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The taxon Beloniformes represents a heterogeneous group of teleost fishes that show an extraordinary diversity of jaw morphology. I present new anatomical descriptions of the jaw musculature in six selected beloniforms and four closely related species. A reduction of the external jaw adductor (A1) and a changed morphology of the intramandibular musculature were found in many Beloniformes. This might be correlated with the progressively reduced mobility of the upper and lower jaw bones. The needlefishes and sauries, which are characterised by extremely elongated and stiffened jaws, show several derived characters, which in combination enable the capture of fish at high velocity. The ricefishes are characterised by several derived and many plesiomorphic characters that make broad scale comparisons difficult. Soft tissue characters are highly diverse among hemiramphids and flying fishes reflecting the uncertainty about their phylogenetic position and interrelationship. The morphological findings presented herein may help to interpret future phylogenetic analyses using cranial musculature in Beloniformes.

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Morphology of the suspensorial, jaw and opercle musculature of Beloniformes and related species (Teleostei: Acanthopterygii), with a special reference to the m. adductor mandibulae complex

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Key words

Oryzias, *Belone*, *Perca,* Atherinomorpha, feeding, jaw elongation

Abstract

The taxon Beloniformes represents a heterogeneous group of teleost fishes that show an extraordinary diversity of jaw morphology. I present new anatomical descriptions of the jaw musculature in six selected beloniforms and four closely related species. A reduction of the external jaw adductor (A1) and a changed morphology of the intramandibular musculature were found in many Beloniformes. This might be correlated with the progressively reduced mobility of the upper and lower jaw bones. The needlefishes and sauries, which are characterised by extremely elongated and stiffened jaws, show several derived characters, which in combination enable the capture of fish at high velocity. The ricefishes are characterised by several derived and many plesiomorphic characters that make broad scale comparisons difficult. Soft tissue characters are highly diverse among hemiramphids and flying fishes reflecting the uncertainty about their phylogenetic position and interrelationship. The morphological findings presented herein may help to interpret future phylogenetic analyses using cranial musculature in Beloniformes.

Introduction

The jaw anatomy of Beloniformes, the needlefishes and their allies, is very diverse. As such, they received reasonable attention in osteological, phylogenetic as well as ontogenetic analyses (Rosen and Parenti, 1981; Boughton *et al.*, 1991; Lovejoy *et al.*, 2000, 2004). The taxon includes small, short-snouted and duckbilled ricefishes (Adrianichthyidae) (Parenti, 1987), which live in flooded Asian rice fields. Halfbeaks (hemiramphids), another group, are characterised by an elongated lower jaw. The flying fishes (Exocoetidae) have short snouts; whereas the sauries (Scomberesocidae) and needlefishes (Belonidae), which are adapted to fast swimming and fish hunting, have elongated upper and lower jaws with extended teeth rows (Nelson, 2006). Although the drastic ontogenetic changes of the jaws have been previously studied in their external shape (Boughton *et al.*, 1991; Lovejoy *et al.*, 2004), the anatomy of the fully formed cranial musculature has received little attention.

Beloniformes belong to the Atherinomorpha (Figure 1), which are placed within the Acanthopterygii. The phylogenetic relationships among acanthopterygian groups, which also include taxa such as Perciformes and Mugilomorpha, are controversial (e.g. Stiassny, 1990; Johnson and Patterson, 1993; Parenti, 1993; Parenti and Grier, 2004; Rosen and Parenti, 1981; Wu and Shen, 2004; Nelson, 2006; Setiamarga *et al.,* 2008; Near *et al.,* 2013). Smegmamorpha, Mugilomorpha, or Paracanthopterygii have all been hypothesised to form the sister taxon to Atherinomorpha.

The monophyly of Atherinomorpha is currently accepted (Nelson, 2006; Near *et al.*, 2013). Atheriniformes form the sister group of Cyprinodontea, which comprises Cyprinodontiformes (killifishes and their allies) and Beloniformes (Figures 1B-C). Recently, Li (2001) analysed osteological data of the hyobranchial apparatus and re-established the traditional hypotheses of Berg (1958) and Rosen (1964) of a closer relationship of Adrianichthyidae to Cyprinodontiformes (Figure 1A; see also Temminck and Schlegel, 1846: compared to Yamamoto, 1975). This hypothesis, however, was not based on a cladistic analysis and represents phenetic classifications. These classifications are in strong contrast to several analyses, resulting in a sister group relationship of Adrianichthyidae and Exocoetoidea, comprising the remaining Beloniformes (Figure 1), and Beloniformes as the sister group of Cyprinodontiformes (Collette *et al.*, 1984, Dyer and Chernoff, 1996; Hertwig, 2008; Naruse *et al.*, 1993; Naruse, 1996, Rosen and Parenti, 1981; White *et al.*, 1984).

The phylogenetic relationships within Beloniformes are still a matter of debate. Traditional studies (Rosen, 1964; Rosen and Parenti, 1981) found two major clades within

Beloniformes (excl. Adrianichthyidae), namely Exocoetoidea (flying fishes and halfbeaks) and Scomberesocoidea (sauries and needlefishes), together forming the Exocoetoidei (Collette *et al.*, 1984; Parin and Astakhov, 1982; Rosen, 1964; Figure 1A-B).

Recently, Lovejoy (2000) and Lovejoy *et al.* (2004) proposed the paraphyly of hemiramphids and nested Scomberesocidae inside “Belonidae” (Figure 1C). The paraphyly of hemiramphids was also supported by Tibbetts (1991) and Aschliman *et al.* (2005). The halfbeak *Dermogenys* (which is included in the present study) was found to be a member of the Zenarchopteridae, which comprise a subset of hemiramphids of the Indo-West-Pacific (Anderson and Collette, 1991; Lovejoy, 2000; Meisner, 2001). Zenarchopteridae represents the sister taxon of ~~to~~ the clade formed by needlefishes and sauries (Lovejoy *et al.*, 2004; Aschliman *et al.,* 2005). Other representatives of the traditionally recognized hemiramphids grouped with the Exocoetidae, or as the sister group to the clade Zenarchopteridae + “Belonidae” (Figure 1C).

The complex jaw musculature of Beloniformes has only been studied in a very few species so far, and most published descriptions of beloniform species are superficial and insufficiently illustrated. That makes broad phylogenetic comparisons impossible. The aim of the present study was to illustrate and describe the morphological diversity of cranial musculature of six selected species of Beloniformes in great detail and to compare it to external jaw anatomy. By using manual dissections and histological slide sections I aim to provide a comprehensive anatomical basis for future researchers studying more species in a phylogenetic context.

In the present, pure anatomical study, the great diversity within beloniform subgroups or within non-beloniform groups could not be studied by maintaining the provided extent and detail of illustrations and descriptions. However, I present some considerations about the potential phylogenetic relevance of some characters that have to be tested in future studies. Therefore, four selected near related acanthopterygian species, which may serve as outgroup in future phylogenetic studies, are described. In addition to two atherinomorph species, I included the percomorph *Perca fluviatilis*, which was recently used to define the ancestral pattern of atherinomorph jaw musculature (Hertwig, 2008), and the mugilomorph *Rhinomugil corsula*, which is possibly closer related to Atherinomorpha.

Materials and Techniques

Taxonomic sampling

The cranial anatomy of ten acanthopterygian species was studied (Fig. 2-3, S1-9), including six species of Beloniformes. Specimens from the following collections were used: Phyletisches Museum der Friedrich Schiller Universität Jena, Germany (ISZE), Smithsonian Institution of the National Museum of Natural History Washington, USA (USNM), Naturhistorisches Museum der Burgergemeinde Bern, Switzerland (NMBE).

- Perciformes, *Perca fluviatilis* (Linnaeus, 1758) (ISZE) (Fig. 2A, S1);
- Mugilomorpha, *Rhinomugil corsula* (Hamilton, 1822) (NMBE) (Fig. 2B, S2);
- Atheriniformes, *Atherina boyeri* (Risso, 1810) (NMBE) (Fig. 2C, S3);
- Cyprinodontiformes, *Aplocheilus lineatus* (Valenciennes, 1846) (NMBE) (Fig. 2D, S4);
- Beloniformes, Adrianichthyidae, *Oryzias latipes* (Temminck and Schlegel, 1846) (NMBE) (Fig. 2E, S5);
- Beloniformes, Adrianichthyidae, *Xenopoecilus oophorus* (Kottelat 1990) (NMBE) (Fig. 3);
- Beloniformes, Exocoetidae, *Parexocoetus brachypterus* (Richardson, 1846) (USNM 299385) (Fig. 2F, S6);
- Beloniformes, Hemiramphidae, *Dermogenys pusilla* (Kuhl and van Hasselt, 1823) (NMBE) (Fig. 2G, S7);
- Beloniformes, Belonidae, *Belone belone* (Linnaeus, 1761) (NMBE) (Fig. 2H, S8);
- Beloniformes, Scomberesocidae, *Scomberesox saurus* (Walbaum, 1782) (ISZE) (Fig. S9).

Anatomical observations

Standard procedures for histology and manual dissection are those used by Werneburg (2007) and Werneburg and Hertwig (2009).

For dissection, two or more specimens per species were used. In the first step of dissection (summarised in Figure 2) the lateral view of the skinned head including all muscles in their unaltered place, including the jaw adductor musculature, opercle-, and suspensoric-related musculature, was documented. In the second step, the external section of m. adductor mandibulae (A1) was mostly removed and the course of the internal section of m. adductor mandibulae (A2/3) was depicted. Further steps of dissection did allow inspection of the symplectic in lateral view with the A2/3 completely or partly removed. Finally, the medial view of the jaw apparatus was documented with a focus on the musculature medial of the lower jaw, namely the intramandibular section of m. adductor mandibulae (Aω), the anterior part of m. protractor hyoidei, and m. intermandibularis.

Serial sections were prepared for all species (slice thickness = 12µm), except for *Pe. fluviatilis* and *B. belone* due to the size of these species. The positions of the sections are indicated in the dissection figures (Figures S1-9). For *S. saurus*, a juvenile specimen was used for histological sectioning, whereas for manual dissections and character coding (as for all species), adult specimens were used (Fig. S9).

Nomenclature

Osteological nomenclature follows Weitzman (1962, 1974) with modifications as summarised by Hertwig (2008). Basic myological terminology is that of Werneburg (2011). Fish muscle nomenclature mainly corresponds to that of Winterbottom (1974). The homologisation of particular muscular portions follows Werneburg and Hertwig (2009). The nomenclature of the nervous system refers to Holje *et al.* (1986). For osteological and, if available, for myological comparisons, I relied on Osse (1969) for Perciformes; on Thomson (1954) for Mugilomorpha; on Kulkarni (1948), Rosen (1964), Karrer (1967) and Hertwig (2005, 2008) for Adrianichthyidae and Cyprinodontiformes; on Clemen *et al.* (1997), Greven (1997), Meisner (2001), Shakhovskoi (2002) and Candewalle *et al.* (2002) for hemiramphids; on Khachaturov (1983) and Shakhovskoi (2004) for Exocoetidae; and on Chapman (1943) for Scomberesocidae.

Results

External section of the m. adductor mandibulae complex (A1).

The ancestrally undivided m. adductor mandibulae is differentiated into different muscle sections in teleost fishes, representing a complex of individual muscles, each having a separated origin, course, and insertion. The external section of m. adductor mandibulae complex, A1, is the lateral-most jaw muscle. If present, it originates posteriorly on the suspensorium and/or on the preopercle, it runs rostrad, and has a tendinous insertion to the upper or lower jaw (i.e. Allis, 1897). An A1 is present in *Perca fluviatilis* (Fig. 3A, S1), *Rhinomugil corsula* (Fig. 2B, S2), *Atherina boyeri* (Fig. 2C, S3), *Aplocheilus lineatus* (Fig. 2D, S4), *Oryzias latipes* (Fig. 2E, S5), and *Xenopoecilus oophorus* (Fig. 3) but is absent in all other species studied herein, namely *Dermogenys pussila*, *Parexocoetus brachypterus*, *Belone belone*, and *Scomberesox saurus*.

In *O. latipes*, Hertwig (2008) and Werneburg and Hertwig (2009) described a lateral muscle of the adductor complex with an insertion to the lower jaw. It could be interpreted in two different ways: First, it could represent A1, the possession of which is plesiomorphic. A1 is present in all non-beloniform fishes studied and in *O. latipes*, it autapomorphically would have shifted its insertion to the lower jaw. Second, A1 could be reduced in *O. latipes* (Hertwig, 2005). In that case, one additional step of transformation would be needed, as the internal section of m. adductor mandibulae (A2/3) would be modified secondarily. Hertwig (2005) followed the principle of parsimony and opted for the first explanation. Werneburg (2007) interpreted an insertion of A1 to the maxilla and homologised the muscle to the A1 of the outgroup representatives. After reanalysing, this finding was revised and A1 actually inserts on the posterior edge of the dentary at two-thirds of its height below the coronoid process of this bone and has contact via connective tissue to the lig. maxillo-mandibulare in this species (Werneburg and Hertwig, 2009). Previously, the latter connection was misinterpreted as an upper jaw insertion (Werneburg, 2007).

Wu and Shen (2004) mentioned a small ventrolateral portion of A1, their A1-VL, in two flying fish species. As Hertwig (2005: 39) already pointed out, the homologisations of those authors remain unclear. Moreover, the illustration of that portion is lacking. It appears that Wu and Shen (2004) may have confused this portion with the lateral subdivision of A2/3. Hertwig (2008: 149) wrote: ‘In an extensive comparative study of the m. adductor mandibulae in teleostean fishes, [the authors], however, did not mention a subdivision of A2/3 either in the Mugilomorpha or in the Atherinomorpha, but this is probably down to their limited taxon sample, which comprised only three species of the latter.' If Wu and Shen (2004) actually identified the remainder of A1 as their A1-VL (supported by the fact that an insertion of A1-VL to the maxilla is present), a high interspecific variability may be hypothesised for the flying fishes.

Starks (1916) dissected a belonid species, *Tylosurus acus*, in which he described an A1-muscle. Following the present homologisation, however, that muscle clearly represents the lateral head of the muscle A2/3, which has a similar anatomy as found in *B. belone* (see also below) and *S. saurus* (Fig. 2H, S8-9).

Orientation. The spatial orientation of A1 to the more medial, internal section of m. adductor mandibulae (A2/3) is different among species. In *R. corsula* (Fig. 2B, S2), the A1 is situated ventrolaterally to the lateral head of A2/3 and three-fourths of this head are still visible in lateral view. In *Pe. fluviatilis*, the muscle is situated dorsolateral to the internal section and the complete lateral head (A2/3, lateral) is not covered in lateral view (Fig. 3A, S1). A1 is situated completely lateral to the intermedial head of the internal section of m. adductor mandibulae (A2/3, intermedial) in *Ap. lineatus* (Fig. 2D, S4), *O. latipes* (Fig. 2E, S5; see also Werneburg and Hertwig, 2009), and *X. oophorus* (Fig. 3) and the lateral head (A2/3, lateral) is only covered in its anterior region. Laterally in *At. boyeri* (Fig. 2C, S3), the A1 completely covers the internal section of m. adductor mandibulae (A2/3).

For the ground pattern of Atherinomorpha, Hertwig (2005) proposed that the external (A1) and internal (A2/3) sections are situated next to each other in a horizontal plane. As an outgroup of Atherinomorpha, the author used *Pe. fluviatilis*, in which the A2/3-portions are situated above each other in a horizontal plane (Fig. 3A, S1). In the present study, *R. corsula* was dissected as an additional, potential outgroup species, which is closely related to Atherinomorpha. Similar to Atherinomorpha (*sensu* Hertwig, 2008), the A1 of that species also has to be interpreted to be lateral to the A2/3 in a horizontal plane. As such, that character has to be withdrawn as an autapomorphy of Atherinomorpha. More detailed observation among Percomorpha could identify the orientation of A1 to A2/3 in *Pe. fluviatilis* (Fig. 2A, S1) as autapomorphy of Percomorpha or only of that species. In the latter case, the 'A1 in horizontal plane to A2/3' would need to be interpreted as plesiomorphic among Acanthopterygii. Observations among Mugilomorpha could identify the orientation of A1 to A2/3 as a homoplastic character of *R. corsula* and Atherinomorpha. If all members of Mugilomorpha had an A1 lateral to A2/3, and when following the phylogenetic hypothesis of Stiassny (1990), that spatial orientation would need to be interpreted as a synapomorphy of Mugilomorpha + Atherinomorpha.

Insertion. The tendon of A1 inserts on the lateral face of the anterior part of the maxilla in *Pe. fluviatilis* (Fig. 3A, S1), to the medial face of the middle region of the maxilla in *R. corsula* (Fig. 2B, S2) and *X. oophorus* (Fig. 3), and to the posterior edge of the dentary in *O. latipes* (Fig. 2E, S5). With three tendons, A1 inserts on the processus primordialis (anguloarticularis), to the medial side of the lacrimal, and medially to the anterodorsal tip of the maxilla in *At. boyeri* (Fig. 2C, S3). The A1 inserts with two tendons to the lateral face of the medial part of the maxilla and to the medial face of the lacrimal in *Ap. lineatus* (Fig. 2D, S4).

The insertion of A1 to the jaws is different in all species studied. A definition of homology (e.g. A1 inserts laterally to the maxilla) was not made, because the differences of A1 were too large. Hertwig (2008) observed several atherinomorph species and defined the insertion of A1 at the lateral face of the maxilla to be present in *Pe. fluviatilis* and “Aplocheilidae”. In contrast to *Pe. fluviatilis* (Fig. 2A, S1), however, the A1 inserts on the other end of the maxilla in *Ap. lineatus* (Fig. 2D, S4). The latter species has an additional tendon to the medial face of the lacrimal, a character which was found by Hertwig (2008) to be present in the ground pattern of Atherinomorpha (compare to Alexander, 1967; Parenti, 1993; Stiassny, 1990). For Cyprinodontiformes (incl. *Aplocheilus*), Hertwig (2005) was not able to define an unambiguous constellation of the insertion of A1. However, he argued that the insertion of A1 shifted based on the rotation of the maxilla in this taxon. As such, the insertion of A1 to the lateral face of the maxilla could be interpreted as being plesiomorph among Atherinomorpha.

Internal section of the m. adductor mandibulae complex (A2/3)

The A2/3 usually originates with two or three muscle heads on the suspensoric and on the preopercle and inserts as a consistent muscle to the lower jaw. Muscle heads are defined as partial differentiations of a muscle. They have separated origins or insertions (Werneburg 2007, 2011). Muscle heads gain a descriptive nomenclature herein; the position of the origin (or insertion) and the spatial orientation of them were considered. This nomenclature differs from Winterbottom (1974), because that one is not applicable for muscle heads herein.

A2/3 can have an intramandibular portion. A muscle portion is defined as having a separate origin, course, and insertion, but as having some intertwining fibres or a shared tendon with another muscle portion of the same ontogenetic and/or phylogenetic origin (Werneburg 2007, 2011).

Origin. In *Pe. fluviatilis* (Fig. 3A, S1), *Pa. brachypterus* (Fig. 2F, S6), and *D. pussila* (Fig. 2G, S7), the A2/3 has two muscle heads (A2/3, lateral; A2/3, medial) in its origin. A2/3 originates with three muscle heads (A2/3, lateral; A2/3, medial; A2/3, intermedial) in *R. corsula* (Fig. 2B, S2), *Ap. lineatus* (Fig. 2D, S4), *O. latipes* (Fig. 2E, S5), *X. oophorus* (Fig. 3), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9).

The cyprinodontiform species *Ap. lineatus* (Fig. S4) was found to have three muscle heads in its origin. This corresponds to the findings of Hertwig (2008). To confirm his findings, Hertwig (2008) used histological sections, which permit a much higher accuracy when distinguishing between minute muscle heads. I have seen many of the sections, and used some herein, and can confirm his observations.

Jourdain (1878) described a specimen of *B. belone* ("*vulgaris*"), in which A2/3 was not separated. I dissected several specimens of that species and always found a separation, although I have to note that the differentiation of the lateral and the medial head were difficile. Also, apparently, Jourdain (1878) did not remove the lateral head of A2/3 as he expected A2/3 to represent an undifferentiated muscle mass and hence did not discover the intermedial head of A2/3.

The lateral head of A2/3 originates almost overall at the vertical aspect of preopercle, at the posterior part of the horizontal aspect of the preopercle, as well as on the processus lateralis hyomandibularis in *R. corsula* (Fig. 2B, S2), *Ap. lineatus* (Fig. 2D, S4), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9). It originates at the vertical aspect of the preopercle (but does not reach its dorsal most tip) and at more than half of the horizontal aspect of the preopercle in *D. pussila* (Fig. 2G, S7). In *Pe. fluviatilis* (Fig. 3A, S1) and *Pa. brachypterus* (Fig. 2F, S6), the lateral head originates ventrally at the processus lateralis hyomandibularis, at the ventral third of the vertical aspect of the preopercle, as well as on the processus caudalis quadrati. With a narrow attachment, it only originates on the ventral third of the vertical aspect of the preopercle in *O. latipes* (Fig. 2E, S5) and *X. oophorus* (Fig. 3).

In *Pe. fluviatilis*, the medial head of A2/3 originates from the hyomandibular, the metapterygoid, and the symplectic, as well as from processus lateralis hyomandibularis (Fig. S1). It originates from the hyomandibular and from the metapterygoid in *R. corsula* (Fig. S2) or only from the metapterygoid in *Ap. lineatus* (Fig. S4) and *Pa. brachypterus* (Fig. 2F, S6). It arises from the lateral faces of the quadrate, the symplectic, and the cartilaginous interspaces of the hyopalatine arch, and from the tendon of the m. adductor arcus palatini quadrati in *O. latipes* (Fig. S5) and *X. oophorus* (Fig. 3). The medial head of A2/3 originates ventrally at the sphenotic, laterally at the hyomandibular, and dorsally at the metapterygoid in *D. pussila* (Fig. S7), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9).

Similar to the present study, Hertwig (2005, 2008) found the origin of the medial head of A2/3 to be highly variable. In addition to an adult specimen of *S. saurus*, a juvenile was studied (Fig. 9E-H). In this specimen, a different orientation of the A2/3-heads was found (Werneburg, 2007). One could hypothese that the medial head of A2/3 in the juvenile shifts its origin to a dorsal position and the intermedial head of A2/3 could shift its origin to a more ventral position (two transformation steps). Alternatively, the origin of the medial A2/3-head of the juvenile could shift ventrolaterally to the intermedial head of A2/3 and would be homologous to the intermedial head of A2/3 in the adult. Hence, the intermedial head of A2/3 in the juvenile (then the medial head of the adult) would keep its origin at the sphenotic (one transformation step). Those scenarios are very speculative because they are derived from only one observation. No final answer can be presented, because the variability of that character within *S. saurus* cannot be estimated. The species *D. pussila*, *B. belone*, and *S. saurus* show a very drastic ontogenetic elongation of the lower jaw (Hemiramphidae) or of both jaws (Belonidae, Scomberesocidae) (Boughton *et al.*, 1991; Lovejoy, 2000; Lovejoy *et al.*, 2004). It would be valuable to study if, correlated to the elongation of jaws, changes in the anatomy of the jaw musculature occur (origin, volume, course, insertion). Comparative ontogenetic and electromyographic studies (Focant *et al.*, 1981; Osse, 1969) could help to interpret the specific case mentioned herein. Ontogenetic changes in the anatomy of the jaw musculature were already observed by Hertwig (2005) in representatives of Goodeidae (Cyprinodontiformes: *Crenichthys*). *Nanichthys* (Scomberesocidae) is often not accepted as a 'genus' in a taxonomic sense and is often referred to as a dwarf morphotype of *Scomberesox* (Collette, 2004a; Collette *et al.*, 1984). However, if the juvenile specimen of *S. saurus* studied herein would actually represent a member of a valid genus *Nanichthys*, the arrangement of the A2/3-musculature may serve as a criterion to distinguish both species taxonomically.

The intermedial head of A2/3 is situated between the lateral and the medial head. It originates only on the horizontal aspect of the preopercular in *R. corsula* (Fig. S2). It takes its origin from the horizontal aspect of the preopercle and at the processus caudalis quadrati in *Ap. lineatus* (Fig. S4), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9) and originates only on the processus caudalis quadrati in *O. latipes* (Fig. S5) and *X. oophorus* (Fig. 3). An intermedial head is not present in *Pe. fluviatilis*, *At. boyeri*, *Pa. brachypterus*, and *D. pussila*.

In *At. boyeri* (Fig. S3), A2/3 is separated into two portions (by definition; see above and Werneburg 2011). The muscle portions of A2/3 have separated origins lateral at the posterior part of the suspensoric as well as separated insertions medial to the lower jaw. The medial portion of A2/3 is differentiated into two heads at its origin. The lateral portion of its A2/3 is not separated into heads. Among the species studied herein, and indeed, considering data from Hertwig (2008) regarding several other atherinid species, this condition has to be declared autapomorphic for *At. boyeri* (Atheriniformes).

Orientation. The spatial orientations of the medial and the lateral head of A2/3 are different among species. In *Pe. fluviatilis* (Fig. 2A, S1), *Ap. lineatus* (Fig. S4), *D. pussila* (Fig. 2G, S7), *X. oophorus* (Fig. 3), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9), the medial head of A2/3 is situated dorsally to the lateral head or is at least clearly visible in lateral view. The medial head of A2/3 is situated ventrally to the lateral head in *At. boyeri* (Fig. S3). The lateral head is situated laterally to the medial head and can cover it completely in *R. corsula* (Fig. S2), *O. latipes* (Fig. S5), and *Pa. brachypterus* (Fig. 2F, S6).

The medial and the lateral heads of A2/3 have about the same size in *Pe. fluviatilis* (Fig. S1) and *D. pussila* (Fig. S7). The medial head is relatively narrow when compared to the lateral head in *Pa. brachypterus* (Fig. S6). The lateral head is quite widespread when compared to the medial head. In *R. corsula* (Fig. S2) and *Ap. lineatus* (Fig. S4), the medial head is larger than the lateral head in *O. latipes* (Fig. 2E, S5), *X. oophorus* (Fig. 3), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9).

Insertion. Except for *B. belone* (Fig. 2H, S8) and *S. saurus* (Fig. S9), A2/3 only inserts on the medial side of the lower jaw. In the former species, it also inserts on the coronomeckelian bone, which is only found in these two species. It represents a bone, which is posterodorsally fused with the border of processus primordialis anguloarticularis. Both bones are separated from each other by a clear suture (Werneburg, 2007).

Intramandibular portion. An intramandibular portion of A2/3 is lacking in all Beloniformes. It is present in *R. corsula* (Fig. S2) and has a narrow insertion on the medial face of processus coronoideus dentalis. In *Ap. lineatus* (Fig. S4), it has broad insertions to the processus coronoideus dentalis, to cartilago Meckeli, and to the anguloarticular. It inserts medially to the dentary in *At. boyeri* (Fig. S3) and has a narrow insertion medially to the anguloarticular in *Pe. fluviatilis* (Fig. S1).

The configuration of the intramandibular portion of A2/3 is different among non-beloniforms species. As the criterion of homology, the intramandibular portion is defined to originate from an A2/3-associated aponeurosis or tendon herein. Hertwig (2008), who observed few species of Beloniformes (*O. latipes* and some hemiramphids), argued for an autapomorphic reduction of an intramandibular portion of A2/3 within Beloniformes, which I can confirm herein.

Intramandibular muscles possibly act in positioning the jaw (Karrer, 1967: “Stellbewegung”). Hertwig (2005, 2008) mentioned the reduction of intramandibular muscles and found a correlation between the loss of those muscles and a reduced mobility of particular bone elements. For *Empetrichthys latos* (Cyprinodontiformes), he noticed an ontogenetic reduction of intramandibular muscles. The movement of upper jaw bones in Beloniformes may be coupled to the movement of the lower jaw (see above) and hence they may underlie large mechanical stresses in fish hunting species. To withstand those forces, the bones of the lower jaw may have a higher degree of fusion resulting in the tendency to reduce intramandibular musculature.

Like Hertwig (2008), I defined an intramandibular portion of A2/3 as present in *Pe. fluviatilis*. However, the configuration of the intramandibular musculature of *Pe. fluviatilis* could be interpreted differently. In the present study, two intramandibular muscles were differentiated. First, an intramandibular portion of A2/3 is described as originating from the tendon of A2/3 by only a few muscle fibres. It narrowly inserts on the medial face of the anguloarticulare. Second, an intramandibular m. adductor mandibulae (Aω) is described, which is tendinously originating from the preopercular and the quadrate. That muscle has a flat insertion medially to the dentary, to cartilago Meckeli, and to the anguloarticular.

In contrast, Osse (1969) only described one intramandibular muscle for *Pe. fluviatilis*. That muscle, “*Aω*” in Osse (1969), has one origin at the tendon of A2/3. This “*Aω*” also has a narrow attachment to the anguloarticular, one tendinous attachment to the prearticular/quadrate and one flat insertion to the medial face of the lower jaw. Osse (1969) combined the *Aω* and the intramandibular portion of A2/3 of the present study as his “*Aω*”. Therefore, he did not differentiate the course of muscle fibres and other associated structures. The fibres of the intramandibular portion of A2/3 of the present study run anteroventrad. The fibres of the Aω were found to originate as a double fibred muscle from the tendon originating from the prearticular/quadrate. However, some fibres also originate from the tendon of A2/3, which is only partly fused with the tendon of Aω. While both tendons fuse, the course of the Aω-tendon is still separable (Figure S1D). The fusion of the tendons and the origin of some Aω-fibres at the A2/3-tendon may have persuaded Osse (1969) to define only one intramandibular muscle.

One additional interpretation of intramandibular muscle configuration is possible. If a tendinous insertion of A2/3 to the tendon of Aω is hypothesised, the origin of some Aω-fibres may have been shifted to the tendon of A2/3. In that case, no intramandibular portion of A2/3 would exist in *Pe. fluviatilis*. If this configuration is a plesiomorphic condition of Acanthopterygii, the character should also be interpreted as a reversal within Beloniformes. In contrast, if one hypothesises the intramandibular portion of A2/3 to be independently reduced in *Pe. fluviatilis*, the character should be considered as homoplastic in *Pe. fluviatilis* (Percomorpha) and Beloniformes. To clarify that controversy, additional species of Percomorpha and Acanthopterygii need to be observed in great detail, but this was out of the scope of the present study.

Intramandibular section of the m. adductor mandibulae complex (Aω)

The intramandibular section of the m. adductor mandibulae complex (Aω) connects the suspensoric with the medial face of the lower jaw.

Origin. It originates with a tendon anteriorly at the medial face of the symplectic in *Pa. brachypterus* (Fig. S6) and *D. pussila* (Fig. S7). It originates directly at the ventral and the anterior edge of the quadrate in *O. latipes* (Fig. S5). In *R. corsula* (Fig. S2), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9), Aω originates broadly on the medial face of the quadrate and a part of the muscle can have a tendinous origin. It attaches with a tendon anteroventrally to the medial face of the quadrate in *At. boyeri* (Fig. S3) and *Ap. lineatus* (Fig. S4); and in *Pe. fluviatilis* (Fig. S1), it originates with a tendon anteriorly at the medial face of the horizontal aspect of the preopercular and to a small amount medially at the middle area of processus caudalis quadrati. The Aω is absent in *X. oophorus*.

Hertwig (2005) defined as a common character of hemiramphids: The origin of the flat tendon of Aω is situated at a part of the symplectic, which points rostrad. He studied species of *Hyporhamphus*, *Nomorhamphus*, and *Hemiramphodon*. Due to the diverging observation in *D. pussila* herein (Fig. S7), this character on the origin of Aω cannot be confirmed to be diagnostic for all hemiramphids. However, as that character was also found in *Pa. brachypterus* (Fig. S6), a potential synapomorphic character of (Exocoetidae + Hemiramphidae) is identified and a possible monophyly of Hemiramphidae could be indicated (Collette *et al.,* 1984; Rosen, 1964; Rosen and Parenti, 1981). This would contradict the works of Aschliman *et al.* (2005) and Lovejoy *et al.* (2004), who found "Hemiramphidae" paraphyletic. In the work of Lovejoy *et al.* (2004), the Zenarchopteridae (among others *Dermogenys*, *Hemiramphodon*, *Nomorhamphus*) oppose the paraphyletic "Belonidae“ (incl. Scomberesocidae) and *Hyporhamphus* belongs to a group, which opposes (Zenarchopteridae + ”Belonidae). Several species of ”Hemiramphidae“ that are closely related to Exocoetidae in the work of Lovejoy *et al.* (2004), as well as several other species of the remaining groups of Beloniformes need to be observed to gain a better understanding on how that character is distributed. The absence of Aω was documented for some atherinomorph species by Hertwig (2008) and the reduction must have occurred several times independently.

Shape. The Aω represents a double-feathered muscle in *Pe. fluviatilis* (Fig. S1), *At. boyeri* (Fig. S3), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9), in which one of the resulting muscle parts may project to a far caudad direction. The Aω is a parallel fibred muscle in *O. latipes* (Fig. S5) and *Pa. brachypterus* (Fig. S6) and a simple feathered muscle in *Ap. lineatus* (Fig. S4).

Insertion On the medial face of the lower jaw, the Aω (when not differentiated into heads) inserts broadly to the dentary, cartilago Meckeli and/or to the anguloarticular in *Pe. fluviatilis* (Fig. S1), *At. boyeri* (Fig. S3), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7). It inserts broadly to the dentary, to the anguloarticular, and to the cartilago Meckeli, whereby a ventral part in feathered muscles inserts far anteriorly to the medial face of the dentary in *B. belone* (Fig. S8) and *S. saurus* (Fig. S9). It inserts the ventral part of the dentary in *Ap. lineatus* (Fig. S4) and posteriorly to the dentary and medially at the cartilago Meckeli in *O. latipes* (Fig. S5).

In *R. corsula* (Fig. S2), Aω is separated into two heads at the level of the quadrate. The lateral head inserts broadly to the medial face of the dentary and cartilago Meckeli. The medial head of Aω inserts ventrally to the medial face of the dentary and anteriorly to the medial face of the anguloarticular.

Hertwig (2005, 2008) has shown that the configuration of Aω is highly variable among Cyprinodontiformes. In comparison, this can also be concluded for the species observed herein.

M. intermandibularis

M. intermandibularis connects the contralateral dentaries at their medial faces. The cross-section of m. intermandibularis is +/- round in *At. boyeri* (Fig. S3). It is big-bellied oval in *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *O. latipes* (Fig. S5), and *X. oophorus* (Fig. 3); i.e. it is at its maximum twice as broad as high. It is elongated oval in *Ap. lineatus* (Fig. S4), *Pa. brachypterus* (Fig. S6), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9); i.e. it is (mostly much) more than twice as broad as high.

In each species studied, several specimens were observed and a tendency of a rounder cross-section of the muscle was found in *At. boyeri* (Fig. S3). In addition, the assignment to big-bellied or elongated oval has to be understood as a tendency in the variability of the specimens observed.

The m. intermandibularis is parallel fibred and has no tendinous origin at the dentary in

Pe. fluviatilis (Fig. S1), *At. boyeri* (Fig. S3), *Pa. brachypterus* (Fig. S6), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9). However, it is spindle-shaped and has a tendinous origin at the dentary in *R. corsula* (Fig. S2), *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. S5), and *X. oophorus* (Fig. 3).

M. protractor hyoidei

Origin. The m. protractor hyoidei connects the branchial apparatus with the lower jaw. It originates laterally at the ceratohyal in *Pe. fluviatilis* (Fig. S1), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7), with two heads ventrally and laterally at the ceratohyal and at the anterior tips of the branchiostegal rays in *O. latipes* (Fig. S5), ventrally to the ceratohyal in *R. corsula* (Fig. S2), *At. boyeri* (Fig. S3), *Ap. lineatus* (Fig. S4), and *X. oophorus* (Fig. 3) and medially to the ceratohyal in *B. belone* (Fig. S8) and *S. saurus* (Fig. S9).

