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Ingmar Werneburg¹,*

¹ Museum für Naturkunde, Leibniz-Institut für Evolutions- & Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Invalidenstraße 43, 10115 Berlin / Germany

* i.werneburg@gmail.com

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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 m. adductor mandibulae complex belongs to one of the most intensively studied soft tissues in vertebrates. It primarily moves the skeletal elements associated to the mandibular arch and is the main head and the most powerful feeding musculature. The m. adductor mandibulae complex is highly adapted to different feeding strategies among vertebrate clades and, as such, experienced a large amount of diversification. Its anatomy is informative for different phylogenetic levels and a mutual evolution with jaw and skull anatomy can be observed (e.g., Diogo, 2008; Diogo and Abdala, 2010; Datovo and Vari, 2013).

Among teleost fishes, 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 (Figure 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 morphological and molecular analyses, which result in a sister group relationship of Adrianichthyidae and Exocoetoidea, comprising the remaining Beloniformes (Figure 1), and Beloniformes as the sister group of Cyprinodontiformes (Rosen and Parenti, 1981; Collette et al., 1984; White et al., 1984; Naruse et al., 1993; Dyer and Chernoff, 1996; Naruse, 1996, Hertwig, 2008).

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 (Rosen, 1964; Parin and Astakhov, 1982; Collette et al., 1984; Figure 1A-B).

Recently, Lovejoy (2000) and Lovejoy et al. (2004) proposed the paraphyly of hemiramphids and nested Scomberosocidae 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 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 very few species so far, and most published descriptions of beloniform species are superficial and insufficiently illustrated, making broad scale phylogenetic comparisons impossible. 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 (Stiassny, 1990; Setiamarga *et al.*., 2008; Near *et al.*, 2013). A preliminary character mapping is presented.
Materials and Techniques

Taxonomic sampling

The cranial anatomy of ten acanthopterygian species was studied, including six species of Beloniformes (Figure 2-20). 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) (Figures 2A, 5);
- Mugilomorpha, *Rhinomugil corsula* (Hamilton, 1822) (NMBE) (Figures 2B, 6-7);
- Atheriniformes, *Atherina boyeri* (Risso, 1810) (NMBE) (Figures 2C, 8-9, 12D);
- Cyprinodontiformes, *Aplocheilus lineatus* (Valenciennes, 1846) (NMBE) (Figures 2D, 10-11);
- Beloniformes, Adrianichthyidae, *Oryzias latipes* (Temminck and Schlegel, 1846) (NMBE) (Figures 2E, 12A-C, 13);
- Beloniformes, Adrianichthyidae, *Xenopoecilus oophorus* (Kottelat 1990) (NMBE) (Figure 3);
- Beloniformes, Exocoetidae, *Parexocoetus brachypterus* (Richardson, 1846) (USNM 299385) (Figures 2F, 14-15);
- Beloniformes, Hemiramphidae, *Dermogenys pusilla* (Kuhl and van Hasselt, 1823) (NMBE) (Figures 2G, 16-17);
- Beloniformes, Belonidae, *Belone belone* (Linnaeus, 1761) (NMBE) (Figures 2H, 18);
- Beloniformes, Scomberesocidae, *Scomberesox saurus* (Walbaum, 1782) (ISZE) (Figures 19-20).

For a phylogenetic analysis, published information on further beloniform, namely hemiramphid species, *Hyporhamphus unifasciatus* (Ranzani, 1841), *Nomorhamphus* sp. aff. *ravnaki* (Brembach, 1991), and *Hemirhamphodon phaiosoma* (Bleeker, 1852), were included (Table 1, Figure 4). According to the new findings of Werneburg and Hertwig (2009), the data on *O. latipes* was modified when compared to Hertwig (2005, 2008) and Werneburg (2007).

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 6, 8, 10, 12, 14, 16, 19). For S. saurus, a juvenile specimen was used for histological sectioning (Figure 20), whereas for manual dissections and character coding (as for all species), adult specimens were used (Figure 20).

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 Mugiliformes; on Kulkarni (1948), Rosen (1964), Karrer (1967) and Hertwig (2005, 2008) for Adrianichthyidae and Cyprinodontiformes; on Clemen et al. (1997), Greven (1997), Meisner (2001), and Shakhovskoi (2002) for hemiramphids; on Khachaturov (1983) and Shakhovskoi (2004) for Exocoetidae; and on Chapman (1943) for Scomberesocidae.

Character evolution

Using PAUP* (Swofford, 2003), a character mapping was performed. Therefore, the topology of Lovejoy et al. (2004) was used as template to arrange the phylogeny of the beloniform species
studied herein and of three additional hemiramphid species (Figure 4; cf. Figure 1C). For the interrelationship of major acanthopterygian groups, the present study follows the findings of Stiassny (1990), Setiamarga et al. (2008), and Near et al. (2013). Therein, Percomorpha form the sister taxon to Ovalentaria. Consequently a polarisation of characters is given. The topology for the character mapping was drawn using the move branch function in Mesquite 2.01 (Maddison and Maddison, 2007).
**Results and Discussion**

**Characters and character mapping**

In total, 37 soft tissue characters are described and discussed below. The character matrix can be found in Table 1. The results of the character mapping are listed in Table 2. Therein, the consensus of Acctran and Deltran optimizations are documented. Due to the particular focus on the morphological descriptions and illustration of this study, the taxonomic sampling is limited. Also the available data from the literature record is limited. As such, I avoid discussing the character changes in detail. They should serve as orientation and summary of character distribution of the species studied herein. The phylogenetic relevance of the characters should be subject of evaluation and discussion in future, more quantitative analyses of the cranial musculature of Beloniformes. Those studies may also consider more closely related species for the comparison with Atherinomorpha.

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

The 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 (Diogo, 2008; Diogo and Abdala, 2010). 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).

**General appearance.** An A1 is present in *Perca fluviatilis* (Figures 2A, 5), *Rhinomugil corsula* (Figures 2B, 6-7), *Atherina boyeri* (Figures 2C, 8-9, 12D), *Aplocheilus lineatus* (Figures 2D, 10-11), *Oryzias latipes* (Figures 2E, 12A-C, 13), and *Xenopoecilus oophorus* (Figure 3) [character state 0] but is absent in all other species studied herein, namely *Dermogenys pussila, Parexocoetus brachypterus, Belone belone,* and *Scomberesox saurus* [state 1].

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* (Figures 2H, 18-20).

**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* (Figures 2B, 6-7), the A1 is situated ventrolaterally to the lateral head of A2/3 and three-fourths of this head are still visible in lateral view [state 0]. 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 (Figures 2A, 5) [state 1]. A1 is situated completely lateral to the intermedial head of the internal section of m. adductor mandibulae (A2/3, intermedial) in *Ap. lineatus* (Figures 2D, 10-11), *O. latipes* (Figures 2E, 12A-C, 13; see also Werneburg and Hertwig, 2009), and *X. oophorus* (Figure 3) and the lateral head (A2/3, lateral) is only covered in its anterior region [2(2)]. Laterally in *At. boyeri* (Figures 2C, 8-9, 12D), the A1 completely covers the internal section of m. adductor mandibulae (A2/3) [state 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 (Figures 2A, 5). 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* (Figures 2A, 5) 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* (Figures 2A, 5) [state 0], to the medial face of the middle region of the maxilla in *R. corsula* (Figures 2B, 6-7) and *X. oophorus* (Figure 3) [state 1], and to the posterior edge of the dentary in *O. latipes* (Figures 2E, 12A-C, 13) [state 2]. 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* (Figures 2C, 8-9, 12D) [state 3]. 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* (Figures 2D, 10-11) [state 4].

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* (Figures 2A, 5), however, the A1 inserts on the other end of the maxilla in *Ap. lineatus* (Figures 2D, 10-11). 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 plesiomorphic 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; their position of origin (or insertion) and the spatial orientation 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* (Figures 2A, 5), *Pa. brachypterus* (Figures 2F, 14-15), and *D. pussila* (Figures 2G, 16-17), the A2/3 has two muscle heads (A2/3, lateral; A2/3, medial) in its origin [state 0]. A2/3 originates with three muscle heads (A2/3, lateral; A2/3, medial; A2/3, intermedial) in *R. corsula* (Figures 2B, 6-7), *Ap. lineatus* (Figures 2D, 10-11), *O. latipes* (Figures 2E, 12A-C, 13), *X. oophorus* (Figure 3), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 1].

