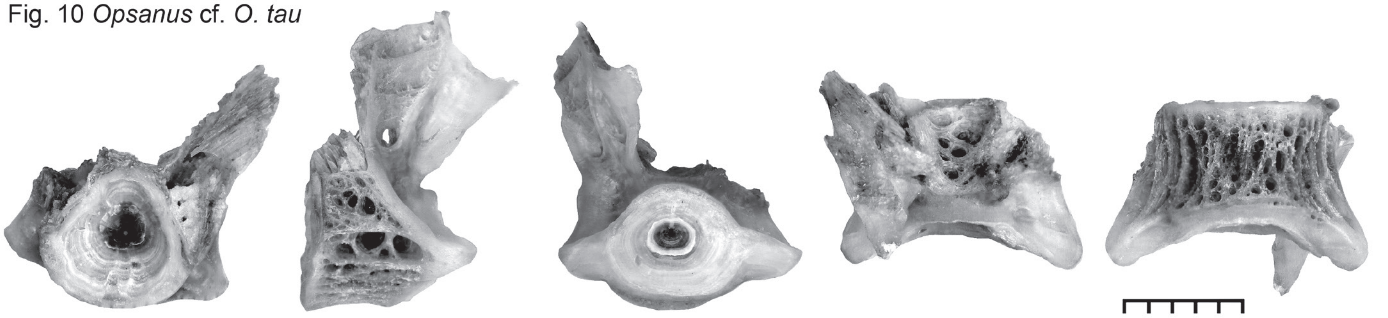


Plate 3. First centrum of Beryciformes and Acanthopterygii – Holocentriformes and Batrachoidiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 8. Beryciformes: Berycidae: *Beryx decadactylus,* CMNFI 1966-0459.8.
Figure 9. Holocentriformes: Holocentridae: *Holocentrus ascensionis,* CMNFI 1987-0334.1.
Figure 10. Batrachoidiformes: Batrachoididae: *Opsanus* cf. *O. tau,* CMNFI 1976-0099.1.

consider this tentative with much more work required. These are marine fishes, many pelagic, with some rarely entering fresh water (Nelson et al. 2016). The members of this order differ in whether or not the neural arch is fused to the centrum, as well as the orientation of the anterior facet. The bone texture varies from honeycomb to smooth.

Family 10. Scombridae – this family is found in tropical to subtropical seas. The first centrum of scombrids is elongate, being longer than high, with a fused neural arch. The anterior and posterior facets are of similar size, with the posterior one circular and the anterior one varying from almost circular to pinched-in at the top by the exoccipital facets. The exoccipital facets are relatively small, circular and widely separated. They are oriented anteromedially. The transverse processes are positioned at the dorsal edge of the centrum and extend for a short distance posteriorly. The bone texture is mostly fine anastomosing ridges forming a honeycomb pattern.

a. Scombridae – *Scomber scombrus* (UAMZ DB13, Plate 4, Fig. 11) is found in the North Atlantic and Mediterranean. The neural arch is fused to the centrum and the small, round facets for the exoccipitals are positioned laterally, extending from the midpoint of the centrum to above the dorsal surface. They extend anterior to the articular facet but not as much as in *S. japonicus*. These facets are oriented anteromedially. Both anterior and posterior articular facets are circular, of similar size, and both are oriented vertically so that the centrum is rectangular in lateral view with equal dorsal and ventral lengths. The centrum is longer than it is high. The lateral sides of the centrum and the facets for the exoccipitals are covered in a network of bone forming a multitude of small round to oval pits. This bone texture continues over the ventral surface of the centrum, as well as onto the neural arch. There is a large pit on the proximal and mid-lateral part of the neural arch on both sides. The transverse processes are oriented posteriorly, and are positioned at the posterodorsal edge of the centrum above midheight. There are no large pits on either the dorsal or ventral surface of the centrum.

b. Scombridae – *Scomber japonicus* (UAMZ F8901, Plate 4, Fig. 12) is an Indo-Pacific fish. Our specimen is from a Mediterranean fish market. The neural arch is fused to the centrum, and does not project laterally past the body of the centrum. The circular anterior and posterior facets are about the same size, with the notochordal foramen positioned at about the midpoint. The small, round exoccipital facets are located laterally, widely separated, and do not extend dorsally beyond the centrum surface. These facets are oriented anteromedially, and extend well anterior to the articular facet for the basioccipital, much more so than those of *S. scombrus*. A thick lateral ridge is present at the interface of the neural arch and the centrum, which extends from the exoccipital facet to the transverse process. The short, rounded, transverse processes are located above the midheight of the centrum (i.e., higher than in *S. scombrus*), and project posteriorly. The bone texture appears smoother than in the other scombrids examined. The cells are smaller and the ridges are relatively thicker, but the ventral and dorsal surfaces retain a distinct honeycomb pattern. This pattern is also found on the lateral surface below the lateral ridge where there is a deep depression with a small central pit. The rest of the lateral surface and the neural arch lack the honeycomb texture and are smooth. The anterior facet is vertical so that the centrum has a similar dorsal and ventral length and is rectangular in lateral view.

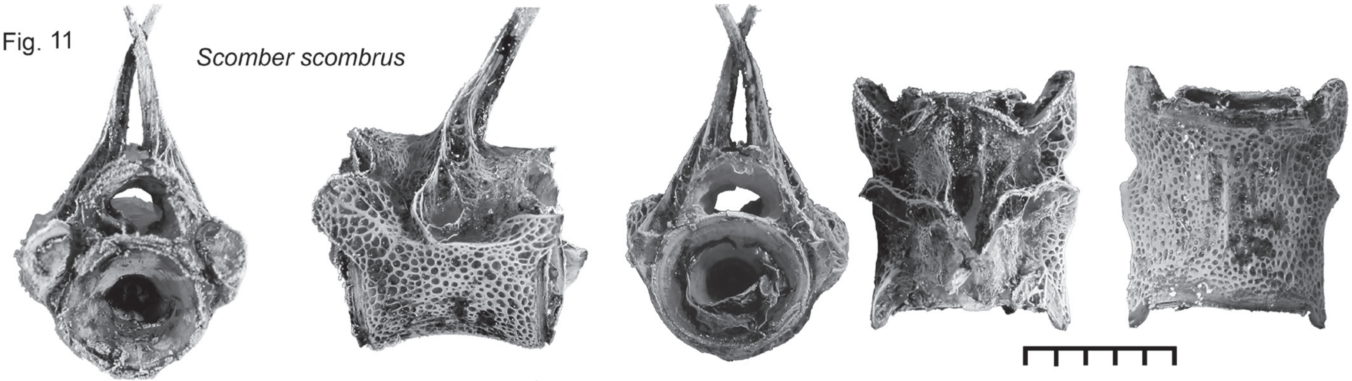
c. Scombridae – *Scomber* sp. (UAMZ F4886, Plate 4, Fig. 13). Although we are unsure of the specific identity of this specimen, we include it as it shows great similarity with *Scomber scombrus*, but is significantly different from that species, thus documenting some of the range of variation in the genus. The neural arch is fused to the centrum. The exoccipital facets are fairly small, oval, positioned dorsolaterally and oriented anteromedially. The anterior facet is sub-circular, being flattened on either side where it meets the exoccipital facets, and oriented anteriorly. The posterior facet is circular and of similar size to the anterior one. The centrum is longer than high and has equal dorsal and ventral lengths (i.e., it is rectangular in lateral view). The lateral and ventral sides of the centrum have a finer network of bone than in *Scomber scombrus*, and this bone texture is prominent on all surfaces of the centrum and neural arch. There are no large pits on the dorsal or ventral surface of the centrum. There is a lateral pit on the side of the neural arch. There is no strong lateral ridge as in *S. japonicus*. This specimen is more similar to *S. scombrus* (rather than *S. japonicus*) and could be conspecific with the differences seen being caused by individual variation.

d. Scombridae – *Rastrelliger brachysoma* (UAMZ AM10, Plate 4, Fig. 14) is found in the Pacific Ocean from Southeast Asia to Australia, although it may enter brackish water. The neural arch is fused to the centrum. The arch is restricted in width between the exoccipital facets, but expands laterally behind the facets. There is a second opening above the arch formed by the bases of the neural spine being separated from one another. The anterior and posterior facets are circular and of equal size, and both are oriented vertically. The centrum is strongly constricted in the middle portion between the anterior and posterior facets. The notochordal foramen is positioned just above the midpoint on both anterior and posterior facets. The round exoccipital facets are widely separated, positioned almost level with the dorsal surface of the centrum, and oriented anteromedially. They project farther anteriorly than the anterior facet of the centrum. The bone texture is almost smooth on the lateral surface of the centrum, but flattened ridges surrounding small cells are more distinct on the ventral and dorsal surfaces, as well as on the neural arch. There are no large pits on the dorsal and ventral surfaces, but a deep depression is present on the lateral side of the centrum, below a lateral flange. The large transverse processes project posteriorly and have a flattened dorsal surface for articulation of the anterior extensions of the neural arch of the following centrum. The centrum is only slightly longer than high.

Family 11. Pomatomidae – *Pomatomus saltatrix* (ROM R.5161, Plate 5, Fig. 15) occasionally enters brackish waters. It is wide-spread in tropical and subtropical waters of the Atlantic, Indian, and southwest Pacific oceans. The neural arch is autogenous. The large exoccipital facets are positioned laterally, oriented anterodorsally, and extend over the dorsal surface of the centrum to meet in the midline anteriorly. They are irregular, between circular and square in shape. The anterior articular facet is circular and oriented anteroventrally; it is slightly smaller than the circular posterior facet. The anterior facet is angled so that the centrum is slightly shorter along the ventral surface than the dorsal in lateral view. The bone texture is formed of thick ridges interspersed with more numerous thin ridges that define small pits of cells. The texture on the dorsal half of the lateral surface has a more open network. There is a single, deep dorsal concavity on the centrum. There are no pits on the ventral surface but there is a medial depression. The transverse processes are oriented posteriorly, and positioned at about the midpoint of the vertical height of the centrum. The centrum length and height are roughly equal.

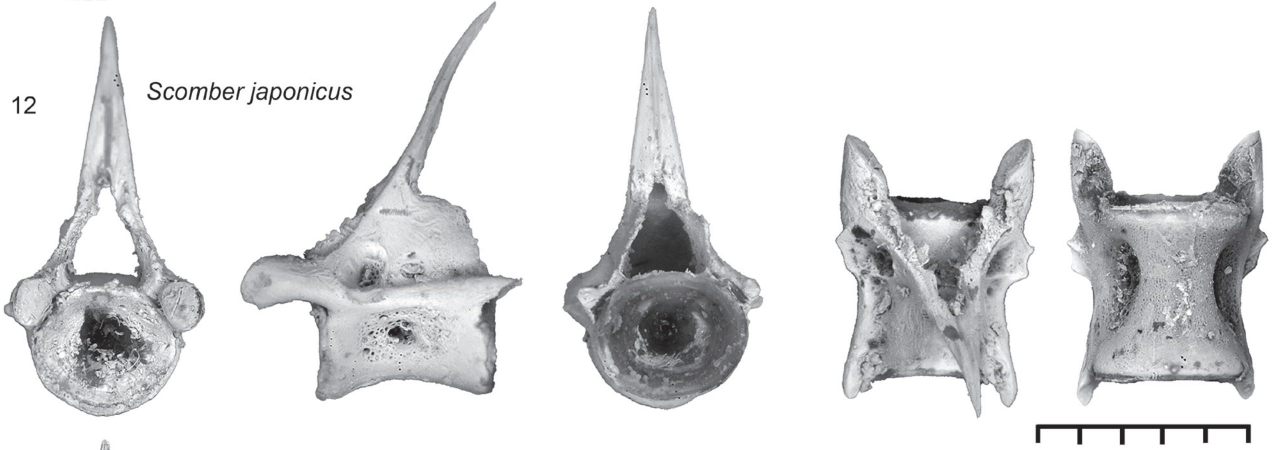
Family 12. Stromateidae – *Pampus argenteus* (UAMZ F8924, Plate 5, Fig. 16) is found in the Indo-West Pacific. Our specimen seems somewhat deformed in that it is not bilaterally symmetrical; however, details can still be determined. The neural arch is autogenous. The exoccipi-

Fig. 11



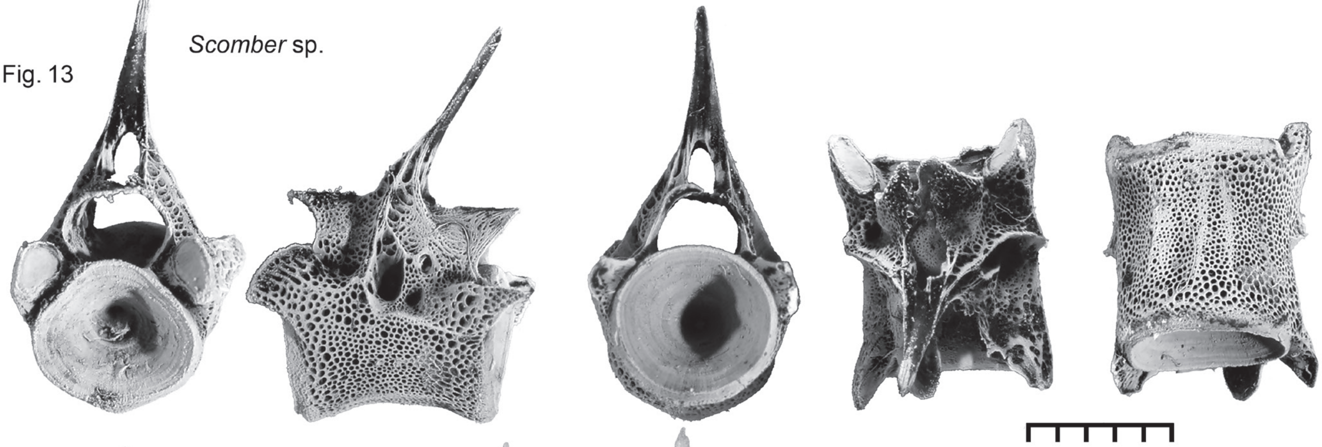
Scomber scombrus

Fig. 12



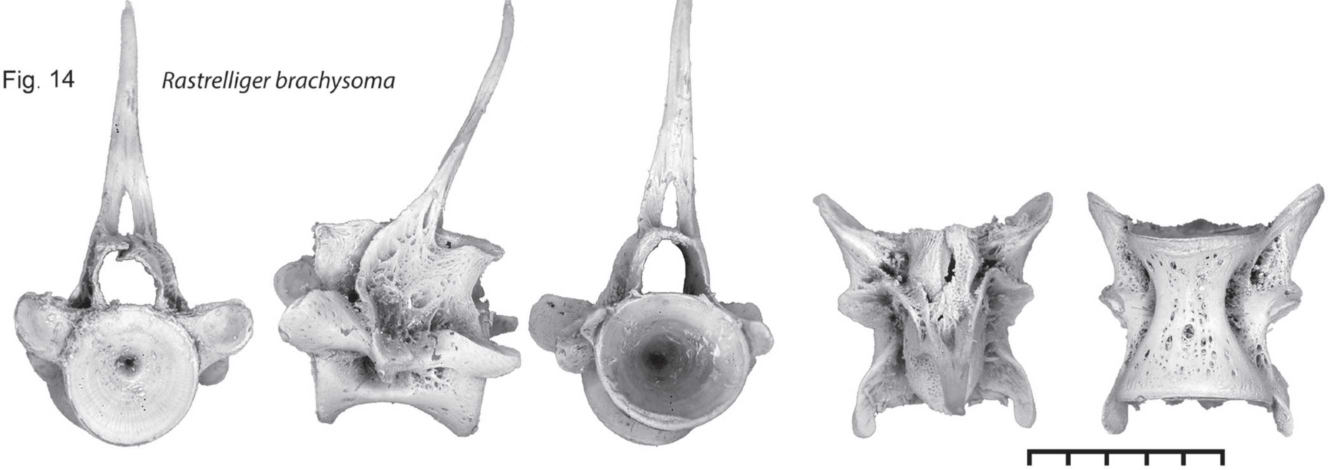
Scomber japonicus

Fig. 13



Scomber sp.

Fig. 14



Rastrelliger brachysoma

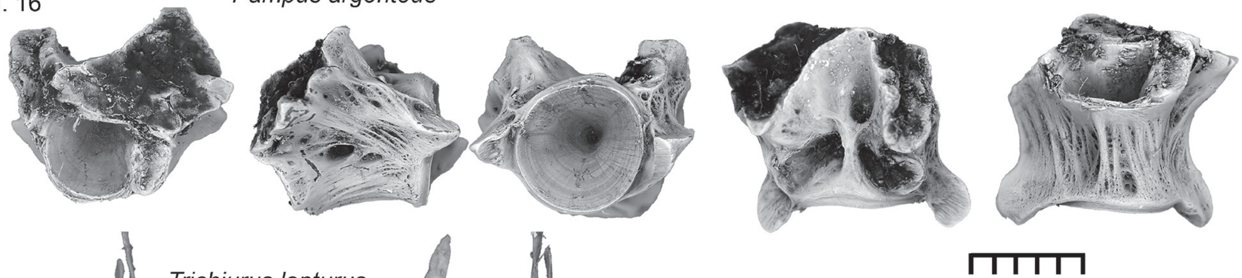
(Opposite page) Plate 4. First centrum of Acanthopterygii – Scombriformes (Scombridae) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 11. Scombriformes: Scombridae: *Scomber scombrus*, UAMZ DB13
Figure 12. Scombriformes: Scombridae: *Scomber japonicus*, UAMZ F8901.
Figure 13. Scombriformes: Scombridae: *Scomber* sp., UAMZ F4886.
Figure 14. Scombriformes: Scombridae: *Rastrelliger brachysoma*, UAMZ AM10.

Plate 5. First centrum of Acanthopterygii – Scombriformes (Pomatomidae, Stromateidae and Trichiuridae) and Syngnathiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 15. Scombriformes: Pomatomidae: *Pomatomus saltatrix*, ROM R.5161.
Figure 16. Scombriformes: Stromateidae: *Pampus argenteus*, UAMZ F8924.
Figure 17. Scombriformes: Trichiuridae: *Trichiurus lepturus*, UAMZ AM6.
Figure 18. Syngnathiformes: Mullidae: *Mullus surmulentus*, ROM R.5316.

Fig. 15

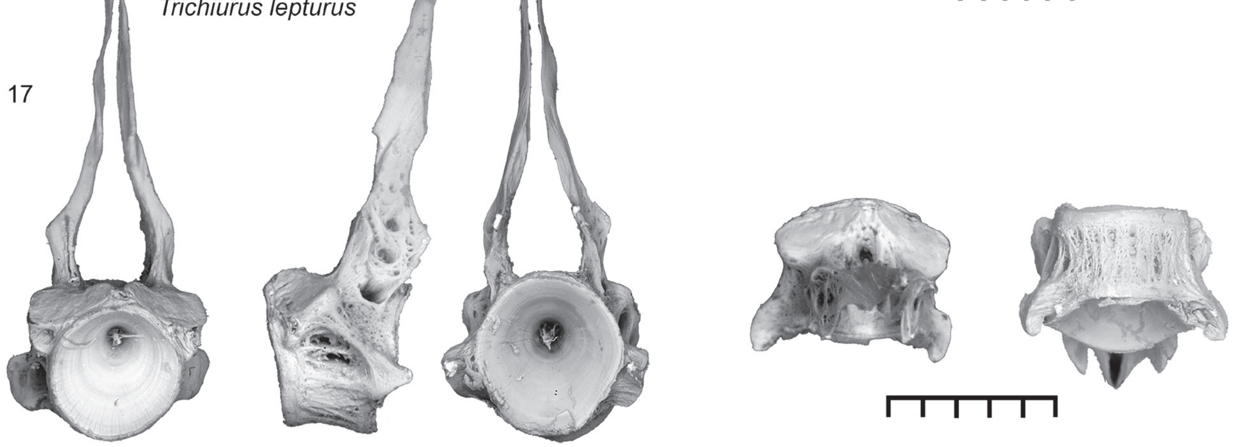
Pomatomus saltatrix

Fig. 16



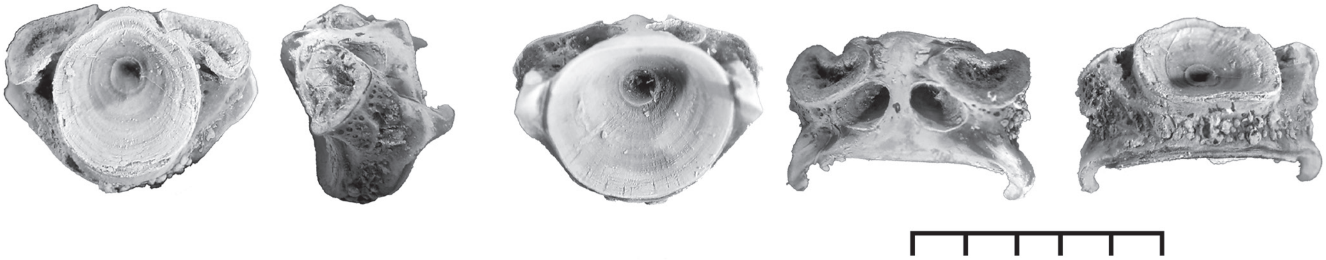
Pampus argenteus

Fig. 17



Trichiurus lepturus

Fig. 18



Mullus surmuletus

tal facets are very large compared to the anterior facet, positioned dorsally, and meet one another in the midline anteriorly. They are oriented more dorsally than anteriorly. The anterior and posterior articular facets are circular and almost vertical such that the centrum is only slightly shorter along the ventral surface than the dorsal surface in lateral view. There is a small pit on the left lateral surface but none on the right and the surrounding bone is mostly smooth with numerous striations but no deep cells. The transverse processes are oriented posterolaterally, and are positioned on the posterodorsal portion of the centrum. The dorsal surface of the centrum bears a single median pit anteriorly, and a pair of pits posteriorly (for the neural arch). The ventral surface of the centrum has no large pits, but the bone texture is striated. The length and height of the centrum are roughly equal, although the exoccipital facets extend dorsally above the surface of the centrum.

Family 13. Trichiuridae – *Trichiurus lepturus* (UAMZ AM6, Plate 5, Fig. 17) inhabits tropical and warm temperate marine and brackish coastal waters globally. The neural arch is fused to the centrum, but the two halves of the neural spine are not fused. The anterior and posterior facets are sub-circular to drop-shaped, with the anterior one slightly smaller and the notochordal foramen positioned more dorsally on the anterior facet. The exoccipital facets are sub-circular to kidney bean-shaped, oriented dorsally, separated from one another only by a small gap, and at the level of the dorsal surface of the centrum. They do not extend anteriorly past the level of the anterior facet, but overlie almost half of the dorsolateral surface of the centrum, restricting the neural arch to the posterior half of the centrum. The bone texture varies. On the lateral surface it is formed by roughly parallel ridges interconnected by smaller ridges and there are pits below the exoccipital facet. On the ventral surface, it has a more honeycomb texture. There is a single, large, median pit on the dorsal surface but none on the ventral or lateral surfaces. The anterior facet is only slightly inclined and the centrum height is only slightly greater than the length, such that the centrum is almost square in lateral view. The transverse processes are below midheight of the centrum, oriented posteroventrally, and quite broad.

Order 9. Syngnathiformes – the pipefishes and seahorses are predominantly marine fishes found in temperate and tropical waters with some species ranging into cooler waters and a few restricted to fresh water (Nelson et al. 2016). The first few anterior vertebrae are elongated compared to those in the rest of the column (e.g., Cantalice and Alvarado-Ortega 2016; Murray 2022), or fused to form a long bony structure (Aulostomidae). Because they are so distinct, we do not include them here. The suborder Mulloidei is included in Syngnathiformes by Betancur-R et al. (2017).

Family 14. Mullidae – *Mullus surmulentus* (ROM R.5316, Plate 5, Fig. 18) inhabits the eastern Atlantic Ocean, as well as the Mediterranean and Black seas. The neural arch is autogenous. The triangular to kidney bean-shaped facets for articulation with the exoccipitals are positioned laterally but do not protrude above the dorsal surface of the centrum and are well separated from one another in dorsal view. In lateral view, these facets are in line with the anterior articular facet for the basioccipital, not extending farther forward. The anterior facet is oval and curved such that only the dorsal part faces slightly anteroventrally while the rest faces anteriorly. The posterior facet is broader and more rounded than the anterior one. The centrum is short, being about twice as high as it is long. The lateral and ventral surfaces are ornamented with small protruding bumps, and the ventral edge is about one third shorter than the dorsal edge. There are two large, oval pits on the dorsal surface for the neural arch, but no pits on the ventral surface. The small transverse processes are positioned dorsal to the middle of the vertical height of the centrum and are hooked medially.

Order 10. Synbranchiformes – the swamp eels are found in tropical and subtropical fresh water (rarely brackish or marine) and are represented by two suborders. The only family in the suborder Synbranchoidei (Synbranchidae) is noted as having a first vertebra with lateral flanges and an articular plug fused to the centrum (Nelson et al. 2016) to create an opisthocoelic vertebra.