Course. A fusion with the contralateral m. protractor hyoidei occurs at the level of the jaws or suspensoric and united, they travel rostrad in *R. corsula* (Fig. S2), *Ap. lineatus*, *O. latipes* (Fig. S5), *X. oophorus* (Fig. 3) (in relation to the jaw joint, the protractor fuses more anteriorly in *X. oophorus* when compared to *O. latipes*), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7) and anteroventrally at the fused mm. protractor hyoidei a tendon can be formed on each side. Such a fusion does not occur in *Pe. fluviatilis* (Fig. S1), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9). In *At. boyeri* (Fig. S3), at the level of the anguloarticular, the muscles fuse only in their ventral regions; they separate on the level of the dentary in order to insert independently of the contralateral muscle to the dentary.

When reaching m. intermandibularis, m. protractor hyoidei has a flat shape in *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. S5), and *X. oophorus* (Fig. 3), or it is about as broad as high in *Pe. fluviatilis* (Fig. S1), *At. boyeri* (Fig. S3), *Pa. brachypterus* (Fig. S6), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9). At this level, m. protractor hyoidei already differentiated into two heads. The dorsal head is flat and the ventral head is as high as broad in *R. corsula* (Fig. S2).

When reaching the dentary, the flat shape of the muscle in *Ap. lineatus* (Fig. S4) and *O. latipes* could be hypothesized as being an autapomorphic character of Cyprinodontoidei *sensu* Rosen (1964) (Fig. 1A).

Insertion. M. protractor hyoidei inserts dorsally to the insertion of m. intermandibularis at the dentary and covers at least the posterodorsal area of the latter muscle in *Ap. lineatus* (Fig. S4), *Pa. brachypterus* (Fig. S6), and *S. saurus* (Fig. S9). In *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *O. latipes* (Fig. S5), *D. pussila* (Fig. S7), and *B. belone* (Fig. S8), it inserts ventrally to m. intermandibularis at the dentary. It inserts dorsally as well as ventrally of m. intermandibularis to the dentary in *X. oophorus* (Fig. 3).

The ventral part of m. protractor hyoidei extends into a long tendon, which reaches the anterior tip of the lower jaw in *D. pussila* (Fig. S7) and *B. belone* (Fig. S8). It does not extend into a long tendon to reach the anterior tip of the lower jaw in *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *At. boyeri* (Fig. S3), *O. latipes* (Fig. S5), and *X. oophorus* (Fig. 3).

The anteroventral elongation of musculature in the region of the dentary seems to be associated with the elongated lower jaw within Beloniformes. In *D. pussila* (Fig. S7) and *B. belone* (Fig. S8), also a ventral insertion of m. adductor mandibulae (Aω) to the anterior tip of the lower jaw can be recognised. Besides the latter muscle, m. intermandibularis is also extended far rostrad in *S. saurus* (Fig. S9), however, in this species m. protractor hyoidei does not reach the anterior tip of the lower jaw. Referring to Haszprunar (1998), one could argue that the elongation of a muscle within the lower jaw is simply an adaptation correlated to food ingestion and hence, it would not have a value for phylogenetic questions. However, as noted by De Pinna (1991) and Haas (2003), such adaptations can be informative on particular hierarchical levels.

M. adductor arcus palatini

The anterior portion of m. adductor arcus palatini, the only portion of this muscle studied herein, originates along the whole parasphenoid and inserts dorsally along the entire suspensoric in *R. corsula* (Fig. S2), *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. 2E, S5), *X. oophorus* (Fig. 3), and *D. pussila* (Fig. 2G, S7) (in addition to other small attachments). In contrast, it originates on the posterior part of the parasphenoid and inserts on the posterior region of the suspensoric in *Pe. fluviatilis* (Fig. 2A, S1), *At. boyeri* (Fig. 2C, S3), *Pa. brachypterus* (Fig. 2F, S6), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9).

M. levator arcus palatini

M. levator arcus palatine originates on the skull roof behind the eye, runs ventrally, and inserts dorsally to the posterior part of the suspensoric.

Origin. It originates broadly on the sphenotic in *Pa. brachypterus* (Fig. 2F, S6) and *D. pussila* (Fig. 2G, S7). In *R. corsula* (Fig. 2B, S2), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9), it originates on a ridge of the sphenotic, the processus sphenoticus, and some fibres originate directly on the sphenotic. The muscle arises via a short tendon from the ventral edge of the transverse process of the sphenotic and runs ventrad along the posterior margin of the orbit, dorsally from the hyomandibular, and with few fibres from the sphenotic in *O. latipes* (Fig. 2E, S5) and *X. oophorus* (Fig. 3). It originates ventrally at the dermosphenotic in *At. boyeri* (Fig. 2C, S3) and from the autosphenotic and with some fibres at the sphenotic in *Pe. fluviatilis* (Fig. 2A, S1) and *Ap. lineatus* (Fig. 2D, S4).

The m. levator arcus palatini plesiomorphically originates at the autosphenotic and with some fibres at the sphenotic. This condition is also visible in *Ap. lineatus* (Fig. S4) and could be assumed as being plesiomorphic for all Cyprinodontiformes (compare to Hertwig, 2005; Karrer, 1967).

Course. During its course from origin to insertion, the thickness of m. adductor arcus palatini hardly changes in *R. corsula* (Fig. 2B, S2), *O. latipes* (Fig. 2E, S5), and *X. oophorus* (Fig. 3). It broadens more than twice in all other species.

M. levator arcus palatini runs dorsally of the medial and lateral head of A2/3 and does not run between both heads heads in *Pe. fluviatilis* (Fig. 2A, S1), *R. corsula* (Fig. 2B, S2), *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. 2E, S5), *X. oophorus* (Fig. 3), and *Pa. brachypterus* (Fig. 2F, S6). It is clearly situated between the lateral and the medial head of A2/3 in *D. pussila* (Fig. S7) or it is only partly surrounded by the lateral and by the medial head of A2/3 in *B. belone* (Fig. 2H, S8) and *S. saurus* (Fig. S9).

Insertion. On the lateral face of the suspensoric of *Pe. fluviatilis* (Fig. S1), *Ap. lineatus* (Fig. S4), *Pa. brachypterus* (Fig. S6), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9), m. levator arcus palatini inserts on the hyomandibular and to the metapterygoid. With some fibres, it also can attach anteriorly to the processus lateralis hyomandibularis. In *O. latipes* (Fig. S5) and *X. oophorus* (Fig. 3), it inserts on the broad face of praeopercular and posterodorsally to the symplectic. In *R. corsula* (Fig. S2) and *At. boyeri* (Fig. S3), it inserts on the hyomandibular, anteriorly to the processus lateralis hyomandibularis, to the metapterygoid, and to the broad face of the preopercular.

Kulkarni (1948) identified the metapterygoid as being reduced within Adrianichthyidae. This suggestion was only based on his observations in *Horaichthys setnai* and *O. melastigma*. Werneburg and Hertwig (2009) identified a horizontal suture in the 'symplectic' (*sensu* Kulkarni, 1948) of *O. latipes*, which could represent the border of the metapterygoid. In histological sections and hence in 3d-reconstructions (Werneburg and Hertwig, 2009), such a differentiation of bones was not visible. As such, the situation remains unclear.

M. dilatator operculi

M. dilatator operculi connects the opercle with the skull roof. It originates ventrally at the lateral face of the sphenotic in *Pa. brachypterus* (Fig. 2F, S6), *X. oophorus* (Fig. 3), and *S. saurus* (Fig. S9). It originates laterally at the sphenotic, at the autosphenotic, and with some fibres possibly at the anteroventral area of the pterotic in *Pe. fluviatilis* (Fig. 2A, S1), *At. boyeri* (Fig. 2C, S3), and *Ap. lineatus* (Fig. 2D, S4). In *R. corsula* (Fig. 2A, S2), *O. latipes* (Fig. 2E, S5), *D. pussila* (Fig. 2G, S7), and *B. belone* (Fig. 2H, S8), it originates laterally at the sphenotic and anteriorly at the lateral face of the pterotic.

Anteriorly, m. dilatator operculi extends almost to the eye and lies dorsally to m. levator arcus palatini in *R. corsula* (Fig. 2A, S2), *At. boyeri* (Fig. 2C, S3), *Ap. lineatus* (Fig. 2D, S4), and *O. latipes* (Fig. 2E, S5). It does not reach the eye region in *Pe. fluviatilis* (Fig. 2A, S1), *X. oophorus* (Fig. 3), *Pa. brachypterus* (Fig. 2F, S6), *D. pussila* (Fig. 2G, S7), *B. belone* (Fig. 2H, S8), and *S. saurus* (Fig. S9).

M. levator operculi

Origin. The m. levator operculi also connects the opercle with the skull roof. It is an undivided muscle with an origin ventrally at the lateral face of the pterotic in all taxa studied, except for *Pe. fluviatilis*. In this species is a bipartite muscle with a large anterior origin ventrally at the lateral face of the pterotic and a small posterior origin ventrally at the ventral situated extrascapula (Fig. 2A, S1).

Insertion. M. levator operculi inserts dorsally to the medial face of the opercle and has a continuous horizontal level of insertion in *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. S5), *X. oophorus* (Fig. 3), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7). It also inserts dorsally at the medial face of the opercle in *B. belone* (Fig. S8) and *S. saurus* (Fig. S9), but it attaches more ventrally to the anterior region of the medial face of the opercle. The muscle inserts dorsally to the medial face and dorsally to the lateral face of the opercle in *At. boyeri* (Fig. S3).

Nerves

The truncus maxillaris infraorbitalis trigemini branches into the ramus mandibularis trigemini and ramus maxillaris trigemini short before or after leaving the neurocranium in *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *At. boyeri* (Fig. S3), and *Ap. lineatus* (Fig. S4) – and dorsally to the suspensoric, the ramus mandibularis trigemini covers the ramus maxillaris trigemini laterally. Contrary, in *O. latipes* (Fig. S5), *X. oophorus* (Fig. 3), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7), it first branches at the level of the eye. In *B. belone* (Fig. S8) and *S. saurus* (Fig. S9), it branches already within the neurocranium. Afterwards, the ramus maxillaris trigemini splits into two branches. Dorsally to the posterior part of the suspensoric, the branches align laterally and medially along the course of ramus mandibularis trigemini. On the level of the jaw joint, the branches of ramus maxillaris trigemini change their course into an anterodorsad direction and enter the upper jaw. Ramus mandibularis trigemini travels anteroventrad to the lower jaw.

The ramus mandibularis facialis branches after leaving the hyomandibular laterally to the suspensoric in order to run with two branches to the medial side of the suspensoric in *At. boyeri* (Fig. S3), *Ap. lineatus* (Fig. S4), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9). In *Pe. fluviatilis* (Fig. S1), *R. corsula* (Fig. S2), *O. latipes* (Fig. S5), *Pa. brachypterus* (Fig. S6), and *D. pussila* (Fig. S7) it branches differently. The course of that nerve could not be followed in *X. oophorus* (Fig. 3).

Ligaments

The lig. premaxillo-maxilla spans broadly between premaxilla and maxilla in *B. belone* (Fig. S8) and *S. saurus* (Fig. S9) and between the proximal ends of the premaxilla and the maxilla in all other species.

Hertwig (2008) argued for the absence of the ligament in Beloniformes and mentioned an extensive area of connective tissue instead. Based on arguments of Werneburg (2013b), I homologise this tissue with the broad ligament found in other taxa.

The primordial ligament is present as a lig. maxillo-anguloarticulare between the maxilla and the anguloarticular in *Pe. fluviatilis* (Fig. 2A, S1) and *At. boyeri* (Fig. 2C, S3). The ligament is absent in all other species.

A ligament, which connects the palatine and the upper jaw, is present as lig. palato-maxilla between palatine and maxilla in *At. boyeri* (Fig. S3), *Ap. lineatus* (Fig. S4), *O. latipes* (Fig. S5), *X. oophorus* (Fig. 3), and *Pa. brachypterus* (Fig. S6). It is present as lig. palato-premaxilla between palatine and premaxilla in *Pe. fluviatilis* (Fig. S1) or absent in *R. corsula* (Fig. S2), *D. pussila* (Fig. S7), *B. belone* (Fig. S8), and *S. saurus* (Fig. S9).

An autapomorphy in the ground pattern of Atherinomorpha may be the presence of a lig. palato-maxilla. The absence of the ligament in *R. corsula* (Fig. S2) and a different attachment of the ligament in *Pe. fluviatilis* makes it impossible to reconstruct the ground pattern.

A lig. parasphenoido-suspensorium is present in *Pe. fluviatilis* (Fig. S1), *At. boyeri* (Fig. S3), and *S. saurus* (Fig. S9). It is absent in all other species.

For *Pe. fluviatilis*, Osse (1969) described two ligaments (his No. XVII and XVIII) that originate from the parasphenoid and insert to the dorsal edge of the suspensoric. This differentiation of the ligament could not be identified in the manual dissections of the present study.

Discussion

In the present study, the variety of jaw, suspensoric, and opercle muscles was described for several acanthopterygian fishes with a focus on Beloniformes. The diversity of jaw muscles within Beloniformes corresponds to the external differences in their jaw morphology. As such, long beaked forms and species with protractible mouths show remarkable differences in their jaw musculature that may be correlated to stiffening or high mobility of jaws.

Most important anatomical differences detected in this study exist in the external jaw musculature of Beloniformes. The jaw adductors belong to the most intensely studied muscles in vertebrates due to their prominent size and variation in the head and their importance for feeding mechanisms (Werneburg, 2013). Among Acanthopterygii, the external section of m. adductor mandibulae (A1) experienced comprehensive diversifications (Wu and Shen, 2004), and among Beloniformes, it can either be present or absent.

The A1 lowers the upper jaw in most fishes. As an autapomorphy of Beloniformes, Mickoleit (2004) mentioned the reduced mobility of bones related to the upper jaw. Hertwig (2005) hypothesised that the reduced mobility of those bones might be correlated with the reduction of A1 within Beloniformes or the displacement of the A1-insertion apart from the upper jaw. In the present study, such a replacement of A1 was discovered in *O. latipes* (Fig. 2E; see also Werneburg and Hertwig, 2009). This species can still move its upper jaw during feeding (pers. obs.), which questions the possibility of a functional correlation of the character pair mentioned by Hertwig (2005, 2008), namely 'A1 no longer attached to upper jaw' and 'non-moveable upper jaw bones'.

Moreover, in the flying fish *Pa. brachypterus*, which has no A1 (Fig. 2F), a protrusible jaw was discovered herein. Therefore, the upper jaw bones are moveable against each other (Figure S6B).

The hemiramphid *Dermogenys pusilla*, which hunts at the surface of the water (Meisner, 2001), is able to easily move its short upper jaw, although the species has no A1 (Fig. 2G). Hence, coupled by ligament attachments, the lifting of the upper jaw appears to be indirectly performed by lowering the lower jaw. A deep coupling of those structures can be hypothesised for most other A1-lacking Beloniformes. In addition, the mobility of the protrusible upper jaw of *Pa. brachypterus* suggests a strong ligament-bone interaction (Figure S6B).

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Among hemiramphids, whose phylogenetic relationship is debated, A1 can be absent (this study: *Dermogenys pussila*; Hertwig 2008: *Hyporhamphus unifasciatus*) or can be present (Hertwig 2008: *Nomorhamphus* sp., *Hemiramphodon phaiosoma*; Rosen 1964: *Arrhamphus brevis*). Also Exocoetidae seem to have members with an A1 (Wu and Shen 2004: *Cypselurus cyanopterus*, *Parexocoetus mento*; but see comments in the Results section) and members without an A1 (this study: *Pa. brachypterus*). The phylogenetic significance of those conditions can first be adequately estimated when more species are observed and more clarity exists about phylogenetic interrelationship. But this requires further detailed and comprehensive observations.

At least for *B. belone* (Fig. 2H) and *S. saurus* (Fig. S9), one may hypothesise that the loss of the A1 could be related to a strong fixation of the upper jaw to the cranium, realised by lig. premaxillo-frontale. Whether the upper jaw of both species is still moveable *in vivo* is not known so far, but is not expected.

As seen in hemiramphids, an elongated lower jaw not necessarily involves the reduction of A1. *Xenopoecilus oophoris*, an adrianichthyid with duckbill-like jaws, also has an A1 (Figure 3), which is attached to the upper jaw. This indicates that also an elongated upper jaw, which possibly was present in the ground pattern of Beloniformes already (Parenti 1987), not necessarily implies the loss of A1. Only the derived condition of two species, *B. belone* and *S. saurus*, which possess a *stiffened* upper jaw, may be clearly correlated to the loss of A1. As such, it can be expected that another belonid, *Potamorrhamphis eigenmannii* (Miranda Ribeiro, 1915), which has a moveable upper jaw *in vivo* (pers. obs.), could have an A1, but this hypothesis needs further observation. The present study shows that the loss of A1 must not be interpreted only in correlation to elongated jaws. Other biomechanical requirements must be considered.

The studied selection of non-beloniform species must be handled with care when choosing them as potential outgroup species (as example see Hertwig, 2008). Compared to the insufficient documentation of the cranial musculature of most acathopterygian groups, the species dissected herein appear to show several derived characters. E.g., *Rh. corsula* has three main components of A2/3. Most mugiliform taxa, however, are reported to have a different arrangement of that muscle (Gosline, 1993: *Agonostomus*; Van Dobben, 1935: *Mugil*; Wu and Shen, 2004: *Chelon*, *Crenimugil*; Starks, 1916: *Mugil*; Eaton, 1935: *Mugil*). As the authors of these studies did not observe histological sections, these findings could represent artefacts caused by the lower resolution of manual dissection.

As representative of the potential sister group to all remaining Beloniformes, the adrianichthyids *Oryzias latipes* and *Xenopoecilus oophorus* were studied herein. Hertwig

(2005, 2008) and Werneburg and Hertwig (2009) already diagnosed several derived characters for *O. latipes* that could be affirmed herein and together with *X. oophorus*, it shares several derived characters. Due to the distinctive morphology of Adrianichthyidae, problems could arise when reconstructing the jaw muscle configuration in the ground pattern of Beloniformes. In addition to several derived characters, the taxon seems to display several plesiomorphic characters shared with Cyprinodontiformes. This finding persuaded Rosen (1964) and Li (2001) to postulate a sister group relationship of Adrianichthyidae + Cyprinodontiformes, named as Cyprinodontoidei (Figure 1A). The present study highlights which characters are most variable among near related species and may assist taxon and character selection in future phylogenetic studies.

Conclusions

The differing external jaw morphology of diverse beloniform fishes is nicely reflected in the anatomy of their jaw musculature. Apparent changes concern the absence or presence of the A1 and arrangements of the intramandibular musculature. Both muscles are coupled to the upper or lower jaw, which are connected by ligaments themselves. The strong attachment of the upper jaw to the neurocranium, as visible in needlefishes and sauries, involves complex rearrangements of the soft tissue of the jaw apparatus.

Acknowledgements

I am deeply indebted to Stefan T. Hertwig (Naturmuseum Bern). His detailed and prospective dissertation on the evolution and functional morphology of the jaw apparatus in Cyprinodontiformes and our discussions were extremely helpful (but I am of course responsible for any remaining mistakes). I am most grateful to Stefan Hertwig, Lynne Parenti, Rolf Beutel, and Manfred Schartl for kindly providing specimens. Janine Ziermann, Martin Fischer, Lennart Olsson, Torsten M. Scheyer are thanked for discussion. Rommy Peterson and Katja Felbel helped with laboratory concerns. Anonymous reviewers gave constructive critics to former versions of the manuscript.

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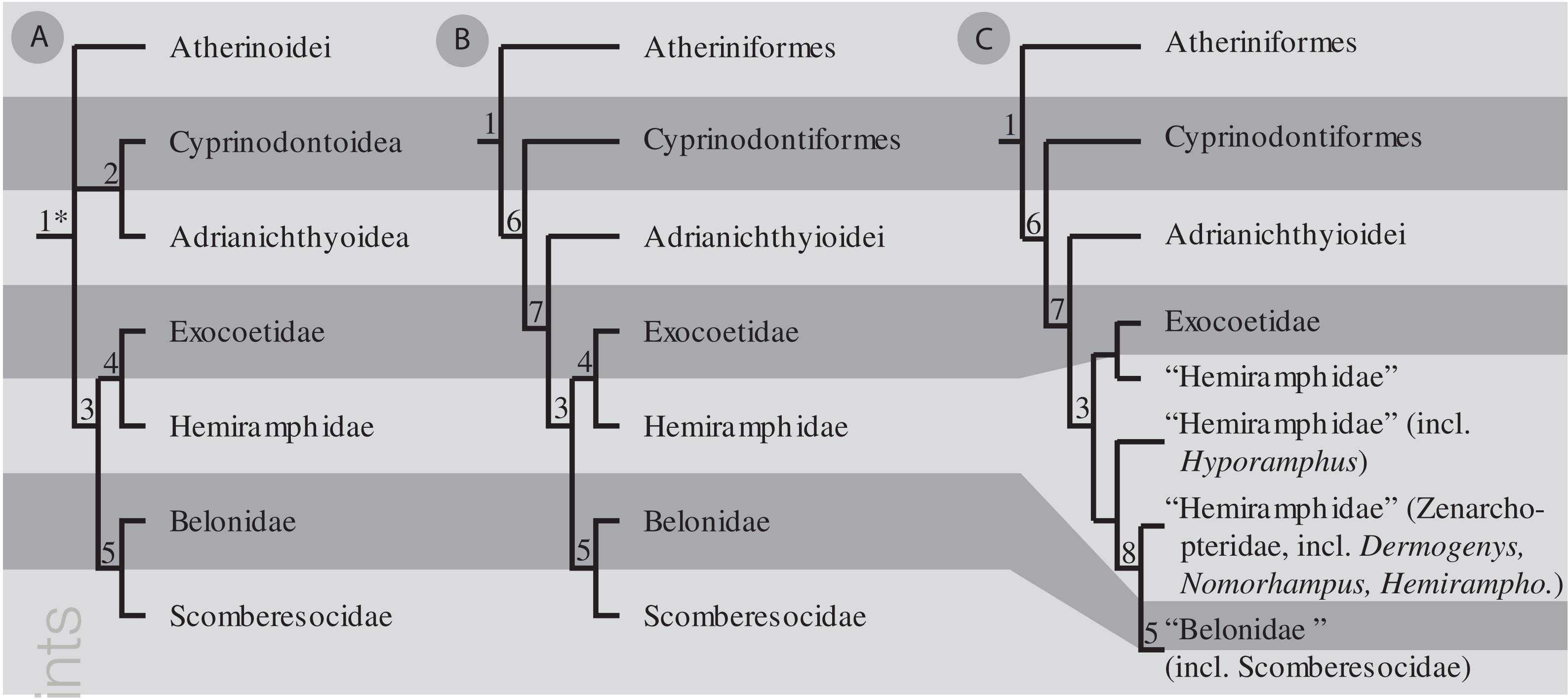
Figures

Figure 1. Alternative topologies for atherinomorph interrelationship as referred in the literature; A) Rosen (1964), B) Rosen and Parenti (1981), C) Lovejoy *et al.* (2004). Note the different arrangement of Cyprinodontea (6), Hemiramphidae, and the position of Scomberesocidae; corresponding taxa are highlighted. Numbers of non-terminal clades: 1 = Atherinomorpha (1*: clade named as "Atheriniformes" by Rosen, 1964), 2 = Cyprinodontoidei, 3 = Exocoetoidei, 4 = Exocoetoidea, 5 = Scomberesocoidea, 6 = Cyprinodontea, 7 = Beloniformes, 8 = N.N.

Figure 2. Overview on the cranial anatomy in the eight species manually dissected in this study. Skin is removed. A) *Perca fluviatilis*, B) *Rhinomugil corsula*, C) *Atherina boyeri*, D) *Aplocheilus lineatus*, E) *Oryzias latipes*, F) *Parexocoetus brachypterus*, G) *Dermogenys pussila*, H) *Belone belone*. Abbreviations of muscles [m. = musculus] and selected bones: A1 = external section of m. adductor mandibulae, A2/3 = internal section of m. adductor mandibulae, AAP = m. adductor arcus palatini, den = dentary, DO = m. dilatator operculi, EA = epaxial musculature, lac = lacrimal, LAP = m. levator arcus palatini; LO = m. levator operculi, max = maxilla, op = opercle, PH = m. protractor hyoidei, pop = preopercle, T = m. trapezius. Drawings not to scale. For detailed labelling, scales, histological sections, and further illustrations see Supplementary Figures.

Figure 3. Serial sections through the head of the duckbilled ricefish *Xenopoecilus oophorus* (Beloniformes, Adrianichthyidae). Slice thickness = 12µm. Section numbers: A) 14, B) 170, C) 206, D) 268, E) 340, F) 440, G) 450 (lenses redrawn), H) 586, I) 648. Bar scale equals 1mm for A-J. Magnifications B', D', I'-J' are not to scale. Compare to the other adrianichthyid studied herein, *Oryzias latipes* (Figure S5).



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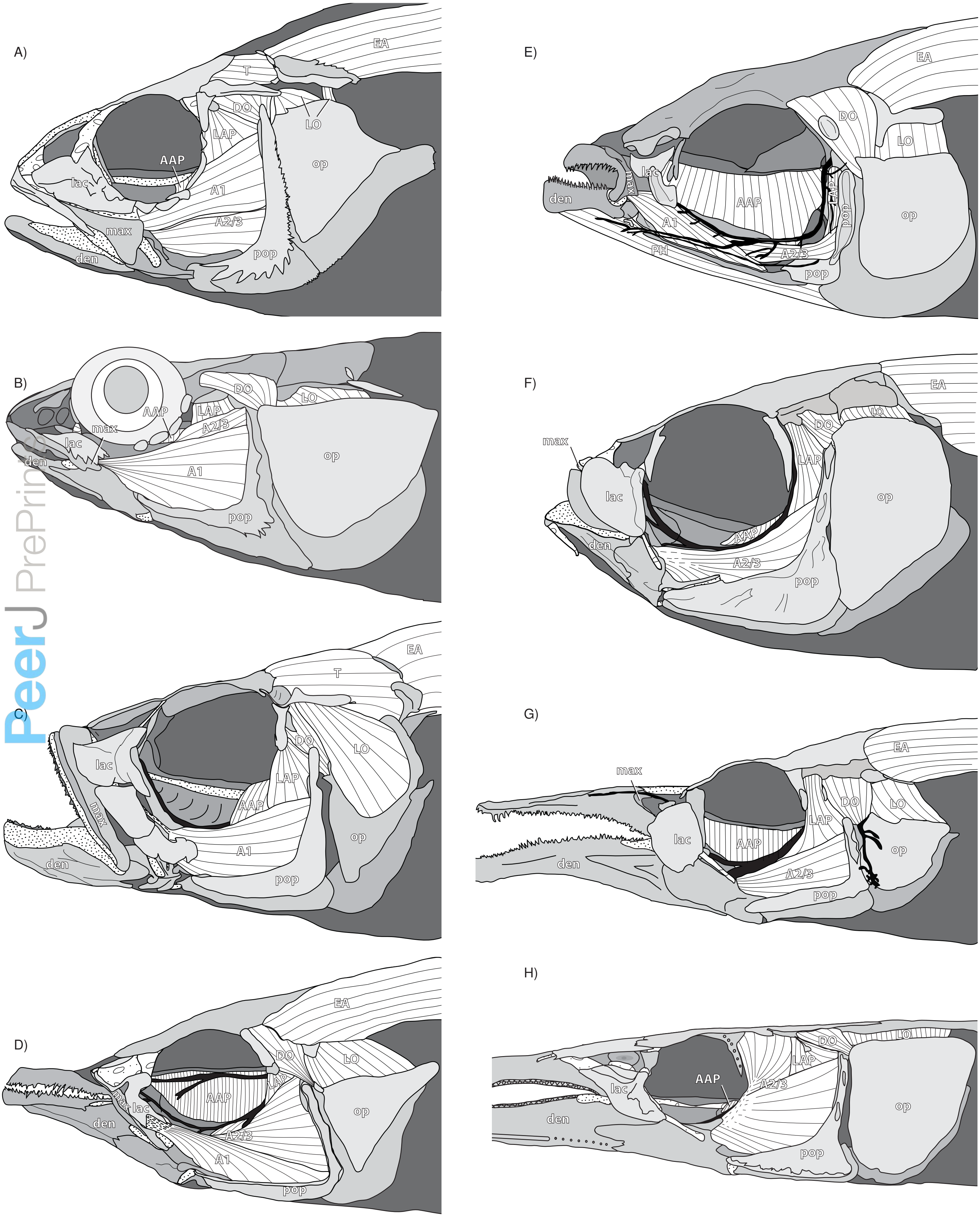
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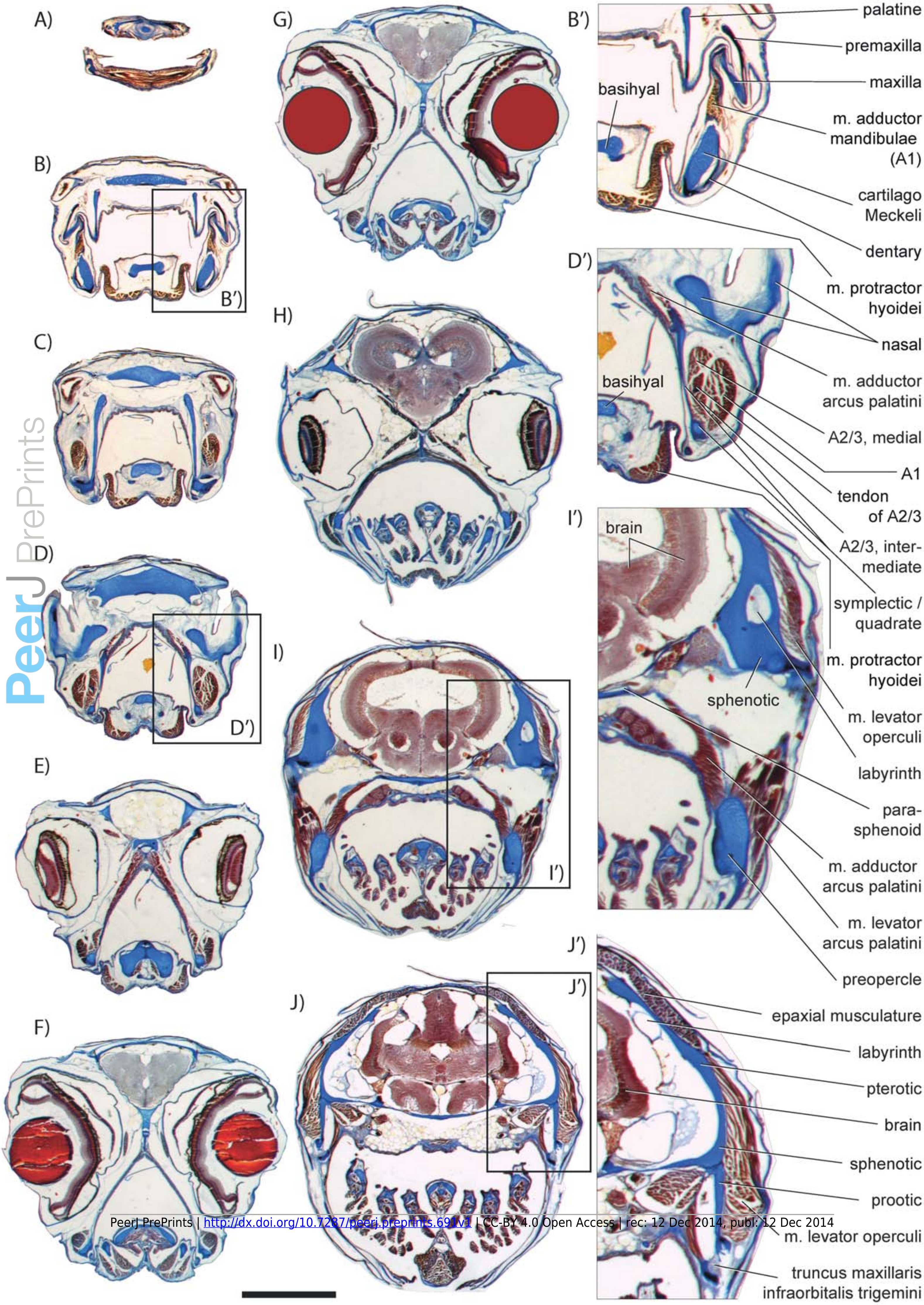
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maxilla
basihyal
m. adductor mandibulae (A1)
cartilago Meckeli
dentary
m. protractor hyoidei
nasal
basihyal
m. adductor arcus palatini
A2/3, medial
A1
tendon of A2/3
A2/3, inter-mediate
symplectic / quadrate
m. protractor hyoidei
brain
sphenotic
m. levator operculi
labyrinth
para-sphenoid
m. adductor arcus palatini
m. levator arcus palatini
preopercle
epaxial musculature
labyrinth
pterotic
brain
sphenotic
prootic
m. levator operculi
truncus maxillaris infraorbitalis trigemini

Paper included Appendix

Figure S1. *Perca fluviatilis*. A-D) Manual dissection. Bar scale equals 5 mm.

Figure S2. *Rhinomugil corsula*. A-D) Manual dissection, E-H) histological sections. Bar scale equals 1 mm in A-D and 2 mm in E-H.

Figure S3. *Atherina boyeri*. A-E) Manual dissection, F-I) histological sections. Bar scale equals 1 mm.

Figure S4. *Aplocheilus lineatus*. A-D) Manual dissection, E-H) histological sections. Bar scale equals 2 mm.

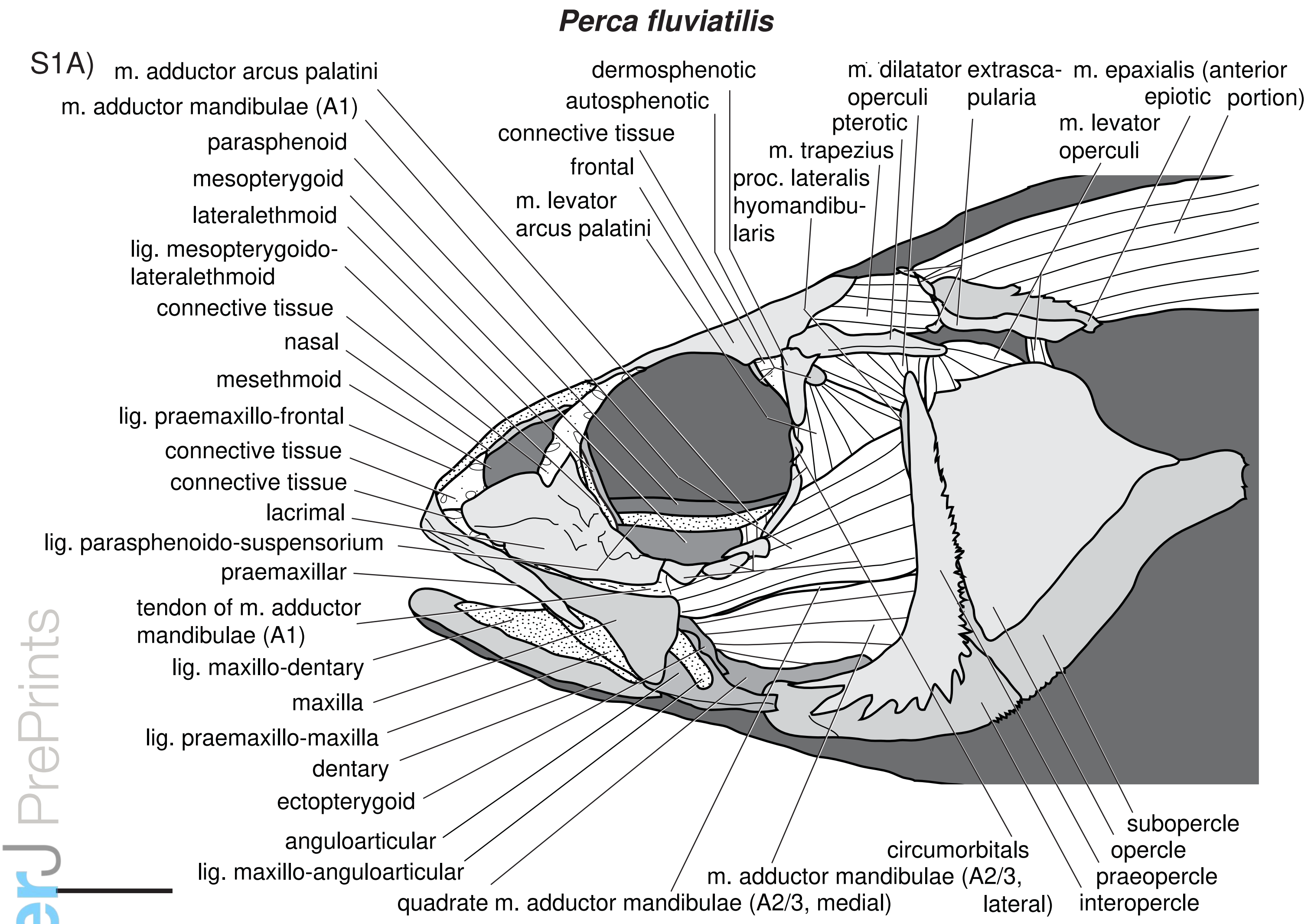
Figure S5. *Oryzias latipes*. A-C) Manual dissection, D-G) histological sections. Bar scale equals 1 mm in A-C and 0.5 mm in E-G. Except for B modified from Werneburg and Hertwig (2009).

