Monograph 1

Phylogenetic Systematics of the Needlefishes (Beloniformes: Belonidae)

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ABSTRACT

Phylogenetic relationships of the family Belonidae with four related families (Scomberesocidae, Zenarchopteridae, Hemiramphidae and Exocoetidae) were reconstructed based on mainly osteological characters. A cladistic analysis resulted in three most parsimonious trees based on characters in 58 transformation series. The family Belonidae is inferred as a non-monophyletic group, due to the family Scomberesocidae nesting within the former, the clade including all belonids and scomberesocids giving rise to two subsequent clades, *viz.*, *Ablennes* + *Potamorrhaphis* + *Pseudotylosurus* + *Strongylura* + *Tylosurus* + *Xenentodon* and *Belone* + *Petalichthys* + *Platybelone* + all scomberesocids. Belonidae is revised to include all belonids and scomberesocids, the two subclades comprising the subfamilies Tylosurinae and Beloninae, respectively. A key to subfamilies is provided for the family.

KEY WORDS: Scomberesocidae, phylogeny, osteology, cladistics, monophyly

INTRODUCTION

Needlefishes (family Belonidae Bonaparte, 1835) include 47 species in 10 genera (Nelson *et al*., 2016), most species being epipelagic in tropical to warm temperate marine waters. However, all species in the South American genera *Belonion* Collette, 1966, *Potamorrhaphis* Günther, 1866 and *Pseudotylosurus* Fernández-Yépez, 1948, the Southeast Asian genus *Xenentodon* Regan, 1911, and three species in the genus *Strongylura* van Hasselt, 1824 are restricted to freshwater (13 species in total), with several additional species of *Strongylura* moving long distances into freshwater (Collette, 2003; Sant'Anna *et al*., 2012; Nelson *et al*., 2016). The family is characterized by both upper and lower jaws extending into long beaks filled with sharp teeth (except for two neotenic species in the genus *Belonion* having a short upper jaw), the third pharyngobranchials separated, relatively small scales on the body (usually 130–350 lateral line scales) and deciduous, dorsal fin rays, usually 11–26 (but up to 43), anal fin rays 12–39, vertebrae 52–97, and no isolated finlets following the dorsal and anal fins (Collette, 2003; Nelson *et al*., 2016). Together with the family Scomberesocidae (sauries), Belonidae forms the superfamily Scomberesocoidea (Collette *et al*., 1984: fig. 184; Nelson *et al*., 2016), included in the suborder Exocoetoidei (Nelson *et al*., 2016) with the superfamily Exocoetoidea (comprising Exocoetidae [flying fishes], Hemiramphidae [halfbeaks] and Zenarchopteridae [viviparous halfbeaks]). Since establishment of the family Belonidae, this family has been treated as valid by many authors (*e.g.*, Gill, 1872; Regan, 1911; Rosen, 1964; Rosen and Parenti, 1981; Collette *et al*., 1984; Nelson *et al*., 2016) for over a century, being distinguished from the family Scomberesocidae by characters such as absence of finlets (*vs*. finlets present in scomberesocids). Boughton *et al*. (1991) inferred the phylogenetic relationships of belonid species based on external morphology (mainly lateral line system) and limited osteological data, but did not show relationships of the family and related taxa, using only two scomberesocid species (other than needlefishes) as outgroups. Lovejoy (2000) analyzed the phylogenetic relationships of the family Belonidae and related taxa (= exocoetoids) from mainly molecular data (484 bp Tmo, 641 bp cyt *b*, 371 bp 16S and 36 morphological, in total 1532 characters) and suggested that the family was non-monophyletic because it included the family Scomberesocidae nested within it. Subsequently, Lovejoy *et al*. (2004) analyzed the phylogenetic relationships of exocoetoids and additional taxa from nuclear gene sequences, and presented similar conclusion. However, none of the above three studies proposed a revised classification, based on the inferred phylogenetic relationships.

The purposes of the present study were: (1) to describe the osteology of Belonidae; (2) to reconstruct the phylogenetic relationships of Belonidae and related taxa; (3) to evaluate the monophyly of the family; and (4) to establish a new classification at the familial level based on reconstructed relationships.

MATERIALS AND METHODS

Examinations of osteology and external morphology were generally made on specimens stained with Alizarin Red-S and Alcian Blue, a specimen of *Belonion dibranchodon* alone was cleared and stained by Potthoff's (1984) technique. Stereomicroscopes with a camera lucida (Leica MZ-12) were used for dissection and sketch-making. In most cases, drawings were made from left side, but when "mirror image" is shown in figure caption, the drawing was made from right side and reversed. Terminology follows Rojo (1991) for general osteology, Fujita (1990) for caudal skeleton and

Freihofer (1978) for nerves. Standard length (SL: *sensu* Hubbs and Lagler, 1958) was measured in specimens, except belonids and scomberesocids. Body length (BL: *sensu* Collette, 1966), defined as the distance from the posterior margin of the subopercle to the base of the caudal fin (= end of hypurals), was measured in belonids and scomberesocids because the elongated upper jaw of most species was easily damaged. Generic and specific names follow Collette and Parin (1970), Hubbs and Wisner (1980), Collette (2003, 2004), Parenti (2008), Aizawa and Doiuchi (2013), Senou (2013a, b) and Lewallen *et al*. (2017). Two specimens each of the belonid *Ablennes hians* (Valenciennes in Cuvier and Valenciennes, 1846) and scomberesocid *Cololabis saira* (Brevoort, 1856) were dissected and examined to clarify intraspecific variation. Figures of these two species were prepared from HUMZ 225353 and HUMZ 227067, respectively, unless otherwise indicated. Areas colored light blue (online version) and gray (printed version) in figures indicate cartilages.

Material examined

Museum collection abbreviations follow Sabaj (2019).

Beloniformes: Exocoetoidei

Belonidae: *Ablennes hians* (Valenciennes in Cuvier and Valenciennes, 1846), HUMZ 225350, 265.2 mm BL, HUMZ 225353, 256.8 mm BL; *Belone belone* (Linnaeus, 1760), HUMZ 229236 (formerly USNM 216681), 203.9 mm BL; *Belonion dibranchodon* Collette, 1966, HUMZ 229211 (formerly INPA-ICT 052117), 34.8 mm BL; *Petalichthys capensis* Regan, 1904, HUMZ 229235 (formerly SAIAB 11930), 167.7 mm BL; *Platybelone argalus argalus* (Lesueur, 1821), HUMZ 229239 (formerly USNM 291425), 166.8 mm BL; *Potamorrhaphis guianensis* (Jardine in Schomburgk, 1843), HUMZ 229240 (formerly USNM 292689), 129.4 mm BL; *Pseudotylosurus angusticeps* (Günther, 1866), HUMZ 229212 (formerly LACM 39672.001), 177.3 mm BL; *Pseudotylosurus microps* (Günther, 1866), HUMZ 229210 (formerly INPA-ICT 004835), 172.5 mm BL; *Strongylura exilis* (Girard, 1854), HUMZ 229241 (formerly USNM 291425), 120.1 mm BL; *Strongylura krefftii* (Günther, 1866), HUMZ 229209 (formerly AMS I.20860-001), 185.6 mm BL; *Strongylura leiura* (Bleeker, 1850), HUMZ 229242 (formerly USNM 206074), 146.3 mm BL; *Strongylura strongylura* (van Hasselt, 1823), HUMZ 229208 (formerly AMS I.25638-001), 176.6 mm BL; *Tylosurus acus imperialis* (Rafinesque, 1810),

HUMZ 229243 (formerly USNM 201438), 238.6 mm BL; *Tylosurus acus melanotus* (Bleeker, 1850), HUMZ 229216 (formerly FRLM 42082), 458.0 mm BL; *Tylosurus gavialoides* (Castelnau, 1873), HUMZ 229213 (formerly QM I.22220), 209.3 mm BL; *Tylosurus punctulatus* (Günther, 1872), HUMZ 229230 (formerly CAS 37463), 155.2 mm BL; *Xenentodon cancila* (Hamilton, 1822), HUMZ 225515, 110.0 mm BL.

Scomberesocidae: *Cololabis saira* (Brevoort, 1856), HUMZ 227067, 140.0 mm BL, HUMZ 228020, 182.3 mm BL; *Elassichthys adocetus* (Böhlke, 1951), HUMZ 229231 (formerly CAS 228231), 34.0 mm BL; *Nanichthys simulans* Hubbs and Wisner, 1980, MCZ 57520, 45.6 mm BL; *Scomberesox saurus* (Walbaum, 1792), HUMZ 213933, 141.6 mm BL.

Hemiramphidae: *Hemiramphus far* (Forsskål, 1775), HUMZ 224363, 175.3 mm SL.

Zenarchopteridae: *Zenarchopterus dunckeri* Mohr, 1926, HUMZ 227347, 72.2 mm SL.

Exocoetidae: *Cypselurus doederleini* (Steindachner in Steindachner and Döderlein, 1887), HUMZ 50216, 245.4 mm SL; *Exocoetus monocirrhus* Richardson, 1846, HUMZ 112152, 146.2 mm SL; *Fodiator acutus* (Valenciennes in Cuvier and Valenciennes, 1847), HUMZ 229232 (formerly SU 52690), 178.9 mm SL; *Parexocoetus brachypterus* (Richardson, 1846), HUMZ 114188, 127.2 mm SL.

Taxa related to Exocoetoidei

Adrianichthyidae (Beloniformes: Adrianichthyoidei): *Oryzias javanicus* (Bleeker, 1854), HUMZ 227068, 28.4 mm SL.

Poeciliidae (Cyprinodontiformes): *Poecilia mexicana Steindachner*, 1863, HUMZ 227069, 40.4 mm SL.

Atherinidae (Atheriniformes): *Atherinomorus pinguis* (Lacepède, 1803), HUMZ 122255, 91.4 mm SL.

SYSTEMATIC METHODOLOGY

The cladistic methodology formulated by Hennig (1966) was adopted for estimation of the phylogenetic

relationship of Belonidae. Outgroup comparisons were adopted to determine character polarity (Watrous and Wheeler, 1981; Wiley, 1981). Character data was analyzed using PAUP* 4.0α161 (Swofford, 2018), including ACCTRAN (accelerated transformation) optimizations, and 100 heuristic searches involving simple addition sequences and TBR (tree bisection and reconnection) branch swapping under the optimality criterion of parsimony. All characters were unweighted. Character evolution was assumed as "unordered" (Fitch parsimony: Fitch, 1971) when two or more characters are recognized in a transformation series. Character evolution in reconstructed phylogenetic relationships was estimated using MacClade version 4.0 (Maddison and Maddison, 2000). Autapomorphies observed only in terminal taxa and variations observed only in outgroups were not used for the analysis because they had no influence on the determination of relationships. Additionally, characters varying due to intraspecific variation were not used for the analysis.

TAXON SAMPLING

1. Monophyly of suborder Exocoetoidei

The monophyly of suborder Exocoetoidei is assessed herein, the suborder being an ingroup of the present analysis. Previous morphological studies, such as Rosen and Parenti (1981), inferred that Exocoetoidei was defined by the following five characters: (1) a median lower pharyngeal tooth plate (= fused fifth ceratobranchials) (see Rosen, 1964); (2) a ventral plate-like process posteriorly on the basioccipital; (3) an elongate lower jaw present during some life history stage at least (Nichols and Breder, 1928); (4) more than three anterior branchiostegal rays; and (5) a single narial opening on each side (Burne, 1909). Additionally, Collette *et al*. (1984) inferred that Exocoetoidei was also defined by two ontogenetic characters, (6) egg oil droplets minute or absent and (7) preanal distance in larvae increasing to about 66% SL. "Anterior branchiostegal rays" (character 4) were defined as "anterior, hair-like branchiostegal rays attached to the hypohyal under the depressed part of the ceratohyal" in Rosen (1964). However, such rays were recognized in only eight (out of 27) exocoetoid species examined here. In fact, of the former, only the belonid *Tylosurus punctulatus* had more than three anterior rays. Furthermore, only a single anterior ray was figured in the hyoid arch of *Dermogenys sumatranus* (Exocoetoidei: Zenarchopteridae) (see Rosen, 1964: fig. 14A). Therefore, character (4) does

not support the monophyly of Exocoetoidei. Characters (3), (6) and (7) were not examined in this study, being ontogenetic. However, characters (1) and (5) were recognized here, in addition to character (2) in all exocoetoids examined (except *Belonion dibranchodon*, all species of *Pseudotylosurus* and *Xenentodon cancila*). Thus, character (2) is also considered to support the monophyly of Exocoetoidei. In addition, the absence of the pterosphenoid in all exocoetoids examined here (*vs*. present in all other species) and the presence of a lateral line in all exocoetoids except the belonid *Belonion dibranchodon* and scomberesocid *Elassichthys adocetus* (*vs*. absent in all other species) were recognized here as characters supporting the monophyly of Exocoetoidei (*i.e.*, five supporting morphological characters in all). Recent molecular phylogenetic studies, including Setiamarga *et al*. (2008) and Betancur-R *et al*. (2017), also indicated that Exocoetoidei form a monophyletic group, the monophyly of Exocoetoidei therefore being strongly supported by both morphological and molecular evidence.

2. Taxon sampling of ingroups

Exocoetoid species were used as ingroups for the phylogenetic analysis, *i.e*., Belonidae, Scomberesocidae, Hemiramphidae, Zenarchopteridae and Exocoetidae (18 genera, 25 species in total) to evaluate the monophyly of Belonidae and determine relationships of exocoetoid species. *Belonion dibranchodon* was not included in the analysis due to the specimen being too small and staining unevenly for accurate observation. Similarly, the very small and damaged (*e.g*., neurocranium) specimen of *Elassichthys adocetus* was excluded as accurate observations were not possible. Consequently, character recognition is not discussed for either species, and "all belonids" and "all scomberesocids" refer to those families except for *Belonion dibranchodon* and *Elassichthys adocetus*, respectively.

3. Taxon sampling of outgroups

Previous morphological (*e.g*., Rosen and Parenti, 1981; Collette *et al*., 1984) and molecular studies (*e.g*., Setiamarga *et al*., 2008; Betancur-R *et al*., 2017) revealed the following relationships: (1) Exocoetoidei and Adrianichthyoidei have a sister relationship, together forming Beloniformes; (2) Beloniformes, Cyprinodontiformes and Atheriniformes form a monophyletic group. Accordingly, outgroups (3 genera, 3 species in total) were employed from each family, *i.e*.,

Adrianichthyidae (Beloniformes: Adrianichthyoidei), Poeciliidae (Cyprinodontiformes) and Atherinidae (Atheriniformes).

COMPARATIVE MORPHOLOGY OF BE-LONIDAE

1. Circumorbitals (Figs. 1, 2)

Description

The circumorbitals include the lachrymal and dermosphenotic. All elements are paired.

The lachrymal (= first infraorbital) is a triangular or circular bone, situated on the anterior margin of the orbit, and connected to the maxilla anteriorly and dentary posteriorly, via ligaments. Posterodorsally, the medial surface of lachrymal has a glenoid cavity articulating with the lateral ethmoid. All species have a posterior tubular structure for a sensory canal, which is discontinuous with those of other bones (Fig. 1).

The tube-like or triangular dermosphenotic (= sixth infraorbital) is attached to the frontal dorsally to form the posterior margin of the orbit and had a tubular structure for a sensory canal. In all species except *Strongylura leiura* and *Xenentodon cancila* (Fig. 2D), the dermosphenotic canal is connected to the frontal canal, whereas the dermosphenotic canal is separated from the frontal canal in *St. strongylura* and *X. cancila*.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 1. *Dermosphenotic sensory canal*. 0: connected to frontal canal; 1: separated from it.

Belonids. The dermosphenotic sensory canal is separated from that of the frontal in *Strongylura leiura* and *Xenentodon cancila* (character 1-1), but connected to the frontal in the other species (character 1-0).

Other ingroups. The dermosphenotic sensory canal is connected to the frontal canal in all other ingroups (character 1-0).

Outgroups. In *Atherinomorus pinguis*, the dermosphenotic sensory canal is connected to the frontal canal (character 1-0), but separated from the frontal in the other outgroups (character 1-1).

Other variation

Lachrymal sensory canal. A lachrymal sensory canal is absent in the scomberesocid *Nanichthys simulans*, but present in other species, including *Belonion dibranchodon* and all outgroups. Thus, absence of the lachrymal sensory canal was considered to be an autapomorphy of *N. simulans*.

2. Neurocranium (Figs. 3–15)

Description

The neurocranium comprises the prevomer, ethmoid, nasal, lateral ethmoid, frontal, sphenotic, pterotic, exoccipital, supraoccipital, epiotic, parasphenoid, basisphenoid, prootic and basioccipital. Of these, the prevomer, ethmoid, supraoccipital, parasphenoid, basisphenoid and basioccipital are unpaired elements, but the others paired. The parietal, pterosphenoid and intercalar are absent.

The oval or T-shaped prevomer is situated anteroventrally on the neurocranium, being separated from the nasal in *Belone belone* (Fig. 4) and *Petalichthys capensis*, but attached to the nasal anterodorsally in all other species (Fig. 3). Note, however, that the prevomer is unossified and its margin obscure in *Belonion dibranchodon* (Fig. 5). The prevomer is posteriorly attached to the parasphenoid and anterolaterally connected to the maxilla and palatine via a ligament. Teeth are present on the ventral surface in *Tylosurus punctulatus*, but absent in other species. Small concavities occur on the ventral surface of the prevomer in *Belone belone* (Fig. 4C). The circular or oblong ethmoid, situated anterodorsally on the neurocranium, is located between the nasals. In *Potamorrhaphis guianensis* (Fig. 7A), all species of *Pseudotylosurus* (Fig. 8A) and *Xenentodon cancila* (Fig. 11A), the ethmoid is covered by the nasals, while the ethmoid is exposed in all other species. Note, however, that the ethmoid is not ossified and its margin obscure in *Belonion dibranchodon* (Fig. 5A).

The rectangular nasal is situated anterodorsally on the neurocranium and attached to the frontal posteriorly
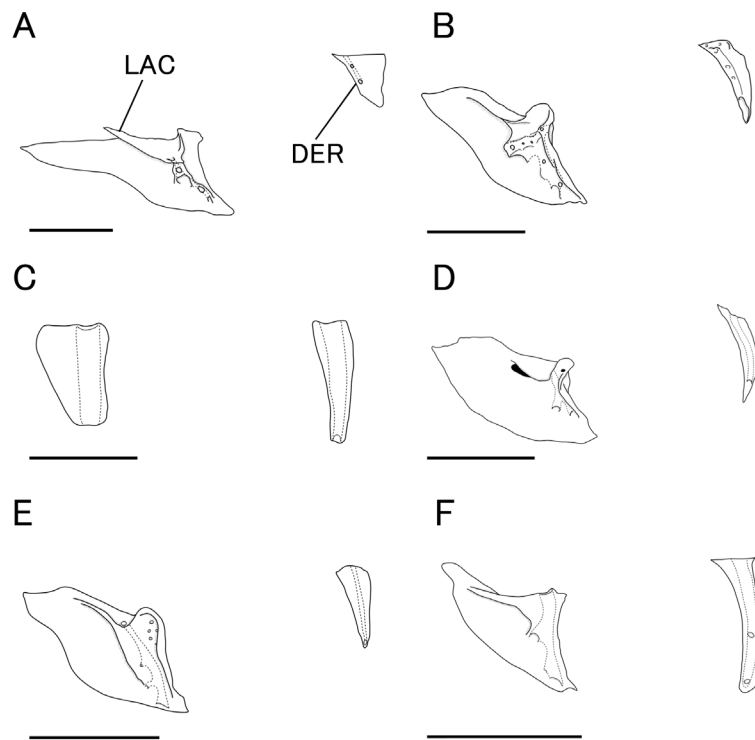
Figure 1. Lateral views of circumorbitals in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon*, mirror image, (D) *Petalichthys capensis*, mirror image, (E) *Platybelone argalus argalus* and (F) *Potamorrhaphis guianensis*. LAC, lachrymal; DER, dermosphenotic. Bars indicate 5 mm (A–B, D–F) and 1 mm (C).
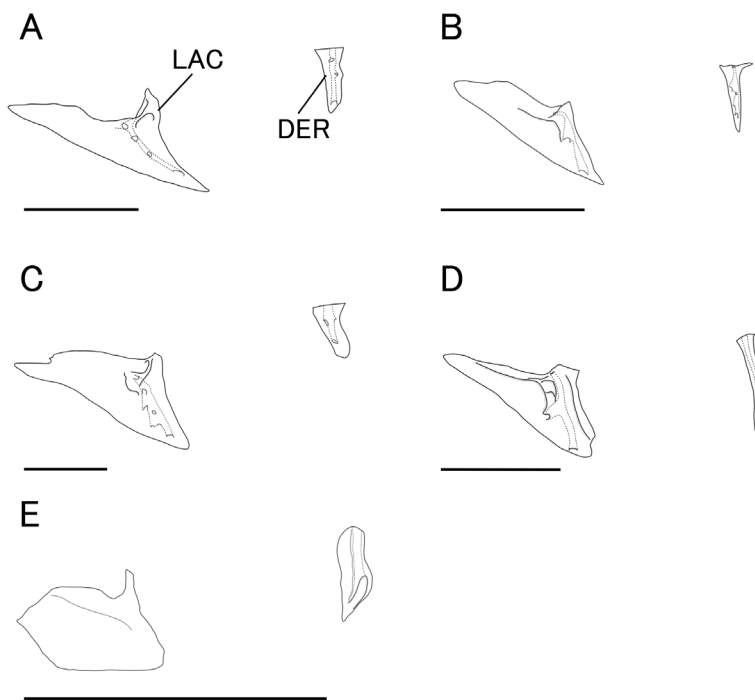
Figure 2. Lateral views of circumorbitals in (A) *Pseudotylosurus angusticeps*, (B) *Strongylura exilis*, (C) *Tylosurus acus imperialis*, (D) *Xenentodon cancila*, mirror image, and (E) *Nanichthys simulans*. Abbreviations as in Fig. 1. Bars indicate 5 mm.

in all species except *Belonion dibranchodon*, in which the nasal is surrounded by a cartilage and thereby attached to the frontal (Fig. 5A). In *Belone belone* (Fig. 4A), *Belonion dibranchodon* (Fig. 5A), *Petalichthys capensis*, *Platybelone argalus argalus* (Fig. 6A) and *Tylosurus acus imperialis*, the paired bones are separated from each other, but attached in all other species. A tubular structure on the nasal for the sensory canal is continuous with the frontal canal. The lateral ethmoid is situated anterolaterally on the neurocranium, forming the anterior wall of the orbit. Although cartilaginous in *Belonion dibranchodon*, the lateral ethmoid shape is clear (Fig. 5B). The lateral ethmoid is attached to the nasal anterodorsally and the frontal posterodorsally, and ventrolaterally articulated with the glenoid cavity of the first infraorbital. The long rectangular or parallelogram frontal is the largest element in the neurocranium, being medially attached to its antimere, anteriorly to the nasal, anteroventrally to the lateral ethmoid, ventrally to the prootic, and posteriorly to the sphenotic, pterotic, epiotic and supraoccipital in all species except *Belonion dibranchodon*, in which the frontal is attached to the cartilaginous lateral ethmoid anteroventrally, and epiotic and supraoccipital posteriorly (Fig. 5). Because the anterior and lateral portions of the frontal are surrounded by a cartilage in this species, the nasal, pterotic and prootic are attached to the frontal via that cartilage. The connection between the frontal and sphenotic is unclear because the margin of the cartilaginous sphenotic of *Belonion dibranchodon* is obscure. The frontal/basisphenoid connection is discussed in the description of the basisphenoid. The dermosphenotic is ventrally attached to the central portion of the frontal, which has a tubular sensory canal structure anteriorly continuous with that of the nasal. The paired frontal canals are interconnected in *Belonion dibranchodon* (Fig. 5A), but separated in other species.

The sphenotic, ossified in all species except *Belonion dibranchodon*, in which it is cartilaginous, is attached to the frontal dorsally, pterotic posteriorly and prootic ventrally. A process is present on the lateral aspect of the sphenotic in all species except *Belonion dibranchodon*, in which the process is absent (Fig. 5B). A tubular structure for the sensory canal is continuous with the frontal and pterotic canals in *Belone belone* (Fig. 4A, B) and *Petalichthys capensis*, but absent in other species. Together with the prootic and pterotic, the sphenotic form a glenoid cavity articulating with a condyle of the hyomandibula. The elongate pterotic is situated posterolaterally on the neurocranium. In *Belonion dibranchodon*, the pterotic is surrounded by cartilage

and not attached directly to any surrounding bones (Fig. 5), whereas the pterotic is attached to the frontal anterodorsally, the epiotic posterodorsally, the prootic anteroventrally and the exoccipital posteroventrally in the other species. In *Belone belone* (Fig. 4A, B) and *Petalichthys capensis*, a tubular structure for the sensory canal is continuous with the sphenotic canal, but absent in the other species. The triangular supraoccipital, situated posterodorsally on the neurocranium, has a backwardly-directed dorsal process. The process is simple in *Petalichthys capensis*, *Pseudotylosurus microps* (Fig. 8A), *Strongylura krefftii*, *St. leiura* (Fig. 9A), *St. strongylura* and *Tylosurus gavialoides*, and bifurcated in the other species. The supraoccipital is attached to the frontal anteriorly, epiotic laterally and exoccipital posteriorly in all species except *Belonion dibranchodon*, in which the supraoccipital is attached to the frontal anteriorly (Fig. 5A). The epiotic and exoccipital are not attached directly to the supraoccipital due to the cartilage around the posterior portion of the supraoccipital in *Belonion dibranchodon* (Fig. 5A).

The exoccipital, situated posteriorly on the neurocranium, is attached to the supraoccipital anterodorsally, epiotic dorsolaterally, pterotic laterally, prootic anteroventrally and basioccipital ventrally in all species except *Belonion dibranchodon*, in which direct attachment is interrupted by cartilage (Fig. 5). The elongate epiotic, located posterodorsally on the neurocranium, is attached to the frontal anteriorly, supraoccipital anteromedially and exoccipital medially in all species except *Belonion dibranchodon*, in which the epiotic is directly attached only to the frontal anteriorly. Posteriorly, the epiotic is surrounded by cartilage, inhibiting direct attachment to other elements (Fig. 5A, B). In *Belone belone* (Fig. 4A, B) and *Petalichthys capensis*, a tubular structure for the sensory canal is continuous with the frontal and posttemporal canal. The long rod-like parasphenoid occupies the ventral portion of the neurocranium, being attached to the prootic dorsally. The parasphenoid/basisphenoid connection is discussed in the description of the basisphenoid. Posteriorly, the parasphenoid is inserted into the basioccipital. Anterodorsally, the parasphenoid is surrounded by cartilage. The basisphenoid is situated on the posteroventral portion of the orbit and attached to the parasphenoid ventrally. Dorsally, the basisphenoid is attached only to the prootic in *Belone belone* (Fig. 4B), *Petalichthys capensis* and *Platybelone argalus argalus* (Fig. 6B), only to the frontal in *Strongylura exilis*, and to both the frontal and prootic in *Belonion dibranchodon* (Fig. 5C), all species of *Pseudotylosurus* (Fig. 8B) and *Potamorrhaphis guianensis* (Fig. 7B). The dorsal

portion of the basisphenoid is attached to the frontal, prootic and parasphenoid in other belonids. The prootic is located on the lateral portion of the neurocranium, its connection with the basisphenoid being discussed in the description of the basisphenoid. The prootic is attached to the frontal, sphenotic, pterotic, exoccipital, basioccipital and parasphenoid in all species except *Belonion dibranchodon*, being directly attached only to the basisphenoid and parasphenoid due to the anterior and posterior portions of the prootic being surrounded by cartilage (Fig. 5B, C).

The basioccipital, situated posteroventrally on the neurocranium, articulates posteriorly with the first vertebra. The basioccipital is attached to the parasphenoid, prootic and exoccipital in all species except *Belonion dibranchodon*, in which the basioccipital is surrounded by cartilage and attached only to the parasphenoid ventrally (Fig. 5C). Posterolaterally-directed processes on both of the basioccipital are present in all species except *Belonion dibranchodon* (absent). A plate-like process is present posteroventrally in all species except *Belonion dibranchodon*, all species of *Pseudotylosurus* (Fig. 8C) and *Xenentodon cancila* (Fig. 11C) (absent).
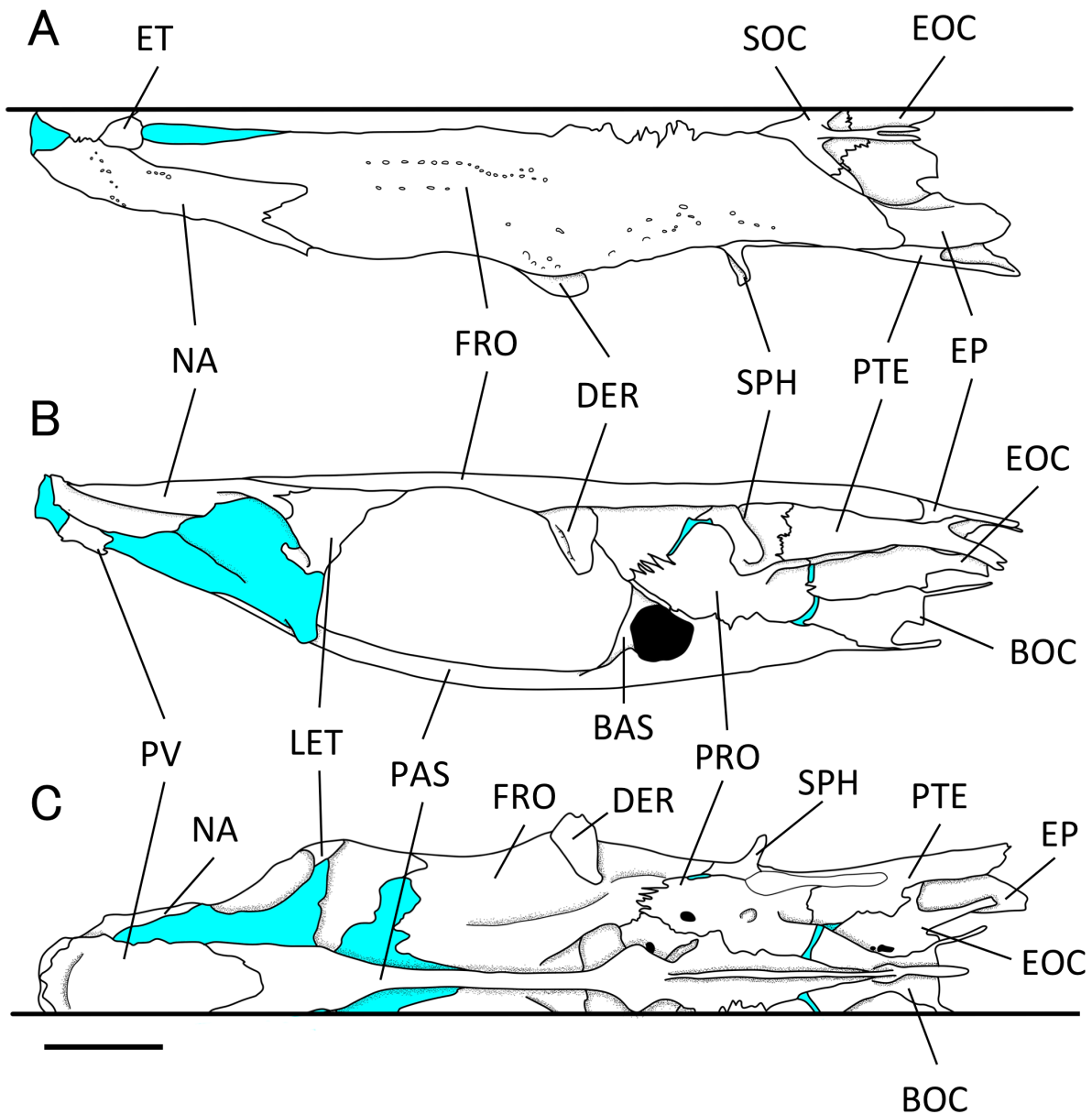

Figure 3. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Ablennes hians*, canals omitted. BAS, basisphenoid; BOC, basioccipital; DER, dermosphenotic; EOC, exoccipital; EP, epiotic; ET, ethmoid; FRO, frontal; LET, lateral ethmoid; NA, nasal; PAS, parasphenoid; PRO, prootic; PTE, pterotic; PV, prevomer; SOC, supraoccipital; SPH, sphenotic. Bar indicates 5 mm.
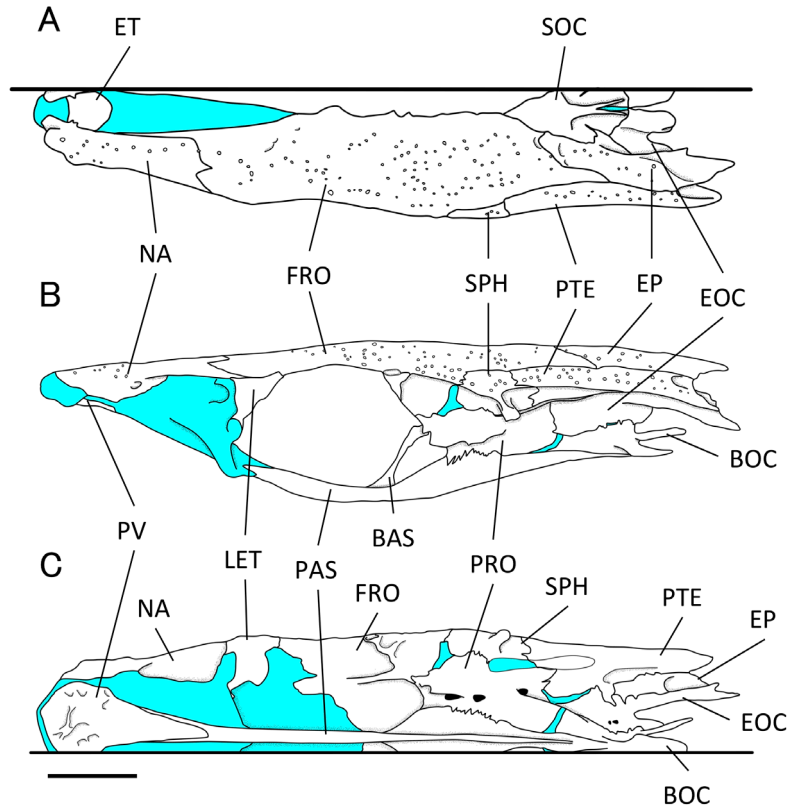
Figure 4. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Belone belone*, canals omitted, Dermosphenotic removed. Abbreviations as in Fig. 3. Bar indicates 5 mm.
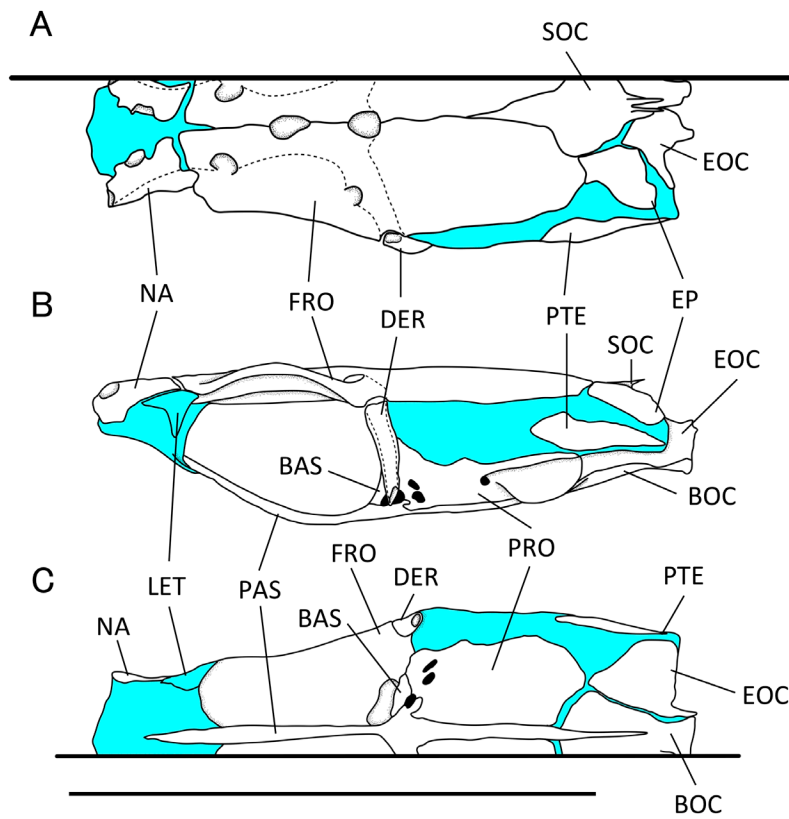