Family 15. Synbranchidae – *Monopterus alba* (ROM R.5206, Plate 6, Fig. 19) is found in Asia. The neural arch is fused to the centrum, and does not project laterally beyond the centrum body. The neural arch bears fairly large accessory processes posteriorly. The first centrum is opisthocoelus. The oval exoccipital facets are oriented dorsally, and are positioned well behind the anterior extent of the anterior facet. The posterior facet is circular and although there is no notochordal foramen, the deepest point of the concavity (where the foramen is normally located) is below the midpoint of the facet. The centrum is longer than tall, with a bone texture that is formed by ridges defining shallow irregular cells that are more oval than circular. There are no large pits on the dorsal, lateral or ventral surfaces. The transverse processes are located above midheight on the centrum, with pointed tips projecting posterolaterally terminating just past the posterior facet. The posterior accessory processes of the neural arch extend farther posteriorly.

Order 11. Anabantiformes – includes fishes that have a suprabanchial or labyrinth organ that allows air-breathing. These are the anabantoids (climbing gouramies, kissing gouramies, gouramies, and fighting fishes), nandoids (leaffishes), and channoids (snakeheads). The first centrum in at least some channoids has ventral accessory processes projecting posteriorly to overlap the centrum behind (Murray 2012).

Fig. 19 *Monopterus alba*

Fig. 20 *Channa striata*

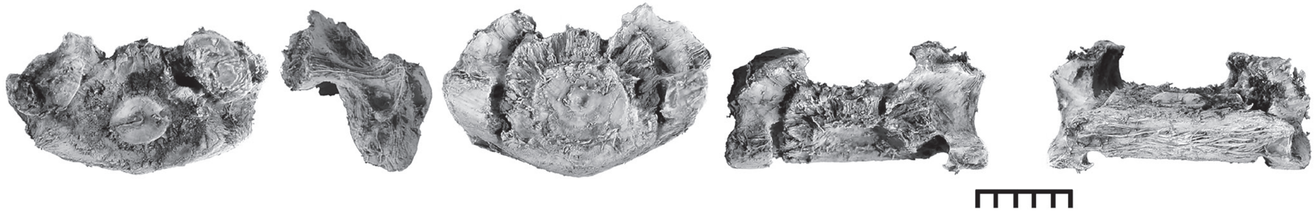


Fig. 21 *Channa micropeltes*

Fig. 22 *Parachanna obscura*

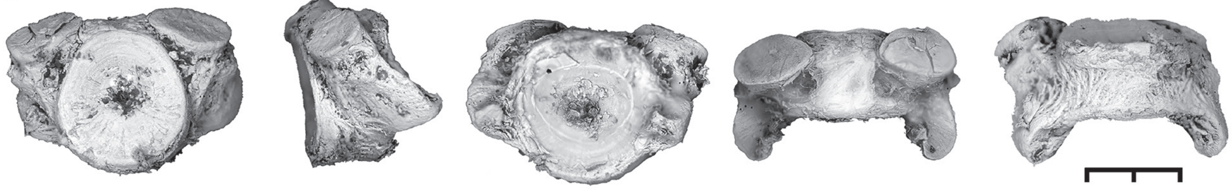


Fig. 23 *Anabas testudineus*

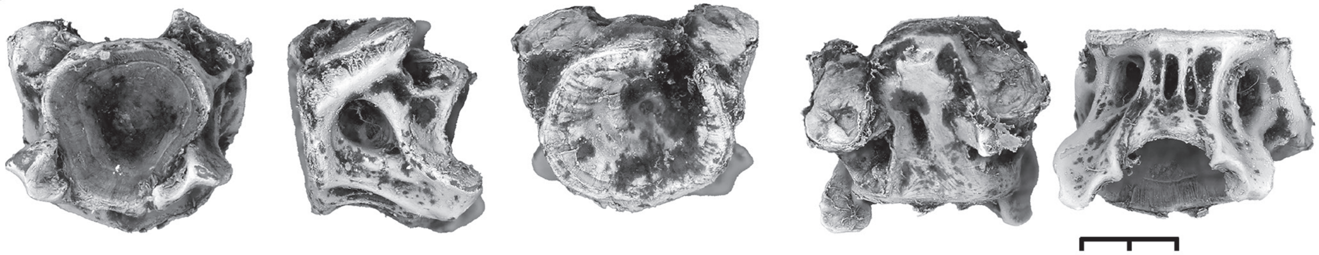


Plate 6. First centrum of Acanthopterygii – Syngnathiformes, Synbranchiformes, and Anabantiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.

Figure 19. Synbranchiformes: Synbranchidae: *Monopterus alba*, ROM R.5206.
Figure 20. Anabantiformes: Channidae: *Channa striata*, UAMZ DB16.
Figure 21. Anabantiformes: Channidae: *Channa micropeltes*, ROM R.5226.
Figure 22. Anabantiformes: Channidae: *Parachanna obscura*, UAMZ #1.
Figure 23. Anabantiformes: Anabantidae: *Anabas testudineus*, UAMZ #x.

Family 16. Channidae – is native to fresh waters of Asia (genus *Channa*) and Africa (genus *Parachanna*). The neural arch is autogenous. There is no ventral pit on the centrum. The large, robust transverse processes extend well behind the centrum.

a. Channidae – *Channa* spp. The centrum is strongly compressed into a disk, with the anterior facet being quite flat, not concave. The facets for the exoccipitals are oval, well separated from one another, and positioned dorsally on the centrum. The transverse processes extend from the midheight of the centrum. The two species presented here differ in whether or not the neural arch is autogenous.

b. Channidae – *Channa striata* (UAMZ DB16, Plate 6, Fig. 20). The neural arch is fused to the centrum, but in the specimen illustrated the arch has been broken off. The exoccipital facets extend well out in front of the anterior facet. They are oriented anteriorly, as is the facet for the basioccipital, but extend farther anterior than the anterior facet so as to form a right angle between the facets for the exoccipitals and that for the basioccipital. The bone texture is fairly smooth with ridges present but no deep spaces between them; the ridges have a tightly woven appearance on the lateral and ventral surfaces. There are no pits on the dorsal or ventral surfaces but a large round pit is located laterally. The transverse processes are short, positioned dorsally, and extend posteriorly.

c. Channidae – *Channa micropeltes* (ROM R.5226, Plate 6, Fig. 21). The neural arch is autogenous. The anterior facet is relatively larger than that of *C. striata*, and the exoccipital facets are relatively lower but still extend above the dorsal surface of the centrum. They do not extend as far anteriorly as those of *C. striata*. The posterior facet is square, slightly larger than the anterior facet; the anterior facet is flat and the posterior one is concave with the concavity deeper than that of *C. striata*. The centrum is short, but not as compressed as in *C. striata*. The bone texture is formed of bundles of ridges; there are no lateral or ventral pits. The pits for the neural arch are small, deep, round and well separated from one another. The transverse processes are longer than those of *C. striata*, and more strongly hooked.

d. Channidae – *Parachanna obscura* (UAMZ #1, Plate 6, Fig. 22). The neural arch is autogenous. The facets for the exoccipitals are rounder than those of *Channa* spp, and oriented more anterodorsally, positioned more or less flush with the dorsal and anterior surfaces of the centrum. They do not extend anteriorly as do those of *Channa striata*. The anterior facet is oval but nearly circular and slightly smaller than the posterior articular facet. The centrum is about twice as high as it is long, with dorsal and ventral lengths being equal. The transverse processes are positioned below the vertical midheight, and are robust, rounded, and project posteriorly. There are no pits on the lateral, or ventral surfaces. The deep, round neural arch pits are closer together than in *Channa micropeltes*. The bone texture is formed by tightly woven ridges with no cells or pits between them.

Family 17. Anabantidae – *Anabas testudineus* (UAMZ #x, Plate 6, Fig. 23) is found in fresh waters of India, China and Southeast Asia. The neural arch on the first centrum is autogenous. The facets for the exoccipitals are roughly round, and well separated.They are located flush with the dorsal surface of the centrum, and oriented almost dorsally. The anterior articular facet is an irregular shape, roughly circular or square, with a fluted edge. The posterior articular facet is more circular, but pinched in between the transverse processes. The bone texture is smooth, with large pits on the lateral, dorsal and ventral surfaces. The transverse processes are positioned low on the centrum, and are robust and rounded. The centrum is about as long as it is high (i.e., not compressed or disk-like), and the anterior articular facet faces vertically such that dorsal and ventral lengths of the centrum are equal. There is a single, median, large pit on the ventral surface, one or more enlarged pits laterally, and a single median pit dorsally in addition to the funnel-shaped paired pits for the neural arch.

Carangaria order incertae sedis – this non-monophyletic assemblage of Betancur-R et al. (2017), includes three orders (Carangiformes, Istiophoriformes, and Pleuronectiformes) as well as several families left as order incertae sedis – Centropomidae, Sphyraenidae, Toxotidae, Leptobramidae, Polynemidae, Menidae and Lactariidae. The family Latidae is included in Centropomidae by Betancur-R et al. (2017), which follows earlier ideas of relationship between these two groups (e.g., Greenwood 1976).

Family 18. Menidae – the placement of this family, with a single species *Mene maculata*, is uncertain. It has been given

(Opposite page) Plate 7. First centrum of Acanthopterygii – Carangaria order incertae sedis, and Carangiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 24. Carangaria: Menidae, *Mene maculata*, UAMZ AM8.
Figure 25. Carangaria: Centropomidae: *Centropomus undecimalis*, ROM R.6579.
Figure 26. Carangaria: Centropomidae: *Lates calcarifer*, UAMZ DB2.
Figure 27. Carangaria: Centropomidae: *Lates niloticus*, UAMZ DB2.
Figure 28. Carangiformes: Carangidae: *Trachinotus carolinus*, UAMZ AM12.
Figure 29. Carangiformes: Carangidae: *Parastromateus niger*, UAMZ F8903.

Fig. 24 *Mene maculata*

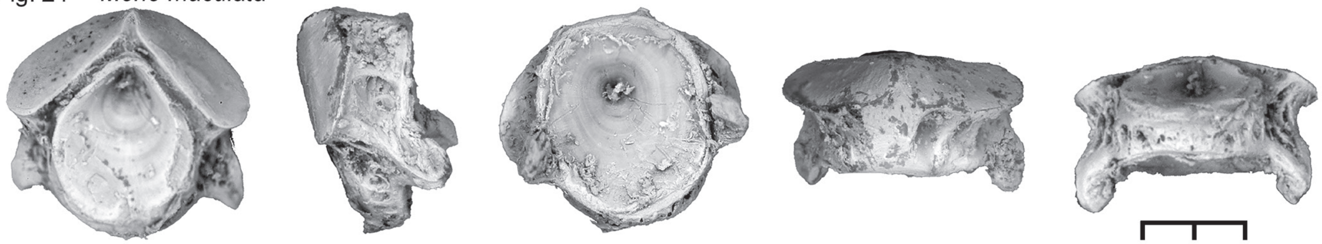


Fig. 25 *Centropomus undecimalis*

Fig. 26 *Lates calcarifer*

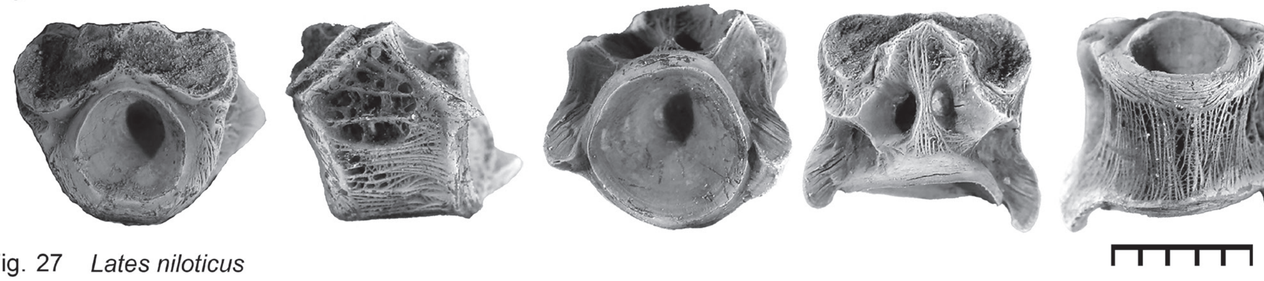
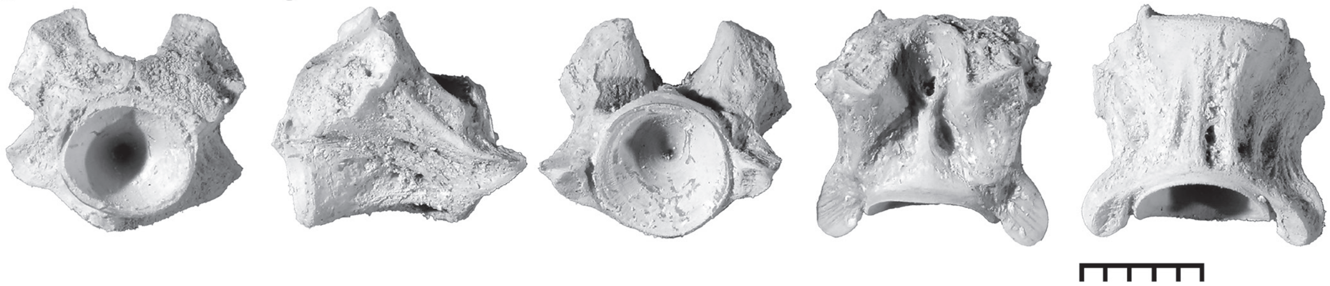


Fig. 27 *Lates niloticus*

Fig. 28 *Trachinotus carolinus*

Fig. 29 *Parastromateus niger*



its own order Meniformes (e.g., Springer and Johnson 2004) or has been placed in Carangiformes (Nelson et al. 2016). Betancur-R et al. (2017) left Menidae as order incertae sedis within their Carangaria, as followed here.

a. Menidae – *Mene maculata* (UAMZ AM8, Plate 7, Fig. 24) is found in marine and brackish coastal waters of the Indo-West Pacific including Southeast Asia and the east coast of Africa. The dorsal half of the anterior facet is strongly constricted by the exoccipital facets, forming a tear drop-shaped facet. The posterior facet has flattened edges, making it round to square in shape. The notochordal foramen is located dorsally in the anterior facet, but closer to the midpoint in the posterior facet. The anterior facet is oriented slightly anteroventrally, so the centrum forms a wedge in lateral view. The exoccipital facets are large, oval, and oriented anteriorly; they are only slightly smaller than the anterior facet. The transverse processes, located below midheight of the centrum, are short, rounded, and extend posteriorly. The bone texture is fairly smooth, with only a few pits on the lower lateral and ventral surfaces. There are no large pits on the centrum. The height of the centrum is about four times its narrowest (ventral) length, or about twice its greatest (dorsal) length.

Family 19. Centropomidae – the composition of this family varies, but at one point it was restricted to the genus *Centropomus*, which is a marine group found in Atlantic coastal waters. Currently it includes all members previously assigned to Latidae, as subfamily Latinae (Betancur-R et al. 2017). Latines are found principally in fresh waters of Africa. The neural arch on the first centrum is autogenous. The anterior facet varies from circular to oval, with the notochordal foramen positioned dorsally. The posterior facet varies in shape but is larger than the anterior facet. The large exoccipital facets are kidney bean-shaped, positioned high on the centrum, and meet one another in the midline, forming a tongue of bone that projects anteriorly. The facets are oriented anterodorsally. The bone texture is formed of bundles of longitudinal, thin, roughly parallel ridges with interconnecting short ridges defining small spaces. There are no large pits on the ventral surface, and the two dorsal pits for the neural arch are confined to the central portion of the centrum separated by a thick ridge. The anterior facet is vertical, with the dorsal and ventral lengths of the centrum similar, forming a rectangular centrum in lateral view.

a. Centropomidae – *Centropomus undecimalis* (ROM R.6579, Plate 7, Fig. 25) inhabits tropical and warm temperate Western Atlantic coastal waters and enters brackish and fresh waters. The anterior facet is oval, taller than wide, and narrower than the oval posterior facet. The dorsal edges of the kidney bean-shaped exoccipital facets project above the level of the dorsal surface of the centrum. The exoccipital facets are smaller in relation to the anterior facet than in the two species of *Lates*, but still large compared to many other taxa, and the tongue of bone that extends between them dorsally is relatively broader. The transverse processes are positioned below midheight of the centrum, and are larger and more medially hooked than those of *Lates* spp. Overall, this centrum is relatively taller than that of *Lates* spp., having a greater height to length ratio.

b. Centropomidae (Latidae) – *Lates calcarifer* (UAMZ DB2, Plate 7, Fig. 26) is a marine fish found in waters of the Indo-west Pacific south to Australia. The neural arch is autogenous. The left and right facets for the exoccipitals are kidney bean-shaped, broadest laterally, and the narrower medial portions of the left and right facet in broad contact in the midline. These facets extend past the dorsal surface of the centrum. The oval anterior facet for the basioccipital is oriented almost vertically. In lateral view, the dorsal edge of the centrum is only slightly longer than the ventral edge, and the length of the centrum is slightly less than its height. The bone on the lateral, ventral and dorsal surfaces of the centrum is striated, or forms small, widely-separated bundles of fibres with pits between bundles restricted to the upper lateral surface. The dorsal surface of the centrum has two oval pits (for the neural arch) separated by a triangle of striated bone depressed into a trough that projects anteriorly between the exoccipital facets. The transverse processes are positioned towards the dorsal surface of the centrum, project posteriorly, and are slightly hooked. The posterior articular facet is almost round, with a wider base than top, and slightly bigger than the anterior facet.

c. Centropomidae (Latidae) – *Lates niloticus* (UAMZ Ln4, Plate 7, Fig. 27) inhabits fresh waters of west, north and east Africa. The first centrum is similar to that of *L. calcarifer*. The neural arch of the first centrum is autogenous, the facets for the exoccipitals are of similar shape and position, but relatively larger than those of *L. calcarifer* and oriented more anteriorly, extending relatively farther above the dorsal surface of the centrum. The anterior facet is circular, and smaller than the posterior articular facet. The ventral portion of the posterior facet is much narrower than in *L. calcarifer*. The neural arch pits are relatively closer together than those of *L. calcarifer*. The bone on the lateral, ventral and dorsal surfaces is striated, but more tightly woven and with numerous small pits more visible than in *L. calcarifer*. The height and width measurements of the centrum are about equal. The slender, hooked transverse processes are located at or just above midheight, and project past the posterior facet.

Order 12. Carangiformes – these are marine fishes including the remoras, jacks, and dolphinfishes among others.

Family 20. Carangidae – Carangidae contains about 30 genera with 147 species found in the Atlantic, Indian and Pacific oceans.

a. Carangidae – *Trachinotus carolinus* (UAMZ AM12, Plate 7, Fig. 28) is found in Atlantic coastal areas of the United States and Brazil and further south, including the Gulf of Mexico. The neural arch is autogenous. The anterior and posterior facets are circular, with the posterior one slightly bigger, and the notochordal foramen positioned at about midheight. The large exoccipital condyles are semi-circular to kidney bean-shaped, with the inner concavity oriented dorsomedially, and are positioned dorsally, extending well above the dorsal surface of the centrum. The facets are oriented anterodorsally, and meet one another in the midline for a very small distance. The transverse processes are positioned just below midheight on the centrum, are broad, and extend posterolaterally; they provide dorsal articular facets for processes on the anteroventral edges of the neural arch of the following centrum. The bone surface bears widely spaced longitudinal ridges forming a network of spaces; there are no large pits on the lateral or ventral surface, and only the paired neural arch pits on the dorsal surface. These are drop-shaped, positioned towards the posterior half of the centrum, and separated by a wide ridge of bone. The anterior facet is almost vertical so that the centrum has equal dorsal and ventral lengths, and the centrum is longer than high giving it a rectangular shape in lateral view.

b. Carangidae – *Parastromateus niger* (UAMZ F8903 Plate 7, Fig. 29) is a reef fish found in Japan, Southeast Asia, Australia, India, and east coast of Africa. The neural spine is autogenous. The anterior and posterior facets are circular, about the same size as each other, and the notochordal foramen is just dorsal to the midpoint. The large exoccipital facets are located dorsal to the anterior facet and oriented almost anteriorly. They are irregular, somewhat L-shaped, being narrower medially than laterally. The anteromedial tips meet one another in the midline. There is a pair of small projections extending anteriorly from either side of the dorsal edge of the anterior facet below the edge of the exoccipital facet; these are unique among the taxa examined. The centrum is 1.3 times longer than high. The transverse processes are just below midheight, and are broadly rounded, extending posteriorly past the posterior facet. The bone texture is formed by strong ridges surrounding depressions that hold a few irregular pits on the lateral and ventral surfaces. Dorsally, the oval pits for the neural arch are positioned posteriorly, with a single median pit placed more anteriorly between the exoccipital facets.

Order 13. Pleuronectiformes – all 14 families of flatfishes have bilaterally asymmetrical bodies, but the first centrum is more or less bilaterally symmetrical as in other acanthomorphs, although the neural spine is inclined laterally. This is a predominantly marine group, with perhaps 10 species found in fresh waters (Nelson et al. 2016).

Family 21. Paralichthyidae – *Paralichthys dentatus* (CMNFI 1987-0327.1; Plate 8, Fig. 30) is found on the east coast of the United States, rarely going north into Canadian Atlantic waters. The tall, narrow neural arch is fused to the centrum. The narrow, oval exoccipital facets are positioned laterally, but oriented almost dorsally; they protrude slightly anterior to the articular facet. The anterior facet is oval and the posterior facet is more circular; the notochordal foramen is position dorsal to the midpoint of the centrum. The centrum is about twice as wide as it is long, and slightly taller than wide. There are no transverse processes. The bone texture is a fine network of longitudinal ridges connected by smaller ridges forming circular to irregular openings.

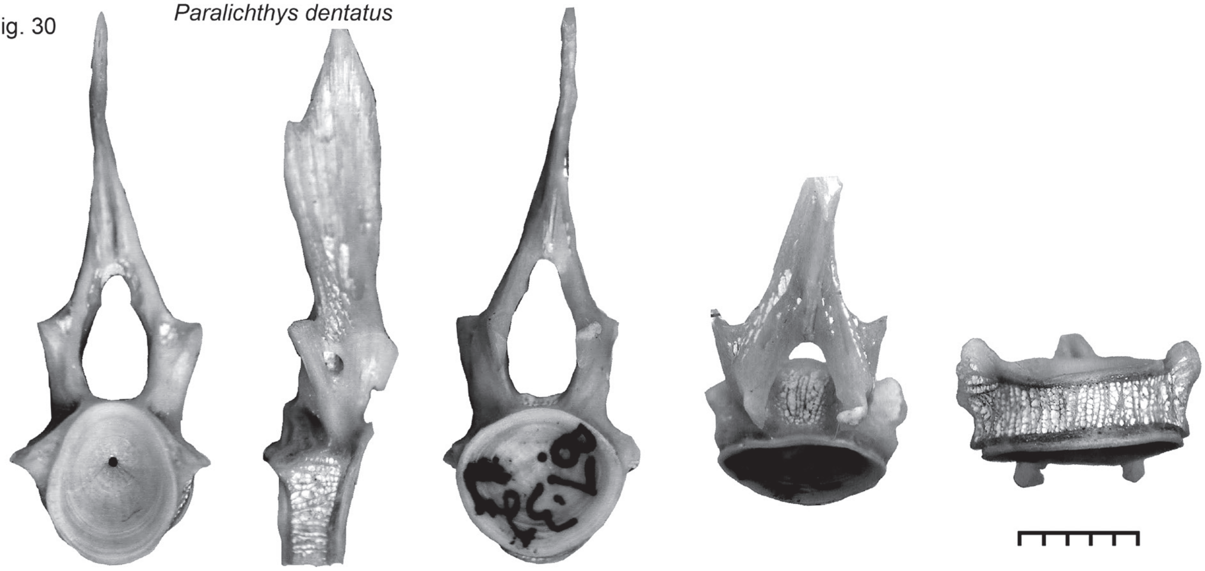
Family 22. Pleuronectidae

a. Pleuronectidae – *Microstomus pacificus* (UAMZ DB7, Plate 8, Fig. 31) is found in the eastern Pacific from Mexico to Alaska. The neural arch is fused to the centrum but broken in our specimen. The small, round to oval facets for the exoccipitals are positioned on the upper half (but below the dorsal surface) of the centrum, and widely separated from one another. They are oriented almost directly dorsally. The anterior articular facet is almost oval, being narrower at the top. The posterior articular facet is broader to become almost square in outline.The notochordal foramen is located dorsal to the midpoint. In lateral view, the length of the centrum is about one quarter the height. The bone on the lateral, dorsal and ventral surfaces of the centrum forms an open network of longitudinal ridges connected by smaller ridges of irregular orientation forming many cells. There are no transverse processes.

b. Pleuronectidae – *Pseudopleuronectes americanus* (ROM R.3240, Plate 8, Fig. 32) is found in the Western Atlantic, along the Canadian and American coasts. The neural arch is fused to the centrum. The anterior facet is similar to that of *Microstomus pacificus* but more pinched dorsally, and the notochordal foramen is located dorsal to the midpoint as in *M. pacificus*. The posterior facet is more oblong (taller than wide). The facets for articulation with the exoccipitals are a little lower on the side of the centrum compared to *M. pacificus*, and relatively larger. The dorsal length of the centrum is longer than the ventral length, giving the centrum a wedge-shape in lateral view. The centrum height is about four times greater than its length. The bone surface on the lateral, dorsal and ventral sides of the centrum is woven a little tighter than in *M. pacificus*. There are no transverse processes.