The cyprinodontiform species *Ap. lineatus* (Figures 10-11) was found to have three muscle heads at 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 difficult. 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.* 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* (Figures 2B, 6-7), *Ap. lineatus* (Figures 2D, 10-11), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 0]. 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* (Figures 2G, 16-17) [state 1]. In *Pe. fluviatilis* (Figure 3A, 5) and *Pa. brachypterus* (Figures 2F, 14-15), 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 quadriati [state 2]. With a narrow attachment, it only originates on the ventral third of the vertical aspect of the preopercle in *O. latipes* (Figures 2E, 12A-C, 13) and *X. oophorus* (Figure 3) [state 3].

**Medial head.** 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 (Figure 5) [state 0]. It originates from the hyomandibular and from the metapterygoid in *R. corsula* (Figures 6-7) [state 1] or only from the metapterygoid in *Ap. lineatus* (Figures 10-11) and *Pa. brachypterus* (Figures 2F, 14-15) [state 2]. 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 quadriati in *O. latipes* (Figures 12A-C, 13) and *X. oophorus* (Figure 3) [state 3]. The medial head of A2/3 originates ventrally at the sphenotic, laterally at the hyomandibular, and dorsally at the metapterygoid in *D. pussila* (Figures 16-17), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 4].

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 (Figures 9E-H). In this specimen, a different orientation of the A2/3-heads was found (Werneburg, 2007). One could hypothesise 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.

**Intermedial head.** 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 (Figures 6-7) [state 0]. It takes its origin from the horizontal aspect of the preopercle and at the processus caudalis quadrati in Ap. lineatus (Figures 10-11), B. belone (Figure 18), and S. saurus (Figures 19-20) [state 1] and originates only on the processus caudalis quadrati in O. latipes (Figures 12A-C, 13) and X. oophorus (Figure 3) [state 2]. An intermedial head is not present in Pe. fluviatilis, At. boyeri, Pa. brachypterus, and D. pussila.

**11Muscle portions.** Unlike in all other species [state 0], A2/3 is laterally separated into two portions (by definition; see above and Werneburg 2011) in At. boyeri (Figures 8-9, 12D) [state 1]. 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 of muscle heads.** The spatial orientations of the medial and the lateral head of A2/3 are different among species. In Pe. fluviatilis (Figures 2A, 5), Ap. lineatus (Figures 10-11), D. pussila (Figures 2G, 16-17), X. oophorus (Figure 3), B. belone (Figure 18), and S. saurus (Figures 19-20), the medial head of A2/3 is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. The medial head of A2/3 is situated ventrally to the lateral head in At. boyeri (Figures 8-9, 12D) [state 1]. The lateral head is situated laterally to the medial head and can cover it completely in R. corsula (Figures 6-7), O. latipes (Figures 12A-C, 13), and Pa. brachypterus (Figures 2F, 14-15) [state
Relative size of muscle heads. The medial and the lateral heads of A2/3 have about the same size in *Pe. fluviatilis* (Figure 5) and *D. pussila* (Figures 16-17) [state 0]. The medial head is relatively narrow when compared to the lateral head in *Pa. brachypterus* (Figures 14-15) [state 1]. The lateral head is quite widespread when compared to the medial head in *R. corsula* (Figures 6-7) and *Ap. lineatus* (Figures 10-11) [state 2]. The medial head is larger than the lateral head in *O. latipes* (Figures 2E, 12A-C, 13), *X. oophorus* (Figure 3), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 3].

Insertion. Except for *B. belone* (Figures 2H, 18) and *S. saurus* (Figures 19-20), A2/3 only inserts on the medial side of the lower jaw [state 0]. In the former species, it also inserts on the coronomeckelian bone [state 1], 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 [state 0]. It is present in *R. corsula* (Figures 6-7) and has a narrow insertion on the medial face of processus coronoideus dentalis [state 1]. In *Ap. lineatus* (Figures 10-11), it has broad insertions to the processus coronoideus dentalis, to cartilago Meckeli, and to the anguloarticular [state 2]. It inserts medially to the dentary in *At. boyeri* (Figures 8-9, 12D) [state 3] and has a narrow insertion medially to the anguloarticular in *Pe. fluviatilis* (Figure 5) [state 4].

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 5D). 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 outside 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* (Figures 14-15) and *D. pussila* (Figures 16-17) [state 0]. It originates directly at the ventral and the anterior edge of the quadrate in *O. latipes* (Figures 12A-C, 13) [state 1]. In *R. corsula* (Figures 6-7), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20), *Aω* originates broadly on the medial face of the quadrate and a part of the muscle can have a tendinous origin [state 2]. It attaches with a tendon anteroventrally to the medial face of the quadrate in *At. boyeri* (Figures 8-9, 12D) and *Ap. lineatus* (Figures 10-11) [state 3]; and in *Pe. fluvialtilis* (Figure 5), 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 [state 4]. The *Aω* is absent in *X. oophorus* [state 5].

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 (Figures 16-17), 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* (Figures 14-15), a potential synapomorphic character of (Exocoetidae + Hemiramphidae) is identified and a possible monophyly of Hemiramphidae could be indicated (Rosen, 1964; Rosen and Parenti, 1981; Collette et al., 1984). This would contradict the works of Lovejoy et al. (2004) and Aschliman et al. (2005), 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.** In *R. corsula* (Figures 6-7), *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 [state 0]. The *Aω* represents a double-feathered muscle in *Pe. fluvialtilis* (Figure 5), *At.
boyeri (Figures 8-9, 12D), D. pussila (Figures 16-17), B. belone (Figure 18), and S. saurus (Figures 19-20), in which one of the muscle parts may project to a far caudad direction [state 1]. The Aω is a parallel fibred muscle in O. latipes (Figures 12A-C, 13) and Pa. brachypterus (Figures 14-15) [state 2] and a simple feathered muscle in Ap. lineatus (Figures 10-11) [state 3].

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 (Figure 5), At. boyeri (Figures 8-9, 12D), Pa. brachypterus (Figures 14-15), and D. pussila (Figures 16-17) [state 0]. 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 (Figure 18) and S. saurus (Figures 19-20) [state 1]. It inserts to the ventral part of the dentary in Ap. lineatus (Figures 10-11) [state 2] and posteriorly to the dentary and medially at the cartilago Meckeli in O. latipes (Figures 12A-C, 13) [state 3].

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

Cross section. M. intermandibularis connects the contralateral dentaries at their medial faces. The cross-section of m. intermandibularis is +/- round in At. boyeri (Figures 8-9, 12D) [state 0]. It is big-bellied oval in Pe. fluviatilis (Figure 5), R. corsula (Figures 6-7), O. latipes (Figures 12A-C, 13), and X. oophorus (Figure 3); i.e. it is at its maximum twice as broad as high [state 1]. It is elongated oval in Ap. lineatus (Figures 10-11), Pa. brachypterus (Figures 14-15), D. pussila (Figures 16-17), B. belone (Figure 18), and S. saurus (Figures 19-20); i.e. it is (mostly much) more than twice as broad as high [state 2].

In each species studied, several specimens were observed and a tendency of a rounder cross-section of the muscle was found in At. boyeri (Figures 8-9, 12D). In addition, the assignment to big-bellied or elongated oval has to be understood as a tendency in the variability of the specimens observed.

Shape. The m. intermandibularis is parallel fibred and has no tendinous origin at the dentary in Pe. fluviatilis (Figure 5), At. boyeri (Figures 8-9, 12D), Pa. brachypterus (Figures 14-15), D. pussila (Figures 16-17), B. belone (Figure 18), and S. saurus (Figures 19-20) [state 0]. However, it is spindle-shaped and has a tendinous origin at the dentary in R. corsula (Figures 6-7), Ap. lineatus (Figures 10-11), O. latipes (Figures 12A-C, 13), and X. oophorus (Figure 3) [state 1].
**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* (Figure 5), *Pa. brachypterus* (Figures 14-15), and *D. pussila* (Figures 16-17) [state 0], with two heads ventrally and laterally at the ceratohyal and at the anterior tips of the branchiostegal rays in *O. latipes* (Figures 12A-C, 13) [state 1], ventrally to the ceratohyal in *R. corsula* (Figures 6-7), *At. boyeri* (Figures 8-9, 12D), *Ap. lineatus* (Figures 10-11), and *X. oophorus* (Figure 3) [state 2] and medially to the ceratohyal in *B. belone* (Figure 18) and *S. saurus* (Figures 19-20) [state 3].

**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* (Figures 6-7), *Ap. lineatus*, *O. latipes* (Figures 12A-C, 13), *X. oophorus* (Figure 3) (in relation to the jaw joint, the protractor fuses more anteriorly in *X. oophorus* when compared to *O. latipes*), *Pa. brachypterus* (Figures 14-15), and *D. pussila* (Figures 16-17) and anteroventrally at the fused mm. protractor hyoidei a tendon can be formed on each side [state 0]. Such a fusion does not occur in *Pe. fluviatilis* (Figure 5), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20) [state 1]. In *At. boyeri* (Figures 8-9, 12D), 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 [state 2].

