

A descriptive myology of *Corydoras aeneus* (Gill, 1858) (Siluriformes: Callichthyidae), with a brief discussion on adductor mandibulae homologies

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Abstract—Cranial and postcranial myology of adult *Corydoras aeneus* is described and results discussed in comparison to other ostariophysan, siluriform and/or loricarioid fishes. Further, a brief discussion on *m. adductor mandibulae* homologies is given providing arguments for the use of the terminology proposed by Diogo and Chardon (2000) in future studies dealing with the myology of Siluriformes. Doing this, we here identified an A_1 OST, A_2 , and A_3' section in *C. aeneus* and recognised the homology of the *m. retractor tentaculi* muscle with the A_3'' . Next to this, the opercular system is discussed, focussing on similarities in this system in both a callichthyid (*C. aeneus*) and loricariid (*Ancistrus* cf. *triradiatus*) representative. In both these families, the *m. dilatator operculi* is enlarged and the direction of the operculo-hyomandibular articulation has shifted. In addition, in both lineages, the *m. hyohyoidei abductor* has also shifted its orientation, acting as an adductor. These similarities seem to corroborate the 'decoupling hypothesis' by Schaefer and Lauder (1986) in which a decoupling of elements in primitive members of a lineage leads to a higher morphological diversity within that lineage combined with the possible acquisition of new functions.

Keywords: adductor mandibulae; Callichthyidae; decoupling hypothesis; morphology; myology.

INTRODUCTION

The genus *Corydoras* (Callichthyidae) is widespread in South America (Gosline, 1940; Nijssen, 1970; Kramer and Braun, 1983) and well known among aquarists for its many ornamental species (Burgess and Quinn, 1992). *Corydoras aeneus* (Gill, 1858) is particularly a very popular species in the trade of freshwater ornamental fish. The species is annually bred and shipped in large quantities all over the world (Tamaru et al., 1997). In the past, *C. aeneus* has already been studied from both

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a morphological and physiological point of view (Kramer and McClure, 1980, 1981; Kramer and Braun, 1983; Huysseune and Sire, 1997) as is also the case for its reproductive biology (Kohda et al., 1995, 2002; Pruzsinszky and Ladich, 1998). However, despite it being commercially bred, the species' ontogeny is poorly known. Only some attention has been paid to the early ontogeny of some aspects of the head in other callichthyids (Hoedeman, 1960), but still a lot of relevant information is lacking. Recently, a descriptive study on the osteology of the species has been published (Huysentruyt and Adriaens, 2005), but a complete overview of the cranial and postcranial myology is still absent. This information, however, is quite relevant for ongoing phylogenetic research on Loricarioidea, to which these callichthyids belong (Reis, 1998; Britto and Castro, 2002; Britto, 2003). In his review, Britto (2003) already stated that the poor knowledge about the phylogenetic relationships among the genera of the Corydoradinae is largely due to the scarcity of data on internal anatomy. The review aims to counter this and provides 71 osteological characters, resolving a large part of this intergeneric phylogeny. However, no myological characters are included in his study. Reis (1998) also mentioned the importance and scarcity of anatomical data on the family level, but he also provided no myological data in his analysis. The lack of myological characters in these various phylogenetic analyses of this group is even more puzzling, considering the fact that Schaefer and Lauder in 1986 already found that, as a consequence of structural innovations in the jaw adductor complex in Loricarioidea, a lot of confusion exists about the homology of these different parts, and thus about their evolutionary history. In addition, Schaefer (1990) has also proposed the presence of a divided *m. adductor mandibulae* as a synapomorphy for the Callichthyidae. Finally, even recent molecular research on the family of the Callichthyidae pointed out that "further analyses of additional morphological data may be very helpful in the understanding of the phylogeny of the Callichthyidae" (Shimabukuro-Dias et al., 2004).