Family 23. Scophthalmidae – *Scophthalmus aquosus* (CMNFI 1986-0090.1; Plate 8, Fig. 33) is found in coastal

Fig. 30

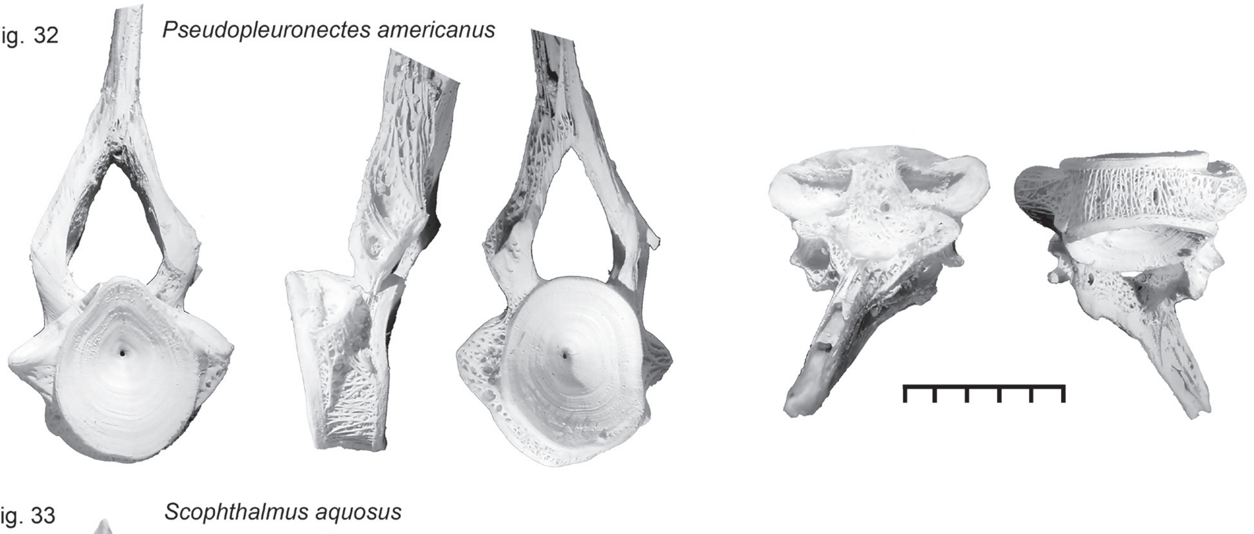


Paralichthys dentatus

Fig. 31

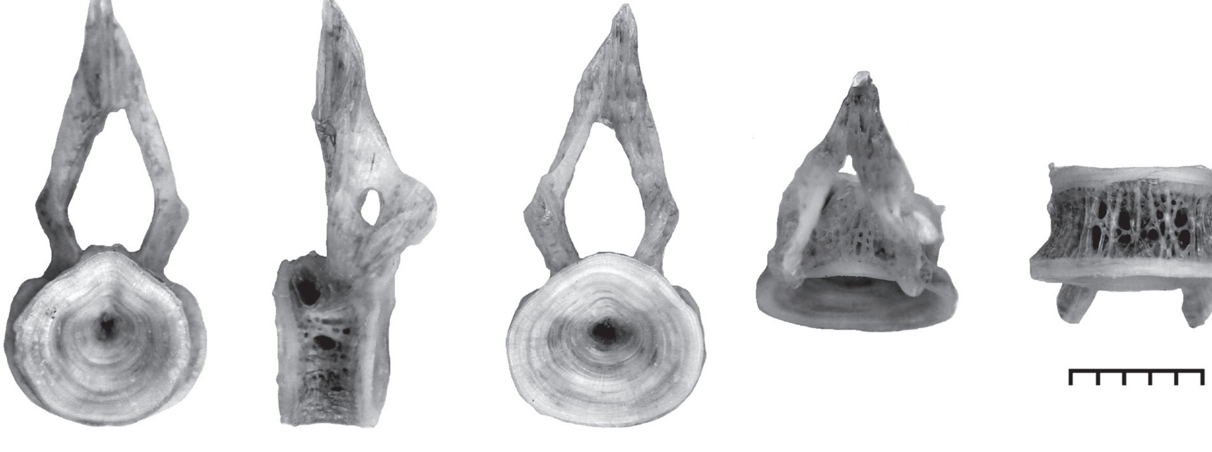
Microstomus pacificus

Fig. 32



Pseudopleuronectes americanus

Fig. 33



Scophthalmus aquosus

(Opposite page) Plate 8. First centrum of Acanthopterygii – Pleuronectiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 30. Pleuronectiformes: Paralichthyidae: *Paralichthys dentatus,* CMNFI 1987-0327.1
Figure 31. Pleuronectiformes: Pleuronectidae: *Microstomus pacificus*, UAMZ DB7 (note: the neural arch and spine are broken).
Figure 32. Pleuronectiformes: Pleuronectidae: *Pseudopleuronectes americanus*, ROM R.3240.
Figure 33. Pleuronectiformes: Scophthalmidae: *Scophthalmus aquosus,* CMNFI 1986-0090.1.

waters of the Western Atlantic from Florida, USA to the Gulf of St. Lawrence. The fused neural arch is tall, but the neural spine is relatively shorter than in the other examined material. The anterior facet is more circular than the other flatfishes, and is similar in size and shape to the posterior facet. The small, oval exoccipital facets are positioned on the dorsal sides of the centrum, and oriented dorsally. There are no transverse processes. The bone texture is similar to the other flatfishes, but the cells are relatively larger.

Order 14. Cichliformes – The family Cichlidae has been removed from its long association with the Labroidei and given its own order (e.g., Betancur-R et al. 2017). The family contains over 200 genera and an estimated more than 1700 species, predominantly inhabiting fresh water, but some species are occasionally found in brackish waters. The subfamily Etroplinae is found in Madagascar, India and Sri Lanka, and subfamily Pseudocrenilabrinae contains all the genera native to Africa.

Family 24. Cichlidae – the first vertebra in cichlids is quite variable. The neural arch is fused to the centrum (although the arch and spine are broken in two of our figured specimens). The anterior facet for articulation with the basioccipital varies in size and shape, and the facets for articulation with the exoccipitals also vary in placement and orientation; however, the anterior facet is oriented anteroventrally such that the centrum is wedge-shaped in lateral view. There are no large pits on the lateral or ventral surfaces; pits may or may not be present on the dorsal surface of the centrum. The bone texture is an open network of cells or small pits between the ridges of bone.

a. Cichlidae, Etroplinae – *Paretroplus menarambo* (UAMZ F9051, Plate 9, Fig. 34) is found in the Sofia River basin of Madagascar. The semicircular to triangular exoccipital facets are oriented almost directly dorsally, and do not meet one another in the midline. The anterior facet is sub-circular, and oriented anteroventrally, with the centrum having a shorter ventral length than dorsal, such that the centrum is slightly wedge-shaped in lateral view. The circular posterior facet is larger than the anterior facet. The bone texture is smoothly ridged with many small depressions (not as deep as cells or pits). There is a pair of large pits on the dorsal surface of the centrum between the neural arch articulations, and a smaller deep pit anterior to these in the midline. There are no lateral or ventral pits. The neural arch is broad at its base, with pointed lateral expansions that extend past the exoccipital facets. The transverse processes are located below midheight, are broadly rounded and project posteriorly.

b. Cichlidae, Pseudocrenilabrinae – *Tyrannochromis nigriventer* (UAMZ AM2, Plate 9, Fig. 35) is a piscivore endemic to Lake Malawi, Africa, where it inhabits shallow water rocky areas. The anterior facet of the first centrum is constricted dorsally by the exoccipital facets. The notochordal foramen is located dorsally in the anterior facet, and centrally in the posterior facet. The posterior facet is sub-circular, having a flattened dorsal margin. The exoccipitals facets are oriented anterodorsally, well separated, and oval in shape. The ventral length is slightly shorter than the dorsal length of the centrum, such that the centrum is a blocky wedge in lateral view. The neural arch is fairly broad at its base, and extends laterally to a pointed tip. There is a posterior median expansion hooking ventrally on each side of the neural arch. The transverse processes are above midheight of the centrum, and project posteriorly, before hooking medially. There are no lateral pits, but two ventral pits are present and a central, circular pit is present dorsally. The bone texture is fairly smooth.

c. Cichlidae, Pseudocrenilabrinae – *Cyphotilapia frontosa* (UAMZ F8936, Plate 9, Fig. 36) is a rock-dwelling omnivorous fish endemic to the northern part of Lake Tanganyika in Africa. The anterior facet is circular and small, about the same size as the exoccipitals facets, and oriented anteroventrally. The circular posterior facet is about twice as large as the anterior facet, with the notochordal foramen located dorsal to the midpoint. The exoccipital facets are kidney bean-shaped, with the concave edge facing posteriorly. These facets are oriented anterodorsally, and are close to one another but do not meet in the midline. There are no pits on the dorsal, ventral or lateral surfaces and the bone texture is smoother than in the other cichlids, with broad, flat expanses of bone and only a few small pits particularly on the ventral surface. The neural arch is broad at its base and the rounded sides extend laterally past the exoccipital facets. The transverse processes are below midheight and angle posteroventrally.

Order 15. Mugiliformes – this order, containing a single family (Mugilidae, with ~20 genera and ~150 species) has a history of being difficult to place taxonomically (Stiassny 1992; see summary in Nelson et al. 2016). Species are found in fresh, brackish and marine coastal waters.

Fig. 34 *Paretroplus menarambo*

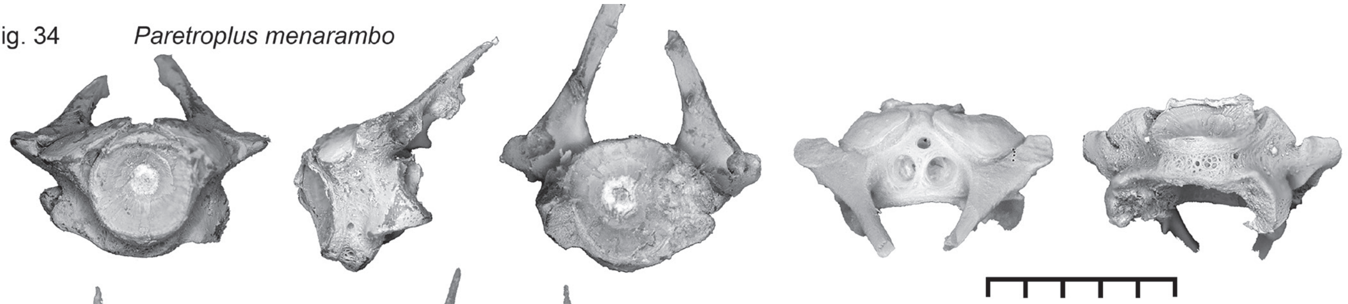


Fig. 35 *Tyrranochromis nigriventer*

Fig. 36 *Cyphotilapia frontosa*

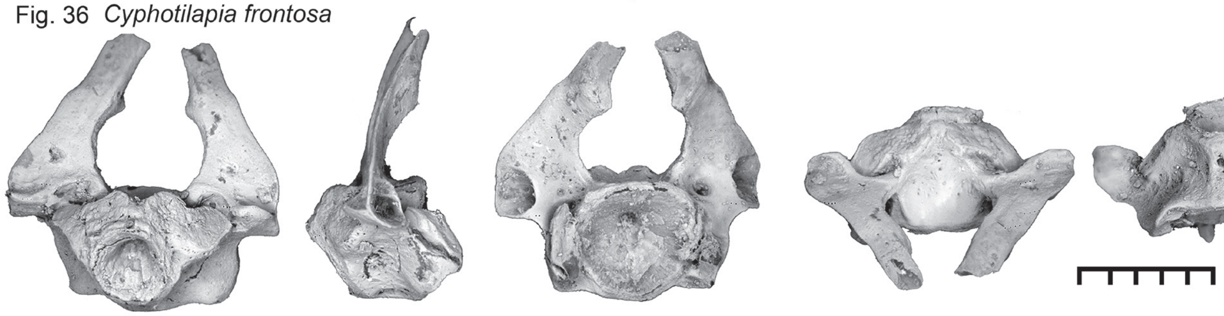


Fig. 37 *Mugil cephalus*

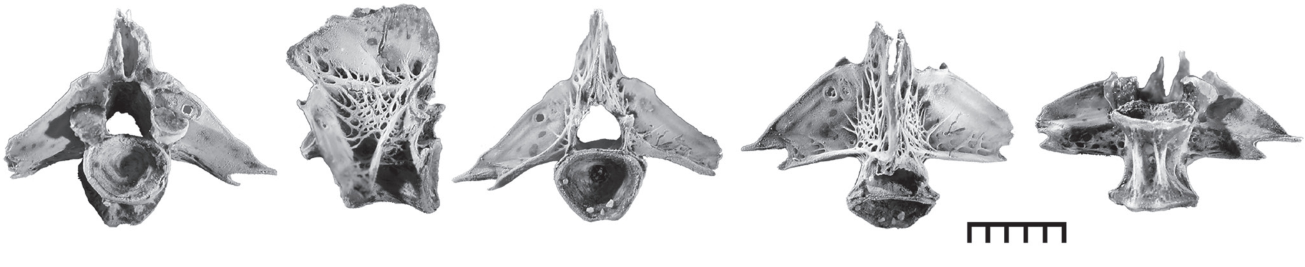


Plate 9. First centrum of Acanthopterygii – Cichliformes and Mugiliformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 34. Cichliformes: Cichlidae: *Paretroplus menarambo*, UAMZ F9051.
Figure 35. Cichliformes: Cichlidae: *Tyrannochromis nigriventer*, UAMZ AM2. The dorsal view is tipped up anteriorly to show the bone under the arch.
Figure 36. Cichliformes: Cichlidae: *Cyphotilapia frontosa*, UAMZ F8936.
Figure 37. Mugiliformes: Mugilidae: *Mugil cephalus*, UAMZ DB9.

Family 25. Mugilidae – *Mugil cephalus* (UAMZ DB 9; Plate 9, Fig. 37) is found in tropical, subtropical and temperate coastal waters globally. In keeping with its history of taxonomic uncertainty, the first centrum of this species is unlike any others we examined. The neural arch is fused to the centrum, and expands laterally into large triangular wings. The arch extends almost the whole length of the centrum. The facets for the exoccipitals are round, positioned on the dorsal surface of the centrum, and widely separated from one another. They are oriented anterodorsally. The anterior articular facet is subcircular but the posterior facet is almost triangular, narrowing ventrally. The anterior facet is slightly angled, such that the ventral length of the centrum is shorter than the dorsal length in lateral view. The centrum is about 1.5 times longer than high. The bone on the lateral, dorsal and ventral surfaces of the centrum is more or less smooth, with a large depression or pit laterally, and a deep, elongate median pit ventrally. The sides of the neural arch and expanded wings bear a network of bone. There are no transverse processes.

Order 16. Labriformes – the wrasses and their relatives are grouped based on the morphology of the pharyngeal jaws. The family Cichlidae has been removed from this order and given its own order (e.g., Betancur-R et al. 2017).

Family 26. Labridae

a. Labridae – *Halichoeres radiatus* (ROM R.2216; Plate 10, Fig. 38) is a marine and brackish water reef fish of the Western Atlantic Ocean, found from the southern USA through the Caribbean and Gulf of Mexico to Brazil. The neural arch on the first centrum is autogenous. The facets for articulation with the exoccipitals are triangular to oblong, positioned near the upper half of the centrum to reach the dorsal surface, and oriented anterodorsally. The facets are retracted posteriorly so that they are slightly posterior to the anterior articular facet; this is unique among the examined material. The anterior facet is oval (taller than wide) and oriented anteriorly (vertical in lateral view). The notochordal foramen is dorsal to the midpoint. The oval posterior articular facet is broader than the anterior facet. The dorsal and ventral lengths of the centrum are equal so that the centrum is rectangular in lateral view. The centrum is short, being about three times higher than long. The network of ridges in the bone on the lateral, dorsal and ventral sides of the centrum is tightly packed such that the bone is mostly smooth, with a few spaces between ridges. There is a single pair of large oval pits (for the neural arch) on the dorsal surface of the centrum, and no large lateral or ventral pits. The robust, large transverse processes project from the ventral edge of the centum and hook dorsally; this is unique among examined material.

b. Labridae – *Tautoga onitis* (CMNFI Z000339; Plate 10, Fig. 39) is found in Atlantic coastal waters off Nova Scotia, Canada south to South Carolina, USA. The neural arch is autogenous. The oval exoccipital facets are positioned laterally, but are large and nearly meet in the midline. The anterior facet is constricted dorsally to form a broad teardrop shape. The posterior facet is slightly depressed to form a wide oval to rectangular shape. The notochordal foramen is just above midheight. The long transverse processes are oriented posteriorly and have a slight medial hook at the ends. They are positioned low on the centrum. The bone texture is a honeycomb of fairly thick ridges separating small cells. There are no large pits present except for the deep, circular, neural arch pits on the dorsal surface.

c. Labridae – *Tautogolabrus adspersus* (CMNFI 1977-0239.1; Plate 10, Fig. 40) has a similar distribution to *Tautoga onitis*, found in Atlantic coastal waters from Newfoundland, Canada to Virginia, USA. The anterior facet is oval in shape and the exoccipital facets are positioned high on the centrum. The centrum is relatively longer than that of *Tautoga onitis*, and the transverse processes are located a little higher on the centrum. The bone texture is smoother, with fewer cells particularly on the ventral surface.

Family 27. Scaridae

a. Scaridae – *Chlorurus* sp. (UAMZ AM1, Plate 10, Fig. 41) and other scarids (parrotfish) are predominantly reef fish found in the Atlantic, Indian and Pacific oceans. The neural arch is fused to the centrum. The centrum bears wings of bone extending laterally and joining with the broad transverse processes at the ventral edge of the centrum to form a projection that underlaps a similar lateral wing on the second centrum. This is unique to this family among our examined material. The anterior facet is sub-circular, being slightly pinched dorsally, and the posterior facet is circular. The notochordal foramen in slightly above the midpoint. The exoccipital facets are relatively large, round, oriented anterodorsally, and meet one another in the midline. The anterior facet is slightly inclined, creating a wedge-shaped centrum in lateral view. The bone texture on the ventral surface is formed by thick ridges separated deep spaces. On the lateral side, a deep pit is positioned above the lateral wing of bone. The transverse processes of *Chlorurus* sp. are extensions of the lateral wing and project posteriorly from the ventral area of the centrum forming long triangular processes.

b. Scaridae – *Scarus vetula* (CMNFI 1987-0312.1; Plate 10, Fig. 42) is a reef fish of the Western Central Atlantic, found in the Gulf of Mexico and Caribbean, reaching south to coastal waters of northern South America. The neural arch is fused to the centrum, and the centrum bears lateral wings of bone as in *Chlorurus* sp. The oval anterior facet is taller than wide, unlike our other scarid example, but the posterior facet is similar in being narrower ventrally

Fig. 38 *Halichoeres radiatus*

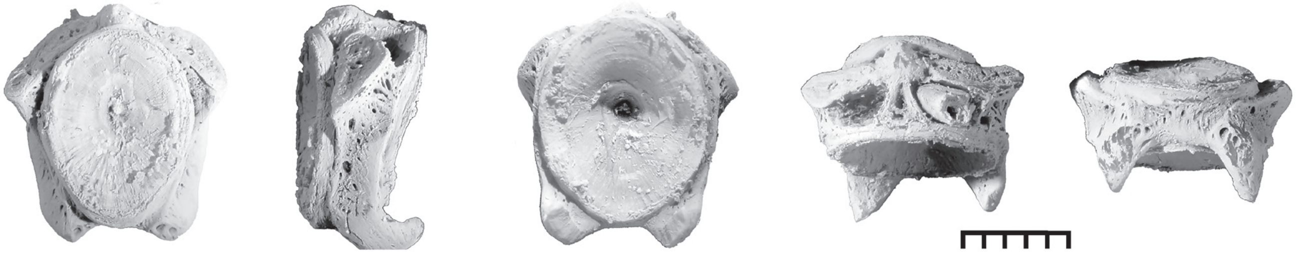


Fig. 39 *Tautoga onitis*

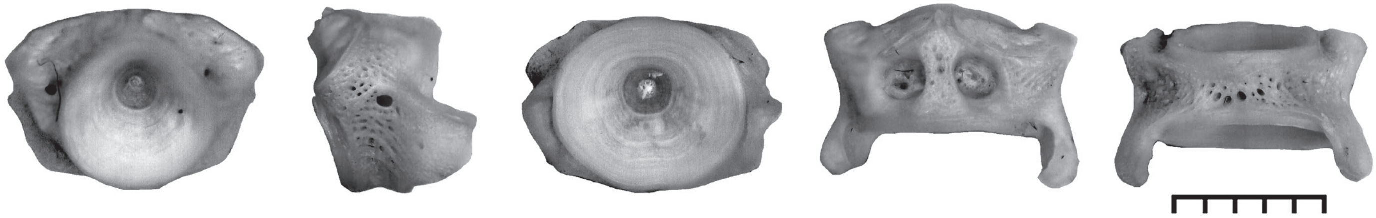


Fig. 40 *Tautogolabrus adspersus*

Fig. 41 *Chlorurus* sp.

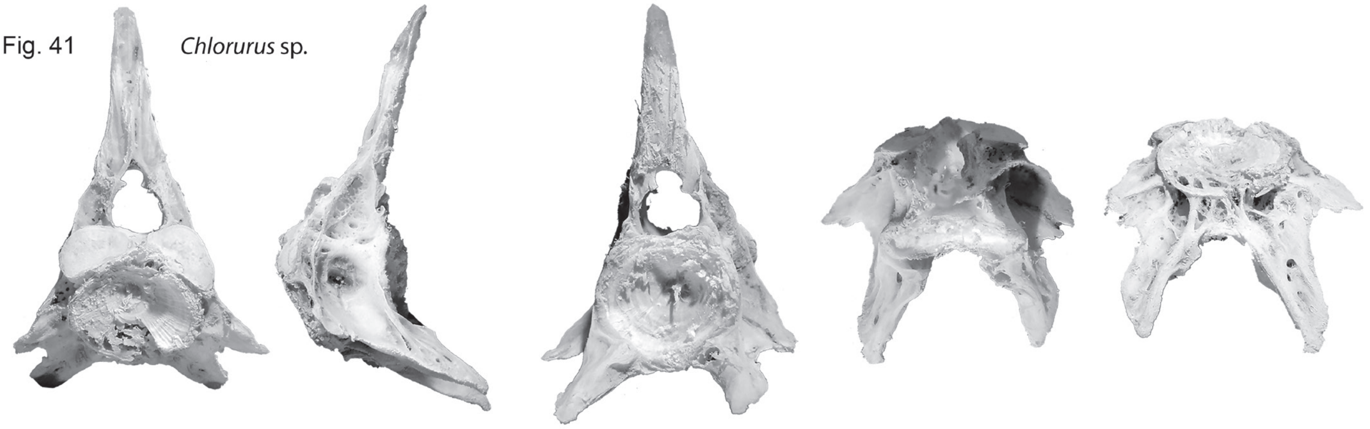
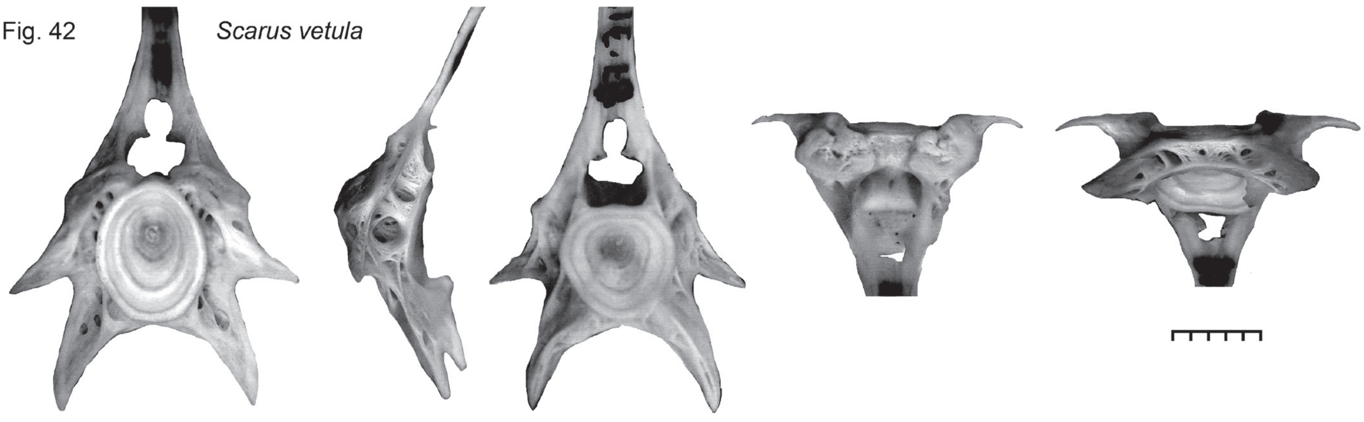


Fig. 42 *Scarus vetula*



(Opposite page) Plate 10. First centrum of Acanthopterygii – Labriformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 38. Labriformes: Labridae, *Halichoeres radiatus*, ROM R.2216 (note, the proximal tip of the broken neural arch is embedded in the right neural arch pit, visible in dorsal view).
Figure 39. Labriformes: Labridae: *Tautoga onitis,* CMNFI Z000339
Figure 40. Labriformes: Labridae: *Tautogolabrus adspersus,* CMNFI 1977-0239.1
Figure 41. Labriformes: Scaridae: *Scarus vetula,* CMNFI 1987-0312.1
Figure 42. Labriformes: Scaridae: *Chlorurus* sp., UAMZ.

than dorsally. The vertebra also differs in the lateral wings being oriented more ventrally, and the exoccipital facets do not meet in the midline. The centrum is relatively shorter (antero-posteriorly) than the *Chlorurus* specimen.