Figure 5. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Belonion dibranchodon*. Abbreviations as in Fig. 3. Bar indicates 5 mm.
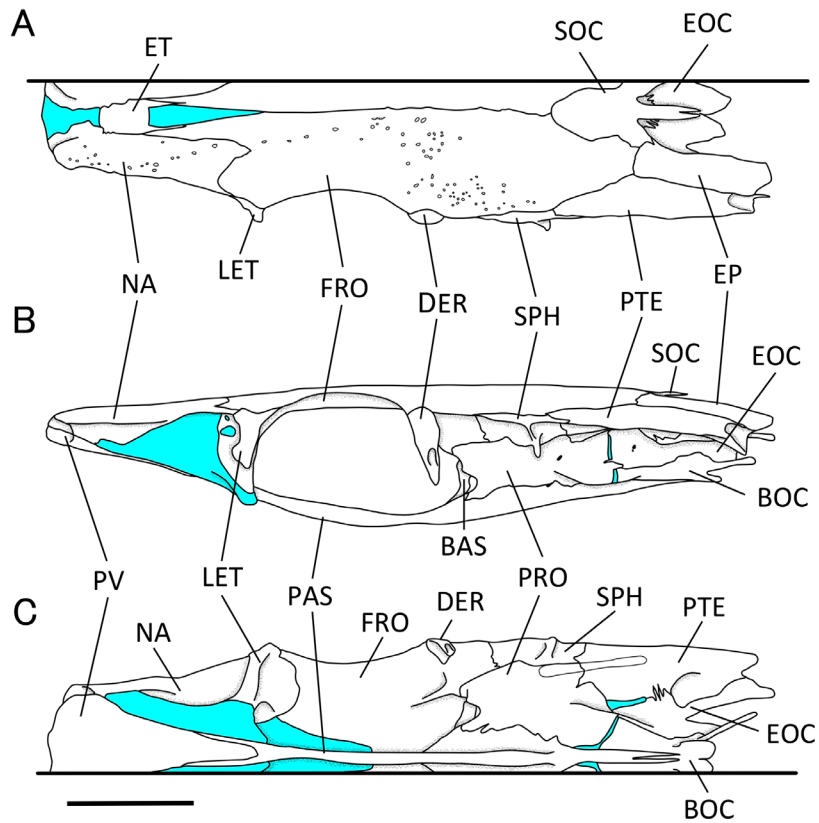
Figure 6. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Platybelone argalus argalus*, canals omitted. Abbreviations as in Fig. 3. Bar indicates 5 mm.
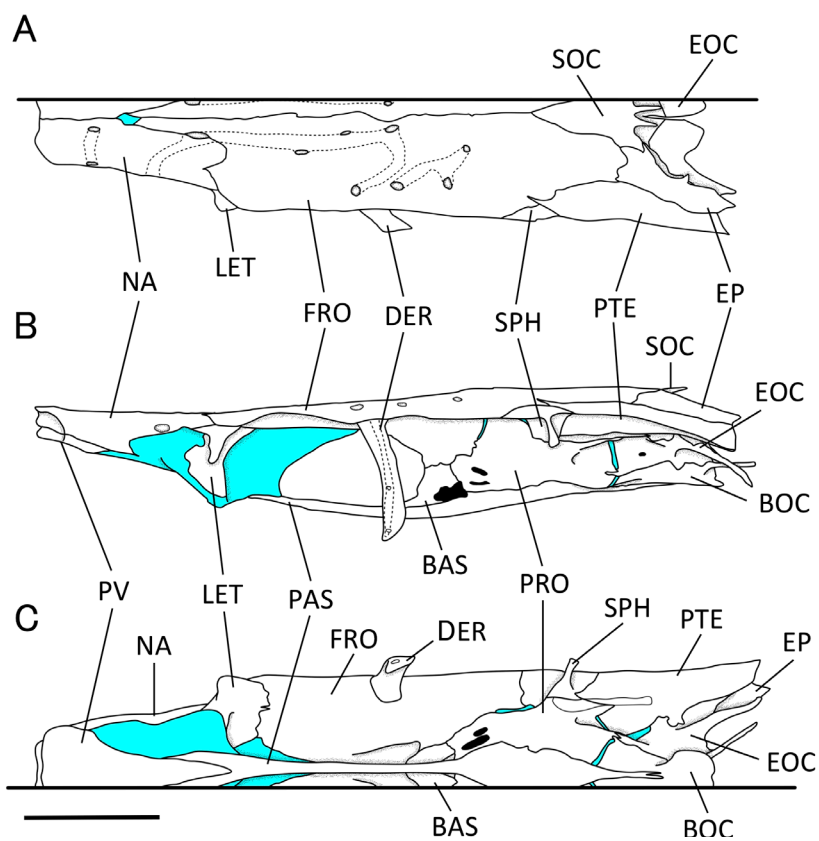
Figure 7. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Potamorrhaphis guianensis*. Abbreviations as in Fig. 3. Bar indicates 5 mm.
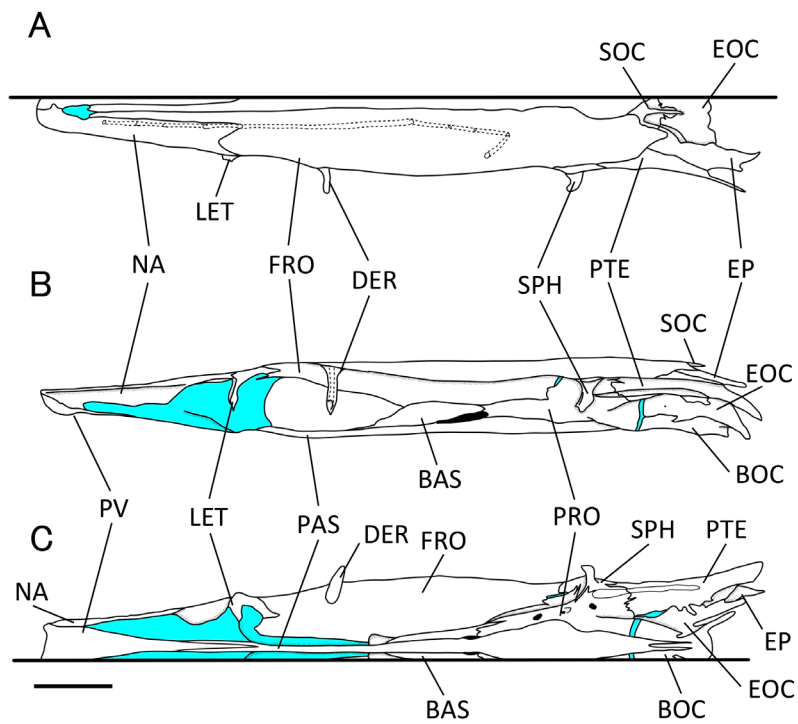
Figure 8. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Pseudotylosurus microps*. Abbreviations as in Fig. 3. Bar indicates 5 mm.
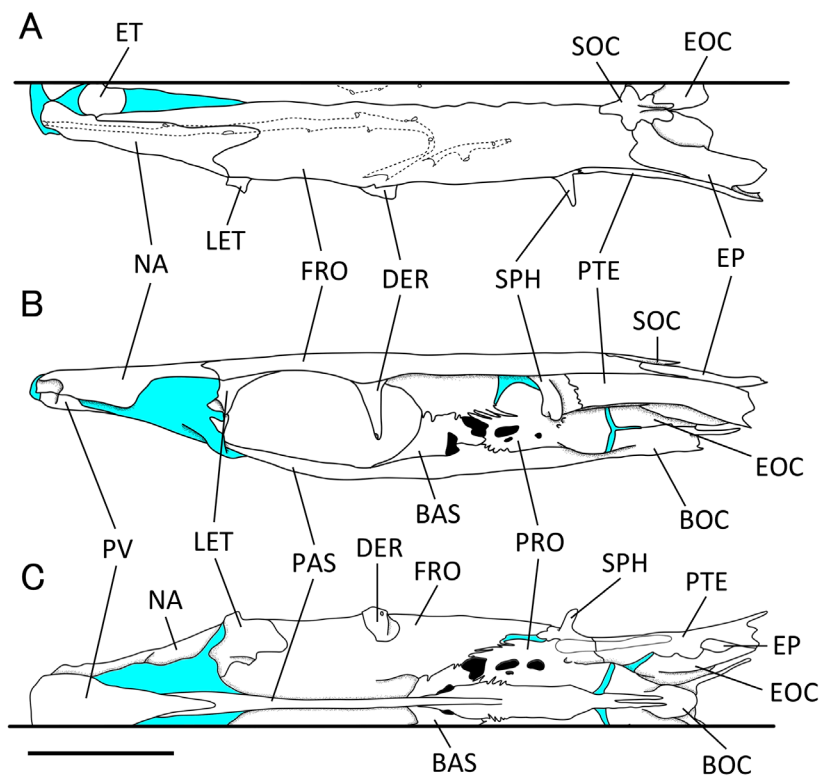

Figure 9. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Strongylura leiura*. Abbreviations as in Fig. 3. Bar indicates 5 mm.
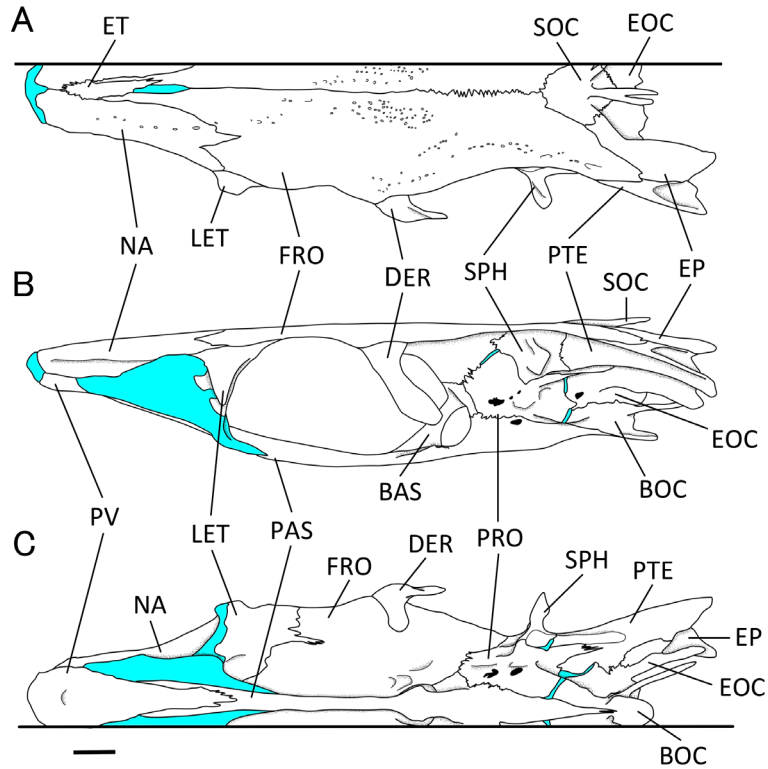
Figure 10. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Tylosurus acus melanotus*, canals omitted. Abbreviations as in Fig. 3. Bar indicates 5 mm.
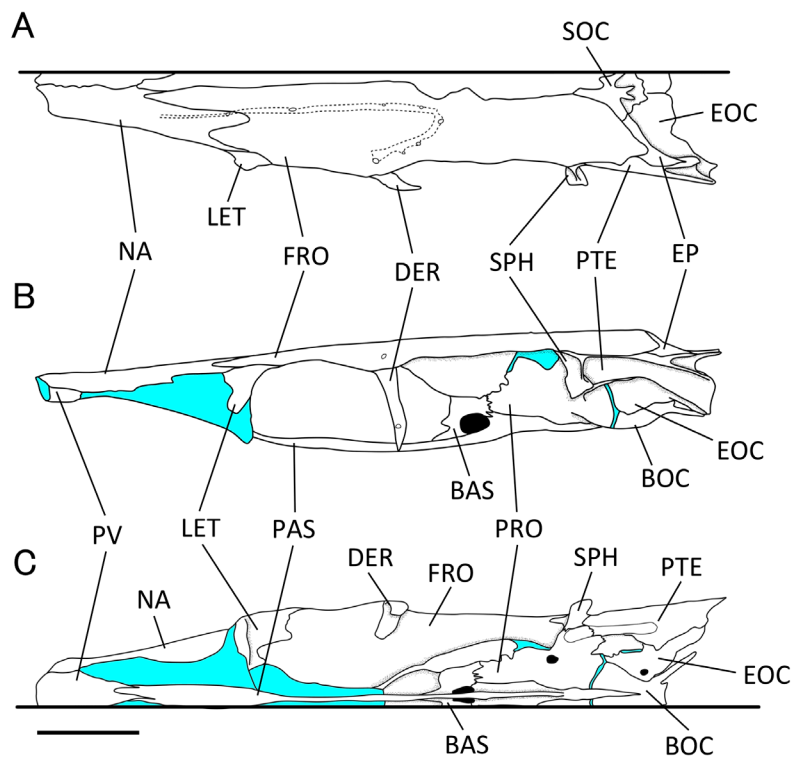
Figure 11. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Xenentodon cancila*. Abbreviations as in Fig. 3. Bar indicates 5 mm.
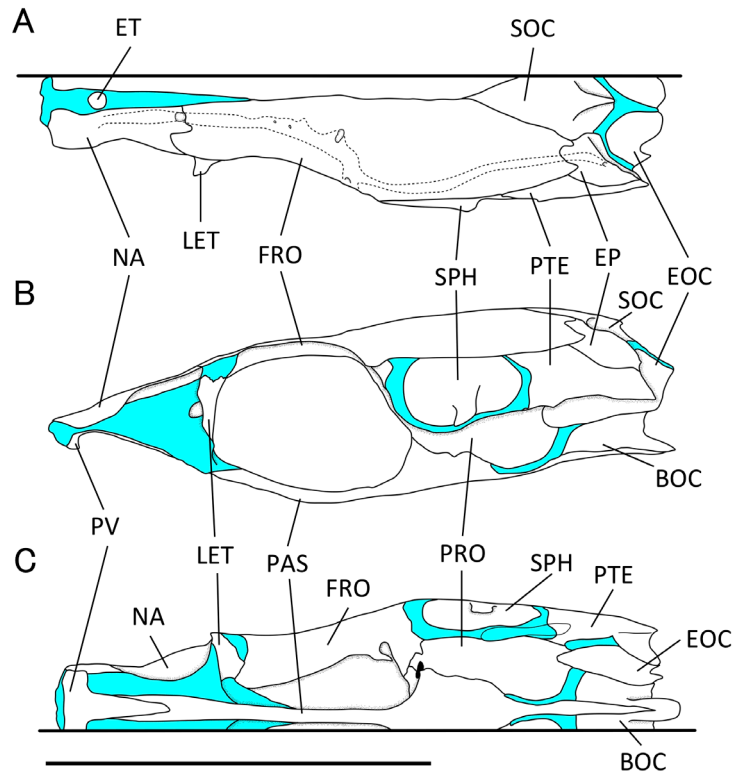
Figure 12. (A) Dorsal, (B) lateral and (C) ventral views of neurocranium in *Nanichthys simulans*. Dermosphenotic removed. Abbreviations as in Fig. 3. Bar indicates 5 mm.
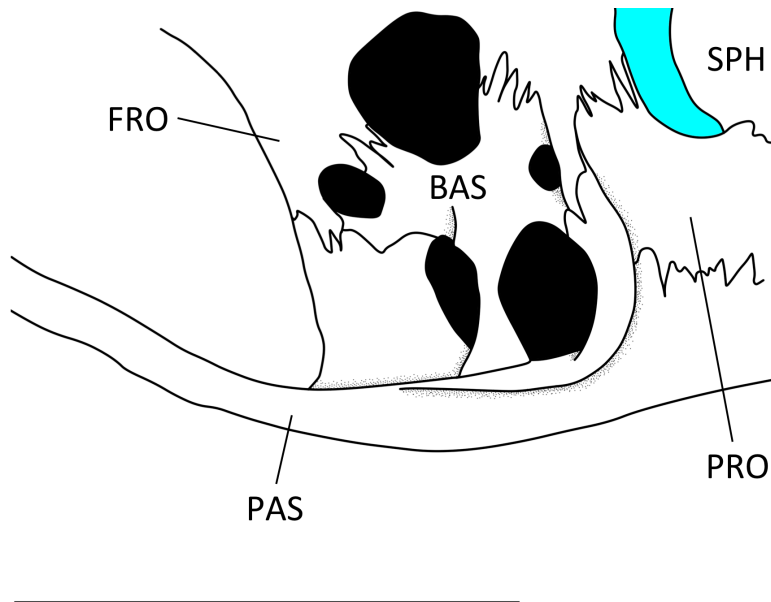
Figure 13. Anterolateral view of basisphenoid and bones attached to basisphenoid in *Scomberesox saurus*. Abbreviations as in Fig. 3. Bar indicates 5 mm.

Figure 14. Dorsal views of neurocranium in (A) *Hemiramphus far* and (B) *Exocoetus monocirrhus*. Abbreviations as in Fig. 3. Bars indicate 5 mm.

Figure 15. (A) Dorsal and (B) ventral views of neurocranium in *Atherinomorus pinguis*. IC, intercalar; PAR, parietal. Other abbreviations as in Fig. 3. Bar indicates 5 mm.
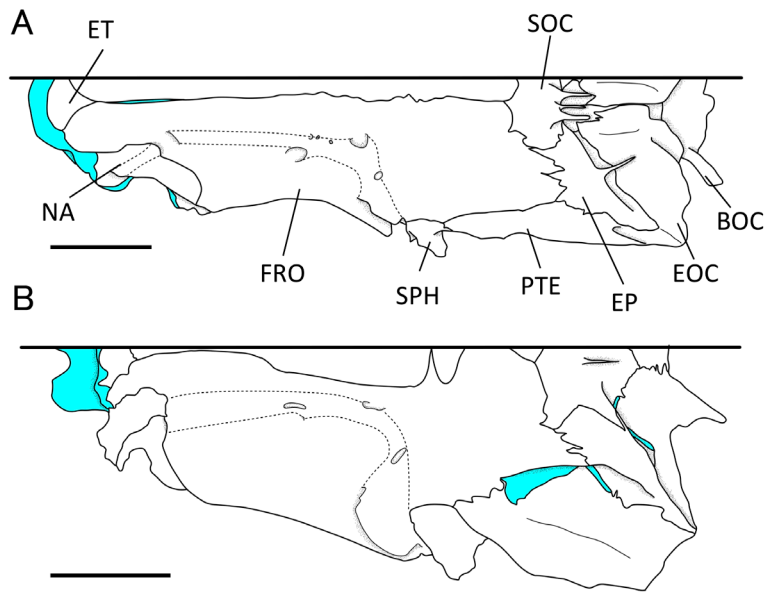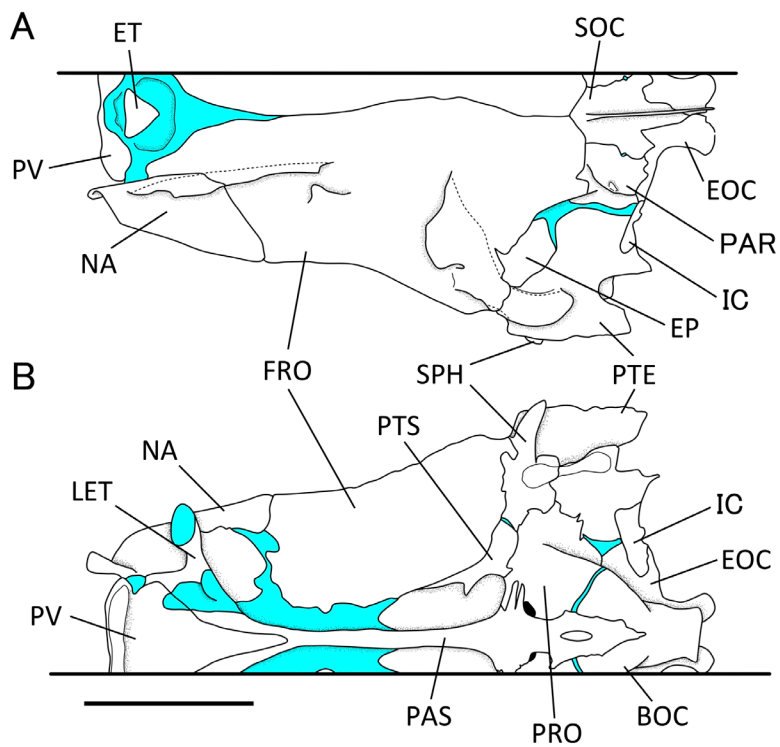
Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 2. *Prevomer and nasal*. 0: separated; 1: attached.

Belonidae. The prevomer is separated from the nasal in *Belone belone* and *Petalichthys capensis* (character 2-0), but attached anterodorsally to the nasal in other species (character 2-1).

Other ingroups. The prevomer is separated from the nasal in all species (character 2-0).

Outgroups. The prevomer is separated from the nasal in all outgroups (character 2-0).

TS 3. *Teeth on prevomer*. 0: absent; 1: present.

Belonidae. Prevomerine teeth are present in *Belone belone* and *Tylosurus punctulatus* (character 3-1), but absent in other species (character 3-0).

Other ingroups. Prevomerine teeth are present in *Parexocoetus brachypterus* (character 3-1), but absent in the other species (character 3-0).

Outgroups. Prevomerine teeth are present in *Atherinomorus pinguis* (character 3-1), but absent in the other outgroups (character 3-0). Remarks. Collette and Parin (1970) reported the presence of prevomerine teeth in *Belone belone* specimens > 200mm BL. Although the specimen examined here is 203.9 mm BL, prevomerine teeth are absent. However, small concavities on the ventral surface of the prevomer, considered to be dental alveoli, are apparent (Fig. 4C). Teeth are believed to either have been removed during a previous study, during which the specimen was dissected, or would have eventually developed with growth in the concavities. Therefore, prevomerine teeth are considered present in *Belone belone* for the present analysis (character 3-1).

TS 4. *Ethmoid*. 0: exposed; 1: covered by nasals.

Belonidae. In *Potamorrhaphis guianensis*, all species of *Pseudotylosurus* and *Xenentodon cancila*, the ethmoid

is covered by the nasals (character 4-1), but exposed in other species (character 4-0).

Other ingroups. The ethmoid is exposed in all species (character 4-0).

Outgroups. The ethmoid is exposed in all outgroups (character 4-0).

TS 5. *Nasals on both sides*. 0: separated; 1: attached.

Belonidae. In *Belone belone*, *Petalichthys capensis*, *Platybelone argalus argalus* and *Tylosurus acus imperialis*, the nasals are separated (character 5-0), but attached to each other in other species (character 5-1).

Other ingroups. The nasals are separated in all species (character 5-0).

Outgroups. The nasals are separated in all outgroups (character 5-0).

TS 6. *Sensory canal of nasal*. 0: present; 1: absent.

Belonidae. A nasal sensory canal is present in all species (character 6-0).

Other ingroups. A nasal sensory canal is absent in *Exocoetus monocirrhus* (character 6-1), but present in other species (character 6-0).

Outgroups. The canal is present in *Atherinomorus pinguis* (character 6-0), but absent in the other outgroups (character 6-1).

TS 7. *Sensory canal of sphenotic and pterotic*. 0: absent; 1: present only in pterotic; 2: present in sphenotic and pterotic.

Belonids. In *Belone belone* and *Petalichthys capensis*, the canal is present in both bones (character 7-2), but absent in other species (character 7-0).

Other ingroups. The canal is absent in all species (character 7-0).

Outgroups. In *Atherinomorus pinguis*, the canal is

present only in the pterotic, being continuous with the frontal canal (Fig. 15A) (character 7-1), whereas the canal is absent in the other outgroups (character 7-0).

TS 8. *Sensory canal of epiotic*. 0: absent; 1: present.

Belonids. The epiotic canal is present in *Belone belone* and *Petalichthys capensis* (character 8-1), but absent in other species (character 8-0).

Other ingroups. The canal is present in all scomberesocids (character 8-1), but absent in other ingroups (character 8-0).

Outgroups. All outgroups lack the canal (character 8-0).

TS 9. *Dorsal portion of basisphenoid*. 0: attached only to prootic; 1: attached only to frontal; 2: attached to frontal and prootic; 3: attached to frontal and parasphenoid; 4: attached to frontal, prootic and parasphenoid.

Belonidae. The dorsal portion of the basisphenoid is attached only to the prootic in *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus* (character 9-0), only to the frontal in *Strongylura exilis* (character 9-1), to the frontal and prootic in all species of *Pseudotylosurus* and *Potamorrhaphis guianensis* (character 9-2), and to the frontal, prootic and parasphenoid in the other species (character 9-4).

Other ingroups. The dorsal portion of the basisphenoid is attached to the frontal and parasphenoid in all scomberesocids (Fig. 13) (character 9-3), but attached only to the prootic in other species (character 9-0).

Outgroups. The dorsal portion of the basisphenoid is attached only to the prootic in *Atherinomorus pinguis* (character 9-0). Outgroups that lacked the basisphenoid were coded as "?" for TS 9.

TS 10. *Processes of basioccipital*. 0: absent; 1: present.

Belonidae. The processes are directed posterolaterally on both sides of the basioccipital in all species (character 10-1). Other ingroups. The processes are absent in *Nanichthys simulans* and all exocoetids (character 10-0), but present in other ingroups (character 10-1).

Outgroups. All outgroups lack basioccipital processes (character 10-0).

TS 11. *Plate-like process of basioccipital*. 0: absent; 1: present.

Belonidae. In all species except for all species of *Pseudotylosurus* and *Xenentodon cancila*, a plate-like process is present on the posteroventral portion of the basioccipital (character 11-1). The process is absent in all species of *Pseudotylosurus* and *X. cancila* (character 11-0).

Other ingroups. The process is present in all species (character 11-1).

Outgroups. All outgroups lack the process (character 11-0).

Remarks. Rosen and Parenti (1981) inferred that the presence of the plate-like process of the basioccipital was one of the characters that defining the suborder Exocoetoidei (see section 1 of TAXON SAMPLING).

Other variations

Frontal canals on each side. The frontal canals are interconnected only in *Belonion dibranchodon*, being separated in all ingroups and outgroups, including *Elassichthys adocetus*. Accordingly, interconnection of the frontal canals is considered to be an autapomorphy of *Belonion dibranchodon*.

Lateral process of sphenotic. A lateral sphenotic process is present in all ingroups, outgroups and *Elassichthys adocetus*, except *Belonion dibranchodon*. Therefore, absence of the process is considered an autapomorphy of *Belonion dibranchodon*.

Dorsal process of supraoccipital. The dorsal supraoccipital process is directed backward in the ingroups, outgroups, *Belonion dibranchodon* and *Elassichthys adocetus*. The process exhibits three morphotypes. It is simple in ingroups *Petalichthys capensis, Pseudotylosurus microps, Strongylura krefftii, St. leiura, St. strongylura, Tylosurus gavialoides, Nanichthys simulans* (Fig. 12A) and *Exocoetus monocirrhus* (Fig. 14B) and outgroups *Oryzias javanicus* and *Atherinomorus pinguis*, but bifurcated in ingroups *Ablennes hians, Belone*

belone, Platybelone argalus argalus, Potamorrhaphis guianensis, Ps. angusticeps, St. exilis, T. acus imperialis, T. a. melanotus, T. punctulatus, Xenentodon cancila, Scomberesox saurus, Zenarchopterus dunckeri, Fodiator acutus and *Parexocoetus brachypterus* and an outgroup *Poecilia mexicana*. The process is trifurcated in ingroups *Hemiramphus far* (Fig. 14A) and *Cypselurus doederleini*. However, in *Cololabis saira*, the process is simple in HUMZ 227067, but bifurcated in HUMZ 228020. Because of this intraspecific variation, conditions of the supraoccipital dorsal process were not adopted for the analysis.

Pterosphenoid. The pterosphenoid is absent in all ingroups, *Belonion dibranchodon* and *Elassichthys adocetus*, but present in all outgroups (Fig. 15B). Accordingly, absence of the pterosphenoid is considered a synapomorphy of exocoetoids (see section 1 of TAXON SAMPLING).

Basisphenoid. The basisphenoid is present in all ingroups, plus *Belonion dibranchodon, Elassichthys adocetus* and an outgroup *Atherinomorus pinguis*, while it is absent in *Oryzias javanicus* and *Poecilia mexicana*. Thus, the condition was not used for the analysis, because of the latter condition having been found only in outgroups.

Cartilaginous and unossified elements. In *Belonion dibranchodon*, many cartilaginous and unossified elements, apparently resulting from neoteny, are noted in the neurocranium (*e.g*., cartilaginous lateral ethmoid and sphenotic, unossified prevomer), that were not found in other species. These elements are therefore considered an autapomorphy of *Belonion dibranchodon*.

3. Jaws (Figs. 16–24)

Description

The jaws include the premaxilla and maxilla in the upper jaw, and dentary, angular, retroarticular and coronomeckelian in the lower jaw. All elements are paired.

The tapered or triangular premaxilla, with many conical teeth on its ventral surface, is attached to the maxilla posteriorly, the upper edge of the posterior margin being connected to the nasal via a ligament. An ascending process is absent. The unpaired rostral cartilage is attached to the posteromedial surface. The premaxillae are interdigitated with each other in all species except *Belonion dibranchodon*, in which they are attached by smooth surfaces. The premaxilla is long in all species except *Belonion dibranchodon* (Fig. 16C) (short). All species have a tubular sensory canal structure on the premaxilla, separated from canals on adjacent bones.

The toothless maxilla is a curved bone, situated on the posterior portion of the upper jaw. Its posteromedial surface has a ligament connected to the posterolateral surface of the dentary. A process on the medial surface, connected to the palatine and a concavity formed by the nasal and prevomer via ligaments is present in all species except *Belonion dibranchodon* (Fig. 16C).

The tapered dentary, with many conical teeth on the dorsal surface, is elongated in all species. The antimeres are interdigitated with each other in all species (Fig. 24A) except *Belonion dibranchodon*, in which they are attached by smooth surfaces. The dentary, connected to the angular posteriorly, has a notch on the medial aspect into which the thin cylindrical meckelian cartilage is inserted. Cartilage on the posterolateral surface on the dentary is absent in all species. A tubular sensory canal structure is continuous with canals on the angular and preopercle in all species except *B. dibranchodon*, in which the canal of dentary is separated from those on the angular and preopercle (Fig. 20C).

The wedge-like angular articulates with the condyle of the quadrate posteriorly and is attached to the retroarticular posteroventrally. A cartilage between the angular and retroarticular is present in all species except *Belonion dibranchodon* (Fig. 20C) (unconfirmed due to poor staining), *Platybelone argalus argalus* (Fig. 21A), *Potamorrhaphis guianensis* (Fig. 21B) and *Xenentodon cancila* (Fig. 22B) in which it is absent. The Meckelian cartilage is posteriorly attached to the convexity on the posteromedial portion of the angular.

The small triangular retroarticular, forming the posteroventral corner of the lower jaw, is connected to the interopercle posteriorly via a ligament.

The small coronomeckelian is attached to the medial surface of the angular and connected to the adductor mandibulae tendon. Its dorsal margin extends over the dorsal margin of the angular in all species.