Figure S6. *Parexocoetus lineatus*. A-D) Manual dissection, E-H) histological sections. Bar scale equals 1 mm.

Figure S7. *Dermogenys pussila*. A-C) Manual dissection, D-G) histological sections. Bar scale equals 1 mm in A-C and 0.5 mm in D-G.

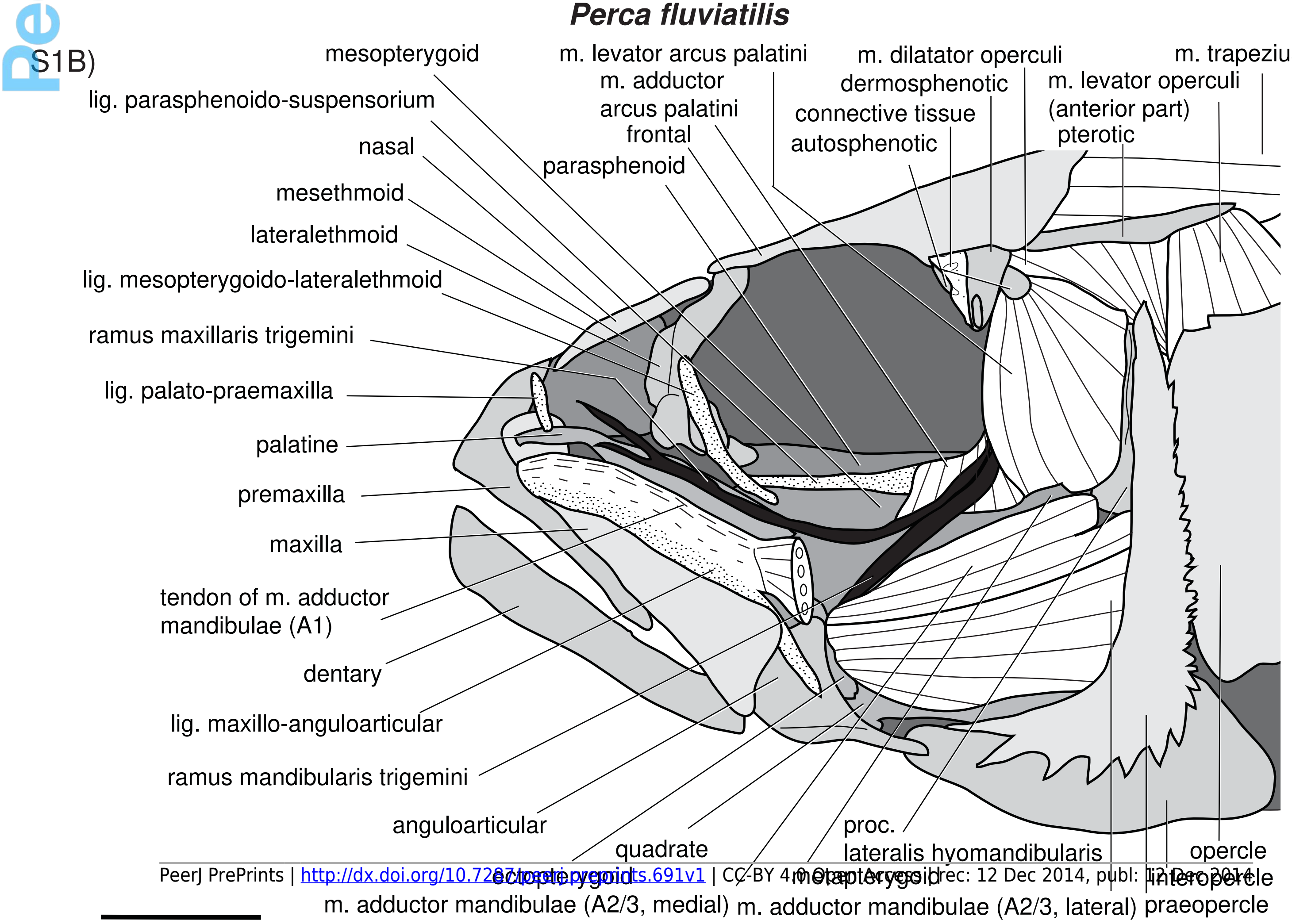
Figure S8. *Belone belone*. A-C) Manual dissection. Bar scale equals 5 mm.

Figure S9. *Scomberesox saurus*. A-D) Manual dissection, E-H) histological sections. Bar scale equals 2 mm in A-D and 0.5 mm in E-H. Adult specimen used for dissection, juvenile specimen used for histology.



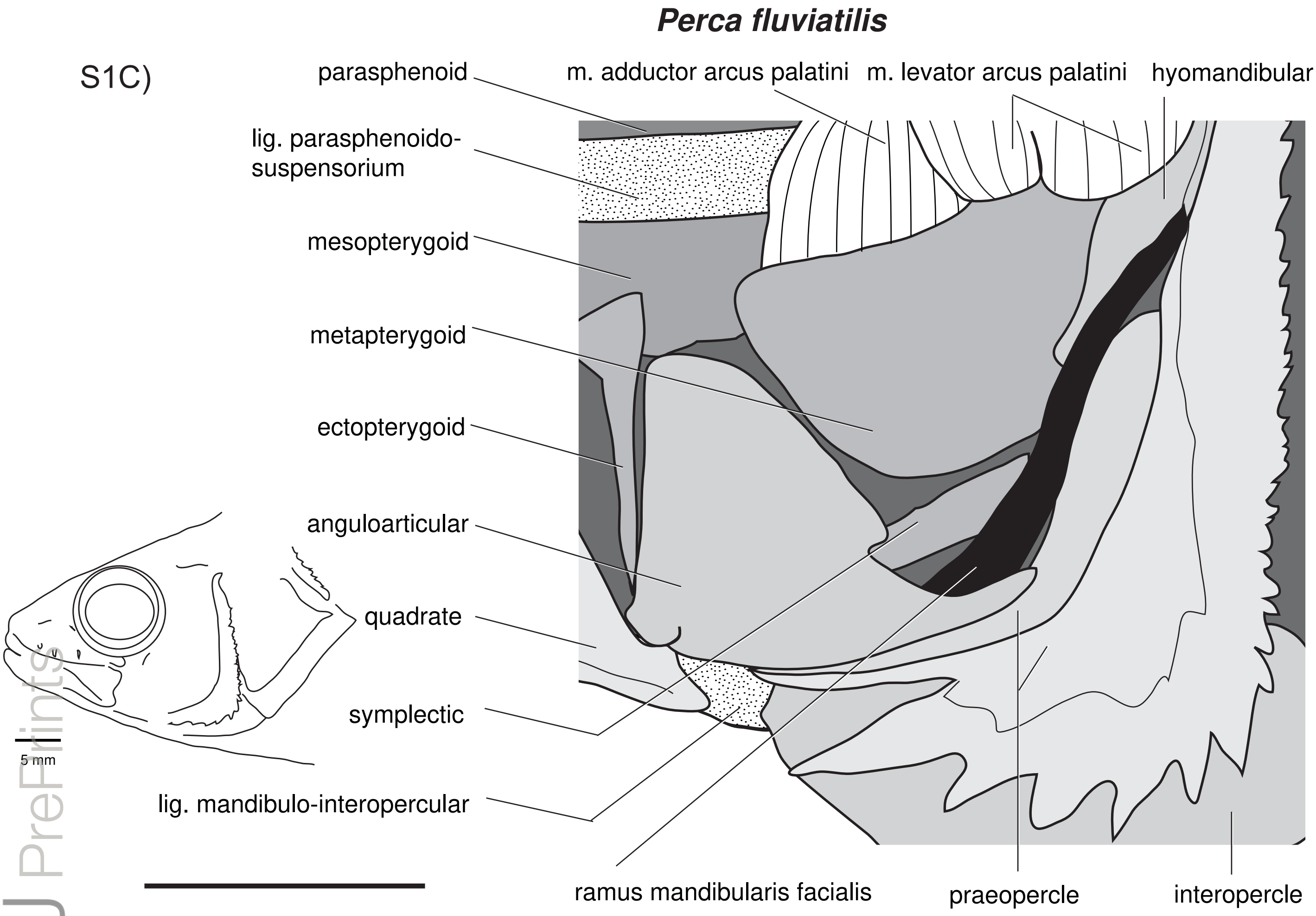
S1A)

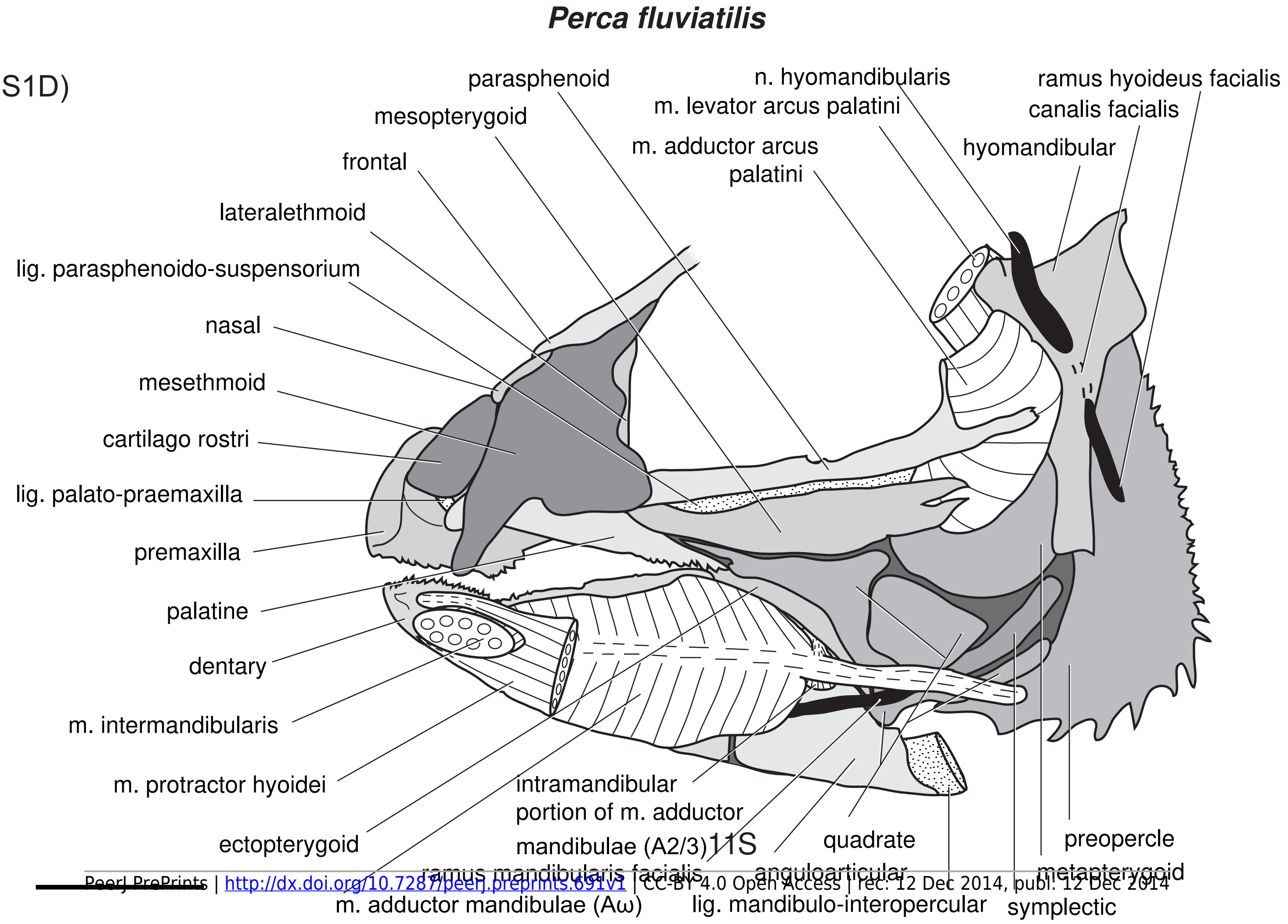
Perca fluviatilis



S1B)

Perca fluviatilis





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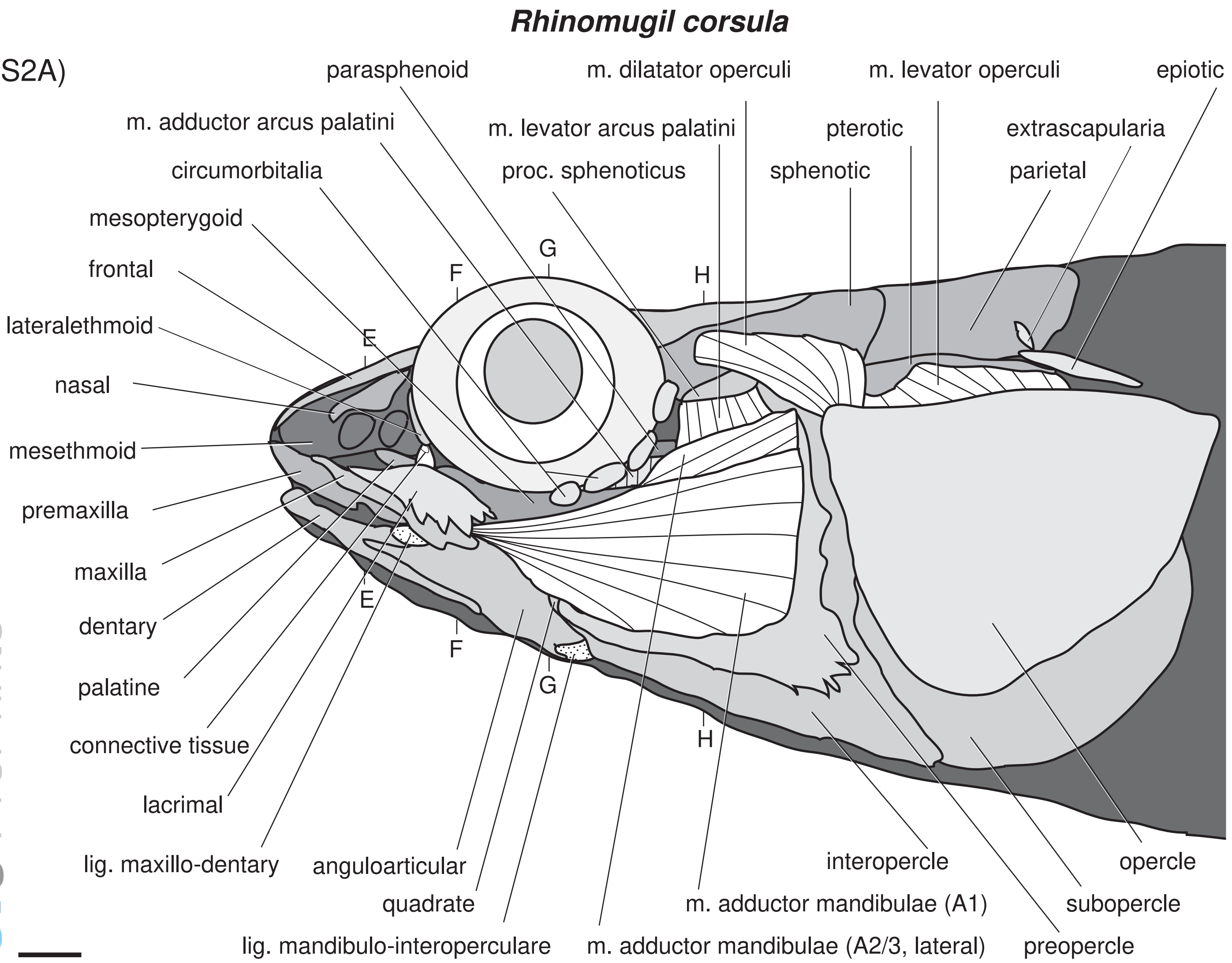
S2A)



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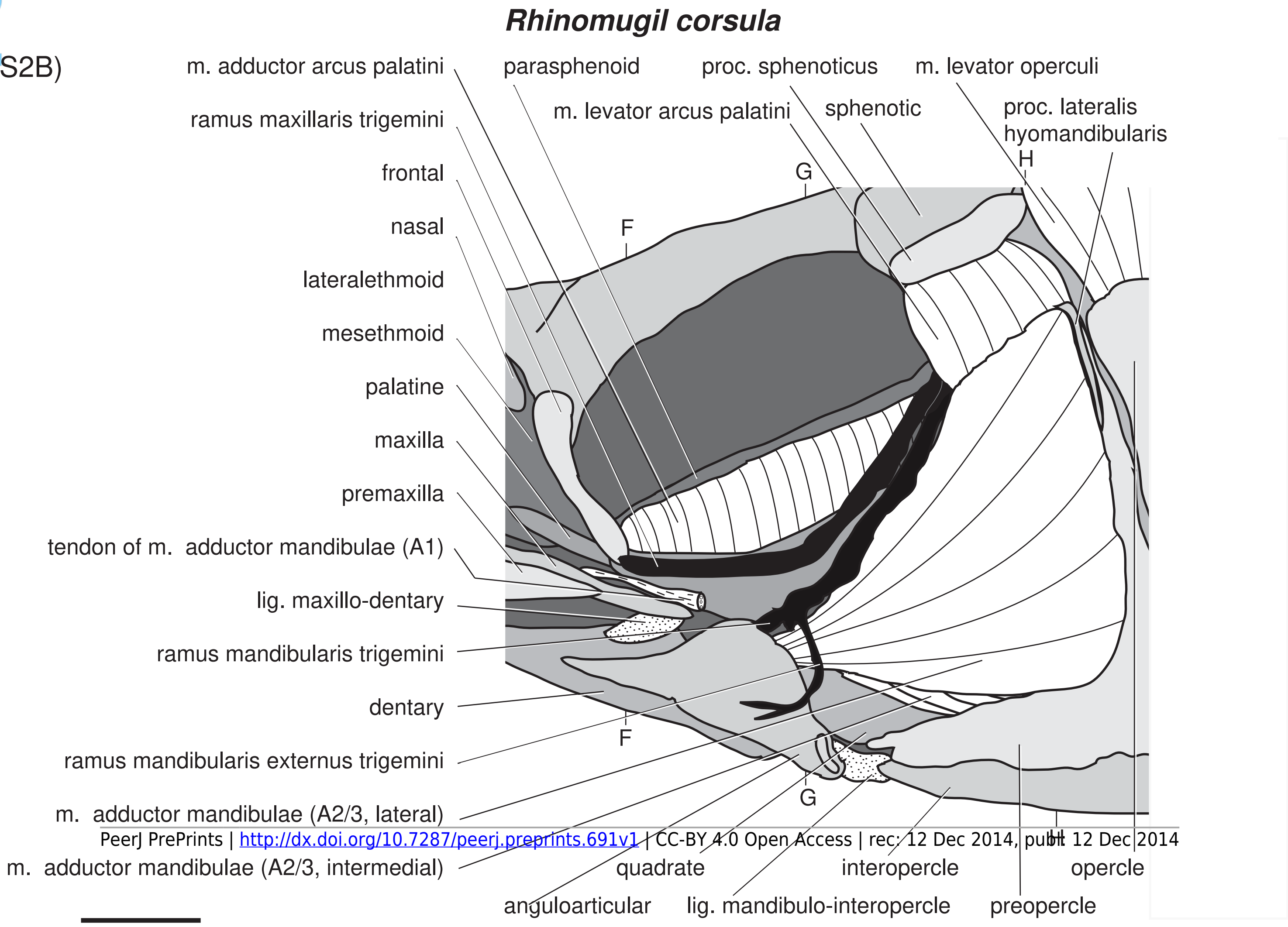

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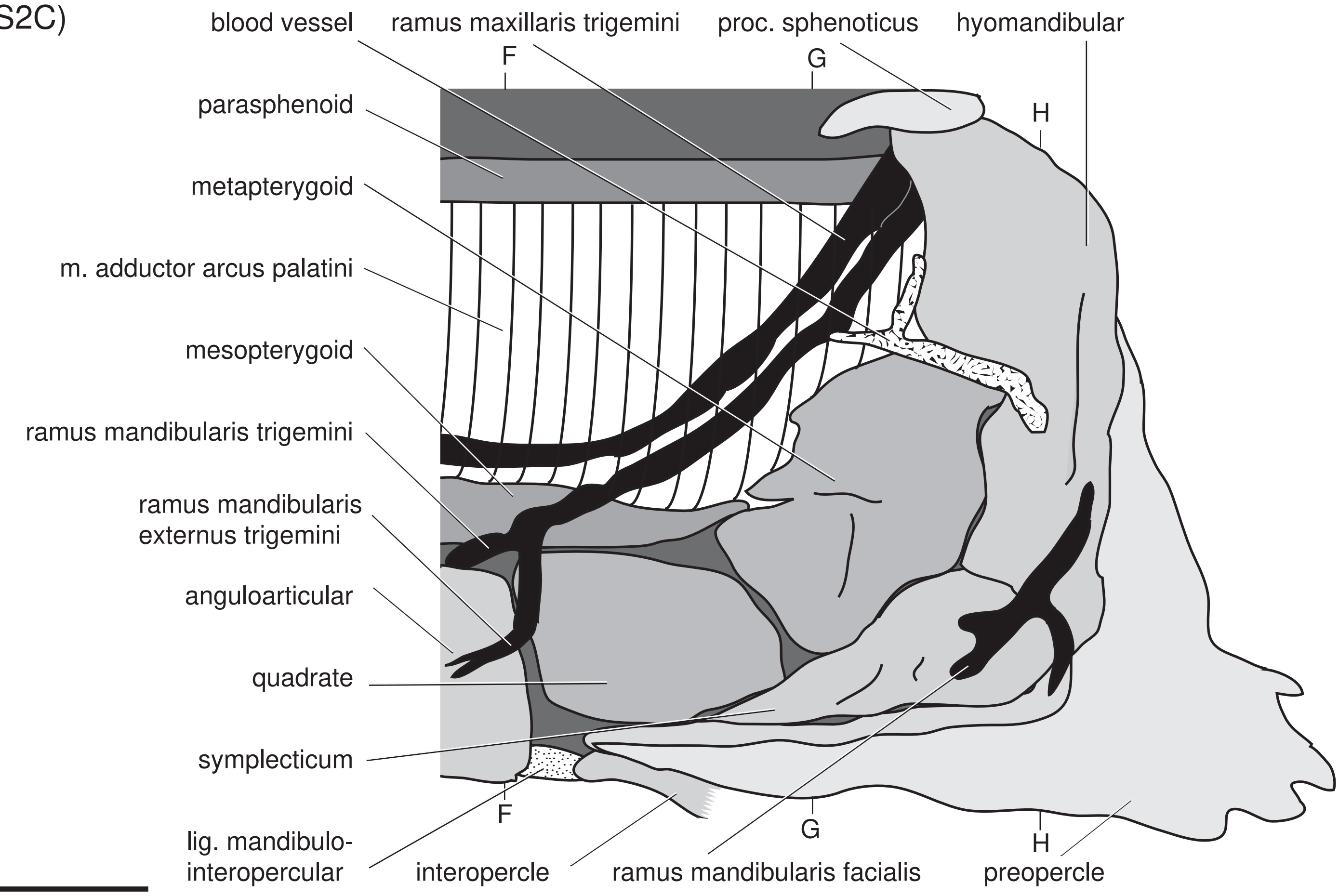
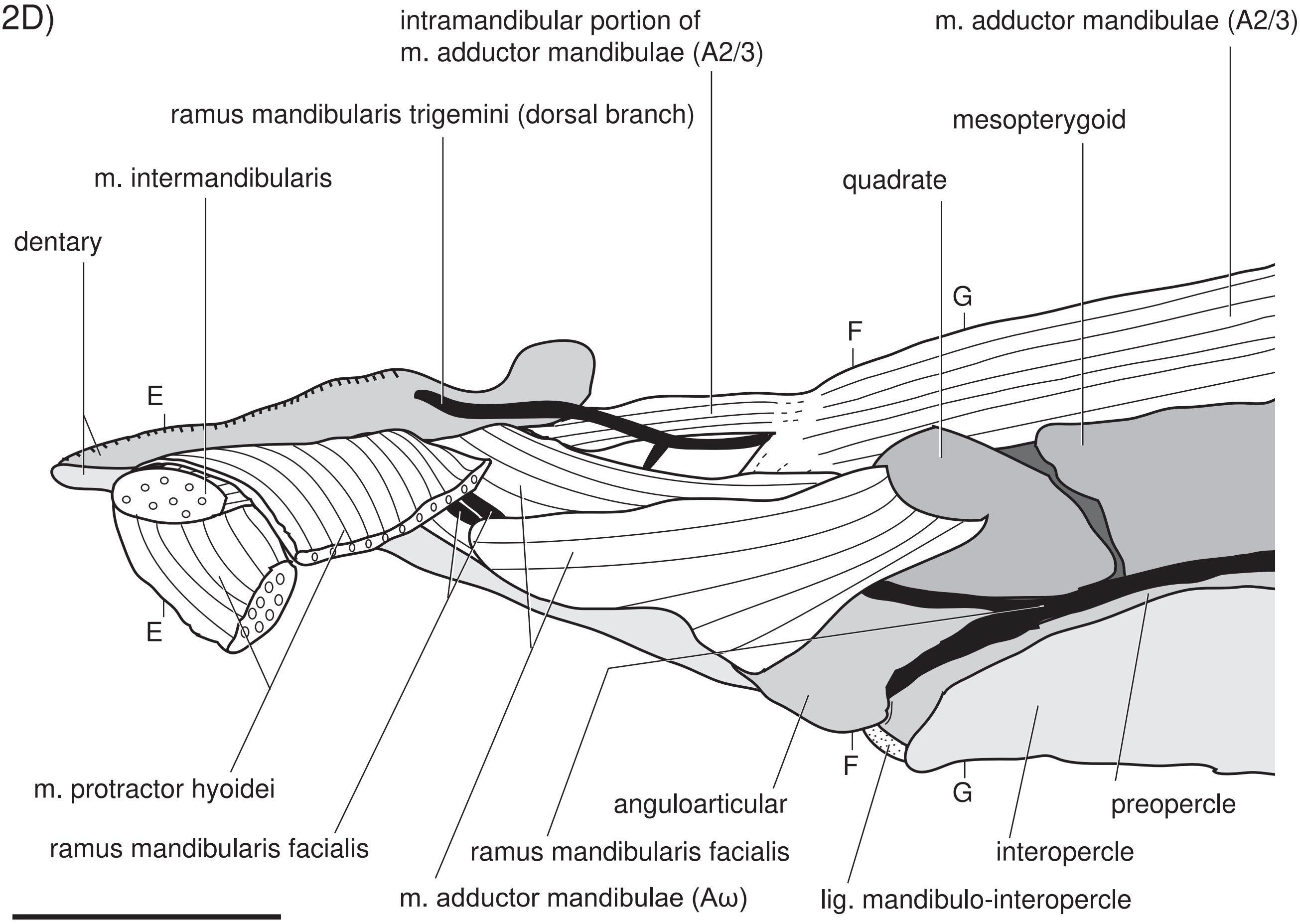
Rhinomugil corsula

S2C)



Rhinomugil corsula

S2D)



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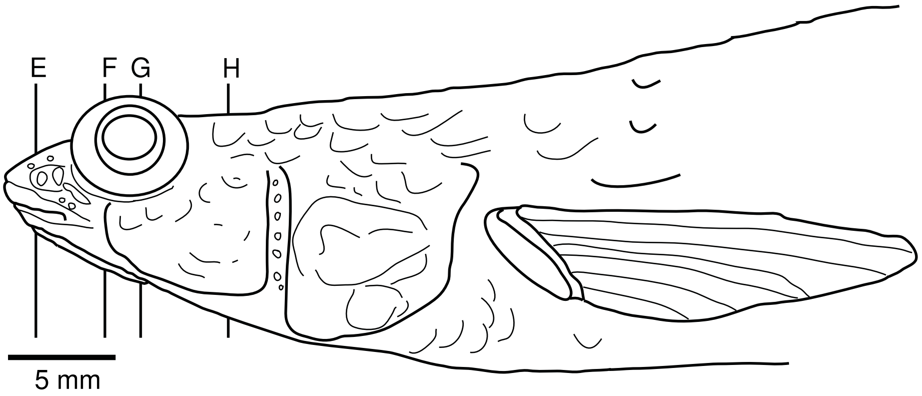
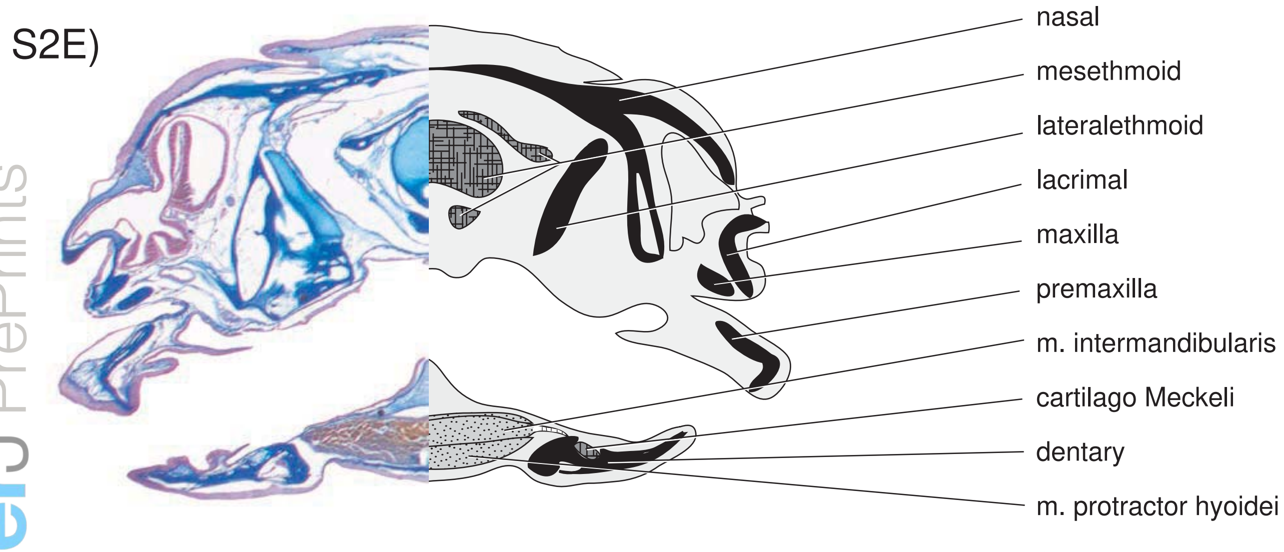
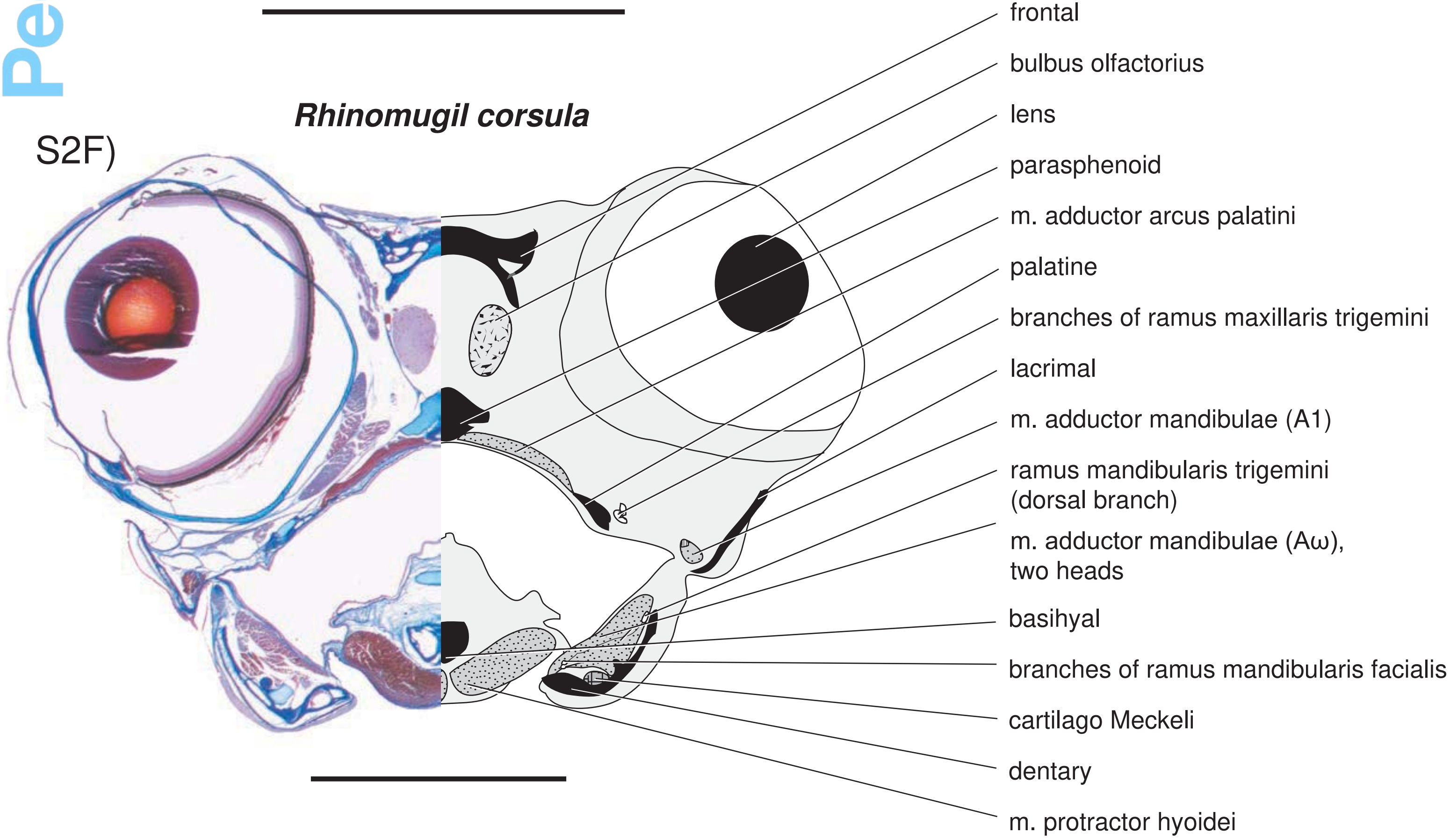
Rhinomugil corsula