Eupercaria order incertae sedis

Family 28. Moronidae – this family contains only two genera, both with species than inhabit fresh, brackish and marine waters: *Morone* in North America and *Dicentrarchus* in Europe and North Africa. The two species of *Morone* we document have similar first centra, but they can be distinguished from one another. The neural arch on the first centrum is autogenous. The facets for the exoccipitals are irregular in shape, being almost square or diamond-shaped, and concave. They are positioned dorsally, almost flush with the dorsal surface of the centrum, and separated from one another by a distinct gap. The anterior and posterior articular facets are almost round; the posterior is slightly larger. The notochordal foramen is just dorsal to the midpoint of the centrum. The bone on the lateral and dorsal surfaces has large pits separated by thin ridges. The dorsal surface bears two, deep, funnel-shaped pits for the neural arch limited to the central part of the centrum, that flare laterally and meet with the tongue of bone between the facets for the exoccipitals to form a triangular surface. Ventrally, there is a single median pit bordered by longitudinal ridges of bone.

a. Moronidae – *Morone chrysops* (UAMZ DB1 and DB15; Plate 11, Figs. 43, 44). This is a freshwater species found in eastern North America, including the Great Lakes. The anterior facet on the first centrum is angled slightly ventrally, resulting in a shorter ventral length than dorsal length of the centrum. The facets for the exoccipitals are oriented anterodorsally. In one specimen, the thin covering of bone surfacing the facets is broken, creating the false impression that the facets form a rim of bone leading to a deep pit which communicates with deep lateral pits on the centrum. The dorsal surface of the centrum bears two median pits (a larger anterior and smaller posterior one) between the neural arch pits in the anterior tongue of bone that lies between the facets for the exoccipitals. The longitudinal striations on the ventral surface of the centrum are widely spaced to form deep spaces between them; these span the length of the centrum. The short transverse processes originate just above midheight on the centrum and project posterolaterally hooking medially at the tip.

b. Moronidae – *Morone saxatilus* (UAMZ F8896, and DB12; Plate 11, Figs. 45, 46). This species is found in marine, brackish and fresh waters of the Western Atlantic and coastal areas as well as the Saint Lawrence River. The first centrum differs from that of *M. chrysops* in a number of features. The anterior and posterior facets of the centrum are slightly taller than wide, and the anterior facet is more vertical. The facets for the exoccipitals are oriented slightly more anteriorly and are positioned a little lower on the centrum. The median pits on the dorsal surface in the tongue of bone between the facets for the exoccipitals are very shallow, with the anterior one being more of a depression rather than a pit, and both are absent in one specimen (not figured). Ventrally, the centrum has a few more longitudinal striations of bone that are more closely packed. The transverse processes are shorter and do not hook as strongly. The two specimens we illustrate differ slightly only in the bone texture on the lateral, dorsal and ventral surfaces of the centrum. In the smaller specimen, the bone texture has more interconnections than in the other, forming numerous small spaces between the ridges.

Order 17. Ephippiformes – spadefishes, members of the Ephippidae, may be included in Acanthuriformes (e.g., Froese and Pauly 2023) or in Moroniformes (Nelson et al. 2016) instead of Ephippiformes as we place them following Betancur-R et al. (2017). These are marine fishes of the Atlantic, Indian and Pacific oceans.

Family 29. Ephippidae – *Chaetodipterus faber* (CMNFI 1986-0068.1; Plate 11, Fig. 47) inhabits reefs of the Western Atlantic coastal waters including the Gulf of Mexico and northern Brazil. The neural arch on the first centrum is autogenous. The large exoccipital facets are positioned dorsally on the centrum and oriented almost directly anteriorly; a triangular tongue of bone separates them in the midline. The anterior facet is oval to circular, and the posterior facet narrows ventrally. The notochordal foramen is dorsal to the midpoint on the anterior facet, but almost at the midpoint on the posterior facet. The centrum is about as high as it is long, but widens laterally towards the posterior end. The blocky transverse processes project posterolaterally. The bone

Fig. 43 *Morone chrysops*

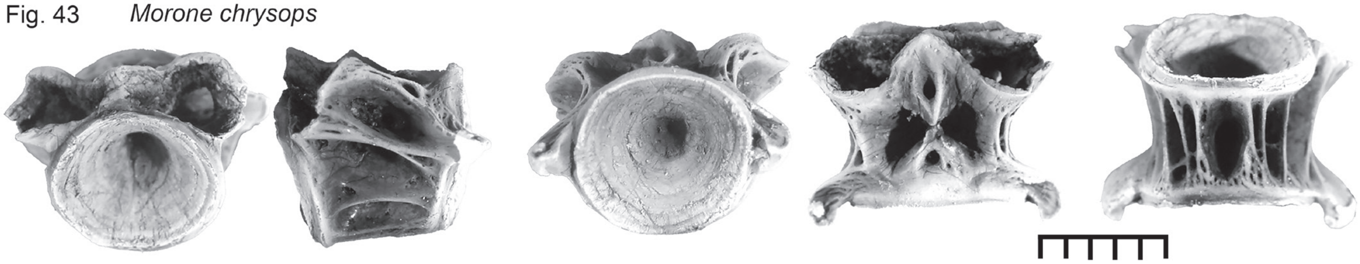


Fig. 44 *Morone chrysops*

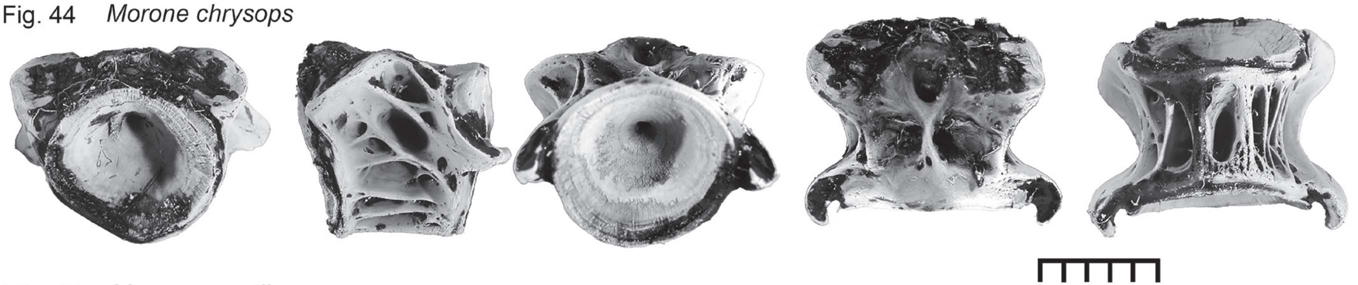


Fig. 45 *Morone saxatilus*

Fig. 46 *Morone saxatilus*

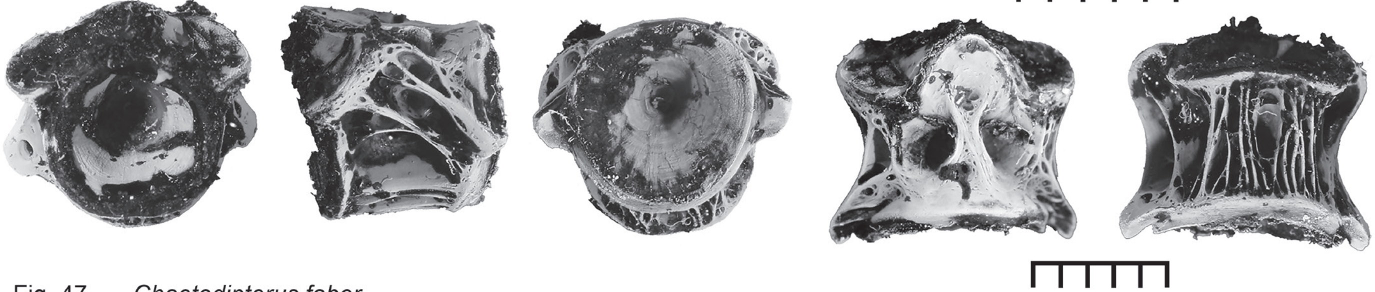


Fig. 47 *Chaetodipterus faber*

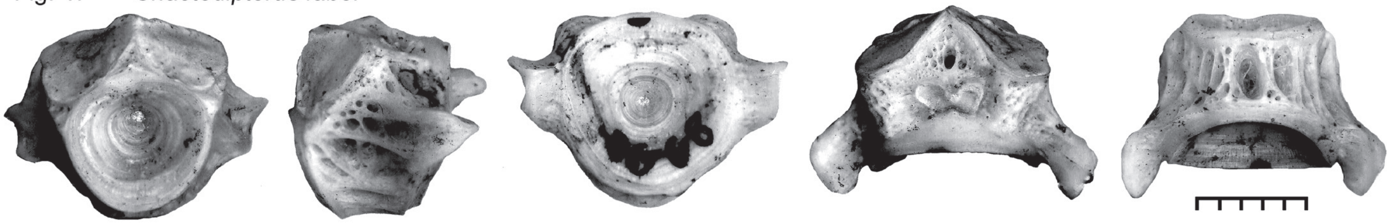
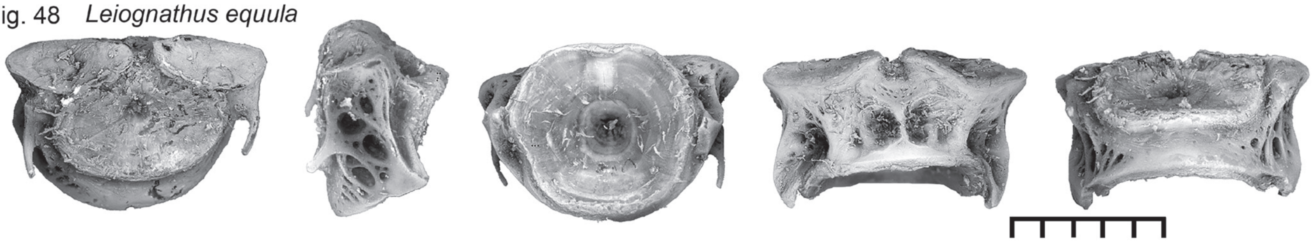


Fig. 48 *Leiognathus equula*



(Opposite page) Plate 11. First centrum of Acanthopterygii – Eupercaria order incertae sedis Moronidae, Ephippiformes and Chaetodontiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 43. Eupercaria: Moronidae: *Morone chrysops*, UAMZ DB1.
Figure 44. Eupercaria: Moronidae: *Morone chrysops*, UAMZ DB15.
Figure 45. Eupercaria: Moronidae: *Morone saxatilus*, UAMZ F8896.
Figure 46. Eupercaria: Moronidae: *Morone saxatilus*, UAMZ DB12.
Figure 47. Ephippiformes: Ephippidae: *Chaetodipterus faber,* CMNFI 1986-0068.1.
Figure 48. Eupercaria: Chaetodontiformes: Leiognathidae: *Leiognathus equula*, UAMZ AM11.

texture is an open network with a larger pit centrally on the ventral surface and a pair of small, oval neural arch pits in the centre of the dorsal surface.

Order 18. Chaetodontiformes – this order contains the butterfly fishes (Chaetodontidae) and ponyfishes (Leiognathidae). Chaetodontids are marine, but leiognathids are found in marine and brackish waters. Both families inhabit the Indo-west Pacific, with butterflyfishes also in the Atlantic, Indian and Pacific oceans. These species have strongly compressed bodies.

Family 30. Leiognathidae – *Leiognathus equula* (UAMZ AM 11, Plate 11, Fig. 48) is found in marine and brackish waters in the Red Sea, Persian Gulf and Indo- Pacific off East Africa south to Australia. The neural arch is autogenous. The anterior facet is almost circular, slightly depressed dorsoventrally, and constricted dorsally between the exoccipital facets. It is sloped so that the dorsal length of the centrum is longer than the ventral length and the centrum is wedge-shaped in lateral view. The posterior facet is slightly larger than the anterior facet, with flattened edges so that it is almost square rather than circular. The exoccipital facets are oriented more anteriorly than dorsally, are oval, and separated from one another by a small distance. The bone texture on the lateral surface is formed by widely spaced, relatively thick ridges creating large openings, but it is smooth on the ventral and dorsal surfaces. The two large, circular neural arch pits on the dorsal surface are close to the midline with only a narrow ridge of bone separating them; there is no ventral pit. The length of the centrum is about 60% of its height. The short transverse processes, which project from the midheight of the centrum, are slightly pointed. Unique to this taxon among those we examined, there are short, pointed projections descending anteroventrally from the ventrolateral edges of the exoccipitals facets.

Eupercaria order incertae sedis

Family 31. Sciaenidae – this family contains almost 70 genera and over 290 species. The drums and croakers are found in the Atlantic, Indian and Pacific oceans. We present four examples of this large family, including one found in fresh waters. In all our examples, the neural arch is autogenous, the centrum has similar height to width to length proportions and the exoccipital facets meet one another over the dorsal surface of the centrum, with a tongue of bone extending anteriorly in dorsal view.

a. Sciaenidae – *Aplodinotus grunniens* (CMNFI 1987-0464.1; Plate 12, Fig. 49), the freshwater drum, is found in North and Central America. The large exoccipital facets broadly meet one another dorsally, with a tongue of bone reaching anteriorly above them. The exoccipital facets are oriented anterodorsally. The circular anterior and almost square posterior facets are inclined to form a wedge-shaped centrum in lateral view. The centrum is about equal in length, width and height. The transverse processes originate from midheight of the centrum and project posteriorly and slightly laterally, extending well beyond the posterior facet. The bone texture is formed of ridges delineating long narrow cells. There is a single, large, median pit ventrally, and a pair of round neural arch pits dorsally.

b. Sciaenidae – *Larimichthys polyactis* (UAMZ F8927, Plate 12, Fig. 50) is a marine species found off the east coast of China and southern Japan. Our figured specimen has an irregular shape indicating it may be somewhat deformed. The anterior facet is sub-circular, compressed dorsally by the exoccipitals facets, and oriented anteriorly. The posterior facet is larger, slightly broader and flattened at its base, and with the notochordal foramen located dorsally. The exoccipital facets are oriented anteriorly, are in the same plane as the anterior facet, and surround the dorsal half or more of the anterior facet. There are no lateral or ventral pits, but small paired pits for the neural arch are present on the posterior part of the dorsal surface of the centrum. The bone texture is an open network of fine ridges with fairly large spaces between them. There is a pair of lateral thickenings or bumps ventrally on the anterior half of the centrum. The transverse processes are low on the centrum, short, and project posteriorly and slightly laterally. The centrum is a little taller than it as long; of the four examined sciaenids, this centrum is the least wedge-shaped in lateral view.

c. Sciaenidae – *Micropogon undulatus* (CMNFI Z000260; Plate 12, Fig. 51) is a marine fish of the US Atlantic coast, including the Gulf of Mexico, and south along the coasts

Fig. 49 *Aplodinotus grunniens*

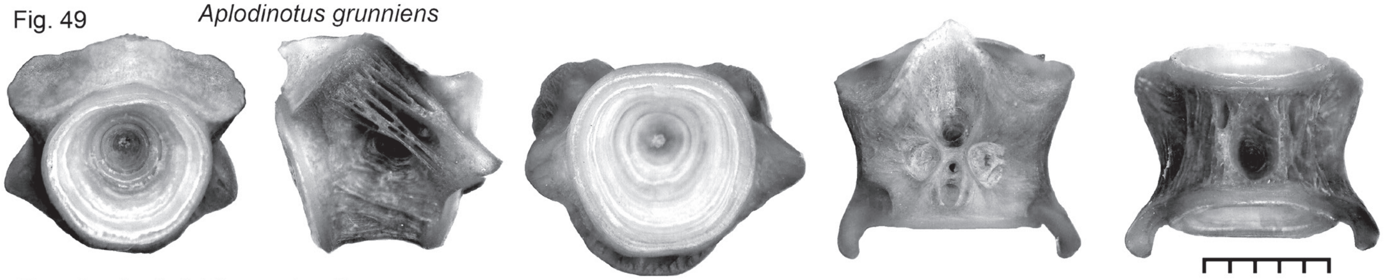


Fig. 50 *Larimichthys polyactis*

Fig. 51 *Micropogon undulatus*

Fig. 52 *Umbrina coroides*

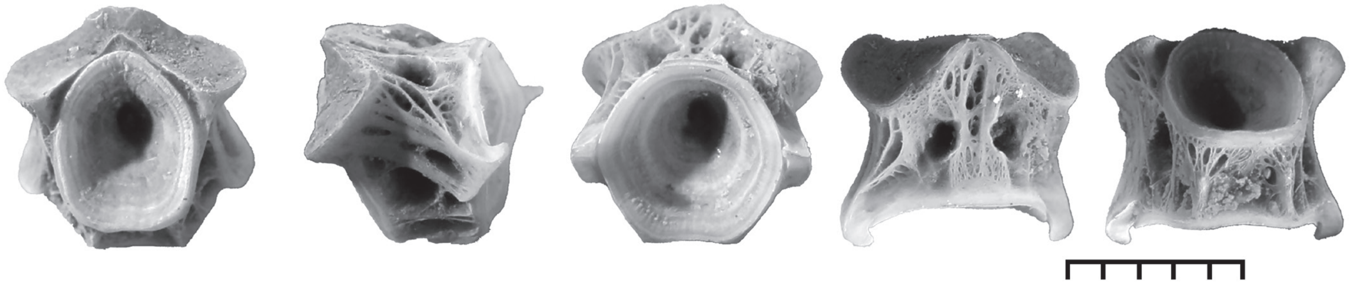


Fig. 53 *Lopholatilus chamaeleonticeps*

Plate 12. First centrum of Acanthopterygii – Eupercaria order incertae sedis Sciaenidae and Latilidae – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 49. Eupercaria: Sciaenidae: *Aplodinotus grunniens,* CMNFI 1987-0464.1.
Figure 50. Eupercaria: Sciaenidae: *Larimichthys polyactis*, UAMZ F8927.
Figure 51. Eupercaria: Sciaenidae: *Micropogonias undulatus,* CMNFI Z000260.
Figure 52. Eupercaria: Sciaenidae: *Umbrina coroides*, ROM R.3090.
Figure 53. Epercaria: Latilidae: *Lopholatilus chamaeleonticeps*, UAMZ F8911.

of Brazil and Argentina. The exoccipital facets of the first centrum are similar to those of *Aplodinotus grunniens*, but less broadly united in the midline. The anterior facet is circular and the posterior facet is only slightly less round. The transverse processes are relatively smaller than those of *Aplodinotus grunniens* and *Umbrina coroides*. The bone texture is more regular, with the ridges paralleling each other on the lateral and ventral surfaces.

c. Sciaenidae – *Umbrina coroides* (ROM R.3090; Plate 12, Fig. 52) is a Western Atlantic species, found in coastal areas of southern North America, Central America and northern South America. The large, triangular facets for the exoccipitals are positioned dorsally and the medial tips meet each other in the midline over the dorsal surface of the centrum. They are oriented anterodorsally and extend dorsally above the body of the centrum. The oval anterior articular facet has a flat ventral edge. The centrum is wedge-shaped in lateral view. The posterior articular facet is wider than the anterior facet. The two round pits for the neural arch on the dorsal surface of the centrum are restricted to the middle of the centrum; there are no pits on the ventral surface. The bone texture dorsally and ventrally is formed by a close network of ridges creating small spaces or cells. On the lateral surface of the centrum, there are larger pits present, with the largest being at midheight. The transverse process is positioned at midheight on the centrum. It is fairly small, oriented posteriorly and slightly hooked. The centrum is slightly taller than long.

Eupercaria order incertae sedis

Family 32. Lopholatilidae – *Lopholatilus chamaeleonticeps* (UAMZ F8911, Plate 12, Fig. 53) inhabits the Western Atlantic in coastal areas from the Canadian Maritimes, to northern South America including the Gulf of Mexico. The neural arch is autogenous. The centrum is short, being about twice as high as it is long, but it is not compressed into a disk, although the concavity of the anterior facet is shallower than the posterior facet. The notochordal foramen is at the midpoint. The oval, anterodorsally-facing exoccipital facets are located dorsally and meet in the midline. The honeycomb bone texture is similar to that of other taxa examined except that the spaces are larger over most of the bone surface. In some areas, the ridges are wider than the spaces, and in other areas, the cells are larger than the ridges. There are no large pits on the lateral or ventral surfaces. The paired dorsal pits for the neural arch are round, close to the midline, and fairly large. There is a small tongue of bone extending between the two exoccipital facets that bears the same texture as the rest of the centrum. The anterior facet is inclined so that the centrum is wedge-shaped in lateral view. The small, pointed transverse processes project from the midheight of the centrum and do not extend posteriorly past the level of the rim of the posterior facet.

Order 19. Lutjaniformes – includes Lutjanidae (snappers) and Haemulidae (grunts). Both are marine families with some members entering brackish waters and are represented in the Atlantic, Indian and Pacific oceans. Caesionidae is considered to be a synonym of Lutjanidae by Betancur-R et al. (2017). The three examples we include are quite dissimilar, with no features appearing to be common among them, with the exception that all have an autogenous neural arch.

Family 33. Caesionidae (= Lutjanidae) – *Pterocaesio chrysozona* (UAMZ AM7, Plate 13, Fig. 54) is a reef fish found in marine waters of the Indo-West Pacific. The neural arch is autogenous. The anterior facet is almost vertical, oriented anteriorly, and tear drop-shaped, being constricted dorsally between the exoccipital facets. The posterior facet is circular. The notochordal foramen is dorsal to the midpoint, but closer to the dorsal edge on the anterior facet than on the posterior facet. The round exoccipital facets are located on the dorsal half of the centrum and extend slightly farther dorsally than the centrum. They are oriented anterodorsally, are separated from one another by a small gap, and project farther anteriorly than the anterior articular facet. The rounded transverse processes are positioned below midheight and project posteriorly beyond the level of the posterior facet. There are two large, round dorsal pits (for the neural arch) and a single relatively large median oval ventral pit on the centrum. The bone texture is smooth dorsally and laterally, but forms a network of a few thick ridges on the ventral surface of the centrum. The centrum is rectangular in lateral view, and is only slightly taller than it is long.