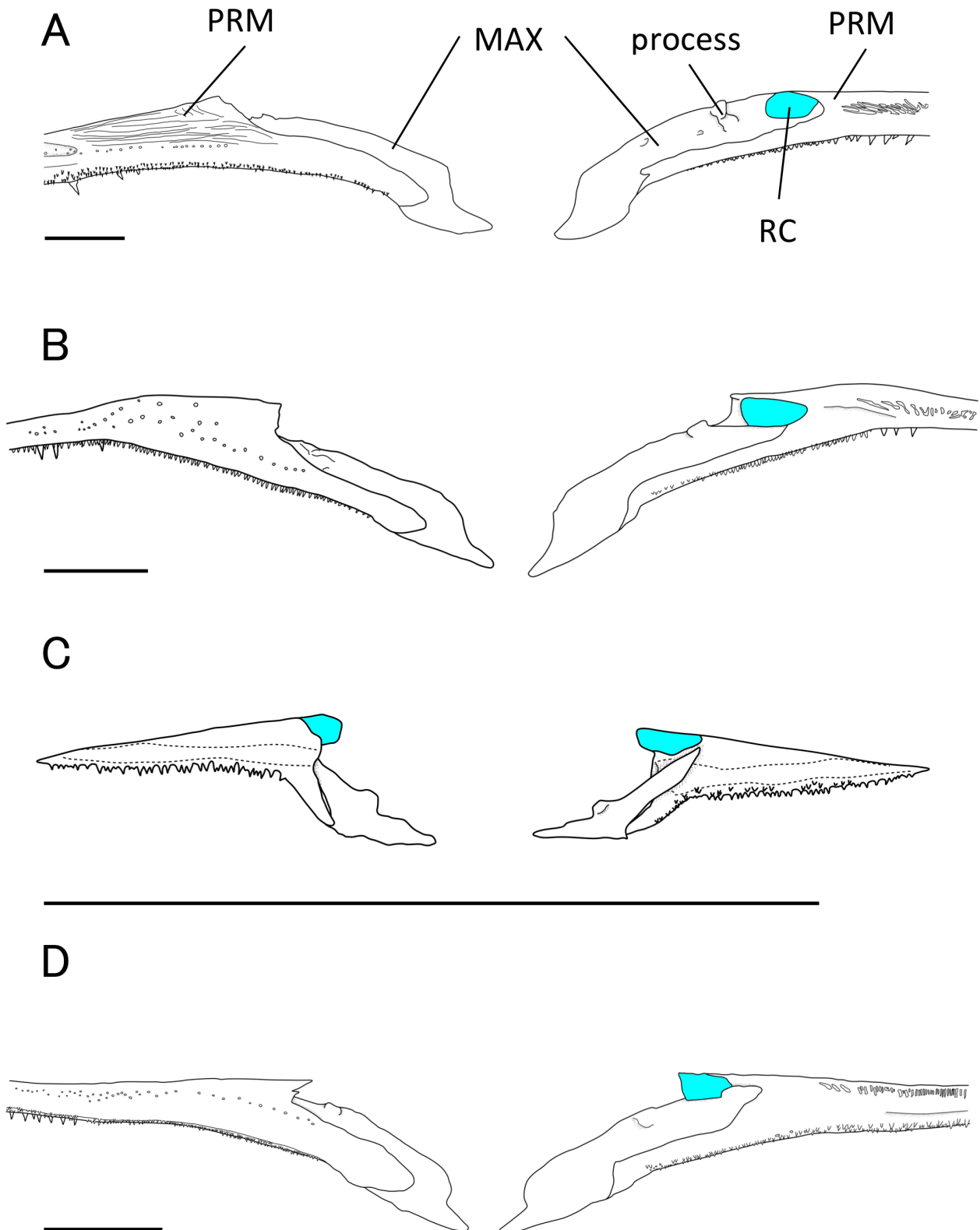**Figure 16.** Lateral views (left) and medial views (right) of upper jaw in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon* and (D) *Petalichthys capensis*. MAX, maxilla; PRM, premaxilla; RC, rostral cartilage. Bars indicate 5 mm.

Figure 17. Lateral views (left) and medial views (right) of upper jaw in (A) *Platybelone argalus argalus*, (B) *Potamorrhaphis guianensis*, (C) *Pseudotylosurus microps* and (D) *Strongylura leiura*. Abbreviations as in Fig. 16. Bars indicate 5 mm.

Figure 18. Lateral views (left) and medial views (right) of upper jaw in (A) *Tylosurus gavialoides*, (B) *Xenentodon cancila* and (C) *Scomberesox saurus*. Abbreviations as in Fig. 16. Bars indicate 5 mm.
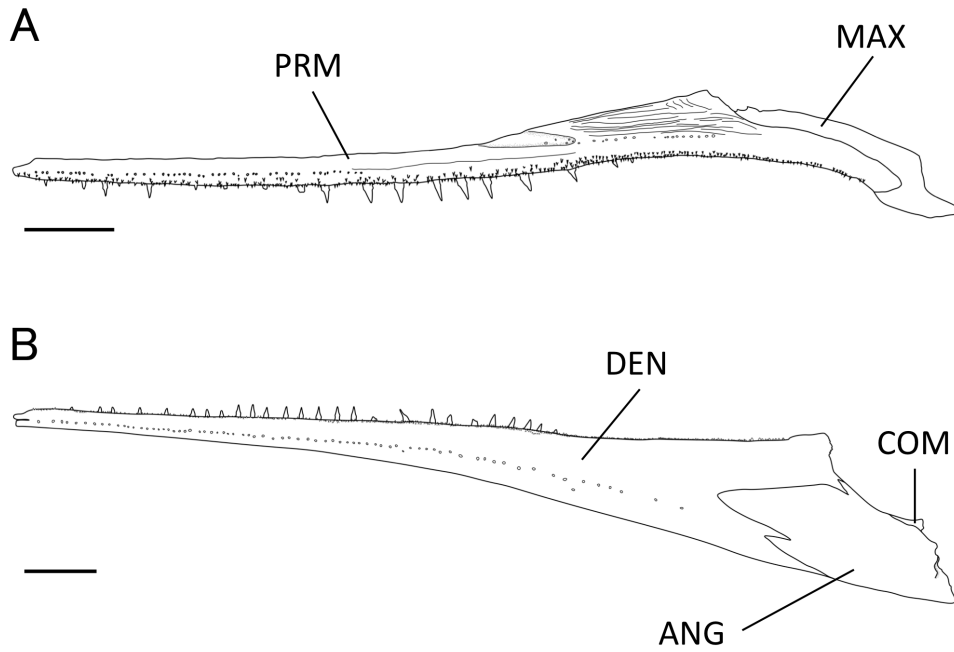
Figure 19. Overall lateral views of jaws of *Ablennes hians* in (A) upper jaw and (B) lower jaw. ANG, angular; COM, coronomeckelian; DEN, dentary; MAX, maxilla; PRM, premaxilla. Bars indicate 5 mm.
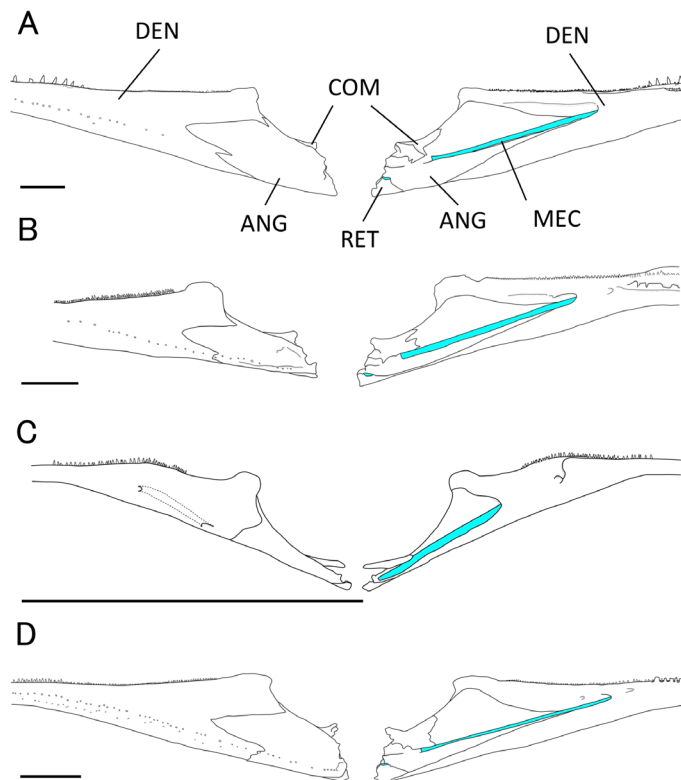
Figure 20. Lateral views (left) and medial views (right) of lower jaw in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon* and (D) *Petalichthys capensis*. ANG, angular; COM, coronomeckelian; DEN, dentary; MEC, meckelian cartilage; RET, retroarticular. Bars indicate 5 mm.
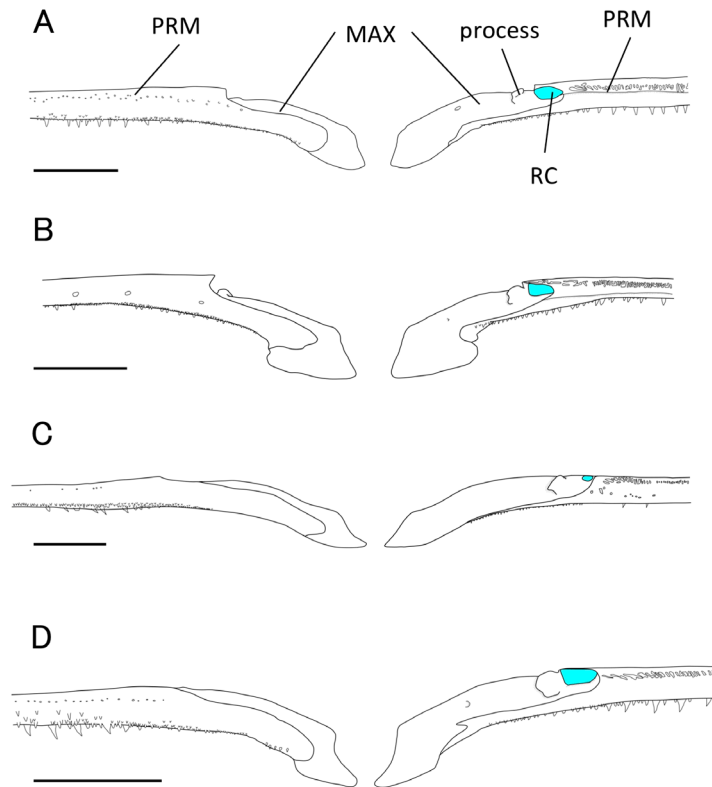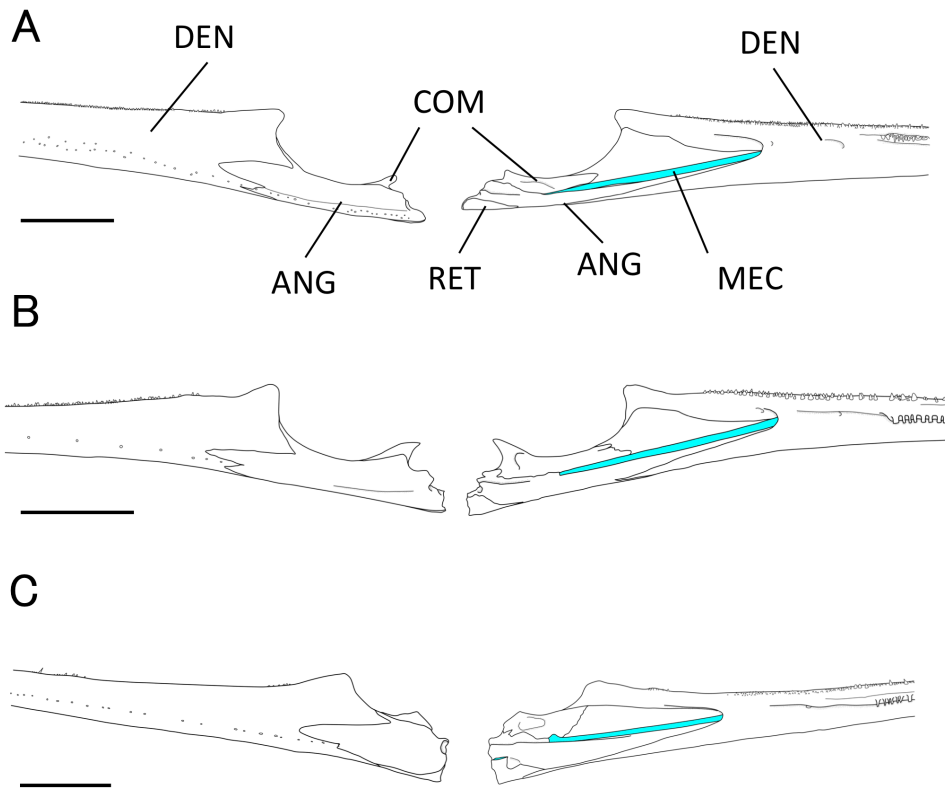
Figure 21. Lateral views (left) and medial views (right) of lower jaw in (A) *Platybelone argalus argalus*, (B) *Potamorrhaphis guianensis*, (C) *Pseudotylosurus microps* and (D) *Strongylura exilis. Abbreviations* as in Fig. 20. Bars indicate 5 mm.
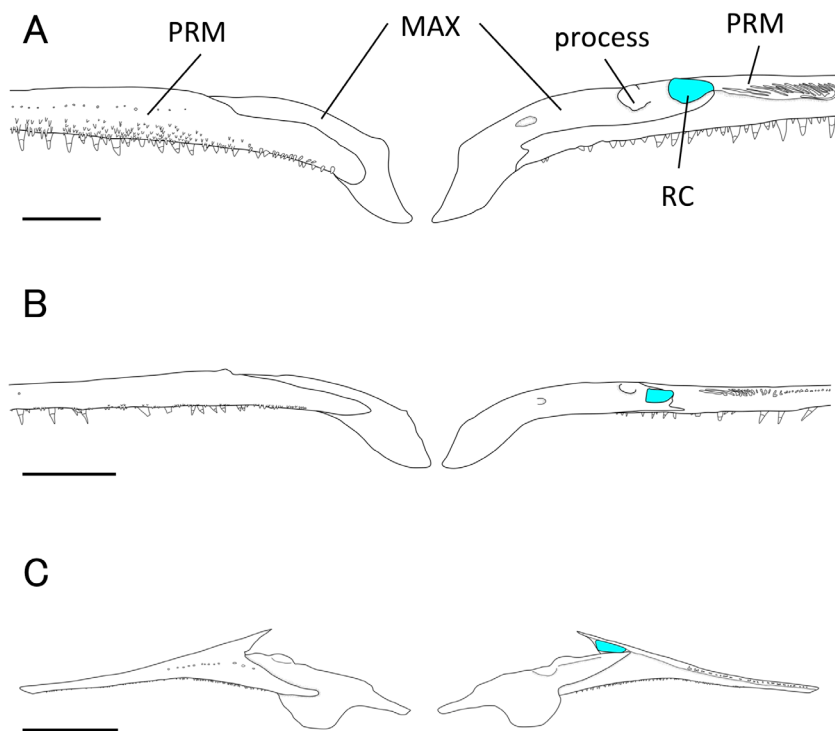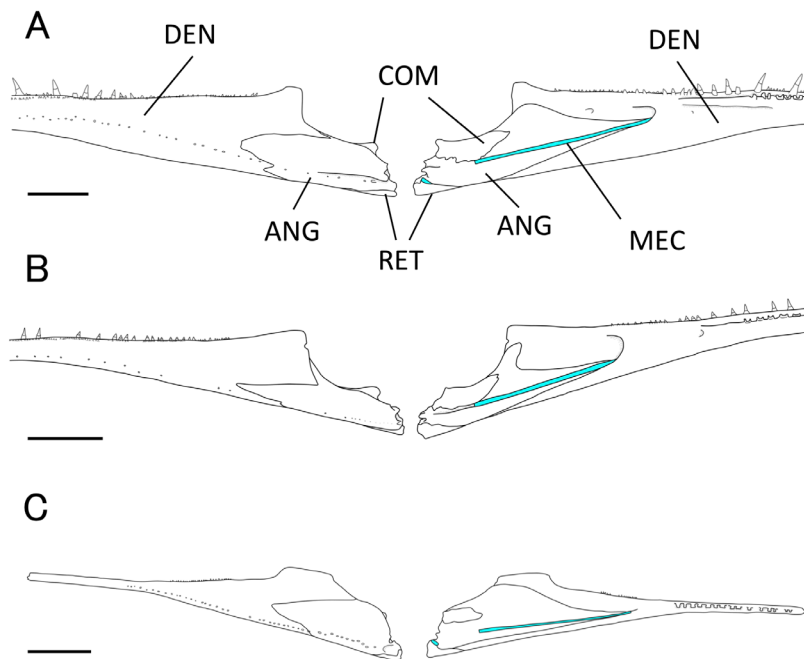

Figure 22. Lateral views (left) and medial views (right) of lower jaw in (A) *Tylosurus punctulatus*, (B) *Xenentodon cancila* and (C) *Scomberesox saurus*. Abbreviations as in Fig. 20. Bars indicate 5 mm.
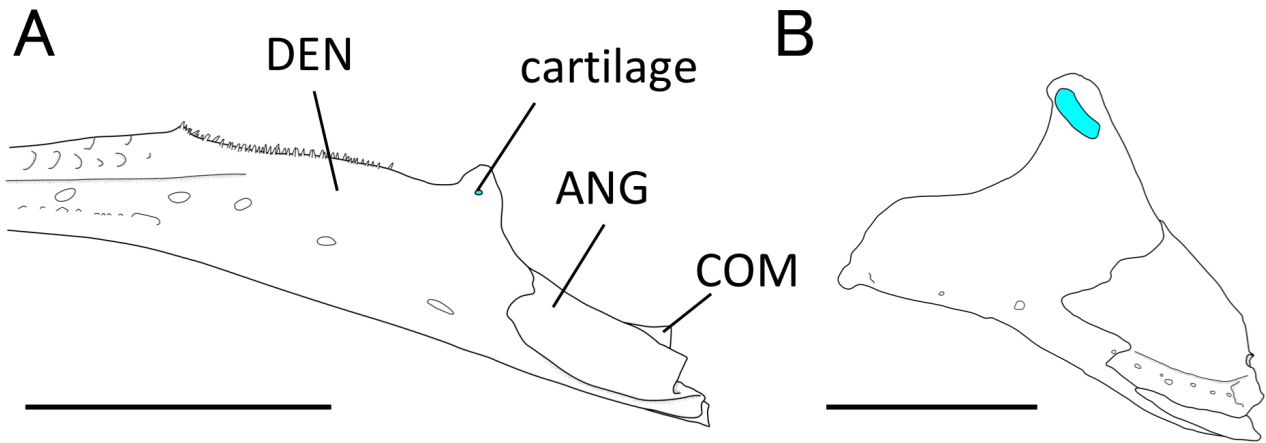
Figure 23. Lateral views of lower jaw in (A) *Zenarchopterus dunckeri* and (B) *Parexocoetus brachypterus*. Abbreviations as in Fig. 20. Bars indicate 5 mm.
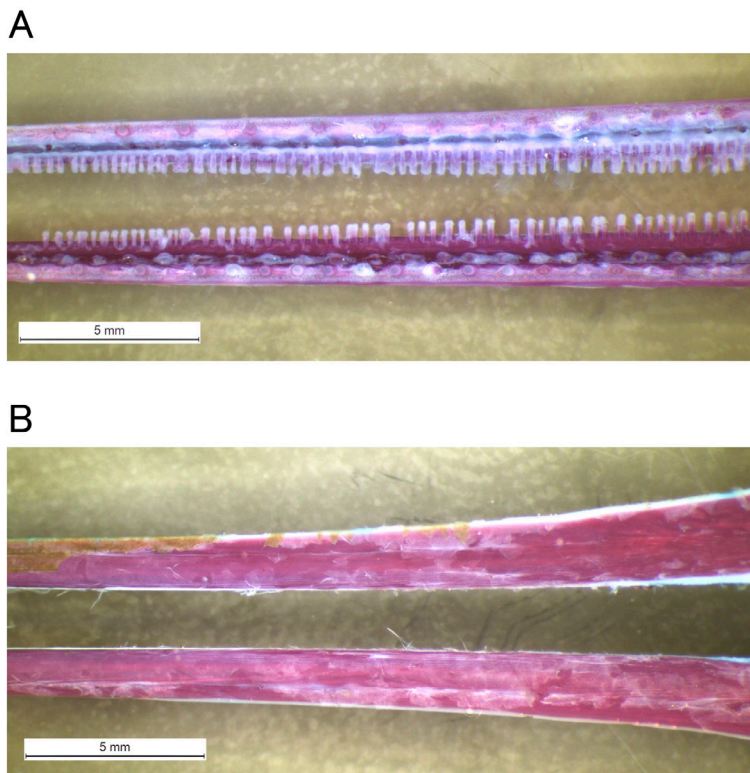
Figure 24. Dorsal views of dentaries on left and right sides in (A) *Pseudotylosurus microps* and (B) *Hemiramphus far*. Dentaries on both sides are detached with each other: (A) shows many small processes which were interdigitated before dissection; (B) with smooth surfaces.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 12. *Premaxilla*. 0: short; 1: long.

Belonidae. The premaxilla is long in all species (character 12-1).

Other ingroups. The premaxilla is long in *Nanichthys simulans* and *Scomberesox saurus* (Fig. 22C) (character 12-1), but is short in other species (character 12-0).

Outgroups. The premaxilla is short in all outgroups (character 12-0).

Remarks. The examined (immature) specimen (45.6 mm BL) of *Nanichthys simulans* lacks long premaxilla and dentary. However, Hubbs and Wisner (1980) reported that the upper and lower jaws were elongate in adults of the species (max. 126 mm SL, usually ca. 100 mm SL), noting also that the lengths of both jaws became relatively greater with growth. Therefore, the premaxilla and dentary of *N. simulans* are treated as long (character 12-1 and 15-1) in the present analysis.

TS 13. *Premaxillae on both sides*. 0: attached by smooth surfaces; 1: interdigitated.

Belonidae. The premaxillae of both sides are interdigitated with each other in all species (character 13-1).

Other ingroups. They are interdigitated with each other in *Scomberesox saurus* (character 13-1), but attached by smooth surfaces in the other species (character 13-0).

Outgroups. In all outgroups, the premaxillae are attached by smooth surfaces (character 13-0).

TS 14. *Sensory canal of premaxilla*. 0: absent; 1: present.

Belonidae. A premaxilla sensory canal is present in all species (character 14-1).

Other ingroups. All scomberesocids have a premaxilla sensory canal (character 14-1), whereas it is absent in other species (character 14-0).

Outgroups. A premaxilla sensory canal is absent in all outgroups (character 14-0).

Remarks. Parin and Astakhov (1982) reported that all Scomberesocoidea (except for the scomberesocid *Elassichthys adocetus*) had the sensory canal of the premaxilla, being unique among teleosts.

TS 15. *Dentary*. 0: short; 1: long.

Belonidae. The dentary is long in all species (character 15-1).

Other ingroups. The dentary is long in *Nanichthys simulans* (see remarks of TS 12), *Scomberesox saurus, Zenarchopterus dunckeri* and *Hemiramphus far* (character 15-1), but short in other species (character 15-0).

Outgroups. The dentary is short in all outgroups (character 15-0).

TS 16. *Cartilage on posterolateral surface of dentary*. 0: absent; 1: present, rudimentary; 2: present, developed.

Belonidae. All species lack the cartilage on the posterolateral surface of the dentary (character 16-0).

Other ingroups. The cartilage is present but rudimentary in *Zenarchopterus dunckeri* (Fig. 23A) (character 16-1), and is present and developed in *Hemiramphus far* and all exocoetids (Fig. 23B) (character 16-2). The cartilage is absent in other species (character 16-0).

Outgroups. All outgroups lack the cartilage (character 16-0).

TS 17. *Dentaries on both sides*. 0: attached by smooth surfaces; 1: interdigitated.

Belonidae. The dentaries on both sides are interdigitated in all belonids (character 17-1).

Other ingroups. The dentaries are interdigitated in all scomberesocids (character 17-1) and attached by smooth surfaces in other ingroups (Fig. 24B) (character 17-0).

Outgroups. The dentaries are attached by smooth surfaces in all outgroups (character 17-0).

TS 18. *Cartilage between angular and retroarticular.* 0: present; 1: absent.

Belonidae. Cartilage is absent between the angular and retroarticular in *Platybelone argalus argalus*, *Potamorrhaphis guianensis* and *Xenentodon cancila* (character 18-1), but present in the other species (character 18-0).

Other ingroups. Cartilage is present in all other ingroups (character 18-0).

Outgroups. *Poecilia mexicana* lacks the cartilage (character 18-1), which is present in all other outgroups (character 18-0).

TS 19. *Dorsal margin of coronomeckelian.* 0: not reaching dorsal margin of angular; 1: extending over dorsal margin of angular.

Belonidae. The dorsal margin of the coronomeckelian extends over the dorsal margin of the angular in all species (character 19-1).

Other ingroups. The dorsal margin of coronomeckelian does not reach the dorsal margin of the angular in *Nanichthys simulans* and all exocoetids (except for *Cypselurus doederleini*) (Fig. 23B) (character 19-0), but extends over the dorsal margin of angular in *Cololabis saira*, *Scomberesox saurus*, *Zenarchopterus dunckeri* (Fig. 23A), *Hemiramphus far* and *Cy. doederleini* (character 19-1).

Outgroups. The dorsal margin of the coronomeckelian does not reach the dorsal margin of the angular in any of the outgroups (character 19-0).

Other variations

Process on medial surface of maxilla. The process is

present in all belonids except *Belonion dibranchodon*, present in *Nanichthys simulans* and *Scomberesox saurus*, but absent in all other ingroups, all outgroups and *Elassichthys adocetus*. Moreover, the premaxilla is elongated in all species that have the process; presence of the process therefore is considered associated with elongation of the premaxilla. Accordingly, this variation was not used in the analysis.

Teeth on jaws. The jaw teeth are conical in all ingroups and outgroups, except for *Hemiramphus far* and *Poecilia mexicana*, in which they are tricuspid and comb-like, respectively. Thus, tricuspid and comb-like teeth are considered autapomorphies of these species.

Sensory canal of lower jaw. The lower jaw sensory canal runs through the dentary and angular, and is connected with the preopercle sensory canal in all belonids except *Belonion dibranchodon*, all scomberesocids including *Elassichthys adocetus*, hemiramphid, zenarchopterid, all exocoetids and the atherinid *Atherinomorus pinguis*. A lower jaw sensory canal is absent but a preopercle sensory canal is present in the adrianichthyid *Oryzias javanicus* and the poeciliid *Poecilia mexicana*. In *Belonion dibranchodon*, the lower jaw sensory canal is present only in the dentary, separated from the preopercle canal. Therefore, the character is considered an autapomorphy of *Belonion dibranchodon*.

4. Suspensorium (Figs. 25–28)

Description

The suspensorium comprises the palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, hyomandibula, preopercle, interopercle, opercle and subopercle. The ectopterygoid is present only in *Belone belone* (Fig. 25B). All elements are paired.

The club-like and toothless palatine forms the anteriormost portion of the suspensorium, and is anteriorly ligamentously connected to the nasal, prevomer and maxillary process. A cartilaginous cap on the anterior tip of the palatine is absent. The posterior part of the palatine is attached to the endopterygoid in the medial aspect and the quadrate in the lateral and medial aspects in all species except *Belone belone*. In *Belone belone*, the posterior part of the palatine is attached to the endopterygoid and quadrate in the

medial aspect, and the ectopterygoid in the lateral aspect (Fig. 25B). A cartilage is surrounded by the palatine, endopterygoid and quadrate in all species except *Belone belone*, in which a cartilage is surrounded by the palatine, ectopterygoid, endopterygoid and quadrate (Fig. 25B).

The ectopterygoid, on the lateral aspect of the suspensorium, is attached to the palatine anteriorly and quadrate posteriorly in *Belone belone* (Fig. 25B).

The endopterygoid is a thin board-like bone, situated on the anterodorsal portion of the suspensorium. In *Tylosurus punctulatus*, teeth are present on the medial surface (Fig. 27A), but absent in other species. Anteriorly, the endopterygoid is medially attached to the palatine, and ventrally, to the quadrate laterally, and the quadrate and symplectic medially. In *Belonion dibranchodon*, the endopterygoid is separated from the metapterygoid (Fig. 25C), whereas the endopterygoid is attached to the metapterygoid posteriorly in other species.

The metapterygoid is located on the central portion of the suspensorium, being anteriorly attached to the quadrate via a lateral cartilage. The metapterygoid is attached to the hyomandibula posteriorly and the symplectic ventrally. In *Belonion dibranchodon*, the metapterygoid is separated from the endopterygoid (Fig. 25C), but is attached to the endopterygoid anteriorly in other species. A metapterygoid lamina is absent in *Belonion dibranchodon*, but present in other species.

The triangular quadrate, situated on the ventral portion of the suspensorium, articulates with the angular anteroventrally. In *Belone belone*, the anterior portion is attached medially to the palatine and laterally to the ectopterygoid (Fig. 25B), but is attached only to the palatine in other species. The quadrate is dorsally attached to the endopterygoid. The posterodorsal portion of the quadrate is attached to the metapterygoid via a lateral cartilage. In *Belonion dibranchodon*, the posteroventral portion of the quadrate is attached only to the symplectic (Fig. 25C), whereas the posteroventral portion of the quadrate is attached to the preopercle and has a notch into which the symplectic is inserted in other species.

The blade-like symplectic is attached to the preopercle ventrally. In all species except *Belonion dibranchodon*, the anterior part is inserted into a notch on the quadrate, whereas it is dorsally attached to the quadrate in *Belonion dibranchodon*. The medial aspect of the symplectic is dorsally attached to the endopterygoid and metapterygoid in all species except *Belonion dibranchodon* (Fig. 25C), in which the symplectic is dorsally attached to the metapterygoid and quadrate. The posterior portion of the symplectic is attached to the hyomandibula via a cartilage. A medial cartilage on the anteriormost portion of the symplectic is absent in *Strongylura strongylura* (Fig. 26D), but present in other species. In all species except *Belonion dibranchodon* and *Potamorrhaphis guianensis*, a foramen crossed by the hyomandibularis incorporates the symplectic, quadrate and preopercle, whereas a foramen is formed by the quadrate and preopercle in *Pot. guianensis* (Fig. 26C). Neither the foramen nor hyomandibularis could be found in the extremely small specimen of *Belonion dibranchodon* examined.

The hyomandibula is situated on the middle of the top of the suspensorium, being attached to the metapterygoid anteriorly, the preopercle ventrally, and the symplectic anteroventrally via a cartilage. Two condyles articulating with glenoid cavities of the preopercle and the neurocranium, respectively, are present on posterior and dorsal portions of the hyomandibula.

The hatchet-like preopercle is attached to the quadrate anterodorsally and the hyomandibula posterodorsally in all species, except *Belonion dibranchodon*. In the middle of the bone, it is attached to the symplectic dorsally. Medially, the preopercle is loosely attached to the interopercle. The preopercle has a tubular sensory canal structure, not continuous with adjacent canals in *Belonion dibranchodon* (Fig. 25C), but anteriorly continuous with the angular canal in other species.

The flat and thin interopercle is loosely attached to the preopercle laterally, and is anteriorly connected to the retroarticular via a ligament and posteriorly attached to the subopercle. The posterodorsal margin of the interopercle is connected to the epihyal via a ligament.

The circular or triangular opercle, on the posterior portion of the suspensorium, anteriorly has a glenoid cavity articulating with the hyomandibular condyle. The opercle overlaps the subopercle ventromedially.

The subopercle is a thin U-shaped bone, situated on the posteroventral portion of the suspensorium and overlapping with the opercle dorsolaterally. Medially, the subopercle supports the branchiostegal rays.
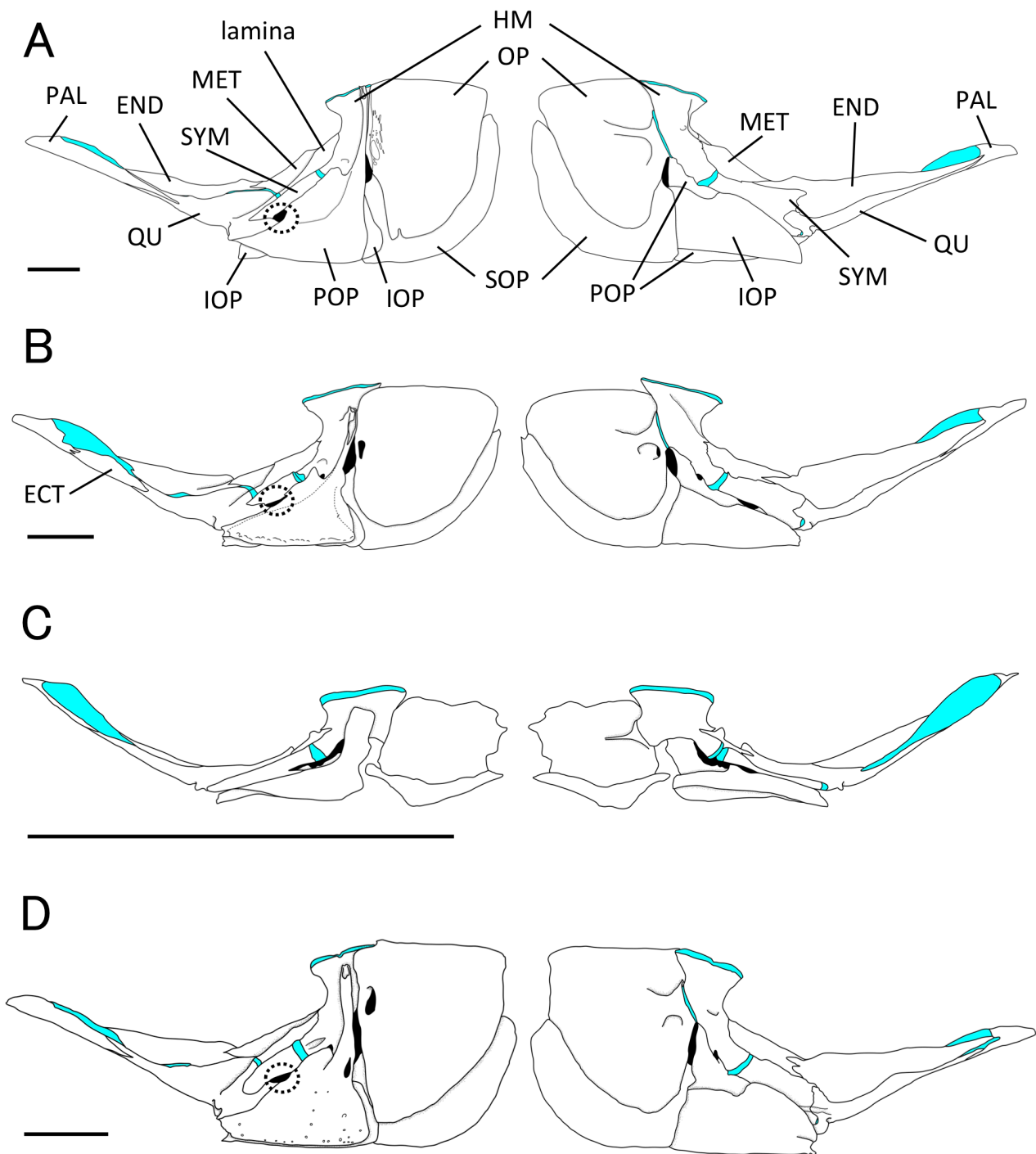
Figure 25. Lateral views (left) and medial views (right) of suspensorium in (A) *Ablennes hians*, canal omitted, (B) *Belone belone*, (C) *Belonion dibranchodon*, canal omitted and (D) *Petalichthys capensis*, canal omitted. ECT, ectopterygoid; END, endopterygoid; HM, hyomandibula; IOP, interopercle; MET, metapterygoid; OP, opercle; PAL, palatine; POP, preopercle; QU, quadrate; SOP, subopercle; SYM, symplectic. Bars indicate 5 mm. Dotted circles in lateral views indicate position of foramen crossed by hyomandibularis.
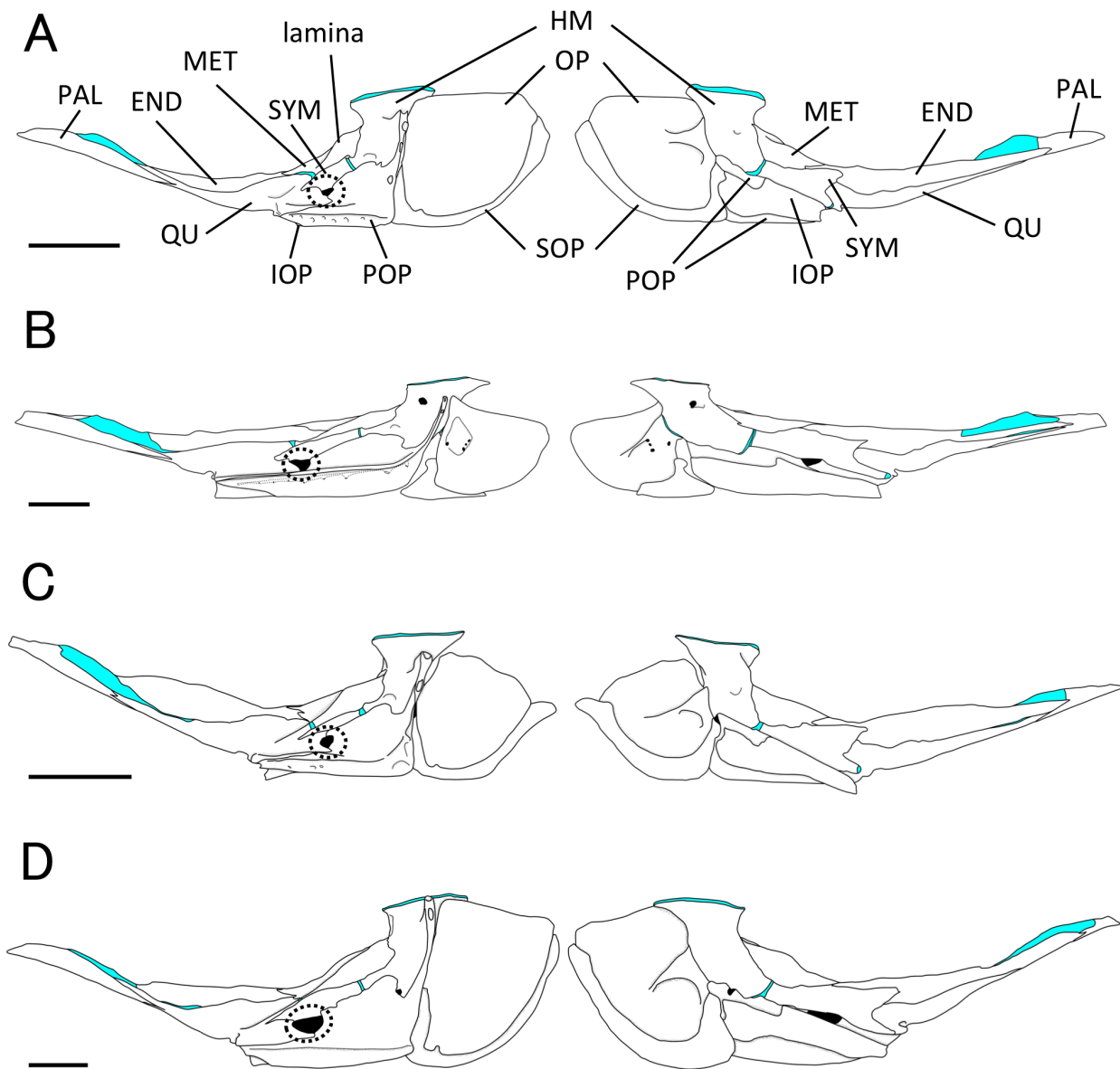
Figure 26. Lateral views (left) and medial views (right) of suspensorium in (A) *Platybelone argalus argalus*, canal omitted, (B) *Pseudotylosurus microps*, (C) *Potamorrhaphis guianensis*, canal omitted and (D) *Strongylura strongylura*, canal omitted. Abbreviations as in Fig. 25. Bars indicate 5 mm. Dotted circles in lateral views indicate position of foramen crossed by hyomandibularis.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 20. *Cartilaginous cap on anterior tip of palatine*. 0: present; 1: absent.