**Anterior part.** When reaching m. intermandibularis, m. protractor hyoidei has a flat shape in *Ap. lineatus* (Figures 10-11), *O. latipes* (Figures 12A-C, 13), and *X. oophorus* (Figure 3) [state 0], or it is about as broad as high in *Pe. fluviatilis* (Figure 5), *At. boyeri* (Figures 8-9, 12D), *Pa. brachypterus* (Figures 14-15), *D. pussila* (Figures 16-17), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20) [state 1]. 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* (Figures 6-7) [state 2].

When reaching the dentary, the flat shape of the muscle in *Ap. lineatus* (Figures 10-11) and *O. latipes* could be hypothesized as being an autapomorphic character of Cyprinodontoidei sensu Rosen (1964) (Figures 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* (Figures 10-11), *Pa. brachypterus* (Figures 14-15), and *S. saurus* (Figures 19-20) [state 0]. In *Pe. fluviatilis* (Figure 5), *R. corsula* (Figures 6-7), *O. latipes* (Figures 12A-C, 13), *D. pussila* (Figures 16-17), and *B. belone*
(Figure 18), it inserts ventrally to the m. intermandibularis at the dentary [state 1]. It inserts dorsally as well as ventrally of m. intermandibularis to the dentary in *X. oophorus* (Figure 3) [state 2].

**Insertion tendon.** The ventral part of m. protractor hyoidei extends into a long tendon, which reaches the anterior tip of the lower jaw in *D. pussila* (Figures 16-17) and *B. belone* (Figure 18) [state 0]. It does not extend into a long tendon to reach the anterior tip of the lower jaw in *Pe. fluviatilis* (Figure 5), *R. corsula* (Figures 6-7), *At. boyeri* (Figures 8-9, 12D), *O. latipes* (Figures 12A-C, 13), and *X. oophorus* (Figure 3) [state 1].

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* (Figures 16-17) and *B. belone* (Figure 18), also a ventral insertion of m. adductor mandibulare (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* (Figures 19-20), 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 at particular hierarchical levels.

**M. adductor arcus palatini**

**Origin and insertion.** 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* (Figures 6-7), *Ap. lineatus* (Figures 10-11), *O. latipes* (Figures 2E, 12A-C, 13), *X. oophorus* (Figure 3), and *D. pussila* (Figures 2G, 16-17) (in addition to other small attachments) [state 0]. In contrast, it originates on the posterior part of the parasphenoid and inserts on the posterior region of the suspensoric in *Pe. fluviatilis* (Figures 2A, 5), *At. boyeri* (Figures 2C, 8-9, 12D), *Pa. brachypterus* (Figures 2F, 14-15), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 1].

**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* (Figures 2F, 14-15) and *D. pussila* (Figures 2G, 16-17) [state 0]. In *R. corsula* (Figures 2B, 6-7), *B. belone* (Figures 2H, 18), and *S. saurus*
(Figures 19-20), it originates on a ridge of the sphenotic, the processus sphenoticus, and some fibres originate directly on the sphenotic [state 1]. 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* (Figures 2E, 12A-C, 13) and *X. oophorus* (Figure 3) [state 2]. It originates ventrally at the dermosphenotic in *At. boyeri* (Figures 2C, 8-9, 12D) [state 3] and from the autosphenotic and with some fibres at the sphenotic in *Pe. fluviatilis* (Figures 2A, 5) and *Ap. lineatus* (Figures 2D, 10-11) [state 4].

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* (Figures 10-11) 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* (Figures 2B, 6-7), *O. latipes* (Figures 2E, 12A-C, 13), and *X. oophorus* (Figure 3) [state 0], whereas in all other species it becomes more than twice as thick [state 1].

**Relation to other muscles.** M. levator arcus palatini runs dorsally of the medial and lateral head of A2/3 and does not run between both heads in *Pe. fluviatilis* (Figures 2A, 5), *R. corsula* (Figures 2B, 6-7), *Ap. lineatus* (Figures 10-11), *O. latipes* (Figures 2E, 12A-C, 13), *X. oophorus* (Figure 3), and *Pa. brachypterus* (Figures 2F, 14-15) [state 0]. It is clearly situated between the lateral and the medial head of A2/3 in *D. pussila* (Figures 16-17) [state 1] or it is only partly surrounded by the lateral and by the medial head of A2/3 in *B. belone* (Figures 2H, 18) and *S. saurus* (Figures 19-20) [state 2].

**Insertion.** On the lateral face of the suspensoric of *Pe. fluviatilis* (Figure 5), *Ap. lineatus* (Figures 10-11), *Pa. brachypterus* (Figures 14-15), *D. pussila* (Figures 16-17), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20), m. levator arcus palatini inserts onto the hyomandibular and to the metapterygoid and with some fibres, it also can attach anteriorly to the processus lateralis hyomandibularis [state 0]. In *O. latipes* (Figures 12A-C, 13) and *X. oophorus* (Figure 3), it inserts on the broad face of the praeopercular and posterodorsally to the symplectic [state 1]. In *R. corsula* (Figures 6-7) and *At. boyeri* (Figures 8-9, 12D), it inserts on the hyomandibular, anteriorly to the processus lateralis hyomandibularis, to the metapterygoid, and to the broad face of the preopercular [state 2].

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**

*Origin.* M. dilatator operculi connects the opercle with the skull roof. It originates ventrally at the lateral face of the sphenotic in *Pa. brachypterus* (Figures 2F, 14-15), *X. oophorus* (Figure 3), and *S. saurus* (Figures 19-20) [state 0]. It originates laterally at the sphenotic, at the autosphenotic, and with some fibres possibly at the anteroventral area of the pterotic in *Pe. fluviatilis* (Figures 2A, 5), *At. boyeri* (Figures 2C, 8-9, 12D), and *Ap. lineatus* (Figures 2D, 10-11) [state 1]. In *R. corsula* (Figures 2A, 6-7), *O. latipes* (Figures 2E, 12A-C, 13), *D. pussila* (Figures 2G, 16-17), and *B. belone* (Figures 2H, 18), it originates laterally at the sphenotic and anteriorly at the lateral face of the pterotic [state 2].

*Shape.* Anteriorly, m. dilatator operculi extends almost to the eye and lies dorsally to m. levator arcus palatini in *R. corsula* (Figures 2A, 6-7), *At. boyeri* (Figures 2C, 8-9, 12D), *Ap. lineatus* (Figures 2D, 10-11), and *O. latipes* (Figures 2E, 12A-C, 13) [state 0]. It does not reach the eye region in *Pe. fluviatilis* (Figures 2A, 5), *X. oophorus* (Figure 3), *Pa. brachypterus* (Figures 2F, 14-15), *D. pussila* (Figures 2G, 16-17), *B. belone* (Figures 2H, 18), and *S. saurus* (Figures 19-20) [state 1].

**M. levator operculi**

*Origin.* The m. levator operculi 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 [state 0], 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 (Figures 2A, 5) [state 1].

*Insertion.* M. levator operculi inserts dorsally to the medial face of the opercle and has a continuous horizontal level of insertion in *Pe. fluviatilis* (Figure 5), *R. corsula* (Figures 6-7), *Ap. lineatus* (Figures 10-11), *O. latipes* (Figures 12A-C, 13), *X. oophorus* (Figure 3), *Pa. brachypterus* (Figures 14-15), and *D. pussila* (Figures 16-17) [state 0]. It also inserts dorsally at the medial face of the opercle in *B. belone* (Figure 18) and *S. saurus* (Figures 19-20), but it attaches more ventrally to the anterior region of the medial face of the opercle [state 1]. The muscle inserts dorsally to the medial face and dorsally to the lateral face of the opercle in *At. boyeri* (Figures 8-9, 12D) [state 2].


**Nerves**

*Truncus maxillaris infraorbitalis trigemini.* 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* (Figure 5), *R. corsula* (Figures 6-7), *At. boyeri* (Figures 8-9, 12D), and *Ap. lineatus* (Figures 10-11) – and dorsally to the suspensoric, the ramus mandibularis trigemini covers the ramus maxillaris trigemini laterally [state 0]. Contrary, in *O. latipes* (Figures 12A-C, 13), *X. oophorus* (Figure 3), *Pa. brachypterus* (Figures 14-15), and *D. pussila* (Figures 16-17), it first branches at the level of the eye [state 1]. In *B. belone* (Figure 18) and *S. saurus* (Figures 19-20), 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 [state 2].