Family 34. Lutjanidae – *Lutjanus campechanus* (UAMZ AM 14, Plate 13, Fig. 55) inhabits the Western Atlantic from southern North America through to northern South America, including the Gulf of Mexico. The neural arch is autogenous. The anterior facet is oval, 1.2 times as high as it is wide. The posterior facet is broader, but still higher than wide. The exoccipital facets are large, semicircular, and oriented almost dorsally; they meet one another in the midline anteriorly below a triangular tongue of bone. The bone texture is a honeycomb formed by anastomosing ridges defining circular to oval spaces with ridges and spaces of equal width. This texture becomes more open (larger spaces) on the dorsal half of the centrum forming what could be defined as large pits (one on the left side and two on the right side) on the lateral surface of our specimen. These are visible below the exoccipital facets in ventral view. There are no large pits ventrally. The paired pits for the neural arch on the dorsal surface of the centrum are round to oval, oriented slightly laterally, and well separated from one another. The robust

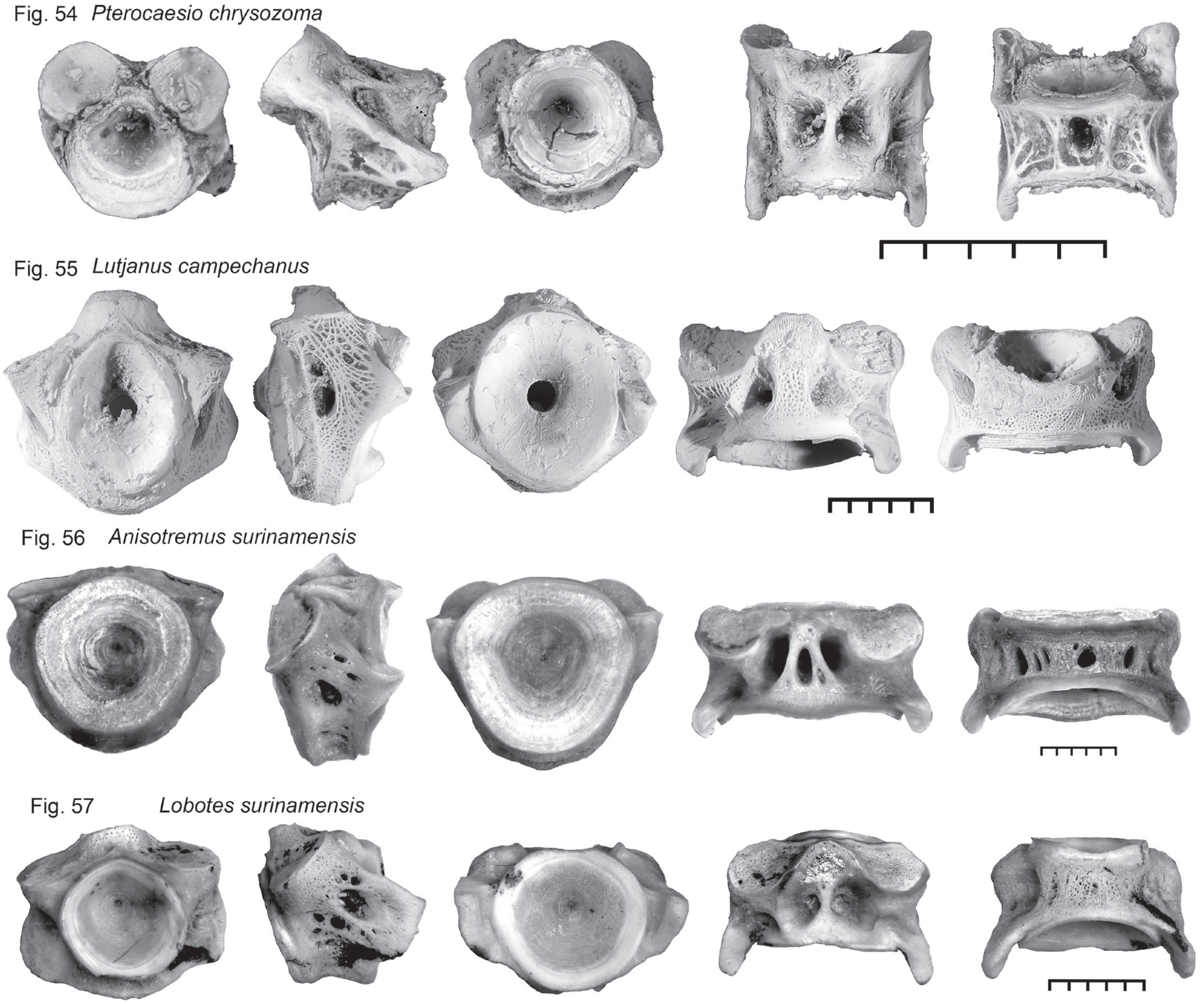


Plate 13. First centrum of Acanthopterygii – Lutjaniformes and Lobotiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 54. Lutjaniformes: Caesionidae: *Pterocaesio chrysozona*, UAMZ AM7.
Figure 55. Lutjaniformes: Lutjanidae: *Lutjanus campechanus*, UAMZ AM 14 (note, this specimen was previously mounted on a wire; the large hole through the centrum is not the notochordal foramen but is an artificial opening drilled to accommodate the wire).
Figure 56. Lutjaniformes: Haemulidae: *Anisotremus surinamensis*, CMNFI Z000447.
Figure 57. Lobotiformes: Lobotidae: *Lobotes surinamensis,* CMNFI Z000446.

transverse processes are positioned just below midheight, extend posteriorly beyond the posterior facet of the centrum for a short distance, and are slightly hooked medially. The centrum is less than half as long as it is high.

Family 35. Haemulidae – *Anisotremus surinamensis* (CMNFI Z000447; Plate 13, Fig. 56) is a reef-associated marine fish found in Atlantic coastal waters of the southern USA to northern South America including the Caribbean and Gulf of Mexico. The irregularly shaped exoccipital faces are positioned dorsally and oriented anterodorsally; they do not quite meet one another in the midline. The almost circular anterior facet narrows ventrally, and the posterior facet is even more constricted ventrally; both have the notochordal foramen positioned just dorsal to the midpoint of the centrum. The centrum is about as tall as it is wide, but the length is only a bit more than half the width. The bone texture is fairly smooth with small, shallow depressions, but there are larger, deeper pits present on the lateral and ventral surfaces, as well as a deep median pit between the pair of neural arch pits on the dorsal surface. The rounded transverse processes are fairly short, but extend posterolaterally beyond the posterior facet.

Order 20. Lobotiformes – this order includes Lobotidae, Hapalogenyidae and Datnioididae according to Betancur-R et al. (2017). *Lobotes* and *Datnioides* were both placed in Lobotidae in the order Spariformes by Nelson et al. (2016), and the family is included in Lobotidae but placed in Acanthuriformes by Froese and Pauly (2023). Hapalogenyidae has also been included in Perciformes (Nelson et al. 2016).

Family 36. Lobotidae – *Lobotes surinamensis* (CMNFI Z000446; Plate 13, Fig. 57) is a benthopelagic fish found in tropical and subtropical marine waters world-wide. The neural arch on the first centrum is autogenous. The exoccipital facets are roughly oval, positioned dorsally and oriented anterodorsally. They meet one another in the midline anteriorly, but are separated posteriorly by a tongue of bone. The anterior facet is smaller than the posterior facet and both are roughly circular with the notochordal foramen positioned above the midpoint. The transverse processes are positioned at midheight and are narrow in dorsal and ventral view, oriented slightly laterally and extend well beyond the posterior facet. The centrum is shorter than it is wide or tall. The bone texture is formed by ridges and small cells or pits on the ventral and lateral surfaces, as well as pits with no ridges on the surface of the exoccipital facet. The neural arch pits are deep and round and there is a deep oval pit on the lateral sides of the centrum between the exoccipital facet and transverse process.

Order 21. Spariformes – incudes only three families according to Betancur-R et al. (2017): Sparidae (porgies), Nemipteridae (threadfin breams) and Lethrinidae (emperor breams). These are all marine and mostly tropical or subtropical.

Family 37. Sparidae – This family is found in tropical and temperate waters of the Atlantic, Pacific and Indian oceans with some species rarely entering brackish or fresh waters. All our examples of this family are similar in that the neural arch on the first centrum is autogenous. The facets for articulation with the exoccipitals are located towards the dorsal surface of the centrum, and oriented anterodorsally. They are oblong or oval in shape, and meet one another in the midline anteriorly. The anterior articular facet is oval to round, angled anteroventrally, with the notochordal foramen slightly dorsal to the midpoint. The posterior facet is also circular and of about the same size or slightly larger than the anterior facet. The centrum is longer along its dorsal surface than along its ventral surface, forming a wedge-shape in lateral view. The bone texture of ridges defining pits or cells is found in all our representatives of this family, but the relative size of the pits and thickness of the ridges vary. The transverse processes are short.

a. Sparidae – *Archosargus rhomboidialis* (UAMZ DB4, Plate 14, Fig. 58) is a reef fish found in marine and brackish waters of the Western Atlantic from Argentina to the southern USA including the Gulf of Mexico. The irregularly-shaped exoccipital facets are located towards the dorsal surface of the centrum, oriented anterodorsally and slightly laterally. They are oblong or oval in shape, and meet one another in the midline anteriorly. The anterior articular facet is oval, angled anteroventrally, with the notochordal foramen slightly dorsal to the midpoint. The posterior articular surface is also oval and of about the same size but broader dorsally. The bone of the lateral and ventral surfaces of the centrum forms a network with fairly large cells. The dorsal surface bears two round pits for the neural arch positioned towards the lateral sides of the centrum, and between them is a smaller oval pit. There is no large pit on the ventral surface. The short transverse processes are positioned at midheight of the centrum and hook slightly medially.

b. Sparidae – *Boops boops* (UAMZ; Plate 14, Fig. 59) inhabits the Eastern Atlantic from Western Africa to Norway, as well as the Mediterranean and Black seas. The relatively large, round facets for the exoccipitals are positioned dorsally and broadly meet one another in the midline anteriorly. They are oriented anterodorsally. The anterior facet is oval, and about 2/3 the diameter of the circular posterior facet. The bone on the lateral and dorsal surfaces of the centrum forms a network of ridges surrounding small pits on the ventral surface but, because the pits are shallow and the ridges are relatively broad, it appears quite smooth. There is a single, round, median pit on the ventral surface, and a larger, round pit low on the lateral surface of the centrum. The small transverse processes are positioned just below midheight on the centrum, and hook slightly medially. The anterior articular facet is angled anteroventrally such that the dorsal length of the centrum is slightly longer than the ventral length, forming a wedge in lateral view.

c. Sparidae – *Diplodus annularis* (UAMZ F8907; Plate 14, Fig. 60) inhabits the Mediterranean Sea, Black Sea and Sea of Azov, with the range extending into the coastal waters of the Eastern Atlantic around Portugal. The exoccipital facets are oval and meet one another in the midline anteriorly; they curve up posteriorly to form a peak over the centrum. The oval anterior facet is oriented anteroventrally, with the notochordal foramen fairly large and situated dorsal to the midpoint. The posterior facet is circular. The bone texture on the centrum is mostly smooth, with a few larger pits on the lateral side. Dorsally, there are two median pits (one anterior and one posterior) between the neural arch pits. There are no pits ventrally. The transverse processes are at midheight on the centrum and project posterolaterally.

d. Sparidae – *Lagodon rhomboides* (CMNFI Z000592; Plate 14, Fig. 61) is a Western Atlantic marine species

Fig. 58 *Archosargus rhomboidalis*

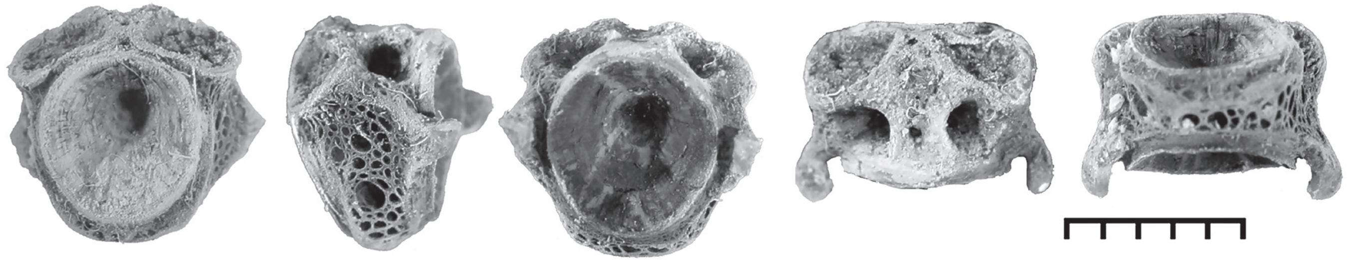


Fig. 59 *Boops boops*

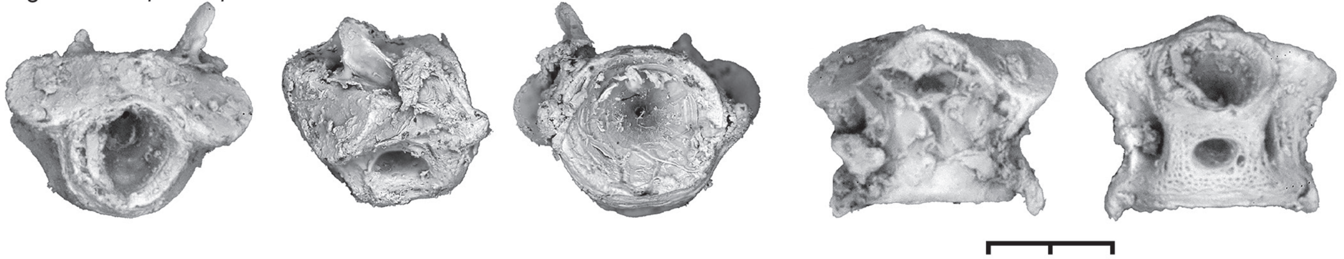


Fig. 60 *Diplodus annularis*

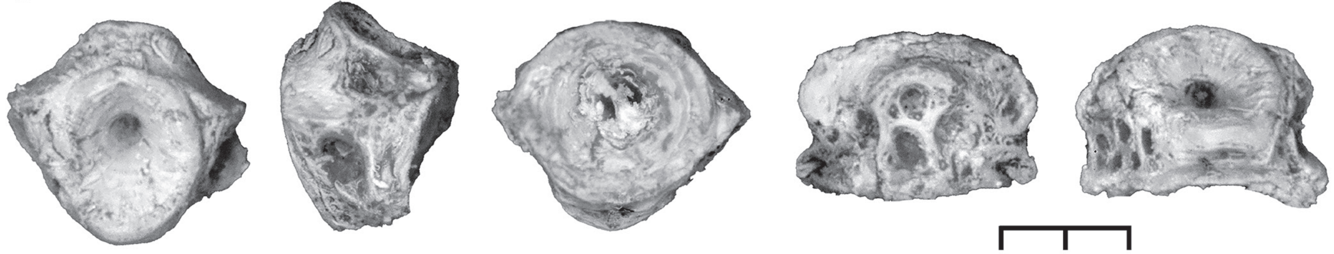


Fig. 61 *Lagodon rhomboides*

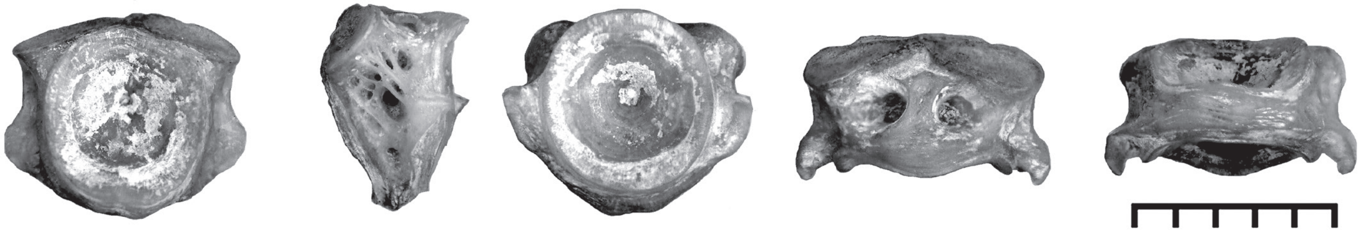


Plate 14. First centrum of Acanthopterygii – Spariformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 58. Spariformes: Sparidae: *Archosargus rhomboidialis*, UAMZ DB4.
Figure 59. Spariformes: Sparidae: *Boops boops*, UAMZ.
Figure 60. Spariformes: Sparidae: *Diplodus annularis*, UAMZ F8907.
Figure 61. Spariformes: Sparidae: *Lagodon rhomboides*, CMNFI Z000592.

found in coastal waters of the USA and Cuba, and in the Gulf of Mexico. The anterior facet is more steeply inclined than in the other taxa except *Spicara maena*, such that the ventral length of the centrum is much shorter than the dorsal length. The exoccipital facets are oriented anterodorsally, forming an almost flat dorsal surface in anterior view. The bone texture on the ventral surface essentially lacks cells and appears as a bundle of ridges.

e. Sparidae – *Pagrus pagrus* (UAMZ; Plate 15, Fig. 62) inhabits marine coastal waters on either side of the Atlantic Ocean, including the Mediterranean Sea. The irregularly-shaped exoccipital facets are smaller than those of *Boops boops*, and oriented more dorsally, but meet broadly in the midline anteriorly. The anterior and posterior articular facets of the centrum are roughly oval, put pinched-in ventrally, with the anterior facet being about 2/3 the diameter of the posterior facet. The notochordal foramen is positioned just dorsal to the midpoint. The bone on the lateral, dorsal and ventral surfaces of the centrum forms a network of ridges surrounding small pits (our specimen has three on the left and five on the right side). Larger pits are present on the lateral surface and a single median depression but no deep pit on the ventral surface. Pits for the neural arch on the dorsal surface of

Fig. 62 *Pagrus pagrus*

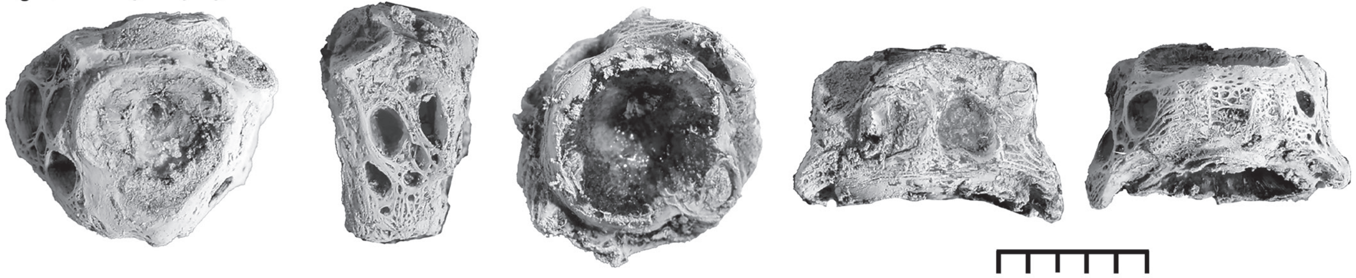


Fig. 63 *Spicara maena*

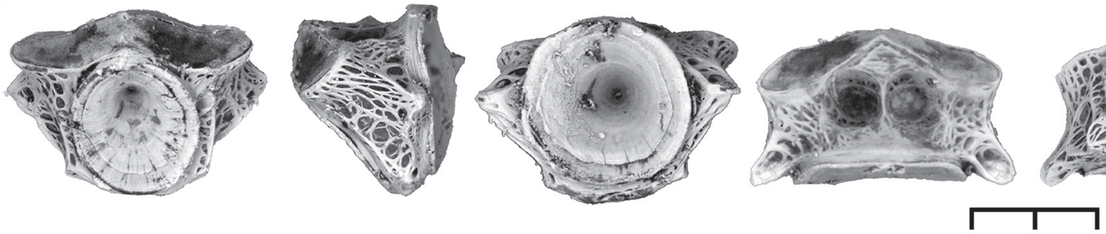


Fig. 64 *Nemipterus virgatus*

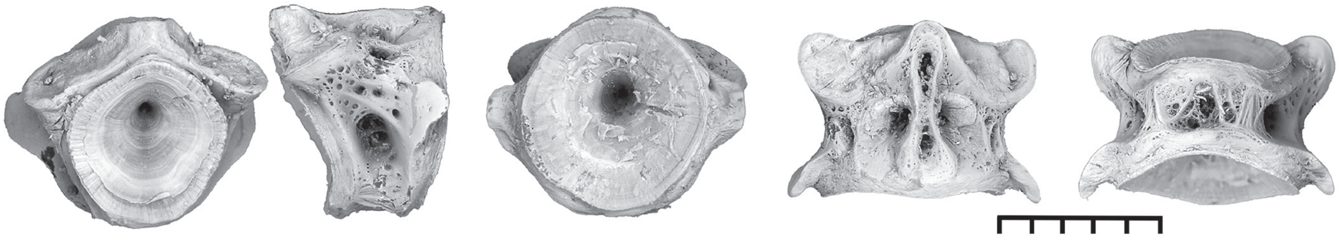


Plate 15. First centrum of Acanthopterygii – Spariformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 62. Spariformes: Sparidae: *Pagrus pagrus*, UAMZ.
Figure 63. Spariformes: Sparidae: *Spicara maena*, UAMZ.
Figure 64. Spariformes: Nemipteridae: *Nemipterus virgatus*, UAMZ AM9.

the centrum are large and round, but confined to the central area of the centrum (i.e., not reaching anterior or posterior edges). In our figured specimen, the left base of the neural arch remains in articulation. The transverse process is very short, only just projecting posterior to the centrum; it is positioned at midheight of the centrum.

e. Sparidae – *Spicara maena* (UAMZ; Plate 15, Fig. 63) is a marine fish found in coastal waters of the Mediterranean and Black seas and in the Eastern Atlantic around Portugal, Morocco, and the Canary Islands. The exoccipital facets are concave, elongate, oval or semicircular, oriented anterodorsally, and curve up the sides of the centrum to meet in the midline. The oval anterior facet is strongly angled, creating a much shorter ventral length than dorsal length for the centrum which is therefore strongly wedge-shaped in lateral view. The posterior facet is larger and circular. The large round pits for the neural arch are positioned just posterior to the exoccipital facets, separated only by a narrow ridge of bone. The bone texture is formed of an open network or honeycomb of ridges surrounding relatively large spaces. There is no pit on the ventral surface. The centrum is slightly higher than long. The transverse processes are short, pointed and oriented posterolaterally.

Family 38. Nemipteridae – *Nemipterus virgatus* (UAMZ AM9, Plate 15, Fig. 64) is found in marine coastal waters of the Indo-West Pacific, north to Japan and south to northern Australia. The neural arch is autogenous. The anterior facet is oval, slightly flattened on either side of the dorsal midpoint by the exoccipital facets, and curved so that the ventral third faces anteriorly and the dorsal two-thirds is oriented anteroventrally. The notochordal foramen is positioned dorsal to the midpoint. The posterior facet is circular and the notochordal foramen is just above the midpoint. The exoccipital facets are semicircular, oriented anterodorsally, and just meet below a dorsal tongue of bone. This tongue of bone has two median pits, one anterior and a second posterior, and is constricted centrally between the two round neural arch pits. There is a single large pit on each lateral surface of the centrum. Ventrally, there is a single median pit. The bone texture is formed of fine ridges and small pits ventrally, but these ridges

Fig. 65 *Holacanthus ciliaris*

Fig. 66 *Siganus guttatus*

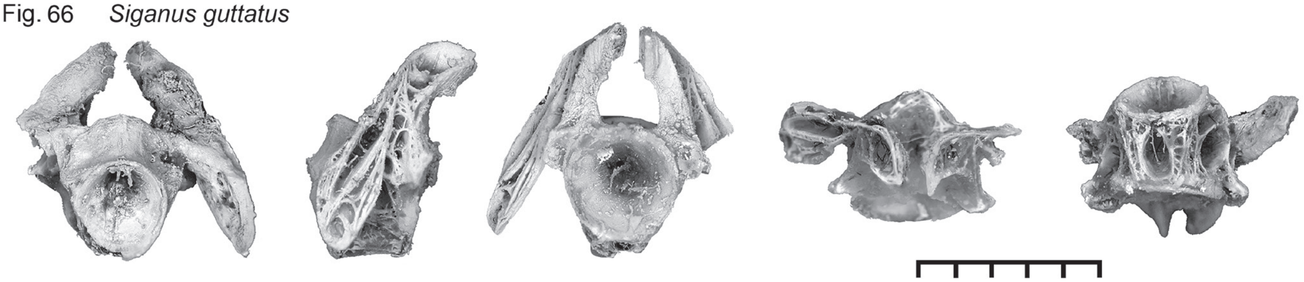


Fig. 67 *Heteropriacanthus cruentatus*

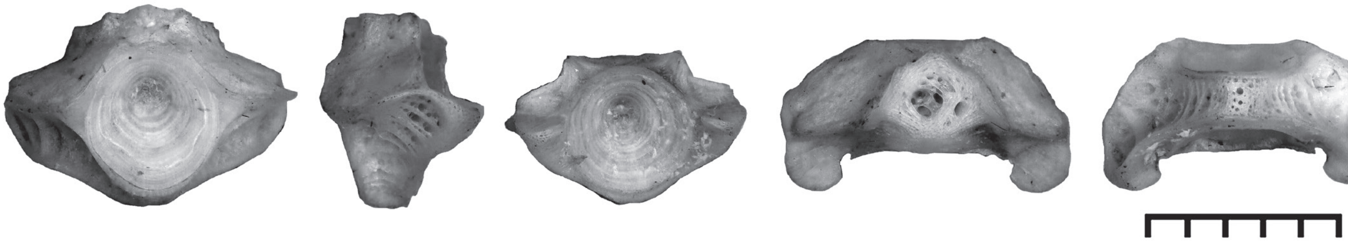


Fig. 68 *Lophius americanus*

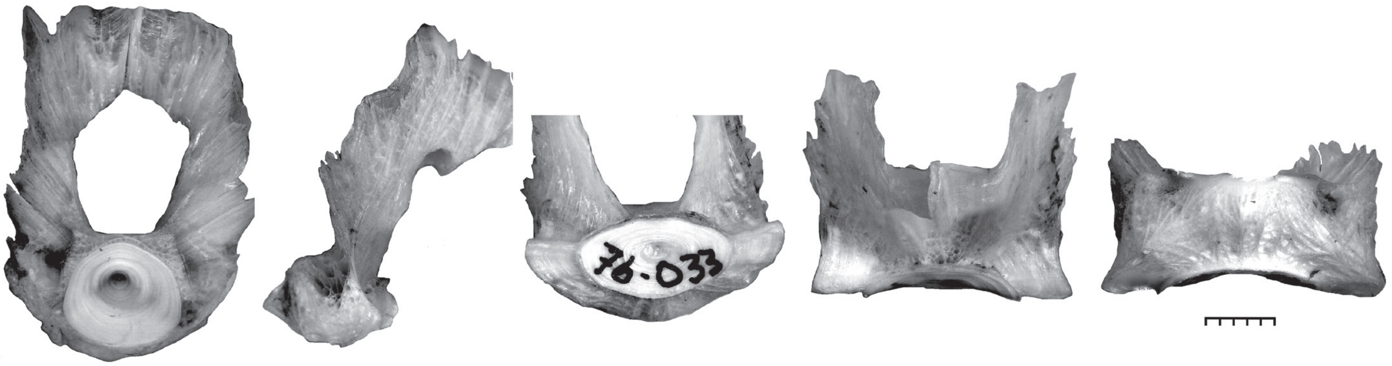


Plate 16. First centrum of Acanthopterygii – Eupercaria order incertae sedis Pomacanthidae and Siganidae, Priacanthiformes and Lophiiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 65. Eupercaria: Pomacanthidae: *Holacanthus ciliaris,* CMNFI 1987-0299.1.
Figure 66. Eupercaria: Siganidae: *Siganus guttatus*, UAMZ AM3.
Figure 67. Priacanthiformes: Priacanthidae: *Heteropriacanthus cruentatus,* CMNFI 1983-268.1.
Figure 68. Lophiiformes: Lophiidae: *Lophius americanus,* CMNFI 1976-0033.1.

are thicker and smoother with larger cells on the lateral surface, and the dorsal surface is almost smooth. The ventral length of the centrum is shorter than the dorsal length, but the curvature of the anterior facet makes the centrum outline in lateral view irregular rather than wedge-shaped. The centrum height is about twice its shortest (ventral) length, and about 1.3 times its greatest (dorsal) length. The short transverse processes are located at midheight of the centrum, and project posterolaterally just beyond the posterior facet rim.