Belonidae. All species lack a cartilaginous cap (character 20-1).

Other ingroups. The cap is present in *Hemiramphus far*, *Zenarchopterus dunckeri*, *Cypselurus doederleini* (Fig. 28A), *Exocoetus monocirrhus* and *Fodiator acutus* (Fig. 28B) (character 20-0), and absent in all scomberesocids (Fig. 27C) and *Parexocoetus brachypterus* (character 20-1).
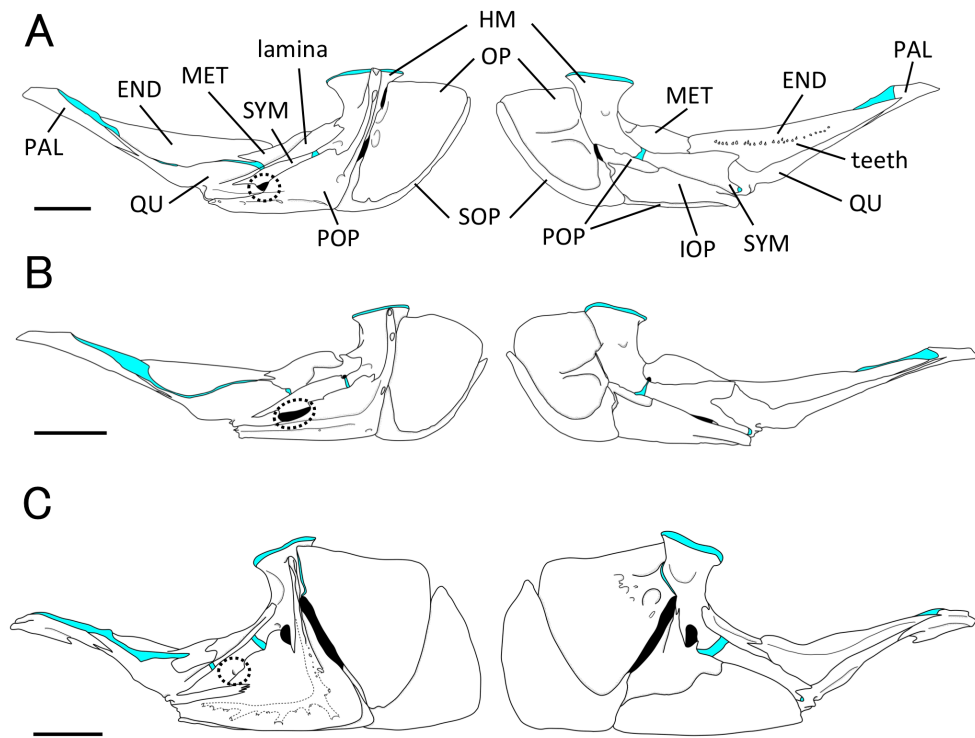
Figure 27. Lateral views (left) and medial views (right) of suspensorium in (A) *Tylosurus punctulatus*, canal omitted, (B) *Xenentodon cancila*, canal omitted and (C) *Cololabis saira*. Abbreviations as in Fig. 25. Bars indicate 5 mm. Dotted circles in lateral views indicate position of foramen crossed by hyomandibularis.

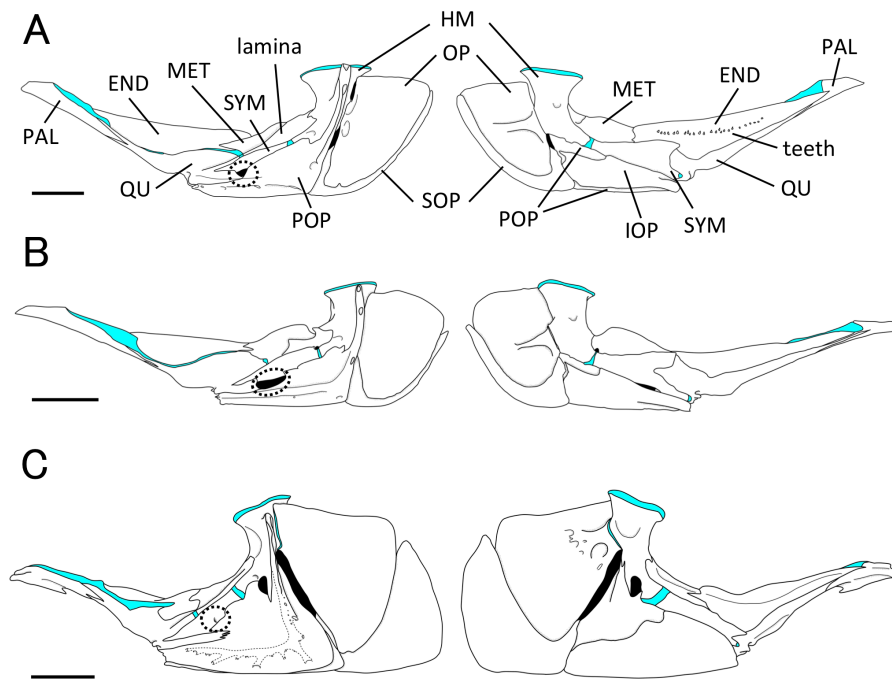**Figure 28.** Lateral views (left) and medial views (right) of suspensorium in (A) *Cypselurus doederleini*, (B) *Fodiator acutus*, canal omitted and (C) *Atherinomorus pinguis*. Abbreviations as in Fig. 25. Bars indicate 5 mm. Dotted circles in lateral views indicate position of foramen crossed by hyomandibularis.

Outgroups. The cap is absent in *Oryzias javanicus*, (character 20-1), but present in the other outgroups (Fig. 28C) (character 20-0).

TS 21. *Teeth on palatine*. 0: absent; 1: present.

Belonidae. Palatine teeth are absent in all belonids (character 21-0).

Other ingroups. Teeth are present in *Parexocoetus brachypterus* (character 21-1), but absent in other species (character 21-0).

Outgroups. Teeth are present in *Atherinomorus pinguis* (Fig. 28C) (character 21-1), but absent in the other outgroups (character 21-0).

TS 22. *Ectopterygoid*. 0: absent; 1: present.

Belonidae. The ectopterygoid is present in *Belone belone* (character 22-1), but absent in other species (character 22-0).

Other ingroups. All other ingroups lack the ectopterygoid (character 22-0).

Outgroups. The ectopterygoid is present in *Atherinomorus pinguis* (Fig. 28C) (character 22-1), but absent in the other outgroups (character 22-0).

TS 23. *Teeth on endopterygoid*. 0: absent; 1: present.

Belonidae. Endopterygoid teeth are present in *Tylosurus punctulatus* (character 23-1), but absent in other species (character 23-0).

Other ingroups. Endopterygoid teeth are present in *Parexocoetus brachypterus* (character 23-1), but absent in other species (character 23-0).

Outgroups. Endopterygoid teeth are present in *Atheri-nomorus pinguis* (Fig. 28C) (character 23-1), but absent in other species (character 23-0).

TS 24. *Metapterygoid lamina*. 0: absent; 1: present.

Belonidae. The metapterygoid lamina is present in all

species (character 24-1).

Other ingroups. The lamina is absent in all species (character 24-0).

Outgroups. The lamina is absent in all outgroups (character 24-0).

TS 25. *Medial cartilage on anteriormost portion of symplectic*. 0: present; 1: absent.

Belonidae. The cartilage is absent in *Strongylura strongylura* (character 25-1), but present in the other species (character 25-0).

Other ingroups. The cartilage is absent in *Cypselurus doederleini* (Fig. 28A) and *Parexocoetus brachypterus* (character 25-1), but present in other species (character 25-0).

Outgroups. The cartilage is absent in *Oryzias javanicu*s (character 25-1), but present in the other outgroups (character 25-0).

TS 26. *Foramen components crossed by hyomandibularis*. 0: symplectic only; 1: quadrate and symplectic; 2: symplectic and preopercle; 3: quadrate, symplectic and preopercle; 4: quadrate and preopercle.

Belonidae. In all species except *Potamorrhaphis guianensis*, the foramen components include the quadrate, symplectic and preopercle (character 26-3), whereas the foramen comprises the quadrate and preopercle only in *Pot. guianensis* (character 26-4).

Other ingroups. The foramen comprises the quadrate and symplectic in *Cypselurus doederleini* (Fig. 28A) and *Exocoetus monocirrhus* (character 26-1), the symplectic only in all scomberesocids (Fig. 27C), *Hemiramphus far* and *Parexocoetus brachypterus* (character 26-0), the symplectic and preopercle in *Fodiator acutus* (Fig. 28B) (character 26-2), and the quadrate, symplectic and preopercle in *Zenarchopterus dunckeri* (character 26-3).

Outgroups. The foramen comprises the quadrate and symplectic in *Poecilia mexicana* (character 26-1), and symplectic only in *Atherinomorus pinguis* (Fig. 28C) (character 26-0). The foramen was not observed in the

Oryzias javanicus specimen, the species therefore was coded as "?" for TS 26.

Other variations

Endopterygoid and metapterygoid. The endopterygoid is separated from the metapterygoid in *Belonion dibranchodon* and *Poecilia mexicana*, whereas the endopterygoid is attached to the metapterygoid in other species, including outgroups and *Elassichthys adocetus*. This variation is not adopted for the analysis due to *Poe. mexicana* being the only analyzed species with the former condition.

Quadrate and preopercle. The quadrate is separated from the preopercle in *Belonion dibranchodon*, but attached to the preopercle in other species. This is considered an autapomorphy of *Belonion dibranchodon*.

5. Hyoid arch (Figs. 29–34)

Description

The hyoid arch comprises the hypohyal, ceratohyal, epihyal, interhyal, branchiostegal rays, urohyal and basihyal. The urohyal and basihyal are unpaired elements, and the others paired. (The basihyal is described and discussed under branchial arches.)

The hypohyal, comprising one element, is situated on the anteroventral portion of the hyoid arch, being attached to a cartilage on the anterior tip of the hyoid arch dorsally and the ceratohyal posteriorly. The dorsomedial portion of the hypohyal is connected to the basihyal anteriorly and the first hypobranchial posteriorly, via a ligament. The posteromedial portion of the hypohyal is connected to the urohyal via a ligament. The antimeres on each side articulate with each other medially.

The elongate and flattened ceratohyal, situated on the middle of the hyoid arch, is attached to the hypohyal anteriorly and the epihyal posteriorly via cartilage. The ventral portion of the ceratohyal is bordered by cartilage.

The short flattened epihyal, situated on the posteriormost portion of the hyoid arch, is attached to the ceratohyal anteriorly. Ventrally, the epihyal is bordered by

cartilage. Posteriorly, the epihyal is connected to the medial surface of the interopercle via a ligament. A cartilage is present on the posterodorsal portion of the epihyal in *Potamorrhaphis guianensis* (Fig. 32), but is absent in other species.

The interhyal is present but rudimentary and buried in ligament between the epihyal and interopercle in *Ablennes hians* (Fig. 29A) and *Potamorrhaphis guianensis* (Fig. 30B), but absent in other species.

The long curved branchiostegal rays number six in *Belonion dibranchodon* (Fig. 29C), nine in *Pseudotylosurus angusticeps* and *Strongylura leiura*, 10 in *Petalichthys capensis* (Fig. 29D), *St. strongylura* and *Xenentodon cancila* (Fig. 31B), 11 in *Platybelone argalus argalus* (Fig. 30A), *Potamorrhaphis guianensis* (Fig. 30B), *Ps. microps* (Fig. 30C) and *Tylosurus gavialoides* (Fig. 31A), 12 in *St. exilis* (Fig. 30D), 13 in *Belone belone* (Fig. 29B), 14 in *Ablennes hians* (Fig. 29A), *St. krefftii*, *T. acus imperialis* and *T. a. melanotus*, and 15 in *T. punctulatus*. They are loosely attached to the lateral aspect of the ceratohyal and epihyal via connective tissue. Two rays are attached to the ceratohyal in *Belonion dibranchodon*, five in *Ps. angusticeps*, six in *Pl. a. argalus*, *St. leiura* and *St. strongylura*, seven in *Pe. capensis*, *Pot. guianensis*, *Ps. microps* and *X. cancila*, eight in *Belone belone* and *T. gavialoides*, nine in *St. exilis*, *St. krefftii* and *T. punctulatus*, and 11 in *Ab. hians*, *T. a. imperialis* and T. *a. melanotus*. Four rays are attached to the epihyal in *Pot. guianensis, Ps. angusticeps* and *St. krefftii*, while three rays are attached in other belonids. One ray is suspended from the cartilage between the ceratohyal and epihyal in *Belonion dibranchodon*, *St. krefftii* and *St. strongylura*. In addition, two anterior branchiostegal rays are supported by connective tissue from the lower portion of the hypohyal in *Belone belone* and *Pl. a. argalus*, compared with six anterior rays in *T. punctulatus*. No rays are supported by the hypohyal in other species examined.

The unpaired thin and tape-like urohyal in the midventral portion of the hyoid arch, is anteriorly connected to the hypohyal on each side via a ligament. The posterior portion of the urohyal is connected to the medial aspect of the pectoral girdle via the sternohyoideus. A dorsal process from the anterior portion of the urohyal is absent in *Petalichthys capensis* (Fig. 33D). The tip of the dorsal process is simple and pointed in *Ablennes hians* (Fig. 33A) and *Belonion dibranchodo*n (Fig. 33C), bifurcated and flat in *Xenentodon cancila* (Fig.
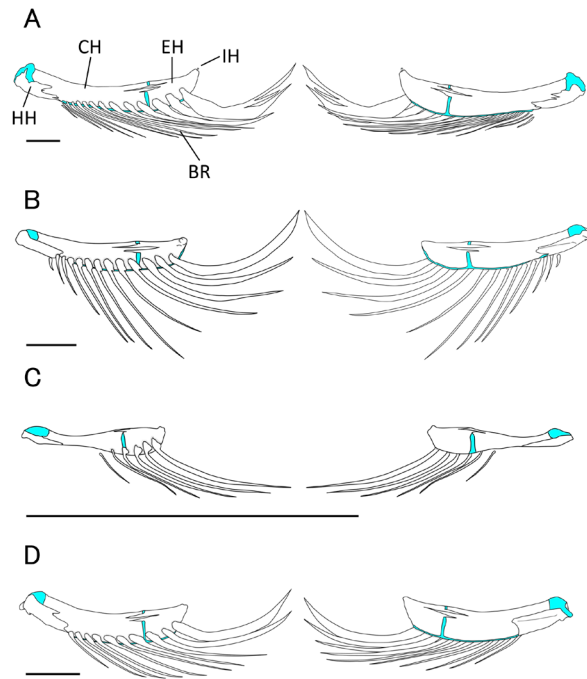
Figure 29. Lateral views (left) and medial views (right) of hyoid arch in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon* and (D) *Petalichthys capensis*. BR, branchiostegal rays; CH, ceratohyal; EH, epihyal; HH, hypohyal; IH, interhyal. Bars indicate 5 mm.
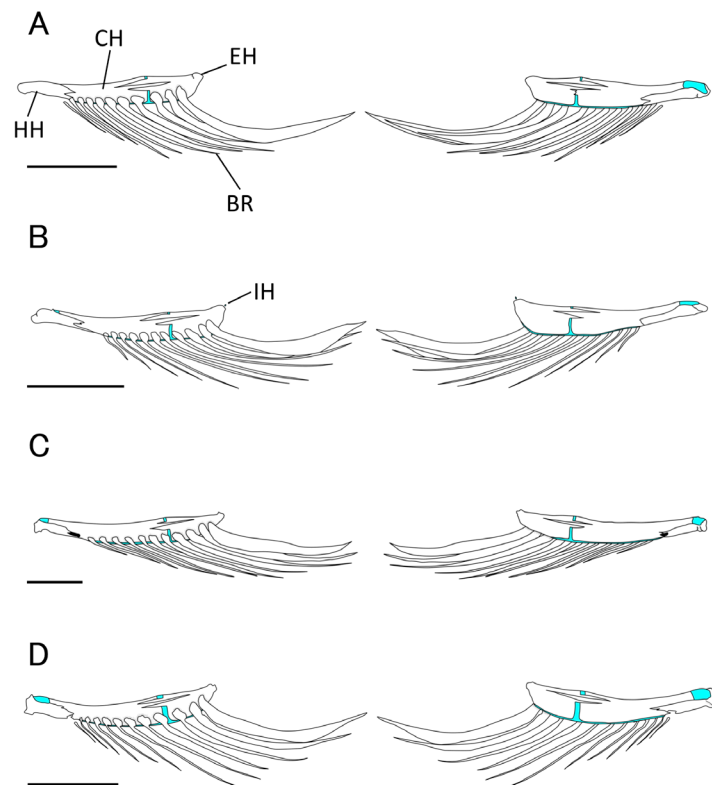
Figure 30. Lateral views (left) and medial views (right) of hyoid arch in (A) *Platybelone argalus argalus*, (B) *Potamorrhaphis guianensis*, mirror image, (C) *Pseudotylosurus microps* and (D) *Strongylura exilis*. Abbreviations as in Fig. 29. Bars indicate 5 mm.
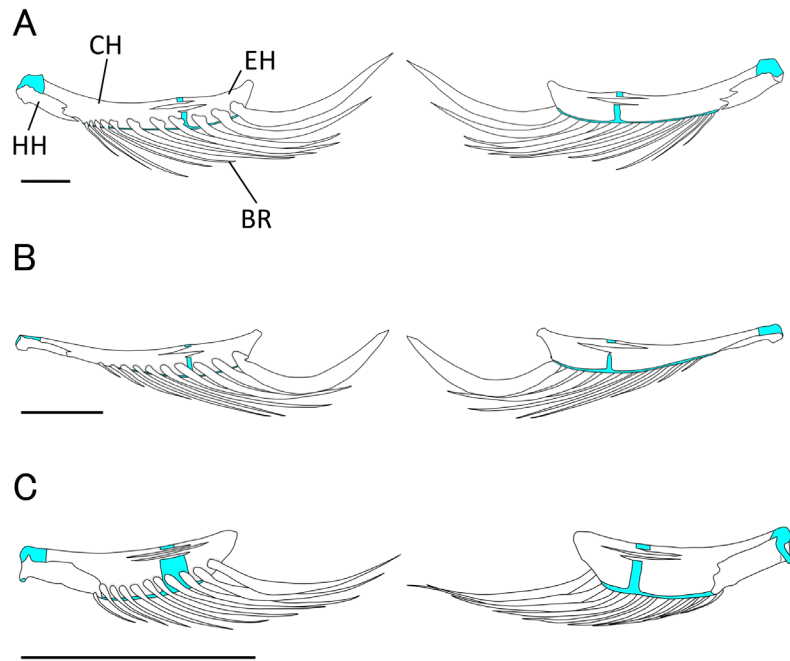
Figure 31. Lateral views (left) and medial views (right) of hyoid arch in (A) *Tylosurus gavialoides*, (B) *Xenentodon cancila* and (C) *Nanichthys simulans*. Abbreviations as in Fig. 29. Bars indicate 5 mm.
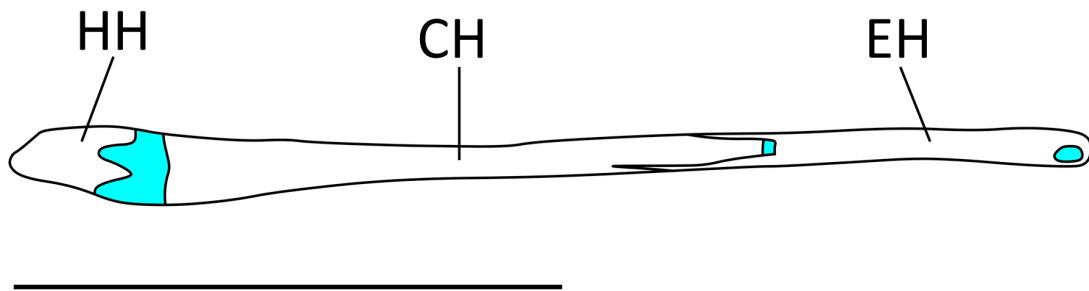
Figure 32. Dorsal view of hyoid arch of *Potamorrhaphis guianensis*, mirror image. Abbreviations as in Fig. 29. Bar indicates 5 mm.
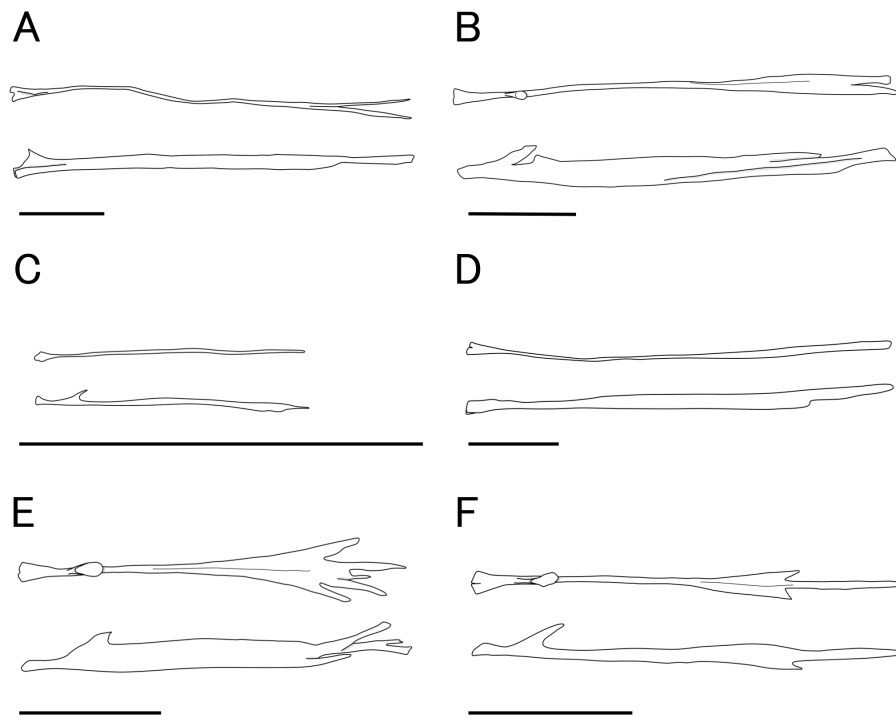
Figure 33. Dorsal views (upper) and lateral views (lower) of urohyal in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon*, (D) *Petalichthys capensis*, (E) *Platybelone argalus argalus* and (F) *Potamorrhaphis guianensis*. Bars indicate 5 mm.

Figure 34. Dorsal views (upper) and lateral views (lower) of urohyal in (A) *Pseudotylosurus angusticeps*, (B) *Strongylura exilis*, (C) *Tylosurus gavialoides*, (D) *Xenentodon cancila* and (E) *Elassichthys adocetus*. Bars indicate 5 mm.

34D), and simple and flat in all other species.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 27. *Cartilage on posterodorsal portion of epihyal.* 0: absent; 1: present.
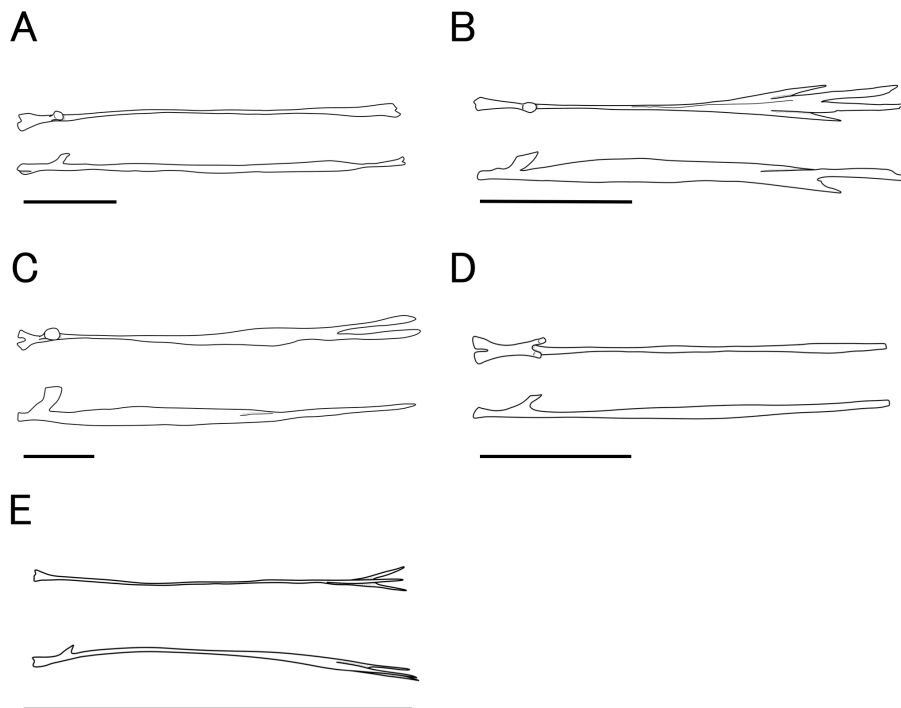
Belonidae. A cartilage is present posterodorsally on the epihyal in *Potamorrhaphis guianensis* (character 27-1), but absent in other species (character 27-0).

Other ingroups. The cartilage is present in *Hemiramphus far* (character 27-1), but absent in other species (character 27-0).

Outgroups. All outgroups lack the cartilage (character 27-0).

TS 28. *Interhyal.* 0: present, developed; 1: present, rudimentary; 2: absent.

Belonidae. The interhyal is present and rudimentary in *Ablennes hians* and *Potamorrhaphis guianensis* (character 28-1), but absent in other species (character 28-2).

Other ingroups. A rudimentary interhyal is present in *Fodiator acutus* (character 28-1), but absent in other species (character 28-2).

Outgroups. The interhyal is absent in *Oryzias javanicus* (character 28-2), but present and welldeveloped in the other outgroups (character 28-0).

Remarks. Rosen and Parenti (1981) inferred that the absence of the interhyal was one of characters that defining the order Beloniformes. In this study, the absence of the interhyal was also recognized in most of the beloniform species. Even though the interhyal is present in belonids *Ablennes hians* and *Potamorrhaphis guianensis*, and exocoetid *Fodiator acutus*, it is small and rudimentary.

TS 29. *Dorsal process of urohyal.* 0: present, tip of process simple and pointed; 1: present, tip of process simple and flat; 2: present, tip of process bifurcated and flat; 3: absent.

Belonidae. The dorsal process of the urohyal is absent in *Petalichthys capensis* (character 29-3). It is present with a simple pointed tip in *Ablennes hians* (character 29-0), present, simple and flat in most other species (character 29-1), and present, bifurcated and flat in *Xenentodon cancila* (character 29-2).

Other ingroups. The process is absent in all exocoetids (character 29-3). It is present with a simple pointed tip in all scomberesocids and *Hemiramphus far* (character 29-0), and present, simple and flat in *Zenarchopterus dunckeri* (character 29-1).

Outgroups. The process is absent in *Oryzias javanicus* (character 29-3) and present, with a simple pointed tip in the other outgroups (character 29-0).

Other variations

Number of branchiostegal rays. The branchiostegal rays vary from six to 15 in Belonidae. Among other ingroups and outgroups, the rays number four in *Oryzias javanicus*, five in *Poecilia mexicana*, six in *Atherinomorus pinguis*, eight in *Elassichthys adocetus*, nine in *Zenarchopterus dunckeri*, 11 in *Nanichthys simulans* and all exocoetids, 12 in *Scomberesox saurus*, 13 in *Hemiramphus far* and 14 in *Cololabis saira*. However, because the homology of each ray was unclear, this variation was not used for the analysis.

Branchiostegal rays attached to ceratohyal and epihyal. The branchiostegal rays are ventrally attached to the lateral aspects of the ceratohyal and epihyal via connective tissue in all ingroups and outgroups. Although the number of rays attached vary in number by species, such variations were not adopted for the present analysis because of the uncertain homology of each ray.

Anterior branchiostegal rays suspended from hypohyal. The branchiostegal rays are also suspended from the lower portion of the hypohyal in belonids *Belone belone*, *Platybelone argalus argalus* and *Tylosurus punctulatus*, scomberesocids *Cololabis saira* and *Nanichthys simulans*, and exocoetids *Cypselurus doederleini*, *Exocoetus monocirrhu*s and *Parexocoetus brachypterus*. Although this condition can be regarded

as apomorphic, this variation was not adopted for the present analysis because the number of branchiostegal rays under the hypohyal is variable (one in *N. simulans* and *Pa. brachypterus*, two in *Belone belone*, *Pl. a. argalus* and *Co. saira*, and three in *Cy. doederleini* and *Ex. monocirrhus*), with uncertain homology of each ray.

6. Branchial arches (Figs. 35–43)

Description

The branchial arches comprise lower and upper parts, the lower including the basibranchials, hypobranchials and ceratobranchials, and the upper including the epibranchials, pharyngobranchials and fourth upper pharyngeal tooth plate. The basibranchials and fifth ceratobranchial are unpaired and the remainder paired. In addition, the gill rakers and basihyal are described in this section.

The spatulate and toothless basihyal is attached to the anteriormost portion of the branchial arches. The basihyal has a cartilaginous margin anteriorly and supports the tongue. The basihyal is connected to the hypohyals ventrally via ligaments and to the first basibranchial posteriorly via connective tissue.

The stick-like basibranchials, comprising three elements, are located on the midline of the lower branchial region, the first being attached to the basihyal anteriorly via connective tissue. The posterior tip of the first basibranchial, with a cartilaginous cap, is attached to the second basibranchial. The second and third basibranchials have cartilaginous caps on their anterior and posterior tips, those of the second basibranchial being attached to the first and third basibranchials, respectively. The second basibranchial is attached anterolaterally between the first hypobranchials on each side and is posteriorly attached to the third basibranchial. The posterior tip of the third basibranchial is connected to a small rhomboid cartilage via connective tissue, the third basibranchial being sandwiched by the second hypobranchials anterolaterally and the third hypobranchials posterolaterally on each side.

The hypobranchials comprise three plate-like bones. The first and second have a cartilaginous portion medially, which articulate with the first and second basibranchials, respectively. The third hypobranchial articulates with the posteromedial potion of the third basibranchial via connective tissue. The third hypobranchial is not found

in *Belonion dibranchodon* due to the small size of the specimen. All hypobranchials have cartilaginous caps on their posterior tips and articulate with the first to third ceratobranchials, respectively.