*Ramus mandibularis facialis.* 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* (Figures 8-9, 12D), *Ap. lineatus* (Figures 10-11), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20) [state 0]. In *Pe. fluviatilis* (Figure 5), *R. corsula* (Figures 6-7), *O. latipes* (Figures 12A-C, 13), *Pa. brachypterus* (Figures 14-15), and *D. pussila* (Figures 16-17) it branches differently [state 1]. The course of that nerve could not be followed in *X. oophorus* (Figure 3).

**Ligaments**

*Lig. premaxillo-maxilla.* This ligaments spans broadly between premaxilla and maxilla in *B. belone* (Figure 18) and *S. saurus* (Figures 19-20) [state 0] and between the proximal ends of the premaxilla and the maxilla in all other species [state 1].

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.

*Primordial ligament.* This ligament is present as a lig. maxillo-anguloarticulare between the maxilla and the anguloarticular in *Pe. fluviatilis* (Figures 2A, 5) and *At. boyeri* (Figures 2C, 8-9, 12D) [state 0]. The ligament is absent in all other species [state 1].
Upper jaw / palatine ligament. A ligament, which connects the palatine and the upper jaw, is present as lig. palato-maxilla between palatine and maxilla in *At. boyeri* (Figures 8-9, 12D), *Ap. lineatus* (Figures 10-11), *O. latipes* (Figures 12A-C, 13), *X. oophorus* (Figure 3), and *Pa. brachypterus* (Figures 14-15) [state 0]. It is present as lig. palato-premaxilla between palatine and premaxilla in *Pe. fluviatilis* (Figure 5) [state 1] or is absent in *R. corsula* (Figures 6-7), *D. pussila* (Figures 16-17), *B. belone* (Figure 18), and *S. saurus* (Figures 19-20) [state 2].

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* (Figures 6-7) and a different attachment of the ligament in *Pe. fluviatilis* makes it impossible to reconstruct the ground pattern.

Lig. parasphenoido-suspensorium. This ligament is present in *Pe. fluviatilis* (Figure 5), *At. boyeri* (Figures 8-9, 12D), and *S. saurus* (Figures 19-20) [state 0]. It is absent in all other species [state 1].

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 performed for the present study.

Conclusions

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 the 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 (Haas, 2001; Diogo, 2008; Diogo and Abdala, 2010; Daza et al., 2011; Konstantinidis and Harris, 2011; Werneburg, 2013; Datovo and Vari, 2013, 2014). 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* (Figures 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 (Figures 2F), a protrusible jaw was discovered herein. Therefore, the upper jaw bones are moveable against each other (Figures 14-15).

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 (Figures 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 (Figures 14-15).

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* (Figure 2H) and *S. saurus* (Figures 19-20), 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,
Potamorrhampsis 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 (Figures 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.

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.

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References

Alexander RM. 1967. Mechanisms of the jaws of some atheriniform fish. Journal of Zoology 151:233-255.

Allis EP. 1897. The cranial muscles and cranial and first spinal nerves of Amia calva. Journal of Morphology 12:487-808.

Anderson WD, III, and Collette BB. 1991. Revision of the freshwater viviparous halfbeaks of the genus Hemiramphodon (Teleostei: Hemiramphidae). Exploration of Freshwaters 2:151-176.

Aschliman NC, Tibbetts IR, and Collette BB. 2005. Relationships of sauries and needlefishes (Teleostei: Scomberesocoidea) to the internally fertilizing halfbeaks (Zenarchopteridae) based on the pharyngeal jaw apparatus. Proceedings of the Biological Society of Washington 118:416-427.

Berg L. 1958. System der rezenten und fossilen Fischartigen und Fische. Berlin: VEB Deutscher Verlag der Wissenschaften.

Boughton DA, Collette BB, and McCune AR. 1991. Heterochrony in jaw morphology of needlefishes (Teleostei: Beloniformes). Systematic Zoology 40:329-354.

Chapman WM. 1943. The osteology of the Pacific Saury, Cololabis saira. Copeia 1943:171-182.

Clemen G, Wanninger AC, and Greven H. 1997. The development of the dentigerous bones and teeth in the hemiramphid fish Dermogenys pusillus (Atheriniformes, Teleostei). Annals of Anatomy 179:165-174.

Collette BB. 2004a. Family Scomberesocidae Müller 1843. California Academy of Science - Annotated checklists of fishes 21:1-6.

Collette BB. 2004b. Family Hemiramphidae Gill 1859 - halfbeaks. California Academy of Science - Annotated checklists of fishes 22:1-35.

Collette BB, McGowen GE, Parin NV, and Mito S. 1984. Beloniformes: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall Jr AW, and Richardson SL, eds. Ontogeny and systematics of fishes. Lawrence: Allen Press Inc., 335-354.

Dasilao JC, Rossiter A, and Yamaoka K. 2002. Adaptive ontogenetic shape change in flyingfish Parexocoetus mento mento. Fisheries Science 68:71-76.

Datovo, A., and Vari, R. P. 2013. The jaw adductor muscle complex in teleostean fishes: Evolution, homologies and revised nomenclature (Osteichthyes: Actinopterygii). PloS One 8(4), e60846.

Datovo, A., and Vari, R. P. 2014. The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes: Actinopterygii): comparative anatomy, synonymy, and phylogenetic implications.
Daza, J. D., Diogo, R., Johnston, P., and Abdala, V. 2011. Jaw adductor muscles across lepidosaurs: a reappraisal. *The Anatomical Record* 294(10), 1765-1782.

de Pinna MCC. 1991. Concepts and tests of homology in the cladistic Paradigm. *Cladistics* 7:367-394.

Diogo, R. 2008. *The Origin of Higher Clades: Osteology, Myology, Phylogeny and Evolution of Bony Fishes and the Rise of Tetrapods.* Science Publishers, Enfield.

Diogo, R., and Abdala, V. 2010. *Muscles of Vertebrates: Comparative Anatomy, Evolution, Homologies and Development.* Science Publishers, Enfield.

Dyer B., and Chernoff B.S., 1996. 1996. Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). *Zoological Journal of the Linnean Society* 117:1-69.

Eaton Jr., T. H. (1935). Evolution of the upper jaw mechanism in teleost fishes. *Journal of Morphology* 58: 157-172.

Focant B, Jacob MF, and Huriaux F. 1981. Electrophoretic comparison of the proteins of some perch (Perca fluviatilis L.) head muscles. *Journal of Muscle Research and Cell Motility* 2:295-305.

Gosline W.A. 1986. Jaw muscle configuration in some higher teleostean fishes. *Copeia* 3:705-713.

Gosline W.A. 1993. A survey of upper jaw musculature in higher teleostean fishes. *Occasional Papers of the Museum of Zoology University of Michigan* 724: 1-26.

Greven H, Wanninger AC, and Clemen G. 1997. Dentigerous bones and dentition in the hemiramphid fish *Dermogenys pusillus* (Atheriniformes, Teleostei). *Annals of Anatomy* 179:21-32.

Haas A. 2001. Mandibular arch musculature of anuran tadpoles, with comments on homologies of amphibian jaw muscles. *Journal of Morphology* 247(1), 1-33.

Haas A. 2003. Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* 19:23-89.

Haszprunar G. 1998. Parsimony analysis as a specific kind of homology estimation and the implications for character weighting. *Molecular Phylogenetics and Evolution* 9:333-339.

Hertwig ST. 2005. Die Evolution der Kiefermuskulatur der Cyprinodontiformes (Teleostei, Acanthopterygii) unter phylogenetischen und funktionsmorphologischen Aspekten [PhD thesis]. 1-170.

Hertwig ST. 2008. Phylogeny of the Cyprinodontiformes (Teleostei, Atherinomorpha): the contribution of cranial soft tissue characters. *Zoologica Scripta* 37:141-174.

Holje L, Hildebrand C, and Fried K. 1986. On nerves and teeth in the lower jaw of the cichlid *Tilapia*
mariae. The Anatomical Record 214:304-311.

Johnson G, and Patterson C. 1993. Percomorph phylogeny: A survey of acanthomorphs and a new proposal. Bulletin of Marine Sciences 52:554-626.

Jourdain S. 1878. Des muscles de l'appareil maxillo-mandibulaire de quelques poissons osseux. Revue des Sciences Naturelles 7: 36-41, pl. 34.

Karrer C. 1967. Funktionell-anatomische und vergleichende Untersuchung des Schädels vom Hechtkärpfling, Belonesox belizanus KNER (Teleostei, Cyprinodontiformes, Poeciliidae).

Zoologisches Jahrbuch für Anatomie 84:191-248.

Khachaturov VA. 1983. The digestive system of flying fishes (Exocoetidae, Beloniformes). Journal of Ichthyology (Voprosy Ikhtiologii) 25:287-293.