However, the various phylogenetic studies to date have managed to resolve the main phylogenetic affinities between the families of the loricarioids (Schaefer, 1990; Reis, 1998; Aquino and Schaefer, 2002), as well as the generic relationships within the callichthyids (Reis, 1997, 1998), but still little information exists on the phylogeny of the highly diverse genus *Corydoras*. Recently, the monophyletic nature of this genus, comprising approximately 140 species, has become uncertain, possibly partially overlapping the currently defined *Brochis* and *Aspidoras* genera (Reis, 1998; Britto, 2003). Consequently, the aim of this study is to provide a full description of the species' adult myology, as a basis for further ontogenetic research on this species, as well as to contribute to future phylogenetic studies.

MATERIALS AND METHODS

For this study we investigated five adult specimens of *Corydoras aeneus*, obtained from an aquarium shop. The specimens were sedated and killed using an overdose

of MS-222 (3-aminobenzoic acid ethyl ester, Sigma), fixed in a 4% formaldehyde solution and preserved in a 70% ethanol solution. These specimens were then investigated and drawn using an Olympus SZX-7 stereomicroscope. To allow a more detailed study of the different muscle bundles, ligaments and fibre directions, one *C. aeneus*-specimen was embedded in Technovit 7100 and 5 μm slices were made using a Reichert-Jung Polycut microtome. These slices were stained with toluidin blue staining. Additional to comparative microscopy, parts of these serial sections were also digitized and used for 3D reconstruction using Amira 3.1.1 software (TGS Europe, France).

RESULTS

For details on skeletal elements in *Corydoras aeneus*, we refer to Huysentruyt and Adriaens (2005). Muscle terminology follows Winterbottom (1974), except where indicated otherwise.

Jaw musculature (figs. 1-4)

The *musculus adductor mandibulae* complex in *Corydoras aeneus* consists of two different muscles, the A_2 and $A_1\text{OST}-A_3'$. The A_2 originates laterally on the hyomandibula, on a ridge near the suture with the metapterygoid and has its insertion on the *ligamentum primordium*. The $A_1\text{OST}-A_3'$ also originates on the hyomandibula, just below the A_2 , but the site of origin of this muscle expands