The ceratobranchials comprise four long stick-like bones (first to fourth ceratobranchials) and a club-like or triangular tooth bearing bone (fifth ceratobranchial). The first to fourth ceratobranchials are paired elements, the fifth being unpaired due to fusion of the bones on both sides. The first to fourth ceratobranchials have cartilaginous caps on their anterior and posterior tips, which articulate with the first to fourth epibranchials, respectively. Anteriorly, the first to third ceratobranchials articulate with the first to third hypobranchials, respectively. The anterior tips of the fourth ceratobranchials on each side are attached to each other and anteriorly to a small piece of cartilage. The anterior tip of the fifth ceratobranchial is cartilaginous, being connected to the anterior tips of the fourth ceratobranchials via connective tissue. Teeth on the dorsal surface of the fifth ceratobranchial are conical and tricuspid in *Belone belone* (Fig. 36B), *Petalichthys capensis* (Fig. 36D) and *Platybelone argalus argalus* (Fig. 37A), and only conical in all other species.

The epibranchials, situated in the dorsolateral portion of the upper branchial arch, comprise the first to fourth epibranchials in all species except *Belonion dibranchodon*, *Pseudotylosurus angusticeps*, *Ps. microps* and *Xenentodon cancila*. They comprise three elements in *Ps. angusticeps* (Fig. 41A) and *X. cancila* (Fig. 41D) (the fourth being absent), three in *Belonion dibranchodon* (Fig. 40C) (the second being absent) and two in *Ps. microps* (the second and fourth being absent). The hatchet-like first epibranchial has cartilaginous caps on its medial and lateral tips, and articulates with the first ceratobranchial ventrolaterally. The medial tip of the first epibranchial is attached to the parasphenoid. The second to fourth epibranchials also have cartilaginous caps on their medial and lateral tips, articulating ventrolaterally with the second to fourth ceratobranchials, respectively. In *Ps. angusticeps*, a cartilaginous cap on the lateral tip of the third epibranchial is absent (Fig. 41A). The second epibranchial articulates medially with the second pharyngobranchial in all belonids, except *X. cancila* in which it is attached to the parasphenoid medially (Fig. 41D). The third and fourth epibranchials articulate with the third pharyngobranchial medially. The dorsolateral process of the second epibranchial is present in all species having the second epibranchial, except *Ps.*
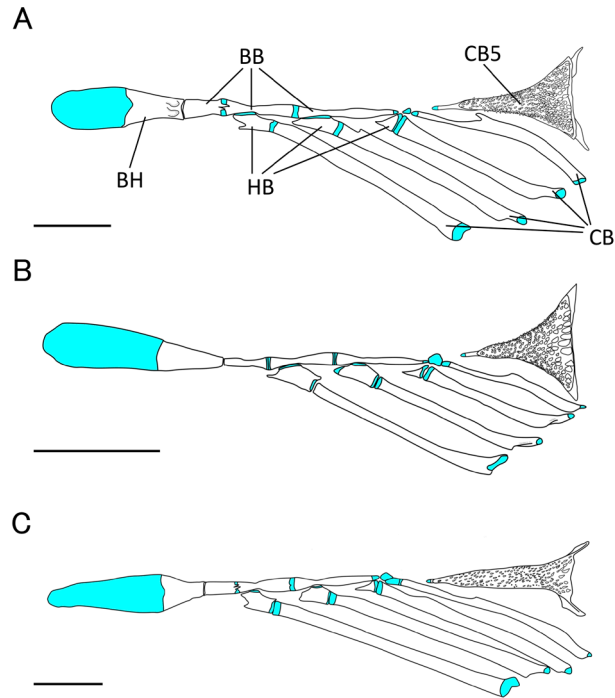
Figure 35. Dorsal views of lower branchial arch in (A) *Belone belone*, (B) *Potamorrhaphis guianensis* and (C) *Tylosurus acus imperialis*. BB, basibranchial; BH, basihyal; CB, ceratobranchial; HB, hypobranchial. Bars indicate 5 mm.
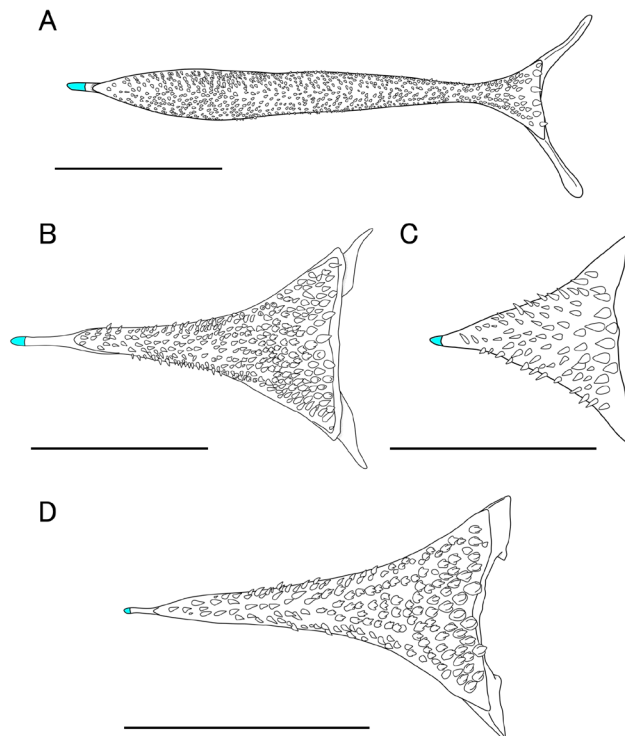
Figure 36. Dorsal views of fifth ceratobranchial in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon* and (D) *Petalichthys capensis*. Bars indicate 5 mm (A–B, D) and 1 mm (C).
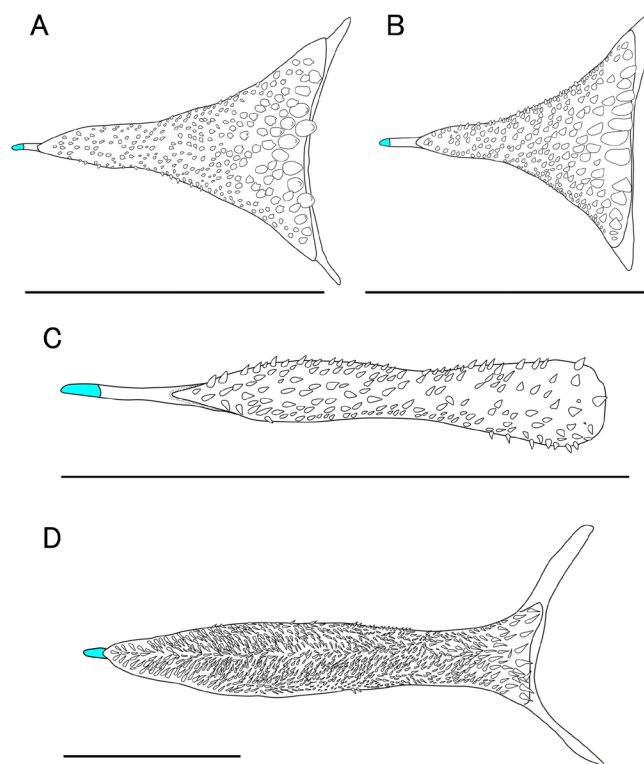
Figure 37. Dorsal views of fifth ceratobranchial in (A) *Platybelone argalus argalus*, (B) *Potamorrhaphis guianensis*, (C) *Pseudotylosurus angusticeps* and (D) *Strongylura krefftii*. Bars indicate 5 mm.
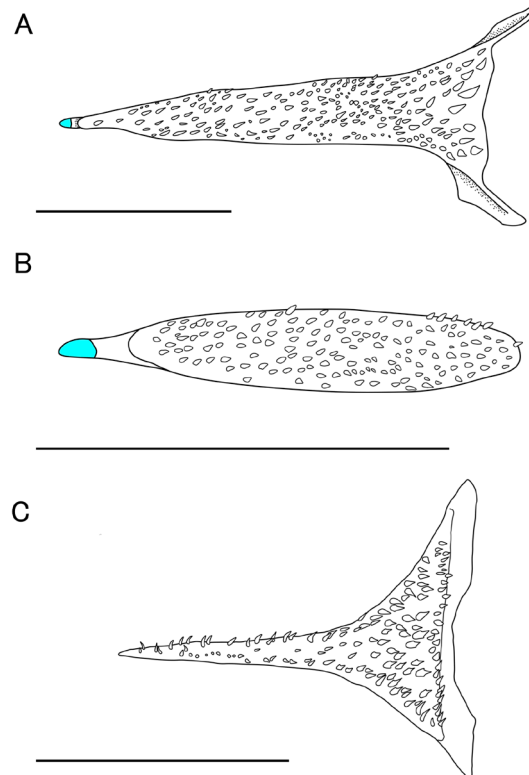
Figure 38. Dorsal views of fifth ceratobranchial in (A) *Tylosurus acus imperialis*, (B) *Xenentodon cancila* and (C) *Scomberesox saurus*. Bars indicate 5 mm.
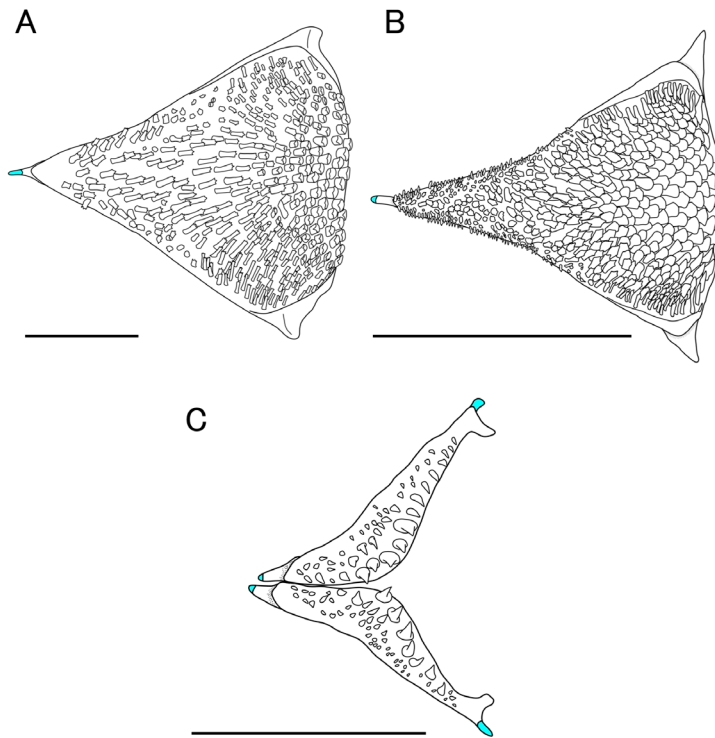
Figure 39. Dorsal views of fifth ceratobranchial in (A) *Hemiramphus far*, (B) *Parexocoetus brachypterus* and (C) *Atherinomorus pinguis*. Bars indicate 5 mm.
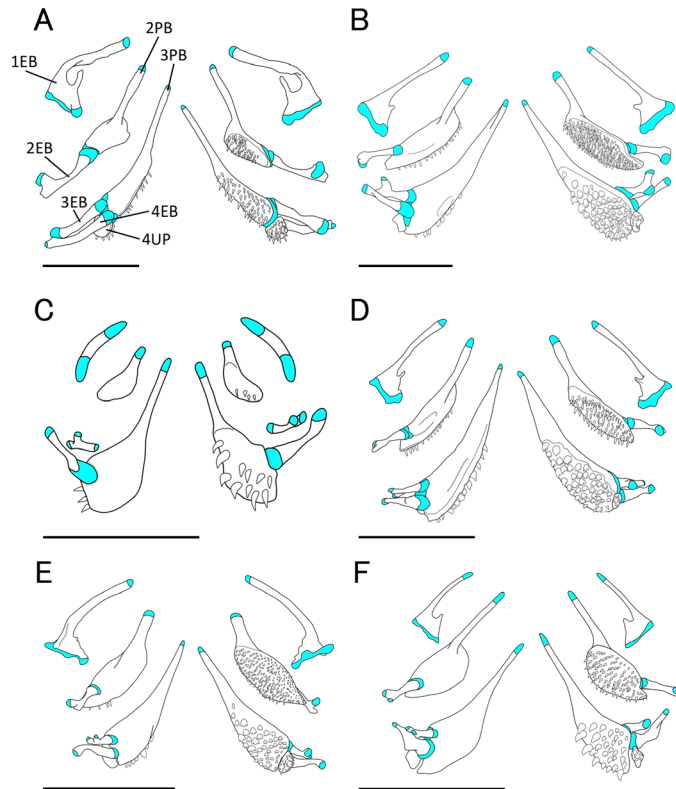

Figure 40. Dorsal (left) and ventral (right) views of upper branchial arch in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Belonion dibranchodon*, (D) *Petalichthys capensis*, (E) *Platybelone argalus argalus* and (F) *Potamorrhaphis guianensis*. EB, epibranchial; PB, pharyngobranchial; UP, upper pharyngeal tooth plate. Bars indicate 5 mm (A–B, D–F) and 1 mm (C).
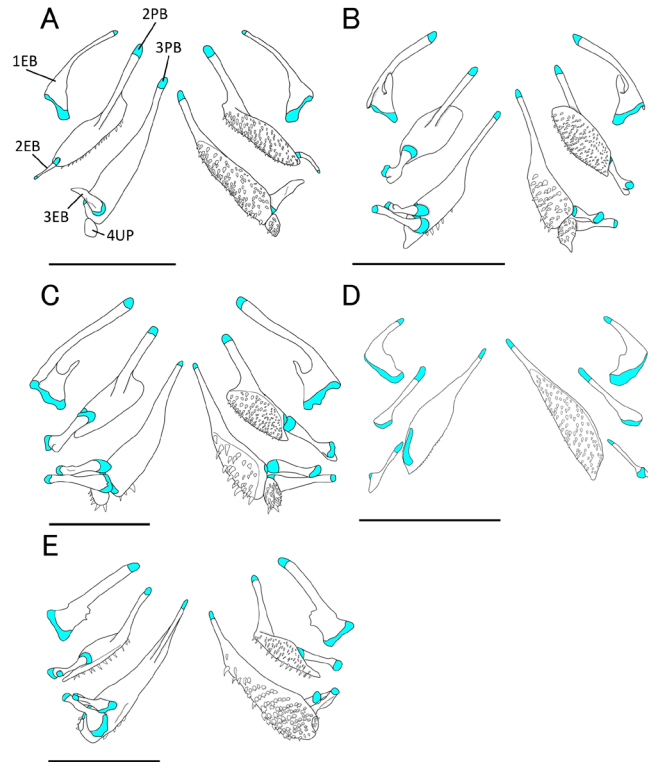
Figure 41. Dorsal (left) and ventral (right) views of upper branchial arch in (A) *Pseudotylosurus angusticeps*, (B) *Strongylura exilis*, (C) *Tylosurus acus imperialis*, (D) *Xenentodon cancila* and (E) *Scomberesox saurus*. Abbreviations as in Fig. 40. Bars indicate 5 mm.
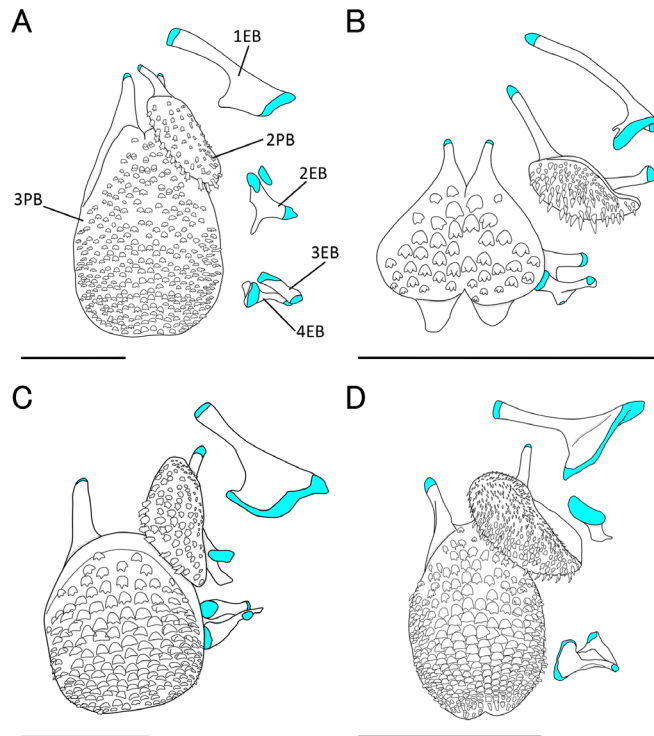
Figure 42. Ventral views of upper branchial arch in (A) *Hemiramphus far*, (B) *Zenarchopterus dunckeri*, (C) *Fodiator acutus* and (D) *Parexocoetus brachypterus*. Abbreviations as in Fig. 40. Bars indicate 5 mm.

A

B

Figure 43. Lateral views of first gill arch in (A) *Petalichthys capensis* and (B) *Xenentodon cancila*.

angusticeps (Fig. 41A), *Strongylura leiura* and *X. cancila* (Fig. 41D). A cartilaginous cap on the process is present in *Potamorrhaphis guianensis* (Fig. 40F), but absent in all other species with a similar process. The dorsal process of the third epibranchial is present in all species except *Ablennes hians* (Fig. 40A) and all species of *Pseudotylosurus* (Fig. 41A). A cartilaginous cap on the dorsal process of the third epibranchial is present in all species with the process, except for *St. exilis* (Fig. 41B), *St. strongylura*, all species of *Tylosurus* (Fig. 41C) and *X. cancila* (Fig. 41D).

The pharyngobranchials, forming the dorsal portion of the oral cavity with the epibranchials and fourth upper pharyngeal tooth plate, include the second and third pharyngobranchials in all species except *Xenentodon cancila* having only the third pharyngobranchial (Fig. 41D). The first pharyngobranchial is absent in all species. The third pharyngobranchials on both sides are separated from each other in all species. The pharyngobranchials have teeth, those on the second pharyngobranchial being conical. Teeth on the third pharyngobranchial are conical and tricuspid in *Belone belone* (Fig. 40B), *Petalichthys capensis* (Fig. 40D) and *Platybelone argalus argalus* (Fig. 40E), but conical in other species.

The fourth upper pharyngeal tooth plate is attached to the posterior portion of the third pharyngobranchial. The fourth upper pharyngeal toothplate is present in all species except *Belonion dibranchodon* (Fig. 40C) and *Xenentodon cancila* (Fig. 41D), in which it is absent. Teeth on the fourth upper pharyngeal tooth plate are conical and tricuspid in *Platybelone argalus*

argalus (Fig. 40E), but conical in other species.

Gill rakers are present in *Belone belone*, *Belonion dibranchodon*, *Petalichthys capensis* (Fig. 43A) and *Platybelone argalus argalus*, but absent in other species (Fig. 43B).

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 30. *Teeth on fifth ceratobranchial.* 0: conical; 1: tricuspid; 2: conical and tricuspid; 3: tricuspid and spatulate.

Belonidae. In *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus*, teeth on the fifth ceratobranchial are conical and tricuspid (character 30-2), but conical in other species (character 30-0).

Other ingroups. The teeth on the fifth ceratobranchial are conical and tricuspid in all scomberesocids (Fig. 38C) and *Cypselurus doederleini* (character 30-2), tricuspid in *Hemiramphus far* (Fig. 39A) (character 30-1), conical in *Zenarchopterus dunckeri* and *Exocoetus monocirrhus* (character 30-0), and tricuspid and spatulate in other exocoetids (Fig. 39B) (character 30-3).

Outgroups. All outgroups have conical teeth on the fifth ceratobranchial (character 30-0).

TS 31. *Dorsolateral process of second epibranchial.* 0: present; 1: absent.

Belonidae. The dorsal process of the second epibranchial is absent (character 31-1) in *Pseudotylosurus angusticeps*, *Strongylura leiura* and *Xenentodon cancila*, but present in other species (character 31-0). *Pseudotylosurus microps* is coded as "?" for TS 31, because of lacking the second epibranchial.

Other ingroups. All species have this process (character 31-0).

Outgroups. The process is absent (character 31-1) in *Oryzias javanicus* and *Poecilia mexicana*, but is present in *Atherinomorus pinguis* (character 31-0).

TS 32. *Cartilaginous cap on dorsolateral process of second epibranchial.* 0: absent; 1: present.

Belonidae. The cartilaginous cap on the dorsolateral process of the second epibranchial is present in *Potamorrhaphis guianensis* (character 32-1), but absent in *Ablennes hians*, *Belone belone*, *Petalichthys capensis*, *Platybelone argalus argalus*, *Strongylura exilis*, *St. krefftii*, *St. strongylura* and all species of *Tylosurus* (character 32-0). All species of *Pseudotylosurus*, *St. leiura* and *Xenentodon cancila* are coded as "?" for TS 32 due to absence of the dorsolateral process of the second epibranchial.

Other ingroups. The cartilaginous cap on the dorsolateral process of the second epibranchial is present in *Scomberesox saurus* and *Cypselurus doederleini* (character 32-1), but absent in other species (character 32-0).

Outgroups. The cartilaginous cap on the dorsolateral process of the second epibranchial is absent in *Atherinomorus pinguis* (character 32-0). Other outgroups are coded as "?" for TS 32 due to absence of the dorsolateral process of the second epibranchial.

TS 33. *Dorsal process of third epibranchial.* 0: present; 1: absent.

Belonidae. In *Ablennes hians* and all species of *Pseudotylosurus*, the dorsal process of the third epibranchial is absent (character 33-1), whereas the process is present in other species (character 33-0).

Other ingroups. All species have the dorsal process of the third epibranchial (character 33-0).

Outgroups. All outgroups have the dorsal process of the third epibranchial (character 33-0).

TS 34. *Cartilaginous cap on dorsal process of third epibranchial.* 0: present; 1: absent.

Belonidae. The cartilaginous cap on the dorsal process of the third epibranchial is absent in *Strongylura exilis*, *St. strongylura*, all species of *Tylosurus* and *Xenentodon cancila* (character 34-1), but present in *Belone belone*, *Petalichthys capensis*, *Platybelone argalus argalus*, *Potamorrhaphis guianensis*, *St. krefftii* and *St. leiura* (character 34-0). *Ablennes hians* and all species of *Pseudotylosurus* are coded as "?" for TS 34, lacking the process on the bone.

Other ingroups. All species have the cartilaginous cap on the dorsal process of the third epibranchial (character 34-0).

Outgroups. All outgroups have the cartilaginous cap on the dorsal process of the third epibranchial (character 34-0).

TS 35. *Fourth epibranchial.* 0: present; 1: absent.

Belonidae. The fourth epibranchial is absent in all species of *Pseudotylosurus* and *Xenentodon cancila* (character 35-1), but present in other species (character 35-0).

Other ingroups. The fourth epibranchial is present in all species (Figs. 41E, 42A–D) (character 35-0).

Outgroups. All outgroups have the fourth epibranchial (character 35-0).

TS 36. *Teeth on second pharyngobranchial.* 0: conical; 1: tricuspid; 2: conical and tricuspid; 3: tricuspid and spatulate.

Belonidae. The teeth on the second pharyngobranchial are conical in all species except *Xenentodon cancila*

(character 36-0). *Xenentodon cancila* is coded as "?" for TS 36 because the second pharyngobranchial is absent.

Other ingroups. The teeth on the second pharyngobranchial are conical in all species of scomberesocids, *Zenarchopterus dunckeri* (Fig. 42B) and *Exocoetus monocirrhus* (character 36-0), are tricuspid in *Hemiramphus far* (Fig. 42A) and *Cypselurus doederleini* (character 36-1), are conical and tricuspid in *Parexocoetus brachypterus* (Fig. 42D) (character 36-2), and are tricuspid and spatulate in *Fodiator acutus* (Fig. 42C) (character 36-3).

Outgroups. The teeth on the second pharyngobranchial are conical in all outgroups (character 36-0).

TS 37. *Third pharyngobranchials on both sides*. 0: separated; 1: attached.

Belonidae. The third pharyngobranchials on both sides are separated from each other in all species (character 37-0).

Other ingroups. The third pharyngobranchial are separated from each other in all scomberesocids (Fig. 41E) (character 37-0), but attached to each other in ingroup species (Fig. 42) (character 37-1).

Outgroups. The third pharyngobranchial are separated from each other in all outgroups (character 37-0).

Remarks. Collette *et al*. (1984) reported that the attached third pharyngobranchials was one of characters defining the superfamily Exocoetoidea. The attached third pharyngobranchials was also recognized in all species of Exocoetoidea in this study.

TS 38. *Teeth on third pharyngobranchial*. 0: conical; 1: tricuspid; 2: conical and tricuspid; 3: tricuspid and spatulate.

Belonidae. The teeth on the third pharyngobranchial are conical and tricuspid in *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus* (character 38-2), but are conical in other species (character 38-0).

Other ingroups. The teeth on the third pharyngobranchial are tricuspid in *Zenarchopterus dunckeri* (Fig. 42B) and *Cypselurus doederleini*, conical and tricuspid in all scomberesocids (Fig. 41E) and *Exocoetus*

monocirrhus (character 38-2), and tricuspid and spatulate in *Hemiramphus far* (Fig. 42A), *Fodiator acutus* (Fig. 42C) and *Parexocoetus brachypterus* (Fig. 42D) (character 38-3).

Outgroups. The teeth on the third pharyngobranchial are conical in all outgroups (character 38-0).

TS 39. *Fourth upper pharyngeal tooth plate*. 0: absent; 1: present.

Belonidae. The fourth upper pharyngeal tooth plate is absent in *Xenentodon cancila* (character 39-0), but present in other species (character 39-1).

Other ingroups. The tooth plate is present in *Cololabis saira* and *Scomberesox saurus* (Fig. 41E) (character 39-1), but absent in other species (Fig. 42) (character 39-0).

Outgroups. The tooth plate is present in *Atherinomorus pinguis* (character 39-1), but absent in other outgroups (character 39-0).

Remarks. Collette *et al*. (1984) reported that the absence of the fourth upper pharyngeal tooth plate was one of characters defining the superfamily Exocoetoidea. In this study, the absence of the fourth upper pharyngeal tooth plate was also recognized in all species of Exocoetoidea.

TS 40. *Teeth on fourth upper pharyngeal tooth plate*. 0: conical; 1: tricuspid; 2: conical and tricuspid.

Belonidae. The teeth on the fourth upper pharyngeal tooth plate are conical and tricuspid in *Platybelone argalus argalus* (character 40-2), but are conical in all other species (character 40-0) except *Xenentodon cancila*, which is coded as "?" for TS 40, because the fourth upper pharyngeal tooth plate is absent.

Other ingroups. The teeth are tricuspid in *Scomberesox saurus* (Fig. 41E) (character 40-1), and conical and tricuspid in *Cololabis saira* (character 40-2). Other species are coded as "?" for TS 40, because they lack the fourth upper pharyngeal tooth plate.

Outgroups. The teeth are conical in *Atherinomorus pinguis* (character 40-0). Other outgroups are coded as "?" for TS 40, because they lack the fourth upper
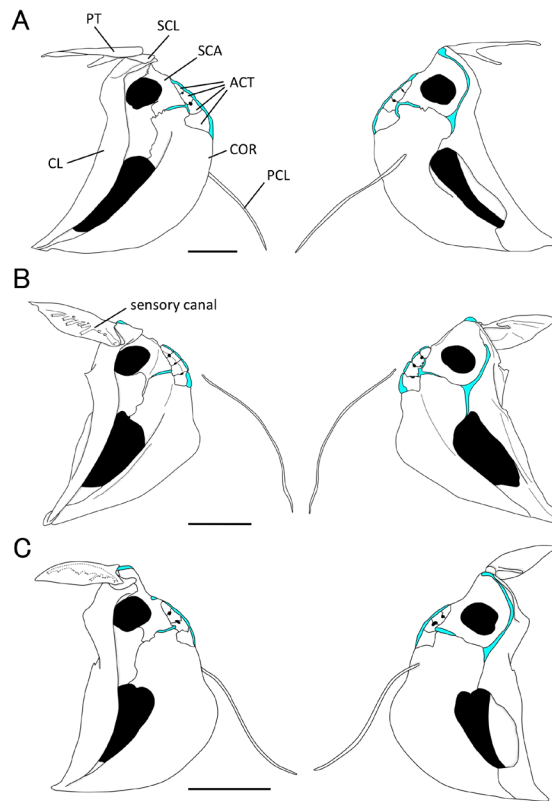
Figure 44. Lateral views (left) and medial views (right) of pectoral girdle in (A) *Ablennes hians*, (B) *Belone belone* and (C) *Petalichthys capensis*, mirror image. ACT, actinost; CL, cleithrum; COR, coracoid; PCL, postcleithrum; PT, posttemporal; SCA, scapula; SCL, supracleithrum. Bars indicate 5 mm.
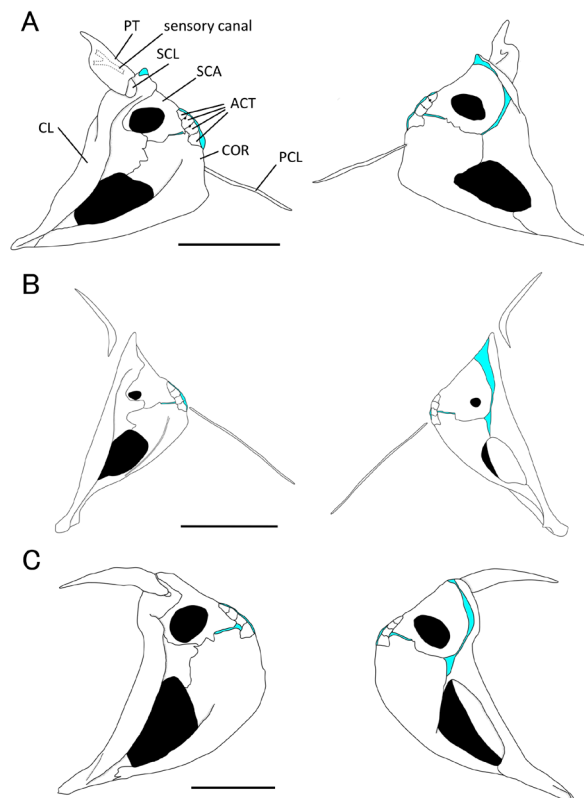
Figure 45. Lateral views (left) and medial views (right) of pectoral girdle in (A) *Platybelone argalus argalus*, (B) *Potamorrhaphis guianensis*, mirror image, posttemporal cut out from cleithrum, and (C) *Pseudotylosurus angusticeps*. Abbreviations as in Fig. 44. Bars indicate 5 mm.
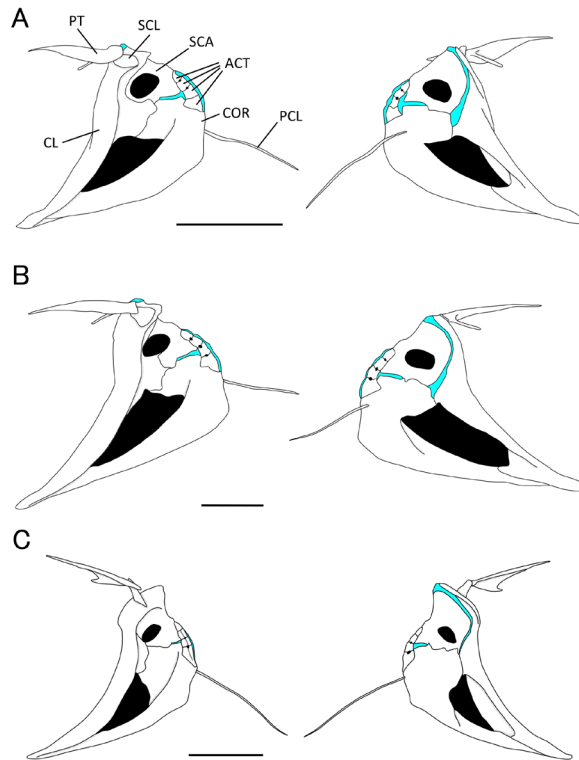
Figure 46. . Lateral views (left) and medial views (right) of pectoral girdle in (A) *Strongylura exilis*, (B) *Tylosurus acus imperialis* and (C) *Xenentodon cancila*, mirror image. Abbreviations as in Fig. 44. Bars indicate 5 mm.
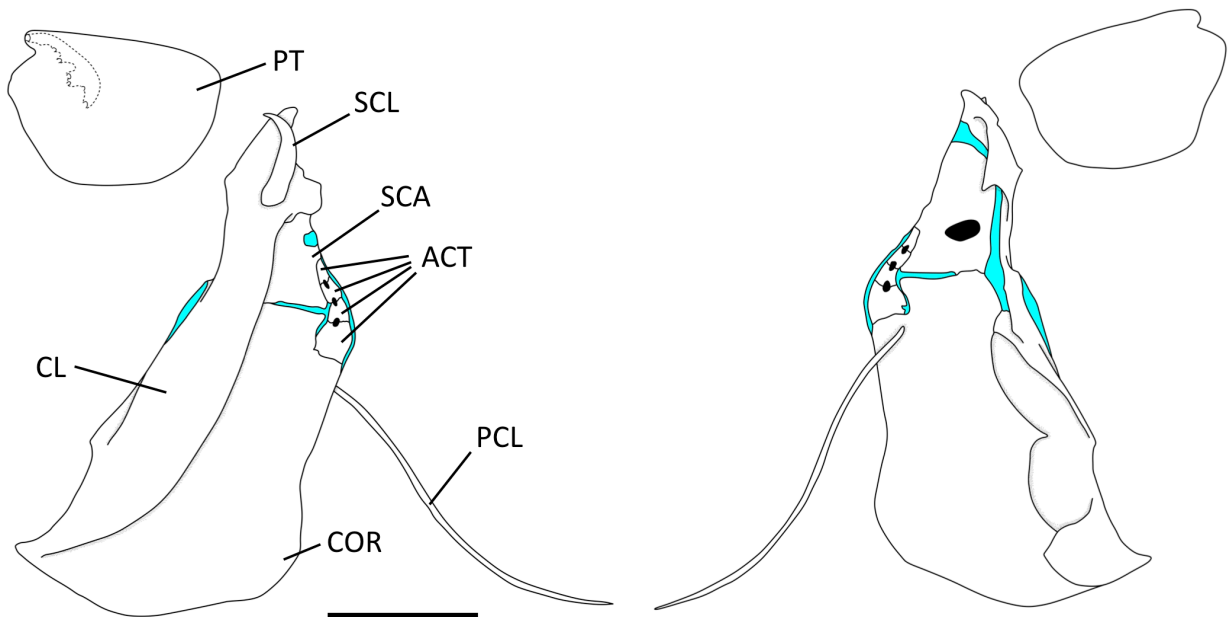
Figure 47. Lateral view (left) and medial view (right) of pectoral girdle in *Cololabis saira*, mirror image, posttemporal cut out from supracleithrum. Abbreviations as in Fig. 44. Bar indicates 5 mm.

pharyngeal tooth plate.