Konstantinidis, P., and Harris, M. P. 2011. Same but different: ontogeny and evolution of the musculus adductor mandibulae in the Tetraodontiformes. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 316(1), 10-20.

Kulkarni CV. 1948. The osteology of Indian cyprinodonts. Part I: comparative study of the head skeleton of Aplocheilus, Oryzias and Horaichthys. Proceedings of the National Institute of Sciences of India 14:65-119.

Li S-Z. 2001. On the position of the suborder Adrianichthyoidei. Acta zootaxonomica Sinica 26:583-588.

Lovejoy NR. 2000. Reinterpreting recapitulation: systematics of needlefishes and their allies (Teleostei: Beloniformes). Evolution 54:1349-1362.

Lovejoy NR, and de Araujo MLG. 2000. Molecular systematics, biogeography and population structure of Neotropical freshwater needlefishes of the genus Potamorrhaphis. Molecular Ecology 9:259-268.

Lovejoy NR, Iranpour M, and Collette BB. 2004. Phylogeny and jaw ontogeny of beloniform fishes. Integrative and Comparative Biology 44:366-377.

Maddison WP, and Maddison DR. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75, http://mesquiteproject.org.

Meisner AD. 2001. Phylogenetic systematics of the viviparous halfbeak genera Dermogenys and Nomorhamphus (Teleostei: Hemiramphidae: Zenarchopterinae). Zoological Journal of the Linnean Society 133:199-283.

Mickoleit G. 2004. Phylogenetische Systematik der Wirbeltiere. München: Verlag Dr. Friedrich Pfeil.
Miranda Ribeiro, A. de [1913]-1915. Fauna brasiliense. Peixes. Tomo V. [Eleutherobranchios, Aspirophoros]. Physoclisti. *Arquivos do Museu Nacional de Rio de Janeiro* v. 17: [1-679] or 755 pp. with title pages, 31 pls., 3 tabs.

Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall Jr AW, and Richardson SL. 1984. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press Inc.

Naruse K. 1996. Classification and phylogeny of fishes of the genus *Oryzias* and its relatives. *The Fish Biology Journal Medaka* 8:1-9.

Near TJ, Dornburg A, Eytan RI, Keck BP, Smith WL, Kuhn KL, Moore JA, Price SA, Burbrink FT, Friedman M, and Wainwright PC. in press. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Science (PNAS)*.

Nelson JS. 2006. *Fishes of the World*. New Jersey: John Wiley and Sons.

Osse JWM. 1969. Functional morphology of the head of the perch (*Perca fluvialitis* L.): An electromyographic study. *Netherlands Journal of Zoology* 19:289-392.

Parenti LR. 1987. Phylogenetic aspects of tooth and jaw structure of the Madeka *Oryzias latipes*, and other beloniform fishes. *Journal of Zoology* 211:561-572.

Parenti LR. 1993. Relationships in atherinomorph fishes (Teleostei). *Bulletin of Marine Science* 52:170-196.

Parenti LR, and Grier HJ. 2004. Evolution and phylogeny of gonad morphology in bony fishes. *Integrated Computational Biology & Philosophy* 44:333-348.

Parin NV, and Astakhov DA. 1982. Studies on the accoustico-lateralis system of beloniform fishes in connection with their systematics. *Copeia* 1982:276-291.

Rosen D. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. *Bulletin of the American Museum of Natural History* 127:217-268.

Rosen DE, and Parenti LR. 1981. Relationships of *Oryzias*, and the groups of atherinimorph fishes. *American Museum Novitates* 2719:1-25.

Setiamarga D, Miya M, Yamanoue Y, Mabuchi K, Satoh T, Inoue J, and Nishida M. 2008. Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes, silversides, and their relatives): The first evidence based on whole mitogenome sequences. *Molecular Phylogenetics and Evolution* 49:598-605.

Shakhovskoi IB. 2002. Cranial Morphology of a Freshwater Halfbeak *Dermogenys siamensis* (Hemiramphidae). *Journal of Ichthyology (Voprosy Ikhtiologii)* 42:565-574.
Shakhovskoi IB. 2004. Skull morphology in the flying fish *Cheilopogon papilio* (Exocoetidae). *Journal of Ichthyology* 44:358-365.

Starks E.C. 1916. The sesamoid articular: a bone in the mandible of fishes. Stanford University Press, Stanford.

Stiassny MLJ. 1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). *American Museum Novitates* 2979:1-33.

Swofford DL. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). 4 ed. Sunderland, Massachusetts: Sinauer Associates.

Swofford DL, Olsen GJ, Waddell PJ, and Hillis DM. 1996. Phylogeny Inference. In: Hillis DM, Moritz C, and Mable BK, eds. *Molecular Systematics*. Sunderland, Massachusetts: Sinauer.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). 4 ed. Sunderland, Massachusetts: Sinauer Associates.

Temminck CJ, and Schlegel H. 1846. Pisces. In: de Siebold P, ed. *Fauna Japonica, Sive Descriptio Animalium quae in Itinere per Japoniam Suscepto annis 1823-30 collegit, notis observationibus et adumbrationibus illustravit*. Leiden, 224-225.

Thomson JM. 1954. The organs of feeding and the food of some Australian mullet. *Australian Journal of Marine and Freshwater Research* 5:469-485.

Tibbetts IR. 1991. The Trophic Ecology, Functional Morphology and Phylogeny of the Hemiramphidae (Beloniformes) PhD thesis. University of Queensland.

Van Dobben WH. 1935. Über den Kiefermechanismus der Knochenfische. *Archives Néerlandaises de Zoologie* 2: 1-72.

Weitzman SH. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* 8:1-77.

Weitzman SH. 1974. Osteology and evolutionary relationships of the Sternoptyhidae with a new classification of Stomioid families *Bulletin of the American Museum of Natural History* 153:327-478.

Werneburg I. 2007. *Vergleichende Morphologie der Kiefermuskulatur der Beloniformes (Teleostei, Atherinomorpha)* [Diploma Thesis at Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, incl. five 3d-movies of Oryzias latipes]. Jena: Digitale Bibliothek Thüringen. URL: [http://www.db-](http://www.db-)
Werneburg I. 2011. The cranial musculature in turtles. *Palaeontologia Electronica* 14:15a:99 pages.

Werneburg I. 2013a. Jaw musculature during the dawn of turtle evolution. *Organisms, Diversity & Evolution* 13:225-254.

Werneburg, I. (2013b). The tendinous framework in the temporal skull region of turtles and considerations about its morphological implications in amniotes: a review. *Zoological Science* 31(3): 141-153.

Werneburg I, and Hertwig ST. 2009. Head morphology of the ricefish, *Oryzias latipes* (Teleostei: Beloniformes). *Journal of Morphology* 270:1095-1106.

White BN, Lavenberg RJ, and McGowen GE. 1984. Atheriniformes: Development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall Jr AW, and Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press Inc., 355-362.

Winterbottom R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia* 125:225-317.

Wu KY, and Shen SC. 2004. Review of the teleostean adductor mandibulae and its significance to the systematic positions of the Polymixiiformes, Lampridiformes, and Triacanthoidei. *Zoological Studies* 43:712-736.

Yamamoto T. 1975. Systematics and Zoogeography. In: Yamamoto T, ed. *Medaka, Biology and Strains*: Yugakusya Publ., 17-29.
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 = Exocoetaidea, 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. 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 Figures 5-20.

Figure 3. The duckbilled ricefish Xenopoecilus oophorus (Beloniformes, Adrianichthyidae). Serial sections through the head. 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, J) 698. Bar scale provided for A-J. Magnifications B’, D’, I’-J’ are not to scale. Compare to the other adrianichthyid studied herein, Oryzias latipes (Figures 12A-C, 13).

Figures 4. Phylogenetic framework. Arrangement of the species studied herein and those of the literature (*) used for the reconstruction of character evolution (character mapping); following Lovejoy (2004; compare to Figures 1C). Outlines indicate the species, which were manually dissected herein; not to scale (compare to Figures 5-20).

[FIGURES 5-20 TO BE VERTICAL IN THE FINAL PDF AND TO APPEAR AFTER THE REFERENCE LIST]
Figure 5. *Perca fluviatilis*. A-D) Manual dissections. Compare to Figure 2A.

Figure 6. *Rhinomugil corsula*. A-D) Manual dissections; levels of histological sections (Figure 7) are indicated. Compare to Figure 2B.

Figure 7. *Rhinomugil corsula*. A-D) Histological sections; compare to Figure 6.

Figure 8. *Atherina boyeri*. A-D) Manual dissections; levels of histological sections (Figure 9) are indicated. For one further manual dissection of this species see Figure 12D. Compare to Figure 2C.

