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The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes: Actinopterygii): comparative anatomy, synonymy, and phylogenetic implications

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Bony fishes of the morphologically diverse infraclass Teleostei include more than 31 000 species, encompassing almost one-half of all extant vertebrates. A remarkable anatomical complex in teleosts is the adductor mandibulae, the primary muscle in mouth closure and whose subdivisions vary in number and complexity. Difficulties in recognizing homologies amongst adductor mandibulae subdivisions across the Teleostei have hampered the understanding of the evolution of this system and consequently its application in phylogenetic analyses. The adductor mandibulae in representatives of all lower teleost orders is described, illustrated, and compared based on broad taxonomic sampling complemented by extensive literature information. Muscle division homologies are clarified via the application of a standardized homology-driven anatomical terminology with synonymies provided to the myological terminologies of previous studies. Phylogenetic implications of the observed variations in the adductor mandibulae are discussed and new possible synapomorphies are proposed for the Notacanthiformes, Ostariophysi, Cypriniformes, Siluriphysi, Gymnotiformes, and Alepocephaloidei. New characters corroborate the putative monophyly of the clades Albuliformes plus Notacanthiformes (Elopomorpha), Argentinoidei plus Esocoidei plus Salmonoidei (Protacanthopterygii) and Hemiodontidae plus Parodontidae (Characiformes). We further confirm the validity of characters from the adductor mandibulae previously proposed to support the monophyly of the Esocoidei and the gonorynchiform clade Gonorynchoidei plus Knerioidei.

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ADDITIONAL KEYWORDS: jaw muscles – musculature – myology – Neoteleostei – Teleostei.

INTRODUCTION

The Teleostei forms one of the largest monophyletic groups across the Vertebrata (Nelson, 2006), with the more than 31 000 extant species in this infraclass representing 96% of all fish biodiversity and approximately one-half of all living vertebrates (IUCN, 2012; Eschmeyer & Fong, 2013). Teleostean fishes are globally distributed throughout almost all aquatic environments in both fresh and marine waters across the spectrum of habits from oceanic depths to precipitous mountain streams. As would be expected given their species-level diversity and their vast range of life styles, teleosts exhibit an astonishing diversity of overall body plans and myriad morphological specializations in all systems.

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Monophyly of the Teleostei is corroborated by a significant series of derived character states (de Pinna, 1996; Arratia, 1999) with the synapomorphies for this group and for its major lineages recently summarized by Wiley & Johnson (2010). Review of that listing demonstrates that almost three-quarters of the vast array of morphological characters delimiting the 180 major lineages of Teleostei involve modifications of the skeleton. The prominence of osteological features in this character set reflects, on the one hand, the extensive exploration of that system across the Teleostei and, on the other, the relatively minor attention directed by systematists towards other anatomical systems (Fig. 1). The negligible percentage of myologically based synapomorphies documented by Wiley & Johnson (2010) derives from both the overall lack of studies on this anatomical system and the difficulties in assembling and comparing myological data from studies focused on small subunits of the Teleostei.

Prime amongst the examples of the difficulties in the incorporation of myological information into higher-level phylogenetic analyses across bony fishes is the adductor mandibulae muscle complex. This muscle mass provides the primary force for mouth closure, a function central to feeding, respiration, and other critical life activities. Most often the adductor mandibulae is subdivided into several subunits of varying degrees of complexity, relative size, and sites of attachment (Winterbottom, 1974; Datovo & Vari, 2013). This trove of potentially phylogenetically informative variation in conjunction with the ready accessibility of the adductor mandibulae along the lateral regions of the head contributed to this muscle being by far the most studied skeletal muscle in teleosts. Indeed, it is often the sole myological complex included in many morphologically based phylogenetic analyses (e.g. Fink & Fink, 1981; Smith-Vaniz, 1984; Castro & Vari, 2004). Notwithstanding its prominence amongst the myological features incorporated into phylogenetic studies, only six of the 42 myological synapomorphies across the Teleostei listed by Wiley & Johnson (2010) involve aspects of the adductor mandibulae. This seeming contradiction is largely a function of the many uncertainties as to the homologies of the subdivisions of the muscle across the expanse of the Teleostei. Absence of such critical basic knowledge renders phylogenetic inferences at more inclusive taxonomic levels impossible or, at best, highly problematic.

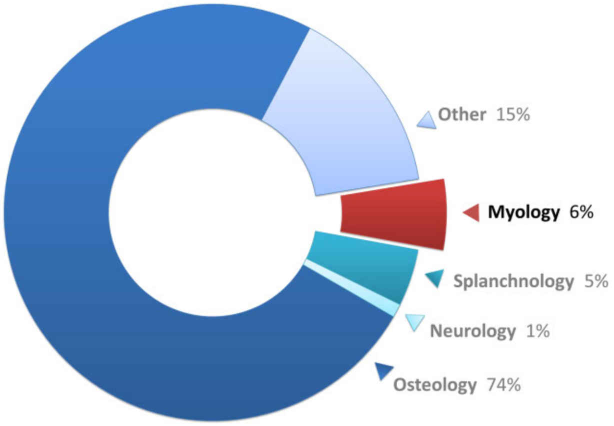


Figure 1. Categories of the morphological synapomorphies delimiting the 180 major groups of the Teleostei listed in Wiley & Johnson (2010).

Lack of information on the homologies of the adductor mandibulae is to a great degree a consequence of the limitations of the alphanumeric terminology (A_1, A_2, A_3, and $A\omega$) initially proposed by Vetter (1878) for this muscle complex and subsequently broadly applied over the 13 following decades. As modified by subsequent authors, the nomenclature originated by Vetter patently failed to reflect the homologies of the components of the adductor mandibulae across many more inclusive clades in the Teleostei. In their overview of the teleostean adductor mandibulae, Datovo & Vari (2013) detailed how the alphanumeric terminology conveyed serious misconceptions as to the evolutionary history of the muscle. Primary amongst these problems was the improper adoption of a model of gain and loss of muscle parts and the use of highly variable attributes as core criteria (i.e. landmarks) for the identification of muscle sections (e.g. the muscular attachment on the maxilla; the path of the ramus mandibularis trigeminus nerve). Perpetuation of this problematic nomenclature for over a century resulted in a striking number of ambiguities. Prime examples are the terms A_1 and A_2, which were applied, respectively, to six and eight different, nonhomologous portions of the muscle in diverse lineages within the Teleostei (Datovo & Vari, 2013). Similarly, no fewer than 11 different designations have been used to refer to a homologous muscle section in a single teleostean order (Datovo & Vari, 2013). Such a degree of pronounced nomenclatural confusion and instability greatly hampered the incorporation of variation in the adductor mandibulae into broader phylogenetic analyses within the Teleostei. Moreover, those results demonstrated the impossibility of adapting the alphanumeric terminology so that it would reflect homologous components of the adductor mandibulae across the Teleostei. As a result, Datovo & Vari (2013) advanced new nomenclatures for both this muscle complex and its associated connective tissue systems in order to achieve congruence between homology and nomenclature and, more importantly, to provide a solid framework that facilitates comparisons amongst the adductor mandibulae components of phylogenetically distant teleosts.

Following on the advances introduced in Datovo & Vari (2013), the present study provides a comprehensive anatomical review of the adductor mandibulae of the lower lineages of the Teleostei, i.e. those not included in the Neoteleostei (Wiley & Johnson, 2010). We describe and illustrate in detail the muscle and associated structures in representatives of all of the 14 orders of basal teleosts and compare our findings with critically pertinent data from the literature. Discordance amongst different studies is discussed and an extensive synonymy for the names previously applied to the components of the adductor mandibulae is presented. We propose several new putative synapomorphies for subgroups within lower teleosts based on new observations and information from the prior literature.

Included in the present analysis is the Ostariophysi, a major lineage within lower teleosts that has long been particularly problematic in terms of questionable homology assumptions for sections of the adductor mandibulae (Gosline, 1989; Diogo & Chardon, 2000a; Datovo & Vari, 2013). In the course of our survey across the Teleostei, we observed that the primitive teleostean condition of the adductor mandibulae is retained in the most generalized members of all major lower teleostean lineages. Neoteleostean fishes conversely demonstrate notable modifications relative to the primitive configuration of the adductor mandibulae and accordingly will be reviewed in a future publication.

MATERIAL AND METHODS

TAXONOMY

Higher-level classification of the Teleostei follows that proposed by Wiley & Johnson (2010). Families not specified in that study are as recognized in Eschmeyer & Fong (2013), except when otherwise noted. The current taxonomic status of the species cited in the synonymies follows Eschmeyer (2013).

MATERIAL

Examined taxa are listed in Table 1. Additional examined comparative material of the Siluriformes, Characiformes, and Neoteleostei is listed in Datovo & Bockmann (2010), Datovo & Castro (2012), and Datovo & Vari (2013), respectively. Examined materials are deposited in the American Museum of Natural History, USA (AMNH); Laboratório de Biologia e Genética de Peixes, Universidade Estadual Júlio de Mesquita Filho, Brazil (LBP); Laboratório de Ictiologia de Ribeirão Preto, Brazil (LIRP); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); and National Museum of Natural History, Smithsonian Institution, USA (USNM). Specimens dissected for analysis of the musculature were double-stained for cartilage and bone following Datovo & Bockmann (2010).

ANATOMICAL TERMINOLOGY

Myology

Insertion is the attachment point of a muscle to the element that moves (or moves to a greater degree) during muscle contraction, whereas origin is the opposite muscle attachment that remains stationary (or moves to a lesser degree) during muscular activity. Skeletal muscles may attach to bones and/or soft tissues. Musculous attachment, whether involving the origin or insertion, is when the fibres of a muscle attach to the skeleton without any intervening macroscopically evident tendon between the muscle and bone (intervening microscopic collagenous tissue is, however, invariably present in all muscle attachments). In a tendinous attachment, the muscle fibres first converge onto a macroscopically evident tendon, which, in turn, attaches to a skeletal element. A subcategory of the tendinous form of attachment is the aponeurotic type of attachment, in which muscle anchorage is achieved via an aponeurosis (see Connective tissues proper, below). In many instances, the attachment of a muscle is both partially musculous and partially tendinous.

Nomenclature for the subunits of the adductor mandibulae complex follows Datovo & Vari (2013). Remaining skeletal musculature is named according to Winterbottom (1974). The terms section or pars of a muscle refer to any identifiable subunit of a muscle whose homology and evolutionary history can be traced across different taxa. Such terms are applied regardless of the degree of separation of the section in question from the adjoining muscle parts (Datovo & Vari, 2013).

Connective tissues proper

Terminology for the connective membranes and ligaments associated with the adductor mandibulae follows Datovo & Vari (2013). Homologous bands of regular connective tissue associating solely with bones in some taxa and with both bones and muscles in other groups are both treated as ligaments. Such a procedure is necessary to avoid the use of alternative qualifiers (ligament in the former case vs. tendon in the latter) for homologous connective tissue bands that only differ in terms of their association, or lack thereof, with muscles (see Johnson & Patterson, 2001; Datovo & Vari, 2013).

Raphe is a linear tendinous suture, or seam, between adjacent muscles or muscle parts. An aponeurosis is any flattened, laminar tendon (Benjamin, Kaiser & Milz, 2008) and, therefore, also consists of regularly arranged collagen fibres (Willard *et al*., 2012). Aponeuroses may progressively differentiate distally into cord-like tendons (Benjamin *et al*., 2008) as exemplified by the intersegmental aponeurosis of the adductor mandibulae in most teleosts (Datovo & Castro, 2012; Datovo & Vari, 2013). In other instances, an aponeurosis may form

Table 1. Material examined

Order	Family	Species	Catalogue number	Examined specimens
Albuliformes	Albulidae	*Albula vulpes*	LIRP 7427	1
			MZUSP 10625	1
Amiiformes	Amiidae	*Amia calva**	USNM 64338	1
Anguilliformes	Anguillidae	*Anguilla reinhardti*	USNM 311978	1
	Congridae	*Ariosoma* sp.	MZUSP 12060	1
Argentiniformes	Argentinidae	*Argentina striata*	MZUSP 17914	1
	Alepocephalidae	*Bajacalifornia burragei*†	USNM 343804	1
		Conocara macropterum†	USNM 410568	1
		Leptoderma sp.†	USNM 410567	1
		Talismania homoptera	USNM 410566	1
		Xenodermichthys copei	MZUSP 86570	1
Characiformes	Distichodontidae	*Xenocharax spilurus*	AMNH 230302	2
			MZUSP 50358	1
Clupeiformes	Denticipitidae	*Denticeps clupeoides*	MZUSP 84776	2
	Pristigasteridae	*Pellona harroweri*	MZUSP 11364	2
Cypriniformes	Cyprinidae	*Carassius auratus*	MZUSP 112353	2
		Danio rerio	MZUSP 112354	3
		Raiamas senegalensis	USNM 271201	1
		Rasbora cephalotaenia	USNM 330848	1
Elopiformes	Elopidae	*Elops lacerta*	MZUSP 84787	1
	Megalopidae	*Megalops cyprinoides*	USNM 102685	1
Gonorynchiformes	Chanidae	*Chanos chanos*	USNM 173572	1
			USNM 347536	1
Gymnotiformes	Gymnotidae	*Gymnotus carapo*	MZUSP 69391	1
	Hypopomidae	*Brachyhypopomus pinnicaudatus*	LIRP 6055	2
	Sternopygidae	*Eigenmannia virescens*†	LIRP 395	2
Hiodontiformes	Hiodontidae	*Hiodon tergisus*	USNM 167970	1
Lepisosteiformes	Lepisosteidae	*Lepisosteus platostomus**	USNM 54983	1
Notacanthiformes	Halosauridae	*Halosaurus pectoralis*	USNM 317567	1
Osteoglossiformes	Arapaimidae	*Arapaima gigas*	MZUSP 26083	1
	Osteoglossidae	*Osteoglossum ferreirai*	USNM 300966	1
Salmoniformes	Esocidae	*Esox americanus*	USNM 237253	1
	Galaxiidae	*Galaxias maculatus*	MZUSP 16600	1
	Osmeridae	*Hypomesus olidus*	USNM 336878	1
		Osmerus mordax	USNM 395752	1
	Salmonidae	*Oncorhynchus mykiss*	MZUSP 85378	1
	Umbridae	*Umbra pygmaea*	USNM 333152	1
Siluriformes	Diplomystidae	*Diplomystes camposensis*†	LBP 3106	1
		Diplomystes mesembrinus†	LBP 449	1
	Nematogenyidae	*Nematogenys inermis*	LBP 1002	1
			MZUSP 88522	2
	Siluridae	*Silurichthys hasseltii*	MZUSP 63489	1

*Outgroup taxon.
†Only partially dissected.

a fibrous laminar cover over a muscle surface (Benjamin *et al*., 2008; Datovo & Castro, 2012). Aponeuroses of this form should not be confused with fasciae, which are thinner membranous sheets composed of irregularly arranged collagen fibres that envelop muscles (Willard *et al*., 2012). Tendons, aponeuroses, and fasciae are usually fully translucent in small and medium-sized specimens of teleosts.

Osteology

Nomenclature for the skeletal components of the neurocranium, lower jaw, and orbital series follows

Patterson (1975), Nelson (1973), and Nelson (1969), respectively. Terminology for the suspensorium (i.e. hyopalatine arch plus opercular series) follows Grande & Bemis (1998), with the term palatine applied to both the ossification demonstrably formed by the fusion of the autopalatine and dermopalatine and when a distinction between these two components is undetermined (Britz, 1996).

Neurology

Terminology for the cranial nerves conforms to the Freihofer (1978) nomenclature.

ILLUSTRATIONS

The results of our survey revealed that some prior publications dealing with diverse taxa in the Teleostei included apparently inaccurate drawings of adductor mandibulae morphology. In order to avoid such problems, we instead illustrate pertinent details of the muscle of the taxa investigated in this study via photographs. This approach unequivocally portrays our observations and underpins discussions of conflicts between our findings and those reported in prior publications. Drawings are presented solely for hypothetical taxa in order to present and illustrate basic patterns of the adductor mandibulae in the Teleostei.

Photographs presented herein are based on multifocal montages derived from the stacking of several individual photographs taken at different focal planes using stereomicroscope systems with attached digital image capture devices or cameras. The final fully focused montage was prepared in CombineZP (Hadley, 2009). Montages were then retouched digitally in Adobe Photoshop CS5 in order to remove artefacts (bubbles, specks, etc.) and imperfections in the original anatomical preparations (e.g. muscles inadvertently stained with Alizarin red or Alcian blue) and to highlight structures of interest via adjustments in contrast, shadows, and channel levels. Nerves were digitally coloured green in order to set them apart from proximate muscle fibres.

GENERAL PATTERN OF THE ADDUCTOR MANDIBULAE IN THE TELEOSTEI

This section briefly characterizes the main subdivisions of the adductor mandibulae of the Teleostei to facilitate the understanding of the subsequent discussions of the morphology of the muscle within each teleostean subgroup investigated in this study. These characterizations follow the conclusions of Datovo & Vari (2013), who critically evaluated the homologies of these subunits of the teleostean adductor mandibulae and introduced a new terminology for the components of the muscle. Datovo & Vari (2013) proposed that it was critical to analyse as many attributes as possible – position, origin, insertion, relationships with adjoining structures, ontogeny, innervation, etc. – in order to arrive at the most parsimonious hypothesis of the homology of a muscle component in each investigated taxon. Thus, single morphological attributes cannot be a priori identified as being universally diagnostic for a specific muscle section across the entirety of the Teleostei. Accordingly, the morphological attributes discussed below and illustrated in Figures 2–5 as characterizing each muscle component are the most general amongst teleosts. Taxa not included in this analysis may demonstrate variation beyond the illustrated conditions. The reader is referred to Datovo & Vari (2013) for more detailed anatomical descriptions and in-depth discussions of the evolution, homologies, and nomenclature of components of the adductor mandibulae and the connective tissues associated with that muscle.

In its simplest configuration, the teleostean adductor mandibulae is composed of two segments, the segmentum facialis and the segmentum mandibularis (Fig. 2). These segments are connected by an intersegmental aponeurosis, with the segmentum facialis originating from the lateral face of the suspensorium and the segmentum mandibularis attaching onto the medial surface of the lower jaw. Both of these muscle segments and the intersegmental aponeurosis may differentiate within the Teleostei into a number of specialized subunits that exhibit varying degrees of differentiation and separation from each other.

Most teleosts have the intersegmental aponeurosis divided into an anterodorsal mandibular tendon, which primarily serves as the site of origin for the segmentum mandibularis, and an anteroventral meckelian tendon that typically attaches to the coronomeckelian bone (Fig. 3). Other tendinous rami may develop from the intersegmental aponeurosis: an anteromedial accessory tendon usually anchoring to the lower jaw, a posteroventral facial tendon attaching to the lateral face of the suspensorium, and a posterodorsal subocular tendon running along the anterodorsal border of the segmentum facialis (Fig. 4). The intersegmental aponeurosis is often partially continuous with the buccal membranes (Figs 2, 3) and some of the ligaments formed within the body of these membranes may merge with the intersegmental aponeurosis. This is the case for the transverse ligament, which differentiates from the buccopalatal membrane and merges with the middorsal portion of the intersegmental aponeurosis (Fig. 4). The faucal ligament, in turn, differentiates from the buccopharyngeal membrane and anteriorly merges into the anteromedial surface of the intersegmental aponeurosis and/or the segmentum mandibularis.

The segmentum facialis often differentiates into three primary sections or partes (singular pars; Fig. 3). The dorsolateral pars malaris usually originates from the

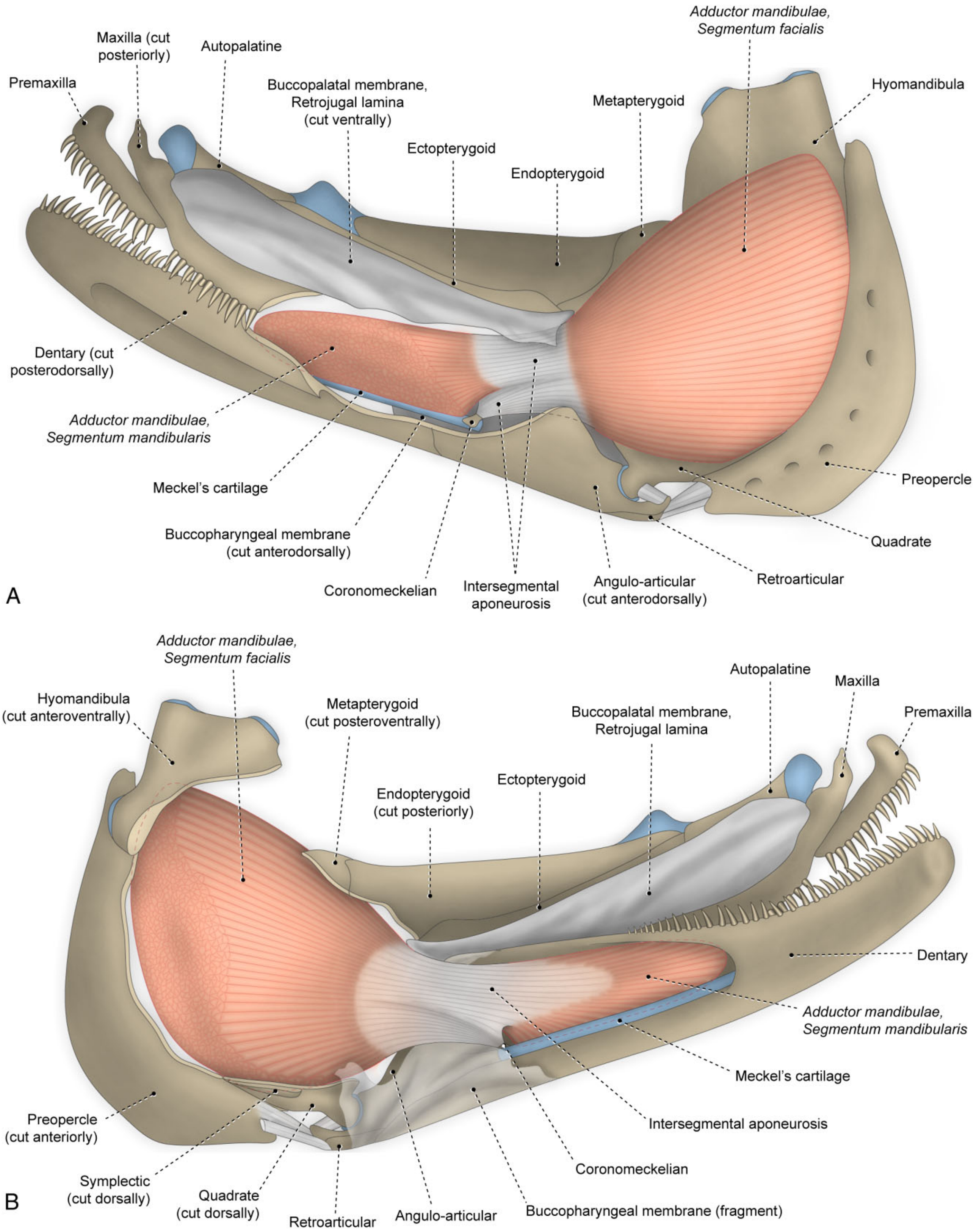


Figure 2. Unspecialized adductor mandibulae of teleosts. Left side muscle and associated structures in hypothetical teleost in (A) lateral and (B) medial views.

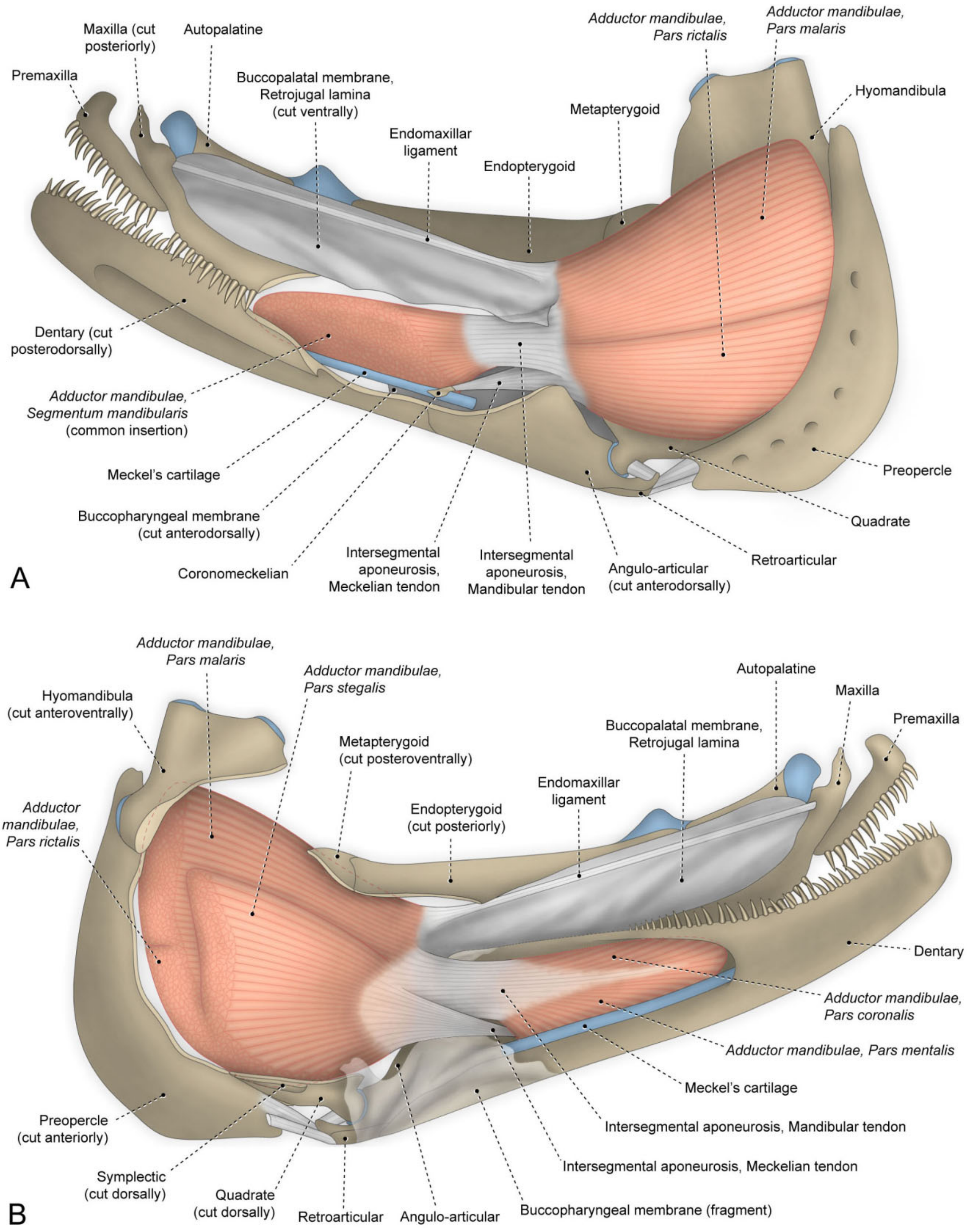


Figure 3. Primary sections of the divided adductor mandibulae of teleosts. Left side muscle and associated structures in hypothetical teleost in (A) lateral and (B) medial views.

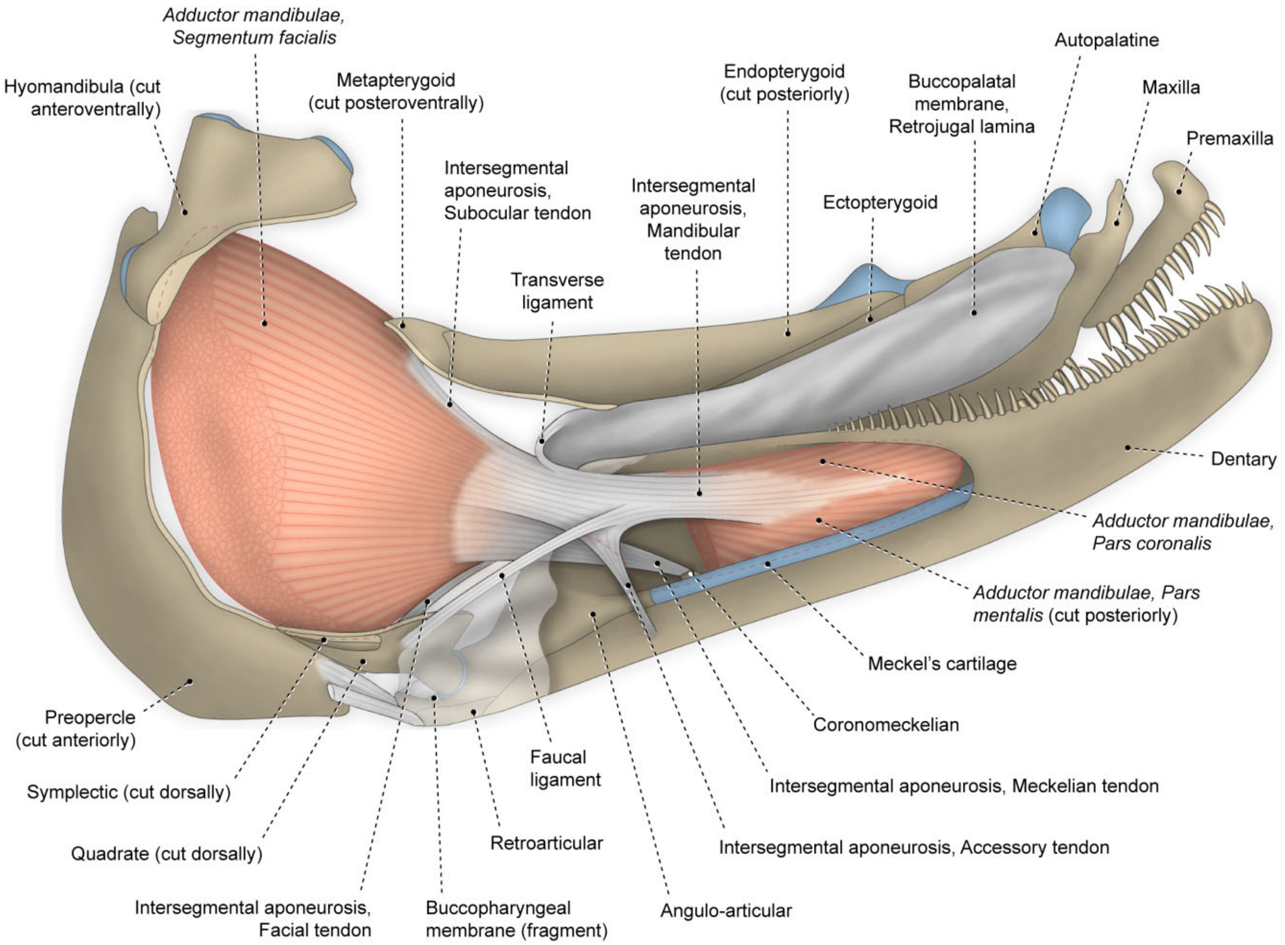


Figure 4. Subdivisions of the intersegmental aponeurosis of teleosts. Left side adductor mandibulae and associated structures of hypothetical teleost in medial view.

dorsal portion (= vertical arm) of the preopercle and the posterodorsal region of the hyomandibula. The ventrolateral pars rictalis typically arises from the ventral portions of the quadrate and preopercle. The medial pars stegalis usually has a more anteriorly situated origin from the metapterygoid and the anterodorsal region of the hyomandibula.

The three primary facial sections (malaris, rictalis, and stegalis) may differentiate further into secondary subsections (Fig. 5) which, in turn, may also additionally divide into tertiary subdivisions, and so forth. The malaris may give rise to an anterodorsal promalaris, which often has a direct connection with the endomaxillar and/or ectomaxillar ligaments, and a posteroventral retromalaris that usually retains an insertion onto the posterodorsal region of the retrojugal lamina (Fig. 5A, B). The rictalis may differentiate into a lateral ectorictalis subsection and a medial endorictalis subsection (Fig. 5C). In such instances, the ectorictalis frequently acquires an insertion onto the lateral region of the retrojugal lamina, whereas the endorictalis retains a connection with the lower jaw. The stegalis may at least partially divide into an anterodorsal epistegalis and posteroventral substegalis (Fig. 5D). These subsections are typically located medial and ventral to the levator arcus palatini, respectively.

The segmentum mandibularis is less frequently differentiated into subunits, although the two primary sections of this muscle segment, the dorsal coronalis and ventral mentalis, are often superficially recognizable along their posteromedial regions (Fig. 3). The mentalis may be further differentiated into a posterior postmentalis and an anterior prementalis (Fig. 5E).

SPECIFIC ANATOMICAL DESCRIPTIONS AND COMPARISONS

The following subsections detail and discuss the alternative morphologies of the adductor mandibulae complex for members in each of the examined orders and selected suborders of lower teleosts. For each order

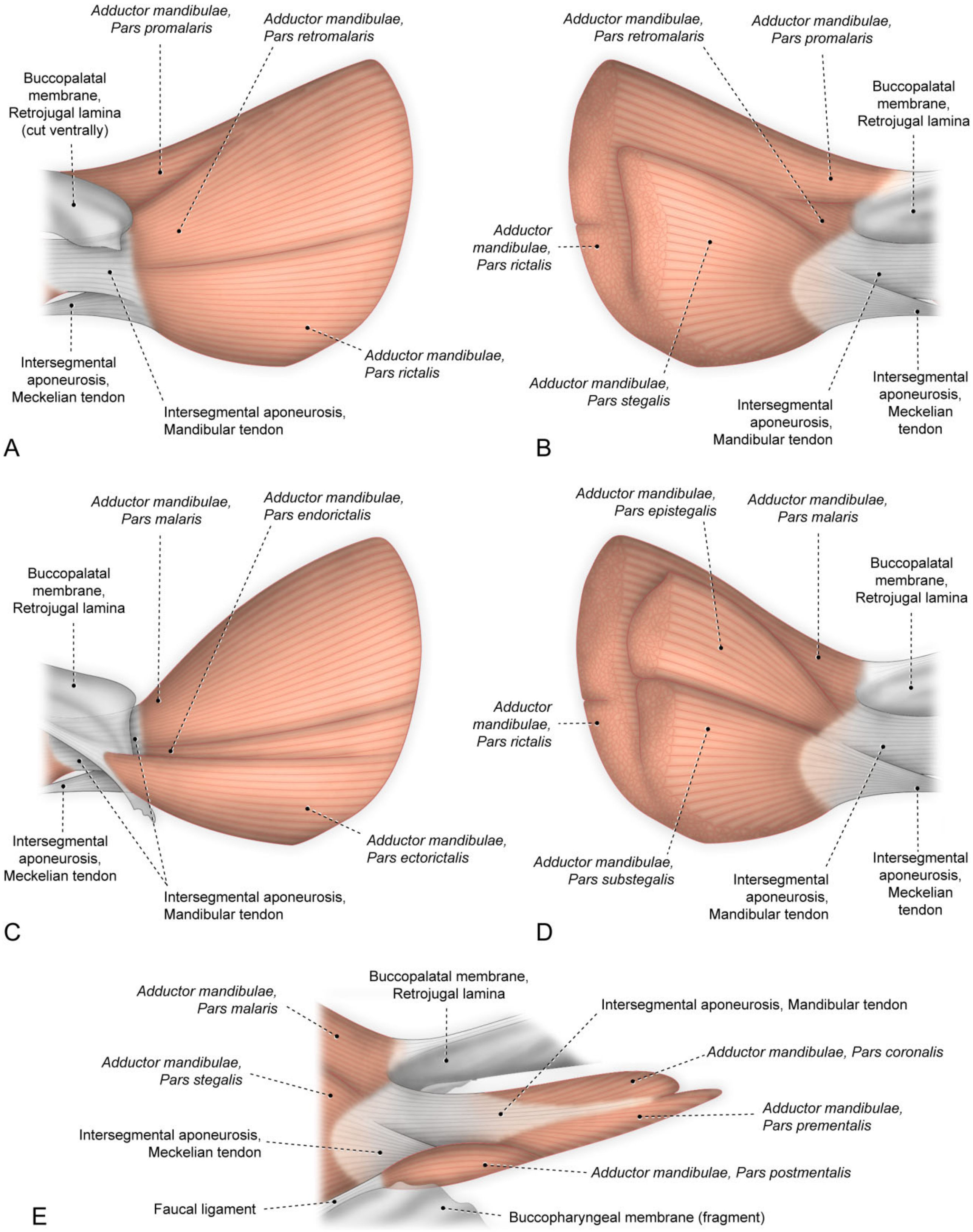


Figure 5. Most common secondary sections of the adductor mandibulae of teleosts. Left side muscle and associated connective tissues in hypothetical teleosts. Subdivided malaris in (A) lateral and (B) medial views; (C) subdivided rictalis in lateral view; (D) subdivided stegalis in medial view; and (E) subdivided mentalis in medial view.

or suborder, we first present a description of the adductor mandibulae in the examined representative(s). This overview is supplemented by comments and comparisons with pertinent data from the literature. Lastly, a list of synonyms is presented for each muscle section reported in previous studies. This facilitates access to information in prior publications within the context of the new terminology for the adductor mandibulae advanced by Datovo & Vari (2013).

Genera to which a synonym applies are specified in the synonymy listings. In instances of subsequent generic reallocation or when significant intrageneric myological divergence was encountered, the species names are provided. These summaries are critical because the applied nomenclature in many prior studies failed to reflect muscle section homologies (Datovo & Castro, 2012; Datovo & Vari, 2013). For example, under the traditional alphanumeric nomenclature of Vetter (1878), the facial sections of the adductor mandibulae are chiefly identified on the basis of their insertion – A_1 for the section inserting on the maxilla, and A_2 and A_3, respectively, for the lateral and medial sections inserting onto the lower jaw. In a rigorous application of these criteria, a homologous section having alternative insertions in different taxa would be identified by different designations. Conversely, a name might be ambiguously applied to nonhomologous sections (e.g. any component of the adductor mandibulae attaching to the maxilla would be termed A_1 notwithstanding dramatically different locations within the overall muscle).

Not all taxa or all muscle sections discussed in earlier analyses could be confidently included in the synonymies because of an absence of critical detail in some prior studies. For example, Gosline (1986) and Friel & Wainwright (1997) explicitly acknowledged that the deeper section of the segmentum facialis (their A_3) was not incorporated in their studies. A similar situation often applies to the segmentum mandibularis (Aω or Aw of most previous studies) that commonly was not investigated in prior studies. Ambiguous or equivocal information from the literature similarly could not be incorporated into the synonymies.

ELOPOMORPHA

ELOPIFORMES

Descriptions

Elops lacerta (Fig. 6)

The segmentum facialis lacks any obvious divisions along its entirety. Origin of this muscle segment is from the preopercle, quadrate, metapterygoid, symplectic, and hyomandibula. At its insertion, the ventromedial fibres of the segmentum facialis, which presumably correspond to the stegalis, converge to a flat meckelian tendon that attaches to the coronomeckelian. The remaining facial muscle mass, which corresponds to the ricto-malaris, inserts on the mandibular tendon and retrojugal lamina that are continuous with each other.