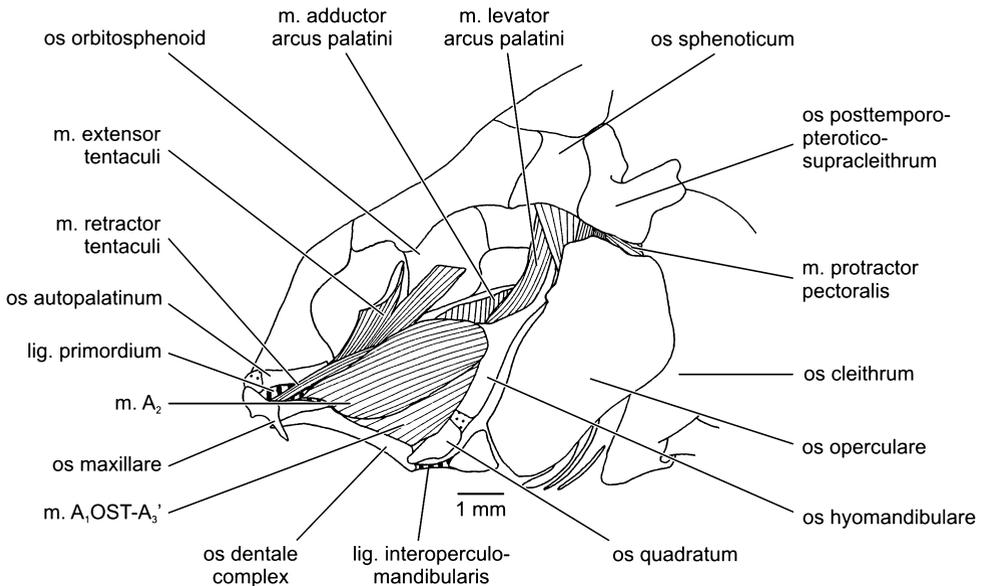
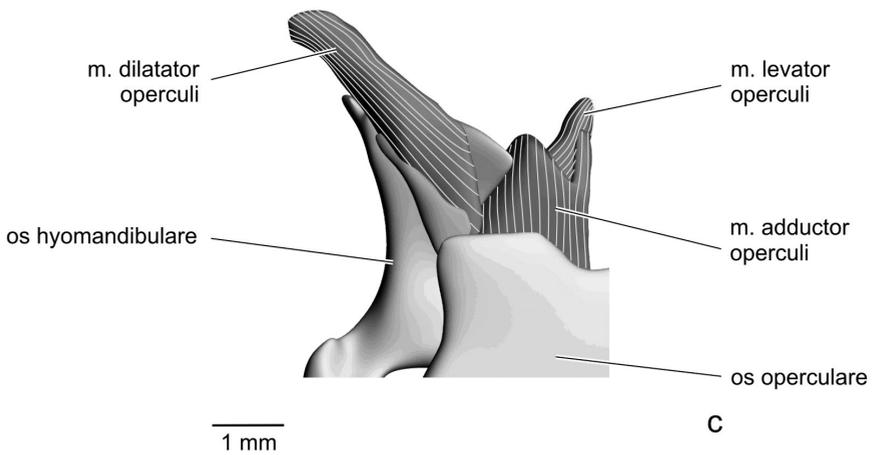
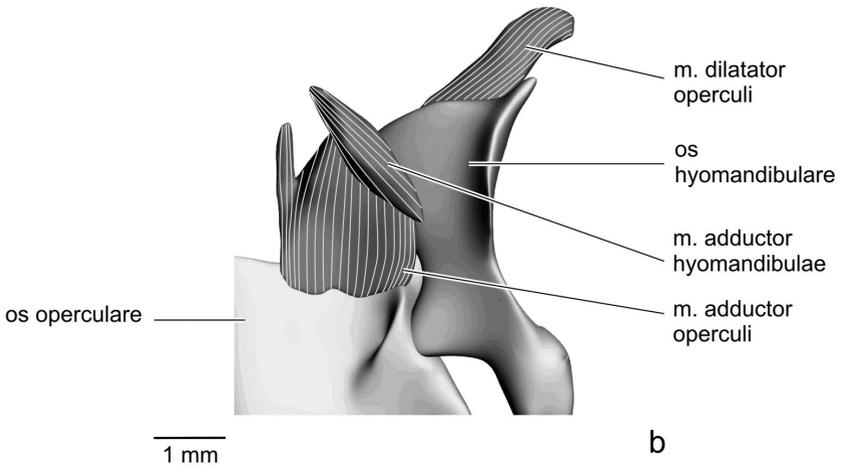
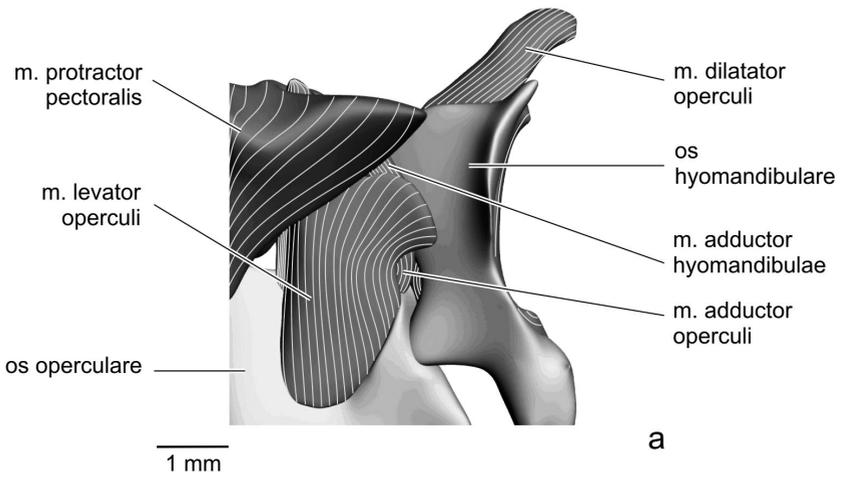


Figure 1. Left lateral view of the cranial musculature of *Corydoras aeneus*. (Eye removed; striping indicates fibre direction.)