Figure 9. *Atherina boyeri*. A-D) Histological sections; compare to Figures 8 and 12D.

Figure 10. *Aplocheilus lineatus*. A-D) Manual dissections; levels of histological sections (Figure 11) are indicated. Compare to Figure 2D.

Figure 11. *Aplocheilus lineatus*. A-D) Histological sections; compare to Figure 10.

Figure 12. Manual dissections. A-C) *Oryzias latipes*; levels of histological sections (Figure 13) are indicated. A and C modified from Werneburg and Hertwig (2009). Compare to Figure 2E. D) *Atherina boyeri*; for other dissections of this species see Figure 8, for histological sections see Figure 9. Compare to Figure 2C.

Figure 13. *Oryzias latipes*. A-D) Histological sections; compare to Figure 12. Modified from Werneburg and Hertwig (2009).

Figure 14. *Parexocoetus lineatus*. A-D) Manual dissections; levels of histological sections (Figure 15) are indicated. Compare to Figure 2F.

Figure 15. *Parexocoetus lineatus*. A-D) Histological sections; compare to Figure 14.
**Figure 16.** *Dermogenys pussila.* A-C) Manual dissections; levels of histological sections (Figure 17) are indicated. Compare to Figure 2G.

**Figure 17.** *Dermogenys pussila.* A-D) Histological sections; compare to Figure 16.

**Figure 18.** *Belone belone.* A-C) Manual dissections. Compare to Figure 2H.

**Figure 19.** *Scomberesox saurus.* A-D) Manual dissections in an adult specimen; approximate levels of histological sections of a juvenile (Figure 20) are indicated.

**Figure 20.** *Scomberesox saurus.* A-D) Histological sections in a juvenile specimen; compare to Figure 19.

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**Tables**

**Table 1.** Character Matrix. X = not applicable; ? = unknown; * = indicating literature data from Hertwig (2008). For the phylogenetic arrangement of species see Figure 4.

**Table 2.** Character evolution within the topology of Lovejoy et al. (2004) (Figure 4). → = direction of character change from taxon 1 to taxon 2; ==> unambiguous character change; --> ambiguous character change.
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 Cyprinodontoidei (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 = Cyprinodontoidea, 7 = Beloniformes, 8 = N.N.
Figure 2

**Overview on the cranial anatomy in the eight species manually dissected in this study.** Skin is removed. 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 Figures 5-20.
3

Figure 3

The duckbilled ricefish *Xenopoecilus oophorus* (Beloniformes, Adrianichthyidae). Serial sections through the head. 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, J) 698. Bar scale provided for A-J. Magnifications B’, D’, I’-J’ are not to scale. Compare to the other adrianichthyid studied herein, *Oryzias latipes* (Figures 2E, 12A-C, 13).
Figure 4

**Phylogenetic framework.** Arrangement of the species studied herein and those of the literature (*) used for the reconstruction of character evolution (character mapping); following Lovejoy (2004; compare to Figures 1C). Outlines indicate the species, which were manually dissected herein; not to scale (compare to Figures 5-20).
Table 1

Character Matrix. X = not applicable; ? = unknown; * = indicating literature data from Hertwig (2008). For the phylogenetic arrangement of species see Figure 4.
| Character complex                        | Character | Aplocheilus lineatus | Atherina boyeri | Belone belone | Dermogenys pusilla | Hemirhamphodon phialosoma* | Hyporhamphus unifasciatus* | Nomorhamphus sp. aff. ravnaki* | Oryzias latipes | Parexocoetus brachypterus | Perca fluviatilis | Rhinomugil corsula | Scomberesox saurus | Xenopoecilus oophorus |
|-----------------------------------------|-----------|----------------------|----------------|-------------|-------------------|-----------------------------|-----------------------------|---------------------------------|----------------|------------------------|-----------------|---------------------|------------------|---------------------|
| General appearance                      |           | 0 0 1 1 0 1 0 0 1 0 0 0 0 1 0 1 0 1 0 0 0 1 0 1 0 |
| Orientation                             |           | 2 3 X X X 2 X 2 X 1 0 X 2 |
| Insertion                               |           | 4 3 X X X 1 X 2 X 0 1 X 1 |
| Orientation of muscle heads             |           | 0 1 0 0 0 0 0 3 2 2 0 0 2 0 0 0 |
| Relative size of muscle heads           |           | 2 X 3 0 ? ? ? 3 1 0 2 3 3 |
| Insertion                               |           | 0 0 1 0 0 0 0 0 0 0 0 0 1 0 |
| Intramandibular portion                 |           | 2 3 0 0 0 0 0 0 0 4 1 0 0 |
| Origin                                  |           | 3 3 2 0 0 0 0 1 0 4 2 2 5 |
| Shape                                   |           | 3 1 1 1 2 2 2 2 2 1 0 1 X |
| Insertion                               |           | 2 0 1 0 ? ? ? 3 0 0 X 1 X |
| Cross section                           |           | 2 0 2 2 2 2 2 1 2 1 1 2 1 |
| Shape                                   |           | 1 0 0 0 ? ? ? 1 0 0 1 0 1 |
| Origin                                  |           | 2 2 3 0 ? ? ? 1 0 0 2 3 2 |
| hyoidei | Course | 0 | 2 | 1 | 0 | ? | ? | ? | 0 | 0 | 1 | 0 | 1 | 0 |
|---------|--------|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Anterior part | 0 | 1 | 1 | 1 | ? | ? | ? | 0 | 1 | 1 | 2 | 1 | 0 |
| Insertion | 0 | 1 | 2 | 2 | 2 | 2 | 2 | 0 | 2 | 2 | 0 | 2 |
| Insertion tendon | X | 1 | 0 | 0 | ? | ? | ? | 1 | X | 1 | 1 | X | 1 |
| M. adductor arcus palatini | Origin and insertion | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| M. levator arcus palatini | Origin | 4 | 3 | 1 | 0 | ? | ? | ? | 2 | 0 | 4 | 1 | 1 | 2 |
| Course | 1 | 1 | 1 | 1 | ? | ? | ? | 0 | 1 | 1 | 0 | 1 | 0 |
| Relation to other muscles | 0 | X | 2 | 1 | ? | ? | ? | 0 | 0 | 0 | 0 | 2 | 0 |
| Insertion | 0 | 2 | 0 | 0 | ? | ? | ? | 1 | 0 | 0 | 2 | 0 | 1 |
| M. dilatator operculi | Origin | 1 | 1 | 2 | 2 | ? | ? | ? | 2 | 0 | 1 | 2 | 0 | 0 |
| Shape | 0 | 0 | 1 | 1 | ? | ? | ? | 0 | 1 | 1 | 0 | 1 | 1 |
| M. levator operculi | Origin | 0 | 0 | 0 | 0 | ? | ? | ? | 0 | 0 | 1 | 0 | 0 | 0 |
| Insertion | 0 | 2 | 1 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| Nerves | Truncus maxillaris infraorbitalis trigemini | 0 | 0 | 2 | 1 | ? | ? | ? | 1 | 1 | 0 | 0 | 2 | 1 |
| Ramus mandibularis facialis | 0 | 0 | 0 | 1 | ? | ? | ? | 1 | 1 | 1 | 1 | 0 | ? |
| Ligaments | Lig. premaxillo-maxilla | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| Primordial ligament | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| Upper jaw / palatine ligament | 0 | 0 | 2 | 2 | ? | ? | ? | 0 | 0 | 1 | 2 | 2 | 0 |
| Lig. paraprophenoide-suspensorium | 1 | 0 | 1 | 1 | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 1 |
Table 2