The ramus mandibularis trigeminus nerve passes external to all of the segmentum facialis.

The segmentum mandibularis is undivided. This segment originates from the flat mandibular tendon and inserts on the dentary and angulo-retroarticular.

Megalops cyprinoides (not illustrated)

The overall morphology of the adductor mandibulae in *Megalops cyprinoides* is similar to that of *Elops lacerta*, with both taxa demonstrating the same basic position and sites of origin and insertion of the muscle. Nevertheless, the muscle sections in these taxa differ in various features. The ricto-malaris and stegalis of *Megalops cyprinoides* are better differentiated from each other anteriorly and the ramus mandibularis trigeminus nerve in that species passes between these muscle sections rather than external to both of them. The ventrolateral facial set of fibres of the adductor mandibulae, which corresponds to the rictalis, is more intimately associated in *Megalops cyprinoides* with a well-defined preangulo-paramaxillar ligament. The tendons of the intersegmental aponeurosis are more obviously separated from each other and an accessory tendon is present in this species vs. absent in *Elops lacerta*. This accessory tendon passes lateral to the meckelian tendon and inserts on the angulo-retroarticular and posterior tip of the coronomeckelian bone.

Remarks

Vrba (1968) provided detailed descriptions of the adductor mandibulae of elopiforms and our observations nearly universally confirm his results despite the different nomenclature applied to the muscles and ligaments in that publication. The author refers to the segmentum facialis as the adductor mandibulae and the segmentum mandibularis as the intramandibularis muscle. Paralleling the observations of the present study, Vrba (1968) also discussed the more obvious differentiation of the subunits of the segmentum facialis in *Megalops* than in *Elops*. In the case of *Megalops* he identified these subdivisions via specific designations, applying A_1A_2 to the ricto-malaris and A_3 to the stegalis.

Other studies similarly reported an undivided segmentum facialis in *Elops* (e.g. Winterbottom, 1974; Diogo & Doadrio, 2008; Diogo, Doadrio & Vandewalle, 2008a; Diogo, Hinits & Hughes, 2008b). Contrary to Vrba (1968), these series of studies designated the entire segmentum facialis as an A2, a procedure potentially leading to the erroneous assumption that the A_1 and A_3 of *Megalops* were absent in *Elops*. As Vrba (1968) inferred, and the present study confirms, all of the facial sections found in *Megalops* are undoubtedly present

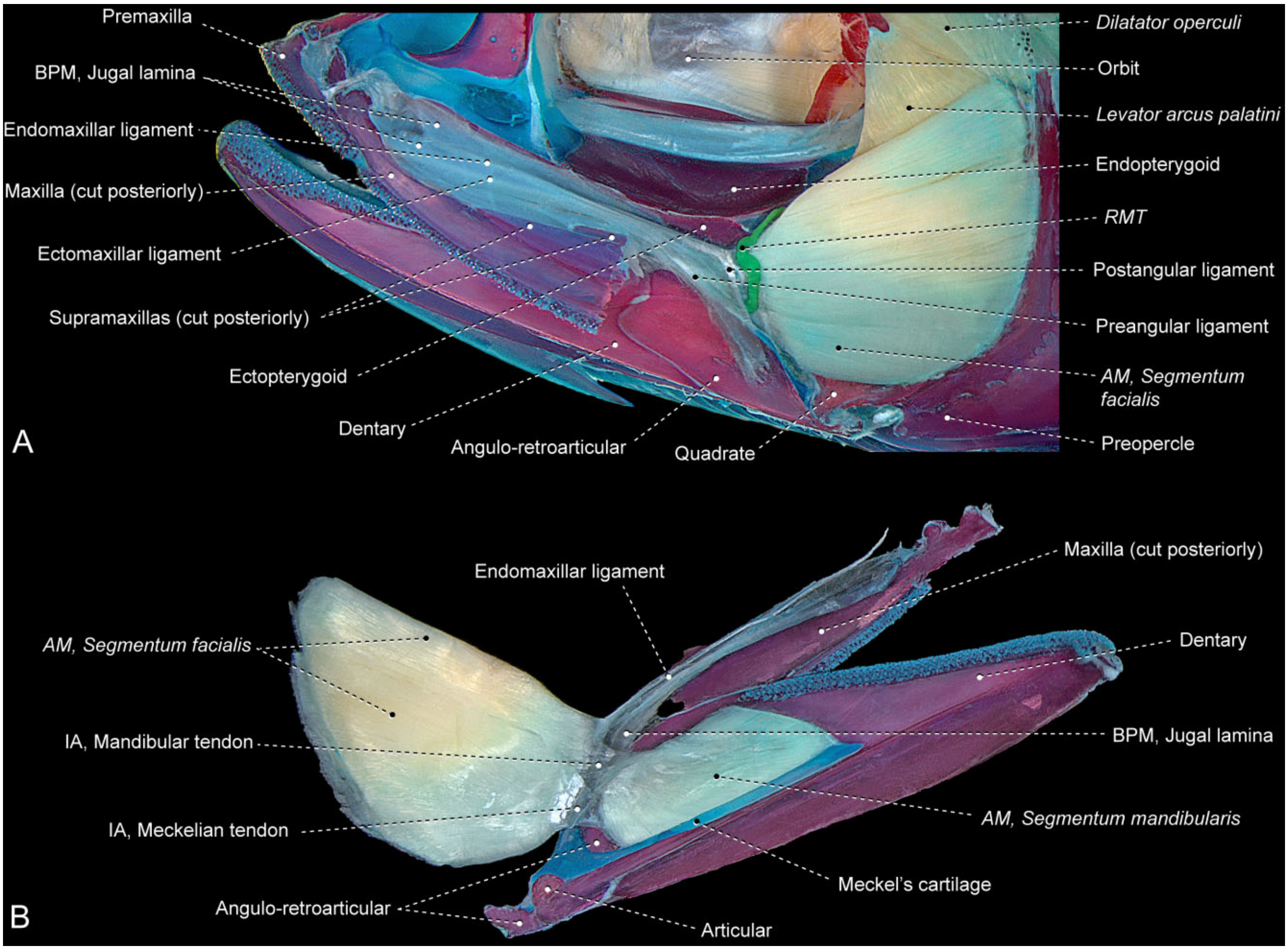


Figure 6. Adductor mandibulae and associated structures of *Elops lacerta* (Elopiformes: Elopidae), MZUSP 84787 (113.7 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

in *Elops*, with the totality of the segmentum facialis exhibiting the same basic origin, insertion, and position in both genera.

Synonymy

Segmentum facialis

A2: Diogo & Doadrio (2008): *Elops*; Diogo *et al*. (2008b): *Elops*; Winterbottom (1974): *Elops*.

Adductor mandibulae: Vrba (1968): *Elops*, *Megalops*.

Pars ricto-malaris

A_1A_2: Vrba (1968): *Megalops*.

Pars stegalis

A_3: Vrba (1968): *Megalops*.

Segmentum mandibularis

Aω: Diogo & Doadrio (2008): *Elops*; Diogo *et al*. (2008b): *Elops*.

Aw: Winterbottom (1974): *Elops*.

Intramandibularis: Vrba (1968): *Elops*, *Megalops*.

ALBULIFORMES

Description

Albula vulpes (Fig. 7)

The three primary sections of the segmentum mandibularis are relatively well differentiated, albeit with these sections partially continuous with each other along some areas of contact. The rictalis originates from the preopercle and quadrate and inserts on the posterior region of coronoid process of the angulo-retroarticular. The posterodorsal portion of this section is mostly aponeurotic and covers a considerable part of the malaris. A small area of the rictalis has its fibres intermingling with the posteroventral region of the malaris. Anteriorly the rictalis is continuous with the stegalis.

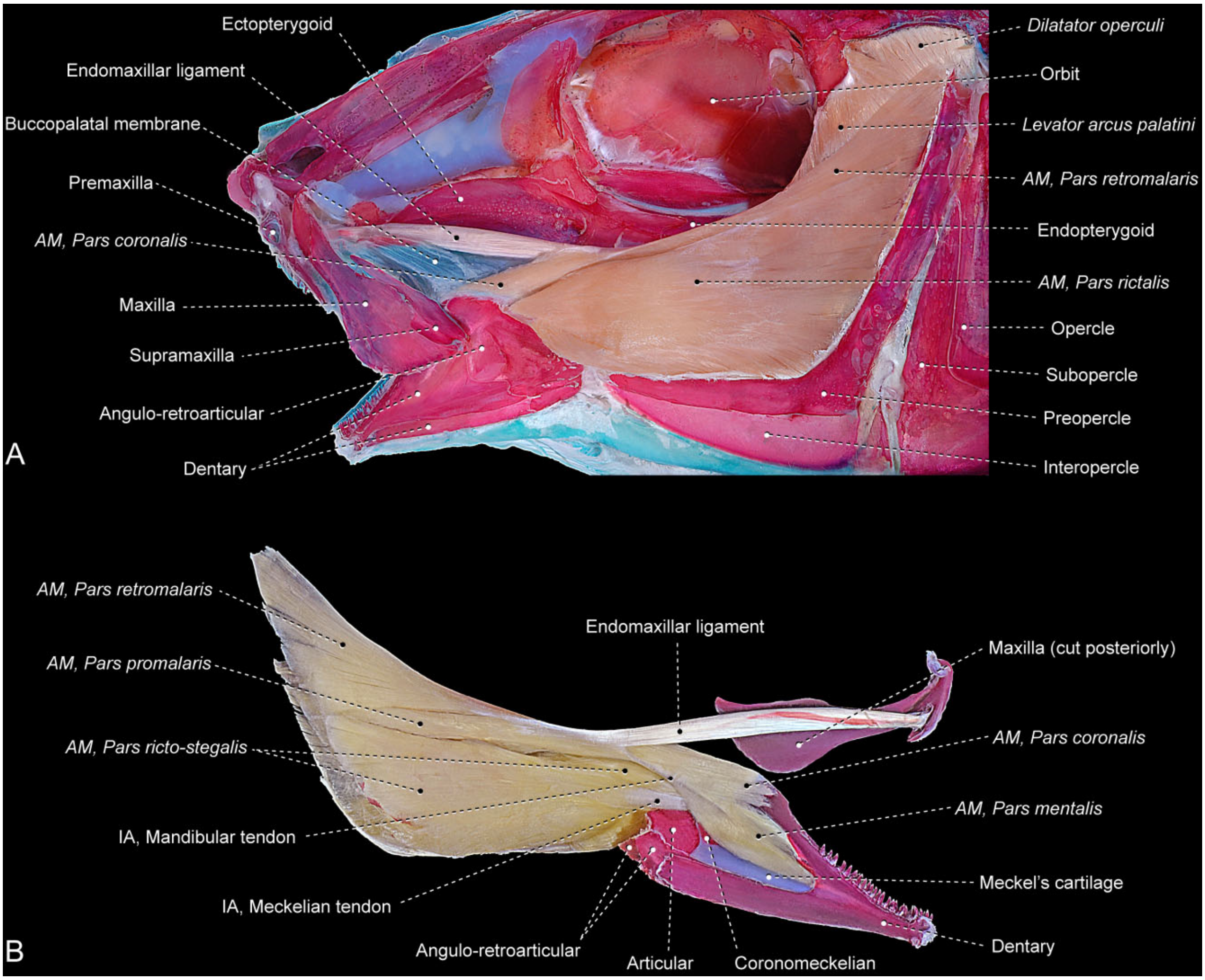


Figure 7. Adductor mandibulae and associated structures of *Albula vulpes* (Albuliformes: Albulidae), LIRP 7427 (189.3 mm standard length). Left side in (A) lateral and (B) medial views; ramus mandibularis trigeminus nerve removed. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis.

The malaris arises from the hyomandibula and converges to the point of junction of the endomaxillar ligament with the mandibular tendon. In the two examined specimens, the malaris shows a partial differentiation into the retromalaris and promalaris from a medial view. The very conspicuous endomaxillar ligament attaches anteriorly to the anteromedial region of the maxilla.

The stegalis extends from the metapterygoid to the meckelian tendon, which is, in turn, completely separate from the mandibular tendon. The meckelian tendon continues anteriorly medial to the segmentum mandibularis to an attachment on the coronomeckelian.

The ramus mandibularis trigeminus nerve runs lateral to the segmentum facialis and transits between the coronalis (dorsally) and the ricto-stegalis (ventrally) in its passage to the lower jaw.

The coronalis extends posteriorly beyond the limits of the lower jaw and originates from the posterior portions of both the mandibular tendon and endomaxillar ligament in their area of confluence. This section inserts onto the dorsomedial surface of the portions of the dentary and angulo-retroarticular forming the coronoid process. The mentalis is posteriorly continuous with the coronalis but anteriorly is well separated from that section. The mentalis arises solely from the mandibular tendon and inserts on the dentary, angulo-retroarticular, and Meckel's cartilage.

Remarks

The morphology of the adductor mandibulae in *Albula vulpes* was previously described by Greenwood (1977) and Wu & Shen (2004). Both analyses recognized that the dorsal-most fibres of the muscle (= malaris) are associated with an endomaxillar ligament and partially separated from the remaining mass of the facial muscle (Fig. 7). Only Greenwood (1977) attributed a distinct name (his A1β) to this portion of the muscle. No similar association of fibres with the endomaxillar ligament was reported for *Pterothrissus*. That genus consequently would have the entire segmentum facialis inserted solely on the lower jaw (Greenwood, 1977).

The coronalis of *Albula* is well differentiated from the mentalis and posteriorly expanded, so as to be visible in a superficial lateral view (Fig. 7). Owing to this degree of differentiation, Greenwood (1977) and Wu & Shen (2004) designated the mentalis as the Aω/Aw, whereas the coronalis was treated as part of the segmentum facialis. *Pterothrissus* was reported as having the coronalis conversely poorly separated from the mentalis and not posteriorly expanded. The entire segmentum mandibularis in this taxon was consequently identified as the Aω by Greenwood (1977).

Synonymy

Segmentum facialis
  A2: Wu & Shen (2004): *Albula*.
  Adductor mandibulae: Greenwood (1977): *Pterothrissus*.

Pars ricto-stegalis
  A2: Greenwood (1977): *Albula*.

Pars malaris
  A1β: Greenwood (1977): *Albula*.

Segmentum mandibularis
  Aω: Greenwood (1977): *Pterothrissus*.

Pars mentalis
  Aω: Greenwood (1977): *Albula*.
  Aw: Wu & Shen (2004): *Albula*.

NOTACANTHIFORMES

Description

Halosaurus pectoralis (Fig. 8)

The retromalaris is superficially distinguishable from the remainder of the segmentum facialis, especially in its distinctly posteriorly displaced origin. The retromalaris arises from the preopercle and hyomandibula and inserts on the subocular tendon and buccopalatal membrane. The promalaris is totally separate from all other facial sections. It arises from a posterodorsal expansion of the metapterygoid and inserts on the retrojugal lamina and more so on the well-differentiated endomaxillar ligament that attaches to the anteromedial region of the maxilla.

The rictalis and stegalis are fully continuous along their expanses, thereby forming a compound ricto-stegalis originating from the metapterygoid, quadrate, and preopercle. The lateral set of fibres of the ricto-stegalis, probably corresponding to the rictalis, inserts on the mandibular tendon, whereas the medial set of fibres, representing the stegalis, converges to the meckelian tendon. This tendon attaches to the posterior portions of Meckel's cartilage.

Posteriorly, the ramus mandibularis trigeminus nerve traverses the segmentum facialis between the promalaris and retromalaris and then proceeds anteriorly between the coronalis dorsally and the ricto-stegalis and mentalis ventrally.

The segmentum mandibularis originates from the mandibular tendon and is well differentiated into the coronalis and mentalis sections. The coronalis extends posteriorly distinctly beyond the posterior border of the lower jaw and is laterally enclosed by the vault-shaped posterodorsal portion of the buccopalatal membrane. Both the coronalis and mentalis insert onto the angulo-articulo-retroarticular.

Remarks

Determination of the homology of the dorsomedial facial section inserting on the maxilla via the endomaxillar ligament is complicated in *Halosaurus pectoralis* (Fig. 8B). At first sight, this muscle section might be considered to represent a dorsal subdivision of the stegalis as proposed by Diogo *et al*. (2008a; their A3-MAX). Comparisons with other species of the Notacanthiformes and Albuliformes cast doubt on that hypothesis of homology. In *Albula*, a partially differentiated medial promalaris has the same basic features as the section in question in the Notacanthiformes: an origin aligned with that of the stegalis and an insertion on the endomaxillar ligament (Fig. 7B). These features suggest that the dorsomedial facial section inserting via the endomaxillar ligament onto the maxilla in *Halosaurus pectoralis* is rather an anteromedial subdivision of the malaris, i.e. the promalaris (Fig. 8B). Further supporting this supposition is the fact that the notacanthiforms *Notacanthus* and *Polyacanthonotus* have the dorsomedial (= promalaris) and dorsolateral (= retromalaris) facial sections sharing an anterior tendinous connection (Greenwood, 1977).

The adductor mandibulae of other halosaurids, although largely similar to that of *Halosaurus pectoralis* (Greenwood, 1977), demonstrates some notable differences. According to Greenwood (1977), other halosaurids have the stegalis fully or partially separated from the rictalis and, at least in *Halosaurus guentheri*, the posterior margin of the retromalaris is aligned with that of the rictalis. Consequently, the two latter sections cannot be discerned from each other in *Halosaurus guentheri* and jointly form a ricto-retromalaris.

The adductor mandibulae of notacanthids demonstrates some notable differences relative to the

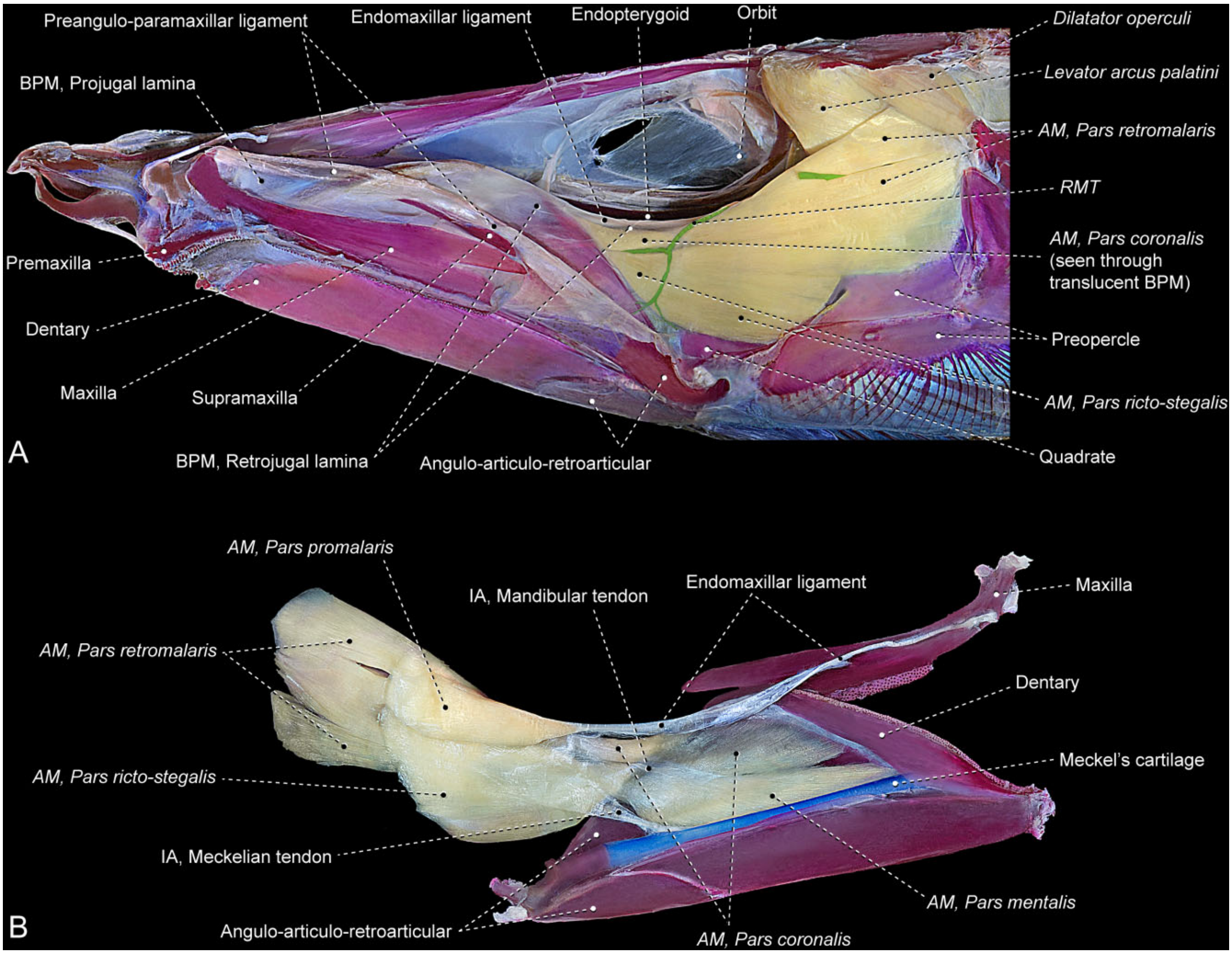


Figure 8. Adductor mandibulae and associated structures of *Halosaurus pectoralis* (Notacanthiformes: Halosauridae), USNM 317567 (518 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

condition in the Halosauridae: the segmentum mandibularis is absent (vs. present); the rictalis inserts on the maxilla (vs. the mandibular tendon); and the promalaris originates medial to the levator arcus palatini (vs. anteroventral to the levator arcus palatini; Greenwood, 1977). In *Polyacanthonotus africanus* and *Notacanthus*, the retromalaris is divided into a dorsolateral retromalaris superioris and a ventromedial promalaris inferioris. *Notacanthus* additionally has a rictalis subdivided into a large ectorictalis and a small endorictalis (Trotti, 1945; Greenwood, 1977).

Synonymy

Pars rictalis
A1α: Greenwood (1977): *Lipogenys*, *Notacanthus*, *Polyacanthonotus*.

Pars ectorictalis
$\mathrm{A1}\alpha^{1}$: Greenwood (1977): *Notacanthus*.
$\mathrm{a}_{1}\beta$: Trotti (1945): *Notacanthus*.

Pars endorictalis
$\mathrm{a}_{1}\alpha$: Trotti (1945): *Notacanthus*.
$\mathrm{A1}\alpha^{2}$: Greenwood (1977): *Notacanthus*.

Pars ricto-retromalaris
A2: Greenwood (1977): *Aldrovandia*, *Halosauropsis*, *Halosaurus*.

Pars retromalaris
A2: Greenwood (1977): *Lipogenys*, *Notacanthus*, *Polyacanthonotus*.

Pars retromalaris superioris
a_2: Trotti (1945): *Notacanthus*.
A2β: Greenwood (1977): *Notacanthus*, *Polyacanthonotus africanus*.

Pars retromalaris inferioris
A2α: Greenwood (1977): *Notacanthus, Polyacanthonotus africanus*.
a_3: Trotti (1945): *Notacanthus*.

Pars promalaris
A1β: Greenwood (1977): *Aldrovandia*, *Halosauropsis*, *Halosaurus*, *Lipogenys*, *Notacanthus*, *Polyacanthonotus*.
A3-MAX: Diogo *et al*. (2008a): *Notacanthus*.
r: Trotti (1945): *Notacanthus*.

Pars stegalis
A3: Greenwood (1977): *Aldrovandia*, *Halosauropsis*, *Halosaurus*, *Lipogenys*, *Notacanthus*, *Polyacanthonotus*.
a_4: Trotti (1945): *Notacanthus*.

Segmentum mandibularis
Aω: Greenwood (1977): *Aldrovandia*, *Halosauropsis*, *Halosaurus*.

ANGUILLIFORMES

Description

Anguilla reinhardti (Fig. 9)

At its origin, the segmentum facialis is divided into an outer much expanded ricto-malaris and two inner

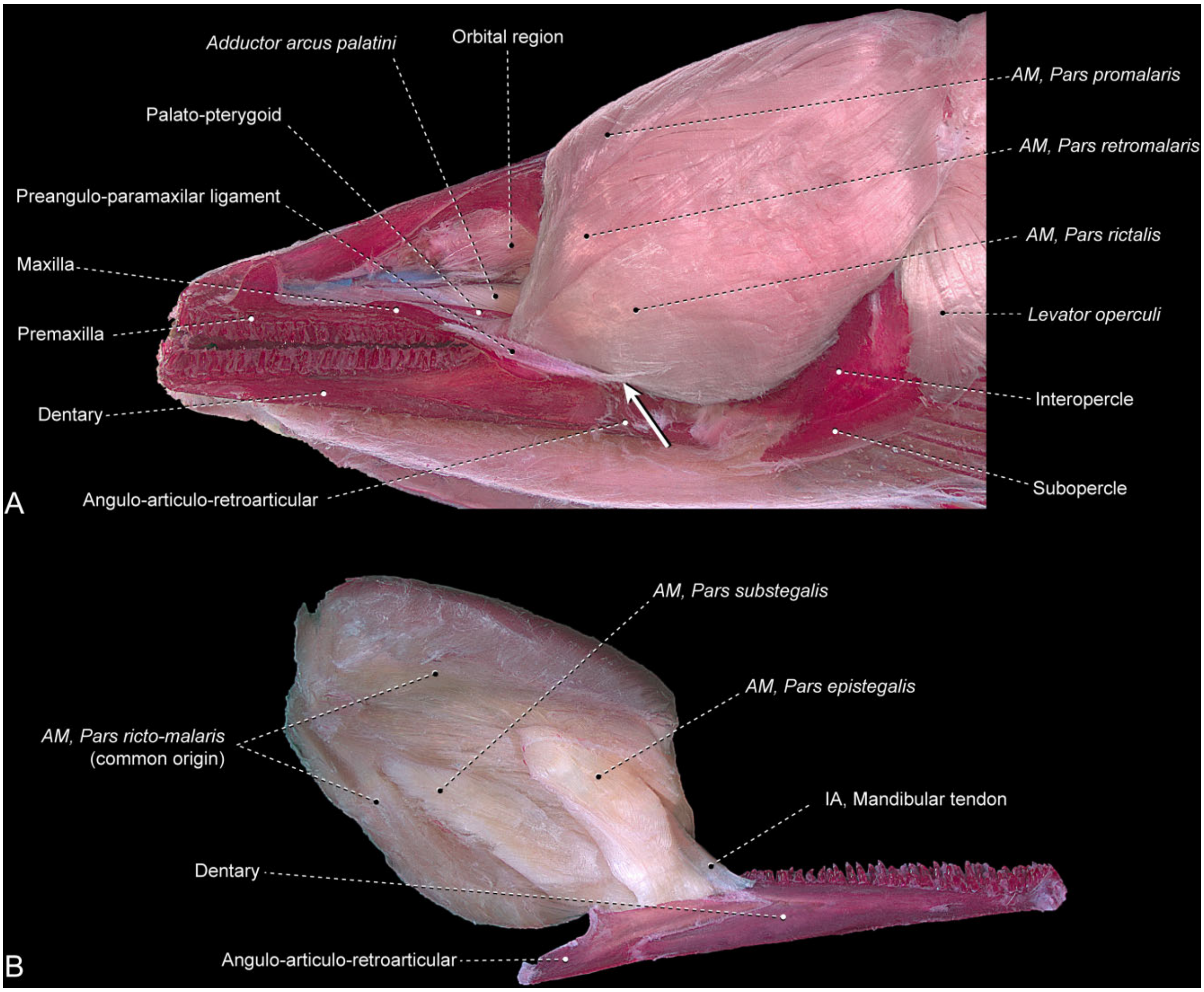


Figure 9. Adductor mandibulae and associated structures of *Anguilla reinhardti* (Anguilliformes: Anguillidae), USNM 311978 (182.4 mm standard length). Left side in (A) lateral and (B) medial views; ramus mandibularis trigeminus nerve removed. Arrow indicates attachment of fibres of the pars rictalis onto the preangulo-paramaxillar ligament. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis.

sections – the epistegalis and substegalis. The ricto-malaris has a broad origin from the preopercle, hyomandibula, pterotic, frontal, parietal, the epaxialis and supracarinalis fasciae, and a midsagittal tendinous raphe shared with its antimere. Fibres of the ricto-malaris attach solely to the cited structures; however, this muscle section extends without attachment over multiple additional bones and muscles. The combination of a broad origin and narrow insertion of this compound section result in the fibres becoming gradually arranged into several bundles that are partially segregated from each other by internal fasciae as they approach the insertion. Three main bundles are more prominent and superficially readily distinguishable. Positionally, the ventral bundle seems to correspond to the rictalis, and the two upper bundles to the retromalaris posteroventrally and promalaris anterodorsally. Most fibres of the rictalis insert on the posterolateral region of the coronoid process of the dentary; however, a few ventrolateral fibres insert onto an inconspicuous preangulo-paramaxillar ligament that attaches to the maxilla. The retromalaris and promalaris insert jointly on the anterior portion of the coronoid process of the dentary, primarily via a robust mandibular tendon.

The stegalis is totally subdivided into two separate subunits, both of which insert on the meckelian fossa along the medial surface of the lower jaw. The epistegalis originates from the pterosphenoid, sphenotic, and pterotic and inserts onto the dentary and angulo-articulo-retroarticular. The substegalis arises from the quadrate and hyomandibula and converges to a conspicuous meckelian tendon that passes lateral to the epistegalis and inserts on the coronomeckelian.

The path of the ramus mandibularis trigeminus nerve could not be determined.

The segmentum mandibularis is absent.

Ariosoma sp. (not illustrated)

The adductor mandibulae is mostly similar to that of *Anguilla reinhardti*. The ricto-malaris has the same origin in the two taxa; however, in *Ariosoma* the rictalis and malaris can only be differentiated from each other anteriorly. In this genus, the fibres of the rictalis attach to a lateral laminar tendon that inserts on the dorsolateral region of the coronoid process of the dentary. There is no connection of the rictalis with the well-differentiated preangulo-paramaxillar ligament. The malaris converges onto a stout mandibular tendon that inserts on the dorsomedial region of the coronoid process of the dentary and the dorsal portion of the coronomeckelian.

The stegalis is completely divided into an epistegalis and a substegalis, both of which are partially continuous with the ricto-malaris at their origins. The substegalis arises from the preopercle, quadrate, and hyomandibula and converges onto a strong meckelian tendon that attaches to the coronomeckelian. The epistegalis originates from the sphenotic and pterosphenoid, passes medial to the substegalis and inserts musculously on the coronomeckelian and angulo-articulo-retroarticular.

The path of the ramus mandibularis trigeminus nerve could not be determined.

The segmentum mandibularis is absent.

Remarks

Homology propositions for the bones of the suspensorium in the Anguilliformes remain unsettled. The metapterygoid that serves as a typical site of origin for the stegalis elsewhere in the Teleostei, is not present as an autogenous element amongst anguilliforms, but is rather possibly fused to the hyomandibula (Belouze, 2001). This fact, in conjunction with other cranial modifications amongst anguilliforms, yields ambiguity in the identification of the stegalis in the anguillid *Anguilla reinhardti* and the congrid *Ariosoma* sp. examined herein, as these species exhibit two distinct shorter inner sections – an anterodorsal section originating from the neurocranium and a posteroventral component arising primarily from the hyomandibula (Fig. 9B). Adams (1919) reported, however, that *Anguilla* sp. has a single shorter inner facial division that bifurcates posteriorly into an anterodorsal bundle with an origin mainly on the neurocranium and a posteroventral bundle with an origin from the suspensorium (his Adm^3). A single, short, medial division of the segmentum facialis that arises from both the hyomandibula and neurocranium is also present in the nettastomatid *Hoplunnis* (Eagderi & Adriaens, 2010b: A3). Based on its internal position and shorter fibres relative to the external facial sections, the single medial division reported by Adams (1919) for *Anguilla* sp. and Eagderi & Adriaens (2010b: A3) for *Hoplunnis* seems to correspond to the entire stegalis. Given that arrangement, the stegalis in the examined material of *Anguilla reinhardti* and *Ariosoma* sp. is interpreted as being completely subdivided into an epistegalis that arises solely from the neurocranium and a substegalis with an origin on the suspensorium. Two inner sections with the same general morphology were also reported for *Anguilla anguilla* (Eagderi & Adriaens, 2010a: A2m and A3) and *Conger conger* (Eagderi & Adriaens, 2010b: A2β and A3).

Only one inner facial section has been reported for *Heteroconger* (Congridae) and *Pythonichthys* (Heterenchelyidae), and in this configuration this section arises solely from the neurocranium (De Schepper, De Kegel & Adriaens, 2007a; Eagderi & Adriaens, 2010a). This inner section may correspond solely to the epistegalis or equate with the entire stegalis. The former hypothesis implies the incorporation of the substegalis into the outer facial sections and the latter proposal requires the migration of the origin of the stegalis to the neurocranium. We surmise that the hypothesis of this muscle being the epistegalis is the more likely; however, both propositions are equally parsimonious in light of the limited available information on adductor mandibulae morphology in taxa closely related to *Heteroconger* and *Pythonichthys*. Consequently, we were unable to incorporate these taxa in our synonymy. Data from De Schepper, Adriaens & De Kegel (2005) and De Schepper, De Kegel & Adriaens (2007b) are difficult to interpret because of the highly modified muscles of the described taxa and, in the case of the first of these publications, also because of some limitations of the associated illustrations.

A tenuous connection of the ventrolateral fibres of the rictalis with the preangulo-paramaxillar ligament is present in at least some components of the Anguillidae (Fig. 9), Heterenchelyidae, and Nettastomatidae. In *Hoplunnis* (Nettastomatidae) the rictalis is differentiated into the ectorictalis and endorictalis (Eagderi & Adriaens, 2010a, b).

Forms of the adductor mandibulae reported in the literature across the Anguilliformes share some notably distinctive features such as the extreme hypertrophy of the superficial portion of the segmentum facialis, which originates from the neurocranium, and the drastic reduction of the segmentum mandibularis (Fig. 9; Adams, 1919; De Schepper *et al*., 2005, 2007a, b; Eagderi & Adriaens, 2010a, b). More extreme modifications of the adductor mandibulae occur in subsets of anguilliforms (A. Datovo pers. observ.; De Schepper *et al*., 2005, 2007b). Thus, future broadly based comparative analyses within the Anguilliformes are necessary to properly elucidate the homologies of the muscle components in many groups within this order.

Synonymy

Segmentum facialis
A2: Wu & Shen (2004): *Echidna*.

Pars rictalis
A2α: Eagderi & Adriaens (2010b): *Conger*, *Hoplunnis*.
A2v: Eagderi & Adriaens (2010a): *Anguilla*.

Pars ectorictalis
A2α ventralis or A2αv: Eagderi & Adriaens (2010b): *Hoplunnis*.

Pars endorictalis
A2α dorsalis or A2αd: Eagderi & Adriaens (2010b): *Hoplunnis*.

Pars ricto-malaris
$A_1 + A_2$: Eaton (1935): *Anguilla*.
Adm^1: Adams (1919): *Anguilla*.

Pars malaris
A1: Eagderi & Adriaens (2010b): *Conger*.
A2β: Eagderi & Adriaens (2010b): *Hoplunnis*.

Pars promalaris
A2β anterior or A2βa: Eagderi & Adriaens (2010b): *Hoplunnis*.
A2a: Eagderi & Adriaens (2010a): *Anguilla*.

Pars retromalaris
A2β posterior or A2βp: Eagderi & Adriaens (2010b): *Hoplunnis*.
A2d: Eagderi & Adriaens (2010a): *Anguilla*.

Pars stegalis
A3: Eagderi & Adriaens (2010b): *Hoplunnis*.
Adm^3: Adams (1919): *Anguilla*.

Pars epistegalis
A3: Eagderi & Adriaens (2010a): *Anguilla*; Eagderi & Adriaens (2010b): *Conger*.

Pars substegalis
A3: Eagderi & Adriaens (2010a): *Anguilla*.
A2β: Eagderi & Adriaens (2010b): *Conger*.

OSTEOGLOSSOMORPHA

HIODONTIFORMES

Description

Hiodon tergisus (Fig. 10)

Despite being largely continuous with each other along much of their lengths, the ricto-malaris and stegalis are clearly discernible at their origins. Fibres of the ricto-malaris extend more posteriorly over the suspensorium than do those of the stegalis. The ricto-malaris originates from the posterior region of the hyomandibula plus the preopercle, symplectic, and quadrate. Fibres of the stegalis, in turn, have a distinct anterior origin on the anterodorsal part of the hyomandibula plus the metapterygoid. Proximate to its insertion, the ricto-malaris undergoes a tenuous subdivision. A ventrolateral set of fibres, corresponding to the rictalis, passes lateral to the ramus mandibularis trigeminus nerve and inserts on the posterior region of the preangular ligament. Dorsolateral fibres that correspond to the malaris run medial to the ramus mandibularis trigeminus nerve to insert on the dentary and the mandibular tendon (see also below).