Rhinomugil corsula

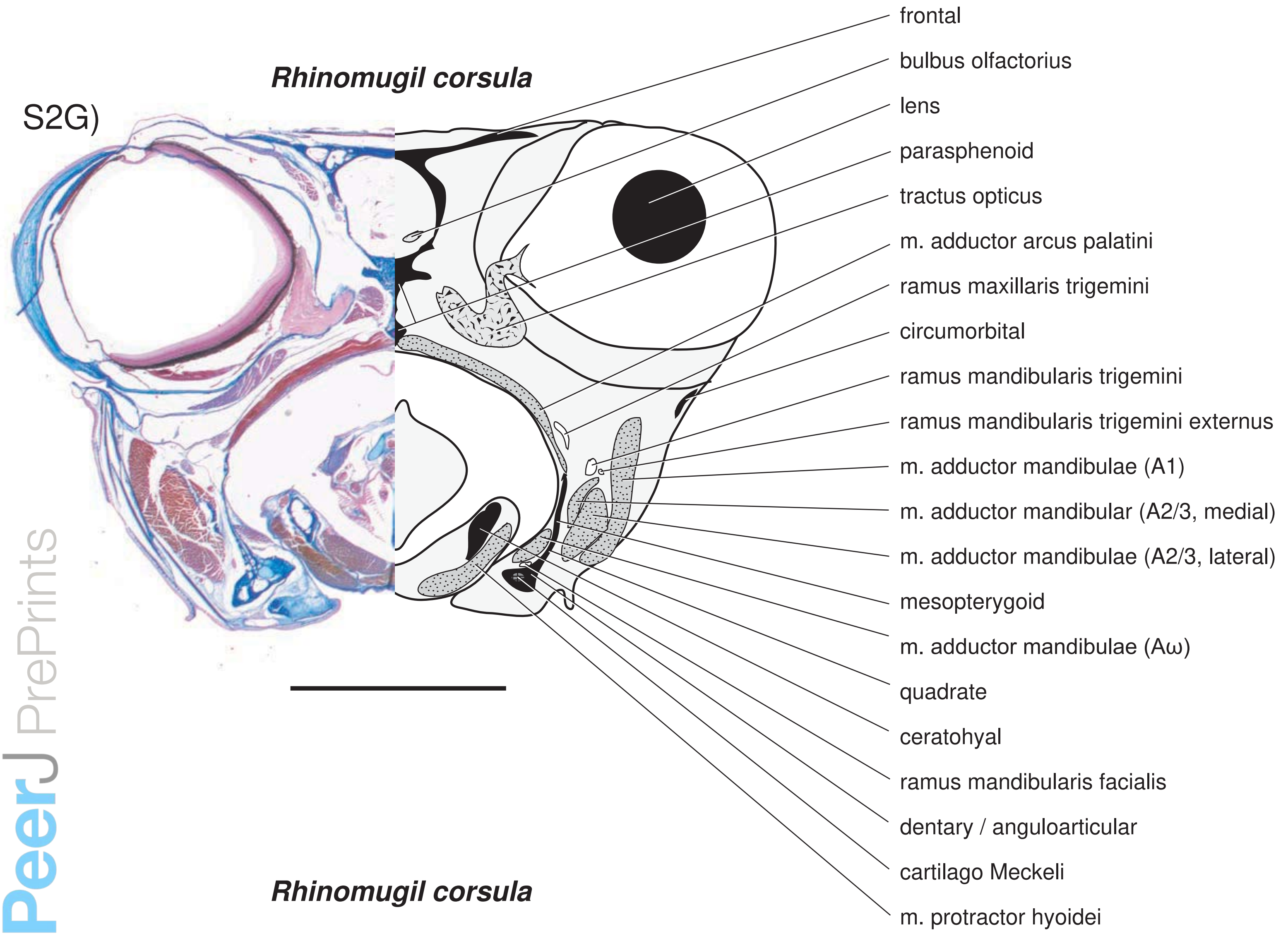


Rhinomugil corsula



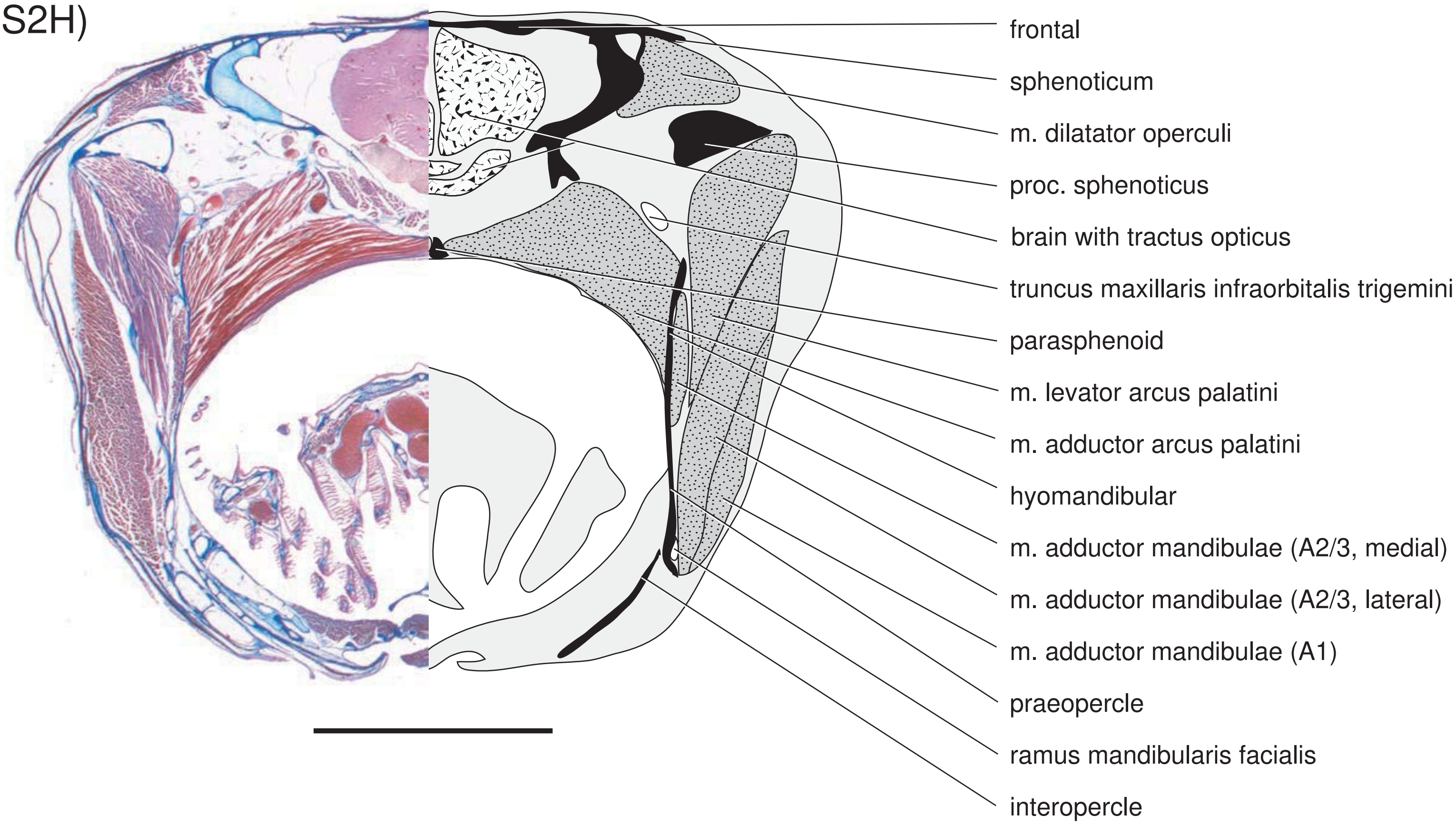
S2G)

Rhinomugil corsula



S2H)

Rhinomugil corsula



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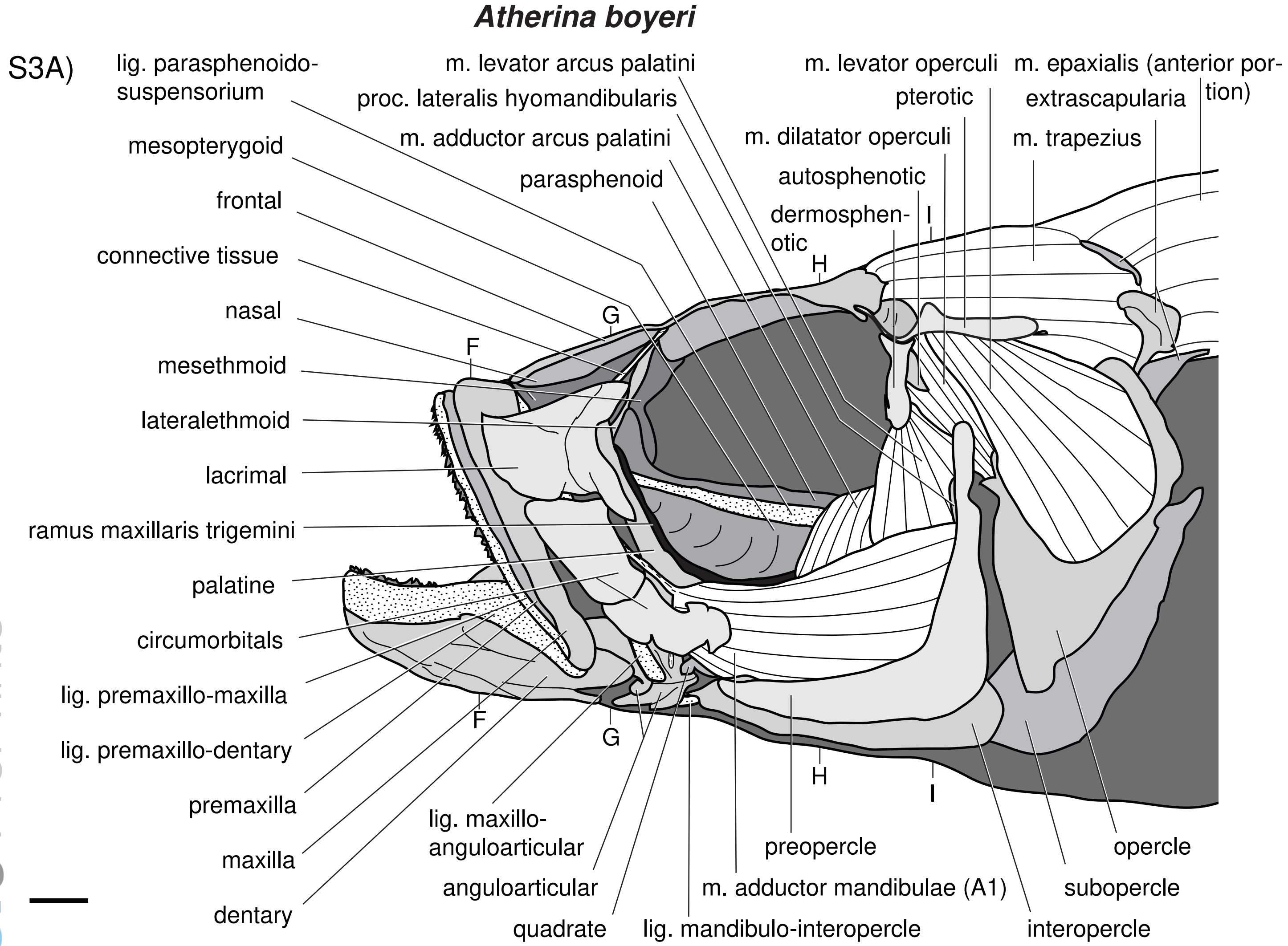
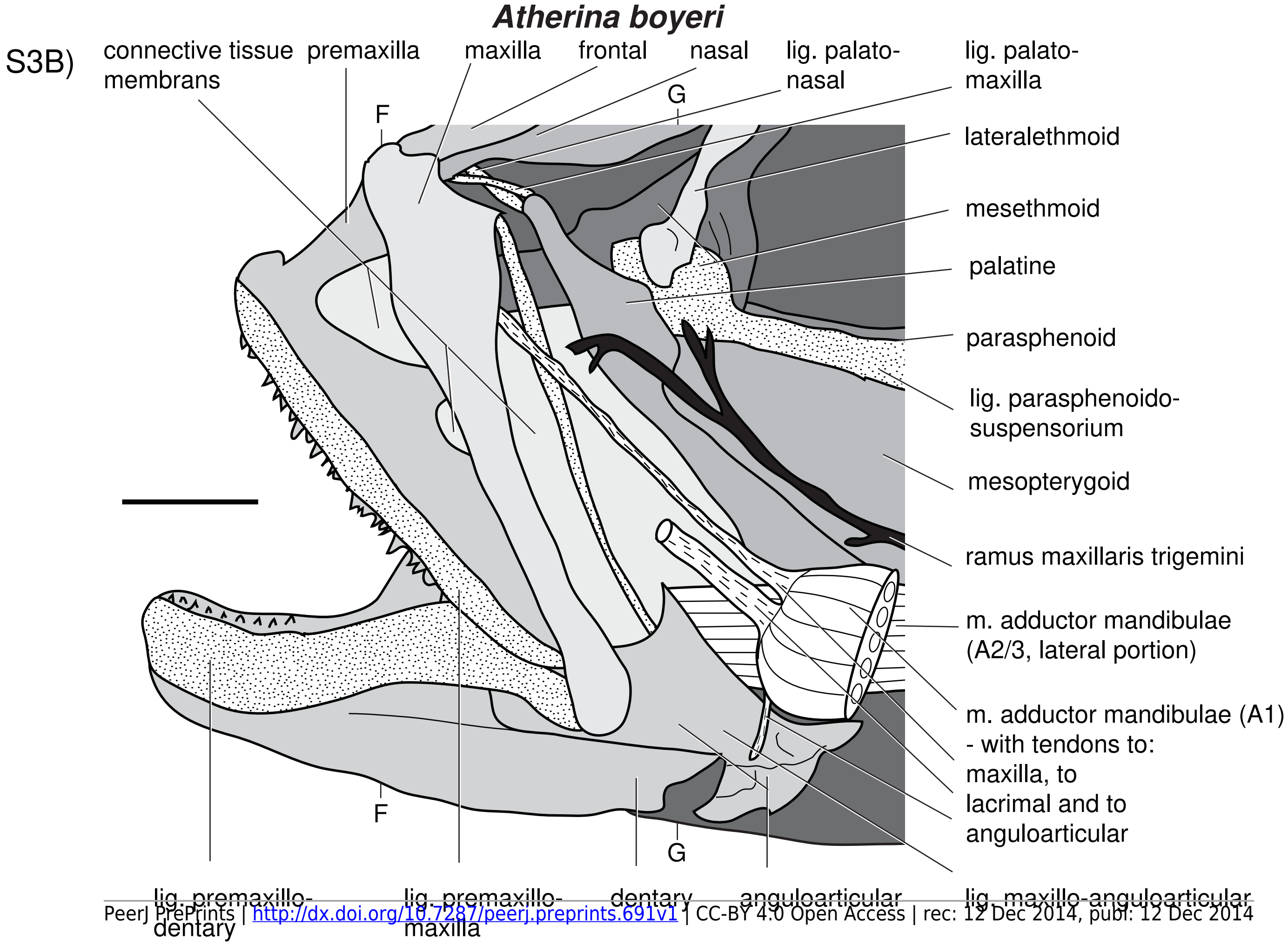


S3A)

Atherina boyeri

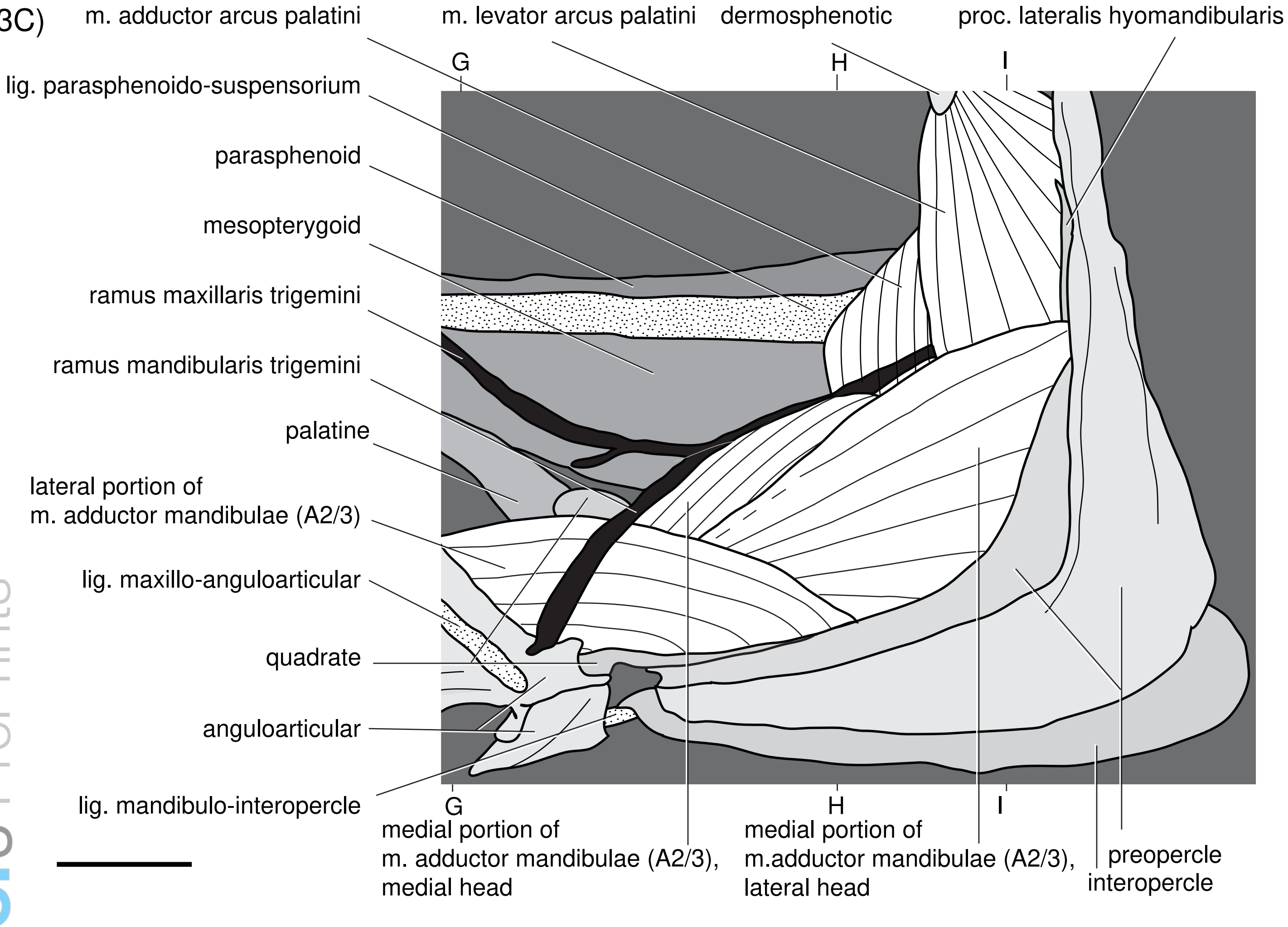


S3B)

Atherina boyeri

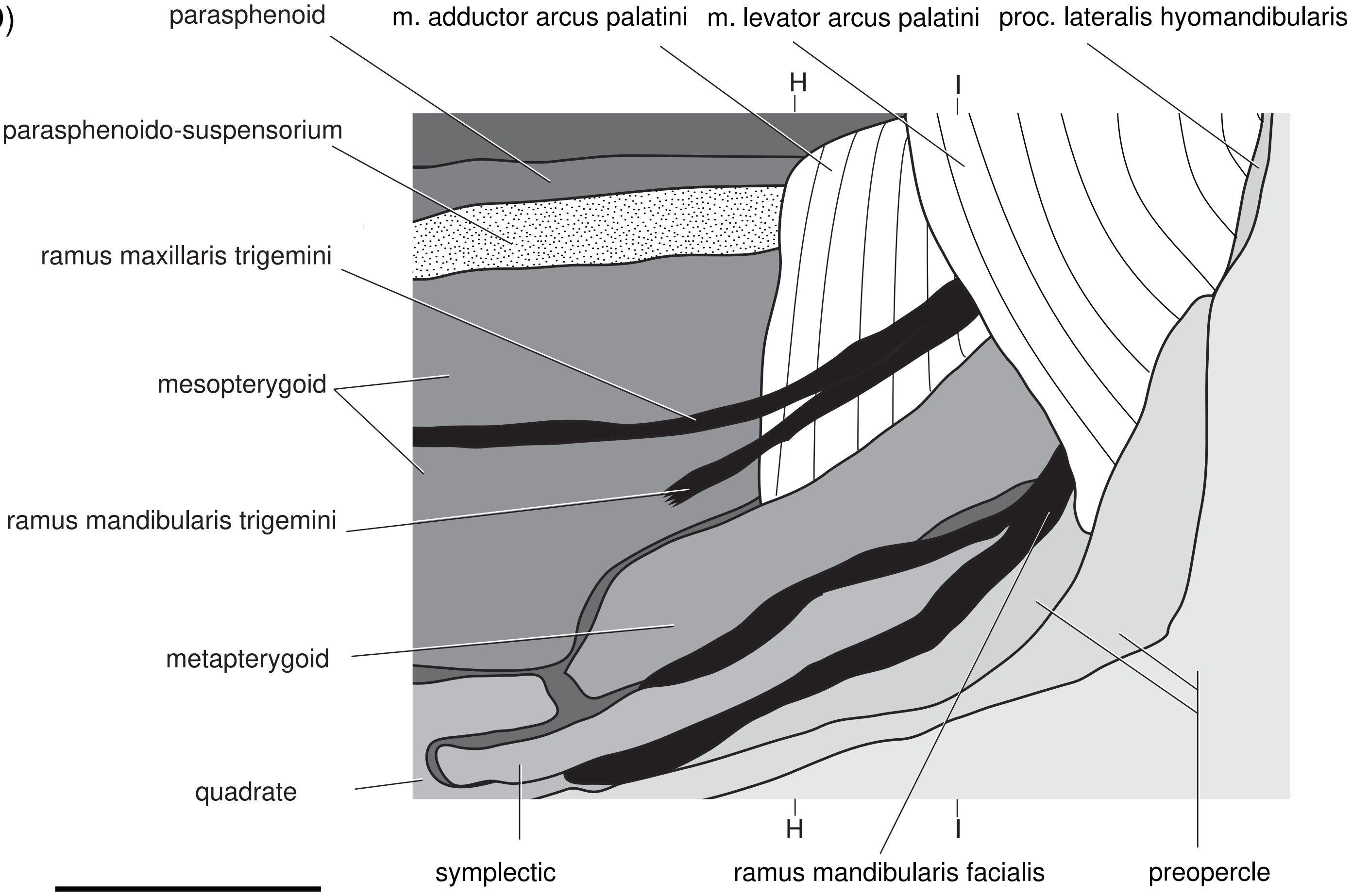
S3C)

Atherina boyeri



S3D)

Atherina boyeri



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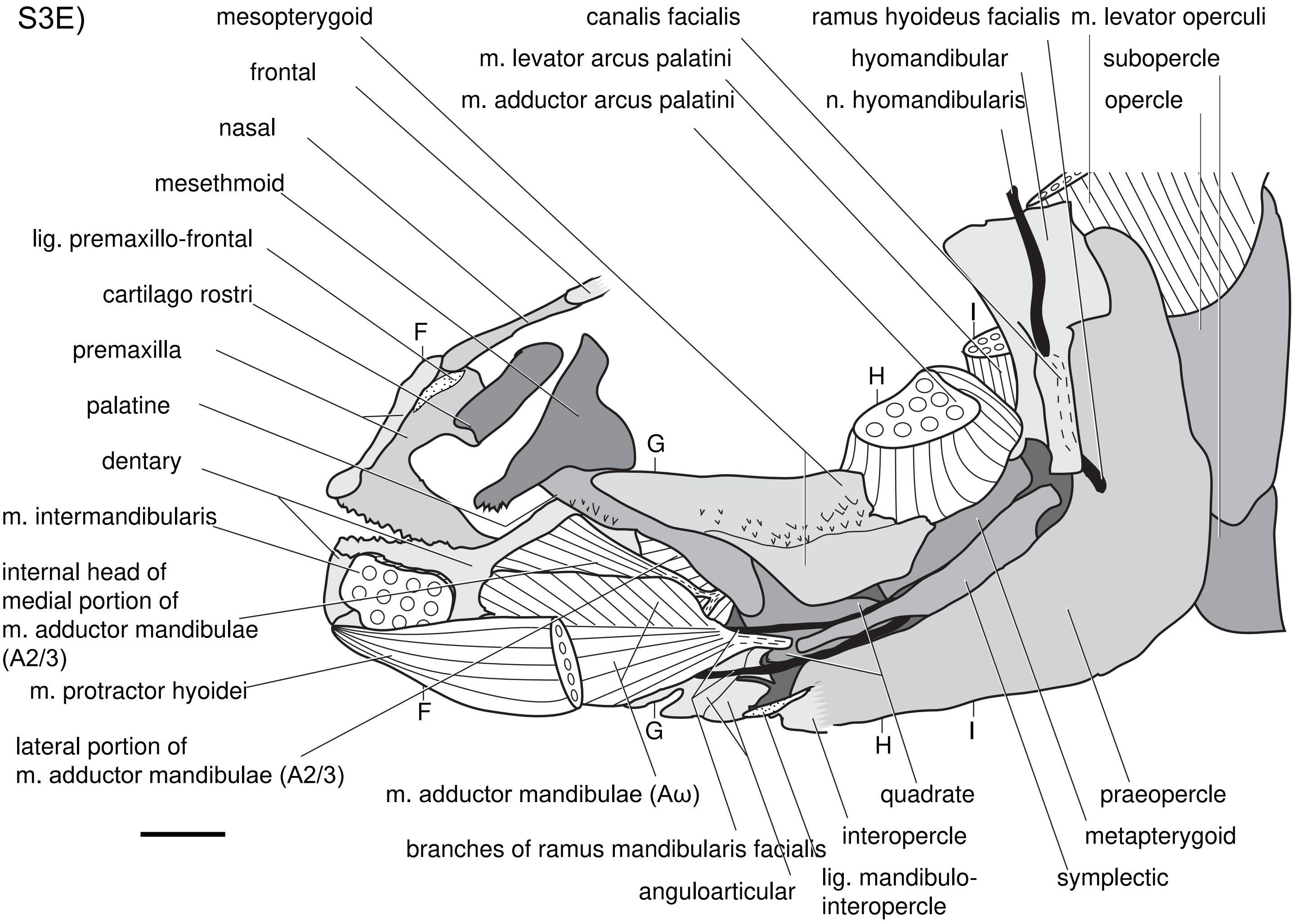
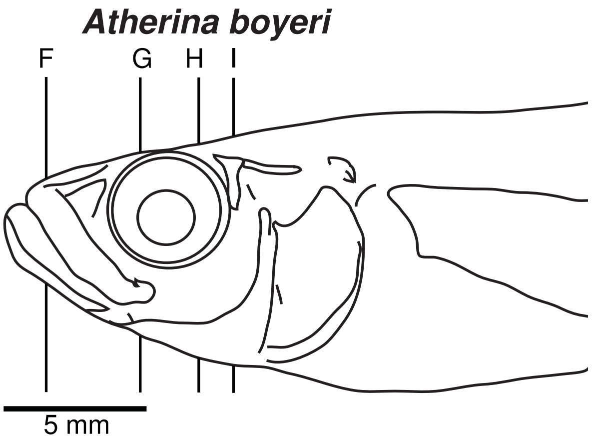
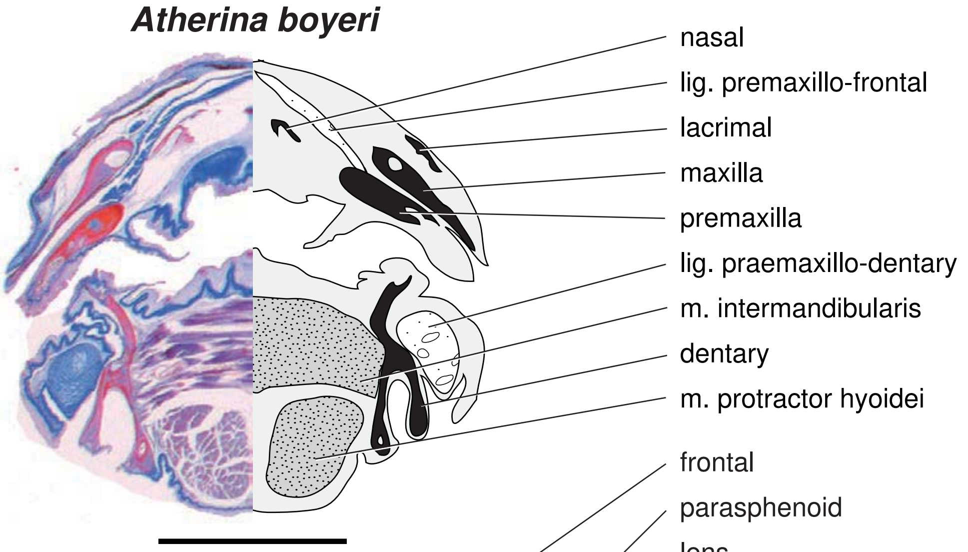
Atherina boyeri

S3E)

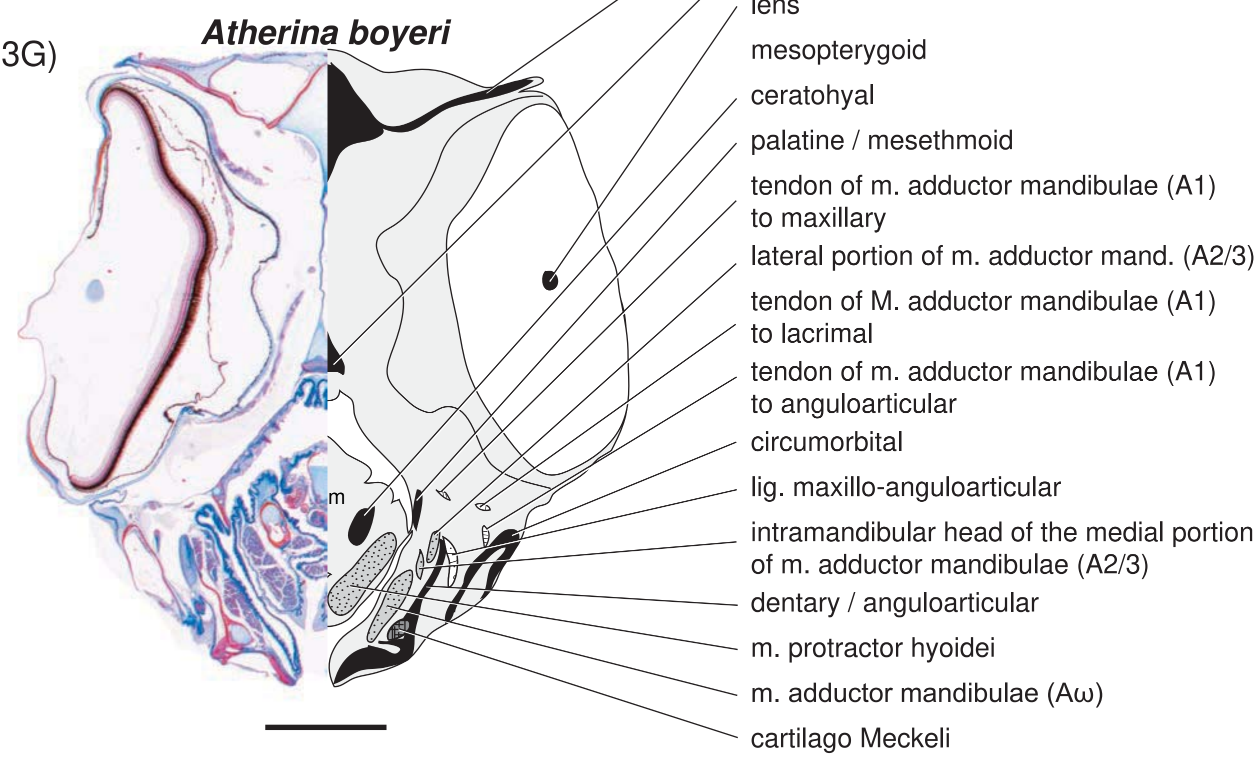



Atherina boyeri
F
G
H
I
5 mm

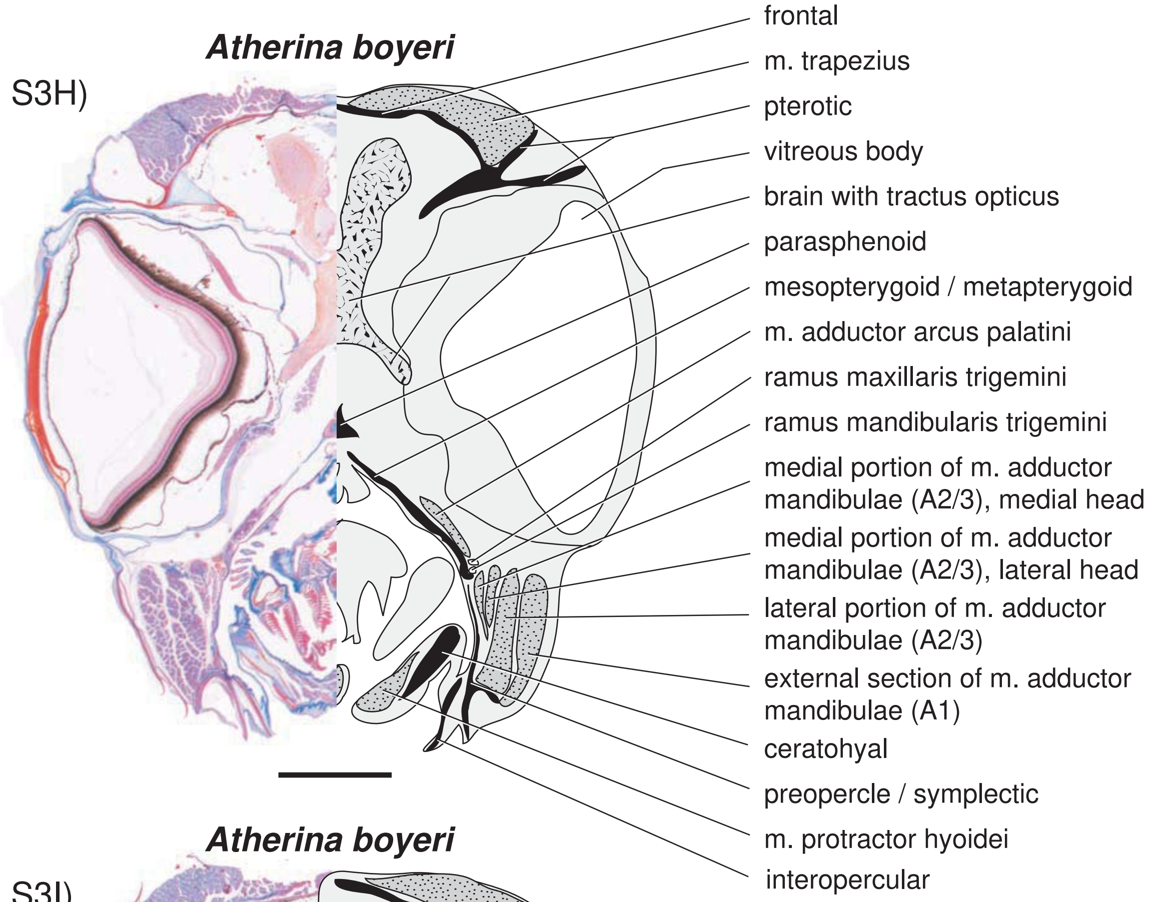
S3F)


Atherina boyeri
nasal
lig. premaxillo-frontal
lacrimal
maxilla
premaxilla
lig. praemaxillo-dentary
m. intermandibularis
dentary
m. protractor hyoidei