Table 2

Character evolution within the topology of Lovejoy et al. (2004) (Figure 4). -> = direction of character change from taxon 1 to taxon 2; ==> unambiguous character change; --> ambiguous character change.
| Character complex                              | Character                        | Pleiomorphic state in taxon 1                                                                 | Derived state in taxon 2                                                                 |
|-----------------------------------------------|----------------------------------|------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| Internal section of m. adductor mandibulae (A2/3) | Spatial orientation             | The medial head of A2/3 is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. | The lateral head is situated laterally to the medial head and can cover it completely [state 2]. |
| Internal section of m. adductor mandibulae (A2/3) | The medial head                 | Originates from the hyomandibular, the metapterygoid, and the symplectic, as well as from processus lateralis hyomandibularis [state 0]. | Originates from the hyomandibular and from the metapterygoid [state 1].                  |
| 12 Internal section of m. adductor mandibulae (A2/3) | Intramandibular portion         | Absent [state 0].                                                                 | Present and has a narrow insertion on the medial face of processus coronoides dentalis [state 1]. |
| Intramandibular section of m. adductor mandibulae (Aω) | Shape                           | Double-feathered muscle, in which one of the resulting muscle parts may project to a far caudal direction [state 1]. | The lateral head inserts broadly to the medial face of the dentary and cartilago Meckeli. The medial head inserts ventrally to the medial face of the dentary and anteriorly to the medial face of the anguloarticular [state 0]. |
| M. intermandibularis                          | Shape                            | Parallel fibre with no tendinous origin at the dentary [state 0]. | Spindle-shaped with tendinous origin at the dentary [state 1]. |
| M. protractor hyoidei                        | Anterior part                    | As broad as high [state 1].                                                                 | The dorsal head is flat and the ventral head is as high as broad [state 2].               |
| M. levator arcus palatini                    | Origin                           | From the autosphenotic and with some fibres at the sphenotic [state 4]. | On a ridge of the sphenotic, the processus sphenoticus, and some fibres originate directly on the sphenotic [state 1]. |
| M. levator arcus palatini                    | Course                           | From origin to insertion, the thickness broadens more than twice [state 1]. | Thickness hardly changes [state 0].                                                      |
| M. levator arcus palatini                    | Insertion                        | On the lateral face of the suspensoric to the hyomandibular and to the metapterygoid and with some fibres, it also can attach anteriorly to the processus lateralis hyomandibularis [state 0]. | On the hyomandibular, anteriorly to the processus lateralis hyomandibularis, to the metapterygoid, and to the broad face of the preopercular [state 2]. |
| M. dilatator operculi                        | Origin                           | Laterally at the sphenotic, at the autosphenotic, and with some fibres possibly at the anteroventral area of the pterotic [state 1]. | Laterally at the sphenotic and anteriorly at the lateral face of the pterotic [state 2]. |
| Ligaments                                    | Primordial ligament              | Present as a lig. maxillo-anguloarticular between the maxilla and the anguloarticular [state 0]. | Absent [state 1].                                                                       |
| Ligaments                                    | Upper jaw / palatine ligament    | Present as lig. palato-maxilla between palatine and maxilla [state 0]. | Absent [state 2]                                                                        |
| Ligaments                                    | Lig. parasphenoido-suspensorium  | Present [state 0].                                                                 | Absent [state 1].                                                                       |
| Ovalentaria                                   |                                   |                                                                                  |                                                                                          |
| Intramandibular section of m. adductor mandibulae (Aω) | Origin                           | Broadly on the medial face of the quadrate and a part of the muscle can have a tendinous origin [state 2]. | With a tendon anteroventrally to the medial face of the quadrate [state 3].               |
| Atherinomorpha                                |                                   |                                                                                  |                                                                                          |
| External section of m. adductor mandibulae (A1) | Insertion                        | To the medial face of the middle region of the maxilla [state 1]. | With three tendons on the processus primordialis (anguloarticularis), to the medial side of the lacrimal, and mediadly to the anterodorsal tip of the maxilla [state 3]. |
| Internal section of m. adductor mandibulae (A2/3) | Muscle portions                 | Does not separate in two portions [state 0]. | Lateral separated into two portions [state 1]. |

**Ovalentaria** → **Rhinomugil corsula**

**Atherinomorpha** → **Atherina boyeri**
| Muscle | Insertion | Description | State 1 | State 2 |
|--------|-----------|-------------|---------|---------|
| M. protractor hyoidei | Dorsally as well as ventrally of m. intermandibularis to the dentary | Ventrally to m. intermandibularis at the dentary | state 2 | state 1 |
| M. protractor hyoidei | A fusion with the contralateral m. protractor hyoidei occurs at the level of the jaws or suspensoric and united, they travel rostrad and anteroventrally at the fused mm. protractor hyoidei a tendon can be formed on each side | 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 | state 2 | state 1 |
| M. adductor arcus palatini | The anterior portion originates along the whole parasphenoid and inserts dorsally along the entire suspensoric (in addition to other small attachments) | Originates on the posterior part of the parasphenoid and inserts on the posterior region of the suspensoric | state 0 | state 1 |
| M. levator arcus palatini | On the lateral face of the suspensoric on the hyomandibular and to the metapterygoid and with some fibres, it also can attach anteriorly to the processus lateralis hyomandibularis | Ventrally to the medial face and dorsally to the lateral face of the opercle with a continuous horizontal level of insertion | state 0 | state 2 |
| M. levator operculi | Dorsally to the medial face of the opercle with a continuous horizontal level of insertion | Dorsally to the medial face and dorsally to the lateral face of the opercle | state 0 | state 2 |

### Ligaments

| Ligaments | Description | State 1 | State 2 |
|-----------|-------------|---------|---------|
| Primordial ligament | Present as a lig. maxillo-anguloarticulare between the maxilla and the anguloarticular | Absent | state 1 |
| Lig. parasphenoido-suspensorium | Present | Absent | state 1 |

### External section of m. adductor mandibulae (A1)

| Insertion | Description | State 1 | State 2 |
|-----------|-------------|---------|---------|
| On the medial face of the middle region of the maxilla | With two tendons to the lateral face of the middle part of the maxilla and to the medially to the medially of the lacrimal | state 1 | state 4 |

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

| Intramandibular portion | Description | State 0 | State 1 |
|--------------------------|-------------|---------|---------|
| Absent | Present with broad insertions to the processus coronoides dentalis, to cartilago Meckeli, and to the anguloarticular | state 0 | state 2 |

### Intramandibular section of m. adductor mandibulae (A3n)

| Insertion | Description | State 0 | State 2 |
|-----------|-------------|---------|---------|
| On the medial face of the lower jaw, the Ao (when not differentiated into heads) inserts broadly to the dentary, cartilago Meckeli and/or to the anguloarticular | On the ventral part of the dentary | state 0 | state 2 |

### M. protractor hyoidei

| Insertion | Description | State 1 | State 2 |
|-----------|-------------|---------|---------|
| Ventrally to the insertion of m. intermandibularis at the dentary and covers at least the posterodorsal area of the latter muscle | state 0 | state 2 |

### M. dilatator operculi

| Origin | Description | State 1 | State 2 |
|--------|-------------|---------|---------|
| Laterally at the sphenotic, at the autosphenotic, and with some fibres possibly at the anteroventral area of the pterotic | Ventrally at the lateral face of the sphenotic | state 1 | state 0 |

### Nerves

| Trunclus maxillaris infraorbitalis trigemini | Description | State 0 | State 1 |
|------------------------------------------|-------------|---------|---------|
| Branches into the ramus mandibularis trigemini and ramus maxillaris trigemini short before or after leaving the neurocranium | First branches at the level of the eye | state 0 | state 1 |

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

| Lateral head | Description | State 0 | State 3 |
|--------------|-------------|---------|---------|
| Originates almost overall at the vertical aspect of preopercle, at the posterior part of the | With a narrow attachment, it only originates on the ventral third of the vertical aspect of the preopercle | state 0 | state 3 |
|                           | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
|---------------------------|----------------------|-----------|--------|--------------------|--------|---------------------------------------|
| M. adductor mandibulae (A2/3) | Present [state 0].   | To the medial face of the middle region of the maxilla [state 1]. | With three muscle heads in its origin (A2/3, lateral; A2/3, medial; A2/3, intermedial) [state 1]. | Ventrally at the processus lateralis [state 2]. | Ventrally to the ceratohyal [state 2]. |
| M. protractor hyoidei     | Medially to the ceratohyal [state 2]. | Medially to the ceratohyal [state 2]. | Laterally at the ceratohyal [state 0]. | Laterally at the sphenotic and anteriorly at the lateral face of the pterotic [state 2]. | Laterally at the ceratohyal [state 0]. |
| M. dilatator operculi     | Its anterior portion originates along the whole parasphenoid and inserts dorsally along the entire suspensoric [state 0]. | Ventral to the lateral face of the sphenotic [state 0]. | Its anterior portion originates on the posterior part of the parasphenoid and inserts on the posterior region of the suspensoric [state 1]. | Laterally at the sphenotic and anteriorly at the lateral face of the pterotic [state 2]. | Laterally at the ceratohyal [state 0]. |

### Beloniformes → Exocoetoidea

|                           | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
|---------------------------|----------------------|-----------|--------|--------------------|--------|---------------------------------------|
| M. protractor hyoidei     | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
| M. adductor mandibulae (A2/3) | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |

### Exocoetoidea → Parexocoetus lineatus

|                           | Orientation of muscle heads | Relative size of muscle heads | Lateral head | Insertion |
|---------------------------|-----------------------------|-------------------------------|--------------|-----------|
| Internal section of m. adductor mandibulae (A2/3) | The medial head is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. | The medial head is larger than the lateral head [state 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 [state 0]. | Dorsally as well as ventrally of m. intermandibularis to the dentary [state 2]. |
| Internal section of m. adductor mandibulae (A2/3) | The medial head is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. | The medial head is larger than the lateral head [state 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 [state 0]. | Dorsally to the insertion of m. intermandibularis at the dentary and covers at least the posterodorsal area of the latter muscle [state 0]. |