The fibres of the stegalis converge to the medial portions of the intersegmental aponeurosis. Within this aponeurosis, the mandibular and meckelian tendons, albeit poorly differentiated, are still discernible from each other. The meckelian tendon, onto which most of the fibres of the pars stegalis attach, is flat along

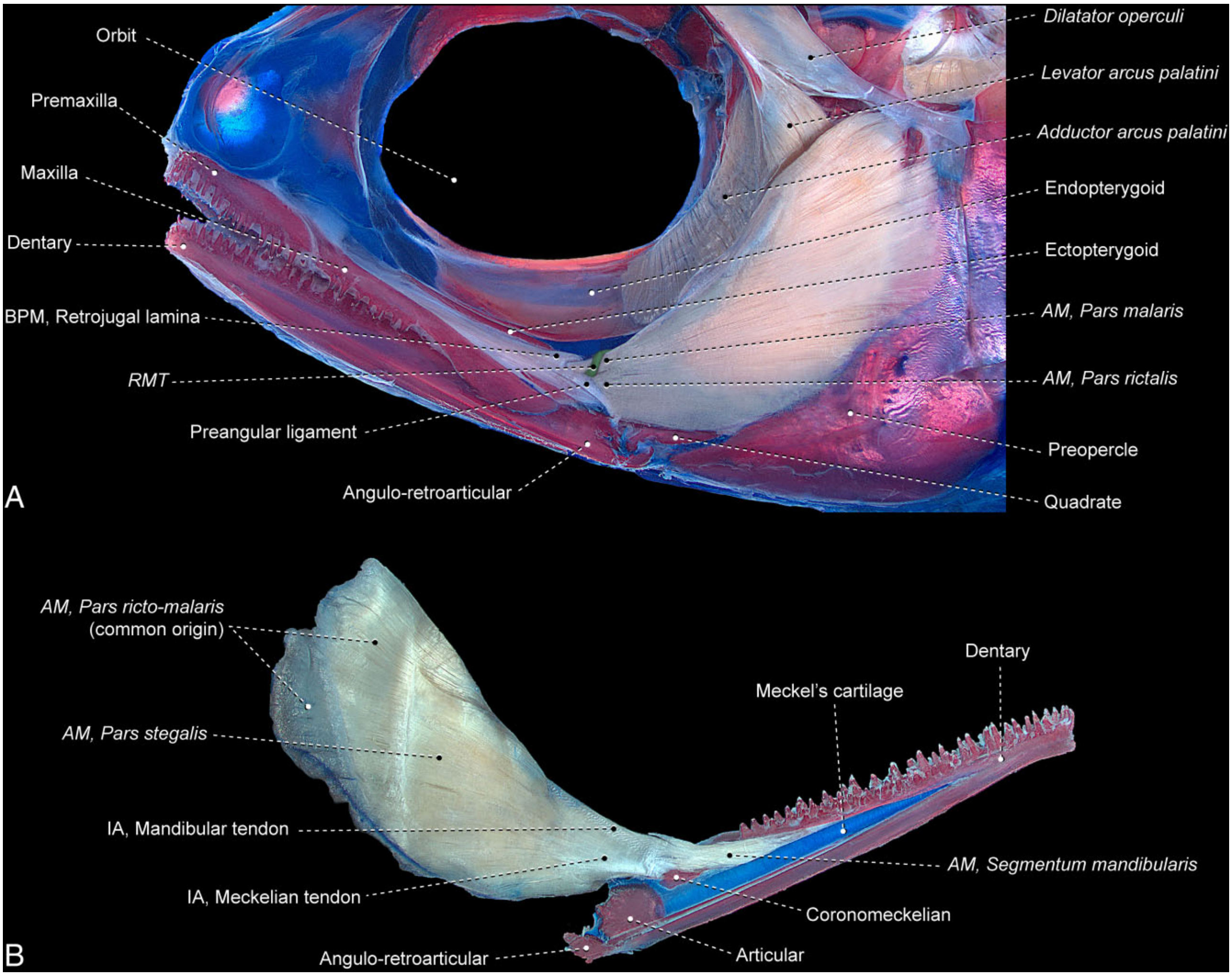


Figure 10. Adductor mandibulae and associated structures of *Hiodon tergisus* (Hiodontiformes: Hiodontidae), USNM 167970 (17.8 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

its medial surface and attaches to the coronomeckelian. The mandibular tendon, by contrast, has a characteristic undulated surface texture and receives the muscle fibres of the malaris and a small number of fibres from the stegalis.

Anteriorly, the mandibular tendon serves as the site of origin of a small, undivided segmentum mandibularis that inserts onto the medial surface of the dentary.

Remarks

Components of the segmentum facialis in *Hiodon*, the sole extant genus of the Hiodontiformes, are mostly undifferentiated from each other and thereby form a largely continuous muscle mass (Fig. 10). This morphology is similar to that characteristic of the Elopiformes (Fig. 6). As in the case of the Elopiformes, the evidence from positional correspondence and muscle attachments unequivocally documents the presence in *Hiodon* of all three of the typical primary facial sections of the Teleostei (rictalis, malaris, and stegalis), albeit these muscle sections in the genus exhibit only an incipient degree of differentiation.

Synonymy

Segmentum facialis
A2: Diogo & Doadrio (2008): *Hiodon*.

Segmentum mandibularis
Aω: Diogo & Doadrio (2008): *Hiodon*.

OSTEOGLOSSIFORMES

Description

Osteoglossum ferreirai (Fig. 11)

The ricto-malaris originates from the fascia of the levator arcus palatini, the quadrate, symplectic, hyomandibula, and preopercle. Although the ricto-malaris remains fully undivided along its entirety, a partial differentiation between the dorsal malaris and the ventral rictalis is perceptible anterolaterally by the different orientations of the fibres of these sections. The dorsal set of fibres corresponding to the malaris abruptly deflects ventrally yielding a rounded anterior profile, whereas the fibres of the rictalis continue in a nearly rectilinear trajectory towards their insertion. The combined ricto-malaris inserts primarily on the mandibular tendon, with some ventrolateral-most fibres additionally inserting directly onto the angulo-articular.

The stegalis is largely continuous laterally with the ricto-malaris. However, the limits of the stegalis are easily distinguishable from a medial view by its shorter fibres and anterodorsally displaced site of origin from the metapterygoid and hyomandibula. The stegalis is partially separated dorsally from the ricto-malaris, with the ramus mandibularis trigeminus nerve passing

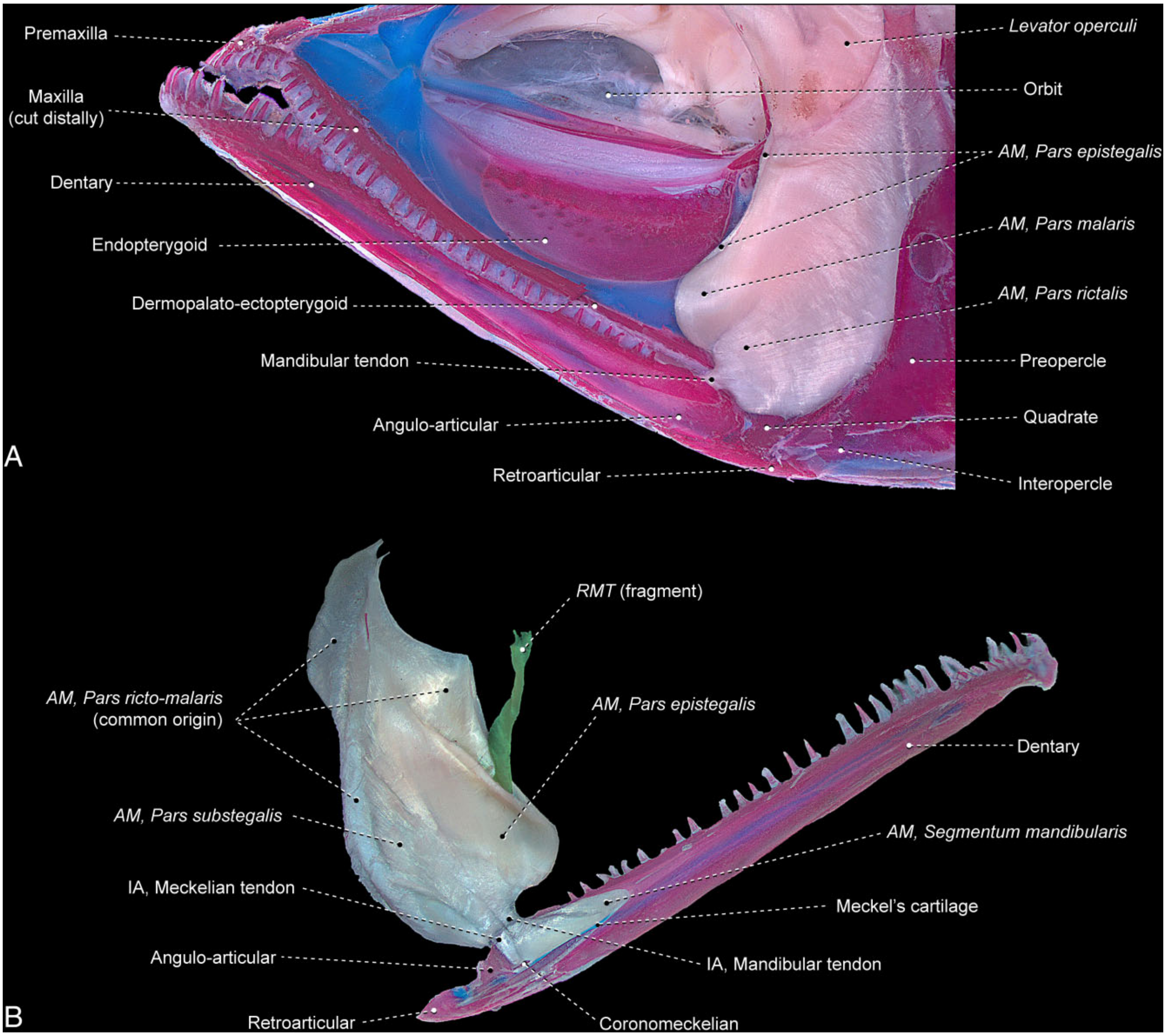


Figure 11. Adductor mandibulae and associated structures of *Osteoglossum ferreirai* (Osteoglossiformes: Osteoglossidae), USNM 300966 (58.3 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

between these two muscle sections. A distinctly less obvious, partial differentiation into an epistegalis and a substegalis is apparent medially. Anteriorly, the epistegalis joins the malaris and inserts on the dorsal portion of the intersegmental aponeurosis that differentiates anteriorly into the mandibular tendon. The substegalis converges onto the ventral region of the intersegmental aponeurosis, which in turn, differentiates anteriorly into a meckelian tendon that inserts on the coronomeckelian.

The segmentum mandibularis is not differentiated into subsections and originates from the mandibular tendon. This muscle segment inserts onto the anguloarticular and the dentary.

Arapaima gigas (not illustrated)

The segmentum mandibularis is mostly undivided along its anteroposterior expanse. The ricto-malaris arises from the quadrate, preopercle, hyomandibula, and infraorbitals 3 + 4 and 5. In the examined specimen, the ricto-malaris remains undifferentiated into subunits along most of its expanse. Near to their insertion, the dorsal fibres that correspond to the malaris, however, form a partially separate muscle bundle that abruptly deflects ventrally towards the lower jaw. The ventral set of fibres of the ricto-malaris, which is homologous to the rictalis, continues in a nearly rectilinear trajectory to its insertion. Both the malaris and rictalis insert musculously and via the mandibular tendon onto the angular and dentary.

The stegalis is continuous with the ricto-malaris but is discernible from a medial view because of its more anterior origin on the metapterygoid and symplectic and its insertion on the meckelian tendon. This tendon, which is completely separated from the mandibular tendon, splits anteriorly into a dorsal and a ventral division, both of which insert onto the coronomeckelian.

The ramus mandibularis trigeminus nerve passes medial to the segmentum facialis and then continues between the mandibular and meckelian tendons.

The segmentum mandibularis is absent.

Remarks

As in the case of many other basal groups in the Teleostei (e.g. Elopiformes and Hiodontiformes), all of the three primary facial sections of the adductor mandibulae present across the Teleostei are undoubtedly identifiable in *Osteoglossum ferreirai* and *Arapaima gigas*. These primary sections – rictalis, malaris, and stegalis – are discernible notwithstanding the pronounced degree of continuity between them (Fig. 11).

Several modifications of the adductor mandibulae were reported by Kershaw (1976) for taxa elsewhere in the Osteoglossiformes. Synonymization of the highly modified muscle divisions reported in that study must be considered tentative. For the osteoglossid *Scleropages formosus*, Kershaw (1976) described a lateral facial section (her A2) with dorsally and ventrally distinguishable sets of fibres that jointly converge to a tendon that serves as the site of origin for a mandibular segment (her Aw). Such a description is almost identical to the ricto-malaris of *Osteoglossum ferreirai* detailed above. Kershaw's A3 in *Scleropages formosus* similarly conforms to our substegalis. Her A1 is similar in most aspects to the epistegalis in *Osteoglossum ferreirai*, except for its insertion on the maxilla in *Scleropages formosus* rather than the intersegmental aponeurosis in *Osteoglossum ferreirai*. These synonymies apparently also apply to the muscle divisions of *Pantodon buchholzi*, which has an epistegalis inserting on both the maxilla and lower jaw (Kershaw, 1976: A1).

Kershaw's (1976) A1 in *Osteoglossum bicirrhosum* occupies the dorsolateral region of the segmentum facialis and, furthermore, has the exact same sites of origin as the malaris in *Osteoglossum ferreirai* (i.e. from the levator arcus palatini fascia and the vertical arm of the preopercle). Therefore, the muscle identified as the A1 in *Osteoglossum bicirrhosum* by Kershaw probably corresponds to the malaris instead of the epistegalis as discussed above for *Scleropages* and *Pantodon*. Kershaw (1976) illustrated, but did not describe, the A3 of *Osteoglossum bicirrhosum*, which renders it impossible to precisely determine the identities of this section and of the A2 in this species.

The segmentum facialis in the Arapaimidae inserts solely on the lower jaw (present study; Kershaw, 1976). Kershaw (1976) reported a mostly undivided segmentum facialis in *Heterotis niloticus*, but recognized that this muscle segment is formed by a medial A3 that originates from the metapterygoid (= stegalis) and a lateral A2 (= ricto-malaris). She identified a dorsolateral section in *Arapaima gigas*, termed the A2 (= malaris), and a ventromedial A3 formed by a 'superficial layer' of fibres with an origin from the preopercle (= rictalis) and 'deeper fibres' with an origin from the metapterygoid (= stegalis). In the specimen of *Arapaima gigas* herein examined, the malaris is only partially separated from the remainder of the segmentum facialis along their anterolateral regions. Kershaw (1976) conversely reported a malaris (her A2) that was fully separated from the adjoining facial sections in the individuals of this species that she examined. As the specimens of *Arapaima gigas* examined by Kershaw (1976) are distinctly larger (neurocranial length = 100 and 250 mm) than the individuals of the species herein dissected (neurocranial length = 32.2 mm), it is possible that the degree of separation of the malaris gradually increases during ontogeny, thereby accounting for the observed differences.

Munshi (1960) described the adductor mandibulae of the notopterid *Chitala chitala* (= *Notopterus chitala*).

The reported muscle is so highly modified relative to the morphology of the muscle in other known osteoglossiforms that we cannot arrive at reliable assumptions as to muscle section homologies in this species based solely on published information.

The segmentum mandibularis is absent in the Arapaimidae but present in the Osteoglossidae and Notopteridae (present study; Munshi, 1960; Kershaw, 1976).

Synonymy

Segmentum facialis
A2A3: Kershaw (1976): *Heterotis*.

Pars malaris
A1: Kershaw (1976): *Osteoglossum*.
A2: Kershaw (1976): *Arapaima*.

Pars ricto-malaris
A2: Kershaw (1976): *Heterotis*, *Pantodon*, *Scleropages*.

Pars rictalis
Superficial layer of A3: Kershaw (1976): *Arapaima*.

Pars ricto-stegalis
A3: Kershaw (1976): *Arapaima*.

Pars stegalis
A3: Kershaw (1976): *Heterotis*.
Deeper fibres of A3: Kershaw (1976): *Arapaima*.

Pars epistegalis
A1: Kershaw (1976): *Pantodon*, *Scleropages*.

Pars substegalis
A3: Kershaw (1976): *Pantodon*, *Scleropages*.

Segmentum facialis
Aw: Kershaw (1976): *Osteoglossum*, *Pantodon*, *Scleropages*.

OTOMORPHA

CLUPEIFORMES

Descriptions

Denticeps clupeoides (Fig. 12)

The segmentum facialis lacks any subdivision and originates from the quadrate, symplectic, metapterygoid, hyomandibula, and preopercle. The lateral-most facial fibres insert onto the mandibular tendon and, based on positional correspondence, this muscle portion presumably corresponds to the ricto-malaris. The medial-most set of fibres of the segmentum facialis is slightly shorter than the lateral set and seems to be homologous, at least in part, with the stegalis. These fibres converge to the meckelian tendon that, in turn, inserts on the coronomeckelian.

The ramus mandibularis trigeminus nerve passes external to the segmentum facialis.

At its origin, the segmentum mandibularis of *Denticeps* is well differentiated into three distinct sections. The coronalis and prementalis arise, respectively, from the dorsal and ventral regions of the mandibular tendon. The third section, the postmentalis, originates from a small faucal tendon that attaches to the anteromedial portion of the quadrate. As they continue anteriorly, all three of these mandibular sections progressively conjoin to a common single attachment onto the angulo-articular, dentary, and Meckel's cartilage.

Pellona harroweri (Fig. 13)

Sections within the segmentum facialis are more discernible in *Pellona* than in *Denticeps*. The ricto-malaris of *Pellona* originates from the quadrate, symplectic, and hyomandibula and remains undivided along most of its anteroposterior expanse. The dorsal-most fibres of the ricto-malaris, corresponding to the malaris, insert onto the coronoid area of the retrojugal lamina. This membrane is continuous ventrally with a short, but wide, mandibular tendon. Consequently, the fibres of the ricto-malaris become gradually attached ventrally to the mandibular tendon. The ventral set of fibres in the ricto-malaris attached to the mandibular tendon thus primarily corresponds to the rictalis.

Although not separate from the ricto-malaris, the stegalis is unequivocally distinguishable as a separate unit from a medial view given its more anterior origin from the metapterygoid. The stegalis converges onto the ventral portion of the intersegmental aponeurosis, primarily on the meckelian tendon that is anchored anteriorly to the coronomeckelian.

The ramus mandibularis trigeminus nerve passes lateral to the anterior portion of the segmentum facialis.

The segmentum mandibularis is not differentiated into subparts. This segment originates primarily from the mandibular tendon, although a few posteroventral fibres also arise from the meckelian tendon. Insertion of the segmentum mandibularis is onto the dentary, angulo-articular, and Meckel's cartilage.

Remarks

Diogo & Doadrio (2008) described the adductor mandibulae of *Denticeps clupeoides*, one of the species of clupeiforms that we examined. According to their interpretation, this species bears only a single facial section that they identified as the A2 and lacks the other sections of the segmentum facialis commonly found in most other teleosts. Our observations of *Denticeps clupeoides* confirm the lack of obvious division in the

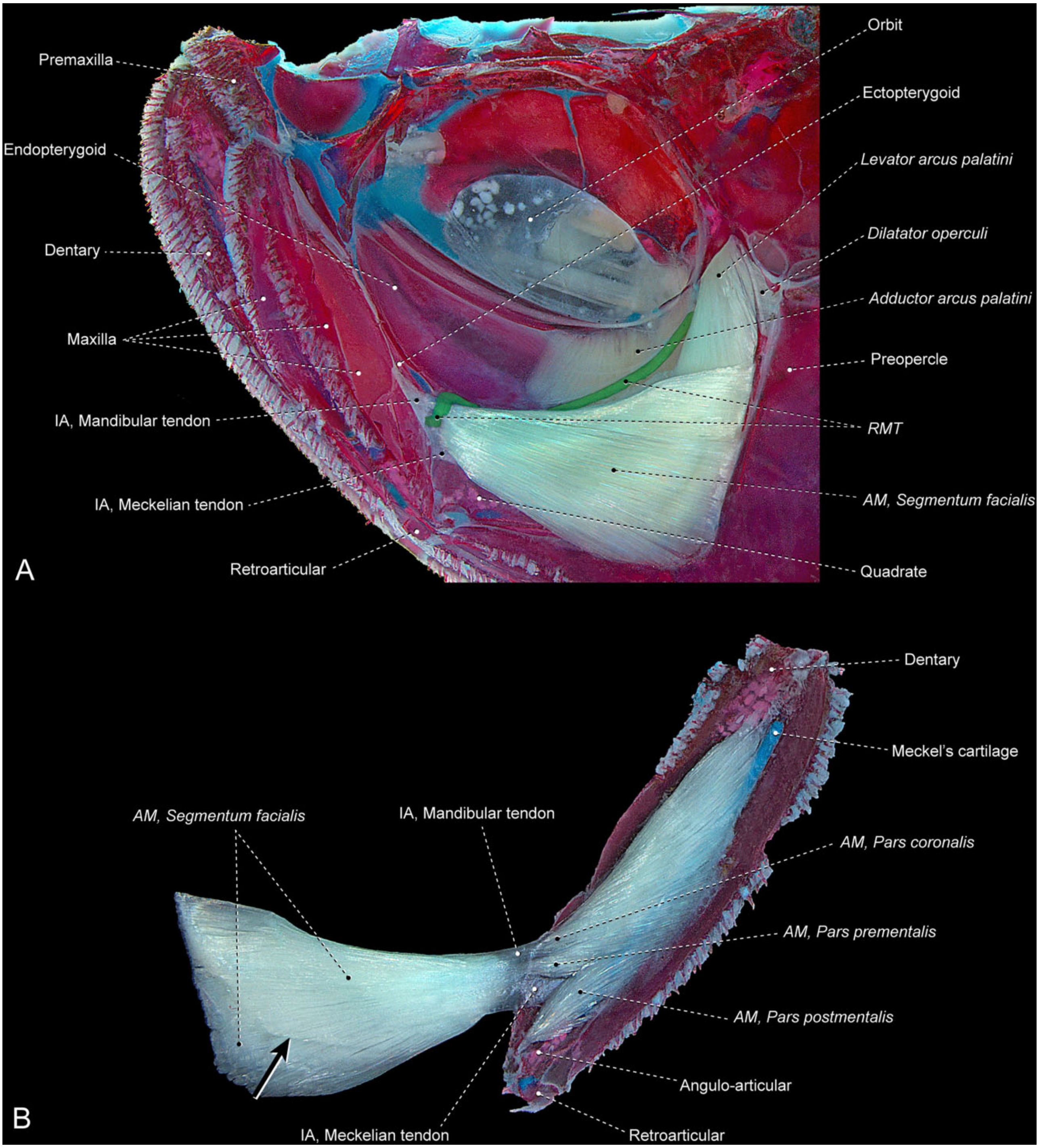


Figure 12. Adductor mandibulae and associated structures of *Denticeps clupeoides* (Clupeiformes: Denticipitidae), MZUSP 84776 (33.9 mm standard length). Left side in (A) lateral and (B) medial views. Arrow indicates shorter set of fibres with more anterior origin possibly representing the posteroventral limit of the stegalis. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

segmentum facialis in this taxon (Fig. 12). Nonetheless, contra Diogo & Doadrio (2008), the evidence indicates that none of the other primary sections of the teleostean segmentum facialis is lost in this taxon, but rather that these sections are present albeit undifferentiated from each other. Supporting this hypothesis is the fact that the undivided segmentum facialis in *Denticeps clupeoides* exhibits the same basic origin, in-

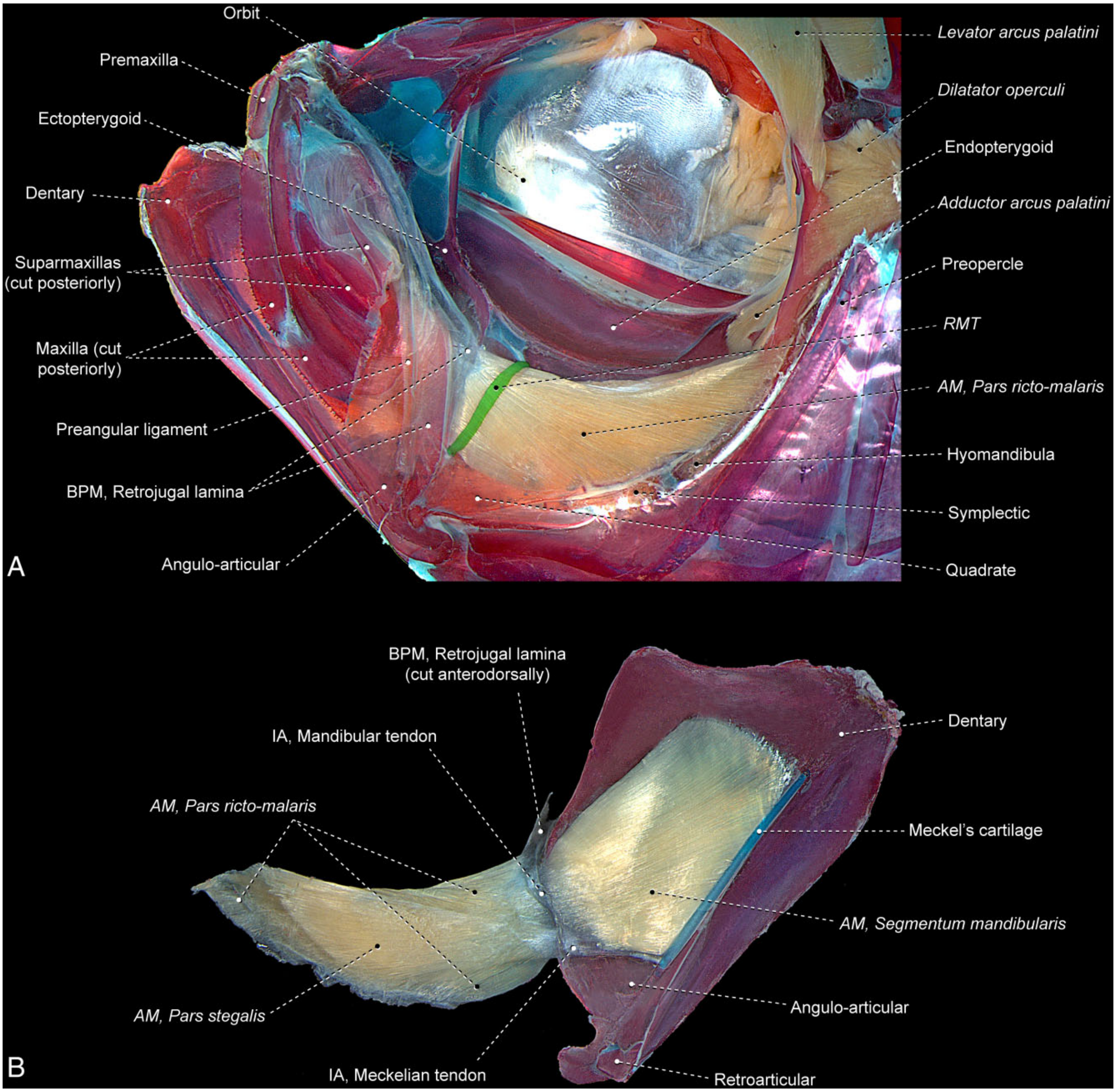


Figure 13. Adductor mandibulae and associated structures of *Pellona harroweri* (Clupeiformes: Pristigasteridae), MZUSP 11364 (74.0 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

sertion, and position of the entire segmentum facialis of other teleosts that have more clearly discernible rictalis, malaris, and stegalis (see Datovo & Vari, 2013), including other members of the Clupeiformes, such as pristigasterids and clupeids (see below). Therefore, as is the case with the elopomorphs *Elops* and *Megalops* and the osteoglossomorph *Hiodon* discussed above, the segmentum facialis of *Denticeps* is formed by the three fundamental sections common across the Teleostei that are poorly differentiated from each other.

The adductor mandibulae in the Clupeidae greatly resembles the configuration encountered in the pristigasterid *Pellona* (Fig. 13), inasmuch as the segmentum facialis in both taxa is also primarily differentiated into two similar sets of fibres: a superficial set associated with both the segmentum mandibularis and the retrojugal lamina, which thus corresponds to the ricto-malaris; and an inner set of fibres directly attached to the lower jaw that clearly corresponds to the stegalis (Eaton, 1935; Munshi, 1960;

Wu & Shen, 2004). As in *Pellona*, the segmentum mandibularis in the Clupeidae is often reported to be mostly undivided (Eaton, 1935; Van Dobben, 1935; Munshi, 1960; Wu & Shen, 2004).

Diogo & Doadrio (2008) also reported the existence of an Aω not differentiated into subparts that originated exclusively from the intersegmental aponeurosis in *Denticeps clupeoides*. Our observations of the same species conclusively demonstrate that the segmentum mandibularis can be differentiated at its origin into three sections. One of these, the postmentalis, which originates from the quadrate, was apparently overlooked by Diogo & Doadrio (2008; compare their fig. 3 with our Fig. 12B).

Synonymy

Segmentum facialis
A_2: Van Dobben (1935): *Clupea*.
A2: Diogo & Doadrio (2008): *Denticeps*.
Adductor mandibulae: Edgeworth (1935): *Clupea*.
Mandibularis: Munshi (1960): *Hilsa ilisha* (= *Tenualosa ilisha*).

Pars ricto-malaris
A_1A_2: Eaton (1935): *Clupea*.
A2: Wu & Shen (2004): *Amblygaster*, *Nematalosa*.
Adductor 1 or Ad_1: Munshi (1960): *Hilsa ilisha* (= *Tenualosa ilisha*).

Pars stegalis
A_3: Eaton (1935): *Clupea*.
A3: Wu & Shen (2004): *Amblygaster*, *Nematalosa*.
Adductor 2 or Ad_2: Munshi (1960): *Hilsa ilisha* (= *Tenualosa ilisha*).

Segmentum mandibularis
A_w or A_ω or intramandibularis: Munshi (1960): *Hilsa ilisha* (= *Tenualosa ilisha*).
Aw: Wu & Shen (2004): *Amblygaster*, *Nematalosa*.
Intramandibularis: Edgeworth (1935): *Clupea*.

Pars corono-prementalis
Aω: Diogo & Doadrio (2008): *Denticeps*.

OSTARIOPHYSI

ANOTOPHYSA

GONORYNCHIFORMES

Description

Chanos chanos (Fig. 14)

The rictalis and malaris are continuous with each other at their origins from the quadrate, symplectic, hyomandibula, and preopercle. Slightly anterior to their origins, the rictalis and malaris become completely separated from each other. The rictalis inserts via a tendon on the anteromedial region of the maxilla. Proximate to its insertion, the muscle fibres of the rictalis become organized into two differentiated, but continuous, bundles that correspond to the ectorictalis (lateral) and endorictalis (medial). The buccopalatal membrane is poorly differentiated from the surrounding connective tissues, but the collagenous reinforced band connecting the insertional tendon of the rictalis to the coronoid process of the lower jaw is presumably derived from connective tissues corresponding to the buccopalatal membrane. This ligament cannot be homologized with any of the main buccopalatal ligaments described in Datovo & Vari (2013) and is herein named the postcoronoid ligament.

The fibres of the malaris converge onto an elongate intersegmental aponeurosis, mainly onto its posterodorsal portion that corresponds to the subocular tendon. The intersegmental aponeurosis runs from the subocular region towards the lower jaw.

The stegalis is well separated from the remaining facial sections along most of its extent. The section arises from the metapterygoid and the palatoquadrate cartilage and inserts along the ventral margin of the intersegmental aponeurosis. The intersegmental aponeurosis bifurcates anteriorly into a ventral meckelian tendon that attaches to the coronomeckelian, and a dorsal mandibular tendon that serves as the site of origin of the segmentum mandibularis.

In the examined specimens, the ramus mandibularis trigeminus nerve passes lateral to the entire segmentum facialis of the adductor mandibulae before continuing onto the medial side of the lower jaw.

The segmentum mandibularis is undivided, but its bipinnate configuration permits the recognition of a coronalis dorsally and mentalis ventrally. Anteriorly these sections cannot be differentiated from each other and the entire segmentum mandibularis inserts on the dentary.

Remarks

Howes (1985a) provided a comprehensive summary of the cranial muscles of representatives of all extant genera of the Gonorynchiformes. In the monotypic *Chanos*, he identified a ventrolateral muscle section (his A_1/a_1) that clearly corresponds to the rictalis (Fig. 14A, C). Howes (1985a) mentioned that this section had two insertional tendons: one that attaches to the maxilla and 'another tendon [that] branches off from the dorsal face of the muscle to join an aponeurosis from which extends A_w' (addition in brackets ours). This latter tendon apparently corresponds to the poorly differentiated postcoronoid ligament that we describe above in *Chanos* (see Fig. 14B, C). Howes (1985a) did not refer to the differentiation of the rictalis in that genus into ectorictalis and endorictalis sections as documented in some subsequent studies (Diogo & Doadrio, 2008; Diogo

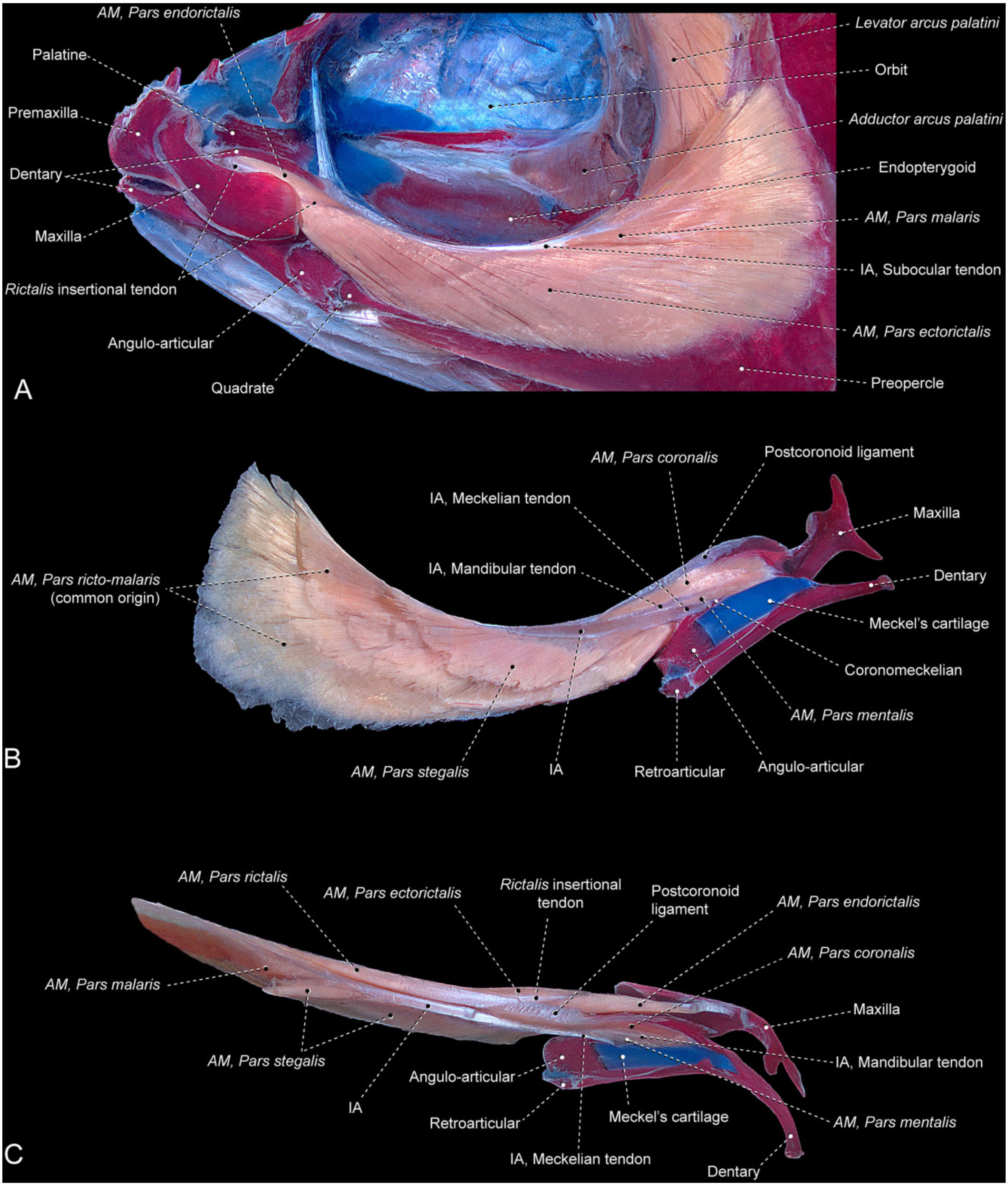


Figure 14. Adductor mandibulae and associated structures of *Chanos chanos* (Gonorynchiformes: Chanidae), USNM 173572 (147.3 mm standard length). Left side in (A) lateral, (B) medial, and (C) dorsal views; ramus mandibularis trigeminus nerve removed. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis.

et al., 2008a; Diogo, 2008b) and herein (Fig. 14A). Amongst all other gonorynchiforms, the rictalis is more obviously subdivided with its subunits explicitly named by Howes (1985a) as the a_1o (= ectorictalis) and a_1i (= endorictalis). According to Howes (1985a), *Gonorynchus* has the endorictalis inserting onto the 'thick connective tissue surrounding the coronoid process' (? = buccopalatal membrane), whereas in all other gonorynchoids, the endorictalis attaches to the maxilla in conjunction with the ectorictalis.

Although the separation of the stegalis from the malaris is somewhat subtle, the stegalis is clearly discernible in the specimens of *Chanos* that we dissected (Fig. 14B, C). One possible consequence of this subtle separation was that the stegalis was not identified as a separate element in any prior analysis of *Chanos* (Howes, 1985a; Diogo & Doadrio, 2008; Diogo *et al*., 2008a; Diogo, 2008b). Thus, the term A2 of prior studies (Howes, 1985a; Diogo & Doadrio, 2008; Diogo *et al*., 2008a; Diogo, 2008b) was applied to both the stegalis and malaris – that is, the stego-malaris of gonorynchiforms. In addition to its insertion on the lower jaw, the stego-malaris according to Howes (1985a) also connects with the lacrimal in *Gonorynchus*, the maxilla and autopalatine in *Cromeria*, and the antorbital, rictal cartilages, and endorictalis in *Phractolaemus*.

The kneriid *Grasseichthys gabonensis* is a miniaturized freshwater fish that exhibits some notable reductive features (Howes, 1985a; Britz & Moritz, 2007). Howes (1985a) identified only one single facial division (his ?A_1) in this species with this section having an origin on the ventral portion of the preopercle and with 'the majority of fibers appearing to insert into the tissue covering the maxilla'. According to Howes 'there is, apparently, no inner muscle (A_2) . . . attaching to the lower jaw' of *Grasseichthys*. *Cromeria*, the sister group of the monotypic *Grasseichthys* (Grande & Poyato-Ariza, 1999), alternatively has an insertion of the ricto-malaris on the maxilla. In light of the qualifications and doubts as to the condition of the muscle in *Grasseichthys gabonensis* expressed by Howes (1985a), it is possible that his ?A_1 might actually refer to the entire segmentum facialis with undifferentiated subdivisions and/or that the connection of this muscle segment with the lower jaw was not noticed by him as a consequence of the very small size of the examined specimens. Additionally corroborating this supposition is the fact that an absence of facial sections of the adductor mandibulae was not encountered in any other teleost either in this study or in that of Datovo & Vari (2013). Thus, if Howes' (1985a) hypothesis proves correct, then *Grasseichthys gabonensis* would be the sole known case of a teleost lacking a connection of the segmentum facialis with the lower jaw and in which some facial sections are in fact lost. Neither condition seems probable in light of the current knowledge of the ontogeny of the adductor mandibulae, in which facial muscle sections are derived from subdivisions of the single muscle mass attached to Meckel's cartilage present in earlier developmental stages (Edgeworth, 1929, 1935; Hernandez, Patterson & Devoto, 2005; Diogo *et al*., 2008b; Konstantinidis & Harris, 2010; Staab & Hernandez, 2010).

The whole adductor mandibulae of the monotypic *Phractolaemus* is modified to a pronounced degree as a function of its highly derived, dorsally opening mouth (Howes, 1985a). Given these striking modifications, the synonymy presented below for this genus is based primarily on the interpretations of Howes (1985a) and should be considered to be tentative.

Within the Gonorynchiformes, a segmentum mandibularis occurs solely in the monotypic Channidae (Howes, 1985a). In the two examined specimens of *Chanos chanos*, the ramus mandibularis trigeminus nerve passes external to the entire segmentum facialis. Howes (1985a), however, reported a passage of this nerve between the rictalis and malaris in this species.