Order 22. Acanthuriformes includes three families, Acanthuridae (surgeonfishes, with over 70 species), Luvaridae (with a single species, the louvar, *Luvarus imperialis*) and Zanclidae (also with a single species, the Moorish idol, *Zanclus cornutus*), all of which are predominantly herbivorous taxa found in marine waters. Betancur-R et al. (2017) left both the Pomacanthidae and Siganidae as order incertae sedis rather than placing them in Acanthuriformes.

Family 39. Pomacanthidae – *Holacanthus ciliaris* (CMNFI 1987-0299.1; Plate 16, Fig. 65) is a reef fish found in Western Atlantic coastal waters of Central America, northern South America, and the southern USA, as well as the Gulf of Mexico and Caribbean. The neural arch is autogenous. The first centrum has a unique shape among specimens examined. The anterior facet is kite-shaped, forming an elongate diamond with the longer point oriented ventrally and curving forward; it is not pierced by the notochord. The posterior facet is circular with the notochordal foramen located dorsal to the midpoint. The oval exoccipital facets are located on the dorsal half of the centrum, somewhat retracted from the level of the anterior facet, and oriented anterodorsally. A thick ridge separates them in the midline. The transverse processes are thick, square, and originate from the ventral surface of the centrum; they project posteriorly well beyond the posterior facet. The bone texture is smooth, with a few small cells or pits on the lateral and ventral surfaces, and a pair of neural arch pits on the dorsal surface.

Family 40. Siganidae – *Siganus guttatus* (UAMZ AM3, Plate 16, Fig. 66) is a marine and brackish coastal reef fish found in the Indo-West Pacific. The neural arch is fused to the centrum and has a long ventrally directed process extending from its base on the lateral side of the centrum (broken on the left side of the figured specimen). This is unique among the species examined (in the scarid *Chlorurus*, a similar lateral expansion of bone originates from the centrum, not the neural arch). The anterior facet is oval and the slightly larger posterior facet is sub-circular, being narrower ventrally than dorsally. The notochordal foramen is located dorsal to the midpoint. The exoccipital facets are broadly connected to one another and also not clearly separated from the centrum, instead being flattened areas on the centrum itself oriented dorsally. They are retracted so that the dorsal surface can articulate with the ventral surface of the exoccipitals which extend posteriorly past the basioccipital on the skull. The ventral length is slightly shorter than the dorsal length (the anterior facet is slightly inclined) to form a slight wedge in lateral view. The centrum is about as long as it is high. The centrum and neural arch are ornamented with an open network of ridges delineating large spaces. There is a single, oval, median pit on each of the ventral, dorsal and lateral surfaces. There are very short processes extending laterally from the bottom of the neural arch (posterior to the long ventrally-directed processes). Because these are on the neural arch, not the centrum, we do not refer to them as transverse processes. This is unique to this taxon among those presented here.

Order 23. Priacanthiformes – includes two families, Priacanthidae and Cepolidae, which were included in Percoidei by Nelson et al. (2017). Priacanthids are tropical to subtropical fish.

Family 41. Priacanthidae – *Heteropriacanthus cruentatus* (CMNFI 1983-0268.1, as *Priacanthus cruentatus*; Plate 16, Fig. 67) is a reef-associated marine fish; the species name is limited to populations of the Atlantic and SW Indian Ocean. There is no neural arch fused to the first centrum. The circular anterior facet is larger, but of similar shape to the posterior facet. The large, oval, anterolaterally-facing exoccipital facets are positioned at midheight on the centrum, and slope to the dorsal surface, but do not meet in the midline. The centrum is wider than high, and higher than long, with the anterior and posterior facets inclined to form a wedge-shape in lateral view. The broad, rounded transverse processes are tall (dorsoventrally) and extend posteriorly from the midheight of the centrum. The bone texture is formed by longitudinal ridges with small cross-ridges delineating circular to oval cells on the lateral and ventral surfaces, with ridges more randomly arranged on the dorsal surface. There are no neural arch pits.

Order 24. Lophiiformes – the anglerfishes inhabit marine waters, with most occurring in deep water. The Lophiidae is considered to be the most primitive family and sistergroup to the rest of the order (Nelson et al. 2016).

Family 42. Lophiidae – *Lophius americanus* (CMNFI 1976-033.1; Plate 16, Fig. 68) is found on the continental shelf in the Western Atlantic from Newfoundland to Florida. The broad neural arch is fused to the first centrum. The anterior facet is almost circular, but the posterior one is depressed into a wide oval. The notochordal foramen is positioned just above the midpoint. The exoccipital facets are oriented anterodorsally. There are no transverse processes. The bone texture is a honeycomb, with the cells being quite shallow. The centrum is twice as wide as it is long and high.

Order 25. Tetraodontiformes – include the puffers, boxfishes, triggerfishes, and porcupinefishes, among others. The relationships of the included families are debated, and more work needs to be done. Seven suborders are recognized by Betancur-R et al. (2017) and well over 400 species are known. These are predominantly marine, but some are restricted to fresh waters.

Family 43. Balistidae – Members of this family are found globally in shallow marine waters associated with coral reefs. In both our examples, the neural arch is fused to the centrum, but the neural spine does not fuse in the midline, with the left and right halves diverging distally and angling anteriorly where they lie along the back of the skull. The centrum is about the same height as width, but the length is shorter, being just over half as long as the height.

The transverse processes are rounded with a slight medial hook and extend well behind the posterior facet. The anterior facet is vertical, and the dorsal and ventral lengths of the centrum are equal, forming a rectangular centrum in lateral view. There are no lateral, ventral, or dorsal pits.

a. Balistidae – unidentified species (UAMZ, Plate 17, Fig. 69). Our specimen was purchased from a grocery store, and was not identified below family level prior to being skeletonized. The anterior facet is almost circular but the posterior facet is oval, being taller than wide. The small, oval exoccipital facets are located on top of the dorsal edge of the centrum at the base of the neural arch, and don't quite meet one another in the midline. They are oriented anterodorsally. The bone texture is formed by anastomosing ridges defining small irregular depressions and cells on all surfaces of the centrum but the cells are deeper around the posterior rim. The transverse processes are positioned at midheight on the centrum.

b. Balistidae – *Balistes capriscus* (CMNFI 1989-0489.1; Plate 17, Fig. 70) is a reef fish of the coastal Western and Eastern Atlantic. The anterior facet is almost circular whereas the posterior one is oval, with the sides pinched in; the notochordal foramen is closer to the dorsal edge in the anterior facet. The exoccipital facets are oriented more dorsally than in the other specimen, and the transverse processes are positioned more ventrally. The bone texture consists of fewer ridges and large cells, instead having more regularly spaced smaller cells, particularly on the ventral surface.

Family 44. Diodontidae – *Chilomycterus schoepfii* (CMNFI Z000877; Plate 17, Fig. 71) is a Western Atlantic inhabitant found in coastal waters from Nova Scotia, Canada, south to Brazil and in the Gulf of Mexico. The neural arch is fused to the first centrum but the left and right halves of the broad neural spine remain unfused and diverge posterolaterally. The circular anterior and posterior facets are of similar size and the notochordal foramen is just dorsal to the midpoint. The exoccipital facets are on the dorsal half of the centrum, face anterolaterally, and are slightly retracted, not reaching as far anterior as the anterior facet. The centrum is much longer than it is high or wide. The transverse processes are positioned towards the dorsal edge of the centrum, are pointed or rounded (the two sides differ in our specimen), and extend posteriorly just beyond the posterior facet. The bone texture on the centrum is formed by thick longitudinal ridges and thinner cross-ridges forming cells; on the neural arch the cells and ridges are much more numerous creating a honeycomb appearance. There are no large pits on any surface.

Order 26. Pempheriformes – contains a number of families but support for them all to be grouped in this order is not strong and more work is needed.

Family 45. Lateolabracidae – *Lateolabrax japonicus* (UAMZ F8926, Plate 17, Fig. 72) inhabits marine, fresh and brackish waters off Japan and the east coast of China. The neural arch is autogenous. The anterior facet and slightly larger posterior facet are almost circular. The notochordal foramen is slightly more dorsally positioned on the anterior facet. The relatively large, round exoccipital facets have a dorsal indentation that makes them almost kidney bean-shaped. They are oriented anterodorsally and meet in the midline below a triangular tongue of bone. The bone texture is formed by an open network of parallel ridges with anastomosing ridges between them delineating irregularly shaped spaces which become quite large on the upper lateral sides. This bone texture continues on the tongue that extends anteriorly between the exoccipital facets. There is a single, narrow, oval median pit on the ventral surface and the round pits for the neural arch on the dorsal surface are located centrally and close to the midline. The anterior facet is curved, such that the ventral length is shorter than the dorsal length of the centrum; the centrum height is less than 1.5 times its ventral length. The rounded transverse processes extend posterolaterally beyond the posterior facet and are located just above midheight of the centrum.

Family 46. Polyprionidae – *Polyprion oxygeneios* (UAMZ AM4, Plate 17, Fig. 73) is circumglobal in southern sub-tropical marine waters off South America, South Africa, Australia, and New Zealand. The neural arch is autogenous but in the figured specimen it is still attached to the centrum by connective tissue. The proximal base of the neural arch expands laterally but does not extend beyond the width of the centrum. The anterior facet of the centrum is oval and pinched-in dorsally, slightly inclined, with the notochordal foramen located just above the midpoint. The posterior facet is circular, with the notochordal foramen located at the midpoint. The exoccipital facets are oriented anterodorsally, widely separated, and project just above the dorsal surface of the centrum. The short trans-

(Opposite page) Plate 17. First centrum of Acanthopterygii – Tetraodontiformes and Pempheriformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 69. Tetraodontiformes: Balistidae: unidentified, UAMZ AMx.
Figure 70. Tetraodontiformes: Balistidae: *Balistes capriscus,* CMNFI 1989-0489.1.
Figure 71. Tetraodontiformes: Diodontidae: *Chilomycterus schoepfii,* CMNFI Z000877.
Figure 72. Pempheriformes: Lateolabracidae: *Lateolabrax japonicus*, UAMZ F8926.
Figure 73. Pempheriformes: Polyprionidae: *Polyprion oxygeneios*, UAMZ AM4.

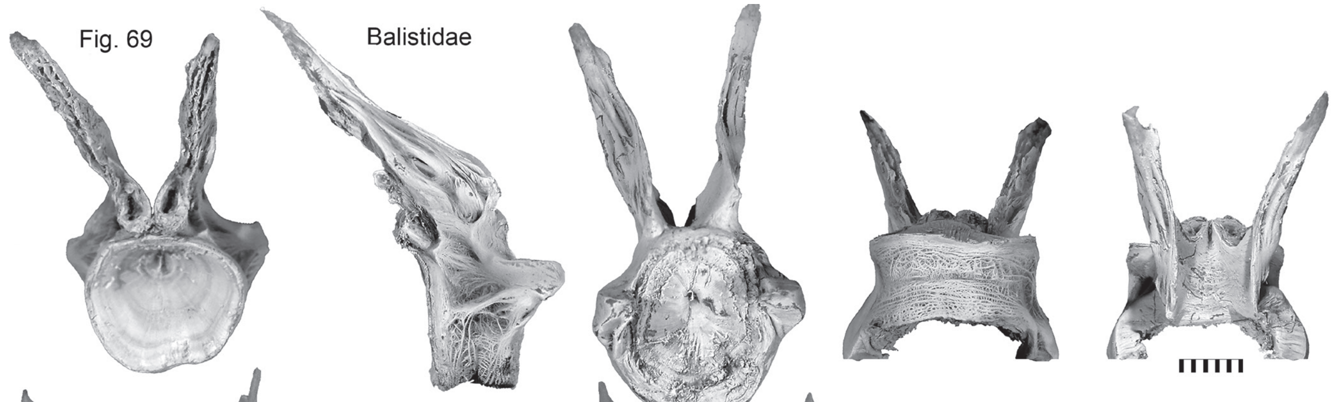


Fig. 69 Balistidae

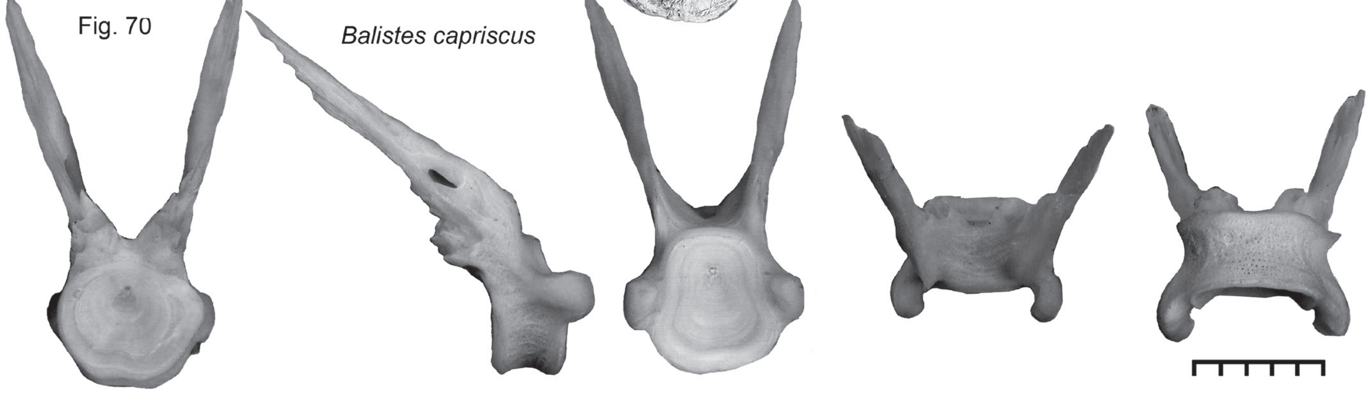


Fig. 70 *Balistes capriscus*

Fig. 71 *Chilomycterus schoepfii*

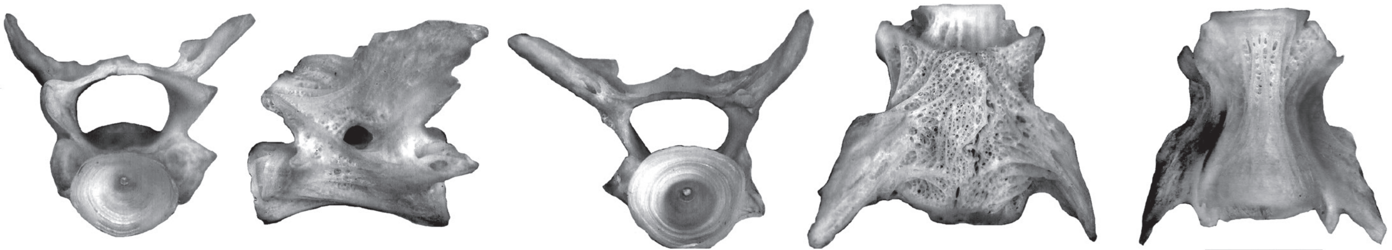


Fig. 72 *Lateolabrax japonicus*

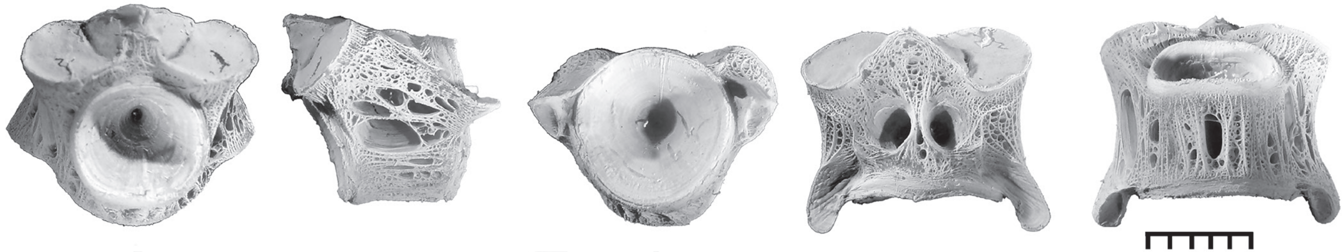


Fig. 73 *Polyprion oxygeneios*

verse processes project posterolaterally. The bone texture is formed of ridges separating fairly large, deep, oval to round cells on the centrum as well as the neural arch and spine. On the ventral surface, these ridges are relatively closer together and the cells are smaller, but the network is more open dorsally and on the lateral surface it forms large openings. There is a single, oval pit on the ventral surface towards the anterior edge. The ventral length is only slightly shorted than the dorsal length of the centrum, such that the shape in lateral view is almost rectangular. The centrum is only slightly higher than it is long.

Order 27. Centrarchiformes – contains four families, Centrarchidae (sunfishes), Elassomatidae (pygmy sunfishes), Enoplosidae (oldwives) and Sinipercidae (Chinese perches). Members of Enoplosidae are marine, found in Australian waters, but the rest are freshwater fishes. Centrarchidae and Elassomatidae are found in North America, and Sinipercidae, as the name implies, is Asian.

Family 47. Centrarchidae – the sunfishes are found in fresh waters of North America. All our specimens have an autogenous neural arch on the first centrum. The anterior articular facet is angled such that the ventral length of the centrum is less than the dorsal length and the centrum is wedge-shaped in lateral view. Both anterior and posterior articular facets are oval to circular and of similar size with the notochordal foramen positioned just above the midpoint. The exoccipital facets are located dorsally on the sides of the centrum. They are oriented anterodorsally and are separated at least partially in the midline by a tongue of bone. The posterior half of the dorsal surface of the centrum bears a pair of deep round pits for the neural arch separated by a ridge of bone. The long transverse processes originate towards the top of the centrum, project well past the posterior facet, and are hooked medially. The bone texture is formed of ridges defining irregularly shaped cells.

a. Centrachidae – *Ambloplites rupestris* (CMNFI 86-0099.1; Plate 18, Fig. 74) inhabits fresh waters of North America, including the St. Lawrence River and Great Lakes. In anterior view, the first centrum appears much broader than the other centrarchids figured because the transverse processes are larger and more ventrally positioned. The anterior and posterior facets are circular. The large exoccipital facets are irregularly shaped and separated from one another in the dorsal midline. There is no large pit on the ventral surface. The bone texture of the lateral surface, below the exoccipital facets, includes a few larger cells. The transverse processes are large, with a distinct medial hook.

b. Centrarchidae – *Lepomis gibbosus* (UAMZ DB5; Plate 18, Fig. 75) is a freshwater fish also reported from brackish waters, found in the eastern North America including the Great Lakes. The exoccipital facets are large, oval to circular, concave, and oriented dorsally. They are positioned on the dorsal surface of the centrum and meet one another in the midline. The anterior and posterior facets are almost circular and of similar size. The ventral surface bears a single round depression. The bone texture is a network of ridges interconnected by shorter ridges to form small circular to oval spaces. The lateral surface is concave on the lower half. The large transverse processes angle posterolaterally, and are relatively long, extending well beyond the posterior articular facet.

c. Centrarchidae – *Lepomis macrochirus* (CMNFI 1980-0174.1; Plate 18, Fig. 76) is found in the Great Lakes as well as the St. Lawrence and Mississippi river basins. The anterior and posterior facets are circular. The exoccipital facets just meet one another in the midline anteriorly, but are separated from one another posteriorly. The bone texture consists of smaller, more numerous cells than the other figured specimens, and the transverse processes are angled more laterally.

d. Centrarchidae – *Micropterus dolomieu* (CMNFI 1976-0055.1; Plate 18, Fig. 77) inhabits the St. Lawrence and Great Lakes basin as well as the Hudson Bay and Mississippi River drainage basins. The anterior facet is oval, and slightly smaller than the more circular posterior facet. The transverse processes are fairly short, and oriented posteriorly. The bone texture has more distinct ridges and larger cells than the other figured centrarchids.

e. Centrarchidae – *Micropterus salmoides* (CMNFI 1986-0072.1; Plate 18, Fig. 78) is found in the same basins as *M. dolomieu*. Both anterior and posterior facets are pinched-in dorsally, forming wide drop-shapes. The tongue of bone between the exoccipital facets is more prominent and pointed compared to the other centrarchids. The cells of the bone texture are deep, irregular in shape, and are more numerous and smaller than those of *M. dolomieu*.

Order 28. Perciformes – this order continues to be the largest order of vertebrates, despite much work in recent decades that has removed subgroups from the order. We examined several families in different suborders as follows:

Percoidei

Family 48. Percidae – in all our examples of percid fishes, the neural arch on the first centrum is autogenous. The facets for the exoccipitals are fairly large compared to the anterior facet, and positioned high on the centrum so that they reach the dorsal surface of the centrum or extend past it. The facets do not meet one another in the midline. The notochordal foramen is relatively large in all our specimens. The bone texture is formed by ridges of bone except in *Etheostoma caeruleum*, but varies among species in how tightly arranged the ridges are. The species also vary in the orientation of the anterior articular facet for the basioccipital, degree of wedge-shape of the centrum, and relative size of the transverse processes.

a. Percidae – *Etheostoma caeruleum* (UAMZ, Plate 19, Fig. 79) is found in freshwaters of eastern North America, in the

Fig. 74 *Ambloplites rupestris*

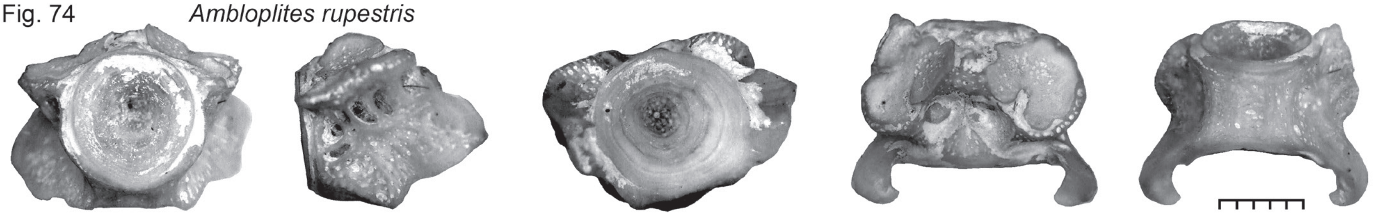


Fig. 75 *Lepomis gibbosus*

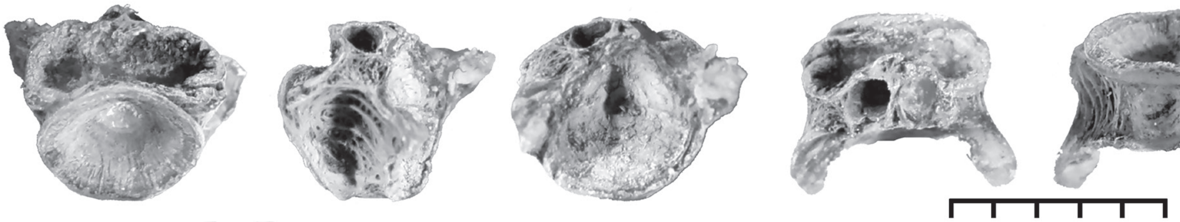


Fig. 76 *Lepomis macrochirus*

Fig. 77 *Micropterus dolomieu*

Fig. 78 *Micropterus salmoides*

Plate 18. First centrum of Acanthopterygii – Centrarchiformes – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 74. Centrarchiformes: Centrarchidae: *Ambloplites rupestris*, CMNFI 1986-0099.1.
Figure 75. Centrarchiformes: Centrarchidae: *Lepomis gibbosus,* UAMZ DB5.
Figure 76. Centrarchiformes: Centrarchidae: *Lepomis macrochirus,* CMNFI 1980-0174.1.
Figure 77. Centrarchiformes: Centrarchidae: *Micropterus dolomieu,* CMNFI 1976-0055.1.
Figure 78. Centrarchiformes: Centrarchidae: *Micropterus salmoides,* CMNFI 1986-0072.1.