TS 41. *Gill rakers*. 0: present; 1: absent.

Belonidae. Gill rakers are present in *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus* (character 41-0), but are absent in other species (character 41-1).

Other ingroups. All species have gill rakers (character 41-0).

Outgroups. All outgroups have gill rakers (character 41-0).

Remarks. The presence of the gill rakers has been recognized as a character to distinguish the genera *Belone*, *Petalichthys* and *Platybelone* from other belonid genera (*e.g*., Collette and Parin, 1970).

Other variation

Shape of fifth ceratobranchial. The fifth ceratobranchial is generally club-like or triangular. However, in some species, the shape is in between these forms, and this variation could not be clearly sorted into either category. Thus, fifth ceratobranchial shape was not used in the analysis.

Fusion of fifth ceratobranchials. The fifth ceratobranchials are fused with each other in all ingroups, plus *Belonion dibranchodon* and *Elassichthys adocetus*, but are autogenous in all outgroups (Fig. 39C). Thus, fusion of the fifth ceratobranchials is considered a synapomorphy of exocoetoids (see section 1 of TAXON SAMPLING).

Second epibranchial. The second epibranchial is absent in *Belonion dibranchodon* (Fig. 40C) and *Pseudotylosurus microps*, but present in all other ingroups, outgroups and *Elassichthys adocetus*. Although the absence of the second epibranchial is considered apomorphic, this condition was not adopted for the analysis due to *Ps. microps* being the only species studied in which the second epibranchial is absent.

Cartilaginous cap on lateral tip of third epibranchial. This element is absent in *Pseudotylosurus angusticeps*, but present in other species including *Belonion dibranchodon* and *Elassichthys adocetus*. Therefore,

absence of the cap is considered an autapomorphy of *Ps. angusticeps*.

First pharyngobranchial. The first pharyngobranchial is absent in all exocoetoids, including *Belonion dibranchodon* and *Elassichthys adocetus*, adrianichthyoid *Oryzias javanicus* and cyprinodontifom *Poecilia mexicana*, but present in atheriniform *Atherinomorus pinguis*. Accordingly, absence of this bone is considered a common character of Beloniformes and Cyprinodontiformes. Rosen and Parenti (1981) reported that the sister relationship of Beloniformes and Cyprinodontiformes was supported by this character.

Second pharyngobranchial. The second pharyngobranchial is absent in *Xenentodon cancila*, but present in other ingroups, outgroups, including *Belonion dibranchodon* and *Elassichthys adocetus*. Therefore, absence of this bone is considered an autapomorphy of *X. cancila*.

7. Pectoral girdle (Figs. 44–47)

Description

The pectoral girdle comprises the posttemporal, supracleithrum, cleithrum, scapula, actinosts, coracoid, postcleithrum and pectoral fin rays. All elements are paired. The supratemporal and mesocoracoid are absent. Elements of the girdle (except for the pectoral fin rays) could not be observed in *Belonion dibranchodon* because the bones are very thin and not well stained.

The thin board or sickle-like posttemporal, on the uppermost part of the pectoral girdle, is ventrally attached to the dorsal surface of the epiotic. In all species, a ventral process is present on the posttemporal and attaches to the posterior portion of the epiotic, except *Potamorrhaphis guianensis* (Fig. 45B) and all species of *Pseudotylosurus* (Fig. 45C) which lack a process. The posttemporal is posteriorly attached to the supracleithrum in all species except *Pot. guianensis*, in which the posttemporal is posteriorly attached to the cleithrum (Fig. 45B) (the supracleithrum being absent). A tubular sensory canal structure on the posttemporal is present in *Belone belone* (Fig. 44B), *Petalichthys capensis* (Fig. 44C) and *Platybelone argalus argalus* (Fig. 45A), but absent in other species.

The supracleithrum, situated between the posttemporal and cleithrum, is absent only in *Potamorrhaphis*
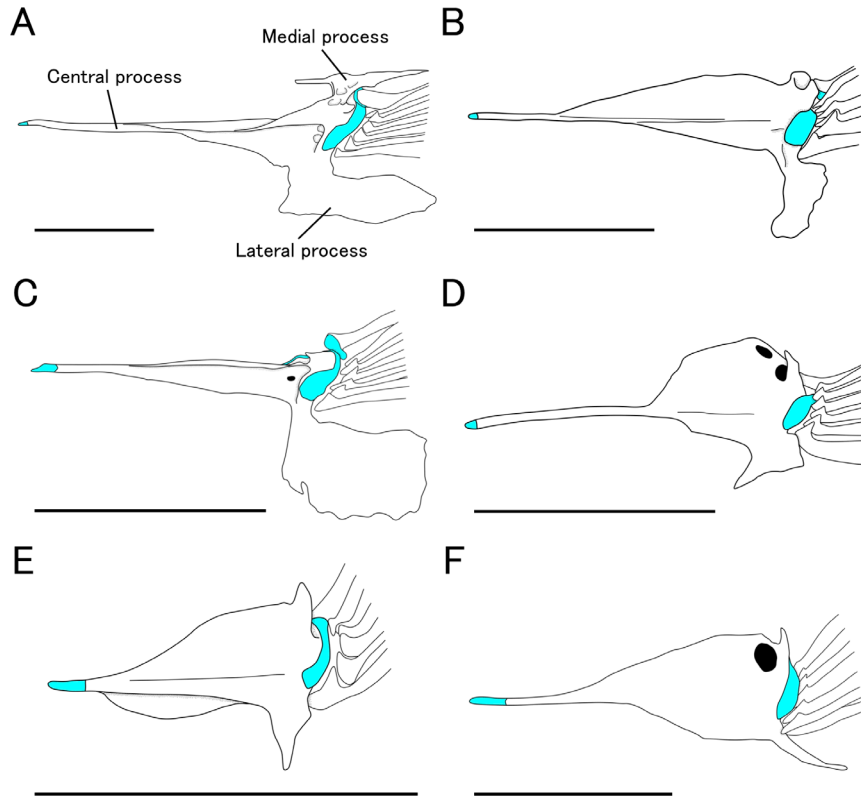
**Figure 48.** Dorsal views of pelvic girdle in (A) *Ablennes hians*, (B) *Belone belone*, (C) *Petalichthys capensis*, mirror image, (D) *Platybelone argalus argalus*, (E) *Potamorrhaphis guianensis* and (F) *Pseudotylosurus microps*. Bars indicate 5 mm.
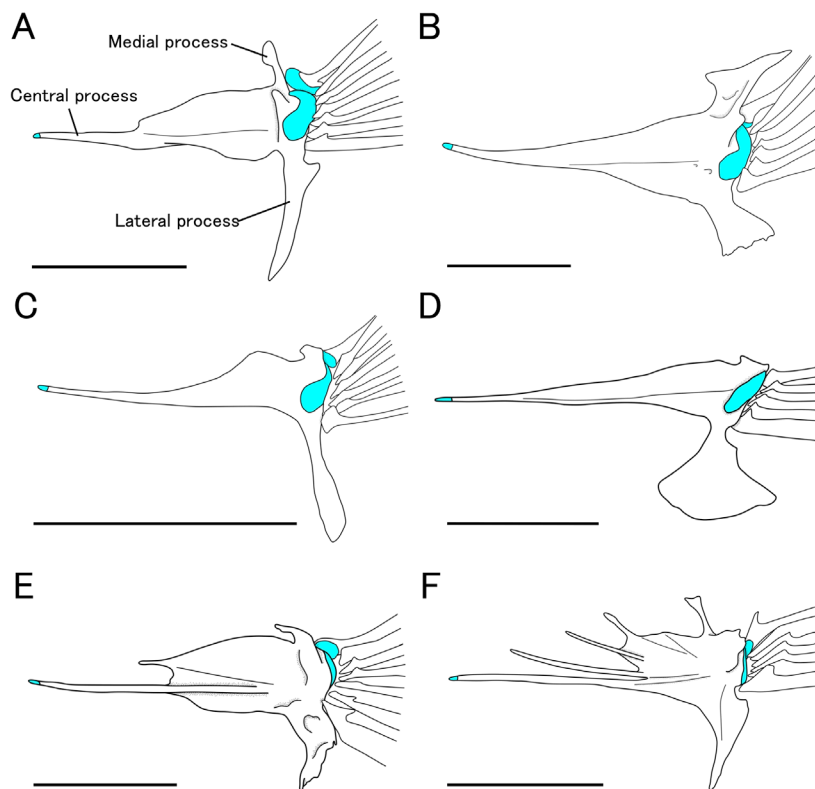
Figure 49. Dorsal views of pelvic girdle in (A) *Strongylura strongylura*, (B) *Tylosurus gavialoides*, mirror image, (C) *Xenentodon cancila*, mirror image, (D) *Nanichthys simulans*, (E) *Hemiramphus far* and (F) *Parexocoetus brachypterus*. Bars indicate 5 mm (A–C, E–F) and 1 mm (D).

guianensis (Fig. 45B).

The cleithrum, located on the anterior portion of the pectoral girdle, is anteroventrally attached to its antimere and dorsally attached to the supracleithrum or posttemporal. The cleithrum is also attached to the scapula posterodorsally and coracoid posteroventrally. Upper and lower foramina are present, between the cleithrum and scapula, and between the cleithrum and coracoid, respectively.

The scapula, on the posterodorsal portion of the pectoral girdle, is directly attached to the cleithrum laterally and via a cartilage medially. The scapula is attached to the first to third actinosts posteriorly and to the coracoid ventrally. A cartilage occurs ventrally in the connection with the coracoid.

The actinosts include four elements, the first, second and upper half of the third being attached to the scapula, and the lower half of the third and fourth to the coracoid. Posteriorly, the actinosts are bordered by cartilage supporting the pectoral fin rays. A foramen is present between each actinost in *Belone belone* (Fig. 44B), *Strongylura strongylura* and all species of *Tylosurus* (Fig. 46B), between the first and second, and second and third, in *Ablennes hians* (Fig. 44A), *Petalichthys capensis* (Fig. 44C), *Platybelone argalus argalus* (Fig. 45A), *St. exilis* (Fig. 46A), *St. krefftii* and *St. leiura*, and between the second and third, and third and fourth, in *Pseudotylosurus microps* and *Xenentodon cancila* (Fig. 46C). All other species lack foramina between the actinosts (Fig. 45B, C).

The crescent-shaped coracoid, situated on the ventroposterior portion of the pectoral girdle, is attached to the cleithrum anteriorly, the scapula dorsally, and the third and fourth actinosts posteriorly. The coracoid is loosely attached to the dorsal portion of the postcleithrum via medial connective tissue.

The long thin postcleithrum is loosely attached to the dorsal portion of the coracoid via medial connective tissue. The postcleithrum is absent in all species of *Pseudotylosurus* (Fig. 45C), but present in other species.

The pectoral fin rays include soft rays only, supported by the posterior margin of the actinosts. They number five in *Belonion dibranchodon*, six in *Potamorrhaphis guianensis*, 10 in all species of *Pseudotylosurus* and *Strongylura strongylura*, 11 in *Petalichthys capensis*,

Platybelone argalus argalus and *St. leiura*, 12 in *Belone belone* and *St. exilis*, 13 in *Ablennes hians*, *St. krefftii*, *Tylosurus acus imperialis*, *T. a. melanotus* and *T. gavialoides*, and 14 in *T. punctulatus* and *Xenentodon cancila*. The pectoral fin is short in all species.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 42. *Ventral process of posttemporal*. 0: present; 1: absent.

Belonidae. The ventral process of the posttemporal is absent in *Potamorrhaphis guianensis* and all species of *Pseudotylosurus* (character 42-1), but present in other species (character 42-0).

Other ingroups. The process is absent in all scomberesocids (Fig. 47) (character 42-1), but present in other species (character 42-0).

Outgroups. The process is absent in *Oryzias javanicus* (character 42-1), but present in other outgroups (character 42-0).

TS 43. *Sensory canal of posttemporal*. 0: absent; 1: present.

Belonidae. The sensory canal of the posttemporal is present in *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus* (character 43-1), but absent in other species (character 43-0).

Other ingroups. The canal is present in all scomberesocids (Fig. 47) (character 43-1), but absent in other ingroups (character 43-0).

Outgroups. All outgroups lack the canal (character 43-0).

TS 44. *Supracleithrum*. 0: present; 1: absent.

Belonidae. The supracleithrum is absent in *Potamorrhaphis guianensis* (character 44-1), but present in other species (character 44-0).

Other ingroups. All species have the supracleithrum
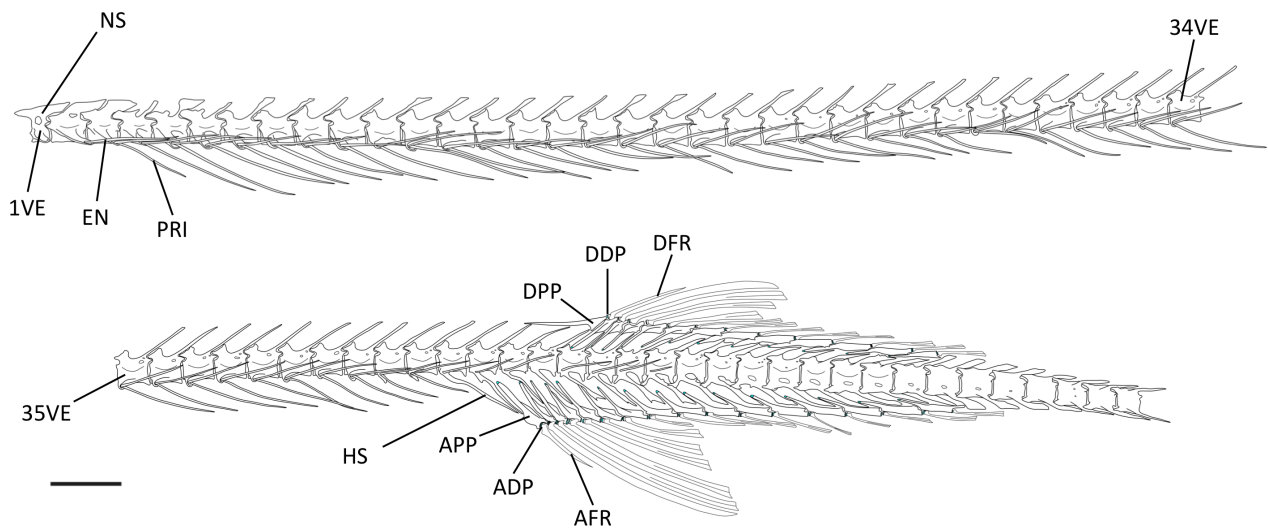
Figure 50. Lateral views of anterior part (upper) and posterior part (lower) of axial skeleton and median fin supports in *Platybelone argalus argalus*. ADP, anal distal pterygiophore; AFR, anal fin ray; APP, anal proximal pterygiophore; DDP, dorsal distal pterygiophore; DFR, dorsal fin ray; DPP, dorsal proximal pterygiophore; EN, epineural; HS, hemal spine; NS, neural spine; PRI, pleural rib; 1, 34 and 35VE, first, thirty-fourth and thirty-fifth vertebra, respectively. Bar indicates 5 mm.
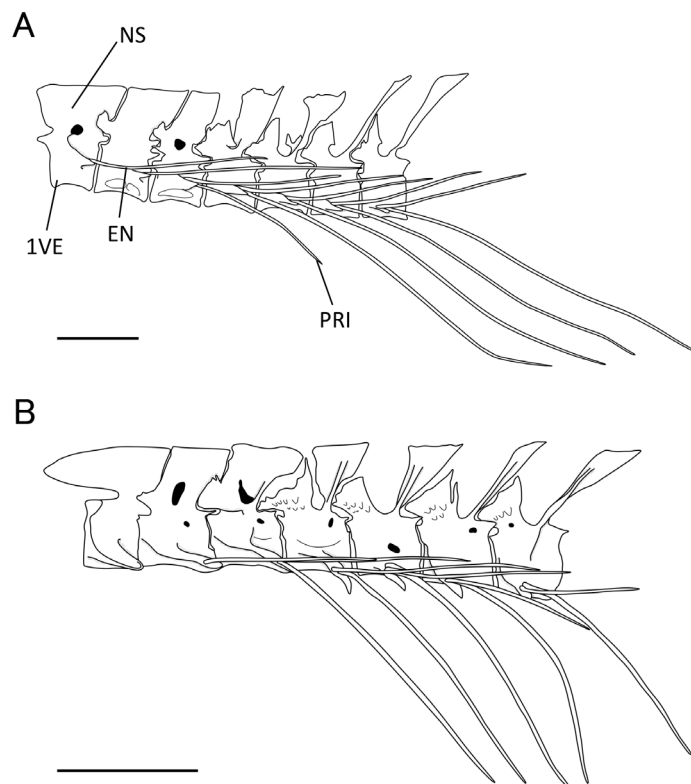
Figure 51. Lateral views of anterior axial skeleton in (A) *Ablennes hians* and (B) *Petalichthys capensis*. Abbreviations as in Fig. 50. Bars indicate 5 mm.
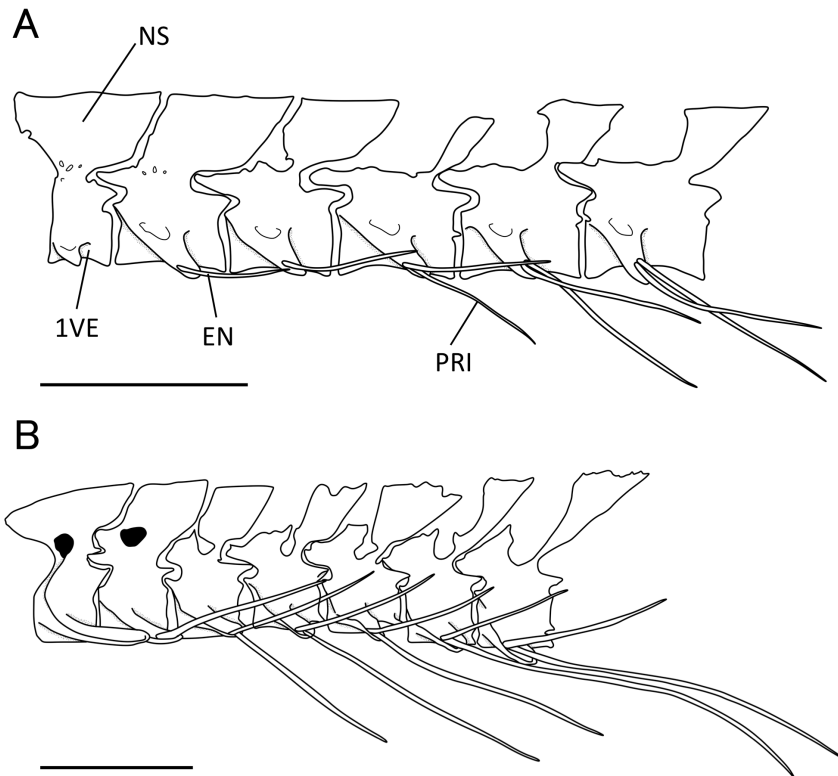
Figure 52. Lateral views of anterior axial skeleton in (A) *Pseudotylosurus angusticeps* and (B) *Tylosurus acus imperialis*. Abbreviations as in Fig. 50. Bars indicate 5 mm.
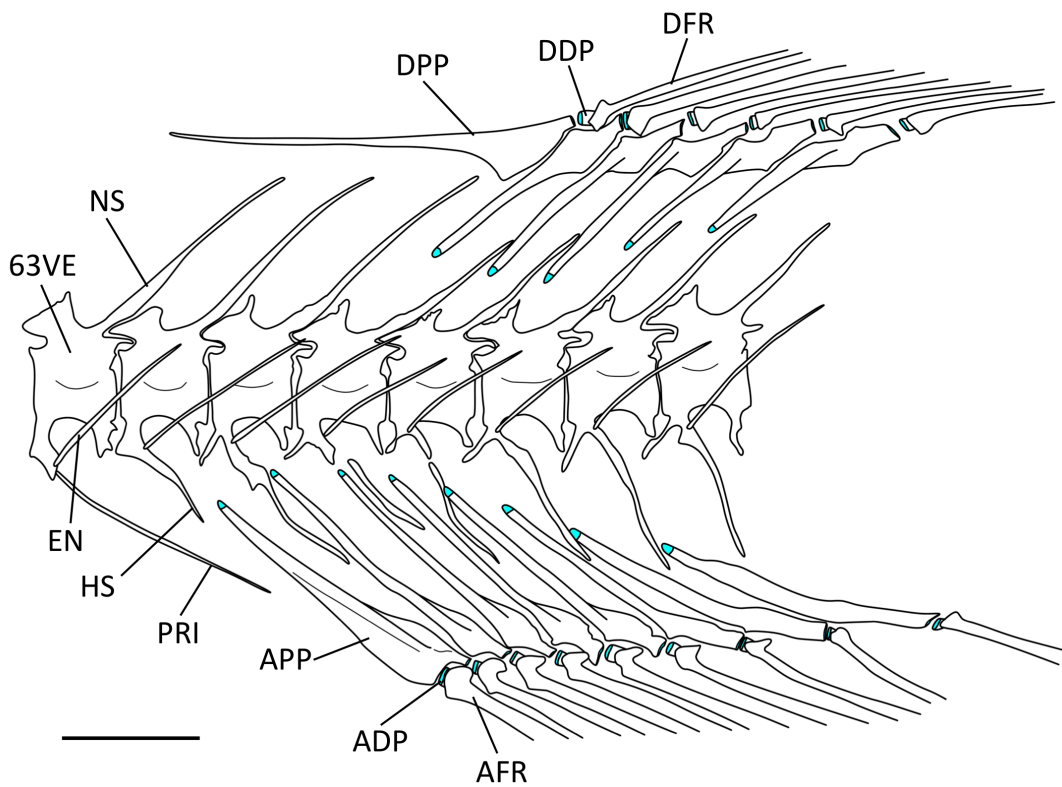
Figure 53. Lateral view of anterior median fin supports in *Tylosurus acus imperialis*. Abbreviations as in Fig. 50. Bar indicates 5 mm.
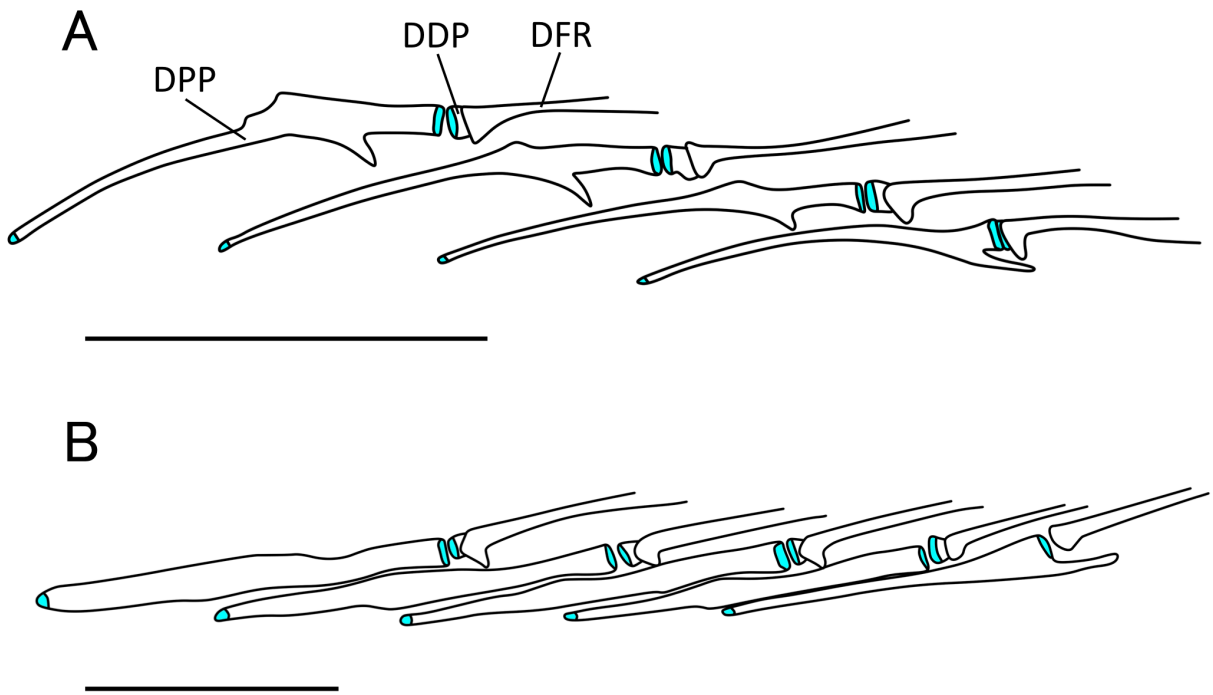
Figure 54. Lateral views of posterior dorsal median fin supports in (A) *Petalichthys capensis* and (B) *Tylosurus acus imperialis*. Abbreviations as in Fig. 50. Bars indicate 5 mm.
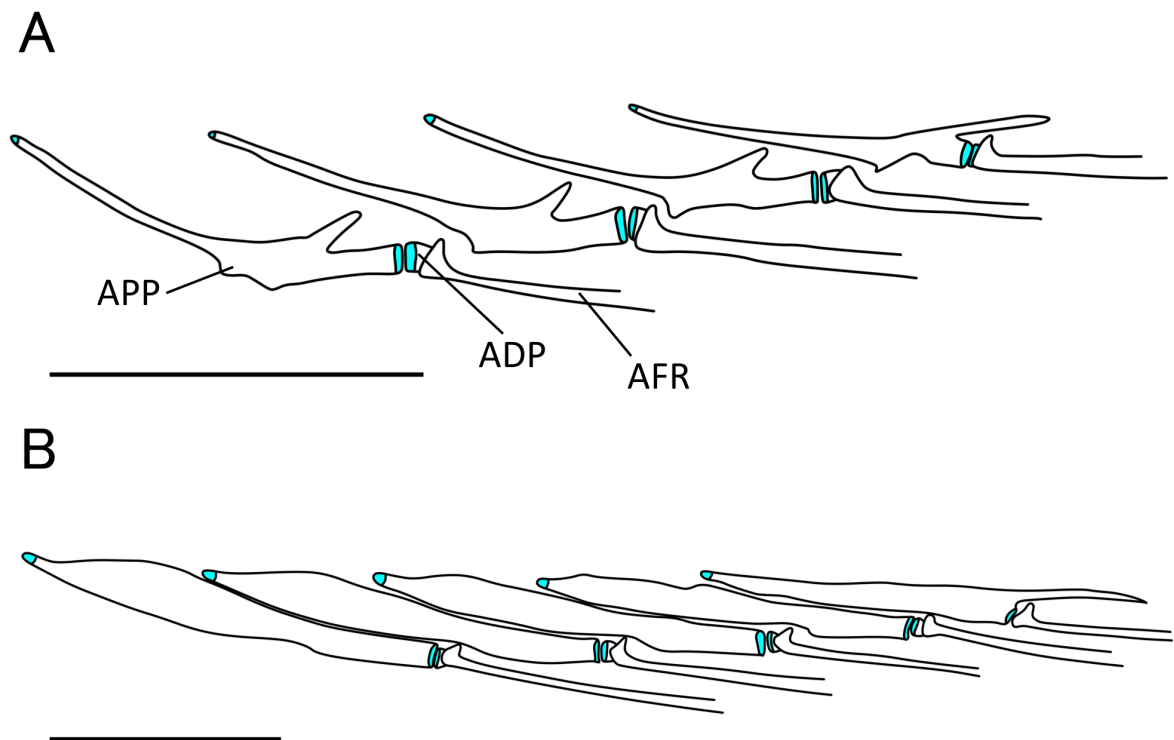
Figure 55. Lateral views of posterior anal median fin supports in (A) *Petalichthys capensis* and (B) *Tylosurus acus imperialis*. Abbreviations as in Fig. 50. Bars indicate 5 mm.
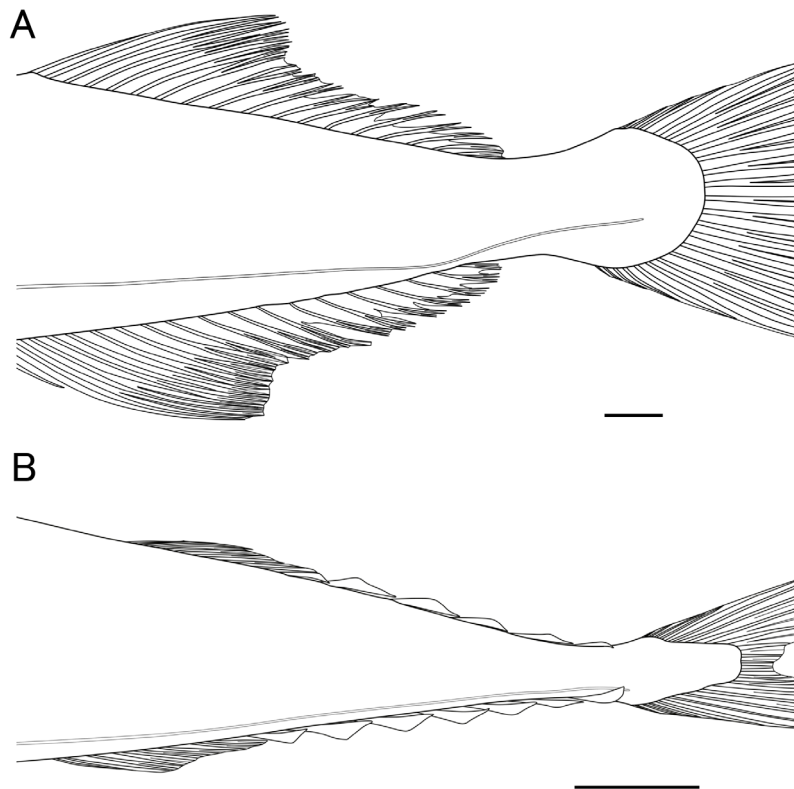
Figure 56. Lateral views of dorsal and anal fins in (A) *Strongylura krefftii*, mirror image, and (B) *Cololabis saira*. Bars indicate 10 mm.

Table 1. Numbers of vertebrae, epineurals, and dorsal and anal proximal pterygiophores in belonids.

|		Vertebrae	Epineurals	Dorsal proximal pterygiophores	Anal proximal pterygiophores
Ablennes hians	HUMZ 225350	55 + 32 = 87	61	23	26
	HUMZ 225353	54 + 31 = 85	61	24	24
Belone belone	HUMZ 229236	54 + 29 = 83	58	19	20
Belonion dibranchodon	HUMZ 229211	36 + 22 = 58	absent	uncounted	uncounted
Petalichthys capensis	HUMZ 229235	45 + 26 = 71	uncounted	17	20
Platybelone argalus argalus	HUMZ 229239	44 + 27 = 71	53	13	16
Potamorrhaphis guianensis	HUMZ 229240	40 + 35 = 75	43	34	27
Pseudotylosurus angusticeps	HUMZ 229212	44 + 27 = 71	50	15	17
Pseudotylosurus microps	HUMZ 229210	45 + 25 = 70	51	14	14
Strongylura exilis	HUMZ 229241	44 + 27 = 71	55	14	17
Strongylura krefftii	HUMZ 229209	40 + 27 = 67	45	17	18
Strongylura leiura	HUMZ 229242	50 + 32 = 82	56	18	23
Strongylura strongylura	HUMZ 229208	39 + 23 = 62	uncounted	14	15
Tylosurus acus imperialis	HUMZ 229243	63 + 32 = 95	51	24	21
Tylosurus acus melanotus	HUMZ 229216	60 + 34 = 94	61	25	22
Tylosurus gavialoides	HUMZ 229213	51 + 28 = 79	uncounted	21	19
Tylosurus punctulatus	HUMZ 229230	51 + 28 = 79	59	21	18
Xenentodon cancila	HUMZ 225515	36 + 21 = 57	uncounted	16	15

(character 44-0).

Outgroups. The supracleithrum is absent in *Oryzias javanicus* (character 44-1), but present in other outgroups (character 44-0).

TS 45. *Foramen between actinosts*. 0: absent; 1: present between each actinost; 2: present between first and second, and second and third, respectively; 3: present between second and third, and third and fourth, respectively.

Belonidae. Foramina are present between each actinost in *Belone belone*, *Strongylura strongylura* and all species of *Tylosurus* (character 45-1), between the first and second, and second and third, in *Ablennes hians*, *Petalichthys capensis*, *Platybelone argalus argalus*, *St. exilis*, *St. krefftii* and *St. leiura* (character 45-2), between the second and third, and third and fourth, in *Pseudotylosurus microps* and *Xenentodon cancila* (character 45-3), but are absent between any actinosts in other species (character 45-0).

Other ingroups. Foramina are present between each actinost in all scomberesocids (Fig. 47), *Hemiramphus far* and *Fodiator acutus* (character 45-1), but absent between any actinosts in other species (character 45-0).

Outgroups. Foramina are present between each actinost in *Atherinomorus pinguis* (character 45-1), but absent between any actinosts in other outgroups (character 45-0).

TS 46. *Postcleithrum*. 0: present; 1: absent.

Belonidae. The postcleithrum is absent in all species of *Pseudotylosurus* (character 46-1), but present in other species (character 46-0).

Other ingroups. All species have the postcleithrum (character 46-0).

Outgroups. All outgroups have the postcleithrum (character 46-0).

TS 47. *Pectoral fin*. 0: short; 1: long.

Belonidae. The pectoral fin is short in all species (character 47-0).

Other ingroups. The pectoral fin is long in all exocoetids (character 47-1), but short in other species (character 47-0).

Outgroups. All outgroups have a short pectoral fin (character 47-0).

Remarks. The well developed long pectoral fin has been known as the characteristic of the exocoetid species (Nelson *et al*., 2016). The exocoetids are distinguishable from the other beloniform families by this character.

Other variations

Shape of posttemporal. The posttemporal is generally thin board or sickle-like, but there is variation in this character in belonids that could not be clearly sorted into either category. Accordingly, posttemporal shape was not used in the analysis.

Number of pectoral fin rays. In belonids, pectoral fin ray numbers vary from five to 14. Number of pectoral fin rays was not used for the analysis because the homology of each ray was unclear.

8. Pelvic girdle (Figs. 48, 49)

Description

The pelvic girdle includes the pelvic bone and pelvic fin rays, all elements being paired. Because the girdle is poorly stained and unclear in *Belonion dibranchodon*, it is excluded from the description.

The thin board-like pelvic bone supports the pelvic fin rays. The pelvic bone is located on the middle and abdominal portions of the body, being separated from the pectoral girdle. The bones on each side are separated from each other. Posteriorly, the pelvic bone is cartilaginous. An anteriorly-directed central process has a cartilaginous cap on its anterior tip. In addition, a pointed or fan-shaped lateral process, and pointed, T-shaped or rounded medial process are present, both variable in size.