Synonymy

Pars rictalis

A_1 or a_1: Howes (1985a): *Chanos*, *Cromeria*, *Gonorynchus*, *Kneria*, *Parakneria*, *Phractolaemus*.

A1-OST: Diogo (2008b): *Chanos*, *Cromeria*, *Parakneria*, *Phractolaemus*; Diogo & Doadrio (2008): *Chanos*; Diogo *et al*. (2008a): *Chanos*.

Pars ectorictalis

A_1o or a_1o: Howes (1985a): *Cromeria*, *Gonorynchus*, *Kneria*, *Parakneria*, *Phractolaemus*.

A1-OST-L: Diogo (2008b): *Chanos*, *Cromeria*, *Parakneria*, *Phractolaemus*; Diogo & Doadrio (2008): *Chanos*; Diogo *et al*. (2008a): *Chanos*.

Pars endorictalis

A_1i or a_1i: Howes (1985a): *Cromeria*, *Gonorynchus*, *Kneria*, *Parakneria*, *Phractolaemus*.

A1-OST-M: Diogo (2008b): *Chanos*, *Cromeria*, *Parakneria*, *Phractolaemus*; Diogo & Doadrio (2008): *Chanos*; Diogo *et al*. (2008a): *Chanos*.

Pars stego-malaris

A_2 or a_2: Howes (1985a): *Chanos*, *Cromeria*, *Gonorynchus*, *Kneria*, *Parakneria*, *Phractolaemus*.

A2: Diogo (2008b): *Chanos*, *Cromeria*, *Parakneria*, *Phractolaemus*; Diogo & Doadrio (2008): *Chanos*; Diogo *et al*. (2008a): *Chanos*.

Segmentum mandibularis

Aω: Diogo & Doadrio (2008): *Chanos*.

A_w: Howes (1985a): *Chanos*.

AW: Diogo (2008b): *Chanos*.

OTOPHYSA

CYPRINIFORMES

Description

Rasbora cephalotaenia (Fig. 15)

The rictalis is fully subdivided into the ectorictalis and endorictalis. The ectorictalis originates from the quadrate and preopercle and inserts tendinously on the lateral face of the maxilla. Although the ventral portion of the endorictalis is partially continuous with the malaris at their origins, these two sections are completely separate from each other along most of their expanse. The endorictalis originates from the quadrate and preopercle and inserts primarily musculously on the posterior portion of the coronoid process of the lower jaw. An inconspicuous transverse raphe is present approximately at the midlength of the endorictalis.

The malaris originates from the hyomandibula, symplectic, and preopercle. Its fibres converge onto the dorsoposterior portion of the elongate intersegmental aponeurosis (= subocular tendon). Anteriorly this aponeurosis subtly divides into a thin mandibular tendon and a robust meckelian tendon that anchors to the coronomeckelian.

Albeit being largely continuous with the malaris, the stegalis is easily discernible from a medial view by its anteriorly displaced origin on the metapterygoid. Fibres of the stegalis attach along the ventral margin of the strap-like intersegmental aponeurosis.

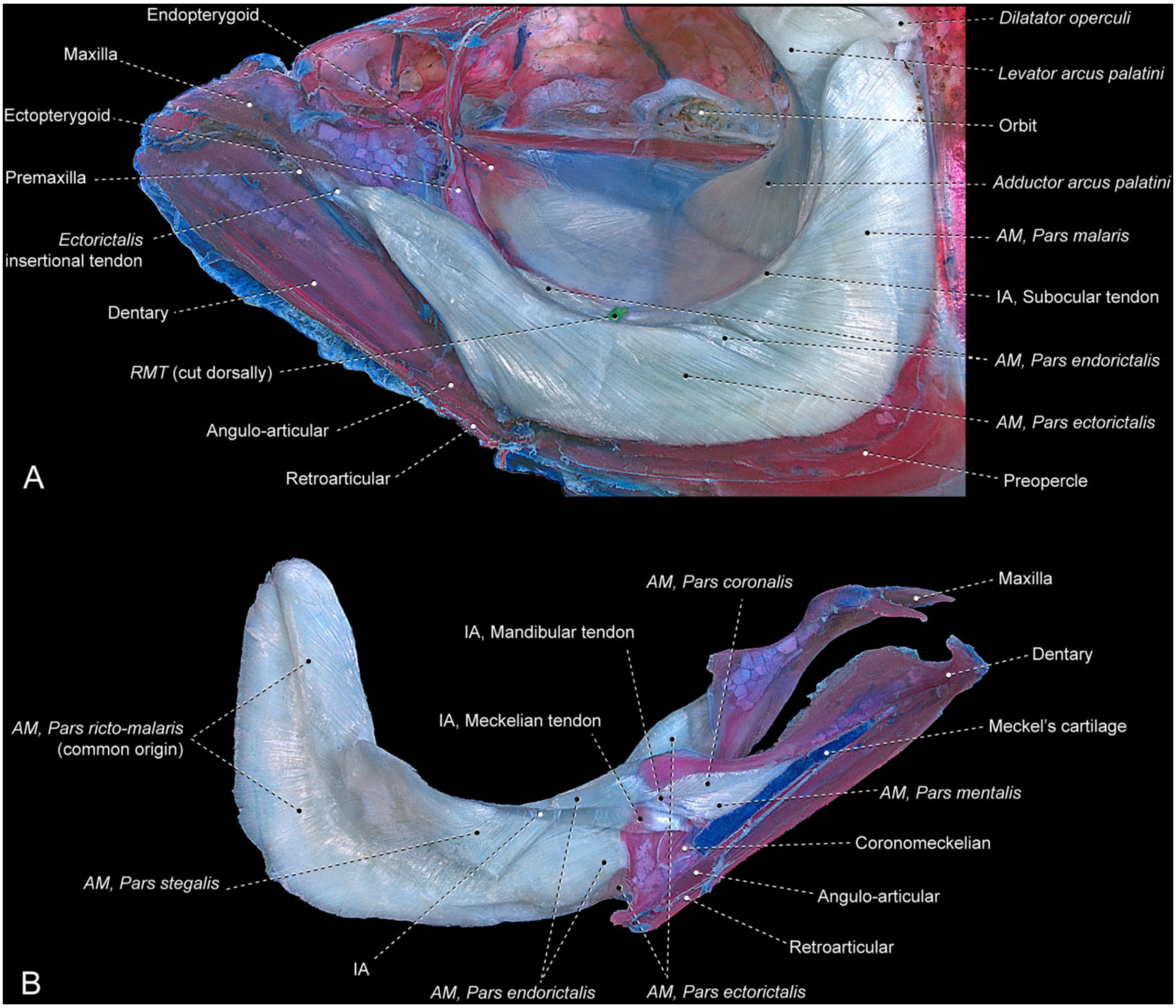


Figure 15. Adductor mandibulae and associated structures of *Rasbora cephalotaenia* (Cypriniformes: Cyprinidae), USNM 330848 (81.2 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

The ramus mandibularis trigeminus nerve traverses the middle of the endorictalis in the course of its passage through the segmentum facialis.

The thin, elongate mandibular tendon serves as the axial tendon of origin for the bipinnate segmentum mandibularis. As a result of this bipinnate configuration, the coronalis and mentalis can be recognized along the posterior portion of the segmentum mandibularis. No distinction between the coronalis and mentalis is apparent anteriorly and the whole segmentum mandibularis inserts on the dentary and Meckel's cartilage.

Danio rerio (not illustrated)

The adductor mandibulae morphology in *Danio rerio* is virtually identical to that of *Rasbora cephalotaenia*, including the presence of a transverse raphe on the endorictalis and a distinguishable stegalis. Neither feature was noted in previous descriptions of the adductor mandibulae of this taxon (cf. Hernandez *et al*., 2005; Hernandez, Bird & Staab, 2007; Diogo & Doadrio, 2008; Diogo *et al*., 2008a, b; Staab & Hernandez, 2010).

Raiamas senegalensis (Fig. 16A)

The ectorictalis originates from the quadrate and preopercle. Shortly anterior to the area of origin, the muscle fibres that arise from the region of the articular condyle of the quadrate differentiate from the remaining sections, thereby yielding a clear subdivision into an ectorictalis superioris and an ectorictalis inferioris. Most of the fibres of the ectorictalis inferioris arise from a ventral tendon attached to the quadrate and spread out anterodorsally to insert on the lateral surface of the maxilla. Towards its insertion, the

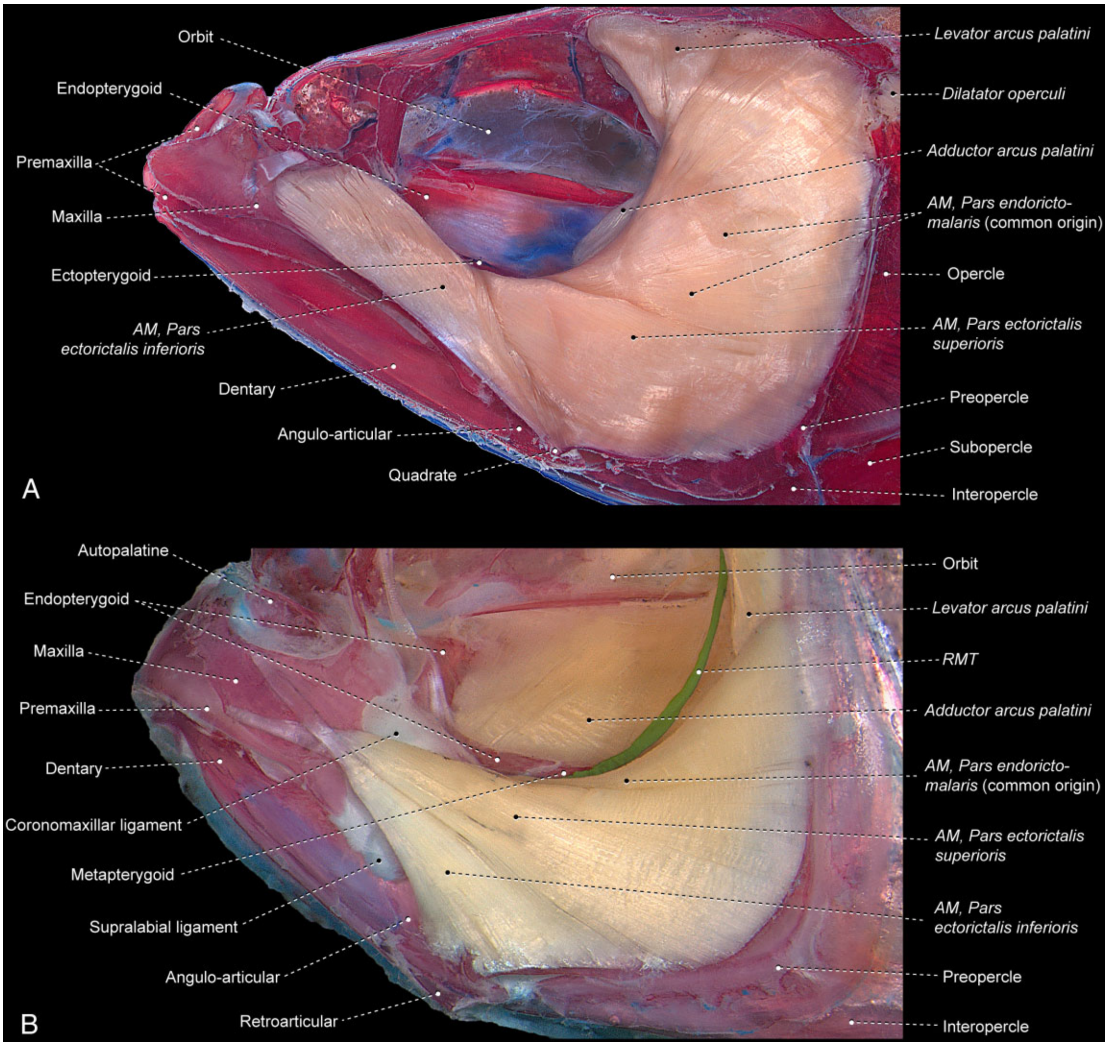


Figure 16. Adductor mandibulae and associated structures of (A) *Raiamas senegalensis* (Cypriniformes: Cyprinidae), USNM 271201 [93.0 mm standard length (SL)] and (B) *Carassius auratus* (Cypriniformes: Cyprinidae), MZUSP 112353 (44.2 mm SL). Left sides in lateral view. Abbreviations: AM, adductor mandibulae; RMT, ramus mandibularis trigeminus nerve.

endorictalis superioris passes medial to the endorictalis inferioris and inserts onto the tendon running along the ventromedial region of the rictalis.

The endorictalis, malaris, and stegalis are largely continuous with each other at their origins, which involve the quadrate, metapterygoid, hyomandibula, preopercle, and pterotic. Proximate to its insertion, the endorictalis separates from the adjacent malaris and attaches primarily musculously on the coronoid process of the dentary. The endorictalis and malaris are further separated from each other by the ramus mandibularis trigeminus nerve that passes between them. Towards its insertion, the fibres of the malaris converge onto the lateral face of the intersegmental aponeurosis.

At its origin, the stegalis is separated into an epistegalis that arises medial to the levator arcus palatini and a substegalis with an origin that can barely be differentiated from that of the malaris. Anteriorly the epistegalis and substegalis conjoin and insert on the intersegmental aponeurosis together with the malaris. Although not readily distinguished from the malaris, the presence of the substegalis section in *Raiamas* can be inferred based on the origin of a set of shorter fibres from the metapterygoid, a typical site of origin for the substegalis in both the Cypriniformes and most other teleosts.

The configuration of the segmentum mandibularis and the insertion of the intersegmental aponeurosis in *Raiamas* are basically similar to that of *Rasbora*.

Carassius auratus (Fig. 16B)

The ectorictalis is completely separated from the underlying facial sections and arises from the preopercle, quadrate, and angulo-articular. Towards its insertion, the ectorictalis progressively separates into two sections – the ectorictalis inferioris and ectorictalis superioris. Each subsection converges onto separate insertional tendons that cross anteriorly and attach to the lateral surface of the maxilla.

At their origins, the endorictalis and malaris cannot be differentiated from each other and thus form an endoricto-malaris. This common origin for these two sections involves the preopercle and hyomandibula. As they proceed toward their insertions, these sections separate. The endorictalis grades into an aponeurosis that inserts along the posterodorsal rim of the angulo-articular and the coronoid process of the dentary. The malaris, in turn, converges to the intersegmental aponeurosis.

The ramus mandibularis trigeminus nerve courses through the segmentum facialis between the malaris and endorictalis. The nerve then continues through the middle of the endorictalis to soon thereafter emerge ventrally between that section laterally and the intersegmental aponeurosis medially prior to its final passage to the lower jaw.

At its origin, the stegalis is readily distinguishable from the endoricto-malaris by its shorter fibres that arise from the metapterygoid. The posterodorsal portion of the stegalis is separated from the adjacent malaris but as these sections proceed anteriorly towards their insertion on the intersegmental aponeurosis, they become fully continuous and indistinguishable from each other. The major part of the intersegmental aponeurosis converges onto the coronomeckelian, thus forming a meckelian tendon. The mandibular tendon is represented solely by a delicate, flat connective tissue band that serves as the site of origin for the tiny segmentum mandibularis.

The segmentum mandibularis consists of an extremely small and delicate bundle of parallel fibres. It originates from the mandibular tendon and inserts on Meckel's cartilage.

Remarks

The segmentum facialis exhibits an outstanding degree of morphological diversification across the Cypriniformes, with the scale of the modifications especially pronounced in the Cobitoidea (*sensu* Conway, 2011). Elucidation of muscle division homologies is challenging when confronted with morphological diversity at this scale. Notwithstanding these complications, tentative hypotheses of homologies can be advanced for adductor mandibulae divisions in most of the prior studies of that system. That said, broader investigations of the adductor mandibulae across the Cypriniformes are clearly necessary in order both to test our proposed synonymy in the more derived members of the order and to evaluate the apparently enormous amount of informative phylogenetic information present in this morphological complex.

The most comprehensive and detailed survey of the cranial musculature of the Cypriniformes to date is that of Takahasi (1925). The adductor mandibulae morphology of the Cyprinidae reported in that study is similar in most aspects to those of the taxa examined herein. Although the cobitoids reported in that study exhibit relatively modified forms of the adductor mandibulae compared with those of cyprinids, the section names applied by Takahasi (1925) seemingly consistently reflect their homology across the entirety of the Cypriniformes. Based on overall obvious topological correspondences between the muscle divisions in the Cypriniformes reported in Takahasi (1925), we confidently infer that his A_1 (or maxillaris) corresponds to the ectorictalis, the A_2 to the endorictalis, the A'_3 to the malaris, and the A''_3 to the stegalis.

The most ventrolaterally located facial division corresponding to the ectorictalis inserts primarily on the lateral surface of the maxilla across all the Cypriniformes (Vetter, 1878; Takahasi, 1925; Edwards, 1926; Eaton, 1935; Van Dobben, 1935; Girgis, 1952;

Munshi, 1960; Weisel, 1960; Alexander, 1966; Ballintijn, van den Burg & Egberink, 1972; Wu & Shen, 2004; Hernandez *et al.*, 2005; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a, b; Staab & Hernandez, 2010; Staab, Ferry & Hernandez, 2012). In some cyprinids, the ectorictalis is undivided (Fig. 15), but in most other Cypriniformes this section is partially, or totally, subdivided into a dorsal ectorictalis superioris and a ventral ectorictalis inferioris (Fig. 16). These two subdivisions may undergo diverse modifications across the Cypriniformes; however, in all known instances the insertion of the ectorictalis superioris on the maxilla is situated medial to the ectorictalis inferioris (Vetter, 1878; Takahasi, 1925; Edwards, 1926; Van Dobben, 1935; Weisel, 1960; Alexander, 1966; Ballintijn *et al.*, 1972; Wu & Shen, 2004; Staab *et al.*, 2012). In many cypriniforms, the origin of the ectorictalis inferioris is expanded anteriorly so as to involve the lower jaw in addition to the quadrate (Fig. 16B). In further advanced morphologies, this section loses its origin from the quadrate (Vetter, 1878; Takahasi, 1925; Edwards, 1926). Some cobitoids have the insertional tendon of the ectorictalis inferioris dorsally shifted and attaching to the kinethmoid (= 'rostral cartilage' of Takahasi, 1925) or the 'connective tissue located between dorsal midline of the premaxillae' and 'the base of the first barbel' (Kim & Kim, 2007). The ectorictalis superioris, in turn, tends to greatly expand dorsally so as to almost entirely cover the inner sections of the segmentum facialis (Takahasi, 1925; Edwards, 1926; Eaton, 1935; Weisel, 1960; Kim & Kim, 2007). Amongst some derived cobitoids, the ectorictalis superioris differentiates into several subsections, some of which may attach to the second pre-ethmoid (Takahasi, 1925; Kim & Kim, 2007). Precise homologies of all these sections remain to a degree unclear, but the dorsal-most of these subsections is particularly interesting because it apparently forms the so-called preorbitalis or praeorbitalis, a muscle that inserts on the lateral ethmoid of some cobitoids (Takahasi, 1925; Kim & Kim, 2007). Such a homology hypothesis is supported by the fact that some taxa have a tendon running from the lateral ethmoid to the dorsomedial portion of the ectorictalis superioris (Takahasi, 1925; Kim & Kim, 2007).

In most, if not all cypriniforms, the ventral facial section positioned immediately medial to the ectorictalis, i.e. the endorictalis, inserts musculously on the coronoid process of the lower jaw (Vetter, 1878; Takahasi, 1925; Girgis, 1952; Munshi, 1960; Alexander, 1966; Ballintijn *et al.*, 1972; Hernandez *et al.*, 2005; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a, b; Staab & Hernandez, 2010). At their insertion, the medial fibres of the endorictalis in some cypriniform taxa pass adjacent to, and are contiguous with, the segmentum mandibularis (Fig. 15B; Takahasi, 1925). The malaris and stegalis are associated with the intersegmental aponeurosis and are, sometimes, largely continuous with one another thereby forming a compound stego-malaris (Takahasi, 1925). The dorsal portion of the stegalis may pass either medial (e.g. *Raiamas*) or anterior (e.g. *Danio* and *Rasbora*) to the levator arcus palatini. In the latter configuration, an unequivocal distinction of the stegalis from the malaris is sometimes impossible (A. Datovo pers. observ.; Takahasi, 1925). The endorictalis also may be continuous with the immediately dorsomedially situated malaris, thereby forming a compound endorictomalaris (e.g. *Carassius*; Girgis, 1952; Munshi, 1960) or endoricto-stego-malaris (Takahasi, 1925; Edwards, 1926; Weisel, 1960; Kim & Kim, 2007). In most, if not all, of these cases, each section apparently still retains its primitive insertion site: the endorictalis attaches to the coronoid process of the lower jaw whereas the fibres of the malaris/stego-malaris converge to the intersegmental aponeurosis.

The ramus mandibularis trigeminus nerve in the Cypriniformes may transit either between the ectorictalis and endorictalis [*Iksookimia*, *Misgurnus*, *Niwaella multifasciata* (= *Kichulchoia multifasciata*); Kim & Kim 2007], through the centre of the endorictalis (*Carassius*, *Danio*, and *Rasbora*; Fig. 15), between the rictalis and malaris (*Raiamas*), or between the malaris and stegalis (*Carassius*; Wu & Shen, 2004).

The segmentum mandibularis is absent in some taxa in the Cyprinidae and apparently across all of the Cobitoidea (Takahasi, 1925).

Howes (1978) examined the adductor mandibulae of *Raiamas bola* (= *Barilius bola*). Comparison of his results with our observations on the congener *Raiamas senegalensis* leads us to conclude that his A1a in *R. bola* corresponds to the ectorictalis inferioris and his A1b to the ectorictalis superioris. The identities of the deeper muscle sections are somewhat uncertain, but the A2 of Howes (1978) possibly corresponds to the endorictomalaris and his A3 to the stegalis. Owing to insufficient information, it is impossible to confidently synonymize the divisions of the adductor mandibulae of most of the other cyprinids surveyed by Howes (1978). For the same reason, the later analyses by that author involving cypriniforms (Howes, 1982, 1984) are also not included in the following synonymy.

Synonymy

Pars ectorictalis

A0: Diogo & Doadrio (2008): *Danio*; Diogo *et al.* (2008a): *Danio*; Diogo *et al.* (2008b): *Danio*.

A_1: Ballintijn *et al.* (1972): *Cyprinus*; Eaton (1935): *Abramis*, *Catostomus*; Takahasi (1925): *Acheilognathus*, *Carassius*, *Cobitis*, *Cyprinus*, *Hymenophysa curta* (= *Parabotia curta*), *Ischikauia*, *Lefua*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Misgurnus*, *Opsariichthys*, *Orthrias* (= *Barbatula*), *Pseudogobio*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*; Vetter (1878): *Barbus*, *Cyprinus*.

A1: Hernandez *et al*. (2007): *Danio*; Staab & Hernandez (2010): *Danio*; Staab *et al*. (2012): *Catostomus*, *Carassius*, *Devario*, *Gila*; Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*), *Zacco*.

A2: Hernandez *et al*. (2005): *Danio*.

Ad_{mx} or maxillaris: Munshi (1960): *Catla*.

Depressor labii superioris: Girgis (1952): *Labeo*.

Maxillary part: Alexander (1966): *Gobio*, *Idus* (= *Leuciscus*).

Maxillaris: Al-Hussaini (1949): *Cyprinus*, *Gobio*, *Rutilus*.

Pars ectorictalis superioris

A'_1: Van Dobben (1935): *Cyprinus*.

A0: Kim & Kim (2007): *Lefua*, *Leptobotia curta* (= *Parabotia curta*), *Misgurnus*, *Orthrias* (= *Barbatula*).

A0 plus preorbitalis: Kim & Kim (2007): *Cobitis*, *Iksookimia*, *Iksookimia choii* (= *Cobitis choii*), *Kichulchoia*, *Koreocobitis*, *Niwaella multifasciata* (= *Kichulchoia multifasciata*).

A1′: Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*).

$A_1\alpha$: Ballintijn *et al*. (1972): *Cyprinus*; Takahasi (1925): *Cobitis*, *Cyprinus*, *Hymenophysa curta* (= *Parabotia curta*), *Lefua*, *Misgurnus*, *Orthrias* (= *Barbatula*), *Pseudogobio*; Vetter (1878): *Cyprinus*.

A1α: Staab *et al*. (2012): *Catostomus*, *Carassius*.

A1b: Howes (1978): *Barilius bola* (= *Raiamas bola*).

Adductor 1 or Adm.1: Edwards (1926): *Catostomus*, *Catostomus nigricans* (= *Hypentelium nigricans*), *Erimyzon*, *Moxostoma*, *Moxostoma melanops* (= *Minytrema melanops*).

Dorsal maxillary part: Alexander (1966): *Gobio*.

Maxillaris dorsalis: Weisel (1960): *Catostomus*.

Maxillaris internal: Al-Hussaini (1949): *Cyprinus*, *Gobio*.

Pars ectorictalis inferioris

A''_1: Van Dobben (1935): *Cyprinus*.

A1″: Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*).

$A_1\beta$: Ballintijn *et al*. (1972): *Cyprinus*; Takahasi (1925): *Cobitis*, *Cyprinus*, *Hymenophysa curta* (= *Parabotia curta*), *Lefua*, *Misgurnus*, *Orthrias* (= *Barbatula*), *Pseudogobio*; Vetter (1878): *Cyprinus*.

A1β: Staab *et al*. (2012): *Catostomus*, *Carassius*.

A1a: Howes (1978): *Barilius bola* (= *Raiamas bola*).

Adductor 2 or Adm.2: Edwards (1926): *Catostomus*, *Catostomus nigricans* (= *Hypentelium nigricans*), *Erimyzon*, *Moxostoma*, *Moxostoma melanops* (= *Minytrema melanops*).

Dorsal maxillary part: Alexander (1966): *Gobio*.

Maxillaris ventralis: Weisel (1960): *Catostomus*.

Maxillaris external: Al-Hussaini (1949): *Cyprinus*, *Gobio*.

Rostralis: Kim & Kim (2007): *Cobitis*, *Iksookimia*, *Iksookimia choii* (= *Cobitis choii*), *Kichulchoia*, *Koreocobitis*, *Lefua*, *Leptobotia curta* (= *Parabotia curta*), *Misgurnus*, *Niwaella multifasciata* (= *Kichulchoia multifasciata*), *Orthrias* (= *Barbatula*).

Pars endorictalis

A1: Hernandez *et al*. (2005): *Danio*.

A1-OST: Diogo & Doadrio (2008): *Danio*; Diogo *et al*. (2008a): *Danio*; Diogo *et al*. (2008b): *Danio*.

A_2: Ballintijn *et al*. (1972): *Cyprinus*; Takahasi (1925): *Acheilognathus*, *Carassius*, *Cyprinus*, *Ischikauia*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Opsariichthys*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*; Vetter (1878): *Barbus*, *Cyprinus*.

A2: Hernandez *et al*. (2007): *Danio*; Staab & Hernandez (2010): *Danio*.

Ad_1': Munshi (1960): *Catla*.

Superficial mandibular part: Alexander (1966): *Gobio*, *Idus* (= *Leuciscus*).

Ventral portion of the levator labii inferioris: Girgis (1952): *Labeo*.

Pars endoricto-malaris

A2α: Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*), *Zacco*.

Ad_1: Munshi (1960): *Catla*.

Levator labii inferioris: Girgis (1952): *Labeo*.

Pars endoricto-stego-malaris

A1-OST: Kim & Kim (2007): *Cobitis*, *Iksookimia*, *Iksookimia choii* (= *Cobitis choii*), *Kichulchoia*, *Koreocobitis*, *Lefua*, *Leptobotia curta* (= *Parabotia curta*), *Misgurnus*, *Niwaella multifasciata* (= *Kichulchoia multifasciata*), *Orthrias* (= *Barbatula*).

A_2A_3: Takahasi (1925): *Acheilognathus*, *Carassius*, *Cobitis*, *Cyprinus*, *Hymenophysa curta* (= *Parabotia curta*), *Ischikauia*, *Lefua*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Misgurnus*, *Opsariichthys*, *Orthrias* (= *Barbatula*), *Pseudogobio*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*.

Adductor 3 or Adm.3: Edwards (1926): *Catostomus*, *Catostomus nigricans* (= *Hypentelium nigricans*), *Erimyzon*, *Moxostoma*, *Moxostoma melanops* (= *Minytrema melanops*).

Mandibularis: Al-Hussaini (1949): *Cyprinus*, *Gobio*, *Rutilus*; Weisel (1960): *Catostomus*.

Pars stego-malaris

A2: Diogo & Doadrio (2008): *Danio*; Diogo *et al*. (2008a): *Danio*; Diogo *et al*. (2008b): *Danio*.

A_3: Ballintijn *et al.* (1972): *Cyprinus*; Takahasi (1925): *Acheilognathus*, *Carassius*, *Cyprinus*, *Ischikauia*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Opsariichthys*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*; Vetter (1878): *Barbus*, *Cyprinus*.

A3: Hernandez *et al.* (2005): *Danio*; Hernandez *et al.* (2007): *Danio*; Staab & Hernandez (2010): *Danio*.

Deep mandibular part: Alexander (1966): *Gobio*, *Idus* (= *Leuciscus*).

Pars malaris

A'_3: Takahasi (1925): *Acheilognathus*, *Carassius*, *Cyprinus*, *Ischikauia*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Opsariichthys*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*.

Ad_1'': Munshi (1960): *Catla*.

Dorsal portion of the levator labii inferioris: Girgis (1952): *Labeo*.

Pars stegalis

A2β: Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*), *Zacco*.

A''_3: Takahasi (1925): *Acheilognathus*, *Carassius*, *Cyprinus*, *Ischikauia*, *Leucogobio güntheri* (= *Gnathopogon elongatus*), *Opsariichthys*, *Pseudorasbora*, *Sarcocheilichthys*, *Richardsonium hakuensis* (= *Tribolodon hakonensis*), *Zacco*.

Ad_3 or Adductor 3: Munshi (1960): *Catla*.

Adductor mandibulae: Girgis (1952): *Labeo*.

Segmentum mandibularis

Aω: Ballintijn *et al.* (1972): *Cyprinus*; Diogo *et al.* (2008b): *Danio*; Hernandez *et al.* (2005): *Danio*; Staab & Hernandez (2010): *Danio*; Vetter (1878): *Barbus*, *Cyprinus*.

Aw: Diogo & Doadrio (2008): *Danio*; Diogo *et al.* (2008a): *Danio*); Howes (1978): *Barilius bola* (= *Raiamas bola*), *Opsariichthys*; Wu & Shen (2004): *Carassius*, *Varicorhinus tamusuiensis* (= *Onychostoma barbatulum*), *Zacco*.

Intra-mandibularis or Ad_w or A_ω: Munshi (1960): *Catla*.

Mentalis or ω: Takahasi (1925): *Carassius*, *Cyprinus*, *Leucogobio guentheri* (= *Gnathopogon elongatus*), *Ischikauia*, *Opsariichthys*, *Zacco*.

CHARACIPHYSAE

CHARACIFORMES

Description

Xenocharax spilurus (Fig. 17)

The rictalis and malaris are continuous with one another at their origins from the quadrate, preopercle, and hyomandibula. Anteriorly, these sections gradually separate and have distinct insertions. The malaris converges onto the dorsal portion of the intersegmental aponeurosis that, in turn, differentiates anteriorly into a mandibular tendon. The rictalis further subdivides anteriorly proximate to its insertion into a small ectorictalis and a larger endorictalis. The ectorictalis attaches to the posterolateral region of the retrojugal lamina, whereas the endorictalis inserts on the coronoid regions of the dentary and angulo-articular.

The ramus mandibularis trigeminus nerve passes between the endorictalis and malaris.

At its origin, the dorsal portion of the stegalis is separated dorsally from the malaris, with the levator arcus palatini passing between these two sections. Ventrolaterally, the stegalis is continuous with the remainder of the segmentum facialis. The fibres of the stegalis arise mainly from the metapterygoid and converge onto the ventral portion of the intersegmental aponeurosis, which separates anteriorly into a meckelian tendon attaching to the coronomeckelian.

As it proceeds distally, the mandibular tendon assumes an aponeurotic form and serves as the site of origin for the entire, undivided segmentum mandibularis. An inconspicuous accessory tendon runs along the posteroventral region of the segmentum mandibularis and is anchored to the angulo-articular. The segmentum mandibularis inserts on the angulo-articular, dentary, and Meckel's cartilage.

Remarks

The adductor mandibulae of the Characiformes was recently reviewed in detail by Datovo & Castro (2012). These authors described the forms of the adductor mandibulae for representatives of all characiform families and clarified the homologies of the muscle divisions within that order. Based on obvious positional correspondence and comparability of attachment sites of the muscle sections detailed in Datovo & Castro (2012), their A1 corresponds to the rictalis, the A1α to the endorictalis, the A1β to the ectorictalis, the A2 to the malaris, the A2α to the promalaris, the A2β to the retromalaris, the A3 to the stegalis, the A3α to the epistegalis, the A3β to the substegalis, and the Aω to the segmentum mandibularis. Datovo & Castro (2012) further hypothesized that the A1γ section, found exclusively in the Acestrorhynchidae and Ctenoluciidae, represents an expansion of what they termed the A1, rather than a subdivision of this section into an A1α and A1β, as is the case elsewhere in the Characiformes. Nevertheless, as discussed in Datovo & Vari (2013), evolutionary events of muscular expansion are almost always associated with events of muscle subdivision and the adoption of distinct terminologies for each of these evolutionary processes is unnecessary. Further research is necessary in order to better determine the precise homologies of the A1 and A1γ in the

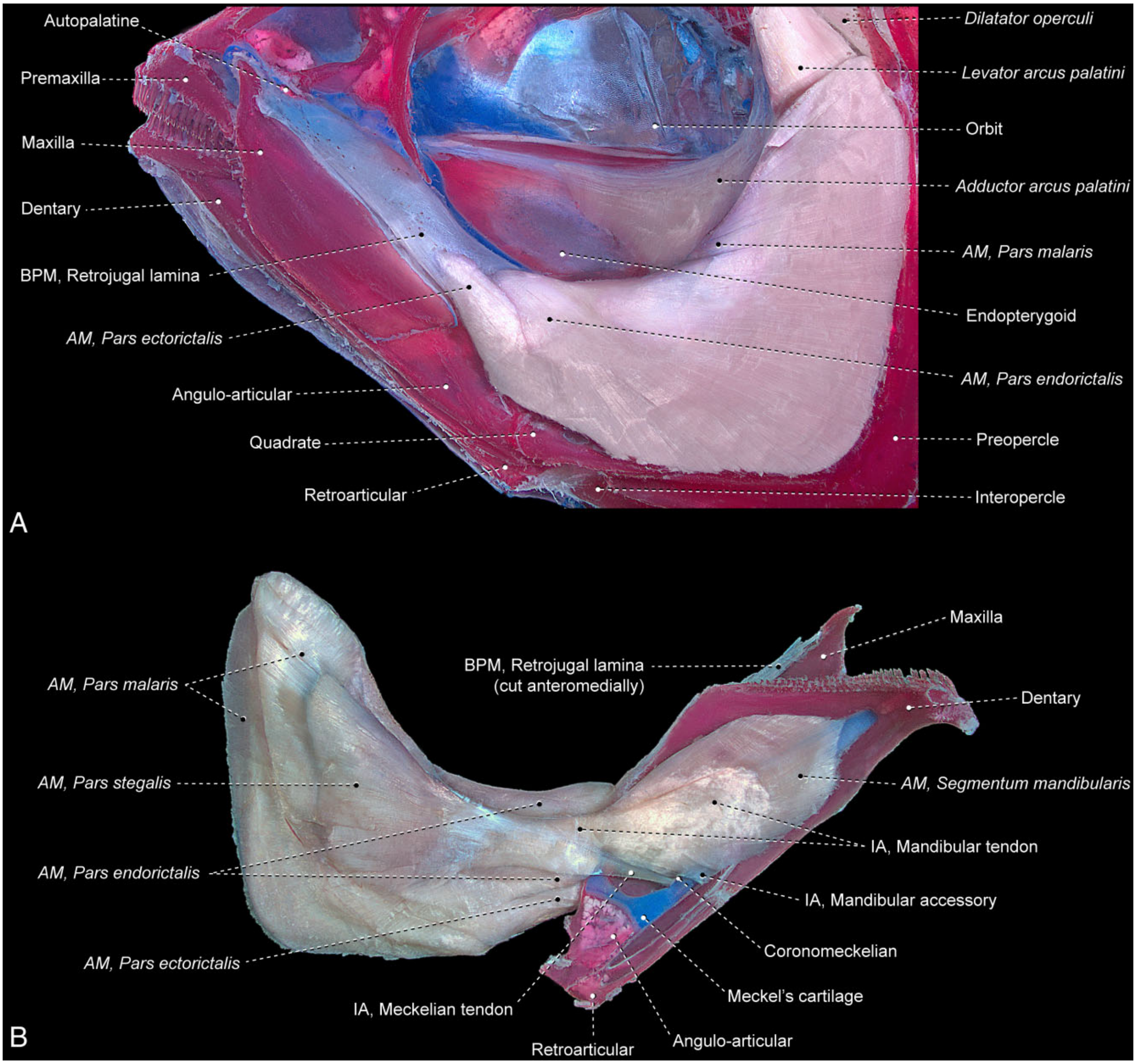


Figure 17. Adductor mandibulae and associated structures of *Xenocharax spilurus* (Characiformes: Distichodontidae), AMNH 230302 (95.2 mm standard length). Left side in (A) lateral and (B) medial views. Ramus mandibularis trigeminus nerve removed. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis.

Acestrorhynchidae and Ctenoluciidae, in particular the possible derivation of the A1γ from the malaris in the Acestrorhynchidae (see Datovo & Castro, 2012: 107). Pending that, and in the interest of nomenclatural simplicity, A1 and A1γ in the Acestrorhynchidae and Ctenoluciidae are herein provisionally synonymized with the ectorictalis and endorictalis, respectively.

The malaris and stegalis are associated anteriorly with the intersegmental aponeurosis across the entirety of the Characiformes (Alexander, 1964; Howes, 1976; Vari, 1979; Gosline, 1989; Datovo & Castro, 2012; Mattox & Toledo-Piza, 2012). The origin of the malaris extends onto the neurocranium in the Acestrorhynchidae, Ctenoluciidae, Cynodontidae, Erythrinidae, Hepsetidae and the characids *Agoniates*, *Acestrocephalus*, *Brycon*, *Bryconops*, *Lignobrycon*, *Salminus*, and *Serrasalmus* (Howes, 1976; Vari, 1995; Datovo & Castro, 2012; Mattox & Toledo-Piza, 2012). In many basal lineages of characiforms (most members of the Distichodontidae and Anostomidae), the rictalis is partially divided into an endorictalis and ectorictalis (Vari, 1983; Datovo & Castro, 2012; Mattox & Toledo-Piza, 2012). In these taxa, the rictalis is associated with both the retrojugal lamina and the lower jaw. Hemiodontidae and Parodontidae are unique within the Characiformes in having the entire rictalis inserting on the maxilla (Datovo & Castro, 2012). All remaining lineages in this order have the rictalis inserted primarily on the lower jaw, although a few fibres of the section occasionally also attach to the infralabial membrane (Alexander, 1964; Winterbottom, 1974; Howes, 1976; Vari, 1979; Lauder, 1981; Machado-Allison, 1983; Gosline, 1989; Datovo & Castro, 2012: 102; Mattox & Toledo-Piza, 2012).