Great Lakes and Mississippi River basins. The widely-separated exoccipital facets are concave, oriented anterodorsally, and are positioned low on the centrum compared to other percids, just reaching the dorsal surface. The anterior articular facet has an irregular oval shape, having both sides pinched in. The posterior facet is oval, with the ventral width greater than the dorsal. The relatively large notochordal foramen is positioned distinctly above the midpoint. The ventral length of the centrum is shorter than the dorsal; the centrum is distinctly wedge-shaped in lateral view. The centrum is about twice as high as it is long. There is a large depression on each lateral surface, no pits on the ventral surface, and only the round neural arch pits on the dorsal surface. The bone surface lacks any networks of ridges. The short, round-

Fig. 79 *Etheostoma caeruleum*

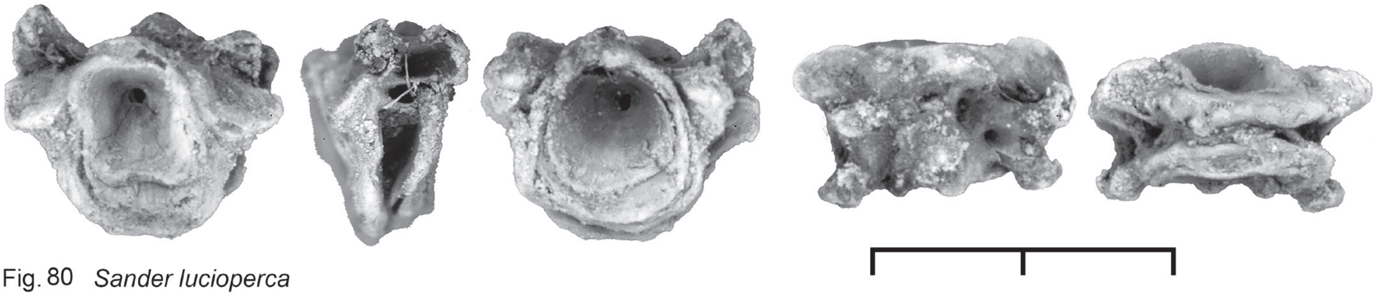


Fig. 80 *Sander lucioperca*

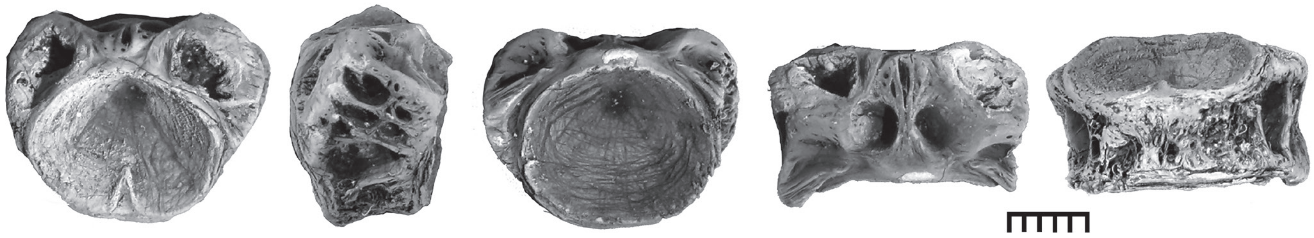


Fig. 81 *Sander lucioperca*

Fig. 82 *Sander canadensis*

Fig. 83 *Sander vitreus*

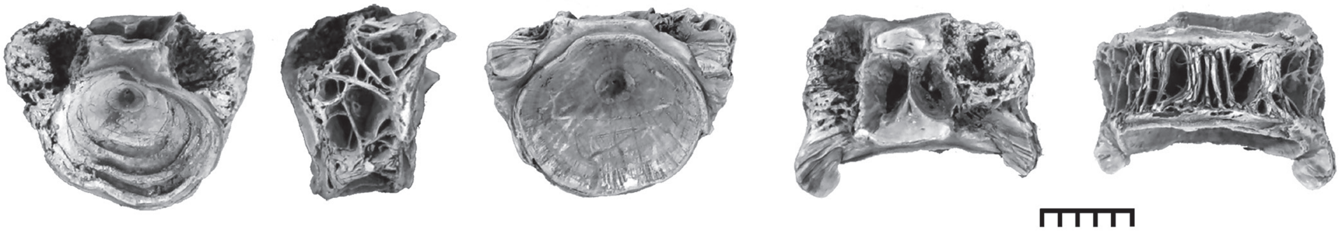


Plate 19. First centrum of Acanthopterygii – Perciformes (Percoidei part 1) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 79. Perciformes: Percoidei: Percidae: *Etheostoma caeruleum,* UAMZ.
Figure 80. Perciformes: Percoidei: Percidae: *Sander lucioperca,* UAMZ F6796.
Figure 81. Perciformes: Percoidei: Percidae: *Sander lucioperca,* UAMZ DB8.
Figure 82. Perciformes: Percoidei: Percidae: *Sander canadensis,* CMNFI 1978-0181.1.
Figure 83. Perciformes: Percoidei: Percidae: *Sander vitreus,* UAMZ F6796.

ed transverse processes are positioned on the dorsal half of the centrum and project posterolaterally.

b. Percidae – *Sander lucioperca* (UAMZ F6796 and DB 8; Plate 19, Figs. 80, 81) is a freshwater fish of Europe. The exoccipital facets are triangular to semicircular (with the broad edge lateral and the tip oriented towards the midline), positioned with the lower edge at midheight of the centrum and extend just to its dorsal surface. The anterior facet is narrower dorsally than ventrally, forming a wide teardrop shape with the notochordal foramen positioned towards the dorsal edge. The posterior articular facet is subcircular. The bone texture forms a more open network of ridges and pits in the smaller specimen. There are two large pits on the dorsal surface for the neural arch, but no large pits on the ventral or lateral surfaces. The ventral length of the centrum is somewhat shorter than the dorsal length (the anterior facet is slanted), forming a slight wedge in lateral view. The centrum is about twice as high as it is long. The short transverse processes are positioned above the midheight of the centrum and project posterolaterally past the posterior facet.

c. Percidae – *Sander canadensis* (CMNFI 1978-0181.1; Plate 19, Fig. 82) inhabits fresh water of Canada and the United States. This species is similar to *S. lucioperca*, but the anterior facet is rounder, and oriented more vertically such that it is less wedge-shaped in lateral view. The ridge of bone separating the neural arch pits on the dorsal surface is quite thick and the transverse processes are oriented more posteriorly.

d. Percidae – *Sander vitreus* (UAMZ F6796; Plate 19, Fig. 83), the walleye, is found in fresh waters throughout North America but is native to the Arctic, Mississippi, and St. Lawrence–Great Lakes basins. The first centrum resembles that of other species in the genus, having roughly circular to drop-shaped anterior and posterior facets, a slight wedge-shape in lateral view, and rounded transverse processes oriented posteriorly. The bone texture is formed of thin ridges delineating irregular cells, which are larger than those of the other species of *Sander*.

d. Percidae – *Perca flavescens* (UAMZ F8745; Plate 20, Fig. 84) is widespread in Canadian fresh waters, and also throughout the United States. The first centrum in this species differs from that of *Sander* spp. in that the centrum is less wedge-shaped, the facets for the exoccipitals are rounder, relatively larger compared to the centrum, and oriented slightly more anteriorly. The anterior facet is rounder. The bone texture is more solid, but still consists of a network of ridges creating spaces between them. The transverse processes are relatively longer and are positioned higher on the centrum, almost at the dorsal edge.

e. Percidae – *Gymnocephalus cernua* (Plate 20, Figs. 85, 86) is a European freshwater fish, but has been introduced elsewhere, including Canada which is where our specimens were collected. The facets for the exoccipitals are relatively very large, oval, and extend above the dorsal surface of the centrum. The bone texture is formed of thicker ridges than in the other percids, and these ridges are anastomosing on the ventral surface of the centrum. The transverse processes are relatively larger than in the other percids.

Serranoidei

Family 49. Serranidae – our two serranid specimens are distinct from one another, but share a few features. The neural arch is autogenous, the exoccipital facets are large, the neural arch pits are large and round, and the bone texture is formed of ridges delineating small cells. But the two taxa differ significantly.

a. Serranidae – *Epinephalus morio* (UAMZ DB11; Plate 20, Fig. 87) is a marine reef species of the Western Atlantic, particularly the Gulf of Mexico and the Caribbean Sea. The exoccipital facets are relatively large, semicircular to rectangular, and located dorsolaterally on the centrum. They are oriented anterodorsally and do not meet in the midline. The round to oval anterior articular facet is oriented almost vertically, and is slightly smaller than the circular posterior facet. The notochordal foramen is positioned dorsal to the midpoint on the anterior facet, but more centrally on the posterior facet. The bone texture on the ventral portion of the lateral surface of the centrum is formed of thin, parallel ridges. A similar bone texture is found on the ventral surface although the ridges are not all parallel; there are rows of circular pits between the ridges. There is no large pit on the ventral surface of the centrum. There is a large lateral opening on the dorsal half of the centrum, and the bone forms a network of striations and vacuities on the side of the exoccipital facet. The dorsal surface of the centrum has two large, round, pits for the neural arch that are separated by a ridge of bone; this bony ridge widens and projects anteriorly as a triangular tongue between the exoccipital facets. The broad transverse processes are above midheight, project posterolaterally and extend just beyond the posterior facet.

b. Serranidae – *Centropristis striata* (CMNFI 86-0066.1; Plate 20, Fig. 88) is a marine fish normally associated with reefs of the Western Atlantic, ranging from the Canadian Maritimes south to the Gulf of Mexico. The anterior facet is oval to drop-shaped, narrower dorsally and taller than wide, whereas the posterior facet is almost circular. The exoccipital facets are kidney bean-shaped, located on the dorsal half of the centrum and oriented almost directly anteriorly. They do not meet one another in the midline. The transverse processes are positioned below midheight on the centrum, and the pointed tips project posterolaterally well past the posterior facet. The bone texture is formed of relatively thick ridges delineating round to oval cells, with no large pits on any surface except for the neural arch pits which are separated by a broad shelf of bone.

Scorpaenoidei

Family 50. Scorpaenidae – *Scorpaena brasiliensis* (CMNFI Z000564; Plate 21, Fig. 89) is a marine, reef-associated fish of the Western Atlantic, found from southern USA to Brazil including the Gulf of Mexico. The neural arch on the first centrum is autogenous. The round anterior facet is oval and the posterior one is circular. Both are oriented vertically so the centrum is rectangular in lateral

Fig. 84 *Perca flavescens*

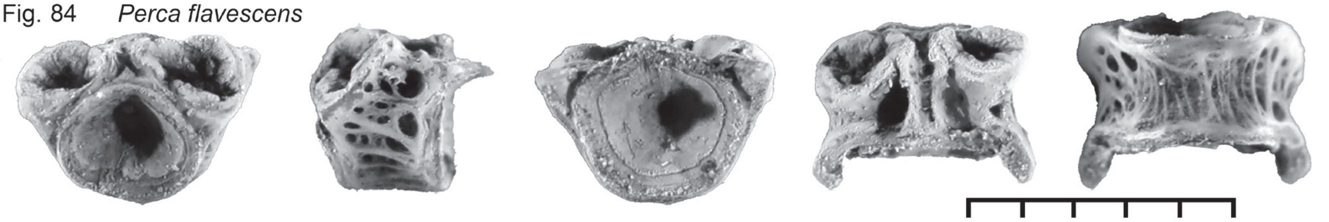


Fig. 85 *Gymnocephalus cernua*

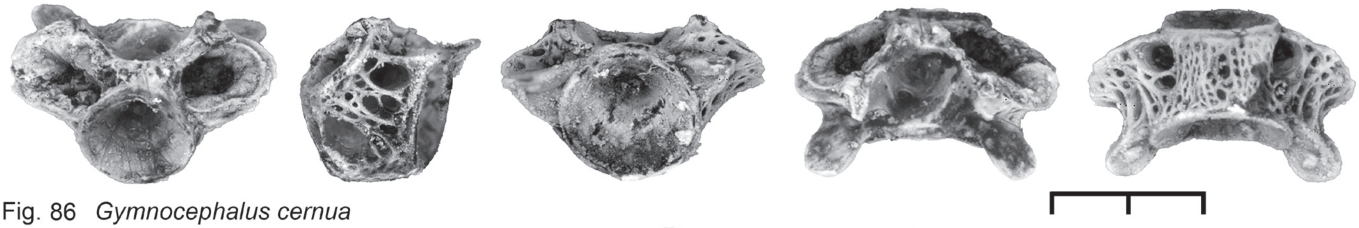


Fig. 86 *Gymnocephalus cernua*

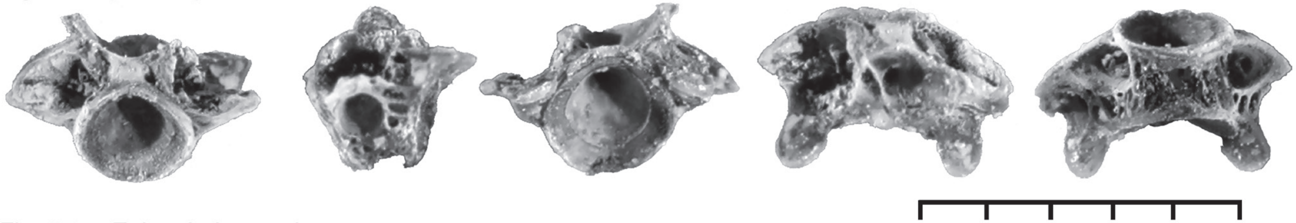


Fig. 87 *Epinephalus morio*

Fig. 88 *Centropristis striata*

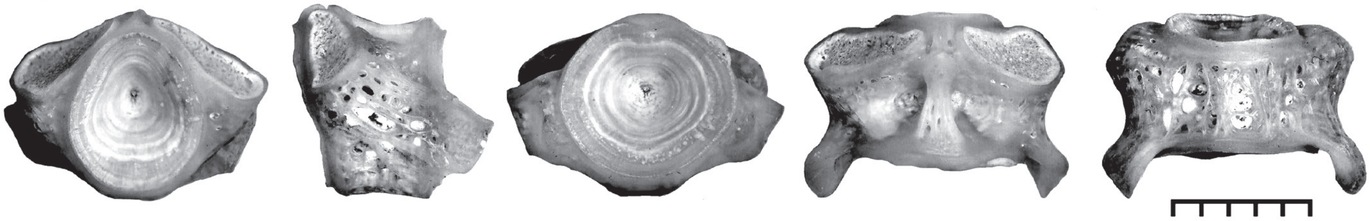


Plate 20. First centrum of Acanthopterygii – Perciformes (Percoidei part 2, and Serranoidei) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 84. Perciformes: Percoidei: Percidae: *Perca flavescens*, UAMZ F8745.
Figure 85. Perciformes: Percoidei: Percidae: *Gymnocephalus cernua*, UAMZ #2.
Figure 86. Perciformes: Percoidei: Percidae: *Gymnocephalus cernua*, UAMZ DB10.
Figure 87. Perciformes: Serranoidei: Serranidae: *Epinephalus morio*, UAMZ DB11.
Figure 88. Perciformes: Serranoidei: Serranidae: *Centropristis striata,* CMNFI 1986-0066.1.

view. The notochordal foramen is at or just above the midpoint. The exoccipital facets extend well above the dorsal surface of the centrum and are oriented anterodorsally. The pointed transverse processes are positioned just above the midheight of the centrum, and are extend posteriorly. The bone texture is formed by thin ridges with sheets of bone delineating irregularly shaped cells. The neural arch pits on the dorsal surface are separated by a broad ridge of bone. There are no large pits on the ventral or lateral surfaces.

Family 51. Sebastidae – *Sebastes mentella* (UAMZ AM5 and UAMZ DB3; Plate 21, Figs. 90, 91) is a marine fish found across the North Atlantic. The neural arch is autogenous. The anterior facet is oval to circular, but slightly pinched inwards dorsally by the exoccipital facets. The posterior facet is heart-shaped with a dorsal indentation. The exoccipital facets are large, round to kidney bean-shaped, and oriented anterodorsally. They extend above the dorsal surface of the centrum but do not meet one another in the midline. The

Fig. 89 *Scorpaena brasiliensis*

Fig. 90 *Sebastes mentella*

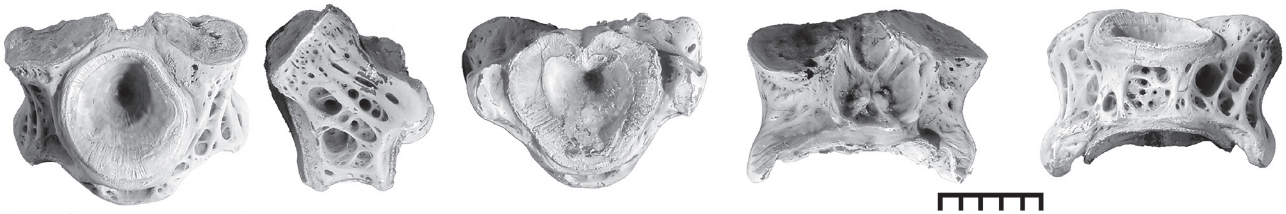


Fig. 91 *Sebastes mentella*

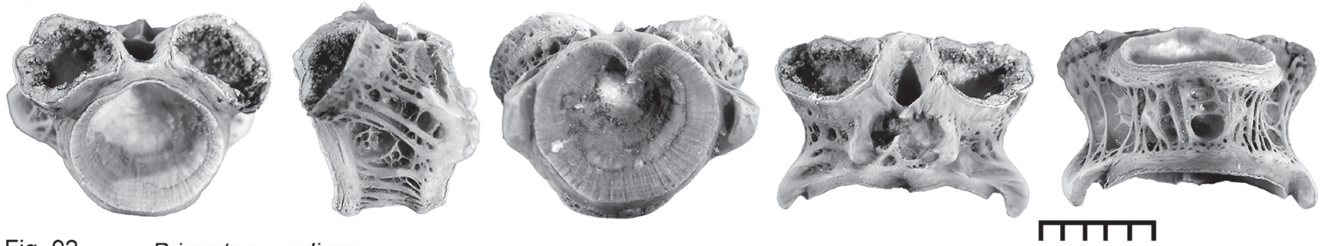


Fig. 92 *Prionotus carolinus*

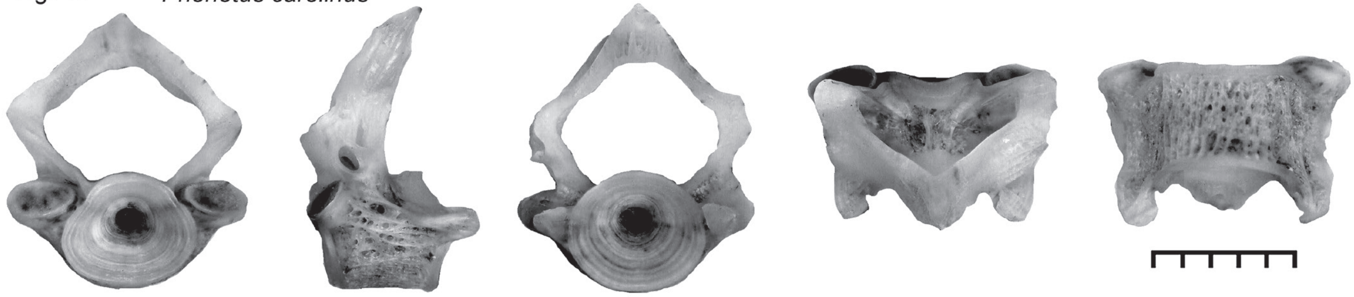


Plate 21. First centrum of Acanthopterygii – Perciformes (Scorpaenoidei) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 89. Perciformes: Scorpaenoidei: Scorpaenidae: *Scorpaena brasiliensis,* CMNFI Z000564.
Figure 90. Perciformes: Scorpaenoidei: Sebastidae: *Sebastes mentella*, UAMZ AM5.
Figure 91. Perciformes: Scorpaenoidei: Sebastidae: *Sebastes mentella*, UAMZ DB3.
Figure 92. Perciformes: Scorpaenoidei: Triglidae: *Prionotus carolinus,* CMNFI 1987-0347.1

bone texture is formed from thick ridges with slightly thinner ridges anastomosing between them and forming circular to oval spaces. Some of these spaces are quite large, but there are no distinct large, deep pits on the lateral or ventral surfaces of the centrum although there is a ventral depression. On the dorsal surface, the 'pits' for the neural arch form shallow depressions that merge together in the midpoint, and have slanting walls forming a funnel-shape rather than a distinct pit. Anterior to these pits there is a shallow trough or depression between the exoccipital facets. The anterior facet is angled only slightly ventrally, so the ventral length of the centrum is only slightly shorter than the dorsal length. The centrum length is about 80% of the height. The broadly rounded transverse processes are located at midheight, and extend posterolaterally.

Triglioidei

Family 52. Triglidae – *Prionotus carolinus* (CMNFI 1987-0347.1; Plate 21, Fig. 92) is a bottom-dwelling coastal marine fish, occasionally found in brackish water, of the Western Atlantic from Nova Scotia, Canada, to Florida, USA including the Gulf of Mexico. The neural arch is fused to the first centrum. The posterior facet is circular and the anterior facet is almost circular, but dorsally it is slightly pinched between the exoccipital facets. The notochordal foramen is located above the centre of the centrum on both facets. The relatively small, oval exoccipital facets are positioned on the sides of the centrum, lateral to the neural arch base, not reaching the dorsal surface, and are oriented anterodorsally. The anterior and posterior facets are vertical so the centrum is rectangular in lateral view. The transverse processes are positioned at midheight on the centrum and are directed posteriorly, with slight medial hooks at their rounded tips. The bone texture is formed by thick longitudinal ridges and thinner cross-ridges forming round to oval cells. There are no large pits on any of the centrum surfaces.

Cottoidei

Family 53. Agonidae – *Hemitripterus americanus* (CMNFI Z000602; Plate 22, Fig. 93) is a marine Atlantic fish inhabiting waters off Labrador, Canada south to Chesapeak Bay, USA. The neural arch is fused to the first centrum. The anterior facet has an irregular shape, being roughly oval but pinched between the exoccipital facets. The posterior facet is almost circular but somewhat flattened ventrally. The notochordal foramen is at about the midpoint in both facets. The anterior facet is slightly inclined such that the centrum has a slightly shorter ventral length than dorsal length. The exoccipital facets are positioned laterally and are broadly separated from each other. They are semicircular and oriented anterodorsally. The transverse processes are situated at the midheight of the centrum but angle dorsally and extend posterolaterally. They are rounded with no median hook. The bone texture is formed by anastomosing ridges delineating circular to oval cells on all surfaces with no large pits.