The pelvic fin rays include six soft rays, the innermost having a cartilaginous cap on its base.
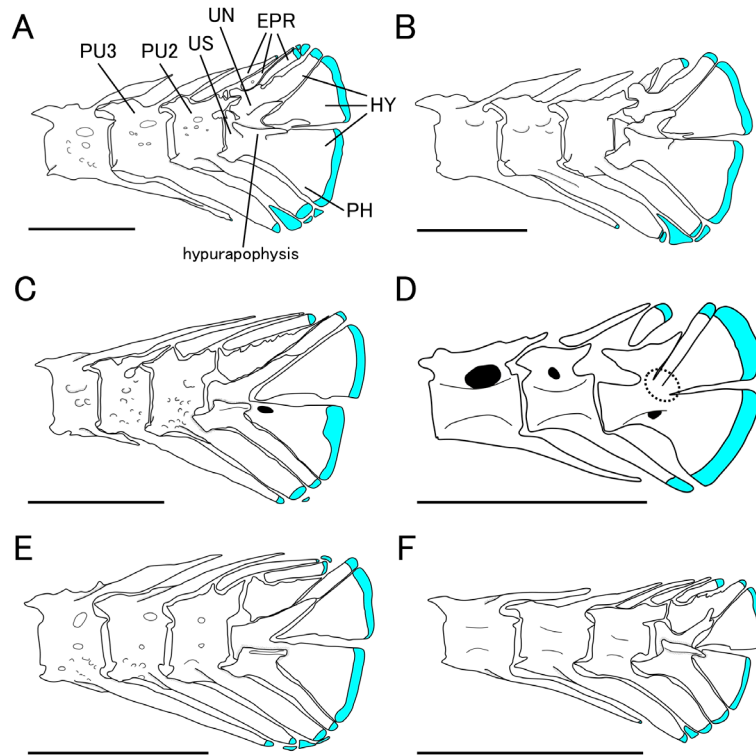
Figure 57. Lateral views of caudal skeleton in (A) *Ablennes hians*, HUMZ 225353, (B) *Ablennes hians*, HUMZ 225350, (C) *Belone belone*, (D) *Belonion dibranchodon*, (E) *Petalichthys capensis* and (F) *Platybelone argalus argalus*. EPR, epural; HY, hypural; PH, parhypural; PU, preural centrum; UN, uroneural; US, urostyle. Bars indicate 5 mm (A–C, E–F) and 1 mm (D). Connection of bones unclear in dotted circle (D).
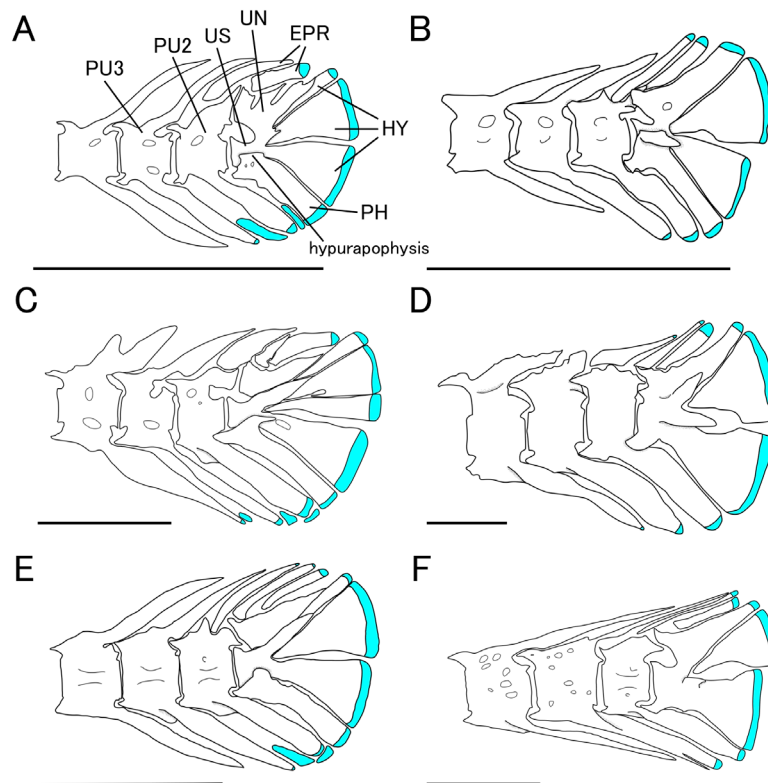
Figure 58. Lateral views of caudal skeleton in (A) *Potamorrhaphis guianensis*, (B) *Pseudotylosurus angusticeps*, (C) *Strongylura strongylura*, (D) *Tylosurus acus melanotus*, (E) *Xenentodon cancila* and (F) *Nanichthys simulans*. Abbreviations as in Fig. 57. Bars indicate 5 mm (A–E) and 1 mm (F).
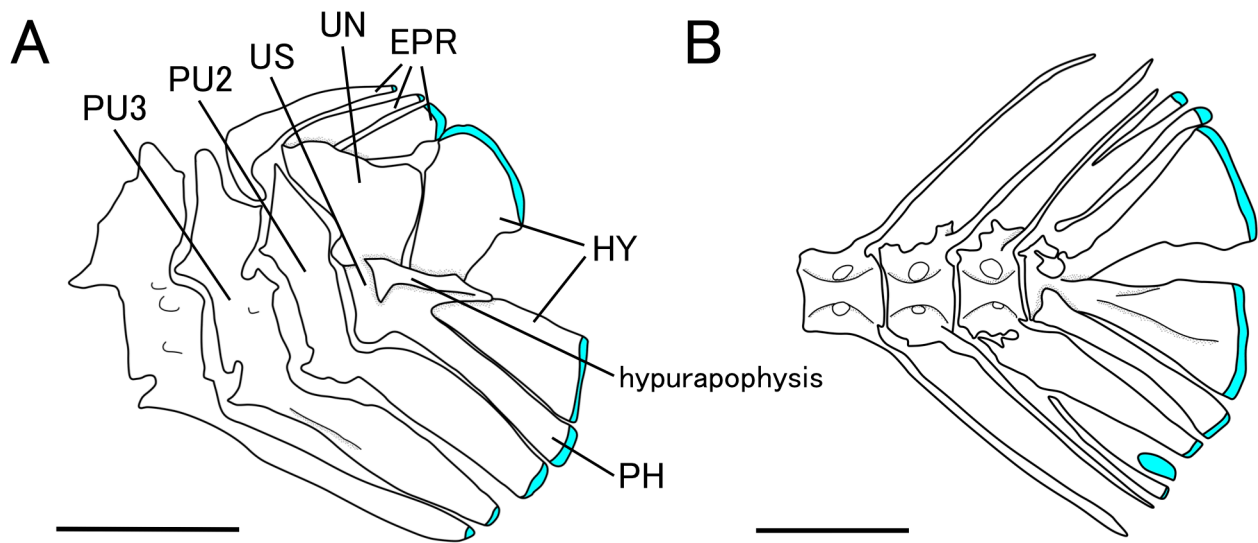
Figure 59. Lateral views of caudal skeleton in (A) *Cypselurus doederleini* and (B) *Oryzias javanicus*. Abbreviation as in Fig. 57. Bars indicate 5 mm (A) and 1 mm (B).

Character recognition

Transformation series (TS) available for phylogenetic analysis

None.

Other variations

Number of central processes. A single central process occurs in all belonids, except *Belonion dibranchodon* (the pelvic bone unclear), and all scomberesocids (Fig. 49D). There are two processes in *Hemiramphus far* (Fig. 49E), *Zenarchopterus dunckeri*, *Cypselurus doederleini* and *Exocoetus monocirrhus*, and four processes in *Fodiator acutus* and *Parexocoetus brachypterus* (Fig. 49F). However, the homology of each process was unclear and the variation was omitted from the analysis.

Shape of lateral and medial processes. The lateral process is generally pointed or fan-shaped, and the medial process pointed, T-shaped or rounded. However, there are variations in these characters in belonids that could not be clearly sorted into either category.

Accordingly, the process shapes were excluded from the analysis.

9. Axial skeleton and median fin supports (Figs. 50–56)

Description

The axial skeleton comprises the vertebrae, pleural ribs (lower series) and epineurals (upper series). Median fin supports include the proximal and distal pterygiophores (Fig. 50). Only the distal pterygiophores are paired, the remainder being unpaired. Supraneurals, stays and medial pterygiophores are absent. The very thin weak distal pterygiophores of *Belonion dibranchodon* are poorly stained, and are accordingly excluded from the description. Dorsal and anal fin ray characters are noted.

The vertebrae include 36 to 63 abdominal and 21 to 35 (including urostyle) caudal elements (Table 1). Each bone supports a neural arch and neural spine dorsally. The first vertebra articulates with the basioccipital anteriorly. The abdominal vertebrae have lateral parapophyses to which pleural ribs and epineurals are

attached. The caudal vertebrae have hemal arches and hemal spines ventrally.

The long thin pleural ribs, located on the anterior portion of the body, surround the internal organs. The dorsal tip of each bone is attached to the parapophysis of the second to last abdominal vertebrae in *Belonion dibranchodon*, but to that of the third to last abdominal vertebrae in all other species except all species of *Pseudotylosurus* (Fig. 52A) and *Tylosurus gavialoides* (attached to the fourth to last abdominal vertebrae).

The long thin epineurals are attached to the parapophyses of the abdominal vertebrae and the lateral aspect of the caudal vertebrae. Absent in *Belonion dibranchodon*, they otherwise number 43 to 61 (Table 1). In *Petalichthys capensis*, *Strongylura strongylura*, *Tylosurus gavialoides* and *Xenentodon cancila*, epineural numbers are unclear due to damage. The first epineural is attached to the parapophysis of the first abdominal vertebra in *Ablennes hians* (Fig. 51A), but to the second abdominal vertebra in other species that have epineurals (Figs. 51B, 52).

The proximal pterygiophores, on the dorsal and anal fin bases and bearing vertebra-associated processes, comprise the major median fin support. The processes of the dorsal proximal pterygiophores are inserted between the neural spines, whereas those of the anal proximal pterygiophores are inserted between the hemal spines. However, the first dorsal proximal pterygiophore process is directed anteriorly and is not inserted between neural spines (Fig. 53). The proximal pterygiophores have cartilaginous caps on the process tips and the posterior ends, respectively. Each posterior cap is loosely attached to an associated distal pterygiophore with which it supports a dorsal or anal fin ray. However, the first anal proximal pterygiophore is attached to two distal pterygiophores and supports two anal fin rays.

The distal pterygiophores are positioned on the base of the dorsal and anal proximal pterygiophores. Each bone is loosely attached to the proximal pterygiophore anteriorly and sandwiched by soft rays laterally. The distal pterygiophores on the last proximal pterygiophores of both dorsal and anal fins are present in *Ablennes hians*, *Belone belone*, *Petalichthys capensis* (Figs. 54A, 55A), all species of *Pseudotylosurus* and *Strongylura krefftii*, but absent in other species (Figs. 54B, 55B).

All the dorsal and anal fins rays are soft rays, numbering 13 to 34 and 15 to 28, respectively. Finlets are absent (Fig. 56A).

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 48. *Finlets*. 0: absent; 1: present.

Belonidae. All species lack finlets (character 48-0).

Other ingroups. Finlets are present in all scomberesocids (Fig. 56B) (character 48-1), but absent in other ingroups (character 48-0).

Outgroups. All outgroups lack finlets (character 48-0).

Remarks. The presence (in Scomberesocidae) or absence (in Belonidae) of the finlets has been recognized as characters to distinguish both families from each other (Nelson *et al*., 2016).

Other variation

Numbers of vertebrae, epineurals and pterygiophores. Vertebral, epineural and pterygiophore numbers vary a great deal by species (Table 1). Because of intraspecific variations in vertebral counts, and dorsal and anal proximal pterygiophore number in *Ablennes hians*, this information was not included in the analysis.

Position of first pleural rib and epineural. The first pleural rib is attached to the first, third or fourth vertebra, whereas the first epineural is attached to the first or second vertebra in belonids. However, the considerable interspecific variation and uncertain homology made the character unsuitable for the analysis.

Epineurals. Epineurals are absent in *Belonion dibranchodon*, but present in both ingroups and outgroups. Lack of epineurals is considered an autapomorphy of *Belonion dibranchodon*.

Distal pterygiophores on last proximal pterygiophores. Distal pterygiophores are present on the last proximal pterygiophores in *Ablennes hians*, *Belone belone*,

Petalichthys capensis, all species of *Pseudotylosurus* and *Strongylura krefftii*, but absent in other belonids. Because the numbers vary by species and had uncertain homology, the character was not adopted for the analysis.

10. Caudal skeleton (Figs. 57–59)

Description

The caudal skeleton comprises second and third preural centra, urostyle, epurals, uroneural, hypurals, parhypural and caudal fin rays.

The second preural centrum, articulating with the third preural centrum anteriorly and urostyle posteriorly, has a neural spine dorsally and hemal spine ventrally. The neural spine is relatively shorter than that of other centra. The hemal spine tip has a cartilaginous cap.

The third preural centrum, articulating with the fourth preural centrum anteriorly and the second preural centrum posteriorly, has a neural spine dorsally and hemal spine ventrally. The hemal spine tip has a cartilaginous cap. The cap is not obvious in *Belonion dibranchodon* due to poor staining (Fig. 57D).

The urostyle, articulating with the second preural centrum anteriorly and fused with the first and second hypurals posteroventrally, is also fused with the uroneural dorsally in *Ablennes hians* (Fig. 57A, B), *Belonion dibranchodon* (Fig. 57D), *Potamorrhaphis guianensis* (Fig. 58A), all species of *Pseudotylosurus* (Fig. 58B), *Tylosurus acus imperialis* and *T. a. melanotus* (Fig. 58D), whereas the urostyle is autogenous from the uroneural in other species. The urostyle is fused with the parhypural in *Ab. hians* (Fig. 57A, B), *Belonion dibranchodon* (Fig. 57D), *Ps. microps*, *T. a. imperialis* and *T. a. melanotus* (Fig. 58D), but is autogenous from the parhypural in other species. The urostyle is autogenous from the third to fourth hypurals in all species except *Belonion dibranchodon*, in which the connection between the urostyle and third to fifth hypurals is unclear because of the small size (Fig. 57D).

The stick-like epurals, located dorsally on the caudal skeleton, comprise two elements in *Ablennes hians* (HUMZ 225350) (Fig. 57B), *Belone belone* (Fig. 57C), *Belonion dibranchodon* (Fig. 57D), *Petalichthys capensis* (Fig. 57E), *Potamorrhaphis guianensis* (Fig. 58A) and all species of *Pseudotylosurus* (Fig. 58B), and three in other species (plus *Ab. hians* [HUMZ 225353] [Fig. 57A]). In *Ab. hians* (HUMZ 225353), *Belone belone* (Fig. 57C), *Pe. capensis* (Fig. 57E), *Ps. angusticeps* (Fig. 58B), *Strongylura krefftii*, all species of *Tylosurus* (Fig. 58D) and *Xenentodon cancila* (Fig. 58E), a cartilaginous cap is present on the dorsal tip of each epural, whereas the cap is present only on the dorsal tip of the most posterior epural in *Ab. hians* (HUMZ 225350) (Fig. 57B), *Belonion dibranchodon* (Fig. 57D), *Platybelone argalus argalus* (Fig. 57F), *Pot. guianensis* (Fig. 58A), *Ps. microps* and *St. strongylura* (Fig. 58C). Cartilaginous caps are present on the dorsal tips of the middle and posterior epurals, but absent on that of the anterior epural in *St. exilis* and *St. leiura*.

The triangular uroneural, situated above the urostyle, is fused with the fifth hypural in *Ablennes hians* (Fig. 57A, B), *Platybelone argalus argalus* (Fig. 57F), all species of *Pseudotylosurus* (Fig. 58B), *Strongylura krefftii*, *Tylosurus acus imperialis* and *T. a. melanotus* (Fig. 58D), but is autogenous from the fifth hypural in other species.

The hypurals, located on the posterior part of the caudal skeleton, comprise up to five elements (conventionally numbered from the most ventral element). The first and second hypurals are fused with each other, forming a 1 + 2 hypural plate. In *Ablennes hians* (Fig. 57A, B), *Belonion dibranchodon* (Fig. 57D), *Pseudotylosurus microps*, *Tylosurus acus imperialis* and *T. a. melanotus* (Fig. 58D), the 1 + 2 hypural plate is fused with the parhypural, whereas the 1 + 2 hypural plate is autogenous from the parhypural in other species. The third and fourth hypurals are fused with each other, forming a 3 + 4 hypural plate in all species except *Strongylura strongylura*, in which they are autogenous (Fig. 58C). The fourth and fifth hypurals are autogenous in all species.

The parhypural is situated below the 1 + 2 hypural plate and the hypurapophysis on the dorsal portion of the parhypural.

The caudal fin rays are supported by the epurals, hypurals, parhypural, and hemal spines of the second and third preural centra. Principal rays number 5 + 7 = 12 in *Potamorrhaphis guianensis*, 8 + 9 = 17 in *Petalichthys capensis* and *Xenentodon cancila*, and 7 + 8 = 15 in other species.

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 49. *Urostyle and uroneural*. 0: fused; 1: autogenous.

Belonidae. The urostyle is fused with the uroneural in *Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus*, *Tylosurus acus imperialis* and *T. a. melanotus* (character 49-0), but is autogenous from the uroneural in other species (character 49-1).

Other ingroups. The urostyle is autogenous from the uroneural in *Cololabis saira*, *Scomberesox saurus* and *Zenarchopterus dunckeri* (character 49-1), but is fused with the uroneural in other species (Figs. 58F, 59A) (character 49-0).

Outgroups. The urostyle is fused with the uroneural in all outgroups (Fig. 59B) (character 49-0).

TS 50. *Urostyle and 1 + 2 hypural plate*. 0: fused; 1: autogenous.

Belonidae. The urostyle is fused with the 1 + 2 hypural plate in all species (character 50-0).

Other ingroups. The urostyle is fused with the 1 + 2 hypural plate in all scomberesocids (Fig. 58F) and *Zenarchopterus dunckeri* (character 50-0), but is autogenous from the 1 + 2 hypural plate in *Hemiramphus far* and all exocoetids (Fig. 59A) (character 50-1).

Outgroups. These bones are fused in all outgroups (Fig. 59B) (character 50-0).

TS 51. *Urostyle and parhypural.* 0: autogenous; 1: fused.

Belonidae. The urostyle is fused with the parhypural in *Ablennes hians*, *Pseudotylosurus microps*, *Tylosurus acus imperialis* and *T. a. melanotus* (character 51-1), but is autogenous from the parhypural in other species (character 51-0).

Other ingroups. These bones are autogenous in *Zenarchopterus dunckeri* (character 51-0), but fused in other species (Figs. 58F, 59A) (character 51-1).

Outgroups. The urostyle and parhypural are autogenous in all outgroups (Fig. 59B) (character 51-0).

TS 52. *Third and fourth hypural*. 0: fused; 1: autogenous.

Belonidae. The third and fourth hypurals are fused in all species (character 52-0) except *Strongylura strongylura*, in which they are autogenous (character 52-1).

Other ingroups. The third and fourth hypurals are fused in all species (Figs. 58F, 59A) (character 52-0) except *Zenarchopterus dunckeri*, in which they are autogenous (character 52-1).

Outgroups. These bones are fused in all outgroups (Fig. 59B) (character 52-0).

TS 53. *Fourth and fifth hypurals*. 0: autogenous; 1: fused.

Belonidae. The fourth and fifth hypurals are autogenous in all species (character 53-0).

Other ingroups. The fourth and fifth hypurals are fused in all exocoetids (Fig. 59A) (character 53-1), but are autogenous in *Hemiramphus far*, *Zenarchopterus dunckeri* and all scomberesocids (Fig. 58F) (character 53-0).

Outgroups. These bones are autogenous in *Atherinomorus pinguis* (character 53-0), but are fused in other outgroups (Fig. 59B) (character 53-1).

TS 54. *Fifth hypural and uroneural*. 0: autogenous; 1: fused.

Belonidae. The fifth hypural is fused with the uroneural in *Ablennes hians*, *Platybelone argalus argalus*, all species of *Pseudotylosurus*, *Strongylura krefftii*, *Tylosurus acus imperialis* and *T. a. melanotus* (character 54-1), but the fifth hypural is autogenous from the uroneural in other species (character 54-0).

Other ingroups. These bones are fused in all scomberesocids (Fig. 58F) (character 54-1), but are autogenous in other species (Fig. 59A) (character 54-0).

Outgroups. These bones are autogenous in all outgroups (Fig. 59B) (character 54-0).

TS 55. *1+2 hypural plate and parhypural*. 0: autogenous; 1: fused.

Belonidae. In *Ablennes hians*, *Pseudotylosurus microps*, *Tylosurus acus imperialis* and *T. a. melanotus*, the 1 + 2 hypural plate and parhypural are fused (character 55-1), whereas they are autogenous in other species (character 55-0).

Other ingroups. These bones are fused in all scomberesocids (Fig. 58F) (character 55-1), but are autogenous in other species (Fig. 59A) (character 55-0).

Outgroups. These bones are autogenous in all outgroups (Fig. 59B) (character 55-0).

Other variations

Urostyle and 3 + 4 hypurals. The urostyle and 3 + 4 hypural plate are autogenous in all ingroups, *Belonion dibranchodon*, *Elassichthys adocetus* and *Atherinomorus pinguis*, but are fused in *Oryzias javanicus* (Fig. 59B) and *Poecilia mexicana*. The character was not used for the analysis because the variation was found only in outgroups.

Number of epurals. Epurals number two or three in all species, including *Belonion dibranchodon* and *Elassichthys adocetus*. However, in *Ablennes hians*, the epurals comprise two elements in HUMZ 225350 (Fig. 57B) and three in HUMZ 225353 (Fig. 57A). Because of this intraspecific variation in *Ab. hians*, epural numbers were not adopted for the analysis.

Cartilaginous cap on dorsal tip of epural. The cartilaginous cap on the dorsal tip of the epural is variable. *Ablennes hians* (HUMZ 225353) has three epurals with a cartilaginous cap present on the tip of each (Fig. 57A). A second specimen (HUMZ 225350) has two epurals, with a cartilaginous cap present only on the tip of the posterior one (Fig. 57B). Because of such intraspecific variation, this character was not used for the analysis.

Number of principal caudal fin rays. Principal caudal fin ray numbers vary from 12 to 17 in belonids. Because the homology of each ray was unclear, this variation was not adopted for the analysis.

11. External morphology (Figs. 60–63)

Description

The narial opening is single (Fig. 60). A lateral line is absent in *Belonion dibranchodon*, but present in other species. The branch of the lateral line under the pectoral fin is absent in *Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus* and *Tylosurus acus imperialis*, whereas it is present in all other species (Fig. 61A) (presence or absence of a branch could not be determined in *T. gavialoides* due to damage to the anterior lateral line scales). A lateral keel on the caudal peduncle is present in *Platybelone argalus argalus* and all species of *Tylosurus* (Fig. 62), but is absent in other species. The caudal peduncle is depressed dorsoventrally in *P. a. argalus* and all species of *Pseudotylosurus* (Fig. 63B), but compressed laterally in other species (Fig. 63A).

Character recognition

Transformation series (TS) available for phylogenetic analysis

TS 56. *Branch of lateral line under pectoral fin*. 0: present; 1: absent.

Belonidae. The branch of the lateral line under the pectoral fin is absent in *Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus* and *Tylosurus acus imperialis* (character 56-1), but present in all other species (except unknown in *T. gavialoides*) (character 56-0). *Tylosurus gavialoides* was coded as "?" for TS 56, because of damage to the anterior lateral line scales in the specimen examined.

Other ingroups. The branch of the lateral line under the pectoral fin is absent in all scomberesocids (Fig. 61B), *Cypselurus doederleini* and *Exocoetus monocirrhus* (character 56-1), but is present in other species (character 56-0).

Outgroups. All outgroups are coded as "?" because they lack the lateral line.
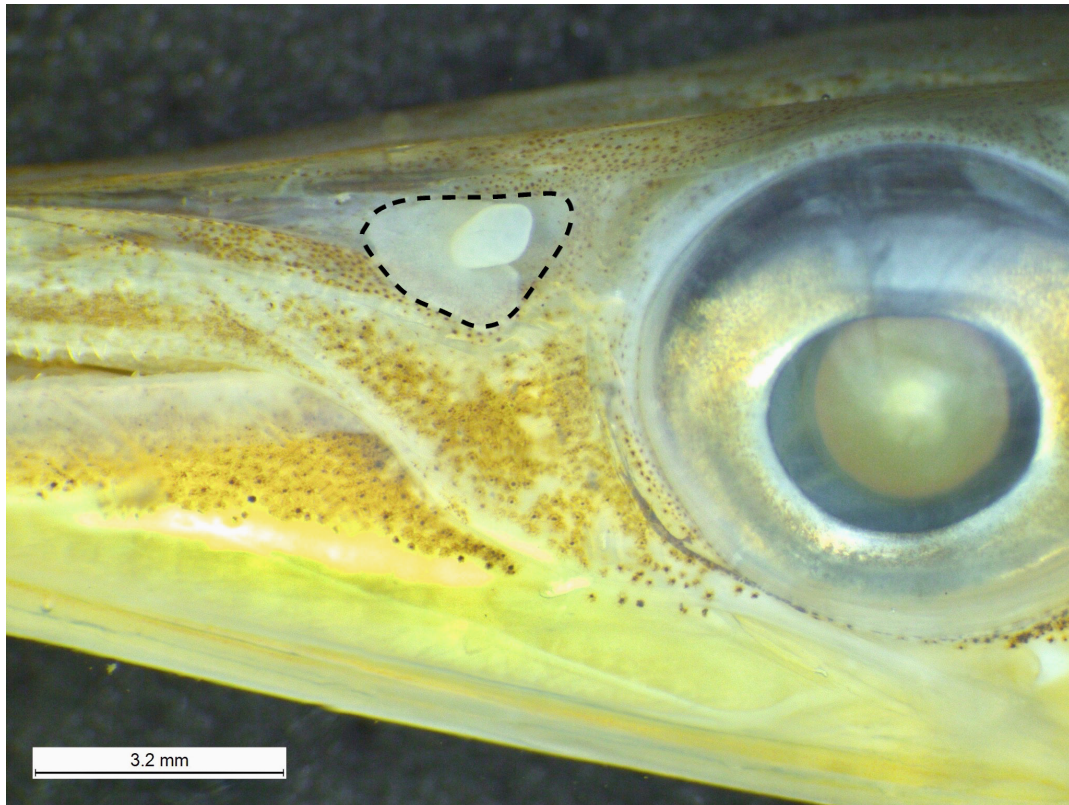
Figure 60. Lateral view of narial opening in *Xenentodon cancila*. Dotted line indicates narial opening.
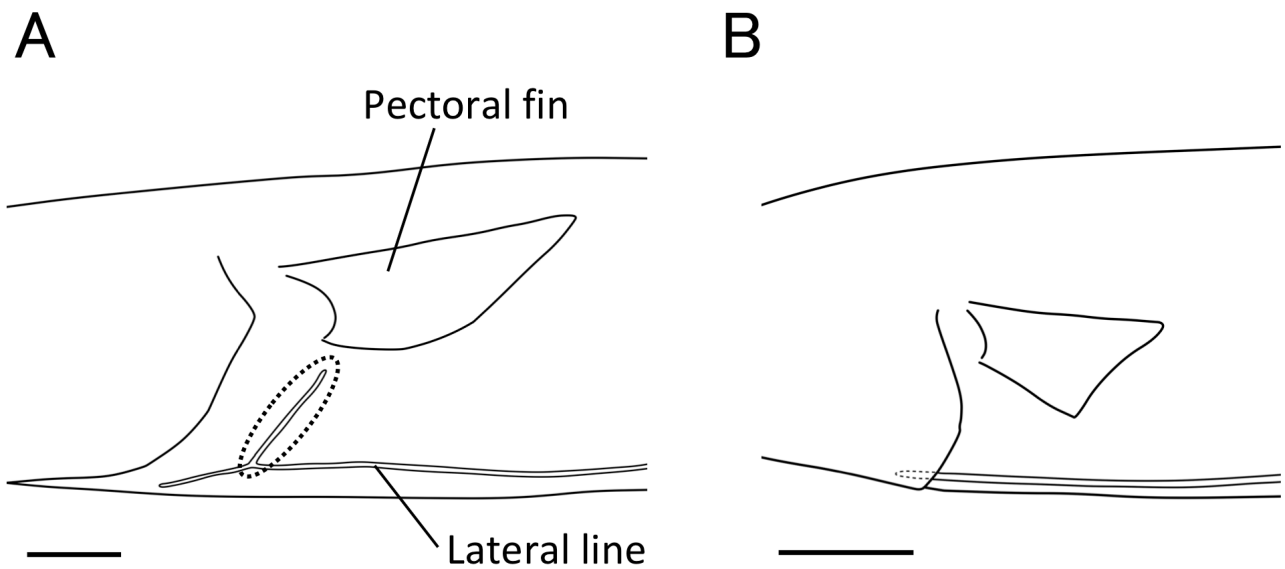
Figure 61. Lateral views of anterior lateral line in (A) *Strongylura krefftii* and (B) *Cololabis saira*. Bars indicate 10 mm. Dotted line indicates branch of lateral line.

Figure 62. Lateral view of caudal peduncle in *Tylosurus acus melanotus*, stained by Alizarin Red-S, mirror image.
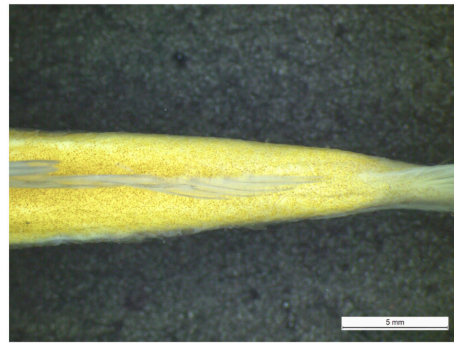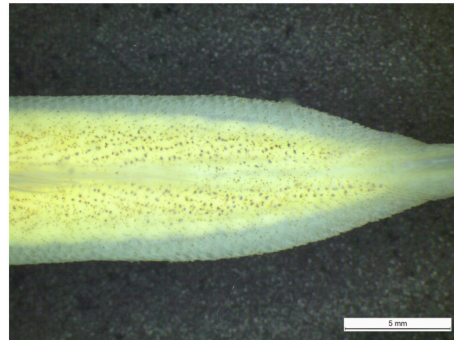
Figure 63. Lateral view (left) and dorsal view (right) of caudal peduncle in (A) *Xenentodon cancila* and (B) *Pseudotylosurus angusticeps*.

Remarks. Parin and Astakhov (1982) reported that the Scomberesocidae differed from Belonidae in the absence of the branch of the lateral line under the pectoral fin (*vs*. the branch present in Belonidae). In this study, the absence of the branch is recognized in all scomberesocid species except *Elassichthys adocetus*, which lacks the lateral line. However, the absence of the branch is also recognized in some species of Belonidae (*Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus* and *Tylosurus acus imperialis*).

TS 57. *Keel on caudal peduncle*. 0: absent; 1: present.

Belonidae. The lateral keel on the caudal peduncle is present in *Platybelone argalus argalus* and all species of *Tylosurus* (character 57-1), but absent in other species (character 57-0).

Other ingroups. All species lack the keel (character 57-0).

Outgroups. All outgroups lack the keel (character 57-0).

Remarks. The presence of the keel on the caudal peduncle has been used to diagnose the genera *Platybelone* and *Tylosurus* (*e.g*., Collette and Parin, 1970; Aizawa and Doiuchi, 2013).

TS 58. *Caudal peduncle*. 0: compressed laterally; 1: depressed dorsoventrally.

Belonidae. The caudal peduncle is depressed dorsoventrally in *Platybelone argalus argalus* and all species of *Pseudotylosurus* (character 58-1), but compressed laterally in other species (character 58-0).

Other ingroups. The caudal peduncle is compressed laterally in all species (character 58-0).

Outgroups. The caudal peduncle is compressed laterally in all outgroups (character 58-0).

Remarks. The dorsoventral depression of the caudal peduncle has been recognized as one of the characters to distinguish the genera *Platybelone* and *Pseudotylosurus* from the other belonids genera (*e.g*., Collette and Parin, 1970; Collette, 1974).

Other variations

Narial opening. The narial opening is single in all ingroups, including *Belonion dibranchodon* and *Elassichthys adocetus*. However, all outgroups have two narial openings. Accordingly, a single narial opening is considered a synapomorphy of exocoetoids (see section 1 of TAXON SAMPLING).

Lateral line. The lateral line is present in all ingroups, but absent in *Belonion dibranchodon* and *Elassichthys adocetus*. The lateral line is absent in all outgroups. The variation was not adopted for the analysis because species with the condition included only outgroups and species not adopted for the analysis. Presence of the lateral line is considered a synapomorphy of exocoetoids (see section 1 of TAXON SAMPLING).

PHYLOGENETIC ANALYSIS

1. Phylogenetic relationships of the family Belonidae and related taxa

Interrelationships of the family Belonidae were reconstructed based on characters in 58 transformation series (Table 2). As the result of the analysis, three equally most parsimonious trees (consistency index 0.48, rescaled consistency index 0.35, tree length 164) were obtained (Fig. 64). Differences were recognized in the relationships of the two clades and one species (*St. strongylura + Tylosurus gavialoides + T. punctulatus* clade [stippled box in Fig. 64], *St. leiura + Xenentodon cancila* clade [gray box in Fig. 64] and *Strongylura exilis*) among the three trees. Topologies of other parts in the three trees are consistent with each other. A strict consensus tree constructed from these (shown in Fig. 65) is accepted as representing the phylogenetic relationships of family Belonidae and related taxa (= suborder Exocoetoidei). Contained taxa and supporting characters of each clade are shown below. Characters labeled "r" or identified by an asterisk indicate reversals and autapomorphies, respectively. The following characters supporting clades in the strict consensus tree are those commonly supporting clades in all three most parsimonious trees.