Datovo & Castro (2012) compared their results with all known prior publications dealing with the adductor mandibulae in the Characiformes. The evidence underlying the synonymization of different components of the muscle in earlier studies is consequently not repeated in this paper.

Pronounced modifications of the adductor mandibulae characterize a few of the characiform taxa reported in the literature (e.g. the distichodontids *Eugnatichthys* and *Ichthyborus*; Vari, 1979) or in some instances the morphology of the system was only partially described. In such instances, the homologies of all muscle divisions could not be confidently elucidated and these taxa are not included in the following synonymy.

Synonymy

Pars rictalis

A_1: Alexander (1964): *Anisitsia notata* (= *Hemiodus unimaculatus*), *Brycon*, *Creatochanes* (= *Bryconops*), *Hoplias*, *Myleus rubripinnis* (= *Myloplus rubripinnis*), *Pyrrhulina*, *Serrasalmus*; Howes (1976): *Acanthocharax*, *Charax*, *Cynodon*, *Cynopotamus*, *Hydrolycus*, *Rhaphiodon*, *Roeboides*, *Roestes*; Machado-Allison (1983): *Piaractus*; Vari (1979): *Citharidium*, *Citharinus*; Vari (1983): *Prochilodus*.

A1: Datovo & Castro (2012): *Agoniates*, *Aphyocharax*, *Astyanax*, *Bivibranchia*, *Brachychalcinus*, *Brycon*, *Bryconexodon*, *Bryconops*, *Caenotropus*, *Chalceus*, *Citharinus*, *Characidium*, *Clupeacharax*, *Creagrutus*, *Ctenobrycon*, *Cyanocharax*, *Deuterodon*, *Exodon*, *Gymnocorymbus*, *Hemibrycon*, *Hemigrammus*, *Hemiodus*, *Hepsetus*, *Hollandichthys*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Jupiaba*, *Knodus*, *Lebiasina*, *Leporellus*, *Leporinus*, *Lignobrycon*, *Metynnis*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Parecbasis*, *Parodon*, *Phenacogrammus*, *Piabina*, *Piabucus*, *Planaltina*, *Poptella*, *Prionobrama*, *Prochilodus*, *Psellogrammus*, *Rhoadsia*, *Roeboides*, *Salminus*, *Serrasalmus*, *Steindachnerina*, *Tetragonopterus*, *Thayeria*, *Triportheus*, *Utiaritichthys*, *Xenocharax*); Mattox & Toledo-Piza (2012): *Acanthocharax*, *Acestrocephalus*, *Acestrorhynchus*, *Aphyocharax*, *Astyanax*, *Boulengerella*, *Brycon*, *Bryconexodon*, *Bryconops*, *Charax*, *Cheirodon*, *Cynodon*, *Cynopotamus*, *Exodon*, *Galeocharax*, *Gnathocharax*, *Gilbertolus*, *Gymnocorymbus*, *Hemiodus*, *Hepsetus*, *Heterocharax*, *Hoplocharax*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Iguanodectes*, *Lonchogenys*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Phenacogaster*, *Roeboides*, *Rhaphiodon*, *Roeboexodon*, *Roestes*, *Salminus*, *Serrasalmus*, *Tetragonopterus*, *Xenocharax*; Winterbottom (1974): *Brycon*, *Creatochanes* (= *Bryconops*).

A1-OST: Diogo *et al*. (2008a): *Brycon*.

A2α: Wu & Shen (2004): *Citharinus*, *Potamorhina*.

AM1: Lauder (1981): *Lebiasina*.

External division: Gosline (1989): *Acestrorhynchus*, *Bivibranchia*, *Brycon*, *Charax*, *Ctenolucius*, *Curimata*, *Hemiodus*, *Hepsetus*, *Hoplias*, *Hydrolycus*, *Piabucina*, *Salminus*.

Pars ectorictalis

A_1: Vari (1979): *Distichodus*, *Hemigrammocharax*, *Nannaethiops*, *Nannocharax*, *Neolebias*, *Xenocharax*.

A1β: Datovo & Castro (2012): *Caenotropus*, *Leporellus*, *Leporinus*, *Prochilodus*, *Steindachnerina*, *Xenocharax*.

A1: Datovo & Castro (2012): *Acestrorhynchus*, *Boulengerella*.

Lateral belly of A1: Mattox & Toledo-Piza (2012): *Xenocharax*.

Ventral division of A_1: Alexander (1964): *Leporinus*.

Pars endorictalis

A_1: Vari (1983): *Leporinus*.

A1α: Datovo & Castro (2012): *Caenotropus*, *Leporellus*, *Leporinus*, *Prochilodus*, *Steindachnerina*, *Xenocharax*.

A1γ: Datovo & Castro (2012): *Acestrorhynchus*, *Boulengerella*.

$A_{2\text{-}1}$: Vari (1979): *Distichodus*, *Hemigrammocharax*, *Nannaethiops*, *Nannocharax*, *Neolebias*, *Xenocharax*.

Dorsal divisions of A_1: Alexander (1964): *Leporinus*.

Medial belly of A1: Mattox & Toledo-Piza (2012): *Xenocharax*.

Pars malaris

A_2: Alexander (1964): *Hoplias*; Vari (1979): *Citharidium*, *Citharinus*; Vari (1983): *Prochilodus*.

A2: Datovo & Castro (2012): *Acestrorhynchus*, *Agoniates*, *Aphyocharax*, *Astyanax*, *Bivibranchia*, *Boulengerella*, *Brachychalcinus*, *Brycon*, *Bryconexodon*, *Bryconops*, *Caenotropus*, *Chalceus*, *Citharinus*, *Characidium*, *Clupeacharax*, *Creagrutus*, *Ctenobrycon*, *Cyanocharax*, *Deuterodon*, *Exodon*, *Gymnocorymbus*, *Hemibrycon*, *Hemigrammus*, *Hemiodus*, *Hepsetus*, *Hollandichthys*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Jupiaba*, *Knodus*, *Lebiasina*, *Leporellus*, *Leporinus*, *Lignobrycon*, *Metynnis*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Parecbasis*, *Parodon*, *Phenacogrammus*, *Piabina*, *Piabucus*, *Planaltina*, *Poptella*, *Prionobrama*, *Prochilodus*, *Psellogrammus*, *Rhoadsia*, *Roeboides*, *Salminus*, *Serrasalmus*, *Steindachnerina*, *Tetragonopterus*, *Thayeria*, *Triportheus*, *Utiaritichthys*, *Xenocharax*; Mattox & Toledo-Piza (2012): *Aphyocharax*, *Bryconexodon*, *Cheirodon*, *Cynodon*, *Exodon*, *Gilbertolus*, *Hemiodus*, *Heterocharax*, *Hoplias*, *Hoplocharax*, *Hydrolycus*, *Lonchogenys*, *Mimagoniates*, *Rhaphiodon*, *Roeboexodon*, *Roestes*, *Serrasalmus*, *Xenocharax*.

A$_{2\text{-m}}$: Vari (1979): *Distichodus*, *Hemigrammocharax*, *Nannaethiops*, *Nannocharax*, *Neolebias*, *Xenocharax*.

A2β: Wu & Shen (2004): *Citharinus*, *Potamorhina*.

AM2: Lauder (1981): *Lebiasina*.

Outer or external part of the internal division: Gosline (1989): *Acestrorhynchus*, *Bivibranchia*, *Charax*, *Hoplias*, *Hydrolycus*, *Piabucina*).

Pars promalaris

A2α: Datovo & Castro (2012): *Acestrorhynchus*, *Agoniates*, *Boulengerella*, *Brycon*, *Bryconops*, *Clupeacharax*, *Hepsetus*, *Hoplias*, *Hydrolycus*, *Lebiasina*, *Salminus*.

Pars retromalaris

A2β: Datovo & Castro (2012): *Acestrorhynchus*, *Agoniates*, *Boulengerella*, *Brycon*, *Bryconops*, *Clupeacharax*, *Hepsetus*, *Hoplias*, *Hydrolycus*, *Lebiasina*, *Salminus*.

Pars stego-malaris

A$_2$: Alexander (1964): *Anisitsia notata* (= *Hemiodus unimaculatus*), *Brycon*, *Creatochanes* (= *Bryconops*), *Pyrrhulina*; Howes (1976): *Acanthocharax*, *Charax*, *Cynodon*, *Cynopotamus*, *Hydrolycus*, *Rhaphiodon*, *Roeboides*, *Roestes*.

A2: Mattox & Toledo-Piza (2012): *Acanthocharax*, *Acestrocephalus*, *Acestrorhynchus*, *Astyanax*, *Boulengerella*, *Brycon*, *Bryconops*, *Charax*, *Cynopotamus*, *Galeocharax*, *Gnathocharax*, *Gymnocorymbus*, *Hepsetus*, *Hyphessobrycon*, *Iguanodectes*, *Odontostilbe*, *Oligosarcus*, *Phenacogaster*, *Roeboides*, *Salminus*, *Tetragonopterus*.

Internal division: Gosline (1989): *Acestrorhynchus*, *Bivibranchia*, *Brycon*, *Charax*, *Ctenolucius*, *Curimata*, *Hemiodus*, *Hepsetus*, *Hoplias*, *Hydrolycus*, *Piabucina*, *Salminus*.

Pars stegalis:

A$_3$: Alexander (1964): *Hoplias*; Vari (1979): *Citharidium*, *Citharinus*, *Distichodus*, *Hemigrammocharax*, *Nannaethiops*, *Nannocharax*, *Neolebias*, *Xenocharax*; Vari (1983): *Prochilodus*.

A3: Datovo & Castro (2012): *Acestrorhynchus*, *Agoniates*, *Aphyocharax*, *Astyanax*, *Bivibranchia*, *Boulengerella*, *Brachychalcinus*, *Brycon*, *Bryconexodon*, *Bryconops*, *Caenotropus*, *Chalceus*, *Citharinus*, *Characidium*, *Clupeacharax*, *Creagrutus*, *Ctenobrycon*, *Cyanocharax*, *Deuterodon*, *Exodon*, *Gymnocorymbus*, *Hemibrycon*, *Hemigrammus*, *Hemiodus*, *Hepsetus*, *Hollandichthys*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Jupiaba*, *Knodus*, *Lebiasina*, *Leporellus*, *Leporinus*, *Lignobrycon*, *Metynnis*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Parecbasis*, *Parodon*, *Phenacogrammus*, *Piabina*, *Piabucus*, *Planaltina*, *Poptella*, *Prionobrama*, *Prochilodus*, *Psellogrammus*, *Rhoadsia*, *Roeboides*, *Salminus*, *Serrasalmus*, *Steindachnerina*, *Tetragonopterus*, *Thayeria*, *Triportheus*, *Utiaritichthys*, *Xenocharax*; Mattox & Toledo-Piza (2012): *Aphyocharax*, *Bryconexodon*, *Cheirodon*, *Cynodon*, *Exodon*, *Gilbertolus*, *Hemiodus*, *Heterocharax*, *Hoplias*, *Hoplocharax*, *Hydrolycus*, *Lonchogenys*, *Mimagoniates*, *Rhaphiodon*, *Roeboexodon*, *Roestes*, *Serrasalmus*, *Xenocharax*; Wu & Shen (2004): *Citharinus*, *Potamorhina*.

AM3: Lauder (1981): *Lebiasina*.

Inner or internal part of the internal division: Gosline (1989): *Acestrorhynchus*, *Bivibranchia*, *Charax*, *Hoplias*, *Hydrolycus*, *Piabucina*.

Pars epistegalis

A$_2$b: Howes (1976): *Cynodon*, *Hydrolycus*, *Rhaphiodon*.

A3α: Datovo & Castro (2012): *Chalceus*, *Hoplias*, *Hydrolycus*, *Lebiasina*.

Pars substegalis

A3β: Datovo & Castro (2012): *Chalceus*, *Hoplias*, *Hydrolycus*, *Lebiasina*.

Segmentum mandibularis

A$_\omega$: Alexander (1964): *Brycon*, *Creatochanes* (= *Bryconops*), *Hoplias*, *Pyrrhulina*.

Aω: Datovo & Castro (2012): *Acestrorhynchus*, *Agoniates*, *Aphyocharax*, *Astyanax*, *Bivibranchia*, *Boulengerella*, *Brachychalcinus*, *Brycon*, *Bryconexodon*, *Bryconops*, *Caenotropus*, *Chalceus*, *Citharinus*, *Characidium*, *Clupeacharax*, *Creagrutus*, *Ctenobrycon*, *Cyanocharax*, *Deuterodon*, *Exodon*, *Gymnocorymbus*, *Hemibrycon*, *Hemigrammus*, *Hemiodus*, *Hepsetus*, *Hollandichthys*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Jupiaba*, *Knodus*, *Lebiasina*, *Leporellus*, *Leporinus*, *Lignobrycon*, *Metynnis*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Parecbasis*, *Parodon*, *Phenacogrammus*, *Piabina*, *Piabucus*, *Planaltina*, *Poptella*, *Prionobrama*, *Prochilodus*, *Psellogrammus*, *Rhoadsia*, *Roeboides*, *Salminus*, *Serrasalmus*, *Steindachnerina*, *Tetragonopterus*, *Thayeria*, *Triportheus*, *Utiaritichthys*, *Xenocharax*; Mattox & Toledo-Piza (2012): *Acanthocharax*, *Acestrocephalus*, *Acestrorhynchus*, *Aphyocharax*, *Astyanax*, *Boulengerella*, *Brycon*, *Bryconexodon*, *Bryconops*, *Charax*, *Cheirodon*, *Cynodon*, *Cynopotamus*, *Exodon*, *Galeocharax*, *Gnathocharax*, *Gilbertolus*, *Gymnocorymbus*, *Hemiodus*, *Hepsetus*, *Heterocharax*, *Hoplocharax*, *Hoplias*, *Hydrolycus*, *Hyphessobrycon*, *Iguanodectes*, *Lonchogenys*, *Mimagoniates*, *Odontostilbe*, *Oligosarcus*, *Phenacogaster*, *Roeboides*, *Rhaphiodon*, *Roeboexodon*, *Roestes*, *Salminus*, *Serrasalmus*, *Tetragonopterus*, *Xenocharax*.

A_w: Gosline (1989): *Brycon*, *Curimata*, *Salminus*; Howes (1976): *Acanthocharax*, *Charax*, *Cynodon*, *Cynopotamus*, *Hydrolycus*, *Rhaphiodon*, *Roeboides*, *Roestes*; Vari (1979): *Citharidium*, *Citharinus*, *Distichodus*, *Hemigrammocharax*, *Nannaethiops*, *Nannocharax*, *Neolebias*, *Xenocharax*.

Aw: Wu & Shen (2004): *Citharinus*, *Potamorhina*.

SILURIFORMES

Descriptions

Nematogenys inermis (Datovo & Bockmann, 2010: figs 1, 2)

All identified facial sections are partially continuous with each other, albeit with differentiation between them perceptible along specific regions of the muscle. The ricto-malaris and stegalis are separated from each other posterodorsally where the levator arcus palatini transits between them. The ricto-stegalis originates solely from the hyomandibula and preopercle in two examined specimens. A third examined specimen exhibits a very subtle tendinous connection between the origin of the malaris and the sphenotic and suprapreopercle. The rictalis and malaris remain continuous with each other medially, but are partially separated laterally. The rictalis inserts musculously on the lateral region of the dentary and angulo-articulo-retroarticular. The lateral-most fibres of the malaris join the rictalis anteriorly to insert on the dorsolateral region of the coronoid process of both the dentary and angulo-articulo-retroarticular. The medial fibres of the malaris merge anteriorly with the stegalis before converging onto an insertional tendon that attaches to the posteromedial rim of the coronoid process of the dentary.

The more anterior origin of the stegalis allows its ready recognition from the ricto-malaris from a medial view. The entire stegalis arises from the quadrate, metapterygoid, hyomandibula, prootic, and sphenotic. Dorsally, the portion of the stegalis, which presumably corresponds to the epistegalis, originates medial to the levator arcus palatini from both the anterodorsal laminar portion of the hyomandibula and the neurocranium. The portion of the muscle lying anteroventral to the levator arcus palatini and with an origin solely on the suspensorium apparently corresponds to the substegalis. Nevertheless, no obvious differentiation between the epistegalis and substegalis is apparent. Anteriorly, a lateral set of fibres of the substegalis passes onto the outer surface of the segmentum facialis and broadly merges with the rictalis to jointly insert on the lateral surface of the dentary. Most fibres of the substegalis continue, however, along the inner surface of the segmentum facialis. This set of fibres joins with the epistegalis to insert musculously on the medial surfaces of the angulo-articulo-retroarticular and coronomeckelian. The dorsal-most portions of the epistegalis merge anteriorly with the dorsomedial fibres of the malaris and converge onto the insertional tendon that is anchored to the posteromedial rim of the coronoid process of the dentary.

The ramus mandibularis trigeminus nerve passes medial to the bulk of the segmentum facialis and then lateral to the insertional tendon common to the dorsal portions of the malaris and stegalis.

The segmentum mandibularis is absent.

Silurichthys hasseltii (Fig. 18)

The ricto-malaris has a broad origin from the quadrate, hyomandibula, preopercle, suprapreopercle, sphenotic, and pterotic. Slightly anterior to their common origin, the rictalis and malaris partially separate from each other along their dorsolateral portions. The rictalis inserts onto the dorsal region of the angulo-articulo-retroarticular, whereas the malaris attaches to a flattened, thin intersegmental aponeurosis. This intersegmental aponeurosis is not obviously differentiated into mandibular and meckelian tendons, although the anterior portion of the aponeurosis serves as the site of origin for the segmentum facialis and the posterior portion attaches to the coronomeckelian and angulo-articulo-retroarticular.

The ramus mandibularis trigeminus passes between the rictalis and malaris.

The stegalis is completely subdivided into a lateral stegalis externa and a medial stegalis interna, both of which have their posterodorsal portions situated medial to the levator arcus palatini (see Remarks below concerning justifications for the identifications of these sections). The stegalis externa originates from the frontal, sphenotic, and hyomandibula and inserts primarily on the intersegmental aponeurosis. The ventral portion of the stegalis externa, however, merges anteriorly with the rictalis and inserts musculously on the angulo-articulo-retroarticular. A few ventrolateral-most fibres of the stegalis externa are visible from a lateral view.

The stegalis interna originates tendinously from the prootic and musculously from the anterior border of the hyomandibula. Anteriorly this section inserts tendinously on the posterior region of the maxilla proximate to the site of attachment of the maxillary barbel.

The segmentum mandibularis arises from the anterior portion of the intersegmental aponeurosis and inserts on the dentary, angulo-articulo-retroarticular, and Meckel's cartilage. The segmentum mandibularis is undifferentiated into sections along its entirety.

Remarks

Members of the Siluriformes usually have a considerable degree of continuity between the rictalis and

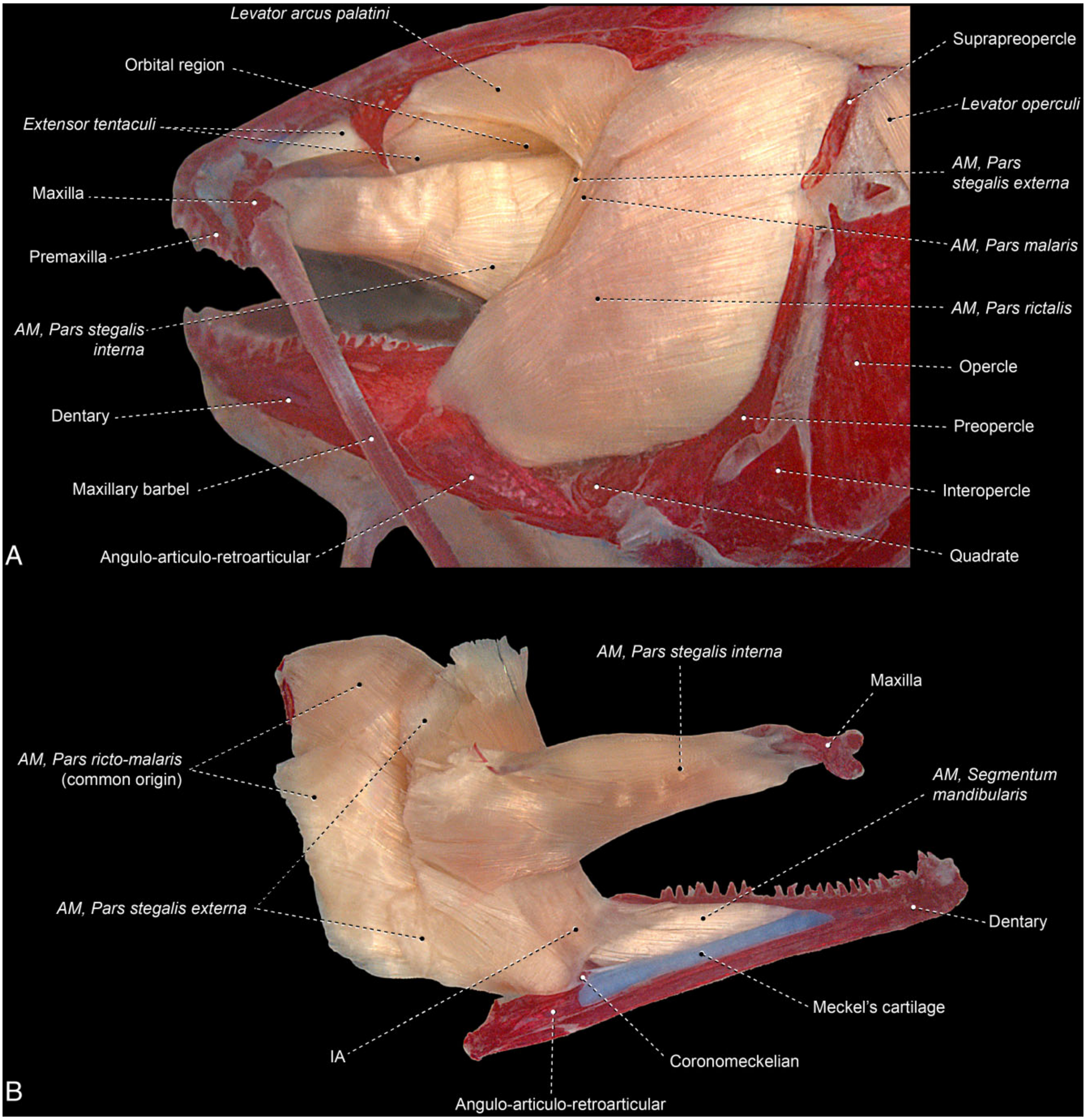


Figure 18. Adductor mandibulae and associated structures of *Silurichthys hasseltii* (Siluriformes: Siluridae), MZUSP 63489 (69.9 mm standard length). Left side in (A) lateral and (B) medial views. Ramus mandibularis trigeminus nerve removed. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis.

malaris. These sections may be differentiated from each other by a partial separation along their lateral portions (Fig. 18; Juge, 1898; Munshi, 1960; Diogo & Chardon, 2000a) and/or by different superficial patterns of fibre orientation (Adriaens & Verraes, 1996; Cabuy *et al*., 1999; Devaere *et al*., 2001; Herrel *et al*., 2002; Schaefer & Provenzano, 2008). In some instances (e.g. Trichomycteridae), the differentiation between the rictalis and malaris is subtle and limited only to the region proximate to their insertions (Datovo & Bockmann, 2010). A completely undifferentiated and undivided ricto-malaris is present in other groups in the order, including some taxa in the Loricariidae, Plotosidae, Siluridae, and Trichomycteridae (Takahasi, 1925; Bornbusch, 1995; Geerinckx *et al*., 2007; Geerinckx, Huysentruyt & Adriaens, 2009; Datovo & Bockmann, 2010). The rictalis is invariably inserted on the lower jaw, usually onto the posterior region of the coronoid process (Takahasi, 1925). In the loricariid *Lithogenes*, the rictalis is partially subdivided into an endorictalis and an ectorictalis (Schaefer & Provenzano, 2008).

In at least some members of most families of the Siluriformes, the origin of the malaris expands dorsally onto the neurocranium (Fig. 18) and in more derived conditions the dorsally enlarged contralateral malares contact each other midsagittally (McMurrich, 1884; Juge, 1898; Takahasi, 1925; Eaton, 1948; Alexander, 1965; Howes, 1985b; Grande & Lundberg, 1988; Lundberg, Bornbusch & Mago-Leccia, 1991; de Pinna & Vari, 1995; Adriaens & Verraes, 1996; Cabuy *et al*., 1999; Devaere *et al*., 2001, 2006; Herrel *et al*., 2002; Rodiles-Hernández *et al*., 2005; Sarmento-Soares & Porto, 2006; de Pinna, Ferraris & Vari, 2007; Shibatta, Muriel-Cunha & de Pinna, 2007; Datovo & Bockmann, 2010). The malaris inserts on the buccopalatal membrane plus the maxilla in the Callichthyidae (see below) and on the lower jaw in both all other examined siluriforms and those for which the muscle was described in the literature (Fig. 18). In some cases where a distinction between the malaris and rictalis is not evident from a lateral view, the malaris can be identified by its anterior association with the mandibular tendon and the segmentum mandibularis (Fig. 18; Takahasi, 1925; Datovo & Bockmann, 2010).

The posterodorsal portion of the stegalis almost always originates medial to the levator arcus palatini (Fig. 18). The origin of this section extends to the neurocranium at least in some species in the Clariidae, Nematogenyidae, Plotosidae, and Siluridae (present study; Takahasi, 1925; Adriaens & Verraes, 1996; Cabuy *et al*., 1999; Devaere *et al*., 2001, 2006; Herrel *et al*., 2002; Datovo & Bockmann, 2010). Anteroventral to the levator arcus palatini, the stegalis is often continuous with, and sometimes almost indistinguishable from, the remaining facial sections.

Identification of the stegalis may be even more problematic because most siluriforms exhibit significant changes in the osteological landmarks typically useful for the identification of the origin and insertion of the stegalis across most teleosts. The hyomandibula of the Siluriformes bears a prominent anterodorsal laminar outgrowth (less pronounced in the Diplomystidae and Nematogenyidae) that extends into the area typically occupied by the metapterygoid in other teleosts (authors' pers. observ.; Fink & Fink, 1981; Arratia, 1992). In turn, the metapterygoid is anteriorly displaced along the suspensorium, consequently assuming the position typically occupied by the endopterygoid and ectopterygoid elsewhere in the Teleostei. As a consequence of these modifications, the stegalis, which usually arises primarily from the metapterygoid in most nonsiluriform teleosts, may arise largely or solely from the hyomandibula in some siluriforms (e.g. derived trichomycterids; Datovo & Bockmann, 2010). Additionally, the coronomeckelian, which typically serves as an insertion site (via the meckelian tendon) for at least part of the stegalis across the Teleostei, is absent in several siluriform taxa (de Pinna, 1993). To further complicate matters, parts of the stegalis may become dissociated from the remainder of that section and become attached to the maxilla, which is reduced to a small, toothless ossification supporting the maxillary barbel across all the Siluriformes except for the Diplomystidae and †Hypsidoridae (Alexander, 1965; Grande, 1987), which resolve as the basal-most members of the order under morphological analyses. This muscle division, which serves to adduct the maxillary barbel, has been designated the adductor tentaculi (McMurrich, 1884; Takahasi, 1925; Eaton, 1948; Alexander, 1965) or, more commonly, the retractor tentaculi (Mahajan, 1971; Howes, 1983; Schaefer, 1990, 1997; Bornbusch, 1995; Adriaens & Verraes, 1996; Cabuy *et al*., 1999; Devaere *et al*., 2001, 2006; Herrel *et al*., 2002; Sarmento-Soares & Porto, 2006; Huysentruyt, Geerinckx & Adriaens, 2007; Geerinckx *et al*., 2009; Huysentruyt, Brunain & Adriaens, 2009). Analysis reveals, however, that different parts of the stegalis have apparently independently become attached to the maxilla in different lineages during the evolution of the Siluriformes. Thus, as is discussed further below, the retractor tentaculi as now utilized is not homologous across the Siluriformes.

In the Ictaluridae and Sisoridae, the part of the segmentum facialis that inserts on the maxilla and the buccopalatal membrane originates from the dorsal region of the hyomandibula, being the only muscle portion situated medial to the levator arcus palatini (McMurrich, 1884; Eaton, 1948; Mahajan, 1971). The remainder of the segmentum facialis in these families originates completely lateral and ventral to the levator arcus palatini. Therefore, the section attached to the maxilla in the Ictaluridae and Sisoridae apparently corresponds to the epistegalis. Association of the epistegalis with the maxilla or buccopalatal membrane also occurs in some trichomycterids (= A3″ of Datovo & Bockmann, 2010). Both the epistegalis and the malaris insert on the maxilla and buccopalatal membrane in the Callichthyidae. The name retractor tentaculi has been used in this family to refer solely to the epistegalis (Howes, 1983; Huysentruyt *et al*., 2007, 2009) or to both the epistegalis and malaris (Geerinckx *et al*., 2009). In the Loricariidae, Astroblepidae, and Scoloplacidae, the epistegalis is attached to the premaxilla (= retractor premaxillae of Howes, 1983; Schaefer, 1990, 1997; Geerinckx *et al*., 2009). The substegalis of loricariids is further divided into an inner substegalis interna and an outer substegalis externa. According to Geerinckx *et al*. (2009), these subsections are derived from the undivided substegalis present earlier in ontogeny. In adult loricariids, the substegalis interna (= retractor palatini of Howes, 1983; Schaefer, 1990, 1997; = retractor veli of Geerinckx *et al*., 2009) becomes attached anteriorly to the buccopalatal membrane, whereas the substegalis externa retains its lower jaw attachment jointly with the ricto-malaris. Munshi (1960) also reported what seems to be a substegalis divided into interna and externa subsections in *Sperata aor* (Bagridae), although in this species both subdivisions retain an insertion on the lower jaw.

Determination of the identity of the so-called retractor tentaculi is more complicated amongst other groups in the Siluriformes, such as the Clariidae and Siluridae. In these families, the part of the segmentum facialis that inserts on the lower jaw is posteriorly divided into two major portions: the first portion lying lateral (= ricto-malaris) and the second medial to the levator arcus palatini (Fig. 18; Juge, 1898; Takahasi, 1925; Bornbusch, 1995; Adriaens & Verraes, 1996, 1997; Cabuy *et al*., 1999; Devaere *et al*., 2001, 2006; Herrel *et al*., 2002). This medial portion of the segmentum facialis has a broad origin that involves the hyomandibula and sometimes also the metapterygoid, quadrate and neurocranium. The retractor tentaculi of clariids and silurids lies completely medial to this inner facial division and also has a broad origin that may also involve the hyomandibula, metapterygoid, quadrate, and neurocranium. Thus, it appears that the entire stegalis in the Clariidae and Siluridae has been subdivided along a parasagittal plane, thereby forming two subsections provisionally named the stegalis externa and stegalis interna (Fig. 18). This division, therefore, apparently does not correspond to a separation of the stegalis into the dorsal epistegalis and ventral substegalis as found elsewhere in the Teleostei. Homology hypotheses for the retractor tentaculi of the Clariidae and Siluridae must be viewed as tentative because they are based upon a comparatively sparse sampling within the hyperdiverse Siluriformes. The identity of the so-called retractor tentaculi of other siluriform groups is even more uncertain given the limited available detailed information on this muscle system in the literature. Additional research centred on the adductor mandibulae is prerequisite for a clarification of the identities of these facial sections across the expanse of the Siluriformes.

As amply documented by Geerinckx *et al*. (2009), and confirmed by our observations, the muscle designated as the retractor tentaculi or muscle ‘a’ in the Loricariidae, Astroblepidae, and Scoloplacidae (Howes, 1983; Schaefer, 1990, 1997; Geerinckx *et al*., 2007) is actually derived from the extensor tentaculi rather than the adductor mandibulae. For this reason, Geerinckx *et al*. (2009) proposed renaming this muscle as the levator tentaculi. A muscle similarly named the retractor tentaculi by Diogo, Chardon & Vandewalle (2003d) and Sarmento-Soares & Porto (2006) in the auchenipterid *Centromochlus heckelii* similarly seems to be clearly derived from the extensor tentaculi, inasmuch as these two muscles are in close contact with each other and given that the supposed retractor tentaculi originates from the anterior portion of the neurocranium rather than from the suspensorium.

As detailed above, the term retractor tentaculi has been applied to at least five different entities: the stegalis interna (Clariidae and possibly Siluridae), epistegalis (Callichthyidae, Ictaluridae, and Sisoridae), malaris and epistegalis jointly (Callichthyidae), a dorsal subdivision of the extensor tentaculi (Loricariidae), and a ventral subdivision of the extensor tentaculi (Auchenipteridae). Owing to this confusing and ambiguous application of the term retractor tentaculi and given that this name in isolation fails to indicate the homologies of the muscle with the corresponding muscle section of other teleosts, we prefer to avoid the use of this term. Use of distinct names for other sections that do not attach to the lower jaw in other siluriform taxa (e.g. retractor premaxillae and retractor veli of derived taxa in the Loricarioidea) should in our opinion be similarly avoided given that the homologies of these muscles were recently clarified (Geerinckx *et al*., 2009).

Many members of the Siluriformes completely lack a segmentum mandibularis. When present (Fig. 18), this segment is often small and has its origin limited to the intersegmental aponeurosis (Takahasi, 1925).

Descriptions of, and nomenclature for, the adductor mandibulae sections in some studies dealing with units in the Siluriformes (Alexander, 1965; Schaefer & Lauder, 1986; Wu & Shen, 2004) lack sufficient detail for homology determinations. Consequently, these publications are not included in the synonymy below.

In a series of at least 28 studies published between 1999 and 2007, 26 of them as sole or first author, Diogo discussed the pectoral and superficial cranial muscles – including the adductor mandibulae complex – of many groups across the breadth of the Siluriformes (Diogo, Vandewalle & Chardon, 1999; Diogo & Chardon, 2000a, b; Diogo, Oliveira & Chardon, 2000, 2001; Diogo, Chardon & Vandewalle, 2001, 2002, 2003a, b, c, d, e, 2004a, b, c, d, 2006a; b; Oliveira *et al*., 2001, 2002; Diogo, 2002, 2004a, b, 2005, 2007a, b; Diogo & Vandewalle, 2003; Diogo & Bills, 2006). As a consequence, the Siluriformes ranks very high amongst orders within the Teleostei in terms of numbers of myological studies. Notwithstanding this impressive number of analyses, these papers did not yield a better understanding of the adductor mandibulae across the order. As an example, Datovo & Bockmann (2010) documented, and our analysis confirms, numerous discrepancies between the observations made in the adductor mandibulae of *Nematogenys inermis* – the single extant member of the Nematogenyidae – and the morphology of the muscle reported by Diogo *et al*. (2006a). Problematic aspects of the study by Diogo *et al*. (2006a) include: inaccuracies in the illustrations and morphological descriptions, misidentification of muscle sections, and an unclear and apparently inconsistent criteria for the recognition of muscle sections (see the detailed analysis in Datovo & Bockmann, 2010: 231, 232). In so far as data as to the morphology of the adductor mandibulae of *Nematogenys inermis* are congruent across all publications by other authors based on multiple examined specimens (present study; Howes, 1983; Datovo & Bockmann, 2010), it is unlikely that intraspecific variation accounts for the highly divergent data of Diogo *et al*. (2006a). Shortcomings in Diogo *et al*.'s (2006a) accounts of the adductor mandibulae in *Nematogenys inermis*, furthermore, are not an isolated case. Rather, personal observations on the morphology of the adductor mandibulae of other siluriforms treated in other publications by Diogo (and in some instances co-authors) demonstrate similar problems.

Further complicating the issue is the fact that the nomenclature for the facial sections of the adductor mandibulae originally proposed in Diogo & Chardon (2000a), and employed thenceforth in all publications by Diogo, fails to reflect the homologies of the muscle sections amongst different orders in the Teleostei. The term A2, for example, was applied in that series of papers to five different muscle sections (Datovo & Vari, 2013: 19). More notably, the terminology proposed by Diogo & Chardon (2000a) fails to reflect the muscle homologies even across different taxa within the Siluriformes. Reflective of this is the fact that although Diogo & Chardon (2000a) recognized that his retractor tentaculi 'is derived from the inner [facial] section of the *adductor mandibulae* (A3)', this homology is implicitly ignored in most of the subsequent studies by Diogo. For example, the adductor mandibulae of the pimelodoid *Pimelodus blochii* is described as having five sections – A1-ost, A2, A3′-d, A3′-v, and A3″ – and no retractor tentaculi in Diogo (2005). The muscle of a second pimelodoid, *Heptapterus mustelinus*, is described in an almost identical repetition of the muscle description of *Pimelodus blochii*, with the same five subdivisions, all exhibiting the same basic characteristics; however, in *Heptapterus mustelinus* a retractor tentaculi is reported as present (Diogo, 2007a). Consequently, in so far as the retractor tentaculi is considered a subdivision of the A3 (Diogo & Chardon, 2000a), at least one of the names A3′-d, A3′-v, or A3″ is inconsistently applied to nonhomologous structures in *Pimelodus blochii* and *Heptapterus mustelinus*. Similar issues apply across nearly all of the publications on siluriforms by Diogo. In light of the scale of the problems in terms of anatomical accuracy, explicitness of data presentation, interpretation of observations, and logical consistency of the publications authored by Diogo, it proved impossible to include the copious amount of data generated by that author into our synonymy or utilize that information for phylogenetic analyses.

Synonymy

Segmentum facialis

A2A3: Datovo, Carvalho & Ferrer (2012): *Trichomycterus*.

Pars ricto-malaris

?A_1 [*sic*]: Howes (1983): *Callichthys*, *Hoplosternum*.

A1-OST plus A2A3′: Adriaens, Baskin & Coppens (2010): *Trichomycterus*.

A_2: Bornbusch (1995): *Belodontichthys*, *Ceratoglanis*, *Hemisilurus*, *Hito* (= *Pterocryptis*), *Kryptopterus*, *Kryptopterus apogon* (= *Phalacronotus apogon*), *Kryptopterus bleekeri* (= *Phalacronotus bleekeri*), *Kryptopterus hexapterus* (= *Micronema hexapterus*), *Kryptopterus micronema* (= *Phalacronotus micronemus*), *Kryptopterus moorei* (= *Micronema moorei*), *Kryptopterus parvanalis* (= *Phalacronotus parvanalis*), *Ompok*, *Ompok eugeneiatus* (= *Kryptopterus eugeneiatus*), *Ompok sabanus* (= *Kryptopterus sabanus*), *Pterocryptis*, *Silurichthys*, *Silurus*, *Wallago*.