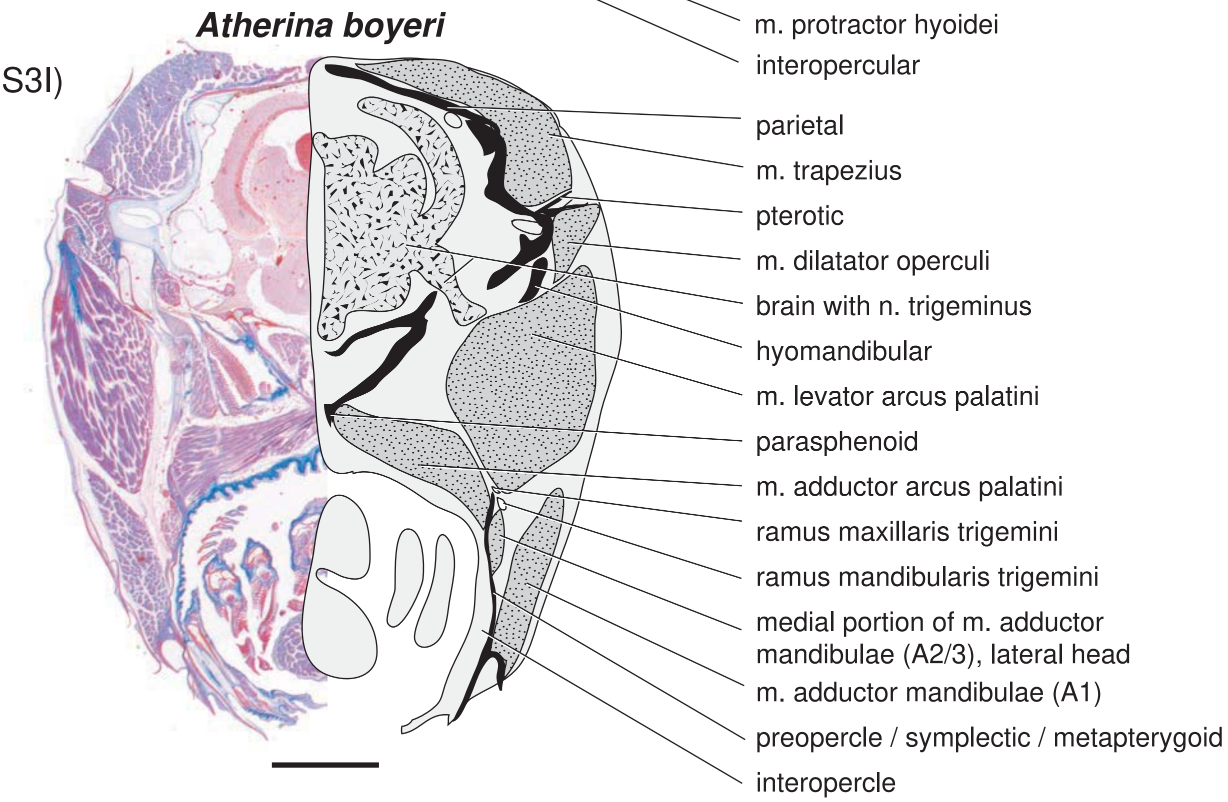
S3G)


Atherina boyeri
frontal
parasphenoid
lens
mesopterygoid
ceratohyal
palatine / mesethmoid
tendon of m. adductor mandibulae (A1) to maxillary
lateral portion of m. adductor mand. (A2/3)
tendon of M. adductor mandibulae (A1) to lacrimal
tendon of m. adductor mandibulae (A1) to anguloarticular
circumorbital
lig. maxillo-anguloarticular
intramandibular head of the medial portion of m. adductor mandibulae (A2/3)
dentary / anguloarticular
m. protractor hyoidei
m. adductor mandibulae (Aω)
cartilago Meckeli
m

S3H)

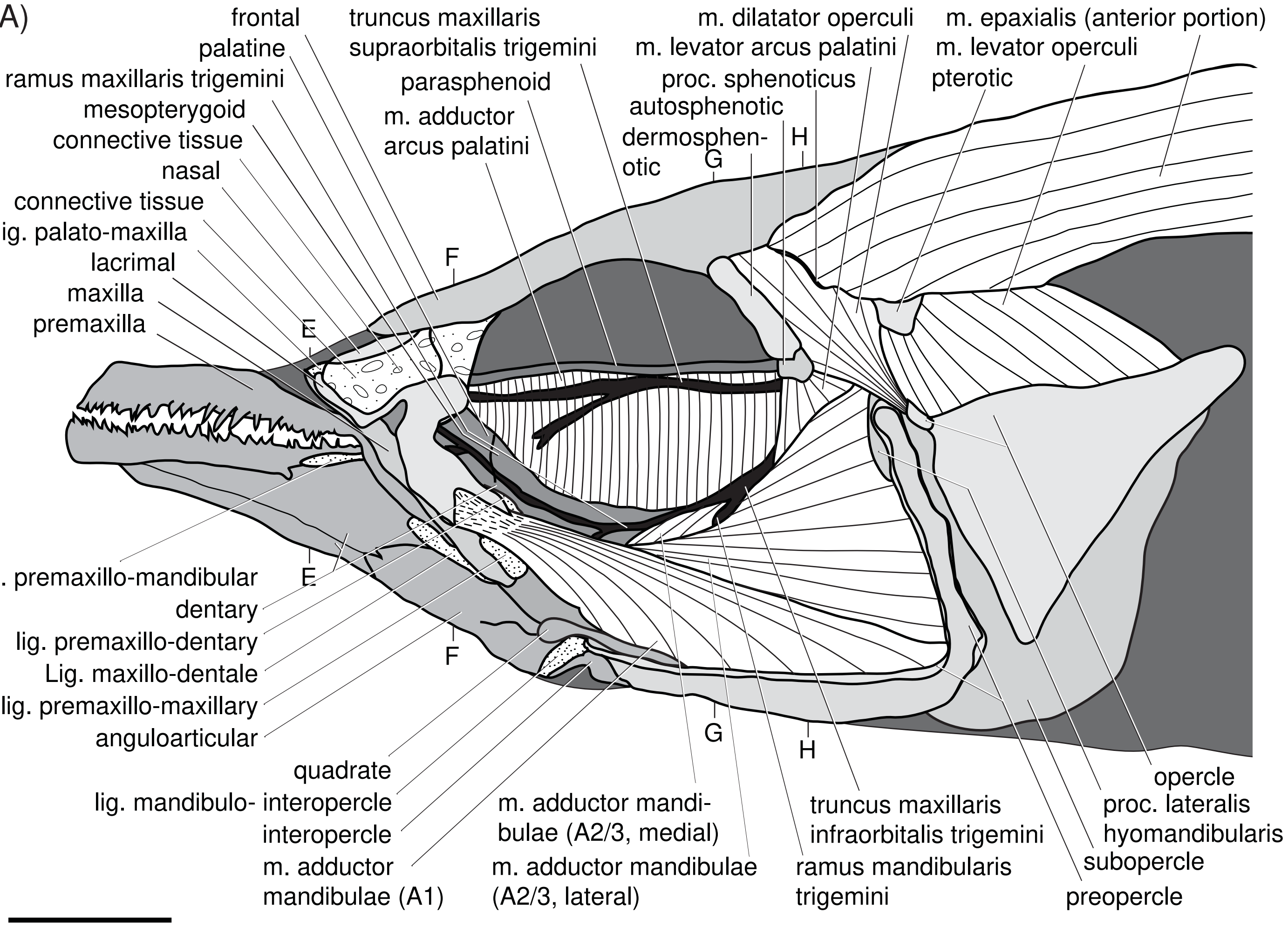

Atherina boyeri
frontal
m. trapezius
pterotic
vitreous body
brain with tractus opticus
parasphenoid
mesopterygoid / metapterygoid
m. adductor arcus palatini
ramus maxillaris trigemini
ramus mandibularis trigemini
medial portion of m. adductor mandibulae (A2/3), medial head
medial portion of m. adductor mandibulae (A2/3), lateral head
lateral portion of m. adductor mandibulae (A2/3)
external section of m. adductor mandibulae (A1)
ceratohyal
preopercle / symplectic
m. protractor hyoidei
interopercular

S3I)


Atherina boyeri
parietal
m. trapezius
pterotic
m. dilatator operculi
brain with n. trigeminus
hyomandibular
m. levator arcus palatini
parasphenoid
m. adductor arcus palatini
ramus maxillaris trigemini
ramus mandibularis trigemini
medial portion of m. adductor mandibulae (A2/3), lateral head
m. adductor mandibulae (A1)
preopercle / symplectic / metapterygoid
interopercle

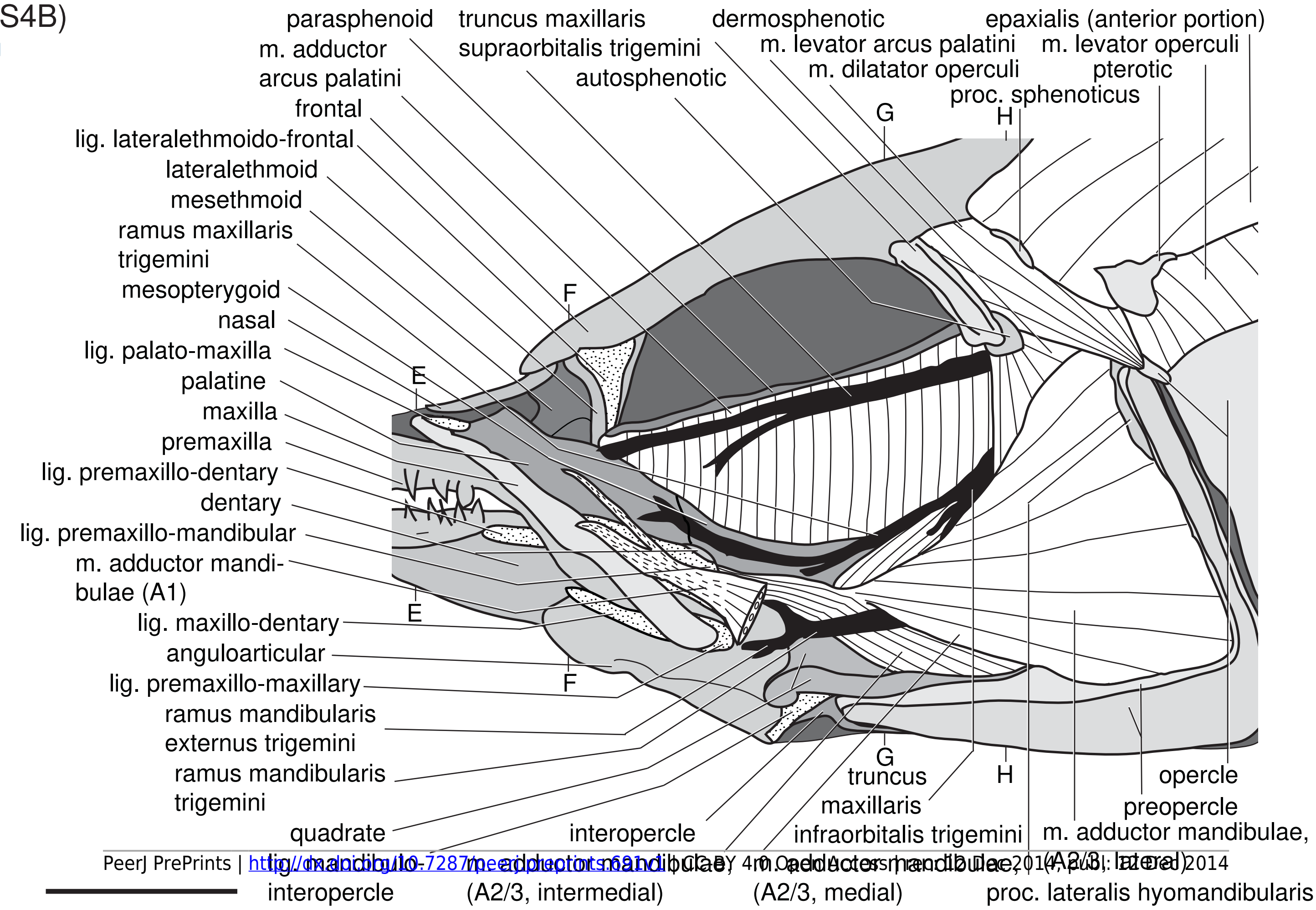
Aplocheilus lineatus

S4A)



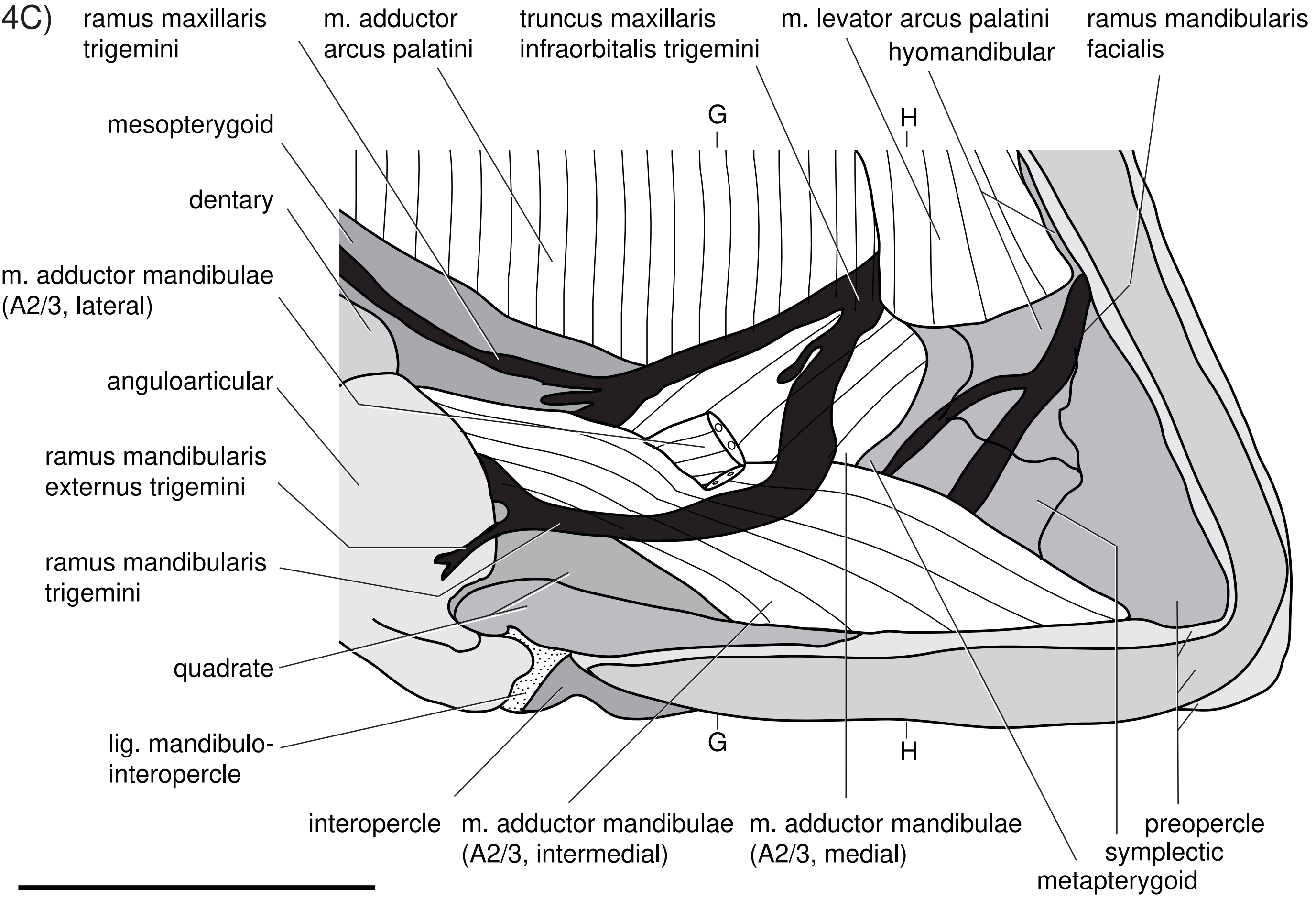
Aplocheilus lineatus

S4B)



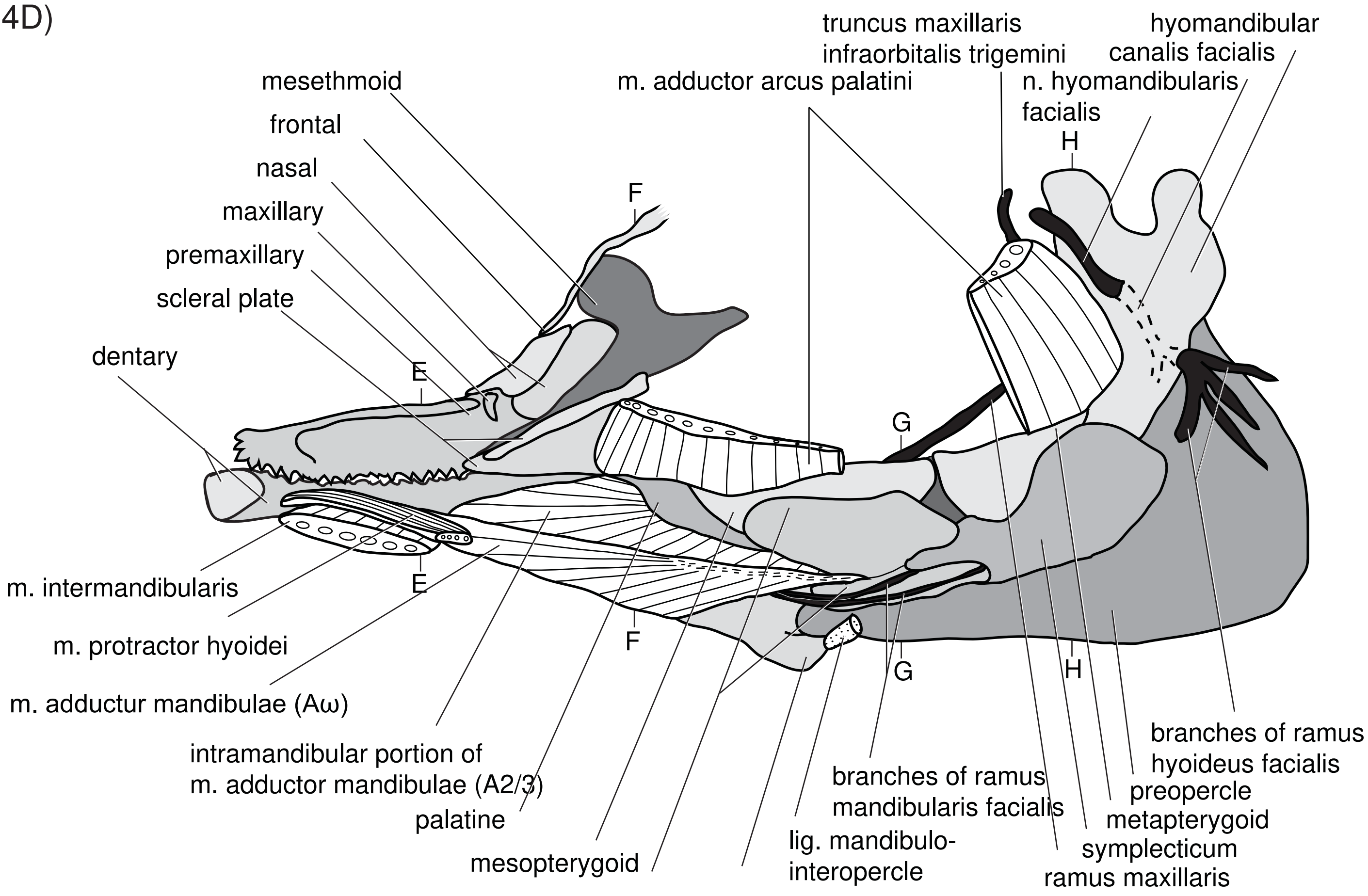
Aplocheilus lineatus

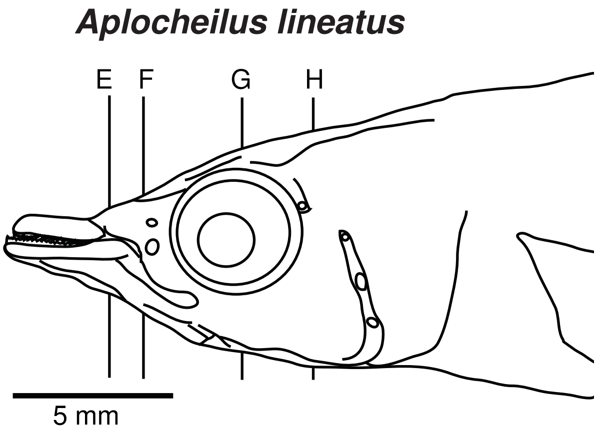
S4C)

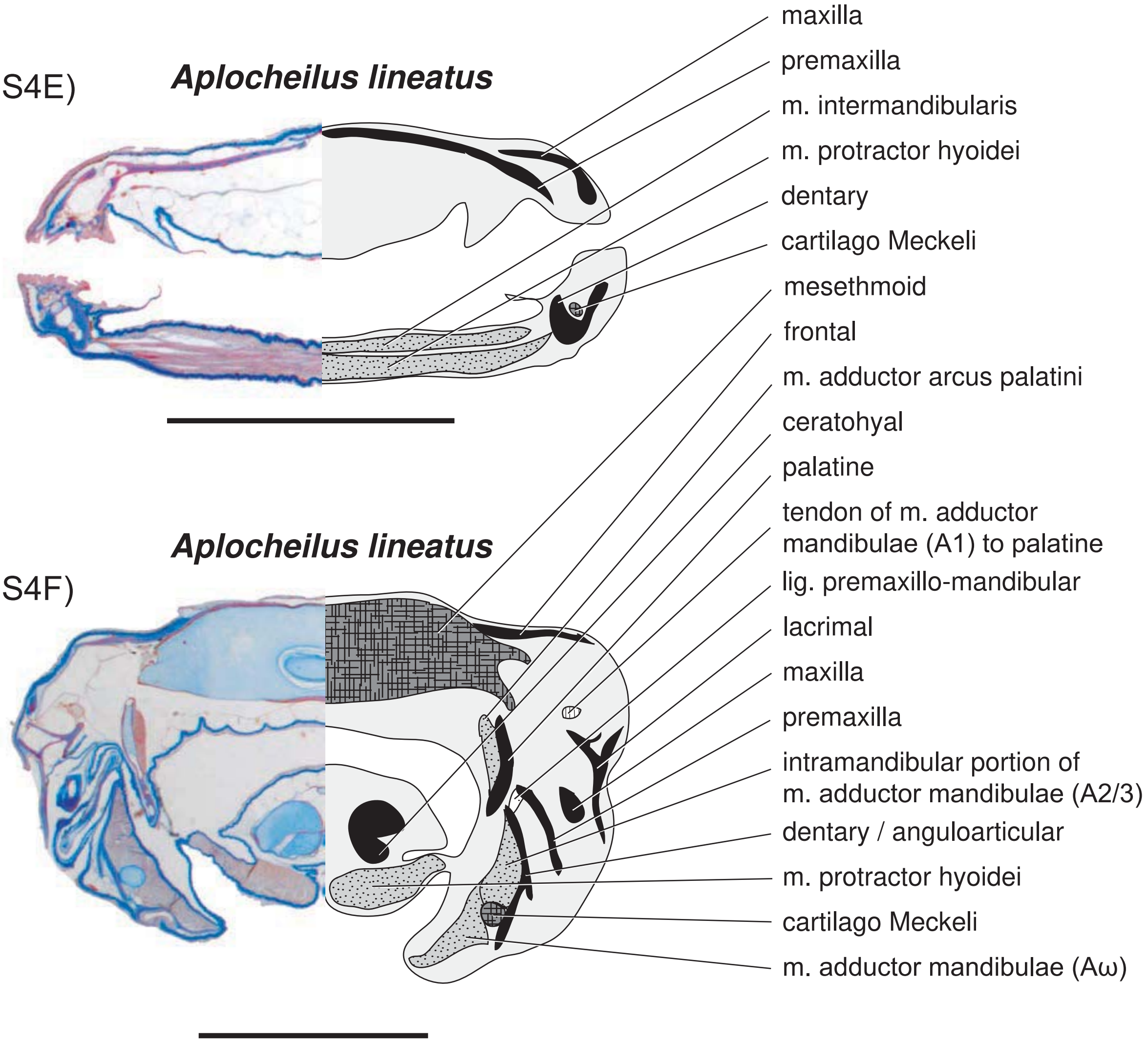


Aplocheilus lineatus

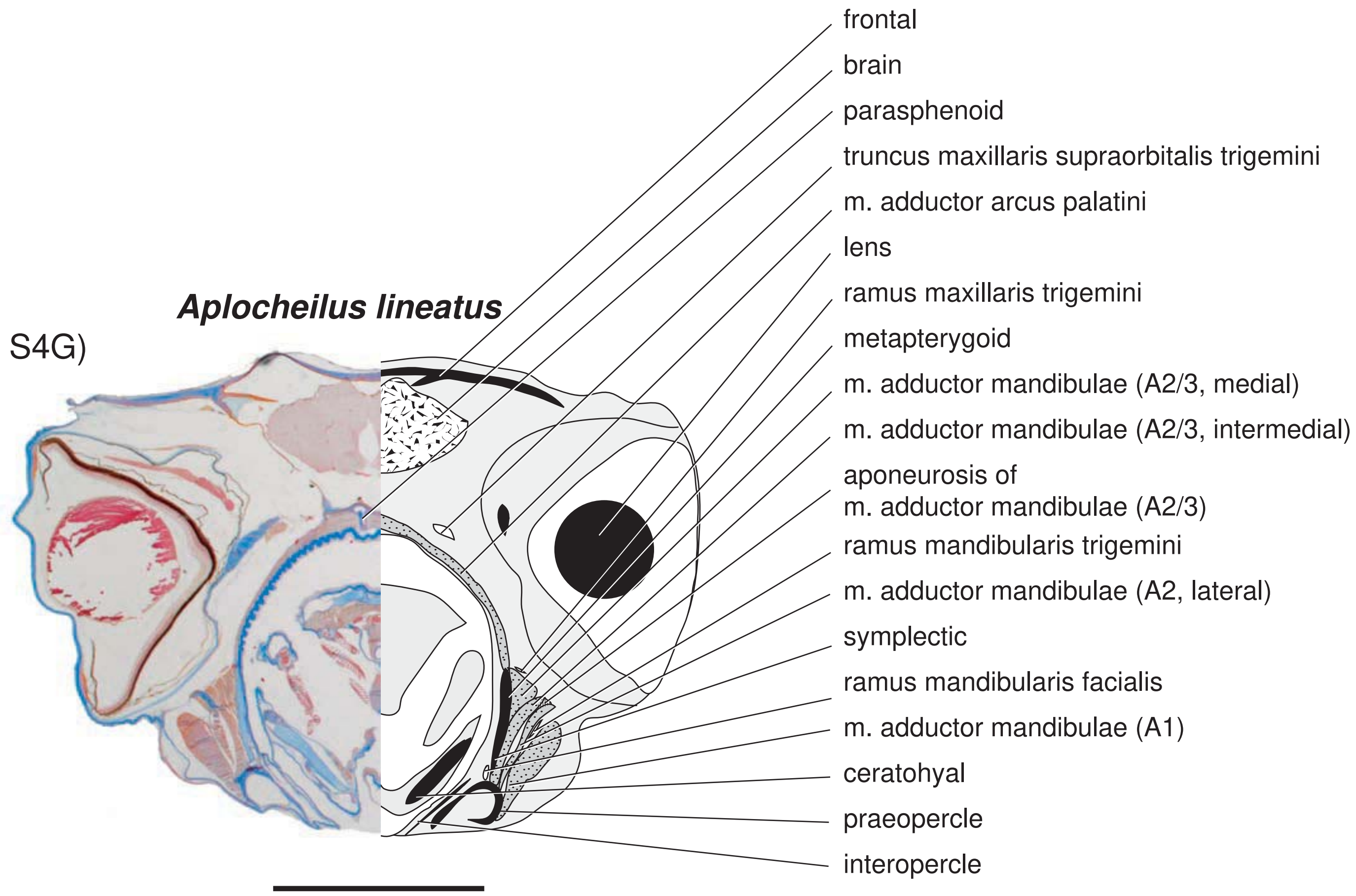
S4D)



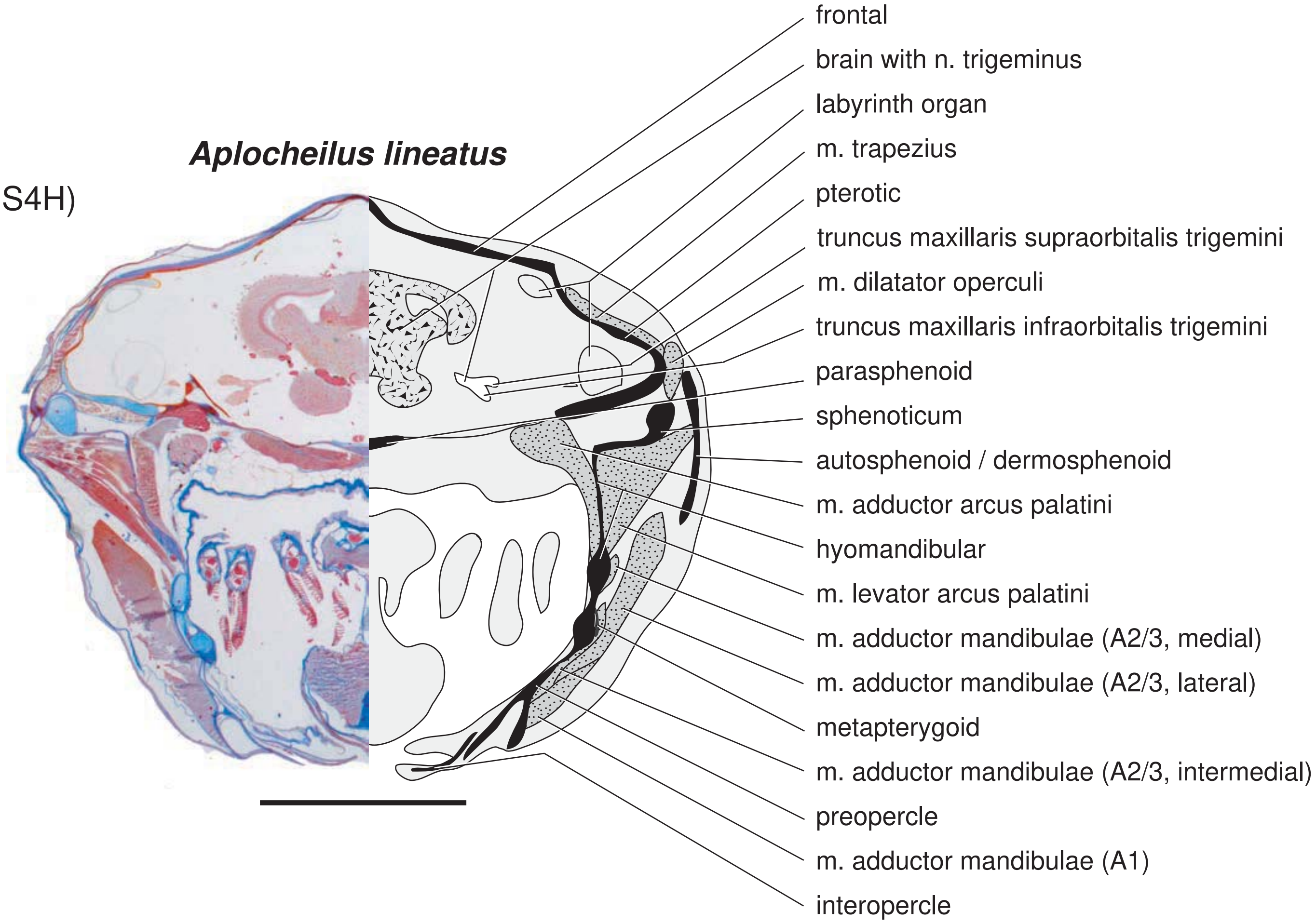

Aplocheilus lineatus
E
F
G
H
5 mm


S4E)
Aplocheilus lineatus
S4F)
Aplocheilus lineatus
maxilla
premaxilla
m. intermandibularis
m. protractor hyoidei
dentary
cartilago Meckeli
mesethmoid
frontal
m. adductor arcus palatini
ceratohyal
palatine
tendon of m. adductor mandibulae (A1) to palatine
lig. premaxillo-mandibular
lacrimal
maxilla
premaxilla
intramandibular portion of m. adductor mandibulae (A2/3)
dentary / anguloarticular
m. protractor hyoidei
cartilago Meckeli
m. adductor mandibulae (Aω)

S4G)



S4H)