Family 54. Anoplopomatidae – *Anoplopoma fimbria* (CMNFI Z000050; Plate 22, Fig. 94) is a deep-water marine fish of the North Pacific. Unlike the other members of this suborder that we figure, the neural arch on the first centrum is autogenous. The circular anterior and posterior facets are almost the same size (the anterior one is a bit smaller) with the notochordal foramen located just above the midpoint. The centrum is twice as wide as it is long, and the width is not quite twice the height. The large, round exoccipital facets are positioned laterally and oriented almost directly anteriorly. The bone texture is a honeycomb of circular cells on all surfaces, with the only large pits present being the pair of

Fig. 93 *Hemitripterus americanus*

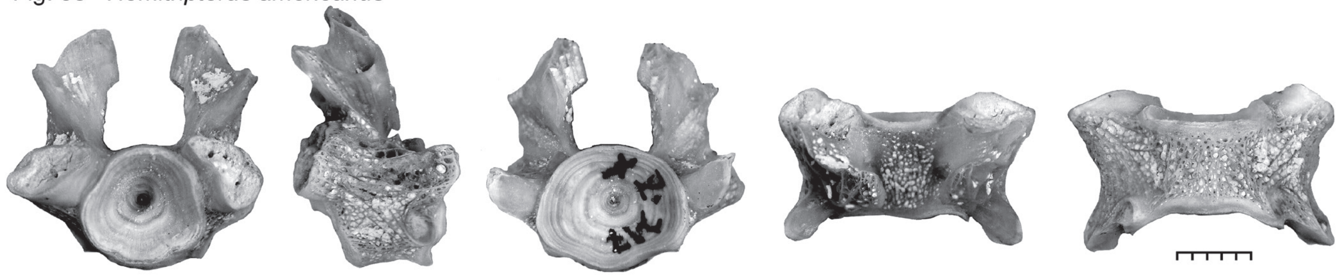


Fig. 94 *Anoplopoma fimbria*

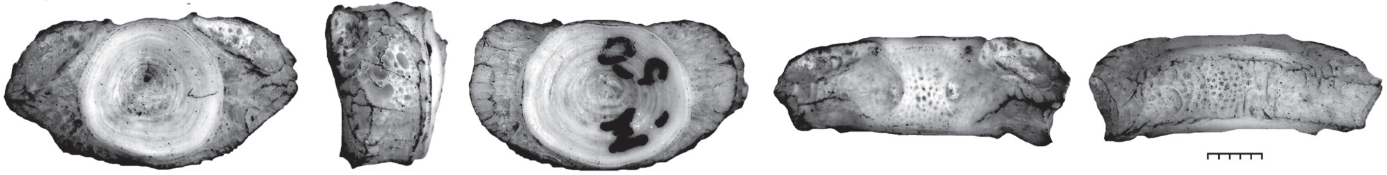


Fig. 95 *Ophiodon elongatus*

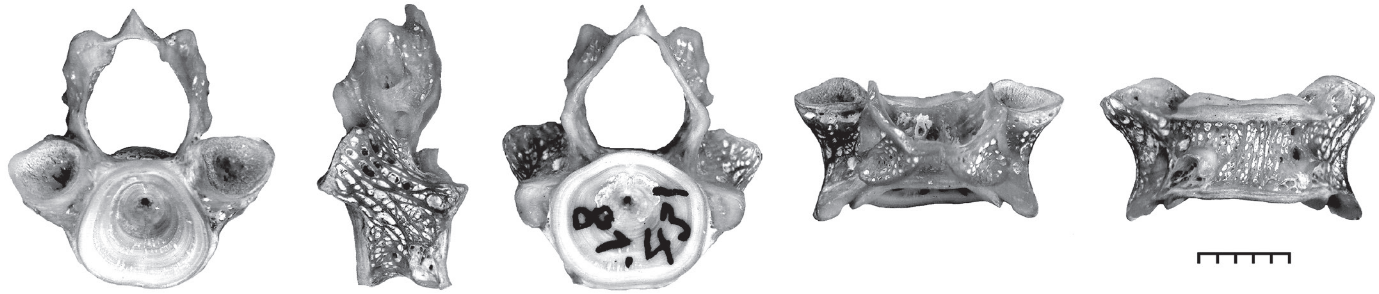


Plate 22. First centrum of Acanthopterygii – Perciformes (Cottoidei, Agonidae, Anoplopomatidae and Hexagrammidae) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.

Figure 93. Perciformes: Cottoidei: Agonidae: *Hemitripterus americanus,* CMNFI Z000602.

Figure 94. Perciformes: Cottoidei: Anoplopomatidae: *Anoplopoma fimbria,* CMNFI Z000050.

Figure 95. Perciformes: Cottoidei: Hexagrammidae: *Ophiodon elongatus,* CMNFI 1987-0431.1.

widely-separated neural arch pits on the dorsal surface. There are no transverse processes.

Family 55. Hexagrammidae – *Ophiodon elongatus* (CMNFI 1987-431.1; Plate 22, Fig. 95) is a marine, demersal fish of the Northeast Pacific. The first centrum of this species is similar to that of the cottids. The neural arch is fused to the centrum and forms a large neural canal. The centrum is slightly wider and taller than it is long. The anterior facet is oval, but wider ventrally than dorsally; the posterior facet is almost circular. The notochordal foramen is located dorsal to the midpoint. The exoccipital facets are positioned laterally, not meeting one another in the midline. They are roughly circular, oriented anterodorsally and project anteriorly farther than the anterior facet. The transverse processes are short, positioned just above midheight on the centrum and project posterolaterally. The bone texture is formed by thick ridges connected by thinner ridges forming irregular cells. There is a pair of larger pits or cells on the ventrolateral surface.

Family 56. Cottidae – Our five examples of sculpins all have the first neural arch fused with the centrum. The anterior and posterior facets are more or less vertical so the centrum is more rectangular than wedge-shaped. The exoccipital facets are large and positioned laterally, and extend anteriorly past the anterior facet to differing degrees. In all, the anterior facet is more-or-less oval, and constricted between the exoccipital facets. The bone texture is formed by ridges delineating small cells.

a. Cottidae – *Cottus ricei* (UAMZ F6720; Plate 23, Fig. 96) is found in freshwaters of North America, from northeastern British Columbia, the Northwest Territories, and Yukon in the north, through the St. Lawrence River, and Great Lakes, and rivers draining into them. The neural arch canal is as broad across as the anterior facet of the centrum. The large, round, exoccipital facets are widely separated, protrude only slightly above the dorsal surface of the centrum, and extend anteriorly farther forward than the anterior articular facet. The anterior facet is a broad oval, but narrower dorsally than ventrally, and faces anteriorly so that the dorsal and ventral lengths of the centrum are essentially equal. The posterior facet is circular and the notochordal foramen is positioned dorsal to the midpoint. The bone texture on the lateral, dorsal and ventral surfaces of the centrum forms a tight network of thin ridges; the ridges are more widely space to form a more open network on the lateral sides of the facets for the exoccipitals and the neural arch. There are two small, round pits on the dorsal surface of the centrum medial to the neural arch, located posterior to the midpoint. There is a single round pit in the midline of the ventral surface. The broadly rounded transverse processes are positioned just above the midheight of the centrum, and project posterolaterally.

b. Cottidae – *Hemilepidotus hemilepidotus* (CMNFI 1989-0505.1; Plate 23, Fig. 97) is a marine sculpin found in the North Pacific. The anterior facet is oval to rectangular, and not as constricted as in the other figured sculpins. The posterior facet is almost diamond shaped; the notochordal foramen is at the mid-point. The exoccipital facets extend much farther anteriorly than, and are almost as large as, the anterior facet. The transverse processes project posteriorly and are relatively short and rounded. The bone texture is fairly smooth, with the small cells being very shallow and the ridges quite thick. There is a pair of well-separated, shallow depressions on the dorsal surface of the centrum.

c. Cottidae – *Leptocottus armatus* (CMNFI 77-0203.1; Plate 23, Fig. 98) is a marine and brackish-water sculpin of the northeastern Pacific Ocean. The anterior and posterior facets are more circular in this species, but the anterior one is wider ventrally. The notochordal foramen is in the centre of both facets. The exoccipital facets are positioned lower than in the other species, being at the midheight of the centrum, and oriented anterolaterally. The transverse processes are positioned higher on the centrum than the exoccipital facets. The centrum is longer than high, unlike the other species in which the height is about the same as the length. The bone texture is similar to that of *Hemitripterus americanus*.

d. Cottidae – *Myoxocephalus polyacanthocephalus* (CMNFI 1987-0455.1; Plate 23, Fig. 99) is found in marine waters of the North Pacific. The anterior facet is constricted dorsally to form a pear-shaped surface and the posterior facet is depressed to form an oval wider than high. The notochordal foramen is positioned towards the dorsal edge on both facets. The centrum is slightly wedge-shaped in lateral view. The large, triangular, concave exoccipital facets are oriented anterolaterally. The transverse facets are positioned at midheight on the centrum, are well-developed and angle posterolaterally. The bone texture is honeycomb-like similar to that of *Leptocottus armatus* and *Hemitripterus americanus*.

Zoarcoidei

Family 57. Anarhichadidae – *Anarhichas denticulatus* (CMNFI 1975-064.1; Plate 24, Fig. 100), a wolffish, is a marine, benthopelagic species of the northern Atlantic, reaching south to Nova Scotia, Canada. The neural arch on the first centrum is autogenous. The anterior articular facet is oval to tear drop-shaped, narrower dorsally. The posterior facet is almost circular, with the notochordal foramen positioned above the midpoint in both facets. Both facets are inclined so that the centrum is strongly wedge-shaped with the ventral length about half the dorsal length. The circular exoccipital facets are retracted behind the anterior facet, and are oriented more dorsally than anteriorly. The long transverse processes are pointed and angle posterolaterally. The bone texture is a honeycomb with anastomosing

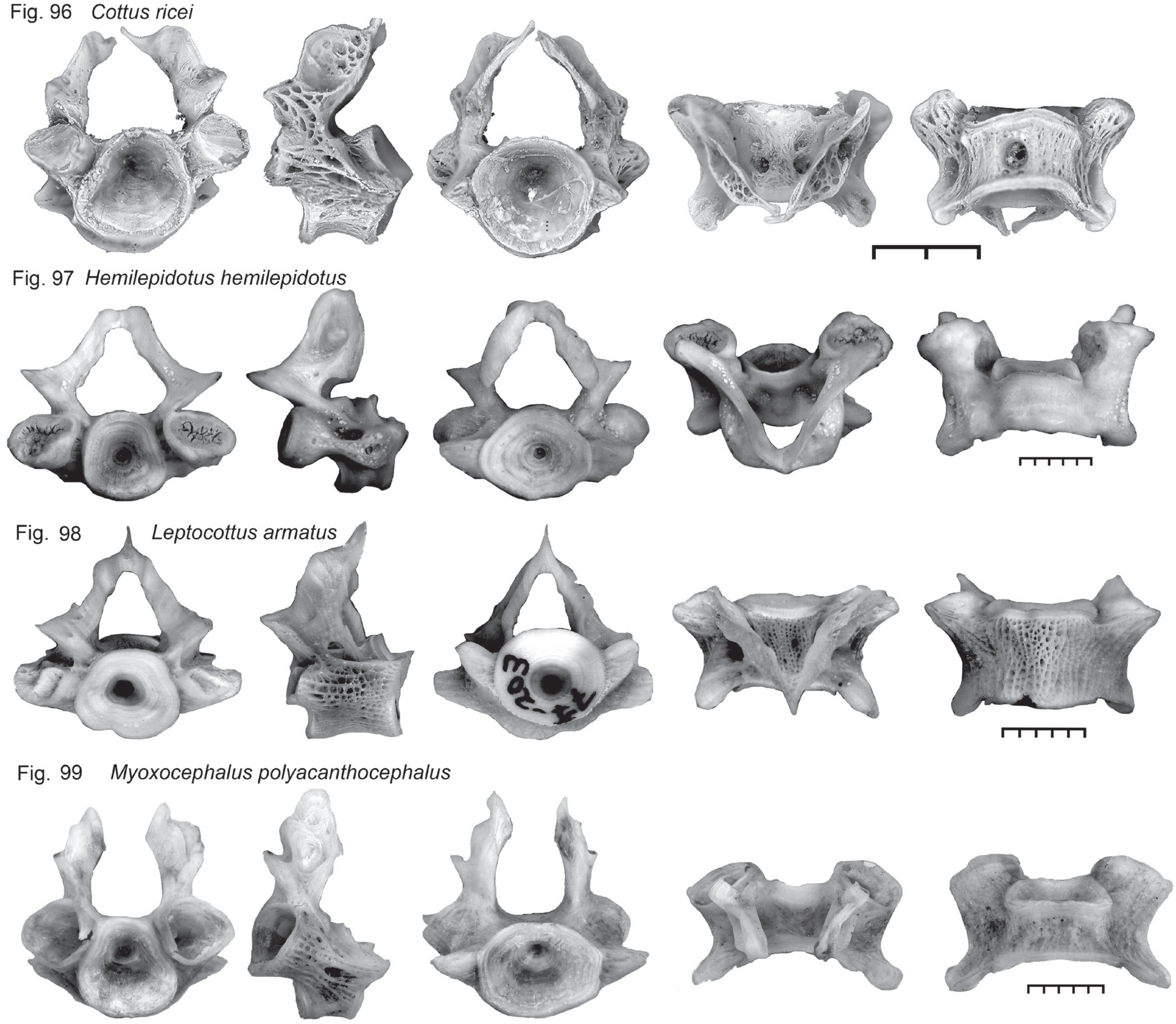


Plate 23. First centrum of Acanthopterygii – Perciformes (Cottoidei, Cottidae) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 96. Perciformes: Cottoidei: Cottidae: *Cottus ricei*, UAMZ F6720.
Figure 97. Perciformes: Cottoidei: Cottidae: *Hemilepidotus hemilepidotus*, CMNFI 1989-0505.1.
Figure 98. Perciformes: Cottoidei: Cottidae: *Leptocottus armatus*, CMNFI 1977-0203.1.
Figure 99. Perciformes: Cottoidei: Cottidae: *Myoxocephalus polyacanthocephalus*, CMNFI 1987-0455.1.

ridges delineating irregularly shaped cells, with the cells being larger on the lateral surface than on the dorsal or ventral surfaces. There are no large pits on any of the surfaces except for the small circular neural arch pits which are well separated and positioned posteriorly on the centrum.

Family 58. Cryptacanthodidae – *Cryptacanthodes maculatus* (CMNFI 87-0329.1; Plate 24, Fig. 101) is a Western Atlantic fish found off the coast of Labrador, Canada, south to New Jersey, USA. It burrows in muddy substrate. The neural arch is autogenous. The vertical anterior and posterior facets are circular, with the notochordal foramen positioned dorsal to the midpoint. The centrum is rectangular in lateral view. The exoccipital facets are positioned laterally, just reaching the dorsal surface of the centrum, and oriented anterodorsally. The transverse processes are located at midheight on the centrum and project posterolaterally. The centrum is about half as long as it is wide or tall. The bone texture is fairly smooth, with broad ridges and shallow cells on the centrum surfaces, with larger cells lateral to the exoccipital

Fig. 100 *Anarhichas denticulatus*

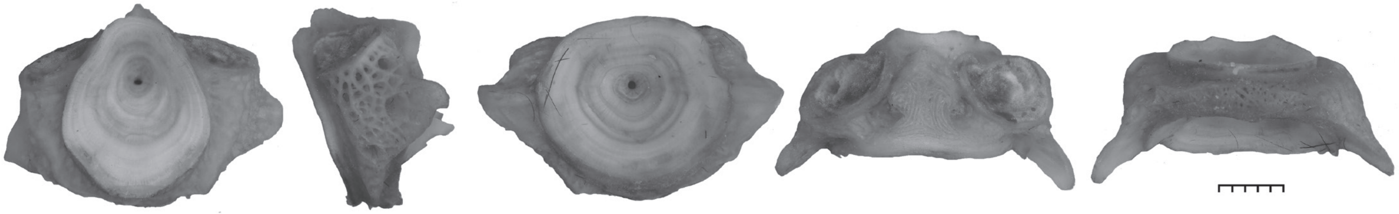


Fig. 101 *Cryptacanthodes maculatus*

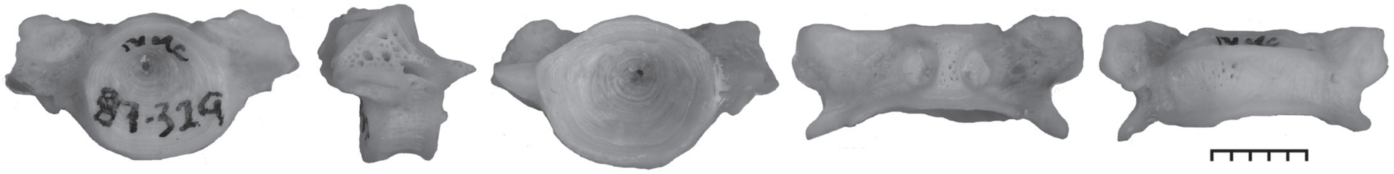


Fig. 102 *Acantholumpenus mackayi*

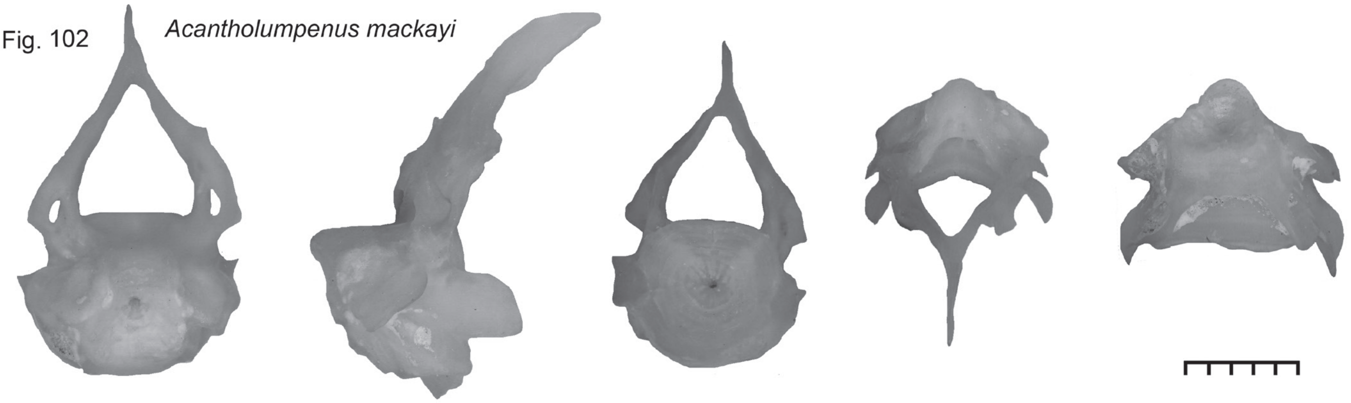


Fig. 103 *Lycodes lavalaei*

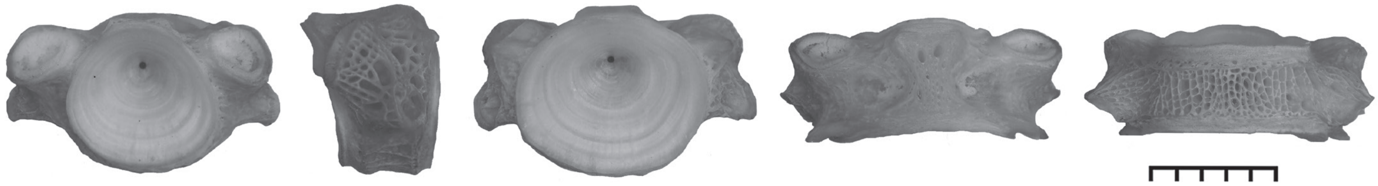


Plate 24. First centrum of Acanthopterygii – Perciformes (Zoarcoidei) – in anterior, left lateral, posterior, dorsal, and ventral views. Anterior towards top of page for the dorsal and ventral views. Scale bars are in millimetres.
Figure 100. Perciformes: Zoarcoidei: Anarhichadidae: *Anarhichas denticulatus,* CMNFI 1975-0064.1.
Figure 101. Perciformes: Zoarcoidei: Cryptacanthodidae: *Cryptacanthodes maculatus,* CMNFI 1987-0329.1.
Figure 102. Perciformes: Zoarcoidei: Stichaeidae: *Acantholumpenus mackayi,* CMNFI 1987-0302.1.
Figure 103. Perciformes: Zoarcoidei: Zoarcidae: *Lycodes lavalaei,* CMNFI 1989-0525.1.

facets. The only large pits are the round neural arch pits on the dorsal surface.

Family 59. Stichaeidae – *Acantholumpenus mackayi* (CMNFI 1987-0302.1; Plate 24, Fig. 102). This genus is placed in Lumpenidae by Froese and Pauly (2023). It is found in the North Pacific and Arctic oceans, in the Bering Sea, and Sea of Okhotsk. Unlike the other zoarcoids figured here, this species has the neural arch fused to the centrum. The anterior facet is pinched-in dorsally between the exoccipital facets; the latter are low on the centrum and oriented anterolaterally. The posterior centrum is circular to square in shape. Both anterior and posterior facets have a centrally-located notochordal foramen. The dorsal surface of the centrum forms an anterior shelf over the anterior facet. The transverse processes are large with the pointed tips oriented posteriorly. The bone texture is smooth, with no ridges or cells and no large pits.

Family 60. Zoarcidae – *Lycodes lavalaei* (CMNFI 1989-0525.1; Plate 24, Fig. 103) is found in Canadian waters of the Atlantic Ocean. The neural arch is autogenous. The anterior and posterior facets are sub-circular with a dorsally-positioned notochordal foramen. The dorsal surface of the centrum forms an anterior shelf over the anterior facet. The circular exoccipital facets are oriented almost anteriorly. The centrum is slightly less than twice as high and wide as it is long. The bone texture is formed of thin longitudinal ridges interconnected by short irregularly oriented ridges forming irregularly shaped cells; these cells are larger on the lateral surface. The only large pits are those for the neural arch, which are widely spaced.

DISCUSSION

Articulated acanthomorph fishes first appear in the fossil record in the mid-Cretaceous, with a number of species recovered from the Albian–Cenomanian deposits of Mexico and Canada, and a significant diversity appearing in the Cenomanian of the USA, the Levant, Europe and Africa (see Murray 2016 for summary). These early acanthomorphs are represented by articulated fossils of relatively small body-size and come from marine deposits. The oldest freshwater acanthomorph fish described, *Spinacaudichthys oumtkoutensis*, is from Cenomanian deposits of Morocco (Filleul and Dutheil, 2001); this species was not assigned to any of the known orders or families within Acanthomorpha.

In North America, the earliest articulated freshwater acanthomorph, collected from Maastrichtian deposits of southern Alberta, was assigned to the paracanthopterygian order Percopsiformes (Murray et al. 2019). However, this taxon as well as other acanthomorphs, have been documented in North America from older freshwater sediments of Coniacian age (Brinkman et al. 2013, 2014) based on isolated elements found in microvertebrate sites. Thus, disarticulated material not only establishes an earlier origin of Acanthomorpha than that suggested by articulated skeletons alone, but also has the potential to provide additional data on early diversity in the group.

As Friedman et al. (2023) noted, articulated acanthomorph material is lacking from Maastrichtian through Eocene aged deposits – a time period they called ‘Patterson’s Gap’. However, North American microvertebrate localities containing disarticulated acanthomorph material of this age have been well studied (e.g., Brinkman et al. 2014; Divay and Murray 2016; Brinkman 2019; Sinha et al. 2021). The survey of the first vertebra of numerous orders and families of acanthomorphs presented here is a first step towards more precise identification of the taxa present, and so provides critical information on acanthomorph diversity during an important period in the early evolution of the group.

We find that there is a correlation between the morphology of the individual centra and the higher level grouping of the species. For example, the presence or absence of fusion between the neural arch and centrum appears to be shared among families within a suborder, with only a few exceptions. One exception is among our representative members of Scorpaenoidei which have an autogenous arch with the exception of *Prionotus*; a second exception is among examined representatives of Cottoidei, which all have fused first neural arches with the exception of *Anoplopoma* in which it is not fused; and the third example is within Zoarchoidei, in which the arches are unfused except in *Acantholumpenus*. If these taxa eventually are found to be unique within their respective suborders, it may indicate an avenue of future research to confirm the relationships of these species. The morphology of the first centum also seems indicative of family, with the figured species of Scombridae, Scaridae, Sparidae, Percidae, and Centrarchidae all have a distinctive bone texture as well an overall morphology that is common to members within each family.

Whether or not the morphology of the centra carries a phylogenetic signal has not been investigated. Because the phylogenetic relationships within Acanthomorpha are still not fully resolved (e.g., Betancur-R et al. 2017) and need much more study, it is premature to attempt to identify features of the centrum that indicate evolutionary relationships. However, the use of centrum morphology could be of great help in other areas; this kind of information is especially useful for looking at diversity changes through time or between geographic regions. Based on the survey of morphology presented here, we should be able to confidently determine changes in diversity across the Cretaceous/Palaeogene boundary. For example, if acanthomorph centra found in Maastrichtian and Palaeocene microvertebrate localities within a local area represent species of the same family, that would indicate that that family survived the end-Cretaceous extinction event.

CONCLUSIONS

Our goals for this project were to test whether or not the morphology of the first centrum of acanthomorphs differs among orders and families, and also to determine if the morphology within a larger clade is consistent to the extent that fossil elements can be confidently attributed at that level. Although our sample is small compared to the vast number of acanthomorph species, it is clear that within this sample, the first centrum has various morphologies that correlate with higher taxonomic groups. We are confident that based on the documentation of this variation, it will be possible to identify many fossil centra to extant acanthomorph families, suborders or orders. This will allow us to gain a better understanding of the timing of origination of some lineages, based on the greater amount of material that is available from microvertebrate localities.

ACKNOWLEDGEMENTS

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