A2: Datovo & Bockmann (2010): *Bullockia*, *Copionodon*, *Haemomaster*, *Hatcheria*, *Homodiaetus*, *Ituglanis*, *Listrura*, *Microcambeva*, *Nematogenys*, *Ochmacanthus*, *Paracanthopoma*, *Parastegophilus*, *Paravandellia*, *Pareiodon*, *Pseudostegophilus*, *Sarcoglanis*, *Scleronema*, *Stauroglanis*, *Trichogenes*, *Trichomycterus*, *Tridentopsis*, *Vandellia*; Schaefer & Provenzano (2008): *Lithogenes*.

A2β: Wu & Shen (2004): *Parasilurus* (= *Silurus*).

$A_2A'_3$: Adriaens & Verraes (1996): *Clarias*; Adriaens & Verraes (1997): *Clarias*; Takahasi (1925): *Fluvidraco* [*sic*] *nudiceps* (= ?*Tachysurus nudiceps* or? *Tachysurus fulvidraco*), *Liobagrus*, *Parasilurus* (= *Silurus*), *Plotosus*, *Pseudobagrus*.

A_2A_3': Cabuy *et al*. (1999): *Clariallabes*, *Clarias*, *Gymnallabes*; Devaere *et al*. (2001): *Channallabes*; Devaere *et al*. (2006): *Platyclarias*; Herrel *et al*. (2002): *Channallabes*, *Clariallabes*, *Clarias*, *Gymnallabes*.

External part: Geerinckx *et al*. (2009): *Ancistrus*; Geerinckx *et al*. (2007): *Ancistrus*.

Portion superficielle or Am_1: Juge (1898): *Silurus*.

Pars rictalis

A_1 or lateral fibres of muscle 'b': Howes (1983): *Ancistrus*, *Astroblepus*, *Chaetostoma*, *Cochliodon* (= *Hypostomus*), *Farlowella*, *Hemiancistrus*, *Hemiodonichthys* [*sic*] (= *Hemiodontichthys*), *Hemipsilichthys calmoni* (= *Pareiorhaphis cameroni*), *Hypoptopoma carinata*

(= *Oxyropsis carinata*), *Hypostomus*, *Hypostomus spinossisimus* [*sic*] (= *Isorineloricaria spinosissima*), *Ixinandria*, *Lipopterichthys*, *Lithoxus*, *Loricaria*, *Loricaria brunneus* (= *Loricariichthys brunneus*), *Loricaria jubata* (*Rineloricaria jubata*), *Loricaria labialis* (= *Loricariichthys labialis*), *Loricaria lanceolata* (= *Rineloricaria lanceolata*), *Loricaria microlepidogaster* (= *Rineloricaria microlepidogaster*), *Loricaria platystoma* (= *Cteniloricaria platystoma*), *Loricaria strigilata* (= *Rineloricaria strigilata*), *Loricaria teffeana* (= *Rineloricaria teffeana*), *Loricaria variegata* (= *Crossoloricaria variegata*), *Loricaria venezeuelae* (*Crossoloricaria venezuelae*), *Metaloricaria*, *Otocinclus nigricauda* (= *Hisonotus nigricauda*), *Panaque*, *Peckoltia pulcher* (*Dekeyseria pulchra*), *Pogonopoma*, *Pogonopomoides* (= *Pogonopoma*), *Pseudancistrus*, *Pseudohemiodon*, *Pterygoplichthys*, *Rhadniloricaria* [*sic*] (= *Rhadinoloricaria*), *Stoniella* [*sic*] (= *Pseudacanthicus*), *Sturisoma*.

A_1OST: Huysentruyt *et al*. (2007): *Corydoras*; Huysentruyt *et al*. (2009): *Corydoras*.

A1-ost: Sarmento-Soares & Porto (2006): *Centromochlus*, *Glanidium*, *Tatia*.

A1-OST plus A2A3′β: Adriaens *et al*. (2010): *Trichomycterus*.

A2′: Datovo & Bockmann (2010): *Bullockia*, *Haemomaster*, *Hatcheria*, *Homodiaetus*, *Ituglanis*, *Listrura*, *Nematogenys*, *Ochmacanthus*, *Paracanthopoma*, *Parastegophilus*, *Paravandellia*, *Pareiodon*, *Pseudostegophilus*, *Sarcoglanis*, *Scleronema*, *Trichogenes*, *Trichomycterus*, *Tridentopsis*, *Vandellia*.

A2α: Wu & Shen (2004): *Pseudobagrus taiwanensis* (= *Tachysurus taiwanensis*).

$A_2A'_3\beta$: Adriaens & Verraes (1996): *Clarias*.

$A_2A_3'\beta$: Cabuy *et al*. (1999): *Clariallabes*, *Clarias*, *Gymnallabes*; Devaere *et al*. (2001): *Channallabes*; Devaere *et al*. (2006): *Platyclarias*.

A2ventral: Schaefer & Provenzano (2008): *Lithogenes*.

Adductor 1 or Ad_1: Munshi (1960): *Mystus aor* (*Sperata aor*).

Adductor mandibulae superficialis: Mahajan (1971): *Sisor*.

External division: Gosline (1989): *Diplomystes*.

External part: Geerinckx *et al*. (2009): *Corydoras*.

Partie latérale de Am_1 or ‘a’: Juge (1898): *Silurus*.

Pars ectorictalis

A2ventral β: Schaefer & Provenzano (2008): *Lithogenes*.

Pars endorictalis

A2ventral α: Schaefer & Provenzano (2008): *Lithogenes*.

Pars malaris

A_2: Huysentruyt *et al*. (2007): *Corydoras*; Huysentruyt *et al*. (2009): *Corydoras*.

A_2 or posterior fibres of muscle ‘b’: Howes (1983): *Ancistrus*, *Astroblepus*, *Chaetostoma*, *Cochliodon* (= *Hypostomus*), *Farlowella*, *Hemiancistrus*, *Hemiodonichthys* [*sic*] (= *Hemiodontichthys*), *Hemipsilichthys calmoni* (= *Pareiorhaphis cameroni*), *Hypoptopoma carinata* (= *Oxyropsis carinata*), *Hypostomus*, *Hypostomus spinossisimus* [*sic*] (= *Isorineloricaria spinosissima*), *Ixinandria*, *Lipopterichthys*, *Lithoxus*, *Loricaria*, *Loricaria brunneus* (= *Loricariichthys brunneus*), *Loricaria jubata* (*Rineloricaria jubata*), *Loricaria labialis* (= *Loricariichthys labialis*), *Loricaria lanceolata* (= *Rineloricaria lanceolata*), *Loricaria microlepidogaster* (= *Rineloricaria microlepidogaster*), *Loricaria platystoma* (= *Cteniloricaria platystoma*), *Loricaria strigilata* (= *Rineloricaria strigilata*), *Loricaria teffeana* (= *Rineloricaria teffeana*), *Loricaria variegata* (= *Crossoloricaria variegata*), *Loricaria venezeuelae* (*Crossoloricaria venezuelae*), *Metaloricaria*, *Otocinclus nigricauda* (= *Hisonotus nigricauda*), *Panaque*, *Peckoltia pulcher* (*Dekeyseria pulchra*), *Pogonopoma*, *Pogonopomoides* (= *Pogonopoma*), *Pseudancistrus*, *Pseudohemiodon*, *Pterygoplichthys*, *Rhadniloricaria* [*sic*] (= *Rhadinoloricaria*), *Stoniella* [*sic*] (= *Pseudacanthicus*), *Sturisoma*.

A2: Sarmento-Soares & Porto (2006): *Centromochlus*, *Glanidium*, *Tatia*.

A2″: Datovo & Bockmann (2010): *Bullockia*, *Haemomaster*, *Hatcheria*, *Homodiaetus*, *Ituglanis*, *Listrura*, *Nematogenys*, *Ochmacanthus*, *Paracanthopoma*, *Parastegophilus*, *Paravandellia*, *Pareiodon*, *Pseudostegophilus*, *Sarcoglanis*, *Scleronema*, *Trichogenes*, *Trichomycterus*, *Tridentopsis*, *Vandellia*.

$A_2A'_3\alpha$: Adriaens & Verraes (1996): *Clarias*.

$A_2A_3'\alpha$: Cabuy *et al*. (1999): *Clariallabes*, *Clarias*, *Gymnallabes*; Devaere *et al*. (2001): *Channallabes*; Devaere *et al*. (2006): *Platyclarias*.

A2A3′α: Adriaens *et al*. (2010): *Trichomycterus*.

A2dorsal: Schaefer & Provenzano (2008): *Lithogenes*.

Adductor 2 or Ad_2: Munshi (1960): *Mystus aor* (*Sperata aor*).

Adductor mandibulae profundus 1 and 2: Mahajan (1971): *Sisor*.

Dorsolateral division of retractor tentaculi: Geerinckx *et al*. (2009): *Corydoras*.

Partie médiale de Am_1 or ‘b’: Juge (1898): *Silurus*.

Pars stego-malaris

Internal division: Gosline (1989): *Diplomystes*.

Pars stegalis

A3: Datovo & Bockmann (2010): *Bullockia*, *Copionodon*, *Haemomaster*, *Hatcheria*, *Homodiaetus*, *Ituglanis*, *Listrura*, *Microcambeva*, *Nematogenys*, *Ochmacanthus*, *Paracanthopoma*, *Parastegophilus*, *Paravandellia*, *Pareiodon*, *Pseudostegophilus*, *Sarcoglanis*, *Scleronema*, *Stauroglanis*, *Trichogenes*, *Trichomycterus*, *Tridentopsis*, *Vandellia*; Wu & Shen (2004): *Parasilurus* (= *Silurus*), *Pseudobagrus taiwanensis* (= *Tachysurus taiwanensis*).

Pars stegalis externa

A_3: Bornbusch (1995): *Belodontichthys*, *Ceratoglanis*, *Hemisilurus*, *Hito* (= *Pterocryptis*), *Kryptopterus*, *Kryptopterus apogon* (= *Phalacronotus apogon*), *Kryptopterus bleekeri* (= *Phalacronotus bleekeri*), *Kryptopterus hexapterus* (= *Micronema hexapterus*), *Kryptopterus micronema* (= *Phalacronotus micronemus*), *Kryptopterus moorei* (= *Micronema moorei*), *Kryptopterus parvanalis* (= *Phalacronotus parvanalis*), *Ompok*, *Ompok eugeneiatus* (= *Kryptopterus eugeneiatus*), *Ompok sabanus* (= *Kryptopterus sabanus*), *Pterocryptis*, *Silurichthys*, *Silurus*, *Wallago*.

A''_3: Adriaens & Verraes (1996): *Clarias*; Takahasi (1925): *Parasilurus* (= *Silurus*).

A_3'': Adriaens & Verraes (1997): *Clarias*; Cabuy *et al.* (1999): *Clariallabes*, *Clarias*, *Gymnallabes*; Devaere *et al.* (2001): *Channallabes*; Devaere *et al.* (2006): *Platyclarias*; Herrel *et al.* (2002): *Channallabes*, *Clariallabes*, *Clarias*, *Gymnallabes*.

Portion profonde or Am_2: Juge (1898): *Silurus*.

Pars stegalis interna

Retractor tentaculi: Adriaens & Verraes (1996): *Clarias*; Adriaens & Verraes (1997): *Clarias*; Bornbusch (1995): *Belodontichthys*, *Ceratoglanis*, *Hemisilurus*, *Hito* (= *Pterocryptis*), *Kryptopterus*, *Kryptopterus apogon* (= *Phalacronotus apogon*), *Kryptopterus bleekeri* (= *Phalacronotus bleekeri*), *Kryptopterus hexapterus* (= *Micronema hexapterus*), *Kryptopterus micronema* (= *Phalacronotus micronemus*), *Kryptopterus moorei* (= *Micronema moorei*), *Kryptopterus parvanalis* (= *Phalacronotus parvanalis*), *Ompok*, *Ompok eugeneiatus* (= *Kryptopterus eugeneiatus*), *Ompok sabanus* (= *Kryptopterus sabanus*), *Pterocryptis*, *Silurichthys*, *Silurus*, *Wallago*; Cabuy *et al.* (1999): *Clariallabes*, *Clarias*, *Gymnallabes*; Devaere *et al.* (2001): *Channallabes*; Devaere *et al.* (2006): *Platyclarias*; Takahasi (1925): *Parasilurus* (= *Silurus*).

Rétracteur du barbillon: Juge (1898): *Silurus*.

Pars epistegalis

A3″: Datovo & Bockmann (2010): *Bullockia*, *Copionodon*, *Hatcheria*, *Ituglanis*, *Listrura*, *Microcambeva*, *Nematogenys*, *Sarcoglanis*, *Scleronema*, *Stauroglanis*, *Trichogenes*, *Trichomycterus*; Sarmento-Soares & Porto (2006): *Centromochlus*, *Glanidium*, *Tatia*.

Adductor 4 or Ad_4: Munshi (1960): *Mystus aor* (*Sperata aor*).

Adductor tentaculi: Eaton (1948): *Ictalurus*; *Amiurus* (= *Ameiurus*).

Dorsomedial division of retractor tentaculi: Geerinckx *et al.* (2009): *Corydoras*.

Retractor premaxillae: Geerinckx *et al.* (2009): *Ancistrus*; Geerinckx *et al.* (2007): *Ancistrus*; Schaefer & Provenzano (2008): *Lithogenes*.

Retractor premaxillae or muscle ‘c’: Howes (1983): *Ancistrus*, *Astroblepus*, *Chaetostoma*, *Cochliodon* (= *Hypostomus*), *Farlowella*, *Hemiancistrus*, *Hemiodonichthys* [*sic*] (= *Hemiodontichthys*), *Hemipsilichthys calmoni* (= *Pareiorhaphis cameroni*), *Hypoptopoma carinata* (= *Oxyropsis carinata*), *Hypostomus*, *Hypostomus spinossisimus* [*sic*] (= *Isorineloricaria spinosissima*), *Ixinandria*, *Lipopterichthys*, *Lithoxus*, *Loricaria*, *Loricaria brunneus* (= *Loricariichthys brunneus*), *Loricaria jubata* (*Rineloricaria jubata*), *Loricaria labialis* (= *Loricariichthys labialis*), *Loricaria lanceolata* (= *Rineloricaria lanceolata*), *Loricaria microlepidogaster* (= *Rineloricaria microlepidogaster*), *Loricaria platystoma* (= *Cteniloricaria platystoma*), *Loricaria strigilata* (= *Rineloricaria strigilata*), *Loricaria teffeana* (= *Rineloricaria teffeana*), *Loricaria variegata* (= *Crossoloricaria variegata*), *Loricaria venezeuelae* (*Crossoloricaria venezuelae*), *Metaloricaria*, *Otocinclus nigricauda* (= *Hisonotus nigricauda*), *Panaque*, *Peckoltia pulcher* (*Dekeyseria pulchra*), *Pogonopoma*, *Pogonopomoides* (= *Pogonopoma*), *Pseudancistrus*, *Pseudohemiodon*, *Pterygoplichthys*, *Rhadniloricaria* [*sic*] (= *Rhadinoloricaria*), *Stoniella* [*sic*] (= *Pseudacanthicus*), *Sturisoma*; Schaefer (1990): *Cochliodon* (= *Hypostomus*), *Hypostomus*, *Isorineloricaria*, *Neoplecostomus*; Schaefer (1997): *Otocinclus*.

Retractor tentaculi: Howes (1983): *Callichthys*, *Hoplosternum*; Huysentruyt *et al.* (2007): *Corydoras*; Huysentruyt *et al.* (2009): *Corydoras*; Mahajan (1971): *Sisor*.

Pars substegalis

A_2: Howes (1983): *Callichthys*, *Hoplosternum*.

A'_3: Huysentruyt *et al.* (2007): *Corydoras*.

A_3': Huysentruyt *et al.* (2009): *Corydoras*.

A3′: Datovo & Bockmann (2010): *Bullockia*, *Copionodon*, *Hatcheria*, *Ituglanis*, *Listrura*, *Microcambeva*, *Nematogenys*, *Sarcoglanis*, *Scleronema*, *Stauroglanis*, *Trichogenes*, *Trichomycterus*; Sarmento-Soares & Porto (2006): *Centromochlus*, *Glanidium*, *Tatia*.

Adductor 3 or Ad_3: Munshi (1960): *Mystus aor* (*Sperata aor*).

Adductor mandibulae profundus 3: Mahajan (1971): *Sisor*.

Internal part: Geerinckx *et al.* (2009): *Corydoras*.

Pars substegalis externa

A_3 or medial fibres of muscle ‘b’: Howes (1983): *Ancistrus*, *Astroblepus*, *Chaetostoma*, *Cochliodon*

(= *Hypostomus*), *Farlowella*, *Hemiancistrus*, *Hemiodonichthys* [*sic*] (= *Hemiodontichthys*), *Hemipsilichthys calmoni* (= *Pareiorhaphis cameroni*), *Hypoptopoma carinata* (= *Oxyropsis carinata*), *Hypostomus*, *Hypostomus spinossisimus* [*sic*] (= *Isorineloricaria spinosissima*), *Ixinandria*, *Lipopterichthys*, *Lithoxus*, *Loricaria*, *Loricaria brunneus* (= *Loricariichthys brunneus*), *Loricaria jubata* (*Rineloricaria jubata*), *Loricaria labialis* (= *Loricariichthys labialis*), *Loricaria lanceolata* (= *Rineloricaria lanceolata*), *Loricaria microlepidogaster* (= *Rineloricaria microlepidogaster*), *Loricaria platystoma* (= *Ctenitoloricaria platystoma*), *Loricaria strigilata* (= *Rineloricaria strigilata*), *Loricaria teffeana* (= *Rineloricaria teffeana*), *Loricaria variegata* (= *Crossoloricaria variegata*), *Loricaria venezeuelae* (*Crossoloricaria venezuelae*), *Metaloricaria*, *Otocinclus nigricauda* (= *Hisonotus nigricauda*), *Panaque*, *Peckoltia pulcher* (*Dekeyseria pulchra*), *Pogonopoma*, *Pogonopomoides* (= *Pogonopoma*), *Pseudancistrus*, *Pseudohemiodon*, *Pterygoplichthys*, *Rhadniloricaria* [*sic*] (= *Rhadinoloricaria*), *Stoniella* [*sic*] (= *Pseudacanthicus*), *Sturisoma*.

A3: Schaefer & Provenzano (2008): *Lithogenes*.

Internal part: Geerinckx *et al*. (2009): *Ancistrus*; Geerinckx *et al*. (2007): *Ancistrus*.

Posterior part of Ad_3: Munshi (1960): *Mystus aor* (*Sperata aor*).

Pars substegalis interna

Anterior portion of Ad_3: Munshi (1960): *Mystus aor* (*Sperata aor*).

Retractor palatini or muscle 'd': Howes (1983): *Ancistrus*, *Chaetostoma*, *Cochliodon* (= *Hypostomus*), *Farlowella*, *Hemiancistrus*, *Hemiodonichthys* [*sic*] (= *Hemiodontichthys*), *Hemipsilichthys calmoni* (= *Pareiorhaphis cameroni*), *Hypoptopoma carinata* (= *Oxyropsis carinata*), *Hypostomus*, *Hypostomus spinossisimus* [*sic*] (= *Isorineloricaria spinosissima*), *Ixinandria*, *Lipopterichthys*, *Lithoxus*, *Loricaria*, *Loricaria brunneus* (= *Loricariichthys brunneus*), *Loricaria jubata* (*Rineloricaria jubata*), *Loricaria labialis* (= *Loricariichthys labialis*), *Loricaria lanceolata* (= *Rineloricaria lanceolata*), *Loricaria microlepidogaster* (= *Rineloricaria microlepidogaster*), *Loricaria platystoma* (= *Ctenitoloricaria platystoma*), *Loricaria strigilata* (= *Rineloricaria strigilata*), *Loricaria teffeana* (= *Rineloricaria teffeana*), *Loricaria variegata* (= *Crossoloricaria variegata*), *Loricaria venezeuelae* (*Crossoloricaria venezuelae*), *Metaloricaria*, *Otocinclus nigricauda* (= *Hisonotus nigricauda*), *Panaque*, *Peckoltia pulcher* (*Dekeyseria pulchra*), *Pogonopoma*, *Pogonopomoides* (= *Pogonopoma*), *Pseudancistrus*, *Pseudohemiodon*, *Pterygoplichthys*, *Rhadniloricaria* [*sic*] (= *Rhadinoloricaria*), *Stoniella* [*sic*] (= *Pseudacanthicus*), *Sturisoma*; Schaefer (1990): *Astroblepus*, *Cochliodon* (= *Hypostomus*), *Hypostomus*, *Isorineloricaria*, *Neoplecostomus*, *Scoloplax*; Schaefer (1997): *Otocinclus*.

Retractor veli: Geerinckx *et al*. (2009): *Ancistrus*; Geerinckx *et al*. (2007): *Ancistrus*; Schaefer & Provenzano (2008): *Lithogenes*.

Segmentum mandibularis

A_w: Gosline (1989): *Ictalurus*.

Aw: Wu & Shen (2004): *Parasilurus* (= *Silurus*), *Pseudobagrus taiwanensis* (= *Tachysurus taiwanensis*).

Mentalis or ω: Takahasi (1925): *Fluvidraco* [*sic*] *nudiceps* (= ?*Tachysurus nudiceps* or ?*Tachysurus fulvidraco*), *Parasilurus* (= *Silurus*), *Plotosus*, *Pseudobagrus*.

Prolongement de Am or Amp: Juge (1898): *Silurus*.

GYMNOTIFORMES

Description

Gymnotus carapo (Fig. 19)

The rictalis is readily distinguishable and almost fully separated from the remainder of the segmentum facialis, with the rictalis continuous with the malaris and stegalis only along its anterodorsal portion. Fibres of the rictalis are arranged into several distinguishable bundles. The entire rictalis section arises from the quadrate, preopercle, and hyomandibula and inserts primarily on the coronoid process formed by the dentary and angulo-articular in addition to the buccopalatal membrane. An additional flat anterolateral tendon emerges from the rictalis immediately internal to the third infraorbital, and grades into a strong subcutaneous layer of connective tissue.

The malaris and stegalis are largely continuous with each other at their common origin from the metapterygoid, hyomandibula, frontal, sphenotic, and parasphenoid, with this origin situated medial to the levator arcus palatini. Towards their insertion, the malaris and stegalis become more obviously differentiated from each other. The anterolateral fibres of the malaris insert onto a superficial anterodorsal aponeurosis of the rictalis, whereas most fibres of the malaris converge onto a strong mandibular tendon that inserts on the medial face of the coronoid processes of the dentary and angulo-articular. The stegalis inserts on the coronomeckelian via the meckelian tendon.

The ramus mandibularis trigeminus nerve could not be located in the examined specimen.

The segmentum mandibularis is absent.

Brachyhypopomus pinnicaudatus (Fig. 20)

Except for a limited intermingling of muscle fibres between the ventral portions of the rictalis and stegalis, all of the three primary facial sections are completely separated from each other. The rictalis originates

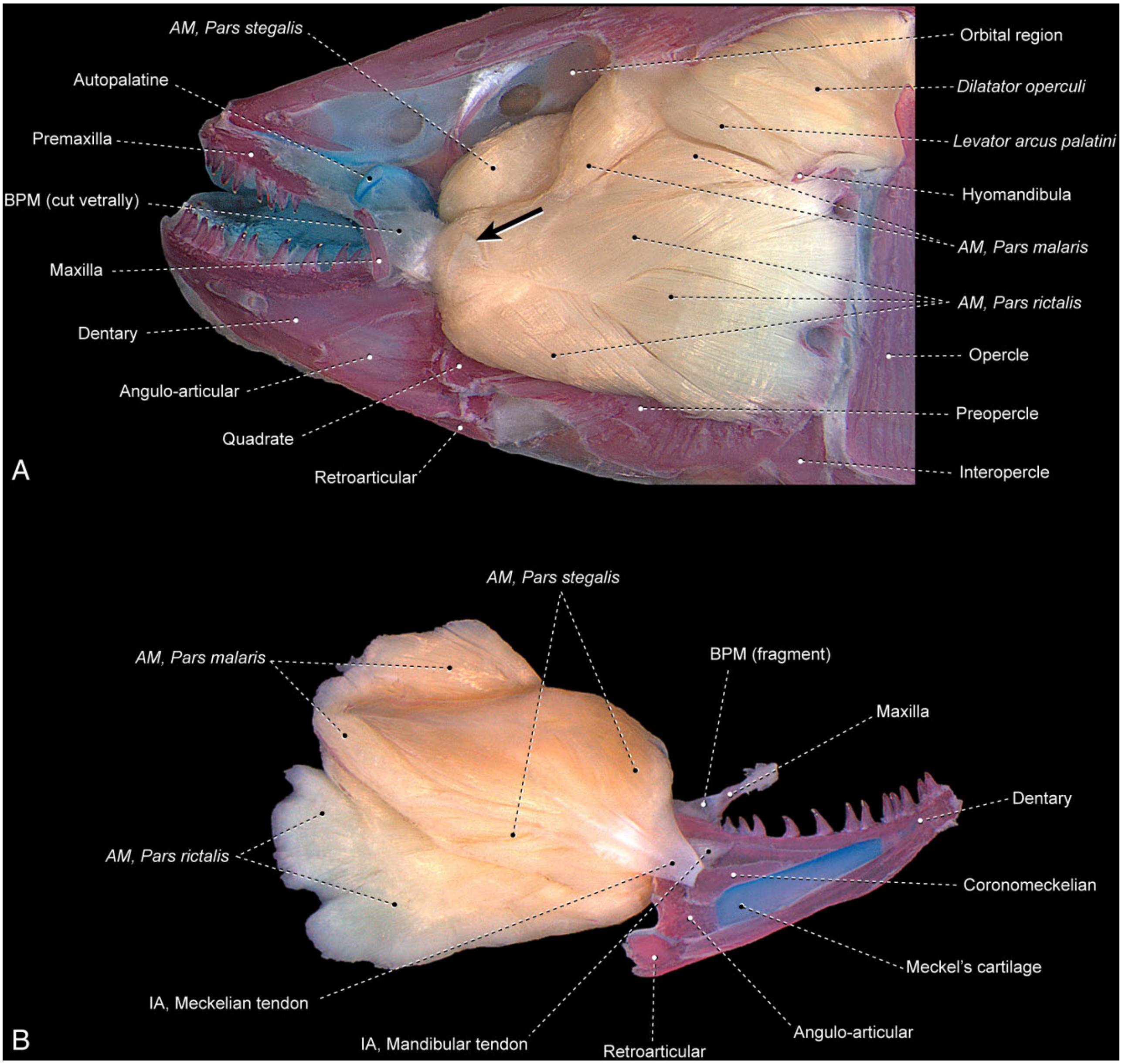


Figure 19. Adductor mandibulae and associated structures of *Gymnotus carapo* (Gymnotiformes: Gymnotidae), MZUSP 69391 (145.0 mm standard length). Left side in (A) lateral and (B) medial views. Arrow indicates tendon fragment leading to subcutaneous layer of connective tissue (cut). Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis.

from the quadrate and preopercle and inserts on the coronoid process of the dentary.

The malaris originates from the hyomandibula, with the posterodorsal portion of the section running between the lateral and the medial sections of the levator arcus palatini. The malaris inserts onto the buccopalatal membrane, primarily onto its anterodorsal portion that firmly attaches to the antorbital and maxilla. This membrane further has a well-differentiated preangular ligament, which anchors to the angulo-articular and also receives a few muscle fibres of the malaris.

The stegalis is the most massive of the facial sections with a broad origin from the quadrate, metapterygoid, hyomandibula, sphenotic, orbitosphenoid, and parasphenoid. This section converges anteriorly onto the intersegmental aponeurosis, which, in turn, subtly differentiates into a ventral portion that inserts on the coronomeckelian (thus, corresponding

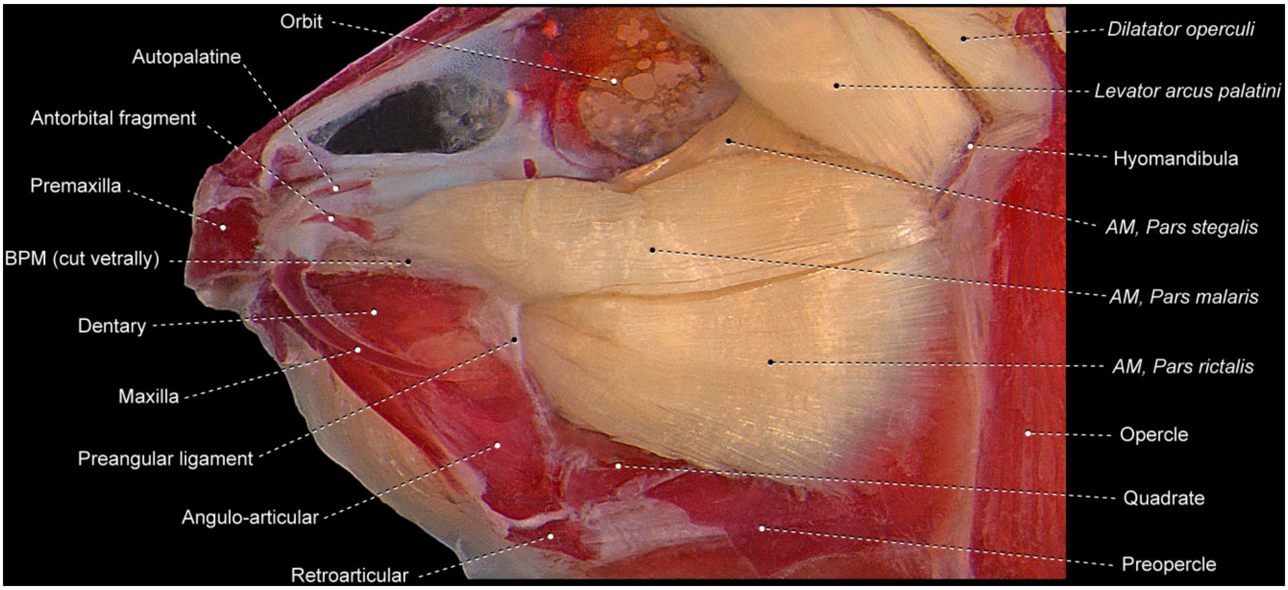


Figure 20. Adductor mandibulae and associated structures of *Brachyhypopomus pinnicaudatus* (Gymnotiformes: Hypopomidae), LIRP 6055 (133.3 mm standard length). Left side in lateral view. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane.

to the meckelian tendon) and a dorsal component that serves as the site of origin for the segmentum mandibularis (thereby corresponding to the mandibular tendon).

The ramus mandibularis trigeminus nerve traverses the segmentum facialis by passing internal to the rictalis and malaris and external to the stegalis.

The segmentum mandibularis is undifferentiated into subsections. It arises from the mandibular tendon and inserts on the medial surface of the dentary and angulo-articular.

Remarks

Aguilera (1986) studied the adductor mandibulae of representatives of all families in the Gymnotiformes. According to that author, the facial fibres of this muscle in the Gymnotidae (*Electrophorus* and *Gymnotus*) are arranged in a convoluted fashion and the segmentum facialis lacks obvious subdivisions. Examination of *Gymnotus carapo* confirms this characterization, although we were, nonetheless, able to confidently identify the three primary facial sections that remain partially differentiated from one another in this species (Fig. 19). The segmentum facialis in the Gymnotidae inserts on the lower jaw and buccopalatal membrane (Fig. 19; Aguilera, 1986). Gymnotids have the dorsolateral portion of the segmentum facialis (= malaris) arising not only from the suspensorium but also from the neurocranium (Fig. 19; Aguilera, 1986), an arrangement unique amongst the Gymnotiformes. The neurocranium further serves in most gymnotiforms as a site of origin of the dorsomedial portion of the segmentum facialis (= stegalis; Fig. 19; Aguilera, 1986).

In the Hypopomidae, Rhamphichthyidae, and Sternopygidae, the malaris is well separated from the remaining facial sections and inserts on the maxilla and/or lacrimal (Aguilera, 1986; Datovo & Vari, 2013). The rictalis and stegalis retain their insertions on the lower jaw with these sections better separated from each other in the Hypopomidae and Sternopygidae than in Rhamphichthyidae (Aguilera, 1986).

The segmentum facialis of the *Adontosternarchus* (Apteronotidae) is overall similar to that in the Hypopomidae and Sternopygidae (Aguilera, 1986), with the only notable difference being that the malaris inserts on both the maxilla and lower jaw in *Adontosternarchus* versus on the maxilla and/or lacrimal in those two families. Identification of the facial sections elsewhere in the Apteronotidae becomes more complicated because the muscle division(s) inserting onto the maxilla may occupy different positions (ventral, posterior, or both dorsal and ventral; cf. Aguilera, 1986; Marrero & Winemiller, 1993), consequently obfuscating a resolution of whether the differences across the family are a function of migration of sections or new attachments to the maxilla. These components of the Apteronotidae are, therefore, not included in our synonymy.

A curious feature of the adductor mandibulae of some gymnotiforms is the presence of filamentous intermuscular bones within the segmentum facialis. Such ossifications have been reported for the gymnotid *Gymnotus carapo*, the apteronotid *Orthosternarchus* *tamandua* and the rhamphichthyids *Iracema caiana*, *Rhamphichthys marmoratus*, and *Rhamphichthys rostratus* (Aguilera, 1986; Albert, 2001; Hilton *et al*., 2007; Carvalho & Albert, 2011). These structures probably represent ossifications of some internal tendons of the adductor mandibulae of these fishes. To our knowledge, such ossifications have not been reported elsewhere in the Teleostei.

Synonymy

Segmentum facialis

Complejo adductor mandibulae: Aguilera (1986): *Electrophorus*, *Gymnotus*.

Pars malaris

A_1: Aguilera (1986): *Adontosternarchus*, *Rhamphichthys*, *Steatogenys*, *Sternopygus*.

Pars rictalis

A_2: Aguilera (1986): *Adontosternarchus*, *Rhamphichthys*, *Steatogenys*, *Sternopygus*.

Pars ricto-stegalis

A_{2-3}: Aguilera (1986): *Rhamphichthys*.

Pars stegalis

A_3: Aguilera (1986): *Adontosternarchus*, *Rhamphichthys*, *Steatogenys*, *Sternopygus*.

Euteleosteomorpha

Protacanthopterygii

Argentiniformes

Argentinoidei

Description

Argentina striata (Fig. 21)

The segmentum facialis is undivided, but the stegalis can be discerned from a medial view by its shorter fibres that have a more anterodorsal origin relative to those of the ricto-malaris. The ricto-malaris arises from the quadrate, symplectic, hyomandibula, and preopercle whereas the stegalis has its origin on the metapterygoid and endopterygoid. Posteriorly, the intersegmental aponeurosis extends as an elongate, conspicuous suborbital tendon onto which most fibres of the segmentum facialis attach. Anteriorly, the intersegmental aponeurosis lacks an obvious subdivision into mandibular and meckelian tendons, but the anteroventral portion of the aponeurosis attaches to the coronomeckelian and, thus, corresponds to the meckelian tendon. The dorsal region of this aponeurosis serves as the site of origin for the medial fibres of the segmentum mandibularis and consequently corresponds to the mandibular tendon.

The ramus mandibularis trigeminus nerve enters into the segmentum facialis of the adductor mandibulae along the lateral face of the intersegmental aponeurosis.

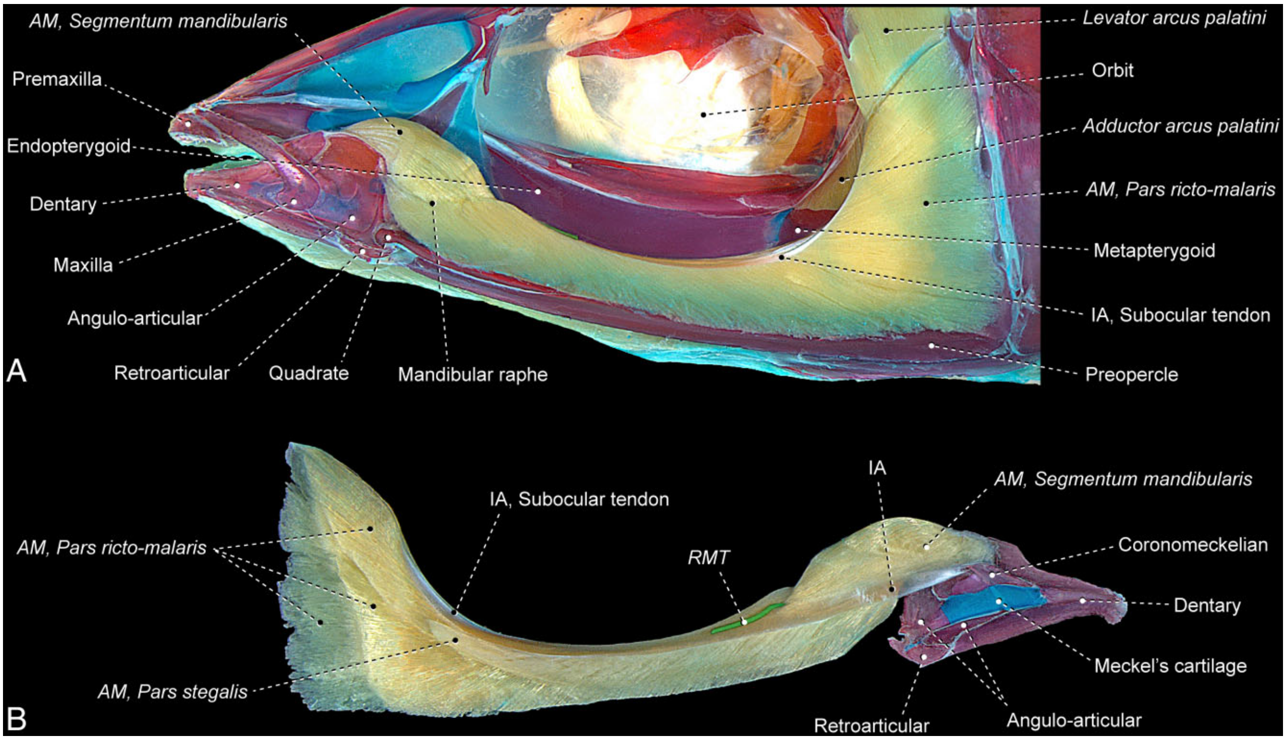


Figure 21. Adductor mandibulae and associated structures of *Argentina striata* (Argentiniformes: Argentinidae), MZUSP 17914 (130.8 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

The segmentum mandibularis is undivided and extends posteriorly for a significant distance, with the major portion of the segment situated beyond the posterior limit of the lower jaw. This segment arises along the anterodorsal part of the intersegmental aponeurosis and, more significantly, from the mandibular raphe that is shared with the anterior portion of the segmentum facialis. The segmentum mandibularis inserts on the medial surfaces of the angulo-articular and the coronoid process of the dentary.