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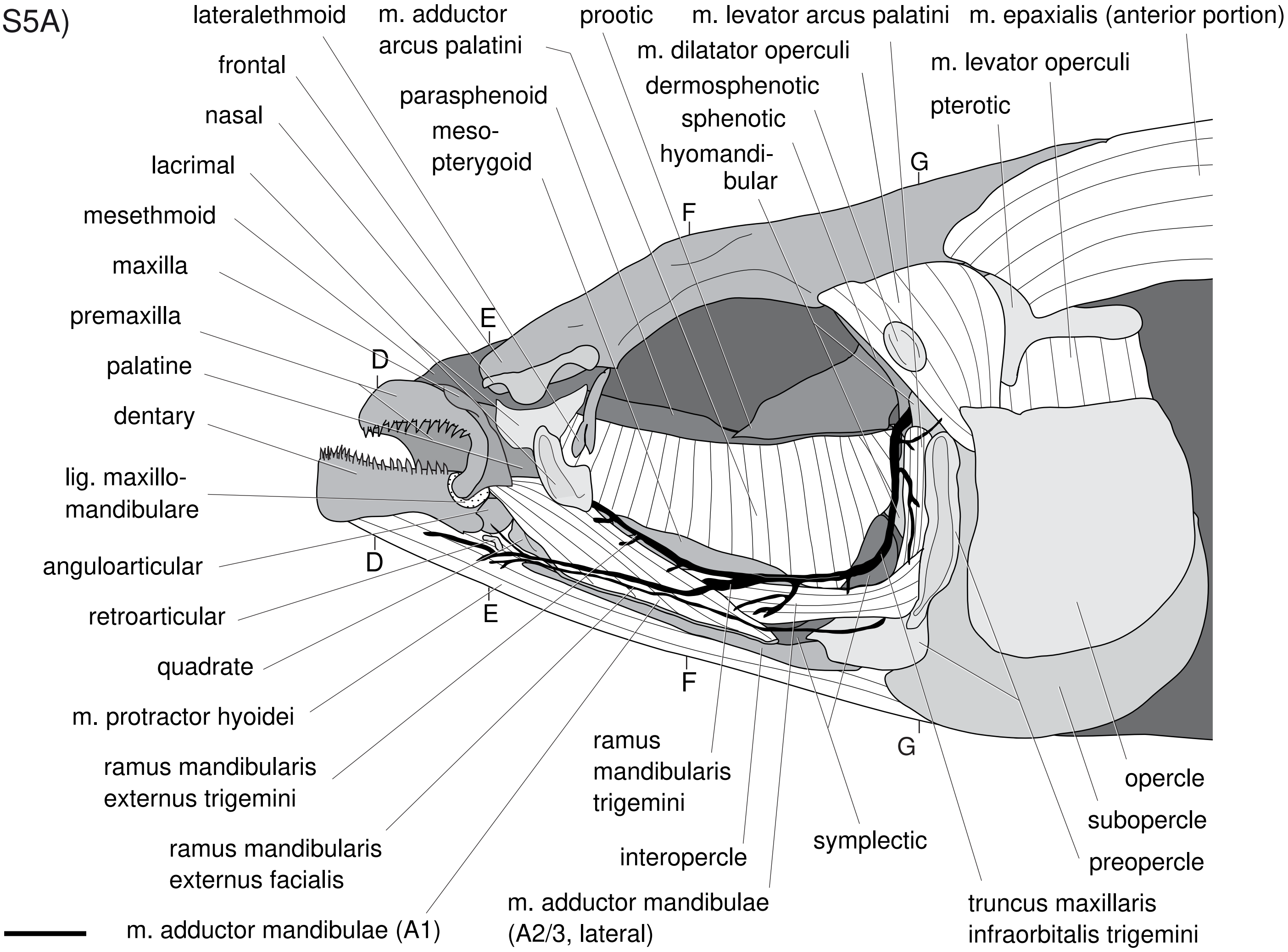
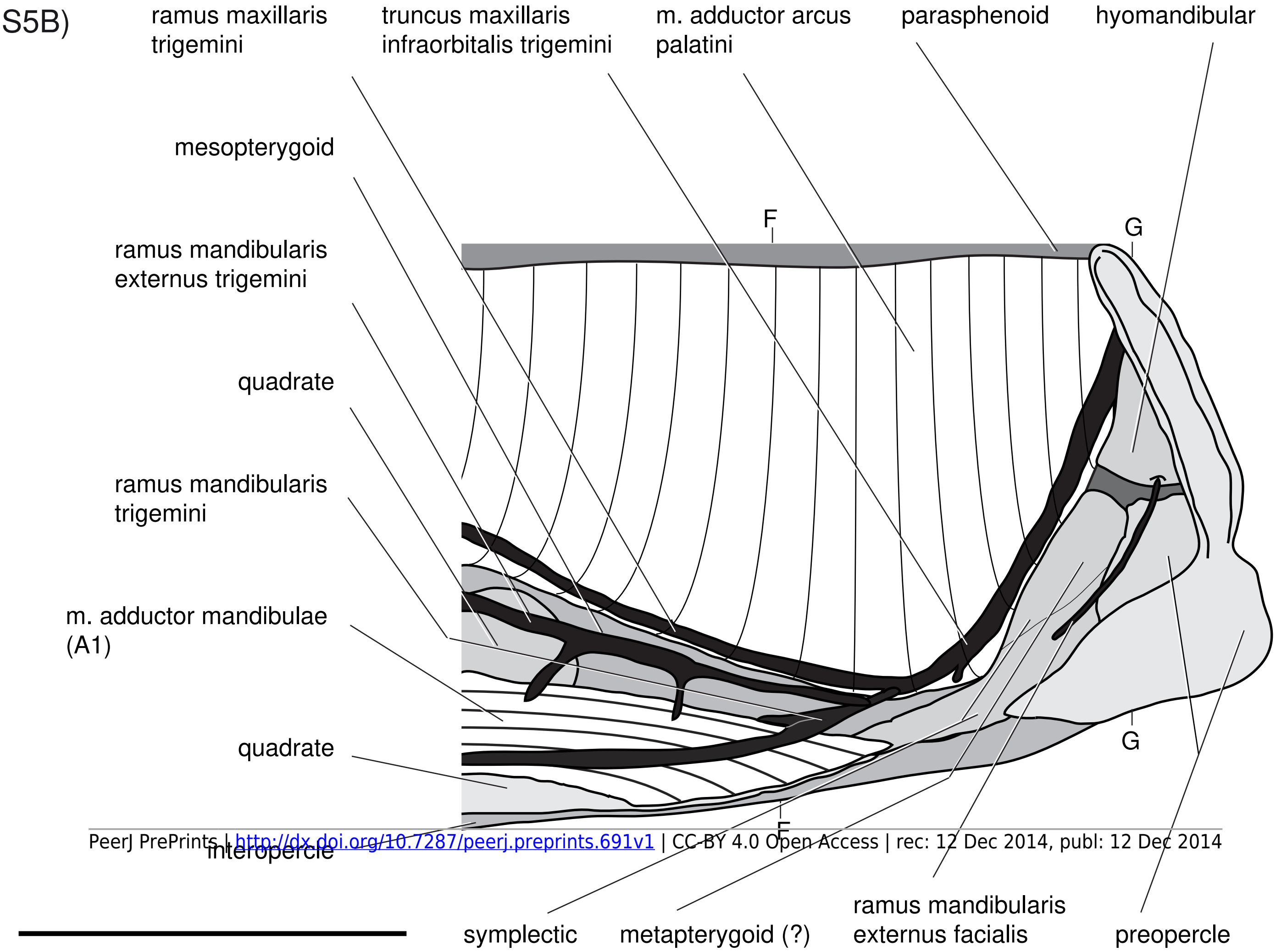
Oryzias latipes

S5A)



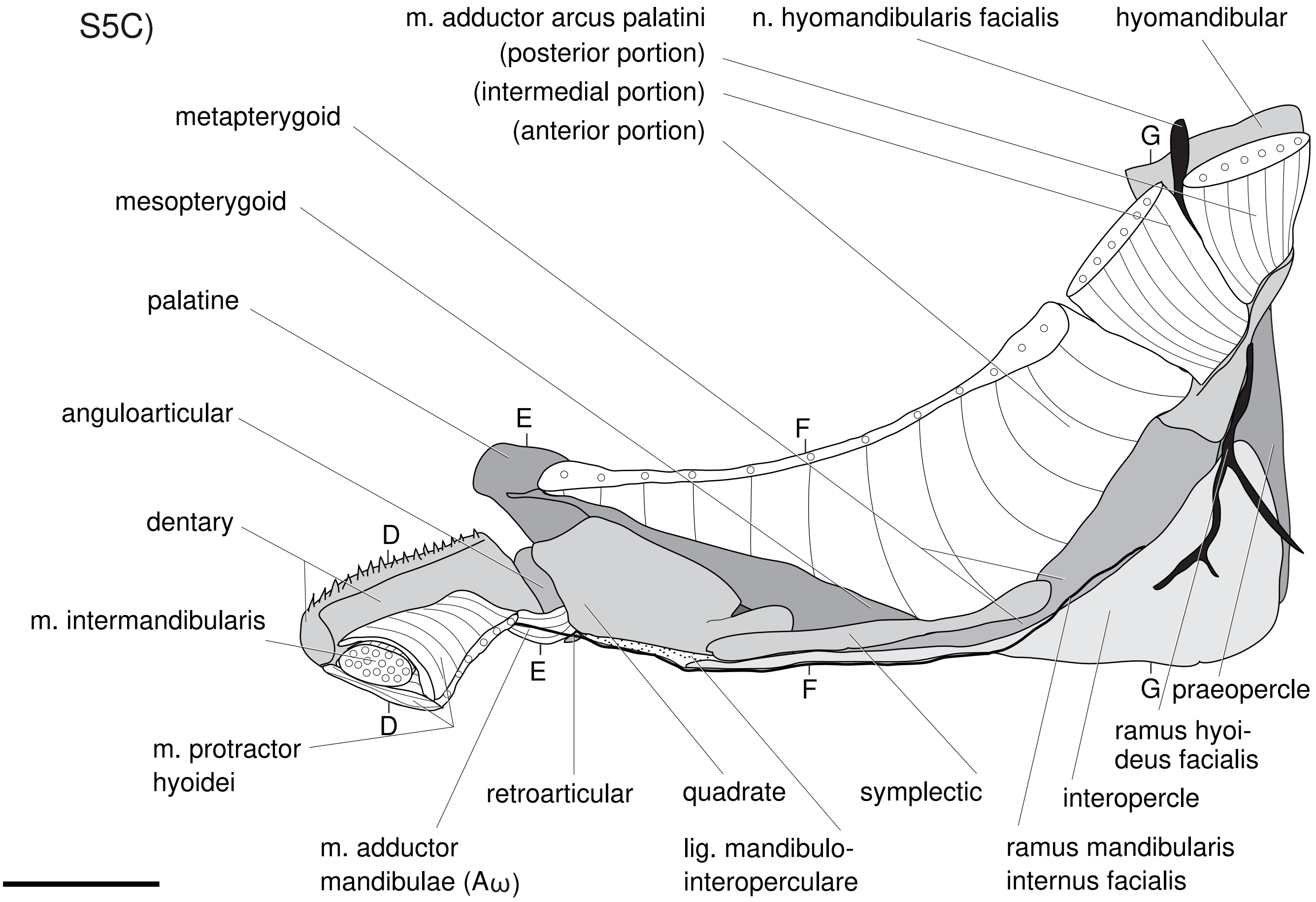
Oryzias latipes

S5B)



S5C)

Oryzias latipes



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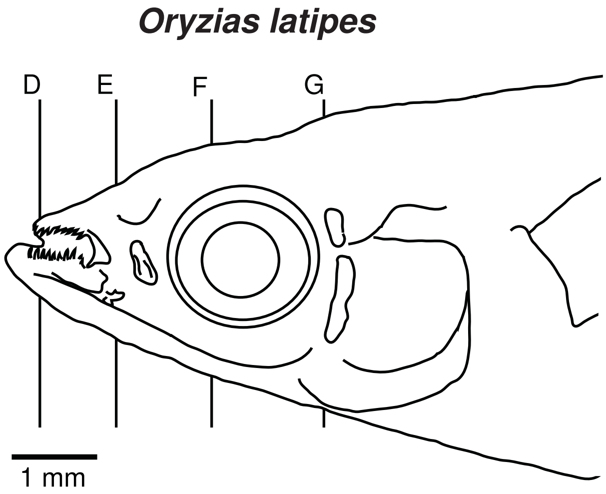

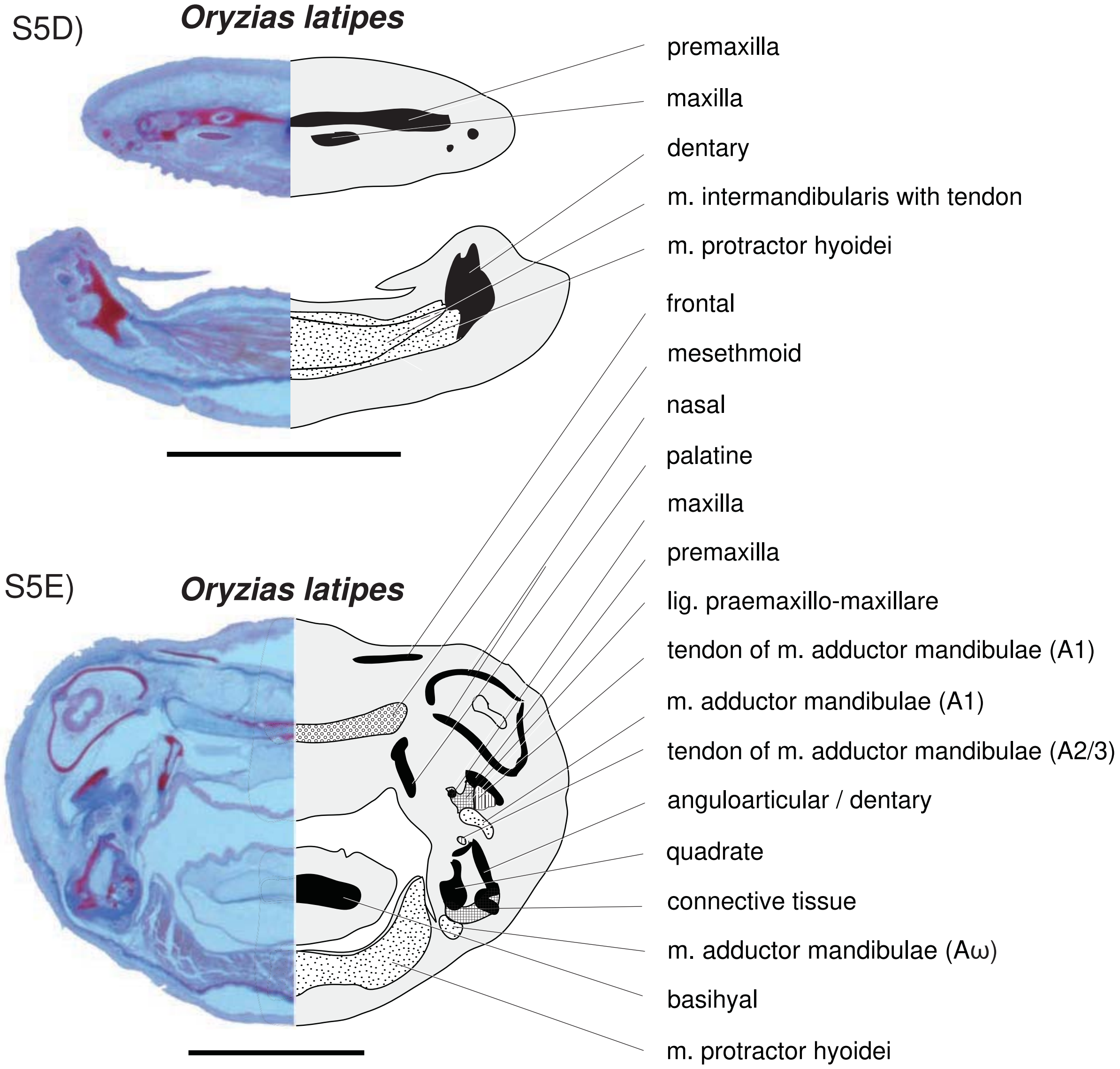

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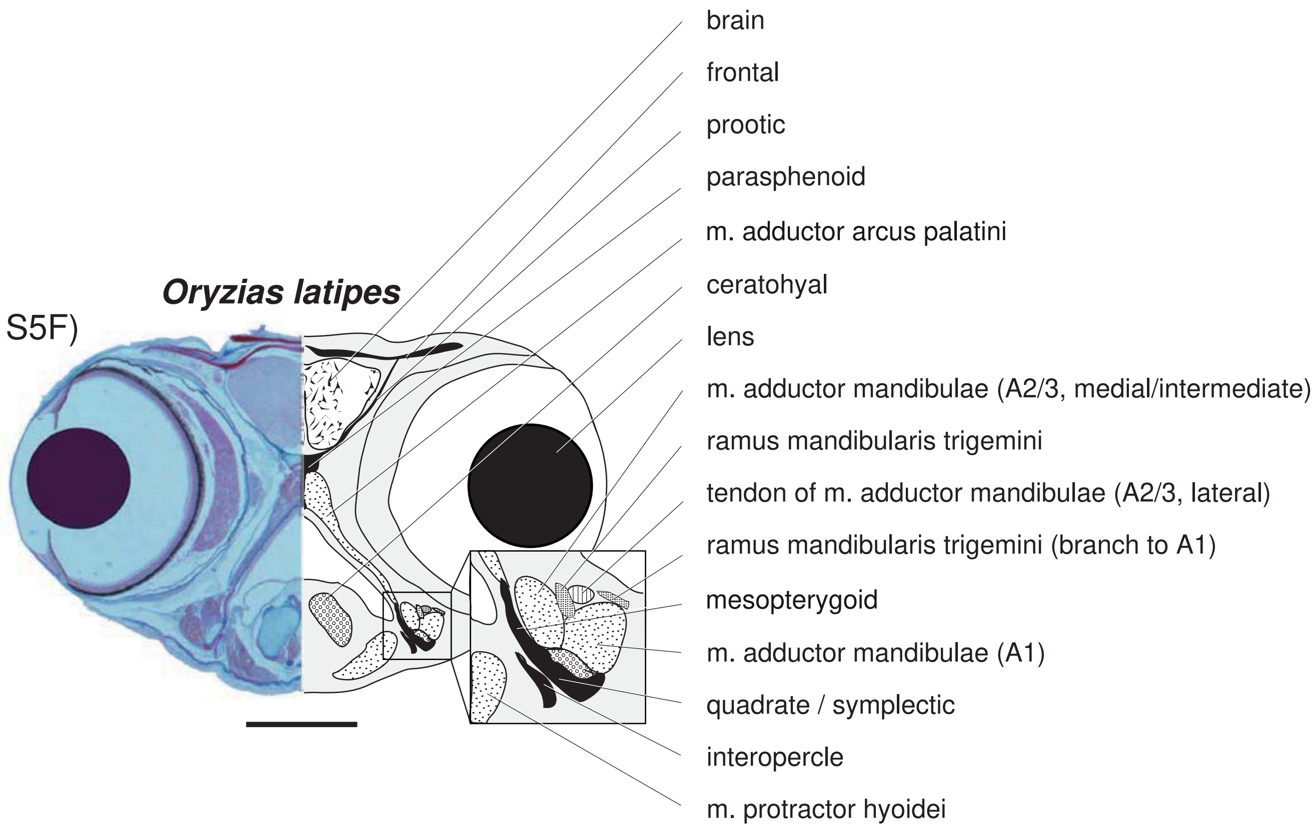

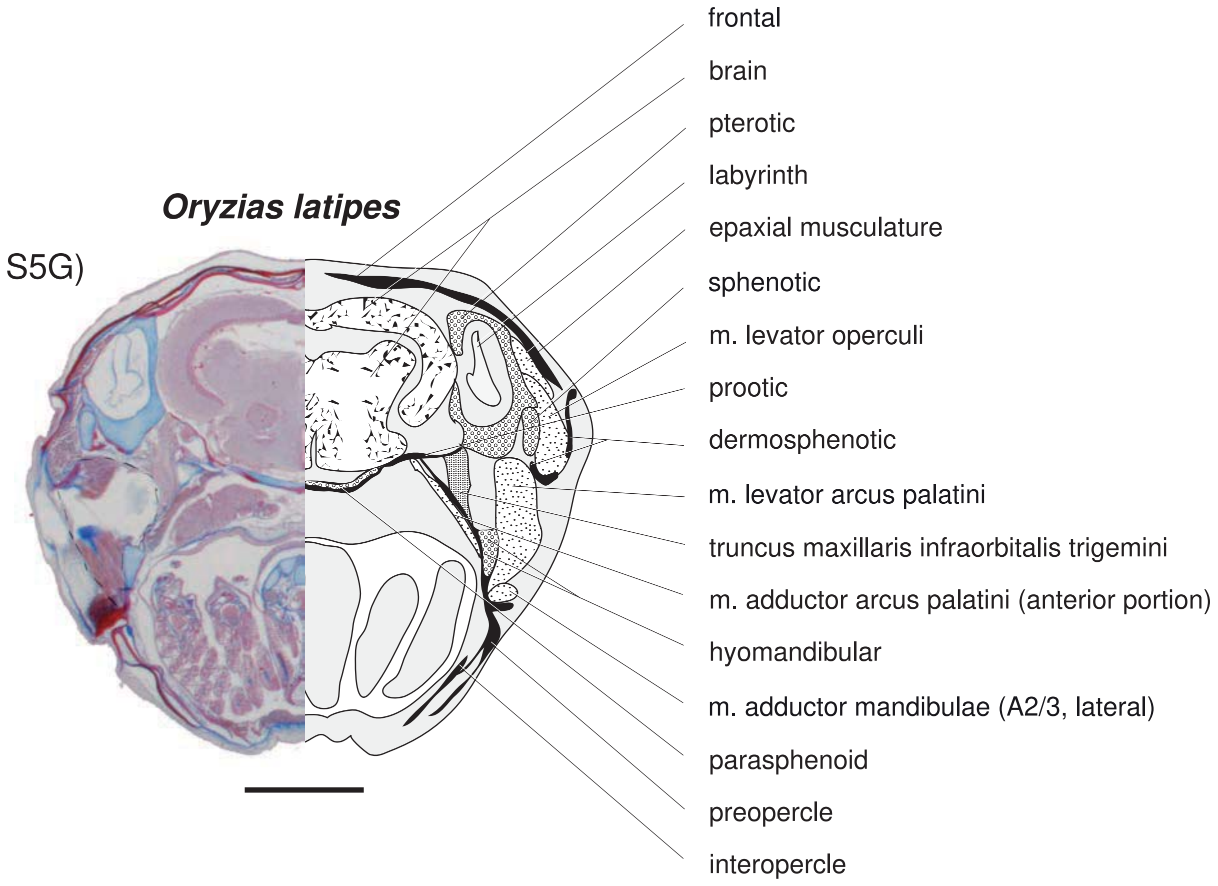

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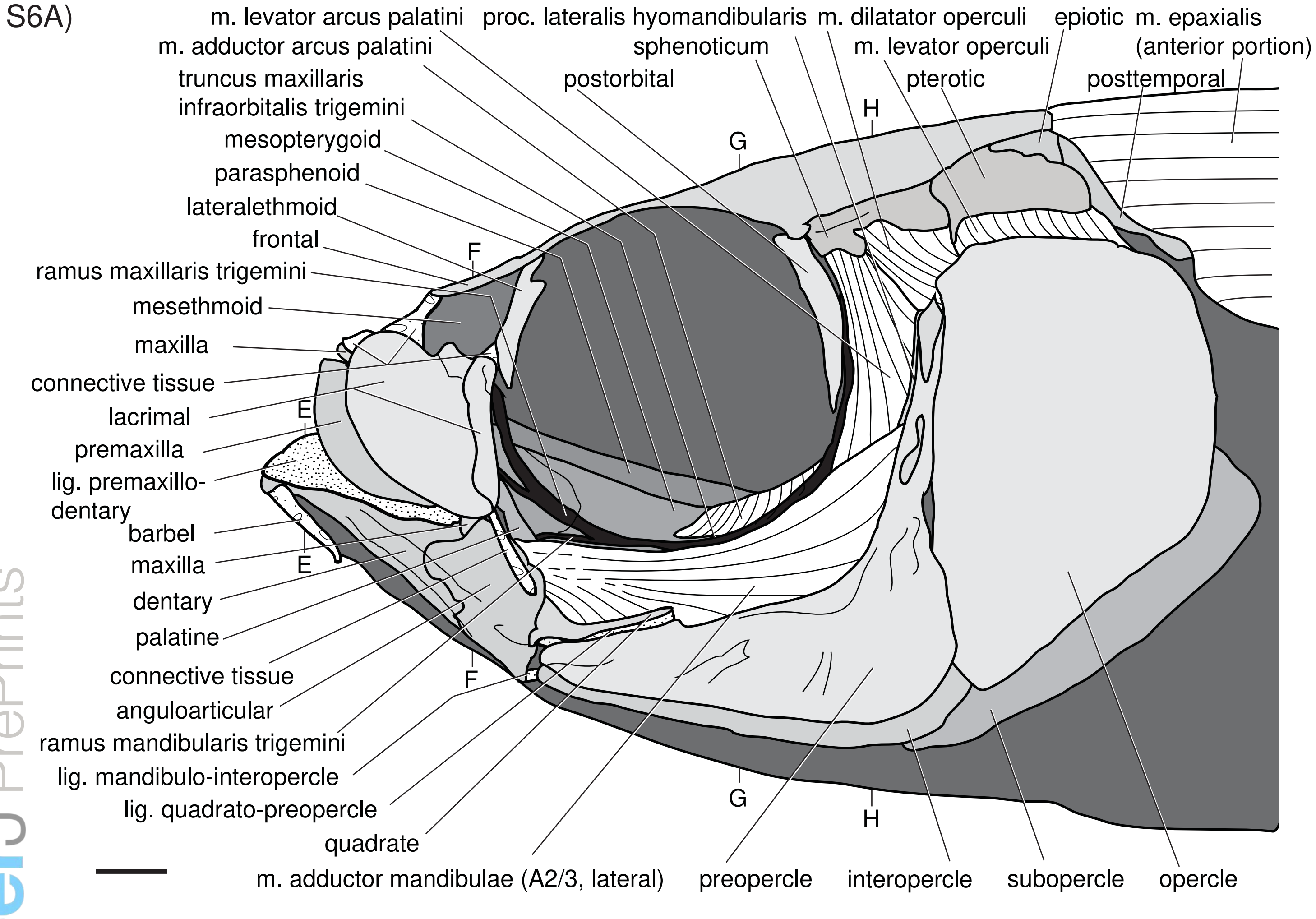
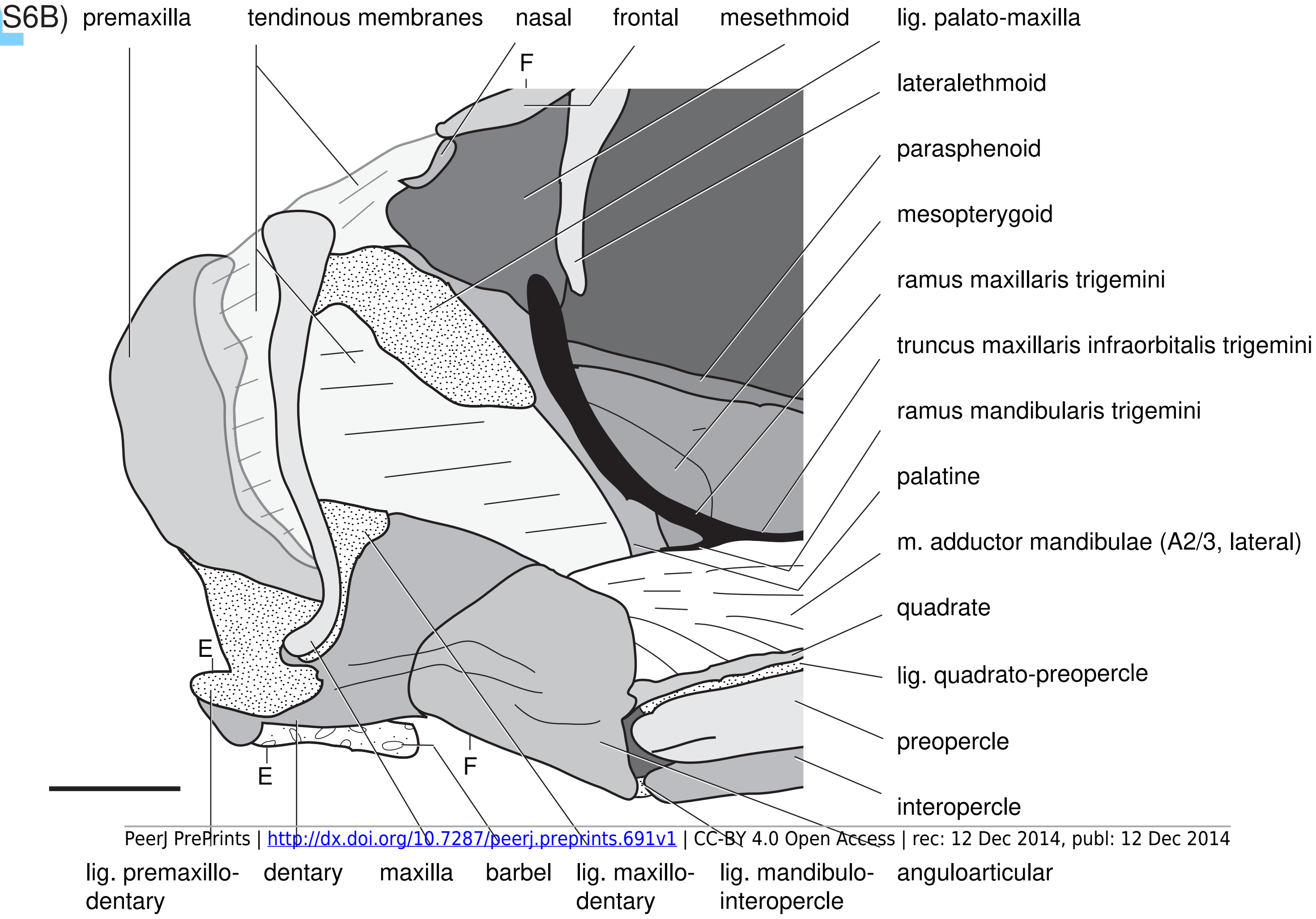
Parexocoetus brachypterus



Parexocoetus brachypterus



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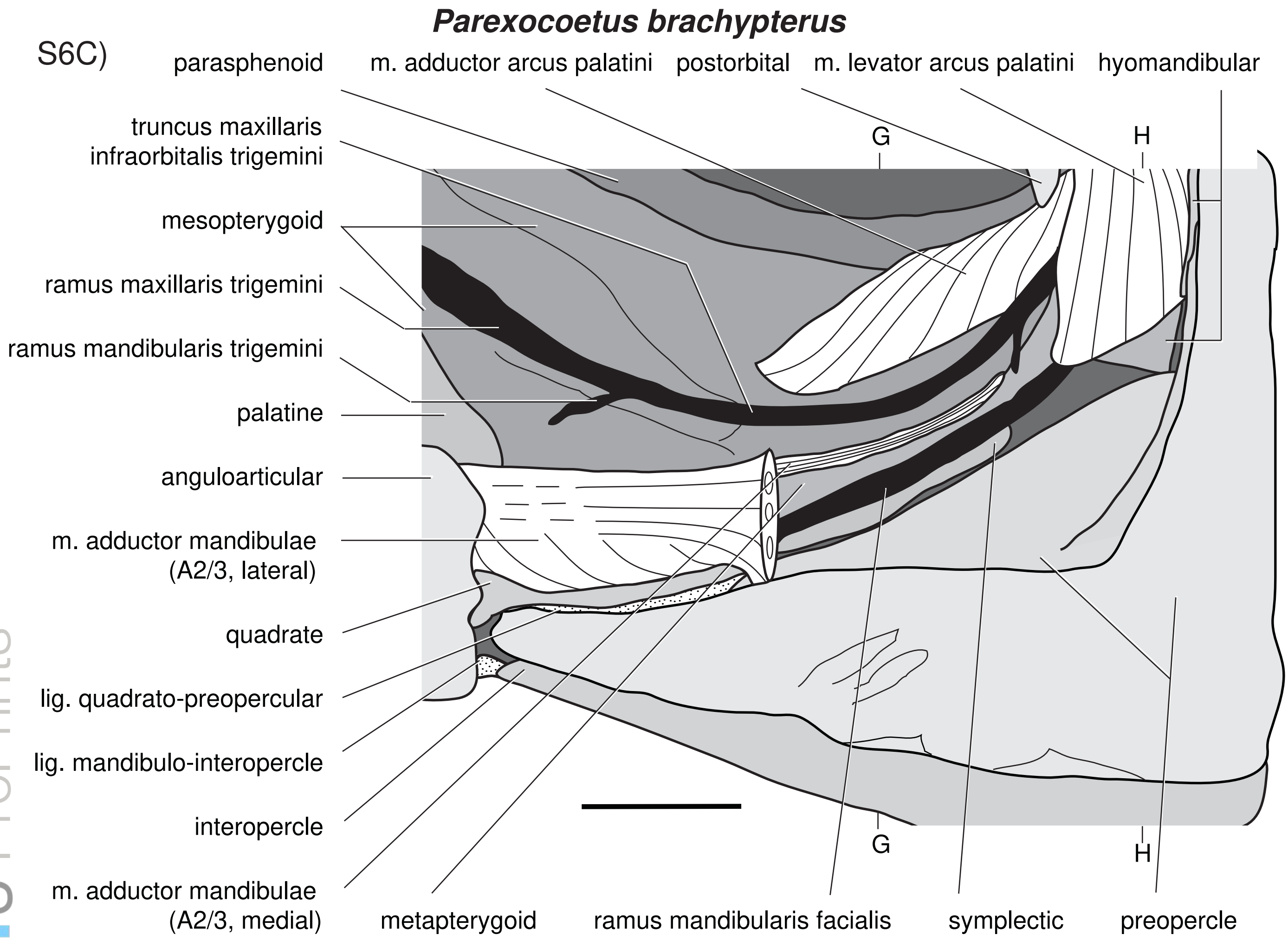
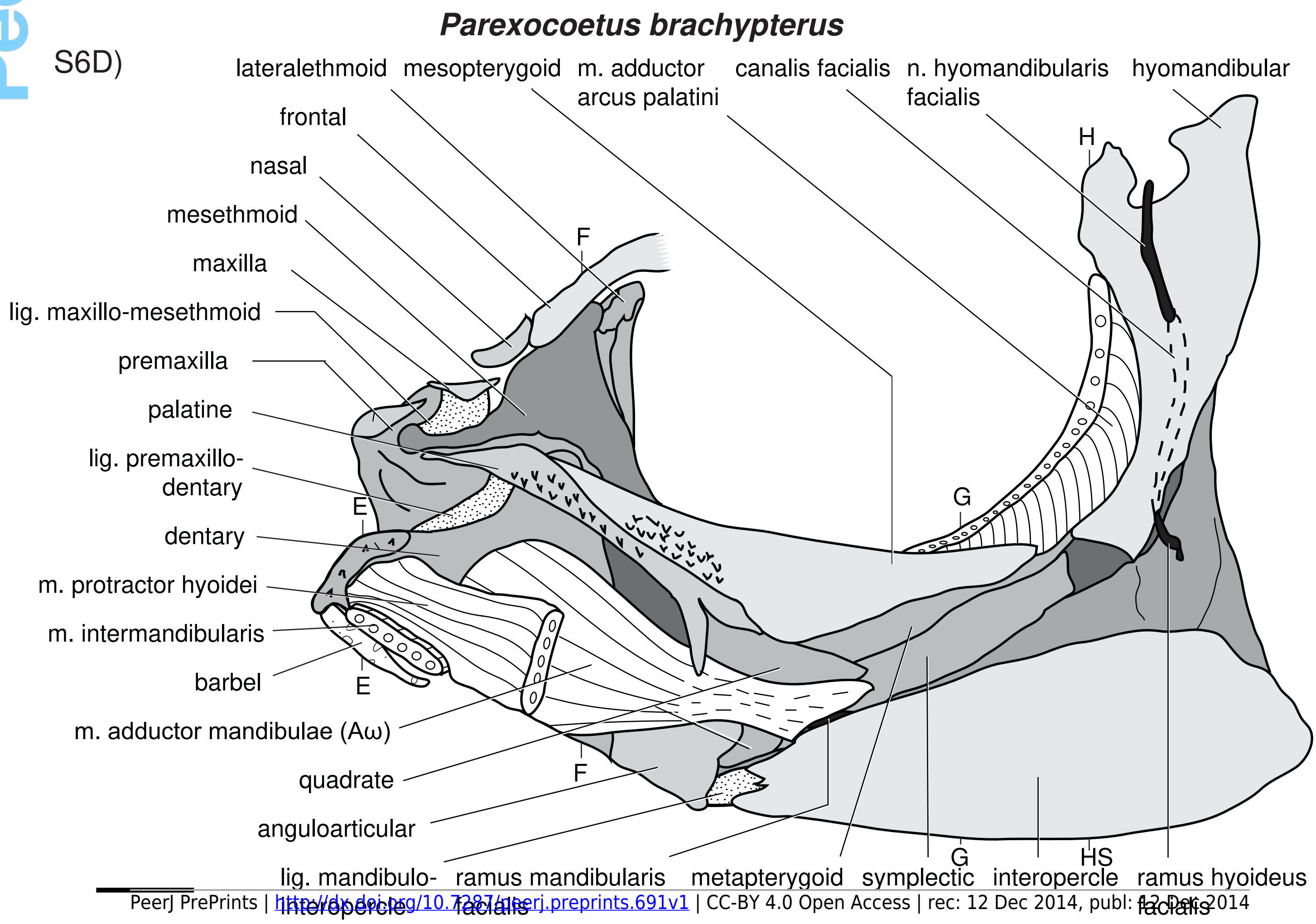
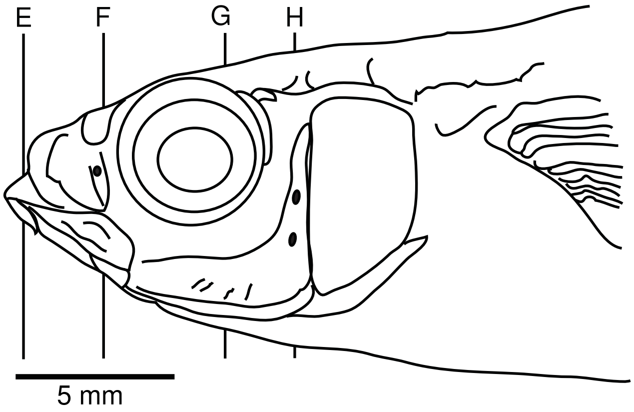
S6C)