### Adrianichthyidae → Oryzias latipes

|                           | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
|---------------------------|----------------------|-----------|--------|--------------------|--------|---------------------------------------|
| Internal section of m. adductor mandibulae (A2/3) | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
| M. protractor hyoidei     | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |

### Adrianichthyidae → Xenoposculus oophorus

|                           | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
|---------------------------|----------------------|-----------|--------|--------------------|--------|---------------------------------------|
| Internal section of m. adductor mandibulae (A2/3) | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |
| M. protractor hyoidei     | Origin and insertion | Insertion | Origin | Spatial orientation | Origin | Ventrally to the ceratohyal [state 2]. |

### Exocoetoidea → Parexocoetus lineatus

|                           | Orientation of muscle heads | Relative size of muscle heads | Lateral head | Insertion |
|---------------------------|-----------------------------|-------------------------------|--------------|-----------|
| Internal section of m. adductor mandibulae (A2/3) | The medial head is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. | The medial head is larger than the lateral head [state 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 [state 0]. | Dorsally as well as ventrally of m. intermandibularis to the dentary [state 2]. |
| Internal section of m. adductor mandibulae (A2/3) | The medial head is situated dorsally to the lateral head or is at least clearly visible in lateral view [state 0]. | The medial head is larger than the lateral head [state 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 [state 0]. | Dorsally to the insertion of m. intermandibularis at the dentary and covers at least the posterodorsal area of the latter muscle [state 0]. |
| **M. levator operculi** | Insertion | Dorsally to the medial face of the opercle and has a continuous horizontal level of insertion [state 0]. | Dorsally to the medial face and dorsally to the lateral face of the opercle [state 2]. |
|------------------------|-----------|--------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|
| **Ligaments**          | Lig. premaxillo-maxilla | Spans between the proximal ends of the premaxilla and the maxilla [state 1]. | Spans broadly between premaxilla and maxilla [state 0]. |

### clade A ➔ clade B

| **Internal section of m. adductor mandibulae (A2/3)** | Lateral head | Originates almost overall at the vertical aspect of the preopercle, at the posterior part of the horizontal aspect of the preopercle, as well as on the processus lateralis byomandibularis [state 0]. | 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 [state 1]. |
|------------------------------------------------------|--------------|--------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|
| **Intramandibular section of m. adductor mandibulae (Aα)** | Shape | A parallel fibred muscle [state 2]. | A double-feathered muscle [state 1]. |

### clade B ➔ Zenarchopteridae

| **M. adductor arcus palatini** | Origin and insertion | Its anterior portion originates on the posterior part of the parasphenoid and inserts on the posterior region of the suspensoric [state 1]. | Its anterior portion originates along the whole parasphenoid and inserts dorsally along the entire suspensoric [state 0]. |

### clade C ➔ Demogenys pussila

| **Internal section of m. adductor mandibulae (A2/3)** | Origin | Two muscle heads (A2/3, lateral; A2/3, medial) in its origin [state 0]. | Three muscle heads (A2/3, lateral; A2/3, medial; A2/3, intermedial) in its origin [state 1] |
|------------------------------------------------------|--------|---------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| **Intramandibular section of m. adductor mandibulae (Aα)** | Insertion | Only on the medial side of the lower jaw [state 0]. | Also on the coronomeckelian bone [state 1]. |

### clade B ➔ clade D

| **Internal section of m. adductor mandibulae (A2/3)** | Origin | With a tendon anteriorly at the medial face of the symplectic [state 0]. | Broadly on the medial face of the quadrate and a part of the muscle can have a tendinous origin [state 2]. |
|------------------------------------------------------|--------|---------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|
| **Intramandibular section of m. adductor mandibulae (Aα)** | Shape | A parallel fibred muscle [state 2]. | A double-feathered muscle, in which one of the muscle parts may project to a far caudad direction [state 1]. |

### clade C ➔ Nomorhamphus sp.

| **External section of m. adductor mandibulae (A2/3)** | Insertion | If not differentiated into heads, on the medial face of the lower jaw, broadly to the dentary, cartilago Meckeli and/or to the anguloarticular [state 0]. | Broadly to the dentary, to the anguloarticular, and to the cartilago Meckeli; a ventral part in feathered muscles inserts far anteriorly to the medial face of the dentary [state 1]. |

### clade B ➔ Zenarchopteridae

| **M. protractor hyoidei** | Origin | Laterally at the ceratohyal [state 0]. | Medially to the ceratohyal [state 3]. |
|--------------------------|--------|--------------------------------------|--------------------------------------|
| **M. protractor hyoidei** | Course | A fusion with the contralateral m. protractor hyoidei occurs at the level of the jaws or suspensoric and united, they travel rostral and anteroventrally at the fused mm. protractor hyoidei a tendon | Such a fusion does not occur [state 1]. |
can be formed on each side [state 0]

| Muscle                  | Origin                              | Insertion                                      | Nerves                                      |
|------------------------|-------------------------------------|-----------------------------------------------|---------------------------------------------|
| M. levator arcus palatini | Broadly on the sphenotic [state 0]. | Dorsally to the medial face and laterally to the lateral face of the opercle [state 2]. | First branches at the level of the eye into the ramus mandibularis trigemini and ramus maxillaris trigemini [state 1]. |
| M. levator operculi  | On a ridge of the sphenotic, the processus sphenoticus, and some fibres originate directly on the sphenotic [state 1]. | Also dorsally at the medial face of the opercle, but it attaches more ventrally to the anterior region of the medial face of the opercle [state 1]. |

| Nerves                      | Ramus mandibularis facialis | Branches differently to state 0 [state 1] |
|-----------------------------|-----------------------------|------------------------------------------|

clade D  Belone belone  clade D  Scomberesox saurus

M. protractor hyoidei  Insertion  Dorsally as well as ventrally of m. intermandibularis to the dentary [state 2].  Dorsally to the insertion of m. intermandibularis at the dentary and covers at least the posterodorsal area of the latter muscle [state 0].

Lig. parasphenoido-suspensorium  Absent [state 1].  Present [state 0].
Figure 5

*Perca fluviatilis. A-D*) Manual dissections. Compare to Figure 2A.
Figure 6

Rhinomugil corsula. A-D) Manual dissections; levels of histological sections (Figure 7) are indicated. Compare to Figure 2B.
Rhinomugil corsula. A-D) Histological sections; compare to Figure 6.
Rhinomugil corsula

A) Rhinomugil corsula

B) Rhinomugil corsula

C) Rhinomugil corsula

D) Rhinomugil corsula
Atherina boyeri. A-D) Manual dissections; levels of histological sections (Figure 9) are indicated. For one further manual dissection of this species see Figure 12D. Compare to Figure 2C.
Figure 9

*Atherina boyeri. A-D* Histological sections; compare to Figures 8 and 12D.
Figure 10

*Aplocheilus lineatus. A-D)* Manual dissections; levels of histological sections (Figure 11) are indicated. Compare to Figure 2D.
Figure 11

*Aplocheilus lineatus. A-D*) Histological sections; compare to Figure 10.
Figure 12

**Manual dissections. A-C)** *Oryzias latipes*; levels of histological sections (Figure 13) are indicated. A and C modified from Werneburg and Hertwig (2009). Compare to Figure 2E. **D)** *Atherina boyeri*; for other dissections of this species see Figure 8, for histological sections see Figure 9. Compare to Figure 2C.
Figure 13

*Oryzias latipes. A-D* Histological sections; compare to Figure 12. Modified from Werneburg and Hertwig (2009).
Figure 14

*Parexocoetus lineatus. A-D* Manual dissections; levels of histological sections (Figure 15) are indicated. Compare to Figure 2F.
Figure 15

*Parexocoetus lineatus.* A-D) Histological sections; compare to Figure 14.
Figure 16

*Dermogenys pussila. A-C* Manual dissections; levels of histological sections (Figure 17) are indicated. Compare to Figure 2G.
Figure 17

*Dermogenys pussila. A-D*) Histological sections; compare to Figure 16.
Figure 18

_Belone belone. A-C) Manual dissections. Compare to Figure 2H._
Figure 19

**Scomberesox saurus. A-D)** Manual dissections in an adult specimen; approximate levels of histological sections of a juvenile (Figure 20) are indicated.
Figure 20

*Scomberesox saurus. A-D)* Histological sections in a juvenile specimen; compare to Figure 19.