Remarks

Except for a barely apparent differentiation of the origin of the stegalis, the segmentum facialis of *Argentina* is otherwise completely undivided (Fig. 21). This configuration is basically universal across the Argentinoidei (see Greenwood & Rosen, 1971; Williams, 1987; Sanford, 2000). Sites of origin and insertion and the relative position of the entire segmentum facialis of argentinoids correspond overall to a combination of the three, basic, primary facial sections of the Teleostei (i.e. malaris, rictalis, and stegalis). As in the case of many other basal teleostean lineages (Elopiformes, Hiodontiformes, and some taxa of the Clupeiformes; see above), it is more parsimonious to hypothesize that all of the three primary portions that compose the segmentum facialis in the Teleostei are present, albeit poorly differentiated from each other, in the Argentinoidei.

A notable common feature in all argentinoids examined in this study and for which the myology has been described, is the posterior extension of the segmentum mandibularis beyond the limits of the lower jaw, with a mandibular raphe connecting this muscle segment with the segmentum facialis (Fig. 21; Greenwood & Rosen, 1971; Williams, 1987; Sanford, 2000). This modification is more pronounced in the Opisthoproctidae (Williams, 1987). *Argentina sphyraena* and *Bathylagus pacificus* have the anterior portion of the adductor mandibulae associated with the retrojugal lamina (Williams, 1987; Sanford, 2000). The ramus mandibularis trigeminus nerve may pass either fully external to the segmentum facialis (*Argentina sphyraena*; Sanford, 2000: fig. 95), lateral to the segmentum mandibularis and then medial to the intersegmental aponeurosis (*Dolichopteryx*; Williams, 1987), or between these two structures (*Argentina striata* and *Argentina silus*; Fig. 21; Williams, 1987).

Synonymy

Segmentum facialis

Posterolateral fibres of AM: Williams (1987): *Dolichopteryx*, *Macropinna*, *Opisthoproctus*.

A2: Williams (1987): *Argentina*, *Bathylagus*; Sanford (2000): *Argentina*.

Segmentum mandibularis

Anterolateral fibres of AM: Williams (1987): *Dolichopteryx*, *Macropinna*, *Opisthoproctus*.

Aw: Williams (1987): *Argentina*, *Bathylagus*; Sanford (2000): *Argentina*.

ALEPOCEPHALOIDEI

Description

Talismania homoptera (not illustrated)

The segmentum facialis originates as a mostly undivided muscle mass from the symplectic, metapterygoid, hyomandibula, and preopercle. Shortly anterior of this common origin, the malaris separates from the remainder of the segmentum facialis to converge onto an ectomaxillar ligament. The anteroventral portion of the ectomaxillar ligament proceeds anteriorly to attach to the anterolateral surfaces of the maxilla and the anterior supramaxilla. The anterodorsal fibres of this ligament gradually disperse into the body of the retrojugal lamina.

The rictalis and stegalis are separated from each other only along their posteroventral portions. These two sections are fully continuous with one another along most of their expanse, thus forming a compound ricto-stegalis. This compound section inserts onto the coronoid region of the buccopalatal membrane and the laterally flattened intersegmental aponeurosis. This aponeurosis divides anteriorly into a meckelian tendon that attaches to the coronomeckelian and a mandibular tendon that serves as the origin for the segmentum mandibularis.

The ramus mandibularis trigeminus nerve passes lateral to the entire segmentum facialis.

The segmentum mandibularis arises from the mandibular tendon and inserts along the dorsal margin of Meckel's cartilage and the medial surfaces of the angulo-articular and dentary. No differentiation into sections is observable within the segmentum mandibularis.

Xenodermichthys copei (Fig. 22)

The segmentum facialis has a restricted origin on the symplectic, hyomandibula, and preopercle and does not demonstrate any division along its entirety. The medial-most fibres of the segmentum facialis, which correspond to the stegalis, converge onto a meckelian tendon that attaches to the coronomeckelian. The posterodorsal portion of the mandibular tendon is continuous with a transverse ligament that, in turn, is continuous with an ectomaxillar ligament. The lateral fibres of the segmentum facialis, presumably corresponding to the ricto-malaris, insert along these three continuous tendinous structures (mandibular tendon, transverse ligament, and ectomaxillar ligament). The anterodorsal portion of the ectomaxillar ligament spreads

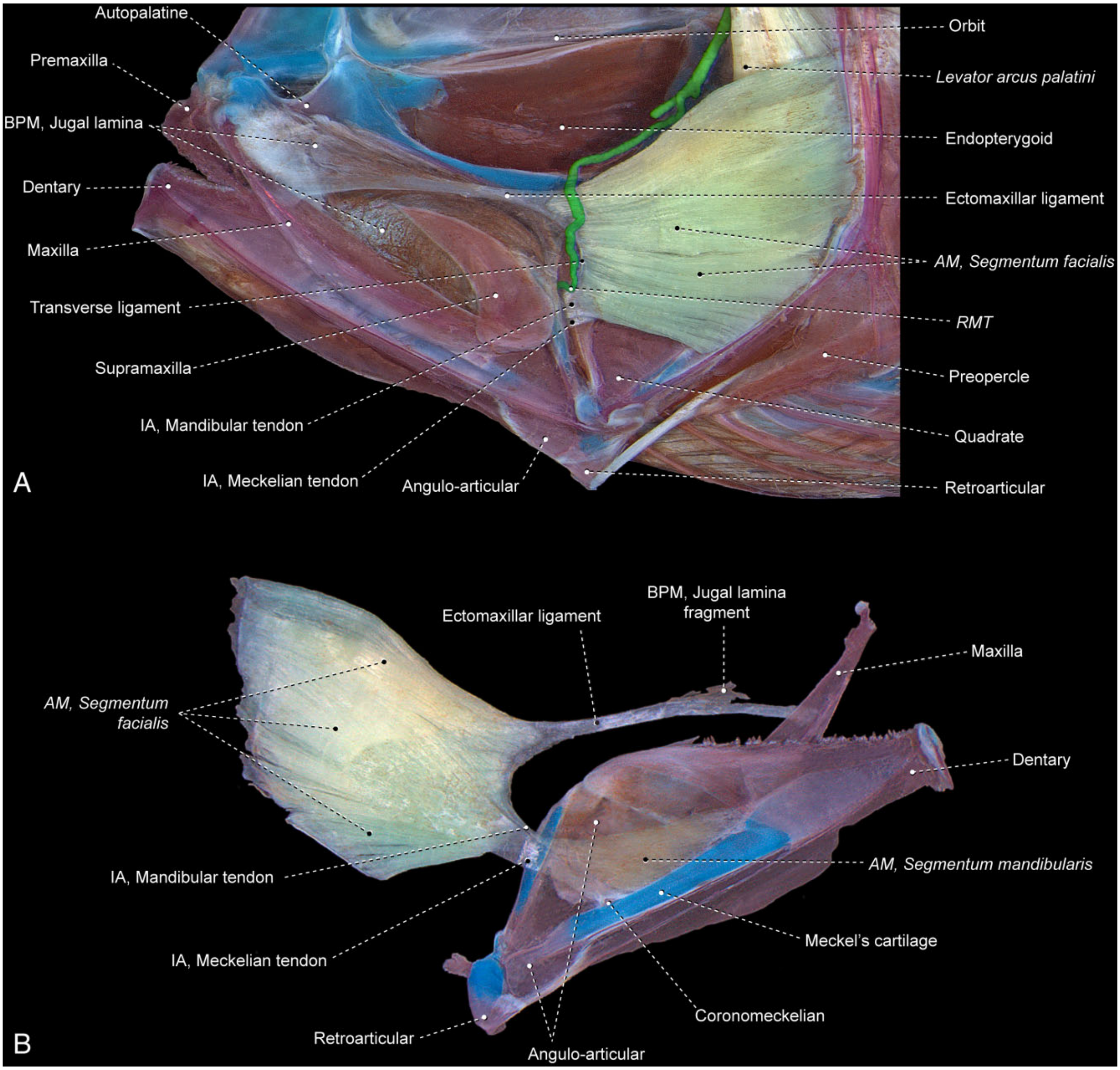


Figure 22. Adductor mandibulae and associated structures of *Xenodermichthys copei* (Argentiniformes: Alepocephalidae), MZUSP 86570 (88.3 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

out into the body of the retrojugal lamina, whereas the anteroventral portion of the ligament continues as a distinct ligament that attaches to the anterolateral surface of the maxilla.

The ramus mandibularis trigeminus nerve passes lateral to the segmentum facialis.

No subunits of the segmentum mandibularis can be discerned. This segment arises from the mandibular tendon and inserts on the angulo-articular and Meckel's cartilage.

Remarks

All alepocephaloids examined in this study and reported in the literature have the anterolateral region of the segmentum facialis associated with the ectomaxillar ligament, which, in turn, inserts on the anterolateral aspects of the maxilla (Fig. 22; Markle, 1980; Markle & Merret, 1980; Markle & Krefft, 1985; Williams, 1987; Patterson & Rosen, 1989; Miya & Markle, 1993; Diogo, 2008a, b; Diogo *et al.*, 2008a). Many other groups in the Alepocephaloidei have an undivided segmentum mandibularis similar with that of *Xenodermichthys* (Fig. 22; A2 of Markle, 1980; Markle & Merret, 1980; Markle & Krefft, 1985; Miya & Markle, 1993; Diogo, 2008a, b; Diogo *et al*., 2008a). Nevertheless, as in the case in the examined specimens of *Talismania homoptera*, other alepocephaloids have the portion of muscle that is directly associated with the ectomaxillar ligament partially, or fully, separated from the remainder of the segmentum mandibularis (= A1 of Markle & Merret, 1980; Williams, 1987). Some species of *Bathylaco* and *Talismania* have what Markle & Merret (1980) and Williams (1987) termed an A1 situated in the middle of the anteroventral expanse of the segmentum facialis, resulting in uncertainty as to whether this muscle section corresponds to the rictalis or malaris. However, this section occupies the dorsolateral portion of the segmentum facialis amongst most alepocephaloids with a separate A1 (present study; Williams, 1987) and clearly corresponds to the malaris, whereas the remaining facial section is equivalent to the ricto-stegalis. The term A2 of prior studies with alepocephaloids was, thus, applied to either the segmentum facialis or the ricto-stegalis, depending on whether a separate malaris (= A1) can be distinguished.

At least some species of *Leptoderma*, *Bajacalifornia*, *Rinoctes*, and *Conocara* have the segmentum mandibularis extending slightly beyond the posterodorsal limits of the lower jaw (A. Datovo pers. observ.; Williams, 1987: fig. 80).

Synonymy

Segmentum facialis

A2: Diogo (2008a): *Alepocephalus*; Diogo (2008b): *Alepocephalus*; Diogo *et al*. (2008a): *Alepocephalus*; Markle (1980): *Asquamiceps*; Markle & Krefft (1985): *Bajacalifornia*; Markle & Merret (1980): *Rinoctes*; Miya & Markle (1993): *Bajacalifornia*; Williams (1987): *Alepocephalus*, *Bajacalifornia*, *Bathytroctes*, *Conocara*, *Leptoderma*, *Mirorictus*, *Narcetes*, *Pellisolus* [= *Mentodus*], *Photostylus*, *Rouleina*, *Xenodermichthys*.

Pars malaris

A1: Markle & Merret (1980): *Leptochilichthys*, *Talismania*; Williams (1987): *Bathylaco*, *Binghamichthys aphos* [= *Talismania aphos*], *Holtbyrnia*, *Platytroctes*, *Sagamichthys*, *Searsia*, *Searsioides*, *Talismania*.

Pars ricto-stegalis

A2: Markle & Merret (1980): *Leptochilichthys*, *Talismania*; Williams (1987): *Bathylaco*, *Binghamichthys aphos* [= *Talismania aphos*], *Holtbyrnia*, *Platytroctes*, *Sagamichthys*, *Searsia*, *Searsioides*, *Talismania*.

Segmentum mandibularis

Aω: Diogo (2008a): *Alepocephalus*.

Aw: Diogo *et al*. (2008a): *Alepocephalus*; Williams (1987): *Alepocephalus*, *Bajacalifornia*, *Bathylaco*, *Bathytroctes*, *Binghamichthys aphos* [= *Talismania aphos*], *Conocara*, *Holtbyrnia*, *Leptoderma*, *Mirorictus*, *Narcetes*, *Pellisolus* [= *Mentodus*], *Photostylus*, *Platytroctes*, *Rouleina*, *Sagamichthys*, *Searsia*, *Searsioides*, *Talismania*, *Xenodermichthys*.

AW: Diogo (2008b): *Alepocephalus*; Markle (1980): *Asquamiceps*; Markle & Merret (1980): *Rinoctes*; Miya & Markle (1993): *Bajacalifornia*.

SALMONIFORMES

ESOCOIDEI

Description

Umbra pygmaea (Fig. 23)

The segmentum facialis arises from the preopercle, symplectic, and metapterygoid. This segment is mostly undivided along its extent, albeit with the three typical primary facial sections of the Teleostei still discernible, thereby indicating an incipient degree of differentiation amongst them. The stegalis is anteroventrally more obviously distinguishable because of its shorter muscle fibres that arise from the metapterygoid and insert on the intersegmental aponeurosis. This aponeurosis is divided anteriorly into a meckelian tendon that inserts on the coronomeckelian, and a mandibular tendon, which serves as the site of origin of the segmentum mandibularis. The lateral-most fibres of the segmentum facialis are superficially arranged into two bundles anteriorly. The dorsal bundle presumably corresponds to the malaris and the ventral bundle to the rictalis. These two external bundles converge anteriorly to a tendon that continues forward to its insertion on the lateral surfaces of the dentary and angulo-articular. The medial-most fibres of the ricto-malaris retain an attachment on the intersegmental aponeurosis in conjunction with the fibres of the stegalis. The retrojugal lamina has a well-differentiated ligament running from the coronoid process of the lower jaw to the anteromedial region of the maxilla, but no muscle fibres of the adductor mandibulae are associated with this ligament. This ligament apparently does not correspond to any of the ligaments most commonly running within the buccopalatal membrane across the Teleostei (see Datovo & Vari, 2013) and is herein termed the precoronoid ligament.

The segmentum mandibularis is completely divided into a coronalis and a mentalis. Posteriorly, the coronalis extends beyond the limits of the lower jaw to arise from the dorsal margin of the intersegmental aponeurosis and from a mandibular raphe that is shared with the inner fibres of the ricto-malaris. Anteriorly, the coronalis inserts on the posterodorsal portion of the dentary. The

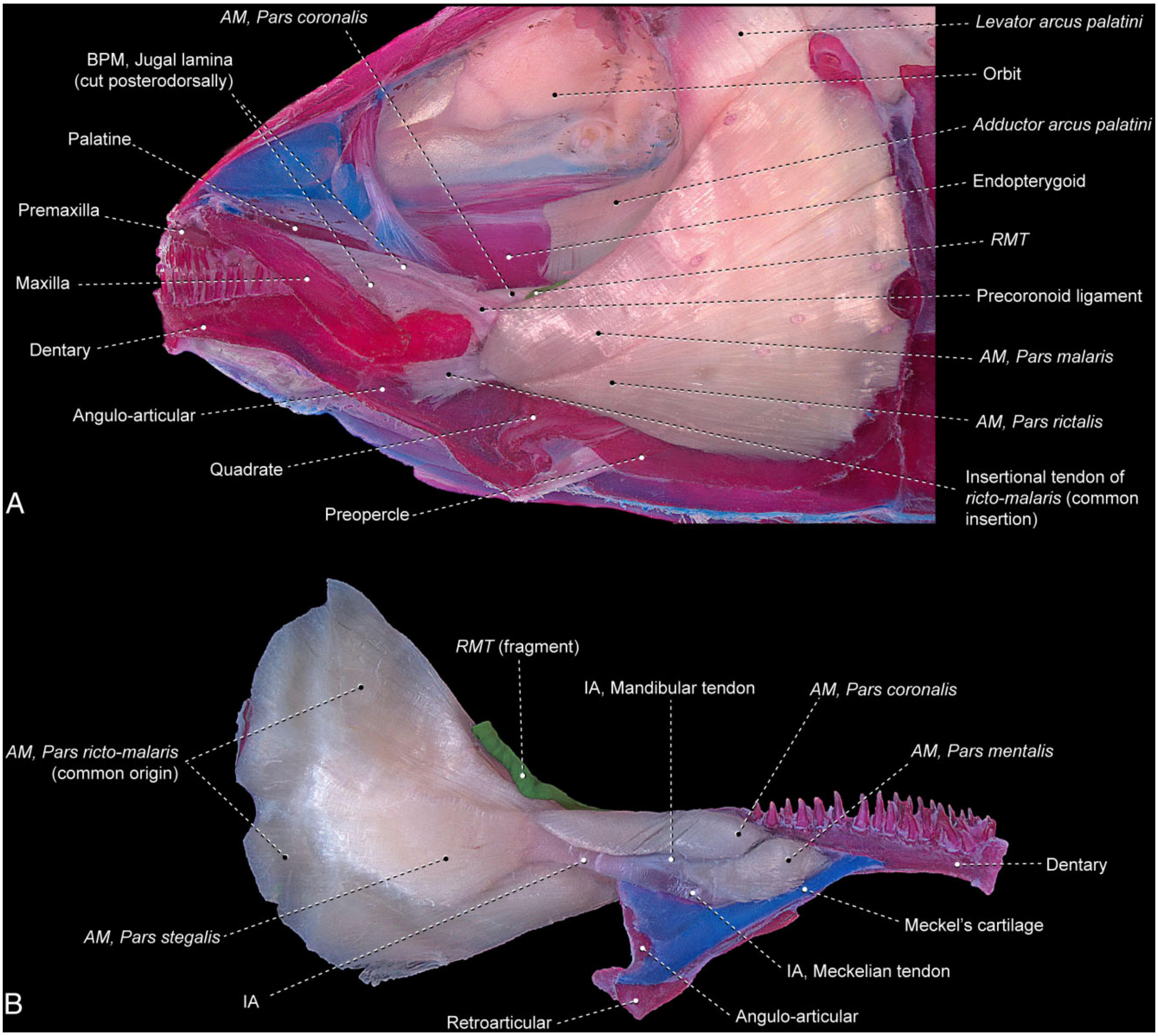


Figure 23. Adductor mandibulae and associated structures of *Umbra pygmaea* (Salmoniformes: Esocoidei: Umbridae), USNM 333152 (58.5 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

mentalis originates from the mandibular and meckelian tendons and inserts onto the angulo-articular and dentary.

The ramus mandibularis trigeminus nerve passes between the ricto-malaris laterally and the posterior portion of the coronalis medially.

Esox americanus (Fig. 24)

The segmentum facialis is divided into completely separate ricto-malaris and stegalis sections. The ricto-malaris has an intricate architecture consisting of some differentiated, but not separated, bundles of muscle fibres. Notwithstanding this differentiation, none of these recognizable bundles seems to fully correspond to either the rictalis or the malaris. The combined ricto-malaris originates from the quadrate, symplectic, preopercle, and hyomandibula. An inner group of fibres from this section passes through an ovoid fenestra bordered by the preopercle and hyomandibula to attach to a prominent posterodorsal process of the hyomandibula that contacts the opercle. The ricto-malaris inserts medially on the mandibular tendon and laterally on the mandibular raphe. As in *Umbra*, a well-differentiated precoronoid ligament is present, but this tissue band does not serve as the attachment site for any muscle fibres.

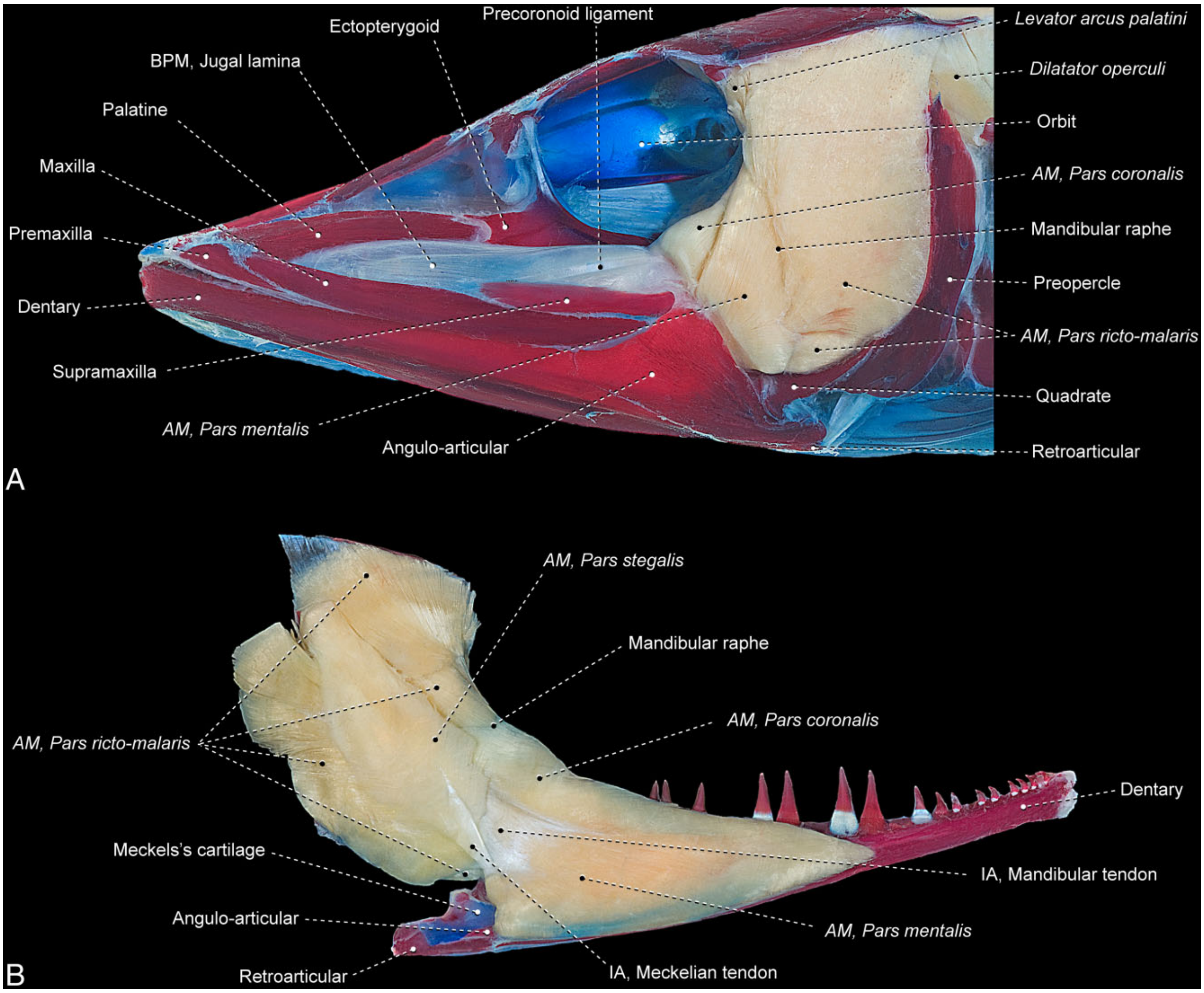


Figure 24. Adductor mandibulae and associated structures of *Esox americanus* (Salmoniformes: Esocoidei: Esocidae), USNM 237253 (158.1 mm standard length). Left side in (A) lateral and (B) medial views. Ramus mandibularis trigeminus nerve removed. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis.

The stegalis originates primarily from the metapterygoid, with a few fibres arising from the posterodorsal process of the hyomandibula and passing through the aforementioned fenestra delimited by the hyomandibula and preopercle. The section inserts on the coronomeckelian via the meckelian tendon.

The ramus mandibularis trigeminus nerve could not be observed in the examined material.

The segmentum mandibularis is a massive element distinctly subdivided posterolaterally into the coronalis and mentalis sections. Both sections originate from the broad mandibular raphe and the medial face of the mandibular tendon, with a few posteromedial fibres arising from the meckelian tendon. The lateral-most fibres of the mentalis insert along the posterodorsal margin of the coronoid process of the angulo-articular. Towards their insertions, the coronalis and mentalis become continuous with one another and insert jointly on the medial surfaces of the angulo-articular, dentary, and Meckel's cartilage.

Remarks

To facilitate the discussion, we follow the traditional classification under which the Esocoidei is divided into two families, the Esocidae and the Umbridae (Greenwood *et al.*, 1966; Nelson, 1972; Eschmeyer & Fong, 2013). Morphology of the adductor mandibulae is relatively consistent across the Umbridae. In all genera of this family the segmentum mandibularis extends beyond the posterodorsal margin of the lower jaw and the rictalis and malaris are differentiated from each other only along their anterolateral portions where they assume a bipinnate arrangement (Fig. 23; Williams, 1987, 1997). In most umbrids, the entire segmentum facialis converges to the intersegmental aponeurosis and lies internal to the ramus mandibularis trigeminus nerve. In *Umbra limi* and *Umbra pygmaea* the insertion of the ricto-malaris shifts laterally, with this section passing lateral to the ramus mandibularis trigeminus nerve and attaching tendinously to the lateral surface of the lower jaw (Fig. 23A; Williams, 1987, 1997). Williams (1987, 1997) suggested that in *Dallia*, the muscle section lying anteromedial to the main facial muscle mass (his A2.dm?) could correspond to a part of the segmentum mandibularis (his Aw) that expanded posteriorly to such an extent that it partially attaches to the suspensorium. Comparisons across the Esocoidei, which also has part of the segmentum facialis greatly expanded posteriorly (see Figs 23, 24), strongly support this assumption as the most parsimonious hypothesis of homology for this muscle division.

Multiple prior studies have discussed the adductor mandibulae of *Esox*, the sole extant genus of the Esocidae (Vetter, 1878; Adams, 1919; Takahasi, 1925; Eaton, 1935; Van Dobben, 1935; Winterbottom, 1974; Williams, 1987, 1997; Sanford, 2000). The morphology of this muscle is relatively similar across all reported species of *Esox*. Contrary to the morphology of umbrids, esocids have the ricto-malaris (the A2 of most previous authors) well separated from the stegalis (the A3 of most previous authors) and the ricto-malaris originates from both the suspensorium and the neurocranium. Adams (1919) adopted a less common terminology, but as his illustrations are derived from those of Vetter (1878), we can confidently infer the homologies of the muscle divisions discussed by Adams (see Synonymy). Most previous studies of several species of *Esox* reported a ricto-malaris not differentiated into subsections and these observations agree with the condition in the examined sample of *Esox americanus*. Williams (1987, 1997) and Winterbottom (1974), alternatively, reported a posterior partial separation between a presumed malaris arising from the neurocranium and a rictalis with an origin on the suspensorium in *Esox lucius* and *Esox americanus*, respectively.

The segmentum mandibularis in esocids is posteriorly expanded to such an extent that some authors misidentified some of its parts as being components of the segmentum facialis. As Winterbottom (1974) concluded and we concur, the sections in *Esox* termed the $A_3\beta$ by Vetter (1878) and $A_1\beta$ by Takahasi (1925) actually correspond to a dorsal division of Winterbottom's (1974) Aw (= segmentum mandibularis), i.e. the coronalis.

Synonymy

Segmentum facialis

A_2: Van Dobben (1935): *Esox*.

A2: Williams (1987): *Dallia*, *Novumbra*, *Umbra*; Williams (1997): *Dallia*, *Umbra*.

A_2A_3: Takahasi (1925): *Esox*.

A2A3: Winterbottom (1974): *Esox*, *Umbra*.

Pars ricto-malaris

A_1A_2: Eaton (1935): *Esox*, *Umbra*.

A_2: Takahasi (1925): *Esox*; Vetter (1878): *Esox*.

A2: Sanford (2000): *Esox*; Williams (1987): *Esox*; Williams (1997): *Esox*; Winterbottom (1974): *Esox*.

Adm^1: Adams (1919): *Esox*.

Pars rictalis

A2β: Williams (1987): *Esox*; Williams (1997): *Esox*; Winterbottom (1974): *Esox*.

Pars malaris

A2α: Williams (1987): *Esox*; Williams (1997): *Esox*; Winterbottom (1974): *Esox*.

Pars stegalis

A_3: Eaton (1935): *Esox*, *Umbra*; Takahasi (1925): *Esox*; Vetter (1878): *Esox*.

A3: Sanford (2000): *Esox*; Williams (1987): *Esox*; Williams (1997): *Esox*; Winterbottom (1974): *Esox*.

Adm^2 plus Adm^3: Adams (1919): *Esox*.

Segmentum mandibularis

A2.dm? [*sic*]: Williams (1987): *Dallia*; Williams (1997): *Dallia*.

Adm^4: Adams (1919): *Esox*.

Aw: Sanford (2000): *Esox*; Williams (1987): *Esox*, *Novumbra*, *Umbra*; Williams (1997): *Esox*, *Umbra*; Winterbottom (1974): *Esox*, *Umbra*.

Pars coronalis

$A_1\beta$: Takahasi (1925): *Esox*.

$A_3\beta$: Vetter (1878): *Esox*.

Pars mentalis

A_ω: Vetter (1878): *Esox*.

OSMEROIDEI

Description

Osmerus mordax (Fig. 25)

The segmentum facialis is mostly undivided along its anteroposterior expanse. Origin of the muscle segment is from the quadrate, symplectic, metapterygoid,

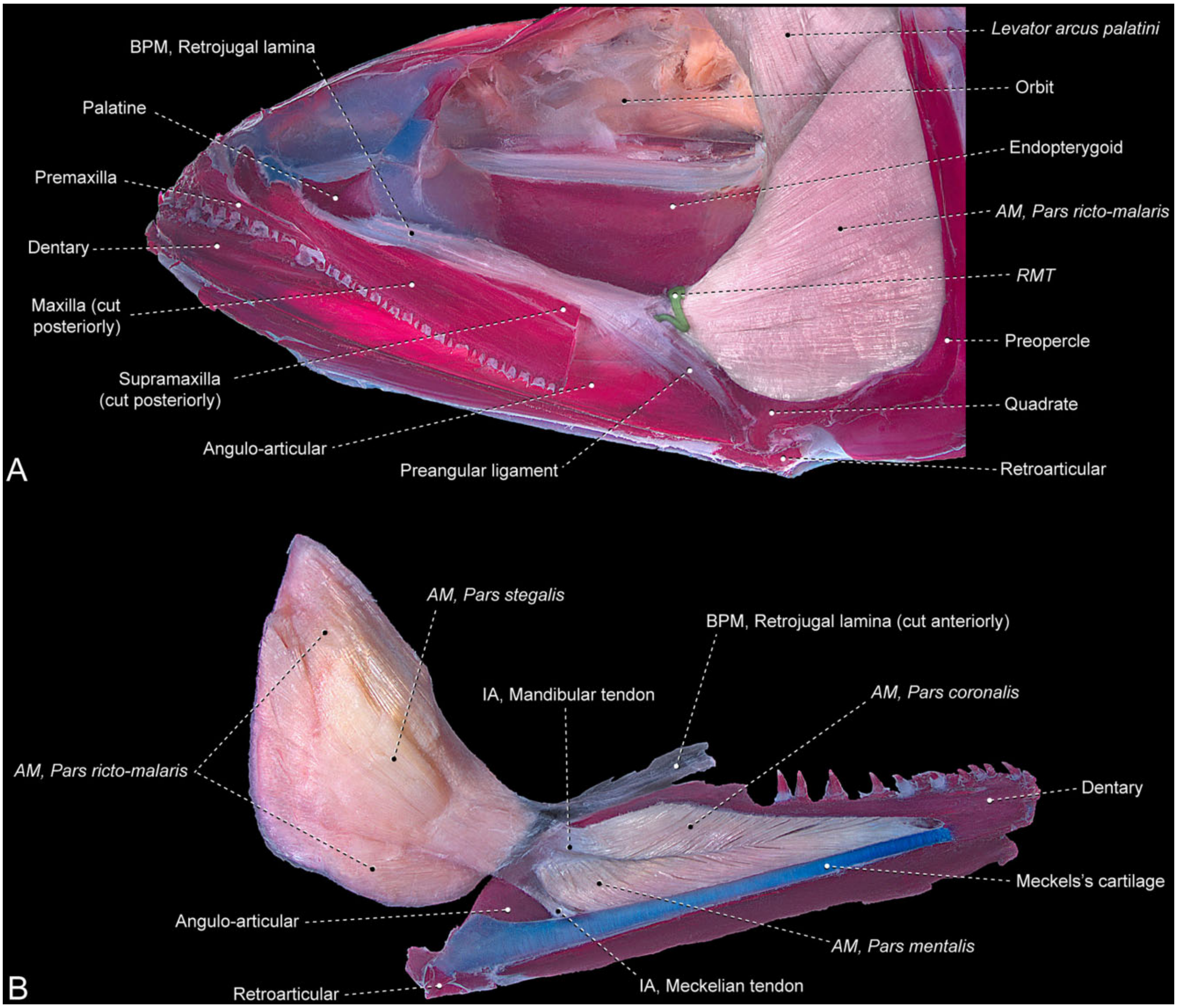


Figure 25. Adductor mandibulae and associated structures of *Osmerus mordax* (Salmoniformes: Osmeroidei: Osmeridae), USNM 395752 (119.5 mm standard length). Left side in (A) lateral and (B) medial views. Abbreviations: AM, adductor mandibulae; BPM, buccopalatal membrane; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

hyomandibula, and preopercle. The lateral-most set of fibres of the segmentum facialis corresponds to the ricto-malaris and inserts on the coronoid region of the retrojugal lamina and the dorsolateral region of the intersegmental aponeurosis. Ventrally, the retrojugal lamina is continuous with the intersegmental aponeurosis and has a partially differentiated preangulo-paramaxillar ligament. From a medial view, the stegalis can be distinguished by its more anterior site of origin on the metapterygoid, with only the dorsal portion of the section separated from the ricto-malaris. The stegalis converges primarily onto the ventral portion of the intersegmental aponeurosis, which, in turn, differentiates anteriorly into the meckelian tendon that inserts on the coronomeckelian.

The ramus mandibularis trigeminus nerve passes lateral to the entire segmentum facialis of the adductor mandibulae.

Only posteriorly is the segmentum mandibularis differentiable into a coronalis and a mentalis as a consequence of the anterior elongation of the mandibular tendon. The entire segmentum mandibularis arises from that tendon and inserts on the angulo-articular and dentary.

Hypomesus olidus (not illustrated)

The morphology of the adductor mandibulae in this species is almost identical to that of *Osmerus mordax*. The only noteworthy differences are that *Hypomesus olidus* has a less pronounced degree of differentiation of the stegalis from the ricto-malaris and of the coronalis from the mentalis.

Galaxias maculatus (not illustrated)

The ricto-malaris originates from the quadrate, symplectic, hyomandibula, and preopercle. As the section proceeds anteriorly, the rictalis and malaris gradually separate from each other only along their dorsolateral portions. The rictalis inserts onto the coronoid region of the retrojugal lamina. The anterolateral fibres of the malaris insert on the retrojugal lamina, whereas the posteromedial fibres of this section converge to the intersegmental aponeurosis. This aponeurosis splits anteriorly into a ventral meckelian tendon that attaches to the coronomeckelian, and a dorsal mandibular tendon that serves as the site of origin for the segmentum mandibularis.

The stegalis is separated dorsally from the ricto-malaris, mainly via the levator arcus palatini that inserts between these sections. The stegalis arises from the metapterygoid and inserts on the intersegmental aponeurosis.

The ramus mandibularis trigeminus nerve passes between the intersegmental aponeurosis and the malaris.

The segmentum mandibularis is posteriorly bipinnate, with the dorsal and ventral components of the segment corresponding to the coronalis and mentalis, respectively. Anteriorly these sections are no longer distinguishable from each other and the entire segmentum mandibularis inserts on the angulo-articular, dentary, and Meckel's cartilage.

Remarks

Many osmeroids have the morphology of the adductor mandibulae similar in most aspects to that of *Osmerus mordax* and *Hypomesus olidus* (Fig. 25; Eaton, 1935; Williams, 1987, 1997; Sanford, 2000; Wu & Shen, 2004). Apparently all osmeroids, with the exception of *Salanx prognathus*, have a ricto-malaris connected with the retrojugal lamina, including its variably discernible embedded ligaments (Fig. 25; Eaton, 1935; Williams, 1987, 1997). In the Galaxiidae, the stegalis is more prominently separated from the ricto-malaris (present study; Williams, 1987, 1997; Sanford, 2000). At least in the material of *Galaxias maculatus* that we examined, the rictalis is partially separated from the malaris and inserts on the posterolateral portion of the retrojugal lamina. A partial separation between rictalis and malaris was not reported by Williams (1987, 1997) for this same species, although all the remaining details of the muscle discussed in that study are congruent with those observed in our material.

The ramus mandibularis trigeminus nerve may pass either external to the segmentum facialis or between this segment and the intersegmental aponeurosis (Fig. 25; Williams, 1987, 1997).

The segmentum mandibularis is present in most osmeroids, but has been reported as absent in *Lepidogalaxias* and *Plecoglossus* (Williams, 1997; Wu & Shen, 2004).

Williams (1987) described and illustrated the adductor mandibulae of *Plecoglossus altivelis* as being divided into four readily discernible facial sections. Conversely, the same species was described (but not illustrated) as having only two facial sections by Wu & Shen (2004). Given the conflicting information in these accounts, *Plecoglossus altivelis* was not included in the following synonymy.

Synonymy

Segmentum facialis

A2: Williams (1997): *Hypomesus*, *Prototroctes*, *Retropinna*; Williams (1987): *Allosmerus*, *Hypomesus*, *Lovettia*, *Mallotus*, *Osmerus*, *Prototroctes*, *Retropinna*, *Salangichthys*, *Salangichthys ishikawae* (= *Neosalangichthys ishikawae*), *Salanx*, *Spirinchus*.

Pars ricto-malaris

A_1A_2: Eaton (1935): *Osmerus*.

A2: Williams (1987): *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lepidogalaxias*, *Neochanna*; Williams (1997): *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lepidogalaxias*, *Neochanna*.

A2a: Sanford (2000): *Galaxias*.

Pars stegalis

A2.dm or dorsomedial division of A2: Williams (1987): *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lepidogalaxias*, *Neochanna*; Williams (1997): *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Lepidogalaxias*, *Neochanna*.

A2b: Sanford (2000): *Galaxias*.

A_3: Eaton (1935): *Osmerus*.

Segmentum mandibularis

Aw: Sanford (2000): *Galaxias*; Williams (1987): *Allosmerus*, *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Hypomesus*, *Lovettia*, *Mallotus*, *Neochanna*, *Osmerus*, *Prototroctes*, *Retropinna*, *Salangichthys*, *Salangichthys ishikawae* (= *Neosalangichthys ishikawae*), *Salanx*, *Spirinchus*; Williams (1997): *Aplochiton*, *Brachygalaxias*, *Galaxias*, *Hypomesus*, *Neochanna*, *Prototroctes*, *Retropinna*.