Parexocoetus brachypterus
parasphenoid
m. adductor arcus palatini
postorbital
m. levator arcus palatini
hyomandibular
truncus maxillaris infraorbitalis trigemini
mesopterygoid
ramus maxillaris trigemini
ramus mandibularis trigemini
palatine
anguloarticular
m. adductor mandibulae (A2/3, lateral)
quadrate
lig. quadrato-preopercular
lig. mandibulo-interopercle
interopercle
m. adductor mandibulae (A2/3, medial)
metapterygoid
ramus mandibularis facialis
symplectic
preopercle
G
H
G
H

S6D)

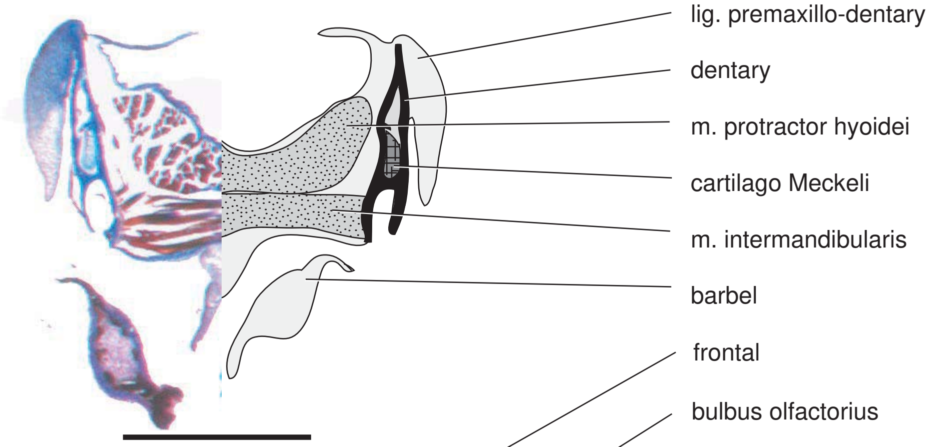

Parexocoetus brachypterus
lateralethmoid
mesopterygoid
m. adductor arcus palatini
canalis facialis
n. hyomandibularis facialis
hyomandibular
frontal
nasal
mesethmoid
maxilla
lig. maxillo-mesethmoid
premaxilla
palatine
lig. premaxillo-dentary
dentary
m. protractor hyoidei
m. intermandibularis
barbel
m. adductor mandibulae (Aω)
quadrate
anguloarticular
lig. mandibulo-interopercle
ramus mandibularis facialis
metapterygoid
symplectic
interopercle
ramus hyoideus facialis
F
H
G
E
E
F
G
HS

Parexocoetus brachypterus



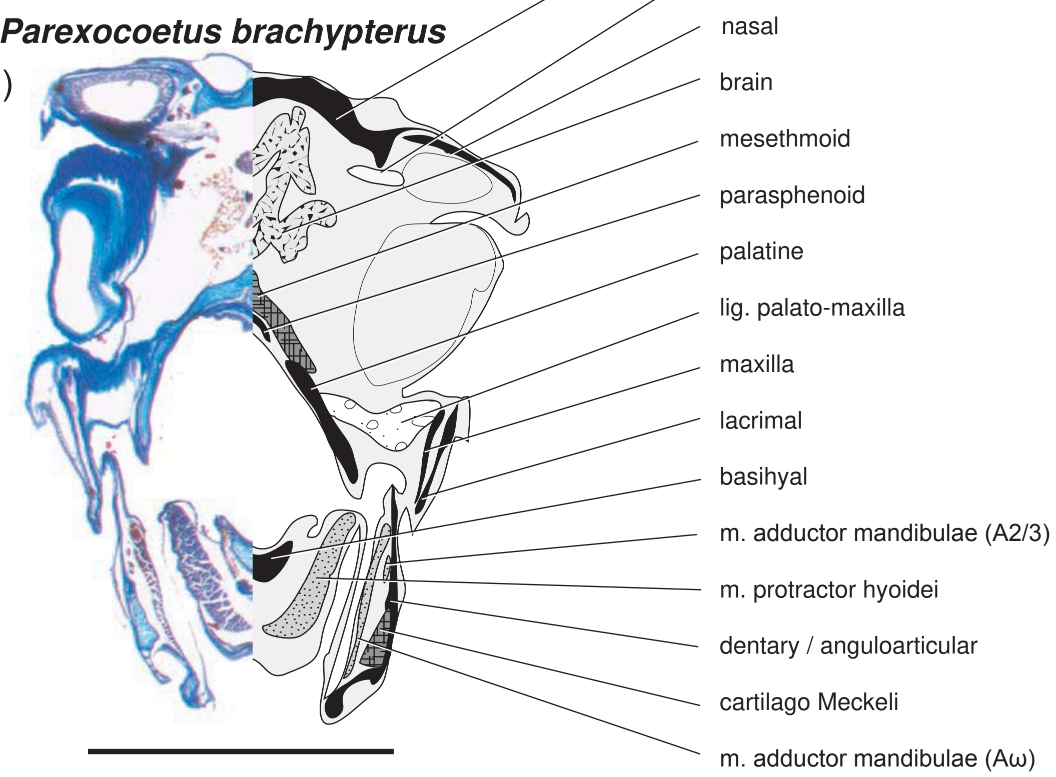
Parexocoetus brachypterus

S6E)



Parexocoetus brachypterus

S6F)



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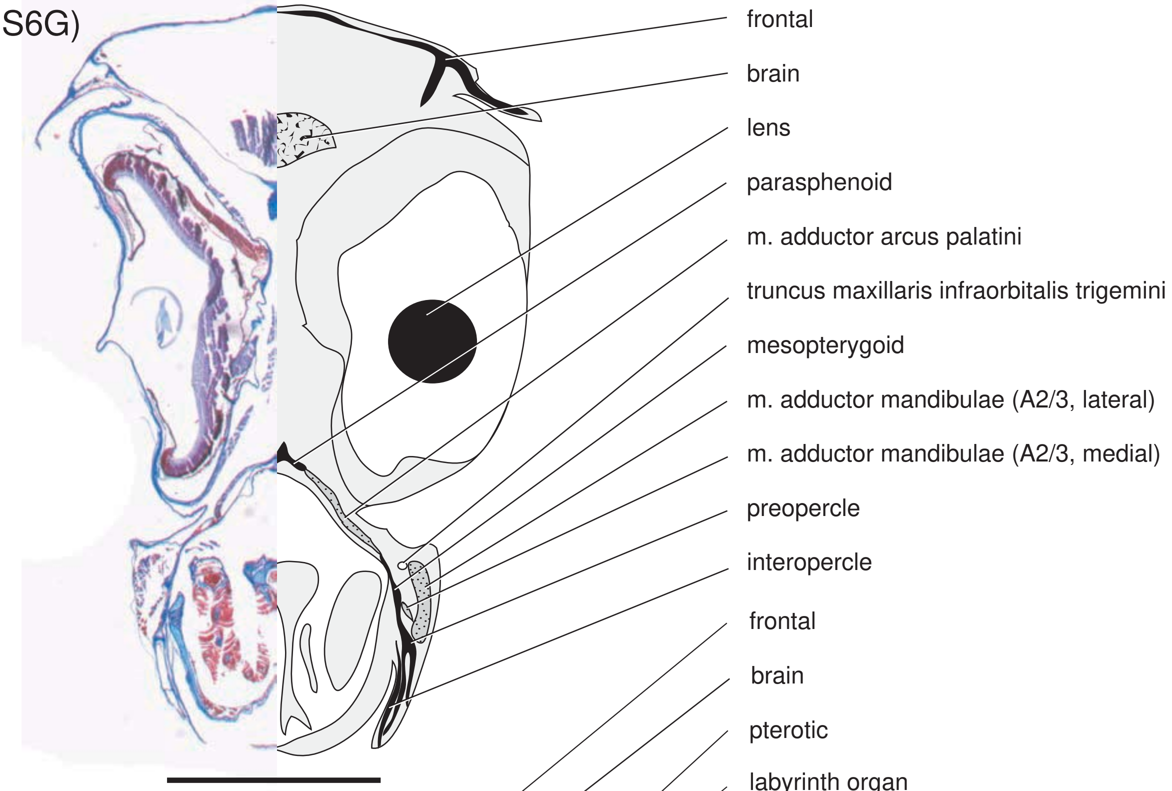
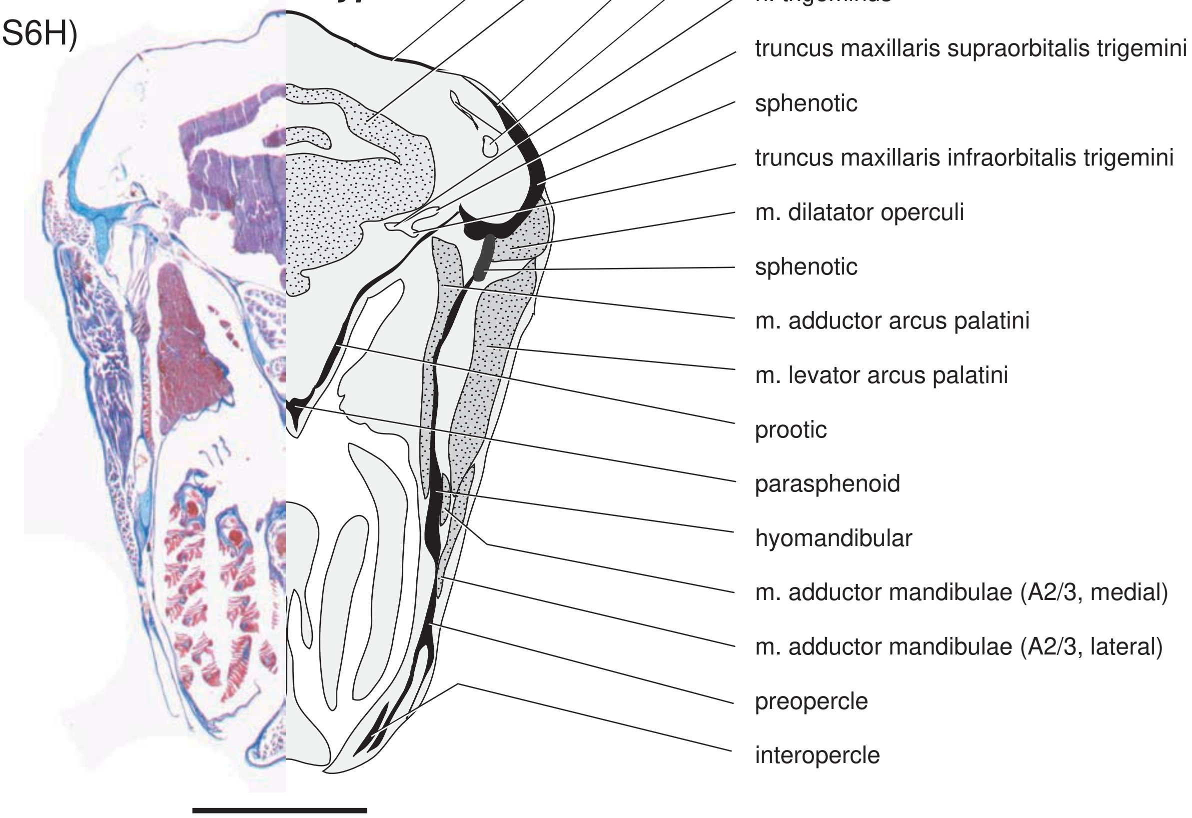
Parexocoetus brachypterus

S6G)



Parexocoetus brachypterus

S6H)



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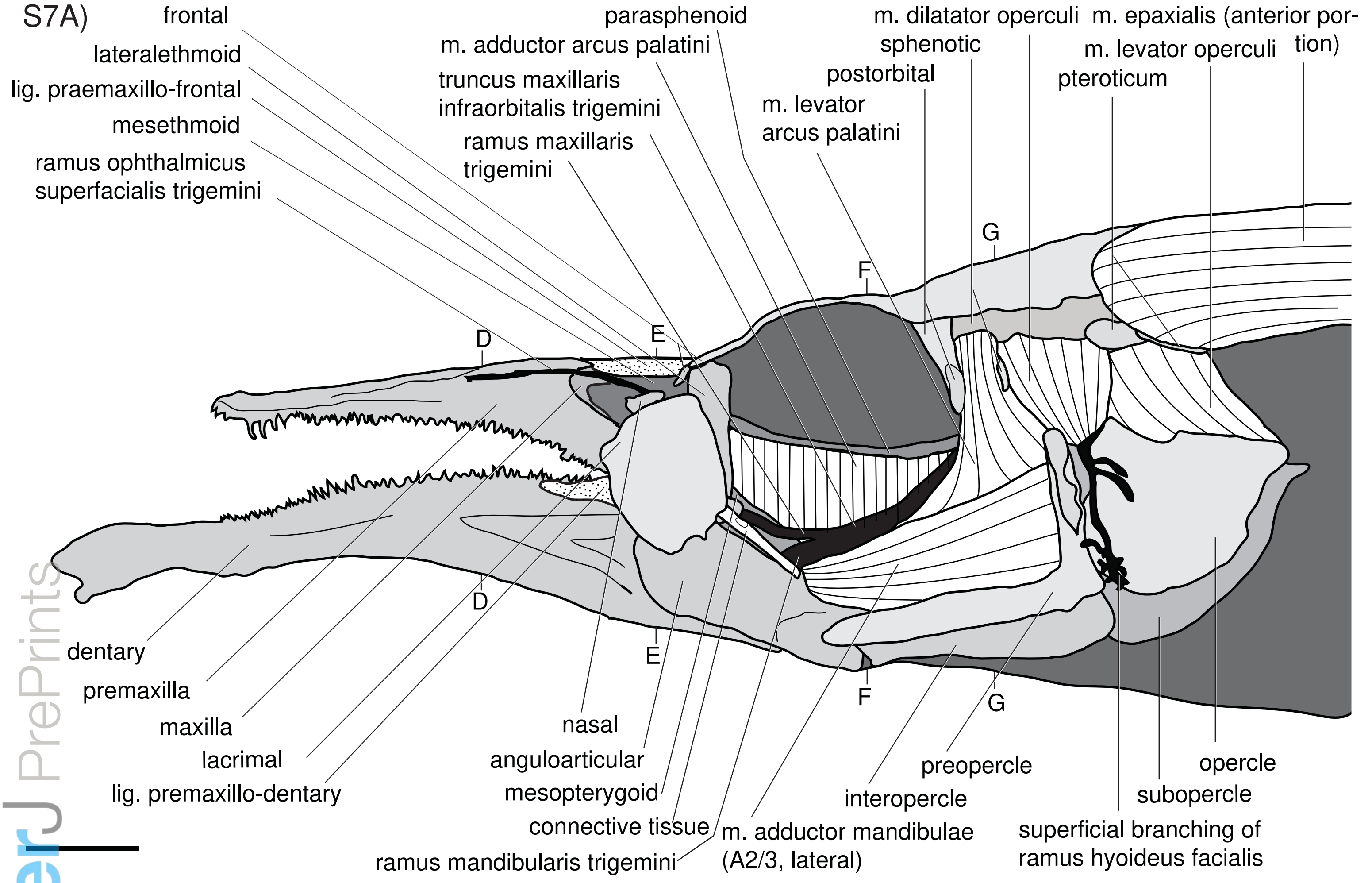
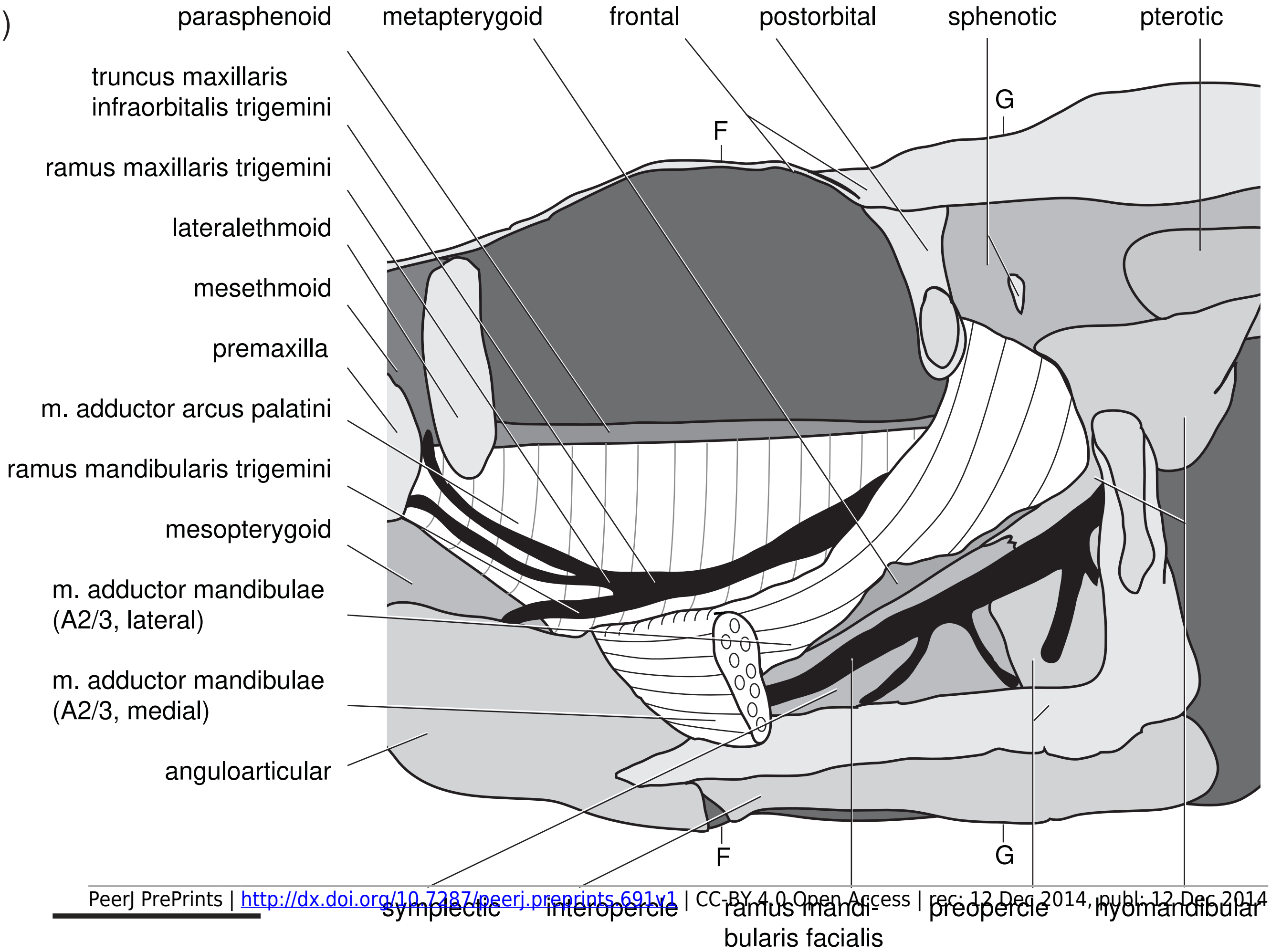
Dermogenys pussila

S7A)



Dermogenys pussila

S7B)



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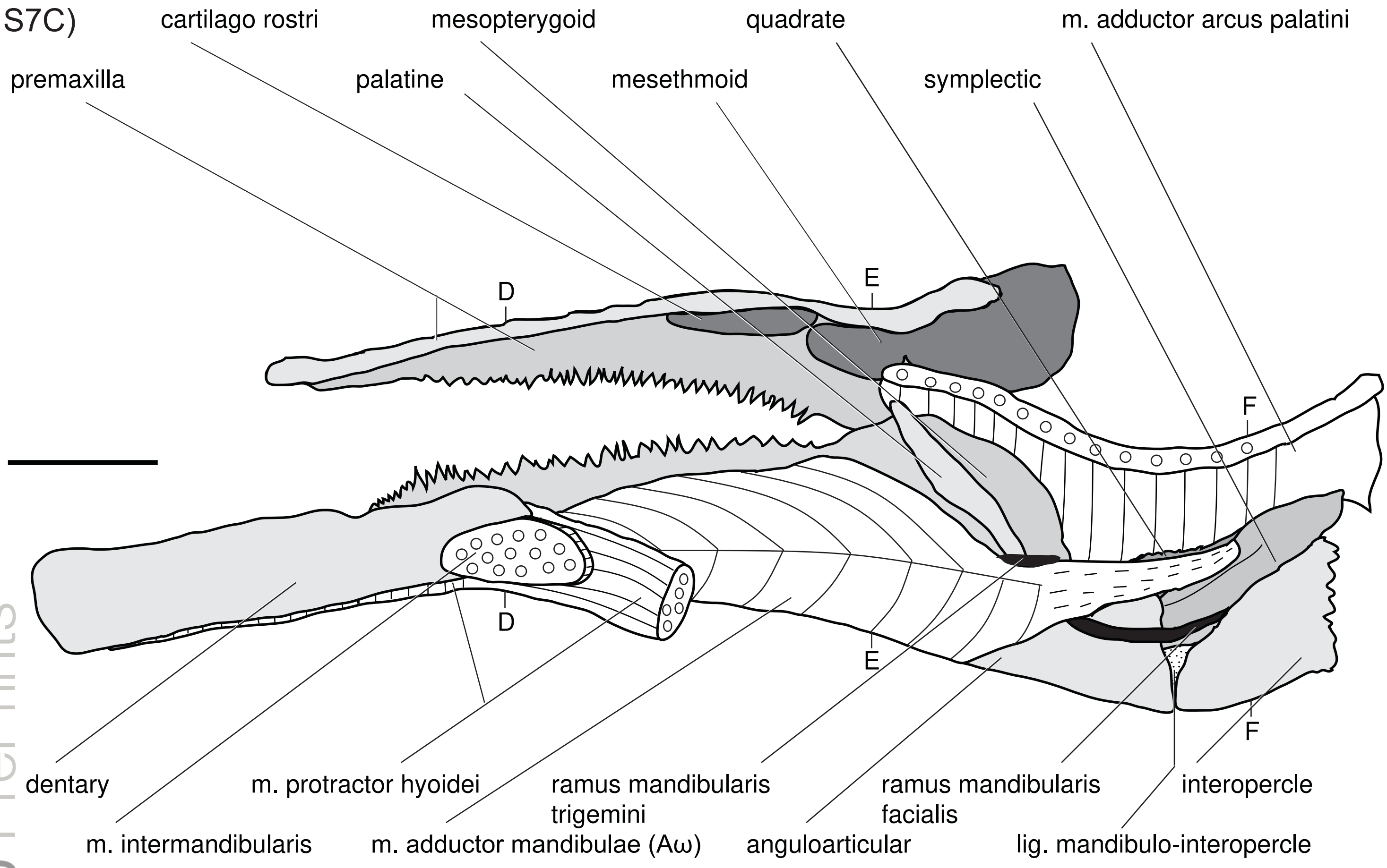
S7C) ***Dermogenys pussila***



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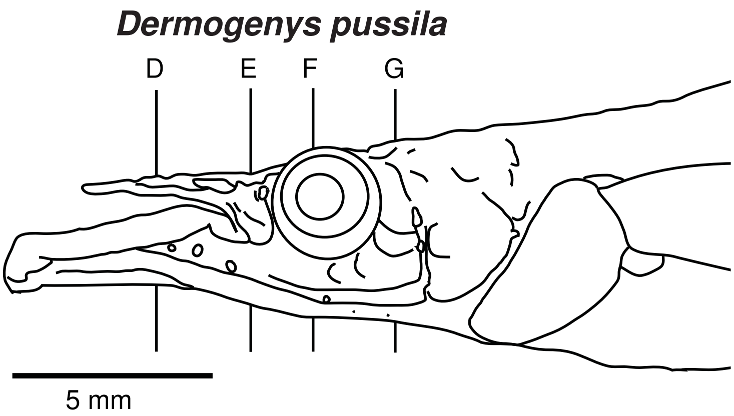
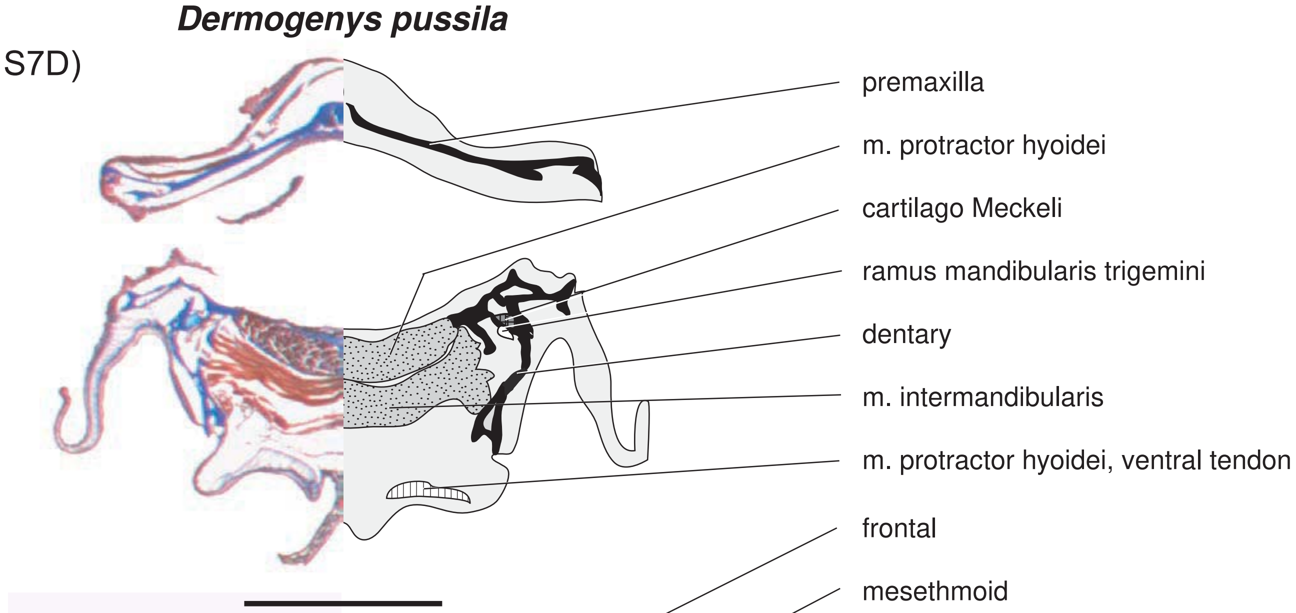
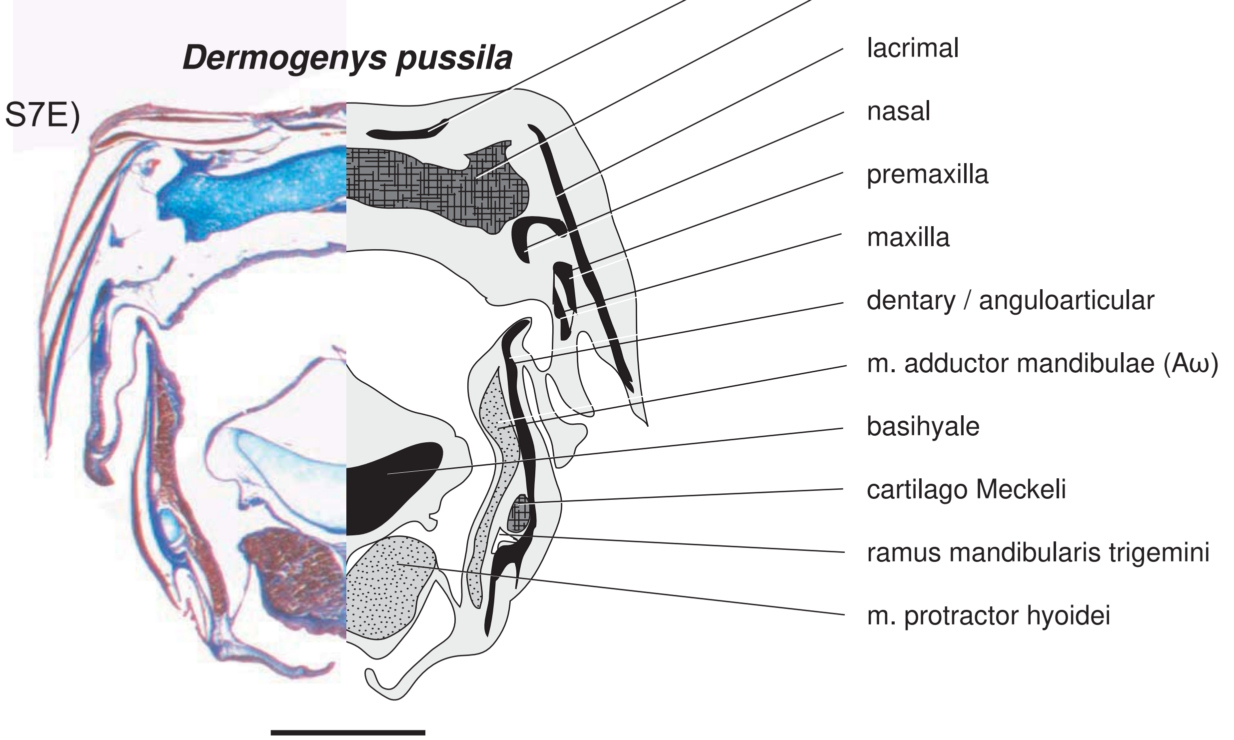
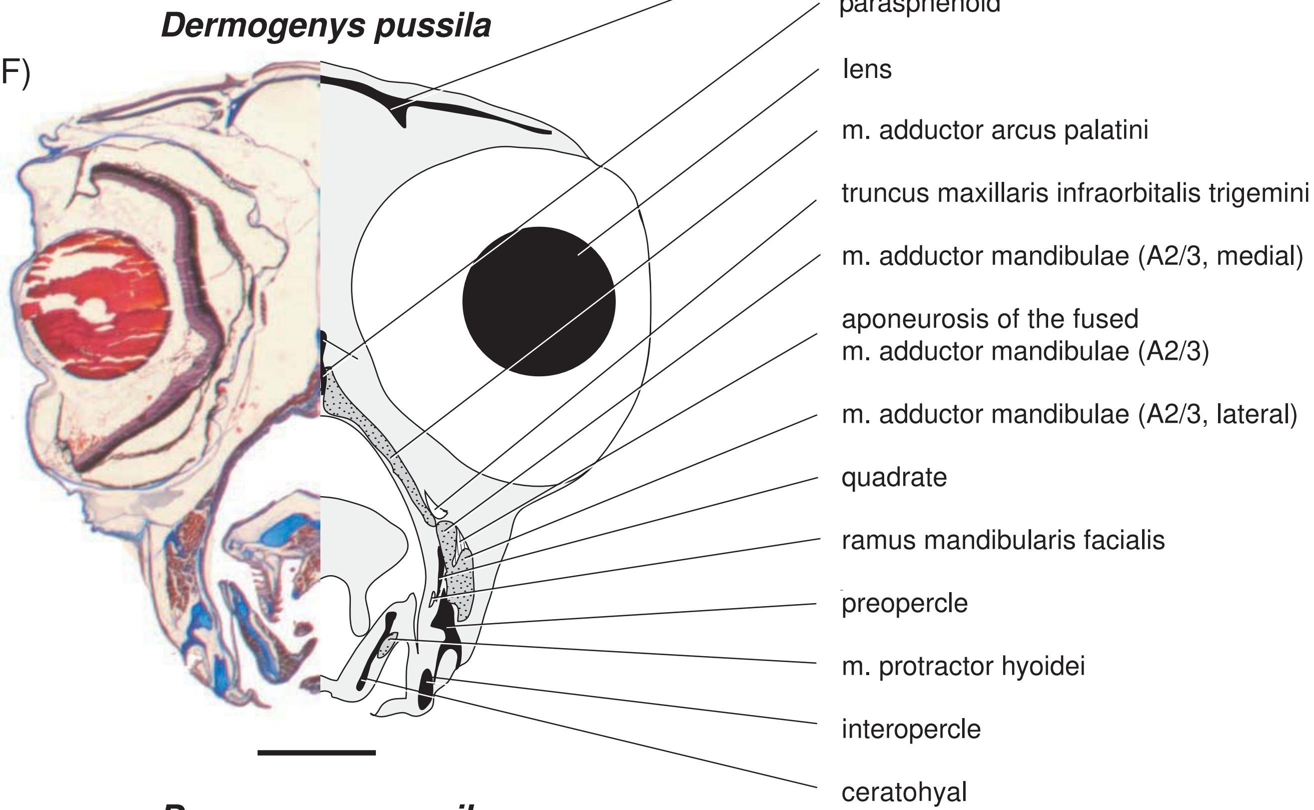

Dermogenys pussila
D
E
F
G
5 mm

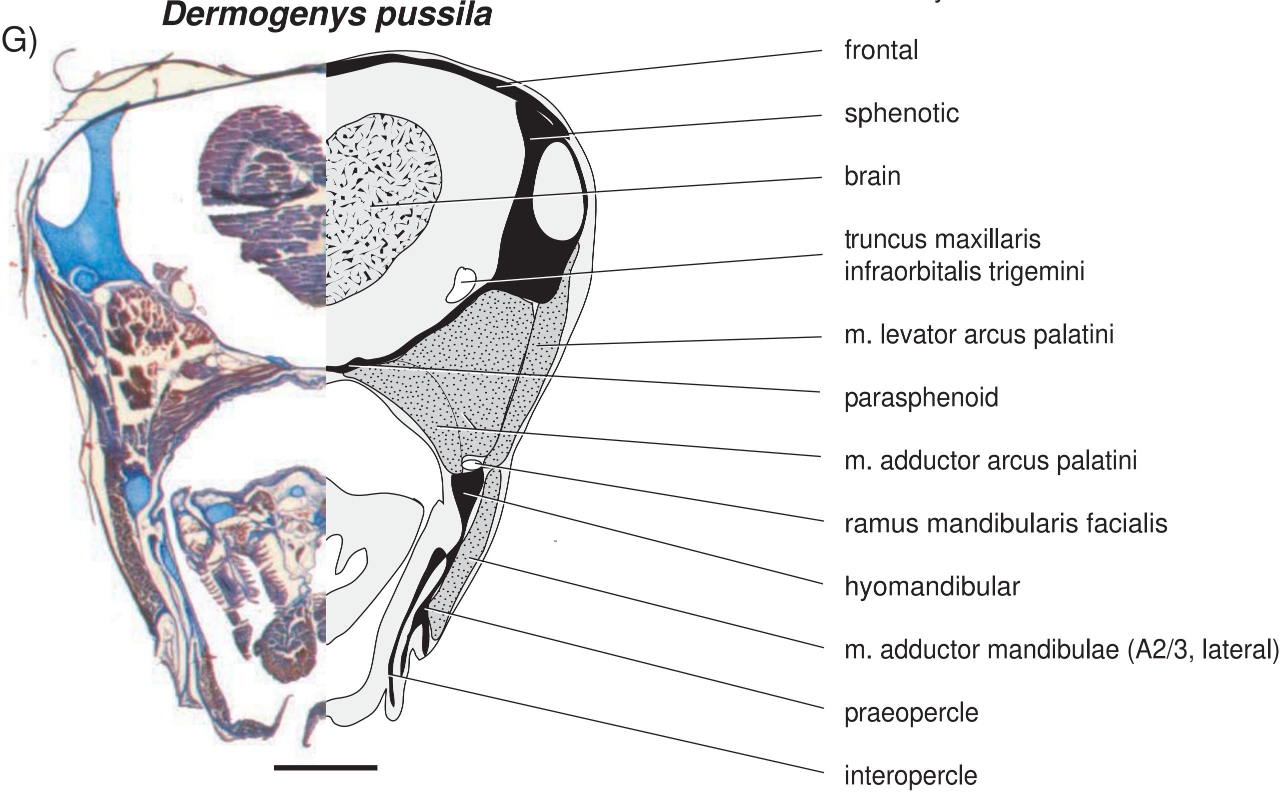

Dermogenys pussila
S7D)
premaxilla
m. protractor hyoidei
cartilago Meckeli
ramus mandibularis trigemini
dentary
m. intermandibularis
m. protractor hyoidei, ventral tendon