Clade A. Includes Exocoetoidei (= all examined ingroups). This clade is supported by six synapomorphies, including five autapomorphies: characters 28-2 (interhyal absent), 10-1* (processes of basioccipital present), 11-1* (plate-like process of basioccipital present), 15-1*
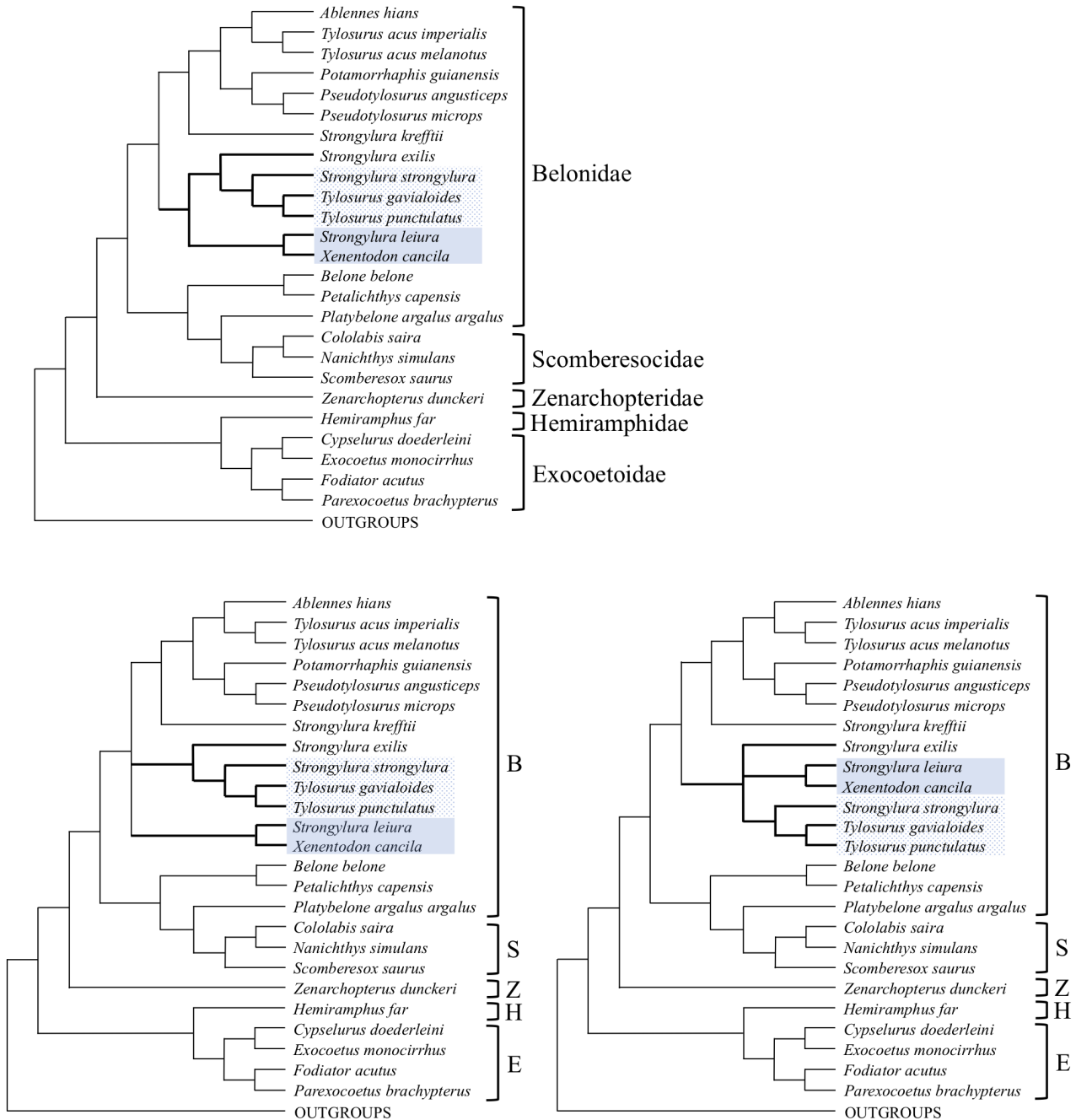
Figure 64. Three equally most parsimonious trees representing phylogenetic relationships of suborder Exocoetoidei. Thick nodes indicate different topology among three trees. Stippled box and gray box indicate *Strongylura strongylura + Tylosurus gavialoides + Tylosurus punctulatus* clade and *Strongylura leiura + Xenentodon cancila* clade respectively.
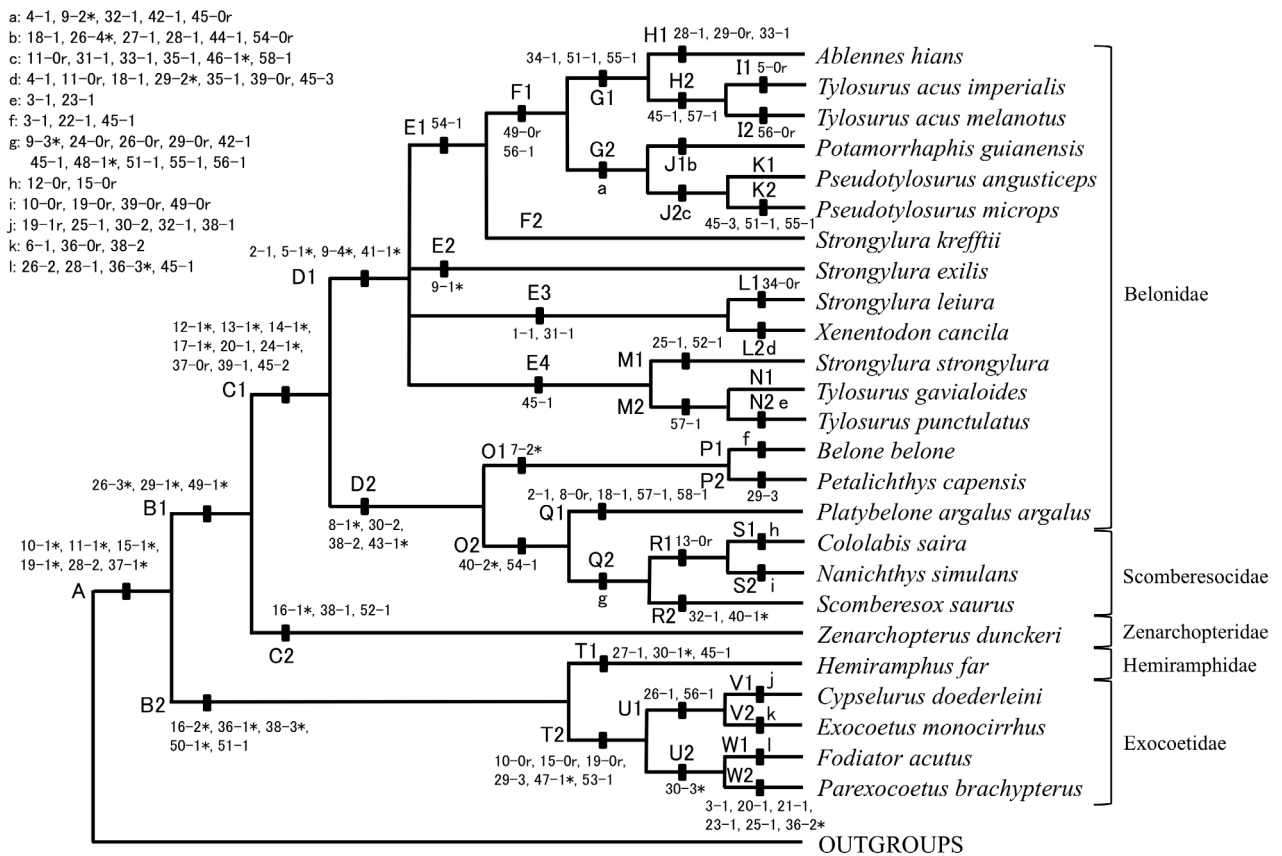
Figure 65. Strict consensus tree of three equally parsimonious trees representing phylogenetic relationships of suborder Exocoetoidei. "r" and asterisk indicate reversal and autapomorphy, respectively.

Table 2. Matrix of characters in 58 transformation series for examined outgroups and ingroups.

Species	Transformation series and characters											
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–58
OUTGROUPS												
Oryzias javanicus	10000	100?0	00000	00001	00001	?0230	1?000	0000?	01010	00000	00100	?00
Poecilia mexicana	10000	100?0	00000	00100	00000	10000	1?000	0000?	00000	00000	00100	?00
Atherinomorus pinguis	00100	01000	00000	00000	11100	00000	00000	00010	00001	00000	00000	?00
INGROUPS												
Belonidae												
Ablennes hians	01001	00041	11111	01011	00010	30100	001?0	00010	10002	00000	10011	100
Belone belone	00100	02101	11111	01011	01010	30212	00000	00210	00101	00010	00000	000
Petalichthys capensis	00000	02101	11111	01011	00010	30232	00000	00210	00102	00010	00000	000
Platybelone argalus argalus	01000	00001	11111	01111	00010	30212	00000	00212	00102	00010	00010	011
Potamorrhaphis guianensis	01011	00021	11111	01111	00010	41110	01000	00010	11010	00000	00000	100
Pseudotylosurus angusticeps	01011	00021	01111	01011	00010	30210	1?1?1	00010	11000	10000	00010	101
Pseudotylosurus microps	01011	00021	01111	01011	00010	30210	??1?1	00010	11003	10000	10011	101
Strongylura exilis	01001	00011	11111	01011	00010	30210	00010	00010	10002	00010	00000	000
Strongylura krefftii	01001	00041	11111	01011	00010	30210	00000	00010	10002	00010	00010	000
Strongylura leiura	11001	00041	11111	01011	00010	30210	1?000	00010	10002	00010	00000	000
Strongylura strongylura	01001	00041	11111	01011	00011	30210	00010	00010	10001	00010	01000	000
Tylosurus acus imperialis	01000	00041	11111	01011	00010	30210	00010	00010	10001	00000	10011	110
Tylosurus acus melanotus	01001	00041	11111	01011	00010	30210	00010	00010	10001	00000	10011	010
Tylosurus gavialoides	01001	00041	11111	01011	00010	30210	00010	00010	10001	00010	00000	?10
Tylosurus punctulatus	01101	00041	11111	01011	00110	30210	00010	00010	10001	00010	00000	010
Xenentodon cancila	11011	00041	01111	01111	00010	30220	1?011	?000?	10003	00010	00000	000
Scomberesocidae												
Cololabis saira	00000	00131	10010	01011	00000	00202	00000	00212	01101	00110	10011	100
Nanichthys simulans	00000	00130	11011	01001	00000	00202	00000	0020?	01101	00100	10011	100
Scomberesox saurus	00000	00131	11111	01011	00000	00202	01000	00211	01101	00110	10011	100
Hemiramphidae												
Hemiramphus far	00000	00001	10001	20010	00000	01201	00000	1130?	00001	00001	10000	000
Zenarchopteridae												
Zenarchopterus dunckeri	00000	00001	10001	10010	00000	30210	00000	0110?	00000	00010	01000	000
Exocoetidae												
Cypselurus doederleini	00000	00000	10000	20010	00001	10232	01000	1110?	00000	01001	10100	100
Exocoetus monocirrhus	00000	10000	10000	20000	00000	10230	00000	0120?	00000	01001	10100	100
Fodiator acutus	00000	00000	10000	20000	00000	20133	00000	3130?	00001	01001	10100	000
Parexocoetus brachypterus	00100	00000	10000	20001	10101	00233	00000	2130?	00000	01001	10100	000

"?" indicates character unspecified.

(dentary long), 19-1* (dorsal margin of coronomeckelian extending over margin of angular) and 37-1* (third pharyngobranchials on both sides attached). Clade A is divided into clades B1 and B2.

Clade B1. Includes Belonidae, Scomberesocidae and Zenarchopteridae. This clade has three autapomorphies: characters 26-3* (foramen crossed by hyomandibularis composed of quadrate, symplectic and preopercle), 29-1* (dorsal process of urohyal present, tip of process simple and flat) and 49-1* (urostyle and uroneural autogenous). Clade B1 is divided into clade C1 and species C2.

Clade B2. Includes Hemiramphidae and Exocoetidae. This clade has five synapomorphies, including four autapomorphies: characters 51-1 (urostyle and parhypural fused), 16-2* (cartilage on posterolateral surface of dentary present and developed), 36-1* (teeth on second pharyngobranchial tricuspid), 38-3* (teeth on third pharyngobranchial tricuspid and spatulate) and 50-1* (urostyle and 1 + 2 hypural plate autogenous). Clade B2 is divided into species T1 and clade T2.

Clade C1. Includes Belonidae and Scomberesocidae. This clade has nine synapomorphies, including five autapomorphies: characters 20-1 (cartilaginous cap on anterior tip of palatine absent), 37-0r (third pharyngobranchials on both sides separated), 39-1 (fourth upper pharyngeal tooth plate present), 45-2 (foramen present between first and second, and second and third actinosts, respectively), 12-1* (premaxilla long), 13-1* (premaxillae on both sides interdigitated), 14-1* (sensory canal of premaxilla present), 17-1* (dentaries on both sides interdigitated) and 24-1* (metapterygoid lamina present). Clade C1 is divided into clades D1 and D2.

Species C2. Includes only the zenarchopterid *Zenarchopterus dunckeri*. This species has three apomorphies, including one autapomorphy: characters 38-1 (teeth on third pharyngobranchial tricuspid), 52-1 (third and fourth hypurals autogenous) and 16-1* (cartilage on posterolateral surface of dentary present and rudimentary).

Clade D1. Includes the belonids *Ablennes hians*, *Potamorrhaphis guianensis* and all species of *Pseudotylosurus*, *Strongylura*, *Tylosurus* and *Xenentodon cancila*. This clade has four synapomorphies, including three autapomorphies: characters 2-1 (prevomer and nasal attached), 5-1* (nasals on both sides attached), 9-4* (dorsal portion of basisphenoid attached to frontal, prootic and parasphenoid) and 41-1* (gill rakers absent). Clade D1 includes polychotomous clades E1, E3 and E4, and species E2.

Clade D2. Includes the belonids *Belone belone*, *Petalichthys capensis* and *Platybelone argalus argalus*, and Scomberesocidae. This clade is supported by four synapomorphies, including two autapomorphies: characters 30-2 (teeth on fifth ceratobranchial conical and tricuspid), 38-2 (teeth on third pharyngobranchial conical and tricuspid), 8-1* (sensory canal of epiotic present) and 43-1* (sensory canal of posttemporal present). Clade D2 is divided into clades O1 and O2.

Clade E1. Includes the belonids *Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus*, *Strongylura krefftii*, *Tylosurus acus imperialis* and *T. a. melanotus*. This clade possesses one synapomorphy, character 54-1 (fifth hypural and uroneural fused). Clade E1 is divided into clade F1 and species F2.

Species E2. Includes only the belonid *Strongylura exilis*. This species possesses one autapomorphy, character 9-1* (dorsal portion of basisphenoid attached only to frontal).

Clade E3. Includes the belonids *Strongylura leiura* and *Xenentodon cancila*. This clade is supported by two synapomorphies: characters 1-1 (sensory canal of dermosphenotic not connecting with frontal) and 31-1 (dorsolateral process of second epibranchial absent). Clade E3 is divided into species L1 and L2.

Clade E4. Includes the belonids *Strongylura strongylura*, *Tylosurus gavialoides* and *T. punctulatus*. This clade has one synapomorphy, character 45-1 (foramen present between each actinost). Clade E4 is divided into species M1 and clade M2.

Clade F1. Includes the belonids *Ablennes hians*, *Potamorrhaphis guianensis*, all species of *Pseudotylosurus*, *Tylosurus acus imperialis* and *T. a. melanotus*, and has two synapomorphies: characters 49-0r (urostyle and uroneural fused) and 56-1 (branch of lateral line under pectoral fin absent). Clade F1 is divided into clades G1 and G2.

Species F2. Includes only the belonid *Strongylura krefftii*, and lacks apomorphies.

Clade G1. Includes the belonids *Ablennes hians*, *Tylosurus acus imperialis* and *T. a. melanotus*. This clade is supported by three synapomorphies: characters 34-1 (cartilage cap on dorsal process of third epibranchial absent), 51-1 (urostyle and parhypural fused) and 55-1 (1 + 2 hypural plate and parhypural fused). Clade G1 is divided into species H1 and clade H2.

Clade G2. Includes the belonids *Potamorrhaphis guianensis* and all species of *Pseudotylosurus*. This clade has five synapomorphies including one autapomorphy: characters 4-1 (ethmoid covered by nasals), 32-1 (cartilage cap on dorsolateral process of second epibranchial present), 42-1 (ventral process of posttemporal absent), 45-0r (foramen between actinosts absent) and 9-2* (dorsal portion of basisphenoid attached to frontal and prootic). Clade G2 is divided into species J1 and clade J2.

Species H1. Species H1 includes only *Ablennes hians* and is supported by three apomorphies: characters 28-1 (interhyal present and rudimentary), 29-0r (dorsal process of urohyal present, tip of process simple and pointed) and 33-1 (dorsal process of third epibranchial absent).

Species H2. Species H2 includes *Tylosurus acus imperialis* and *T. a. melanotus*, and has two synapomorphies: characters 45-1 (foramen present between each actinost) and 57-1 (keel on caudal peduncle present). Species H2 is divided into subspecies I1 and I2.

Subspecies I1. Includes only *Tylosurus acus imperialis* and has one apomorphy, character 5-0r (nasals on both sides separated).

Subspecies I2. Includes only *Tylosurus acus melanotus* and has one apomorphy, character 56-0r (branch of lateral line under pectoral fin present).

Species J1. Includes only *Potamorrhaphis guianensis*, and has six apomorphies including one autapomorphy: characters 18-1 (cartilage between angular and retroarticular absent), 27-1 (cartilage on posterodorsal portion of epihyal present), 28-1 (interhyal present and rudimentary), 44-1 (supracleithrum absent), 54-0r (fifth hypural and uroneural separated) and 26-4* (foramen crossed by hyomandibularis composed of quadrate and preopercle).

Clade J2. Includes the all species of *Pseudotylosurus*. This clade is supported by six synapomorphies including one autapomorphy: characters 11-0r (plate-like process of basioccipital absent), 31-1 (dorsolateral process of second epibranchial absent), 33-1 (dorsal process of third epibranchial absent), 35-1 (fourth epibranchial absent), 58-1 (caudal peduncle depressed dorsoventrally) and 46-1* (postcleithrum absent). Clade J2 is divided into species K1 and K2.

Species K1. Includes only *Pseudotylosurus angusticeps* and has one autapomorphy (cartilaginous cap on lateral tip of third epibranchial absent), which was not included in the present analysis.

Species K2. Includes only *Pseudotylosurus microps*. Species K2 has three apomorphies: characters 45-3 (foramina present between second and third actinosts, and third and fourth actinosts, respectively), 51-1 (urostyle and parhypural fused) and 55-1 (1 + 2 hypural plate and parhypural fused).

Species L1. Includes only *Strongylura leiura* and has one apomorphy, character 34-0r (cartilaginous cap on dorsal process of third epibranchial present).

Species L2. Includes only *Xenentodon cancila*. Species L2 possesses seven apomorphies including one autapomorphy: characters 4-1 (ethmoid covered by nasals), 11-0r (plate-like process of basioccipital absent), 18-1 (cartilage between angular and retroarticular absent), 35-1 (fourth epibranchial absent), 39-0r (fourth upper pharyngeal tooth plate absent), 45-3 (foramina present between second and third actinosts, and third and fourth actinosts, respectively) and 29-2* (dorsal process of urohyal present, bifurcated and tips of processes flat). In addition, clade L2 has one autapomorphy (second pharyngobranchial absent), which

was not adopted for the present analysis.

Species M1. Includes only *Strongylura strongylura* and has two apomorphies: characters 25-1 (medial cartilage on anteriormost portion of symplectic absent) and 52-1 (third and fourth hypurals separated).

Clade M2. Includes the belonids *Tylosurus gavialoides* and *T. punctulatus*, and is supported by one synapomorphy, character 57-1 (keel on caudal peduncle present). Clade M2 is divided into species N1 and N2.

Species N1. Includes *Tylosurus gavialoides* and lacks any apomorphies.

Species N2. Includes *Tylosurus punctulatus* and has two apomorphies: character 3-1 (teeth on prevomer present) and 23-1 (teeth on endopterygoid present).

Clade O1. Includes the belonids *Belone belone* and *Petalichthys capensis*. This clade is supported by one autapomorphy, character 7-2* (sensory canal of sphenotic and pterotic present). Clade O1 is divided into species P1 and P2.

Clade O2. Includes the belonid *Platybelone argalus argalus* and Scomberesocidae. This clade is supported by two synapomorphies, including one autapomorphy: character 54-1 (fifth hypural and uroneural fused) and 40-2* (teeth on fourth upper pharyngeal tooth plate conical and tricuspid). Clade O2 is divided into subspecies Q1 and clade Q2.

Species P1. Includes only *Belone belone* and possesses three apomorphies: characters 3-1 (teeth on prevomer present), 22-1 (ectopterygoid present) and 45-1 (foramen present between each actinost).

Species P2. Includes only *Petalichthys capensis* and has one apomorphy, character 29-3 (dorsal process of urohyal absent).

Subspecies Q1. Includes only *Platybelone argalus argalus*. The subspecies has five apomorphies: characters 2-1 (prevomer and nasal attached), 8-0r (sensory canal of epiotic absent), 18-1 (cartilage between angular and retroarticular absent), 57-1 (keel on caudal peduncle present) and 58-1 (caudal peduncle depressed dorsoventrally).

Clade Q2. Includes Scomberesocidae. This clade is supported by 10 synapomorphies, including two autapomorphies: characters 24-0r (metapterygoid lamina absent), 26-0r (foramen crossed by hyomandibularis composed of only symplectic), 29-0r (dorsal process of urohyal present, tip of process simple and pointed), 42-1 (ventral process of posttemporal absent), 45-1 (foramina present between each actinost), 51-1 (urostyle and parhypural fused), 55-1 (1 + 2 hypural plate and parhypural fused) and 56-1 (branch of lateral line under pectoral fin absent), 9-3* (dorsal portion of basisphenoid attached to frontal and parasphenoid) and 48-1* (finlets present). Clade Q2 is divided into clade R1 and species R2.

Clade R1. Includes the scomberesocids *Cololabis saira* and *Nanichthys simulans*. This clade is supported by one synapomorphy, character 13-0r (premaxillae on both sides attached by smooth surfaces). Clade R1 is divided into species S1 and S2.

Species R2. Includes only *Scomberesox saurus* and has two apomorphies, including one autapomorphy: characters 32-1 (cartilaginous cap on dorsolateral process of second epibranchial present) and 40-1* (teeth on fourth upper pharyngeal tooth plate tricuspid).

Species S1. Includes only *Cololabis saira* and has two apomorphies: characters 12-0r (premaxilla short) and 15-0r (dentary short).

Species S2. Includes only *Nanichthys simulans* and has four apomorphies: characters 10-0r (processes of basioccipital absent), 19-0r (dorsal margin of coronomeckelian not reaching dorsal margin of angular), 39-0r (fourth pharyngobranchial absent) and 49-0r (urostyle and uroneural fused).

Species T1. Includes only the hemiramphid *Hemiramphus far*. This species has three apomorphies, including one autapomorphy: characters 27-1 (cartilage on posterodorsal portion of epihyal present), 45-1 (foramen present between each actinost) and 30-1* (teeth on fifth ceratobranchial tricuspid). In addition, the clade has one autapomorphy (teeth on jaws tricuspid), which was not adopted in the present analysis.

Clade T2. Includes Exocoetidae. This clade is supported by six synapomorphies, including one autapomorphy: characters 10-0r (processes of basioccipital absent), 15-0r (dentary short), 19-0r (dorsal margin of coronomeckelian is not reaching to margin of angular), 29-3 (dorsal process of urohyal absent), 53-1 (fourth and fifth hypurals fused) and 47-1* (pectoral fin long). Clade T2 is divided into clades U1 and U2.

Clade U1. Includes the exocoetids *Cypselurus doederleini* and *Exocoetus monocirrhus* and is supported by two synapomorphies: characters 26-1 (foramen crossed by hyomandibularis composed of quadrate and symplectic) and 56-1 (branch of lateral line under pectoral fin absent). Clade U1 is divided into species V1 and V2.

Clade U2. Includes the exocoetids *Fodiator acutus* and *Parexocoetus brachypterus* and is supported by one autapomorphy, character 30-3* (teeth on fifth ceratobranchial tricuspid and spatulate). Clade U2 is divided into species W1 and W2.

Species V1. Includes only *Cypselurus doederleini* and has five apomorphies: characters 19-1r (dorsal margin of coronomeckelian extending over margin of angular), 25-1 (medial cartilage on anteriormost portion of symplectic absent), 30-2 (teeth on fifth ceratobranchial conical and tricuspid), 32-1 (cartilaginous cap on dorsolateral process of second epibranchial present) and 38-1 (teeth on third pharyngobranchial tricuspid).

Species V2. Includes only *Exocoetus monocirrhus* and possesses three apomorphies: characters 6-1 (sensory canal of nasal absent), 36-0r (teeth on second pharyngobranchial conical) and 38-2 (teeth on third pharyngobranchial conical and tricuspid).

Species W1. Includes only *Fodiator acutus* and has four apomorphies, including one autapomorphy: characters 26-2 (foramen crossed by hyomandibularis composed of symplectic and preopercle), 28-1 (interhyal present and rudimentary), 45-1 (foramen present between each actinost) and 36-3* (teeth on second pharyngobranchial tricuspid and spatulate).

Species W2. Includes only *Parexocoetus brachypterus* and possesses six apomorphies, including one autapomorphy: characters 3-1 (teeth on prevomer present), 20-1 (cartilaginous cap on anterior tip of palatine absent), 21-1 (teeth on palatine present), 23-1 (teeth on endopterygoid present), 25-1 (medial cartilage on anteriormost portion of symplectic absent) and 36-2* (teeth on second pharyngobranchial conical and tricuspid).

2. Comparison with previous studies

The five morphological characters supporting the monophyly of Exocoetoidei (= clade A) were shown in see section 1 of TAXON SAMPLING. In addition to these, the six characters were revealed as synapomorphies of clade A in the present analysis as shown in VI-1. Therefore, the monophyly of Exocoetoidei is supported more strongly by the latter six characters than the former five characters. The family Belonidae and the belonid genera *Strongylura* and *Tylosurus* are inferred as a non-monophyletic group in the present analysis. However, Belonidae (= clades D1, O1 and species Q1) forms a monophyletic group when the family Scomberesocidae (= clade Q2) is included. The genera *Strongylura* and *Tylosurus* form a monophyletic group with the belonid genera *Ablennes*, *Potamorrhaphis*, *Pseudotylosurus* and *Xenentodon*. Additionally, the superfamily Exocoetoidea (= clades B2 and species C2), which includes the families Exocoetidae (= clade T2), Hemiramphidae (= species T1) and Zenarchopteridae (= species C2) (*sensu* Nelson *et al*., 2016) is also inferred as a non-monophyletic group, since Zenarchopteridae is the sister group of the clade including Belonidae and Scomberesocidae in the present analysis. The relationships obtained in the present study corresponded approximately with recent molecular phylogenetic studies, Lovejoy (2000) and Lovejoy *et al*. (2004), in the following points: (1) Belonidae is not a monophyletic group if Scomberesocidae is excluded; (2) genus *Strongylura* is a non-monophyletic group; (3) Zenarchopteridae has a sister relationship with the clade comprising Belonidae and Scomberesocidae, and (4) the superfamily Exocoetoidea is not a monophyletic group.

CLASSIFICATION

Only the classification of clade C1, which includes previous 'Belonidae' and 'Scomberesocidae', is discussed here, since the study examined an insufficient number of zenarchopterid, hemiramphid and exocoetid species (= Exocoetoidea) for a detailed taxonomic classification. Two genera, *Strongylura* and *Tylosurus*, are revealed as non-monophyletic. However, because only four species of *Strongylura* (15 species total: Nelson *et al*., 2016) and three of *Tylosurus* (including two subspecies) (10 species total: Nelson *et al*., 2016) were examined, taxonomic changes at generic rank are not appropriate and all genera of Belonidae regarded as valid (see Collette, 2003) are retained in 'Belonidae'.

1. Family level rank and name

As the result of this study, 'Belonidae' as previously recognized is inferred as a non-monophyletic group, if the family 'Scomberesocidae' is excluded, and therefore requires redefinition. Clade C1, including all belonids and scomberesocids, comprises clades D1 (including the belonid genera *Ablennes*, *Potamorrhaphis*, *Pseudotylosurus*, *Strongylura*, *Tylosurus* and *Xenentodon*) and D2 (including the belonid genera *Belone*, *Petalichthys* and *Platybelone*, and all scomberesocids). Whereas clade C1 is supported by nine synapomorphies, including five autapomorphies, clades D1 and D2 are supported by relatively fewer synapomorphies (D1: four synapomorphies, including three autapomorphies; D2 four synapomorphies, including two autapomorphies). Therefore, familial rank is more appropriately given to clade C1 due to its stronger support. Of the nominal family-group names assigned to type genera included in clade C1 (Belonini Bonaparte, 1835, Scombresocioidei Bleeker, 1859, Tylosuridae Starks, 1906, Strongylurinae Fowler, 1925 and Petalichthyidae Smith, 1949), Belonini has priority (ICZN, 1999: Art. 23.1) and the family name Belonidae is retained.

2. Ranking and naming at subfamilial level

To reflect the presently-determined phylogenetic relationships in Belonidae classification, subfamilial ranking is appropriate for clades D1 and D2, since they are both defined by four synapomorphies and are easily distinguished from each other by absence (clade D1) or presence (clade D2) of gill rakers. Tylosuridae Starks, 1906 and Strongylurinae Fowler, 1925 are both nominal family-group names assigned to type genera included in clade D1. Therefore, Tylosurinae is applied to clade D1, having priority over Strongylurinae (ICZN, 1999: Art. 23.1). Belonini Bonaparte, 1835, Scombresocioidei Bleeker, 1859 and Petalichthyidae Smith, 1949 are all family-group names assigned to type genera included in clade D2, Beloninae having priority (ICZN, 1999: Art. 23.1).

3. Affiliation of species not adopted in the phylogenetic analysis

Belonion dibranchodon

This species has a premaxilla sensory canal (character 14-1), which is an autapomorphy of clade C1. In

addition, the character is unique among teleosts (Parin and Astakhov, 1982). On this basis, the species might be included in clade C1 (Belonidae). However, it lacks the synapomorphies of clades D1 (Tylosurinae) and D2 (Beloninae). Accordingly, although *Belonion dibranchodon* should be presently included in the family Belonidae, its subfamilial affiliation could not be determined.

Elassichthys adocetus

This species has finlets (character 46-1), which is an autapomorphy of clade Q2. Because the character is rare among teleosts, found only in scombrids (mackerels), gempylids (snake mackerels) and some carangids (jacks) (Nelson *et al*., 2016), *Elassichthys adocetus* is placed in clade Q2 (within clade D2) (Beloninae).

4. New classification of Belonidae

The following classification of the family Belonidae, including two subfamilies and 14 genera, is proposed based on the phylogenetic relationships reconstructed in the present study:

Family Belonidae Bonaparte, 1835
Subfamily Tylosurinae Starks, 1906
     Genus *Ablennes* Jordan and Fordice, 1887
     Genus *Potamorrhaphis* Günther, 1866
     Genus *Pseudotylosurus* Fernández-Yépez, 1948
     Genus *Strongylura* van Hasselt, 1824
     Genus *Tylosurus* Cocco, 1833
     Genus *Xenentodon* Regan, 1911
Subfamily Beloninae Bonaparte, 1835
     Genus *Belone* Cuvier, 1816
     Genus *Cololabis* Gill, 1896
     Genus *Elassichthys* Hubbs and Wisner, 1980
     Genus *Nanichthys* Hubbs and Wisner, 1980
     Genus *Petalichthys* Regan, 1904
     Genus *Platybelone* Fowler, 1919
     Genus *Scomberesox* Lacepède, 1803
Incertae sedis in Belonidae
     Genus *Belonion* Collette, 1966

Family Belonidae Bonaparte, 1835

Belonini Bonaparte, 1835: 17 (in a separate distributed in 1835; on p. 274 in journal published in 1940) (type genus: *Belone* Cuvier, 1816).

Scombresocioidei Bleeker, 1859: XXX (type genus: *Scomberesox* Lacepède, 1803).

Tylosuridae Starks, 1906: 781 (type genus: *Tylosurus* Cocco, 1833).

Strongylurinae Fowler, 1925: 3 (type genus: *Strongylura* van Hasselt, 1824).

Petalichthyidae Smith, 1949: 129 (type genus: *Petalichthys* Regan, 1904).

Diagnosis. Sensory canal of premaxilla present (except *Elassichthys*); cartilaginous cap on anterior tip of palatine absent; third pharyngobranchials on both sides separated; scales relatively small, *ca*. 70 to > 350 in lateral line (Nelson *et al*., 2016; this study).

Key to subfamilies of the family Belonidae

1a. Gill rakers absent................. Tylosurinae
1b. Gill rakers present ....Beloninae

Subfamily Tylosurinae Starks, 1906

Tylosuridae Starks, 1906: 781 (type genus: *Tylosurus* Cocco, 1833).

Strongylurinae Fowler, 1925: 3 (type genus: *Strongylura* van Hasselt, 1824).

Diagnosis. Prevomer and nasal attached; teeth on fifth ceratobranchial conical; teeth on third pharyngobranchials conical; gill rakers absent; sensory canal of posttemporal absent (this study).

Subfamily Beloninae Bonaparte, 1835

Belonini Bonaparte, 1835: 17 (in a separate distributed in 1835; p. 274 in journal published in 1840; see van der Laan *et al*., 2014) (type genus: *Belone* Cuvier, 1816).

Scombresocioidei Bleeker, 1859: XXX (type genus: *Scomberesox* Lacepède, 1803).

Petalichthyidae Smith, 1949: 129 (type genus: *Petalichthys* Regan, 1904).

Diagnosis. Prevomer and nasal separated (except *Platybelone*); teeth on fifth ceratobranchial conical and tricuspid; teeth on third pharyngobranchials conical and tricuspid; gill rakers present; sensory canal of posttemporal present (except *Elassichthys*) (this study).

Incertae sedis within Belonidae

Genus *Belonion* Collette, 1966

Belonion Collette, 1966: 7 (type species: *Belonion apodion* Collette, 1966).

Gender. Neuter.

Diagnosis. Frontal canals on right and left sides connected; lateral process of sphenotic absent; many cartilaginous elements present in neurocranium; premaxilla short; lower jaw sensory canal present only in dentary; endopterygoid and metapterygoid not attached; quadrate and preopercle not attached; fourth upper pharyngeal tooth plate absent; first pleural rib attached to second abdominal vertebra; epineurals absent; lateral line absent (this study); branchiostegal rays 6–7 (Collette, 1966; this study); pectoral fin rays 5–6 (Collette, 1966; this study); reproductive maturity attained at *ca*. 25 mm BL (Collette, 1966).

Remarks. Two species, *Belonion apodion* and *Belonion dibranchodon* are included (Collette, 1966).

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