SALMONOIDEI

Description

Oncorhynchus mykiss (Fig. 26)

The rictalis and malaris are continuous with each other at their origins, which involve the quadrate, symplectic, preopercle, and hyomandibula. As the muscle continues anteriorly, the rictalis and malaris become differentiated along their lateral surfaces. Both of these sections insert on the mandibular tendon, which is much shorter medially and becomes laterally continuous with a mandibular raphe shared with the segmentum mandibularis.

The stegalis is partially differentiated into an epistegalis and a substegalis. The latter muscle section is largely continuous with the ricto-malaris but is distinguished, albeit only to a slight degree, at its origin by its shorter fibres that arise from the metapterygoid. The substegalis converges onto the ventral portion of the intersegmental aponeurosis formed jointly by the meckelian and accessory tendons. These tendons are only partially separated from each other and both attach ventrally to the coronomeckelian. The epistegalis originates from the metapterygoid and hyomandibula and is separated dorsally from the ricto-malaris. Insertion of the epistegalis

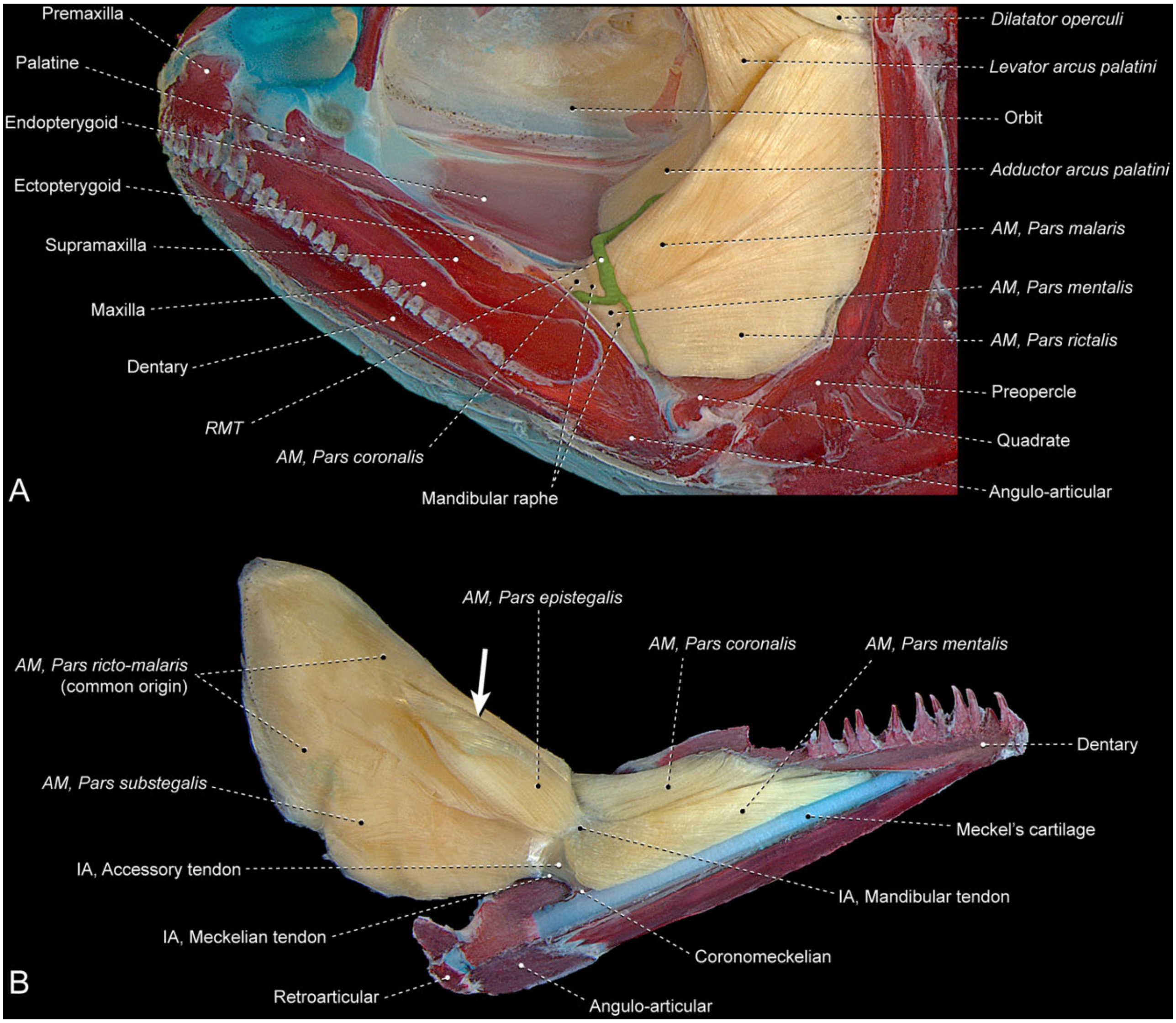


Figure 26. Adductor mandibulae and associated structures of *Oncorhynchus mykiss* (Salmoniformes: Salmonoidei: Salmonidae), MZUSP 85378 (106.4 mm standard length). Left side in (A) lateral and (B) medial views. Arrow indicates dorsal separation between the epistegalis and ricto-malaris. Anterodorsal tip of the dentary in B accidentally cut during dissection. Abbreviations: AM, adductor mandibulae; IA, intersegmental aponeurosis; RMT, ramus mandibularis trigeminus nerve.

is onto the medial regions of the much shortened mandibular tendon.

The segmentum mandibularis is posteriorly differentiated into a coronalis and a mentalis. The coronalis originates from the lateral surface of the mandibular tendon and the dorsal portion of the mandibular raphe, both of which serve as insertion sites for the malaris. The mentalis, in turn, arises from the ventral portion of the mandibular raphe and the medial surface of the mandibular tendon, which serve as insertion sites for the epistegalis and rictalis. Towards their insertions, the coronalis and mentalis become continuous with each other and attach jointly on the dentary, anguloarticular, and Meckel's cartilage.

The ramus mandibularis trigeminus nerve runs along the lateral face of the segmentum mandibularis and then traverses the segmentum mandibularis between the coronalis and the mentalis.

Remarks

Both the segmenta facialis and mandibularis of salmonoids were previously reported as largely undivided (Greene & Greene, 1913; Edgeworth, 1935; Van Dobben, 1935; Lauder & Liem, 1980; Williams, 1987; Sanford, 2000; Wu & Shen, 2004). Although these segments in *Oncorhynchus mykiss* indeed mostly lack subdivisions, all of the primary facial sections typical of the Teleostei are readily recognizable in this species. That said, the degree of differentiation of the sections is often admittedly tenuous (Fig. 26). Incipient degrees of differentiation are also indirectly indicated in the literature information. Although Sanford (2000) reported that the segmentum facialis in all salmonoids lacks any medial division, the accompanying illustration (Sanford, 2000: fig. 92) shows a distinct medial set of fibres in *Salmo* that converges onto a tendon inserted on the coronomeckelian (= the meckelian tendon). This medial facial portion was labelled as the A2(M), which seems equivalent to the stegalis, and the lateral muscle portion as the A2(L), which apparently corresponds to the ricto-malaris. Sanford (2000) also recognized a lateral differentiation between the malaris and rictalis in *Stenodus* (his A2α and A2β sections, respectively), an arrangement similar to that in *Oncorhynchus mykiss* (Fig. 26A).

In most salmonoids the ricto-malaris is connected solely with the segmentum mandibularis via the mandibular tendon and raphe. However, in some taxa a few fibres of the ricto-malaris insert directly on the coronoid region of the lower jaw and/or the retrojugal lamina (Williams, 1987; Sanford, 2000).

Apparently all salmonoids have a medially much shortened mandibular tendon (Fig. 26B) that is transformed laterally into a mandibular raphe (Fig. 26A; Edgeworth, 1935; Lauder & Liem, 1980; Williams, 1987; Sanford, 2000; Wu & Shen, 2004). In most genera, the mandibular raphe and consequently the posterior portion of the segmentum mandibularis extend posterodorsal to the limits of the lower jaw (Williams, 1987; Sanford, 2000).

Synonymy

Segmentum facialis

A_2: Van Dobben (1935): *Salmo*.

A2: Sanford (2000): *Brachymystax*, *Coregonus*, *Hucho*, *Oncorhynchus*, *Prosopium*, *Salmo*, *Salvelinus*, *Stenodus*, *Thymallus*; Williams (1987): *Brachymystax*, *Coregonus*, *Oncorhynchus*, *Prosopium*, *Salmo*, *Salvelinus*, *Stenodus*, *Thymallus*.

A_2A_3: Lauder & Liem (1980): *Salvelinus*.

A2β: Wu & Shen (2004): *Oncorhynchus*.

Adductor mandibulae: Edgeworth (1935): *Salmo*.

Cephalic division: Greene & Greene (1913): *Oncorhynchus*.

Pars rictalis

[At least the lateral part of] A2β: Sanford (2000): *Stenodus*.

Pars malaris

[At least the lateral part of] A2α: Sanford (2000): *Stenodus*.

Pars ricto-malaris

A2(L): Sanford (2000): *Salmo*.

Pars stegalis

A2(M): Sanford (2000): *Salmo*.

Segmentum mandibularis

A_w: Lauder & Liem (1980): *Salvelinus*.

Aw: Sanford (2000): *Brachymystax*, *Coregonus*, *Hucho*, *Oncorhynchus*, *Prosopium*, *Salmo*, *Salvelinus*, *Stenodus*, *Thymallus*; Williams (1987): *Brachymystax*, *Coregonus*, *Oncorhynchus*, *Prosopium*, *Salmo*, *Salvelinus*, *Stenodus*, *Thymallus*; Wu & Shen (2004): *Oncorhynchus*.

Intramandibularis: Edgeworth (1935): *Salmo*.

Mandibular portion: Greene & Greene (1913): *Oncorhynchus*.

PHYLOGENETIC IMPLICATIONS

Implications of various identified specializations of the adductor mandibulae for hypotheses of relationships in lower teleostean fishes are detailed in the following section. Putative myological synapomorphies are preceded by a **bold** number in square brackets. These derived characters are optimized on the cladograms of two recent

Figure 27. Maximum parsimony optimization (accelerated transformation; ACCTRAN) of the identified derived characters of the adductor mandibulae muscle complex superimposed on cladograms of lower teleosts. Topologies based on (A) morphological classification of Wiley & Johnson (2010) and (B) molecular analysis of Near *et al*. (2012). Characters as numbered in the text. When the degree of homoplasies of the same character varies from A to B, the less homoplastic optimization is indicated in red and the most homoplastic optimization in blue; characters in green are equally homoplastic in both topologies. Some character transformations occurring below subordinal levels are not indicated (see Phylogenetic implications).

classifications of the Teleostei (Fig. 27), one based on morphological data (Wiley & Johnson, 2010) and the other based on molecular data (Near *et al*., 2012).

ALBULIFORMES AND NOTACANTHIFORMES

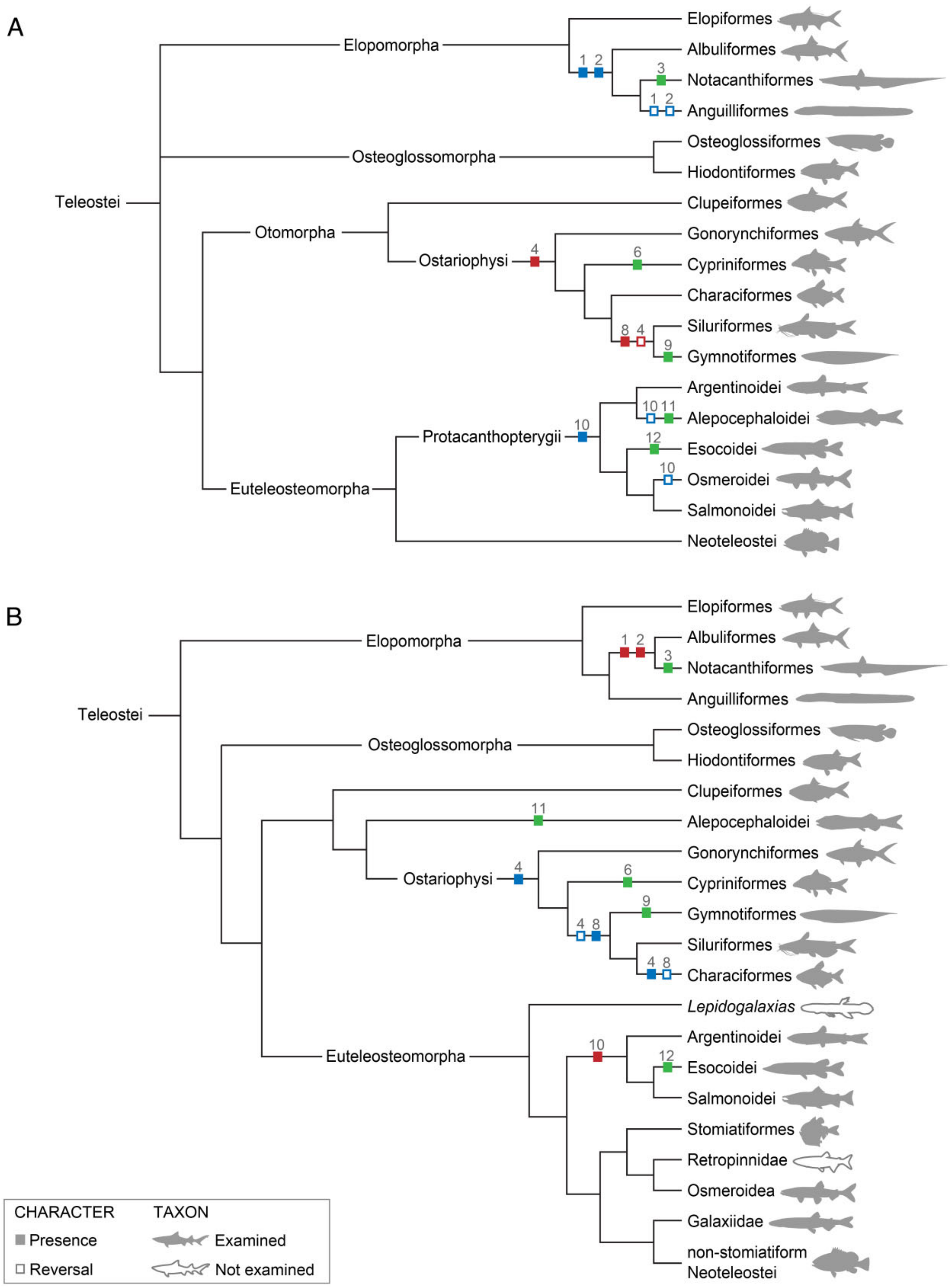
The morphological analyses of Forey (1973) and Forey *et al*. (1996) advanced a hypothesis that the Anguilliformes plus Notacanthiformes form a monophyletic group, which is, in turn, the sister clade to the Albuliformes (Fig. 27A). This scheme of relationships was also arrived at in the molecular studies of Betancur-R *et al*. (2013) and Tang & Fielitz (2012). The sister-group relationship between the Anguilliformes and Notacanthiformes of Forey *et al*. (1996) is supported by several morphological characters, many of them representing losses of character acquired at the base of more inclusive clades (Wiley & Johnson, 2010). This hypothesis of the Anguilliformes as the sister group of the Notacanthiformes, however, disagrees with the conclusions of the majority of morphological studies (Nelson, 1973; Greenwood, 1977; Patterson & Rosen, 1977) and some molecular analyses (Wang *et al*., 2002; Inoue *et al*., 2004; Johnson *et al*., 2011; Near *et al*., 2012) that alternatively propose a sister-group relationship between the Albuliformes and the Notacanthiformes (Fig. 27B). Data from the adductor mandibulae are more congruent with this latter hypothesis. Based on the examined material and data from the literature, most albuliforms and notacanthiforms share two notable derived features of the adductor mandibulae. The first **[1]** is the presence of a conspicuous, well-differentiated endomaxillar ligament connecting the promalaris with the maxilla (Figs 7, 8; Greenwood, 1977). This condition, which is unique to the Albuliformes and the Notacanthiformes amongst lower teleosts (Fig. 27), is paralleled elsewhere in the Teleostei only within the Neoteleostei. *Elops* also exhibits an endomaxillar tendon associated with the segmentum facialis, but the ligament in this genus disperses into the retrojugal lamina before reaching the maxilla. Furthermore, a promalaris cannot be differentiated from the remainder of the segmentum facialis in *Elops*. A second possible synapomorphy for the Albuliformes plus the Notacanthiformes is **[2]** the posterior expansion of the rear portion of the coronalis surpassing the limits of the lower jaw and becoming positioned dorsal to the region of insertion of the rictalis (Figs 7, 8; Greenwood, 1977). This condition is not found elsewhere in the Teleostei (Fig. 27), albeit not universal within both the Albuliformes and Notacanthiformes. Notacanthids lack a segmentum mandibularis and consequently cannot exhibit the noted derived condition. Within the Halosauridae, the posteriorly expanded coronalis is apparently absent in *Aldrovandia gracilis*, albeit present in all other genera of the family (Fig. 8; Greenwood, 1977). One major problem with the hypotheses that these two myological characters represent synapomorphies for the Albuliformes plus the Notacanthiformes is that according to the data in Greenwood (1977), both of these specializations are absent in the Pterothrissidae, an albuliform family that could not be examined in the present study. Characters 1 and 2 would, however, demonstrate a greater degree of homoplasy under the alternative hypothesis under which the Albuliformes is sister to the clade consisting of the Notacanthiformes plus Anguilliformes (Fig. 26A).

NOTACANTHIFORMES

Monophyly of the Notacanthiformes has been supported to date by relatively few characters (see Forey *et al*., 1996). At least one derived condition of the adductor mandibulae in the Notacanthiformes can be hypothesized to be a synapomorphy for the order: **[3]** the complete separation of the promalaris from the remaining muscle sections (Fig. 8B; Greenwood, 1977). Similar arrangements have been observed only in some phylogenetically distant groups within the Holacanthopterygii – specifically the Percopsiformes, Gadiformes, Ophidiiformes, and some Blenniiformes and Tetraodontiformes. All remaining examined teleosts have a promalaris that is either undifferentiated, or only partially separated (Figs 7B, 9A) from the adjoining muscle sections.

OSTARIOPHYSI

The Ostariophysi is one the largest groups within the Teleostei and encompasses almost 70% of all freshwater fishes across the world (Nelson, 2006). Amongst the large monophyletic groups within the Teleostei it is also amongst the best delimited in terms


A
Elopomorpha
Elopiformes
1 2
Albuliformes
3
Notacanthiformes
1 2
Anguilliformes
Osteoglossomorpha
Osteoglossiformes
Hiodontiformes
Teleostei
Clupeiformes
Otomorpha
Gonorynchiformes
4
Ostariophysi
6
Cypriniformes
Characiformes
Siluriformes
8 4
9
Gymnotiformes
Argentinoidei
10 11
Alepocephaloidei
Protacanthopterygii
10
12
Esocoidei
10
Osmeroidei
Euteleosteomorpha
Salmonoidei
Neoteleostei
B
Elopiformes
Elopomorpha
1 2
Albuliformes
3
Notacanthiformes
Teleostei
Anguilliformes
Osteoglossomorpha
Osteoglossiformes
Hiodontiformes
Clupeiformes
11
Alepocephaloidei
Gonorynchiformes
6
Ostariophysi
4
Cypriniformes
9
Gymnotiformes
4 8
Siluriformes
4 8
Characiformes
Lepidogalaxias
10
Argentinoidei
12
Esocoidei
Euteleosteomorpha
Salmonoidei
Stomiatiformes
Retropinnidae
Osmeroidea
Galaxiidae
non-stomiatiform Neoteleostei
CHARACTER
■ Presence
□ Reversal
TAXON
Examined
Not examined

of numbers of morphological synapomorphies (Rosen & Greenwood, 1970; Fink & Fink, 1981, 1996). Fink & Fink (1981) proposed the possession of a ventrolateral A1 section of the adductor mandibulae as a synapomorphy for the Ostariophysi, with a reversal to the absence of this muscle section in the Siluriformes. According to Fink & Fink (1981), the A1 section inserts on the maxilla in basal lineages in the Ostariophysi (gonorynchiforms, cypriniforms, and primitive characiforms), on what the authors termed the ligamentum primordium (= retrojugal lamina) in some characiforms, and on the lower jaw in gymnotiforms. On the basis of these descriptions, the term A1 apparently was applied by Fink & Fink (1981) to several different muscle sections: the rictalis in the case of the Gonorynchiformes (Fig. 14), Gymnotiformes (Fig. 19), and some lineages of the Characiformes (Datovo & Castro, 2012), and the ectorictalis in the case of the Cypriniformes (Figs 15, 16) and basal lineages in the Characiformes (Fig. 17). Furthermore, none of the facial sections of the adductor mandibulae can be considered to be actually absent in the Siluriformes (present study; Datovo & Vari, 2013).

Diogo & Chardon (2000a), following Gosline (1989), also considered the ventrolateral facial section of the adductor mandibulae in the Ostariophysi to be unique to that lineage in the Teleostei and designated this section as the A1-OST, which would also be present in the Siluriformes. However, as demonstrated in Datovo & Vari (2013) and detailed in the muscle synonymies for the Ostariophysi herein, the name A1-OST of Diogo & Chardon (2000a) was also ambiguously applied by those authors to different portions of the adductor mandibulae (rictalis and ectorictalis) in various taxa. Moreover, none of the muscle sections that correspond to the A1 of Fink & Fink (1981) or the A1-OST of Diogo & Chardon (2000a) is, in fact, exclusive to the Ostariophysi. Regardless of their degrees of separation from the adjoining muscle sections, both the rictalis and ectorictalis are present across all of the Teleostei.

All gonorynchiforms (Fig. 14; Howes, 1985a; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a; Diogo, 2008b), all cypriniforms (Figs 15, 16; Vetter, 1878; Takahasi, 1925; Edwards, 1926; Eaton, 1935; Van Dobben, 1935; Girgis, 1952; Munshi, 1960; Weisel, 1960; Alexander, 1966; Ballintijn *et al.*, 1972; Wu & Shen, 2004; Hernandez *et al.*, 2005; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a, b; Staab & Hernandez, 2010; Staab *et al.*, 2012), most basal characiforms (most distichodontids and anostomoids; Vari, 1979; Datovo & Castro, 2012), and the basal-most gymnotiforms (gymnotids; Fig. 19; Aguilera, 1986) have the entire rictalis or, at least, its ventrolateral portion (= ectorictalis) inserted onto the posterolateral face of the buccopalatal membrane. Although the ectorictalis of these groups has often been cited as inserting on the maxilla via a tendon, these insertional tendons are clearly derived from the buccopalatal membrane (present study; Datovo & Castro, 2012; Datovo & Vari, 2013). Even some siluriforms (e.g. *Heptapterus*; A. Datovo pers. observ.) and several derived characiforms (Winterbottom, 1974: 232; Datovo & Castro, 2012: 102) have a tenuous attachment of the rictalis to the buccopalatal membrane, with the connection possibly representing a remnant of the putative ancestral condition for ostariophysans. However, it remains unclear whether the association of at least the ventrolateral portion of the rictalis with the buccopalatal membrane can be considered a synapomorphy for the Ostariophysi or whether it would define a much more inclusive group in the Teleostei. An association of the rictalis with the buccopalatal membrane also characterizes various taxa more or less proximate to the Ostariophysi, such as the basal osteoglossomorph *Hiodon* (Fig. 10), some osmeroids, and, perhaps, also some argentinoids (present study; Williams, 1987, 1997; Sanford, 2000).

These issues aside, the Ostariophysi can apparently be defined by one synapomorphy involving the adductor mandibulae: **[4]** a rictalis differentiated into endorictalis and ectorictalis subsections (Fig. 27A). This condition is present across all of the Gonorynchiformes (Fig. 14; Howes, 1985a; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a; Diogo, 2008b) and Cypriniformes (Figs 15, 16; Vetter, 1878; Takahasi, 1925; Edwards, 1926; Eaton, 1935; Van Dobben, 1935; Girgis, 1952; Munshi, 1960; Weisel, 1960; Alexander, 1966; Ballintijn *et al.*, 1972; Wu & Shen, 2004; Hernandez *et al.*, 2005; Diogo & Doadrio, 2008; Diogo *et al.*, 2008a, b; Staab & Hernandez, 2010; Staab *et al.*, 2012), and basal groups in the Characiformes (most members of the Distichodontidae and Anostomoidea; Vari, 1979; Datovo & Castro, 2012). An undifferentiated rictalis is present as the primitive condition for the Teleostei, as well as in derived characiforms and all gymnotiforms and siluriforms. Amongst lower teleosts, only a few taxa in the Anguilliformes and Notacanthiformes (Elopomorpha) similarly have the ectorictalis and the endorictalis differentiated from one another, but within present concepts of higher-level relationships within the Teleostei, this condition in the Elopomorpha obviously evolved independently from that of the Ostariophysi. Therefore, under the traditional morphological hypothesis of relationships within the Ostariophysi (Fink & Fink, 1981, 1996), the differentiation of the rictalis into ectorictalis and endorictalis sections may be optimized as appearing at the base of the Ostariophysi, with a reversal at the base of the Siluriphysi (= Siluriformes + Gymnotiformes) and other secondary reversals occurring within the Characiformes (Fig. 27A). It is difficult to estimate the number of reversals of this character within the Characiformes as a consequence of the many uncertainties as to the internal phylogenetic relationships in the order (compare the topologies of Ortí & Meyer, 1997; Buckup, 1998; Calcagnotto, Schaefer & DeSalle, 2005; Mirande, 2009, 2010; Oliveira *et al*., 2011). By contrast, phylogenetic analyses based solely on molecular data proposed several alternative hypotheses of relationships amongst the Characiphysae; none of which recovered the monophyly of the Siluriphysi (Siluriformes plus Gymnotiformes; see Ortí & Meyer, 1997; Lavoué *et al*., 2005; Nakatani *et al*., 2011; Near *et al*., 2012; Betancur-R *et al*., 2013). Under such schemes of characiphysan relationships, a rictalis differentiated into the endorictalis and ectorictalis (character 4) would be highly homoplastic across the Ostariophysi and recovered as a synapomorphy for this subcohort only under accelerated transformation (ACCTRAN) optimization (Fig. 27B).

GONORYNCHIFORMES: GONORYNCHOIDEI AND KNERIOIDEI

Fink & Fink (1996) proposed **[5]** the absence of the segmentum mandibularis (= their A_ω) as a synapomorphy supporting the sister-group relationship between the Gonorynchoidei (Gonorynchidae) and Knerioidei (Kneriidae, Phractolaemidae). We confirm that this muscle is primitively present in the generalized members of all basal teleostean orders, including the basal gonorynchiform *Chanos* (Chanoidei). The validity of the character 5 is, thus, indirectly corroborated in the present study (note – this subordinal character not shown on Fig. 26).

CYPRINIFORMES

The Cypriniformes is a monophyletic order diagnosed by several skeletal synapomorphies (Fink & Fink, 1981; Conway *et al*., 2010; Conway, 2011). A first myological synapomorphy is herein proposed for the order: **[6]** the anterior portion of the body of the ectorictalis covering part of the lateral surface of the maxilla when the mouth is closed (Figs 15, 16; Vetter, 1878; Takahasi, 1925; Edwards, 1926; Eaton, 1935; Van Dobben, 1935; Girgis, 1952; Munshi, 1960; Weisel, 1960; Alexander, 1966; Ballintijn *et al*., 1972; Wu & Shen, 2004; Hernandez *et al*., 2005; Diogo & Doadrio, 2008; Diogo *et al*., 2008a, b; Staab & Hernandez, 2010; Staab *et al*., 2012). Such an arrangement was not encountered elsewhere in the Teleostei, other than for a few derived taxa in the Gobiiformes (A. Datovo pers. observ.; Takahasi, 1925: A1β; Van Tassell & Baldwin, 2004: A2 gamma). Given the huge phylogenetic distance between the Cypriniformes and these derived taxa in the Gobiiformes, this specialized condition of the ectorictalis in these groups is more parsimoniously interpreted as parallel acquisitions, with the condition in the Cypriniformes constituting a synapomorphy for the order (Fig. 27).

CHARACIFORMES: HEMIODONTIDAE AND PARODONTIDAE

The Hemiodontidae and Parodontidae are morphologically similar in diverse aspects (Roberts, 1974) and have been grouped together in the subfamily Hemiodontinae by some authors (Regan, 1911; Eigenmann, 1912; Géry, 1959). Roberts (1974) noted various features common to hemiodontids and parodontids, but noted that evidence of a close relationship between these families was 'inconclusive'. Langeani (1998) explicitly enumerated several derived features shared by the two families, but considered such shared similarities as parallelisms in light of the phylogenetic hypothesis proposed by Buckup (1998) under which the two families did not resolve as sister taxa. Amongst the more encompassing cladistic analyses of the Characiformes produced to date, only the molecular study of Calcagnotto *et al*. (2005) proposed the Hemiodontidae and Parodontidae as sister groups. At least one unequivocal and highly distinctive feature of the adductor mandibulae corroborates that hypothesis: **[7]** the entire rictalis inserting solely onto the maxilla (present study; Datovo & Castro, 2012; note – this subordinal character not shown on Fig. 27). This condition is not found elsewhere either within the Characiformes or amongst most other ostariophysans. Within the lower Teleostei, only gonorynchiforms also exhibit a rictalis inserting solely on the maxilla, but such an occurrence is most parsimoniously interpreted to be convergent with that of hemiodontids and parodontids in light of present concepts of relationships amongst ostariophysans.

SILURIPHYSI

A sister-group relationship between the Siluriformes and Gymnotiformes (= Siluriphysi *sensu* Fink & Fink, 1996) is strongly supported by nearly 40 derived morphological characters (Fink & Fink, 1981, 1996). Molecular phylogenies, by contrast, refute this arrangement and propose several alternative hypotheses of relationships amongst the Characiformes (which is often recovered as nonmonophyletic), Siluriformes, and Gymnotiformes (Ortí & Meyer, 1997; Lavoué *et al*., 2005; Nakatani *et al*., 2011; Near *et al*., 2012; Betancur-R *et al*., 2013). A derived character of the adductor mandibulae corroborates the longstanding hypothesis of a monophyletic Siluriphysi: **[8]** the origin of the malaris extending dorsally to an attachment onto the neurocranium (Fig. 27A). This condition is present in most siluriforms, including all members of the primitive families Diplomystidae and Cetopsidae (Fig. 18;

McMurrich, 1884; Juge, 1898; Takahasi, 1925; Eaton, 1948; Alexander, 1965; Howes, 1985b; Grande & Lundberg, 1988; Lundberg *et al*., 1991; de Pinna & Vari, 1995; Adriaens & Verraes, 1996; Cabuy *et al*., 1999; Herrel *et al*., 2002; Rodiles-Hernández *et al*., 2005; Devaere *et al*., 2001, 2006; Sarmento-Soares & Porto, 2006; de Pinna *et al*., 2007; Shibatta *et al*., 2007; Datovo & Bockmann, 2010), and at least in the Gymnotidae (Fig. 19A; Aguilera, 1986), the basal-most gymnotiform family according to the morphologically based phylogenetic analysis by Albert (2001). Members of other gymnotiform families reported by Aguilera (1986) may also have a malaris attached to the neurocranium, but as a consequence of remaining doubts as to the homologies of the facial sections in some gymnotiforms reported in that study, we defer from unequivocally proposing that such an attachment is more general across the order. In the plesiomorphic condition for the Teleostei, the malaris arises solely from the suspensorium. Elsewhere amongst lower teleosts, a malaris originating from the neurocranium is also present only in the Anguilliformes, Esocidae, and some derived taxa within the Characiformes, but such occurrences are more parsimoniously interpreted as convergent with the condition of the Siluriphysi given the overall evidence as to higher-level relationships within the Teleostei. Amongst molecular phylogenies that do not resolve the Siluriphysi as monophyletic, character 8 is optimized with more steps and may be recovered as a synapomorphy for the Characiphysae only under the ACCTRAN algorithm (Fig. 27B).

GYMNOTIFORMES

The Gymnotiformes, one of the morphologically most distinctive groups within the Teleostei, is characterized by the highest number of known synapomorphies amongst all the orders in that infraclass (Fink & Fink, 1981, 1996; Albert, 2001; Wiley & Johnson, 2010). At least one additional synapomorphy, and the first involving myology, can be added to that list: **[9]** the levator arcus palatini passing lateral to the malaris (Fig. 19; Aguilera, 1986; Marrero & Winemiller, 1993). In the vast majority of teleosts, the insertional portion of the levator arcus palatini conversely lies fully medial to the malaris. A levator arcus palatini lateral to the malaris was encountered elsewhere in the Teleostei solely in the Dactylopteriformes, Gadiformes, and Percopsiformes (A. Datovo pers. observ.; Eaton, 1935; Rosen & Patterson, 1969; Howes, 1988; Imamura, 2000; Endo, 2002). Notwithstanding these similarities, in light of the pronounced phylogenetic separation of these orders within the Acanthomorphata, these occurrences in those orders are most parsimoniously interpreted as convergences relative to the condition that characterizes the Gymnotiformes (Fig. 27).

PROTACANTHOPTERYGII

As defined by Wiley & Johnson (2010), the Protacanthopterygii is composed of the Argentiniformes (Argentinoidei and Alepocephaloidei) and Salmoniformes (Esocoidei, Osmeroidei and Salmonoidei). Nevertheless, most phylogenetic analyses of the Protacanthopterygii refuted its monophyly and, more problematically, arrived at highly divergent schemes of relationships for, and within, the group. Whereas some morphological analyses suggest that the Esocoidei (Fink & Weitzman, 1982; Sanford, 1990; Johnson & Patterson, 1996) or both the Esocoidei and Salmonoidei (Williams, 1987; Begle, 1992) should be excluded from the subcohort, all molecular analyses (e.g. Ishiguro, Miya & Nishida, 2003; Lavoué *et al*., 2005, 2007, 2008; Near *et al*., 2012; Betancur-R *et al*., 2013) and one morphological study (de Pinna & Di Dario, 2010) proposed the exclusion of the Alepocephaloidei, which was alternatively hypothesized to be more closely allied to the Otomorpha. Amongst the several different proposals involving the Protacanthopterygii, data from the adductor mandibulae are more congruent with the hypothesis of Near *et al*. (2012), which advances that the Argentinoidei, Esocoidei, and Salmonoidei form a monophyletic group.

Primitively in the Teleostei, the segmenta facialis and mandibularis are separated from each other by a gap in which the elongate intersegmental aponeurosis does not serve as an attachment area for any muscle fibres. In most protacanthopterygians, the anteroventral region of the lateral portion of the segmentum facialis, i.e. the ricto-malaris, instead contacts the posterodorsal limit of the segmentum mandibularis. In this morphological plan, a mandibular raphe that is medially continuous with the mandibular tendon interconnects the contact area between the ricto-malaris and the segmentum mandibularis. This condition characterizes all taxa of the Argentinoidei (Fig. 21; Greenwood & Rosen, 1971; Williams, 1987; Sanford, 2000), Esocoidei (Fig. 23; Winterbottom, 1974; Williams, 1987, 1997), and Salmonoidei (Fig. 26; Edgeworth, 1935; Lauder & Liem, 1980; Williams, 1987; Sanford, 2000; Wu & Shen, 2004). In the Teleostei outside of the Protacanthopterygii, similar conditions are present only in the nototheniiforms *Nototheniops* and *Gymnodraco* and the stromateriform *Peprilus* (A. Datovo pers. observ.; Iwami, 2004), all of which are within the Percomorphacea and, thus, phylogenetically distinctly distant from the Protacanthopterygii. A mandibular raphe is present in a few other groups of the Acanthomorphata, but in such instances the raphe never interconnects the ricto-malaris and segmentum mandibularis as it does in the Protacanthopterygii (e.g. in the Cyprinodontiformes, this raphe only connects the malaris with the coronalis; A. Datovo pers. observ.).

Therefore, **[10]** the possession of a mandibular raphe interconnecting the ricto-malaris and segmentum mandibularis can be optimized as a synapomorphy for the protacanthopterygian clade of Near *et al*. (2012) that is formed by the Argentinoidei, Esocoidei, and Salmonoidei (Fig. 27B). Under the traditional phylogenetic scheme of the Protacanthopterygii, this character would be optimized as a synapomorphy for this subcohort with one reversal in the Alepocephaloidei and another in the Osmeroidei (Fig. 27A).

ALEPOCEPHALOIDEI

The segmentum facialis of the Alepocephaloidei demonstrates a notable feature unique to this group within the lower Teleostei. All alepocephaloids have the anterolateral portion of the segmentum facialis, which may or may not be distinguishable as a separate malaris, converging onto an ectomaxillar ligament that attaches to the anterolateral region of the maxilla (Fig. 22; Markle, 1980; Markle & Merret, 1980; Markle & Krefft, 1985; Williams, 1987; Patterson & Rosen, 1989; Miya & Markle, 1993; Diogo, 2008a, b; Diogo *et al*., 2008a). This condition superficially resembles the configuration of the segmentum facialis in most of the Neoteleostei (see Datovo & Vari, 2013). In these neoteleosts, the malaris is, however, always associated with the endomaxillar ligament (rather than the ectomaxillar ligament) that attaches to the anteromedial region of the maxilla (Datovo & Vari, 2013: fig. 6). Alepocephaloids lack an endomaxillar ligament. Some taxa in the Stephanoberyciformes, Beryciformes, Zoarcoidei, and Scorpaenoidei also have an ectomaxillar ligament in addition to the endomaxillar ligament associated with the malaris. This condition markedly differs from that of the Alepocephaloidei in which only an endomaxillar ligament is present. Furthermore, those fishes are well nested within subgroups of the Acanthopterygii *sensu stricto* (Johnson & Patterson, 1993; Wiley & Johnson, 2010), a taxon so phylogenetically distant from the Alepocephaloidei that the connection between the malaris and the ectomaxillar ligament obviously arose independently in each of the groups. Therefore, this feature: **[11]** the association of the dorsolateral portion of the segmentum facialis (= malaris) solely with the ectomaxillar ligament unambiguously constitutes a synapomorphy for the Alepocephaloidei (Fig. 27).

ESOCOIDEI

Williams (1987) indicated that the Esocoidei is unique within the Protacanthopterygii in possessing a 'coronoid-maxilla ligament' running from the coronoid process of the lower jaw to the posteromedial aspects of the maxilla. This ligament is derived from the jugal lamina and clearly corresponds to the precoronoid ligament as defined in this paper (Figs 23, 24). We confirm the findings of Williams (1987) and conclude that this ligament is unique to the Esocoidei not only amongst the Protacanthopterygii but apparently also across all of the Teleostei. As a consequence, this feature: **[12]** the presence of a precoronoid ligament is hypothesized to be a synapomorphy for the Esocoidei (Fig. 27).

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