Dermogenys pussila
S7E)
frontal
mesethmoid
lacrimal
nasal
premaxilla
maxilla
dentary / anguloarticular
m. adductor mandibulae (Aω)
basihyale
cartilago Meckeli
ramus mandibularis trigemini
m. protractor hyoidei

S7F)



S7G)



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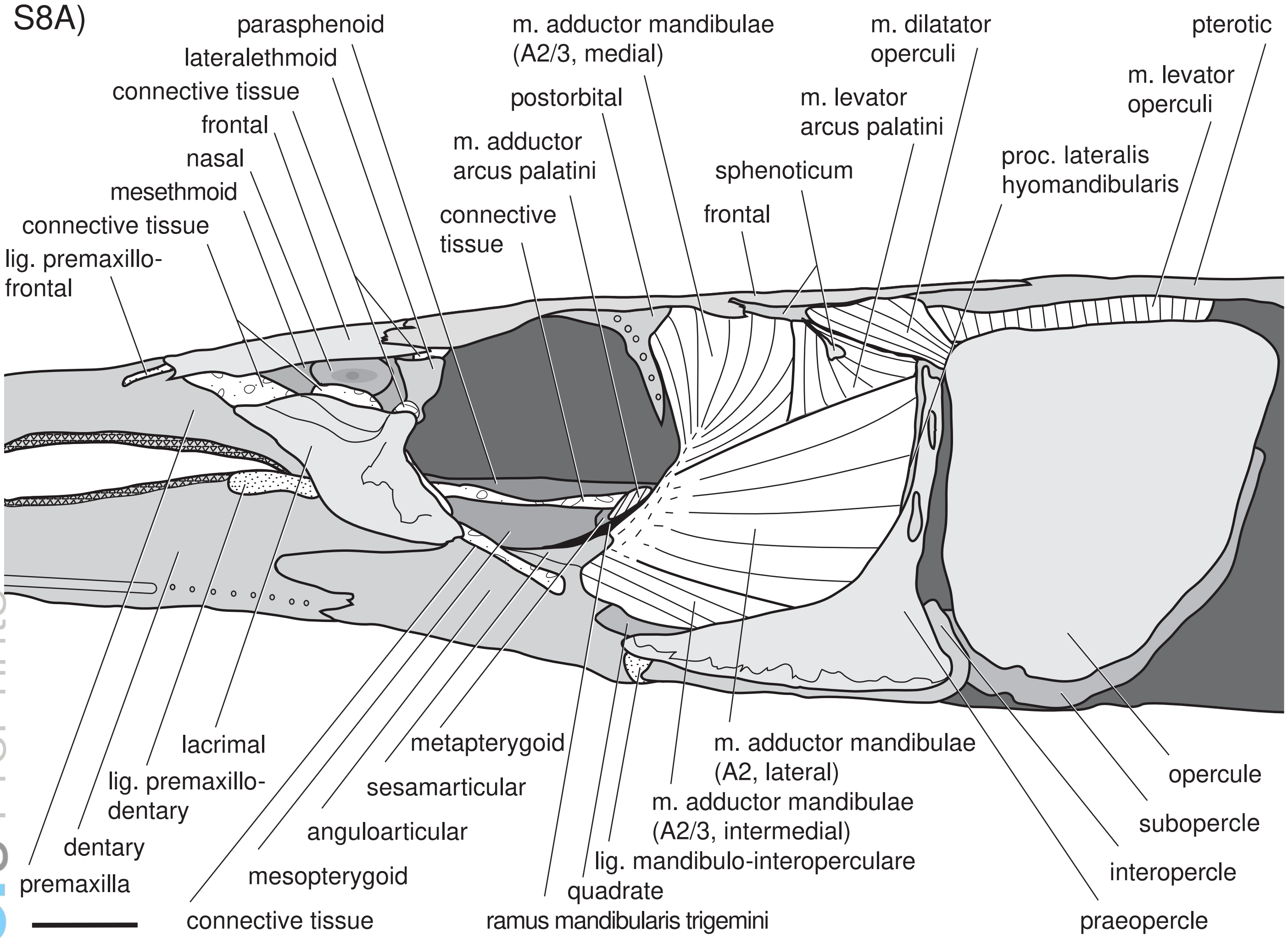
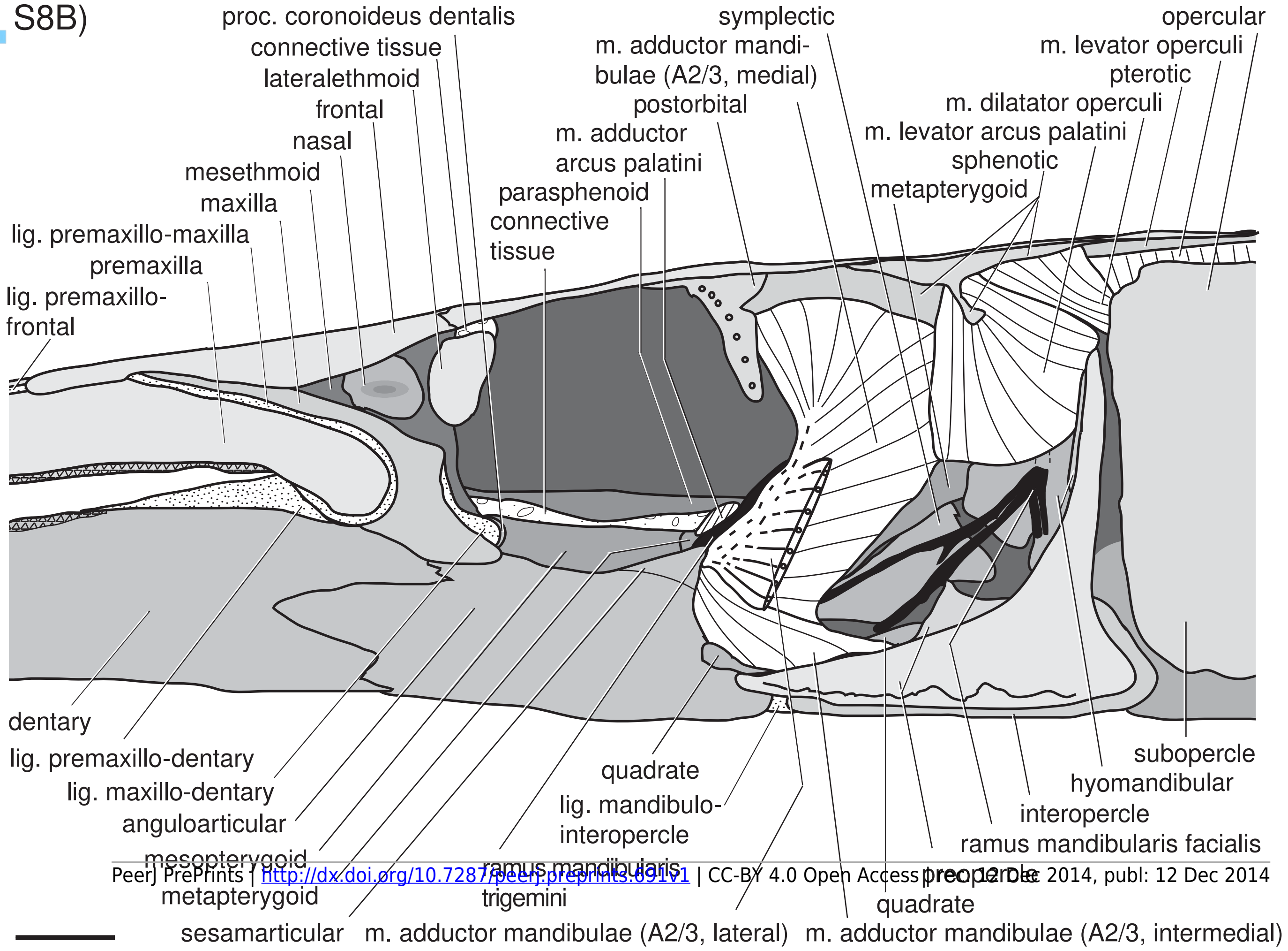
Belone belone

S8A)



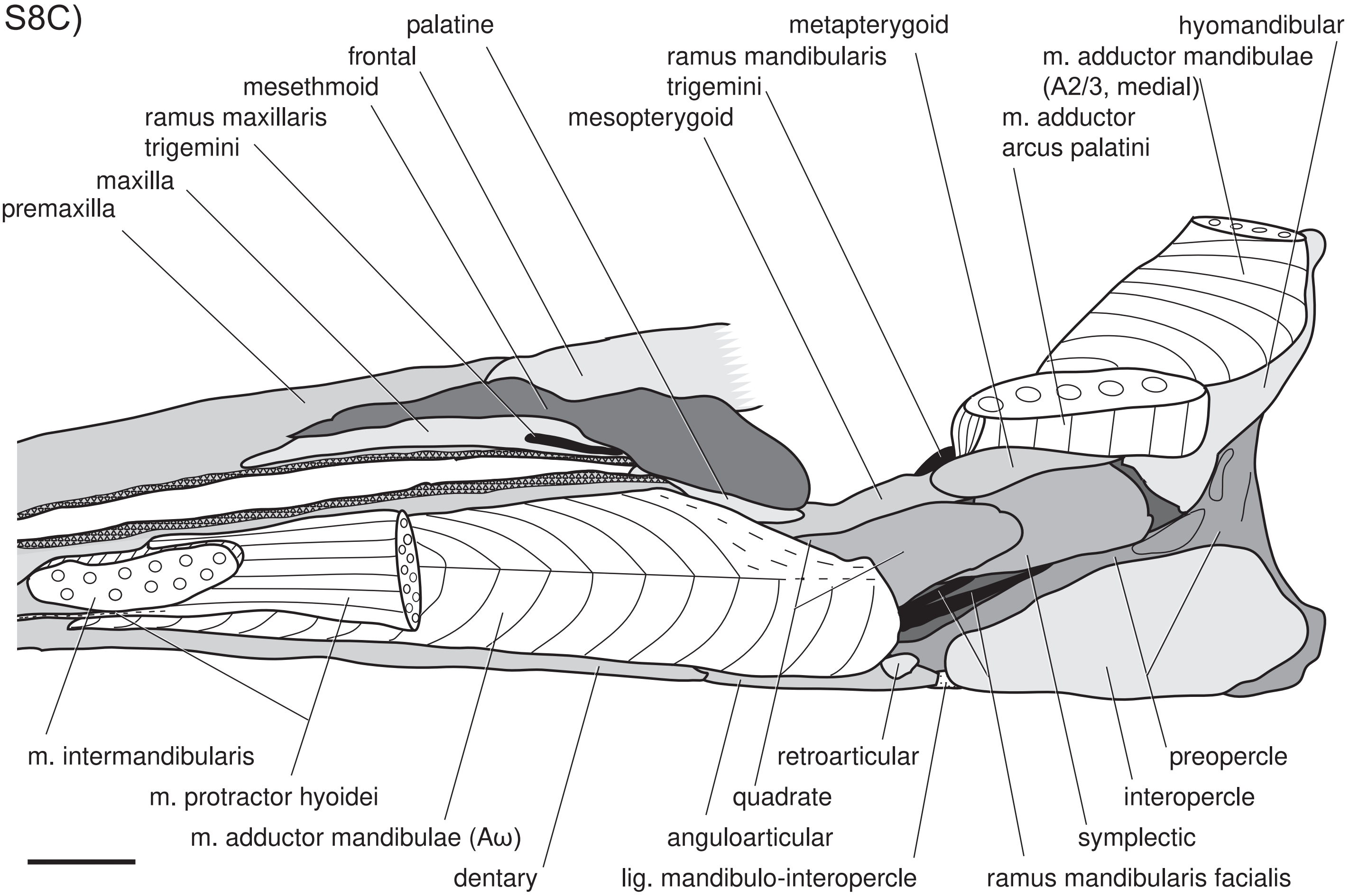
Belone belone

S8B)

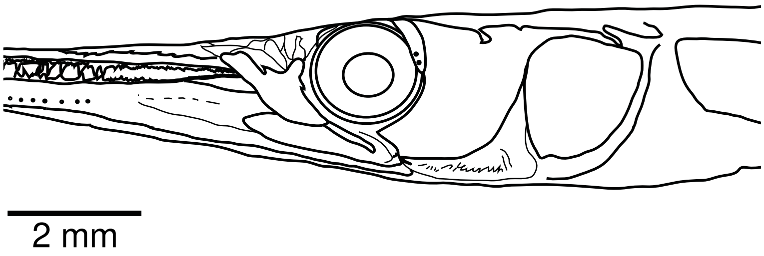


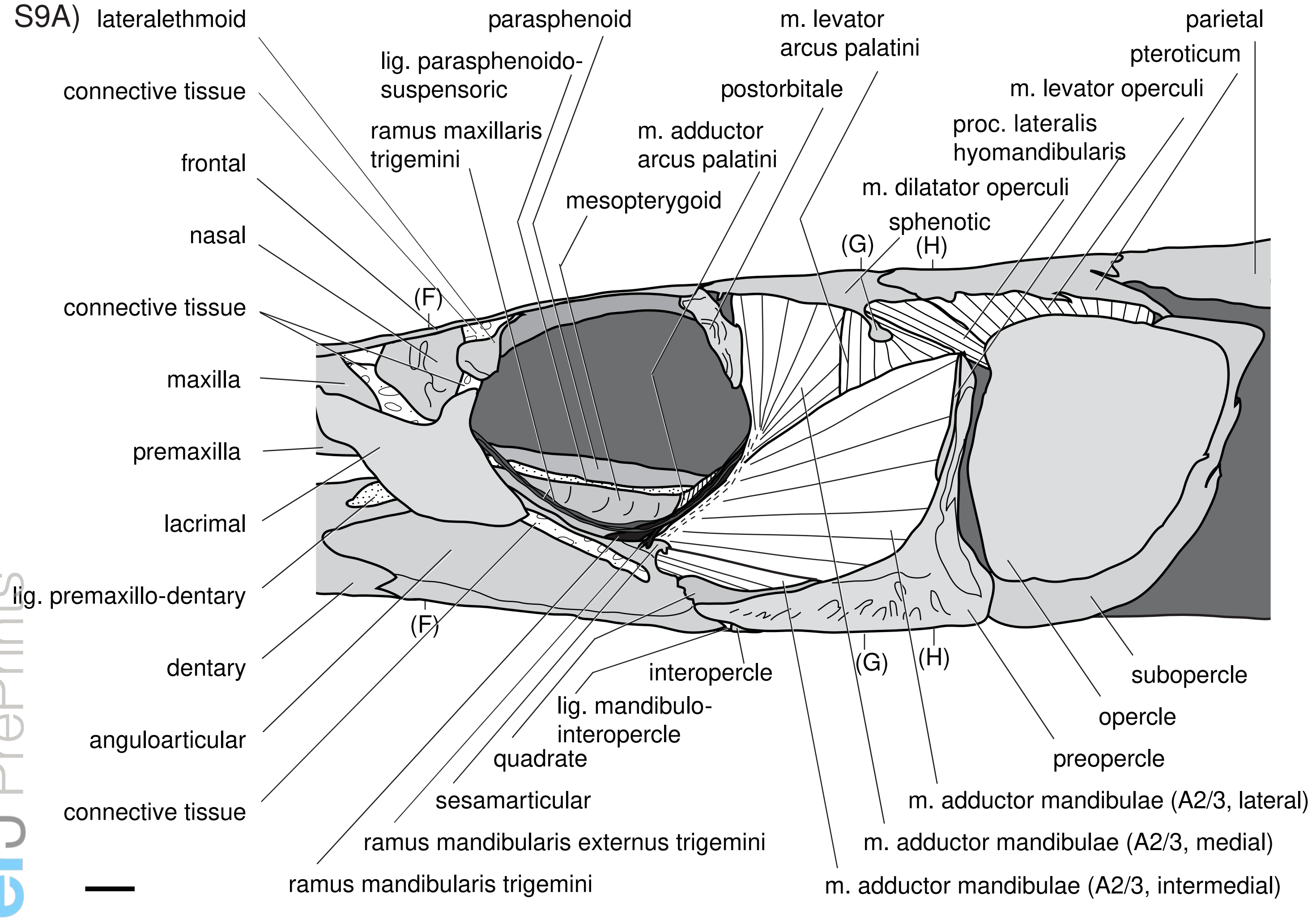
Belone belone

S8C)

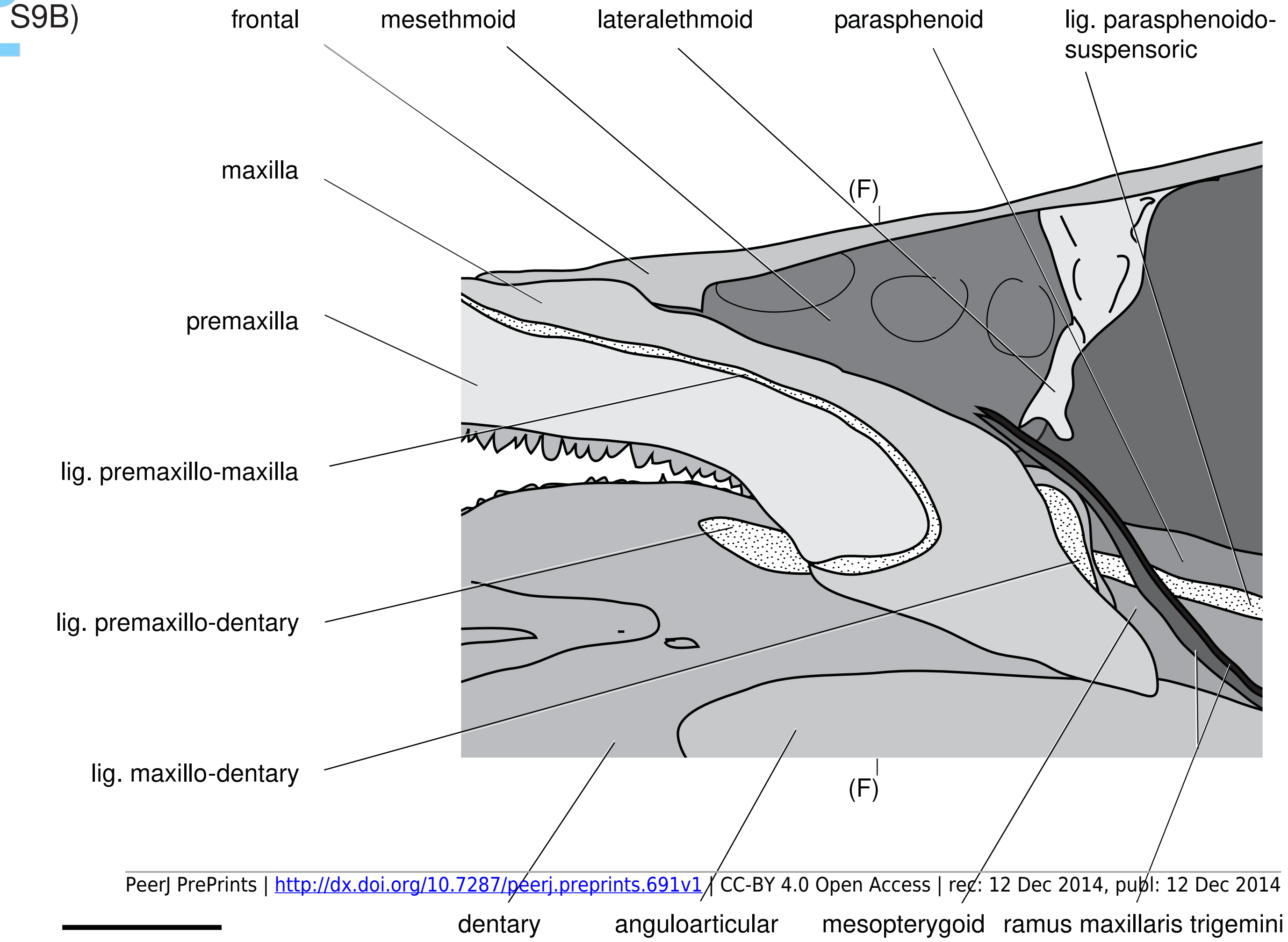


Belone belone





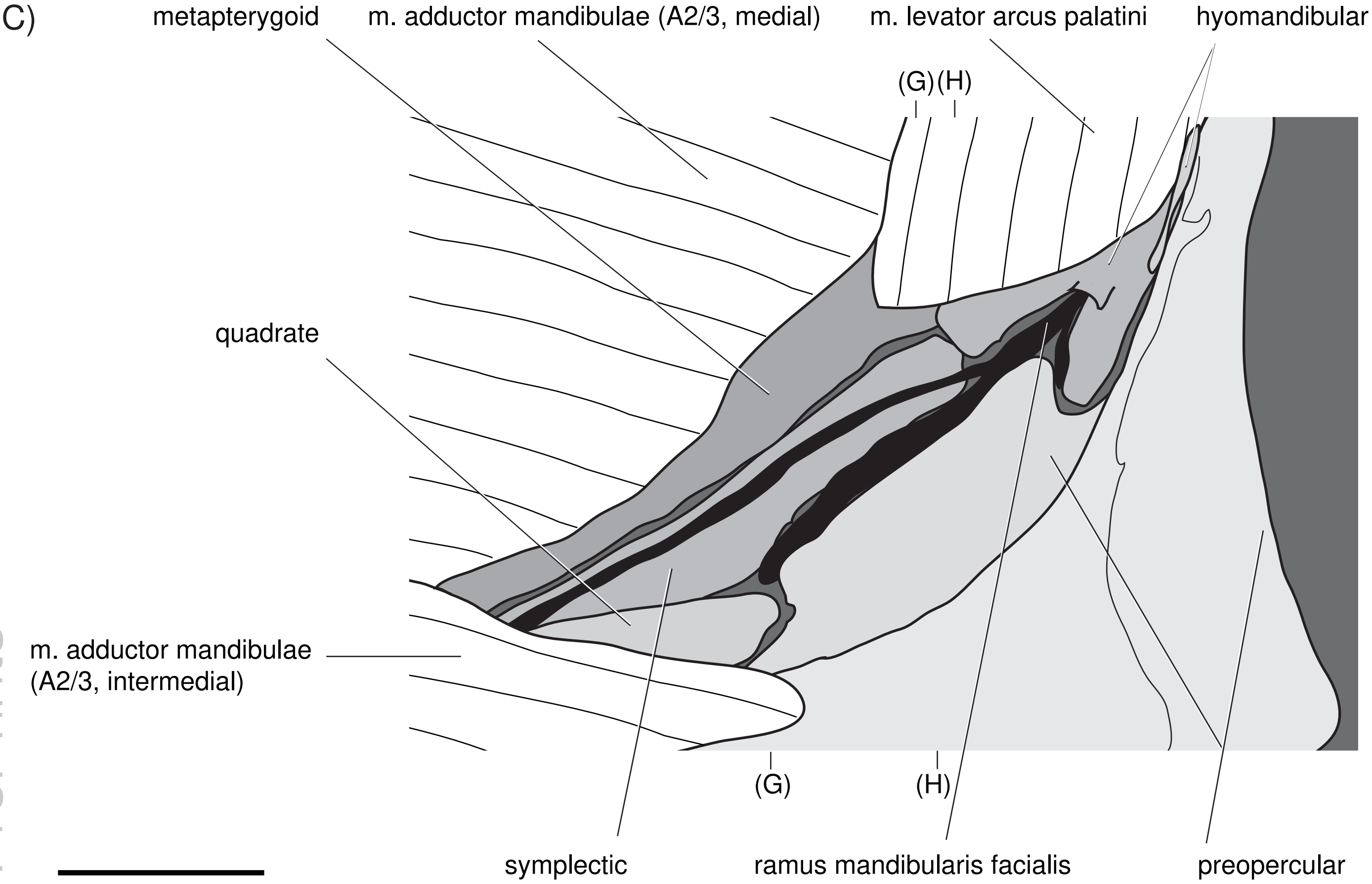
Scomberesox saurus



Scomberesox saurus

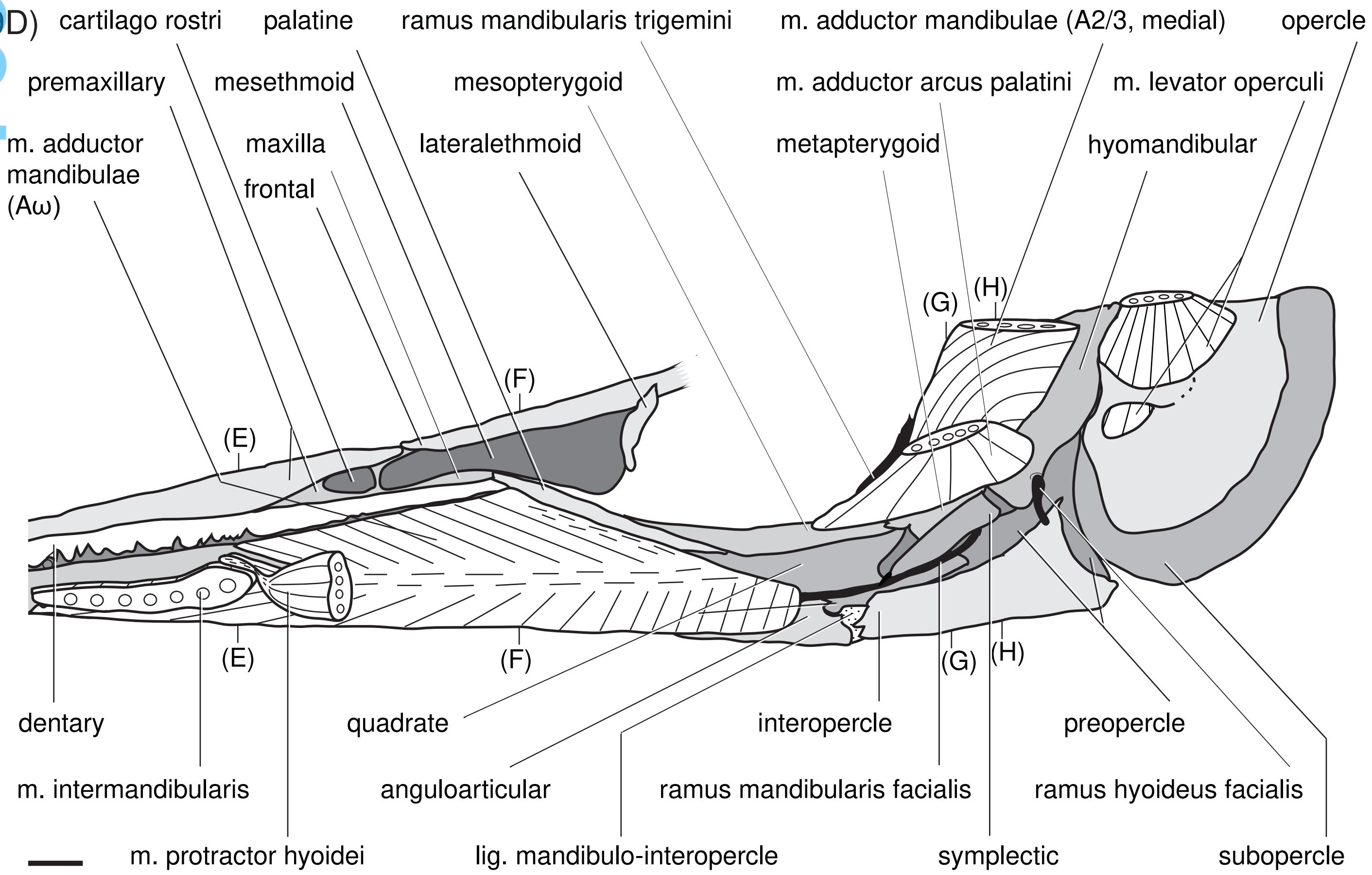
S9C)

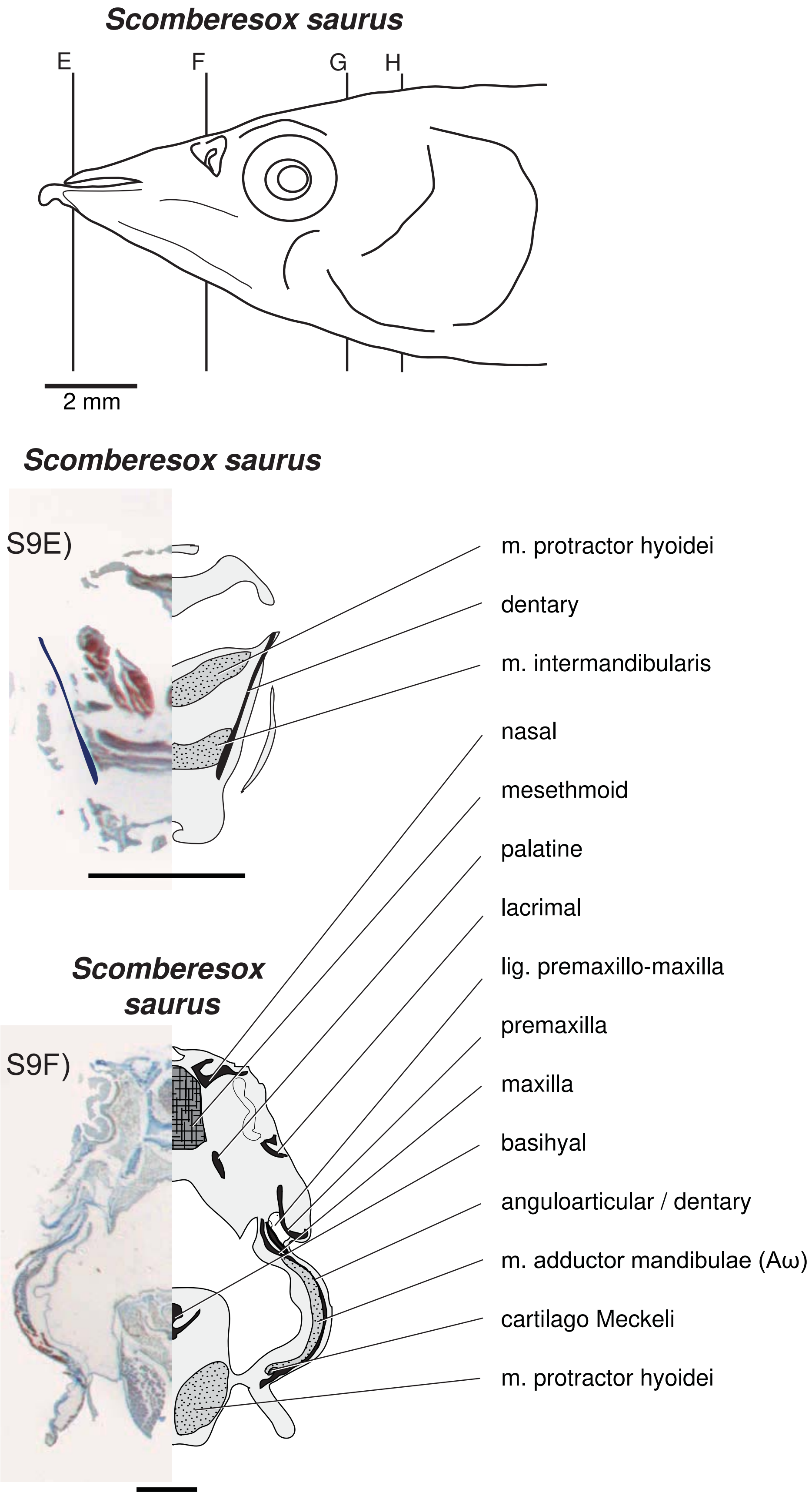
Scomberesox saurus



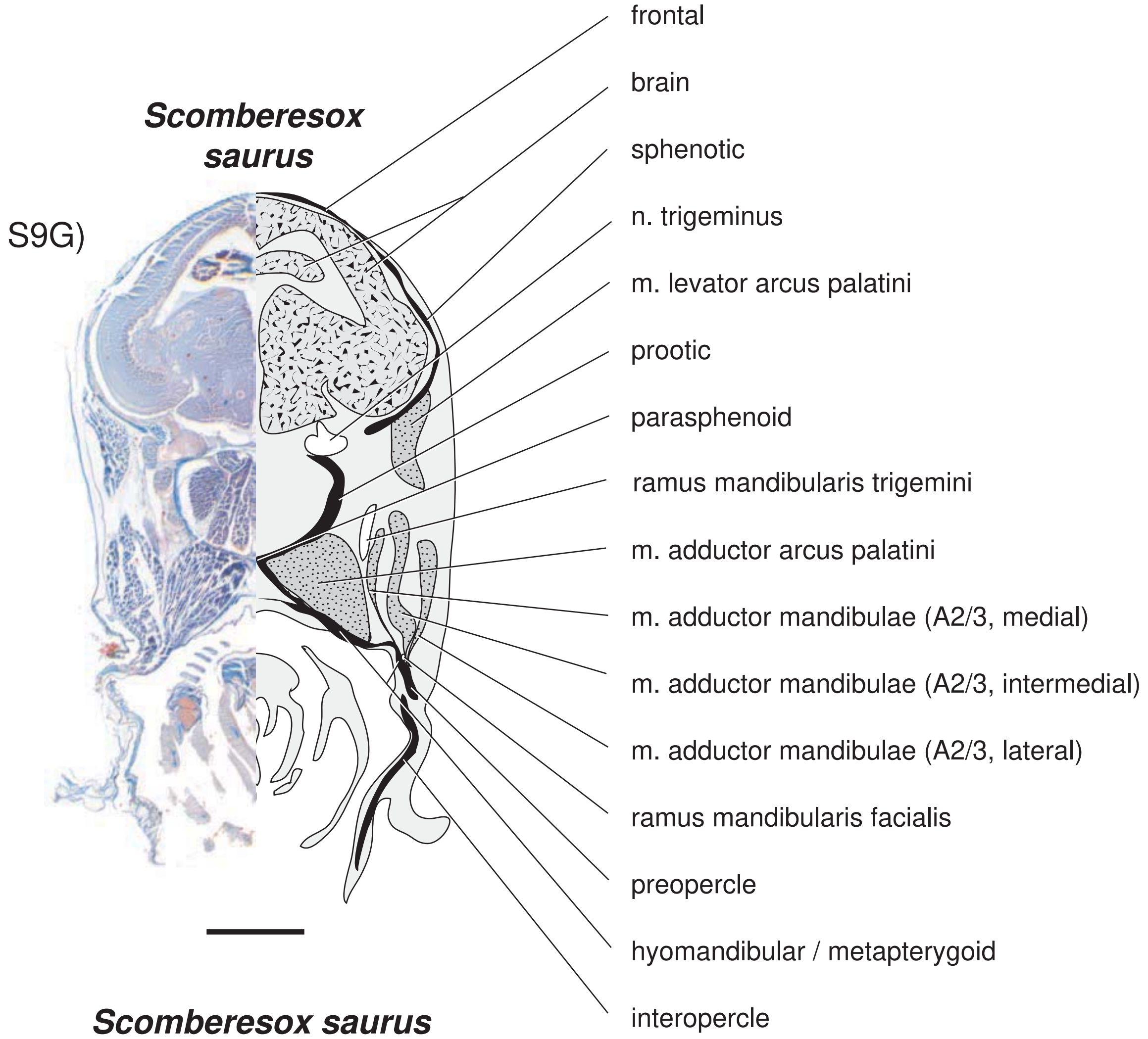
S9D)

Scomberesox saurus




Scomberesox saurus
E
F
G
H
2 mm
Scomberesox saurus
S9E)
m. protractor hyoidei
dentary
m. intermandibularis
nasal
mesethmoid
palatine
lacrimal
lig. premaxillo-maxilla
premaxilla
maxilla
basihyal
anguloarticular / dentary
m. adductor mandibulae (Aω)
cartilago Meckeli
m. protractor hyoidei
Scomberesox saurus
S9F)

Scomberesox saurus



Scomberesox saurus