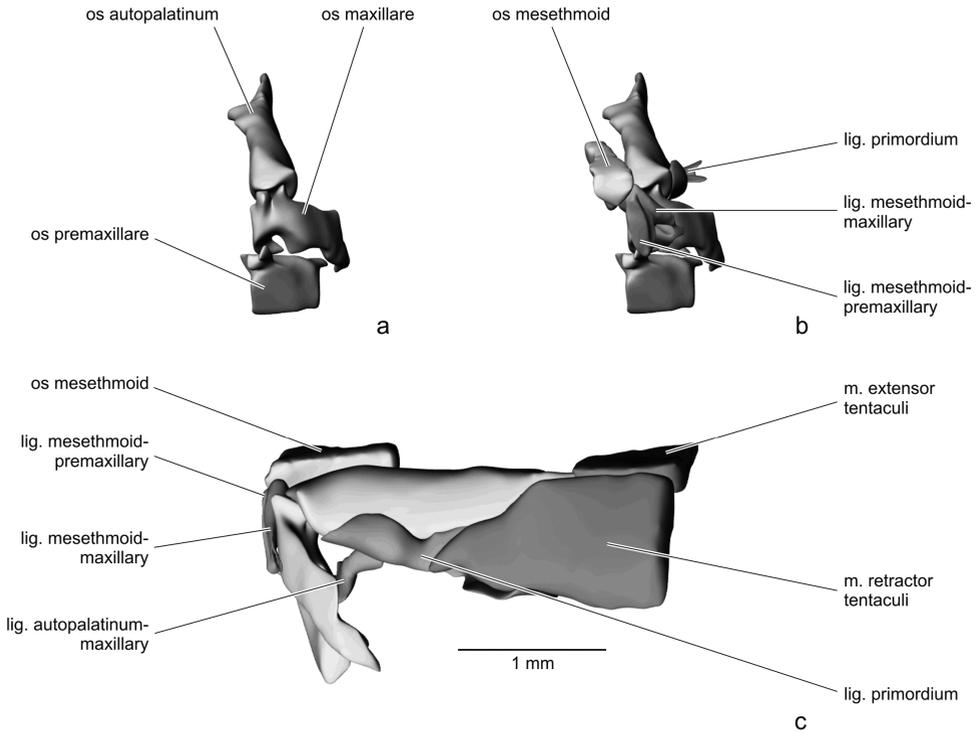


Figure 3. (a) Rostral view of a 3-D reconstruction of the bones of the left autopalatinum-premaxillary-maxillary complex. (b) Rostral view of a 3-D reconstruction of the bones and ligaments of the left autopalatinum-premaxillary-maxillary complex. (c) Lateral view of a 3-D reconstruction of the bones, ligaments and muscles of the left autopalatinum-premaxillary-maxillary complex. (Scale bar only applicable to (c); scale differs in perspective views (a) and (b).)

further ventrally, covering the entire caudal margin of the quadrate bone. The muscle then runs forward, covering the entire suspensorial arch, splitting up at the level of the caudal margin of the lower jaw, with a lateral bundle (A_1OST) inserting on the dorsolateral side of the lower jaw and a medial bundle (A'_3) on the dorsomedial side. Both bundles attach to the lower jaw between the suspensorial joint caudally and the coronoid process rostrally.

The *m. retractor tentaculi* in *C. aeneus* originates on both the hyomandibula and metapterygoid. The muscle then runs medially from both the A_2 and $A_1OST-A'_3$ and, like the A_2 , also attaches to the *lig. primordium*.

Figure 2. (a) Median view of a 3-D reconstruction of the left opercular musculature. (b) Median view of a 3-D reconstruction of the left opercular musculature, protractor pectoralis and levator operculi muscles not shown. (c) Lateral view of a 3-D reconstruction of the left opercular musculature, protractor pectoralis muscle not shown. (Skull roof bones not shown in all reconstructions; striping indicates fibre direction.)

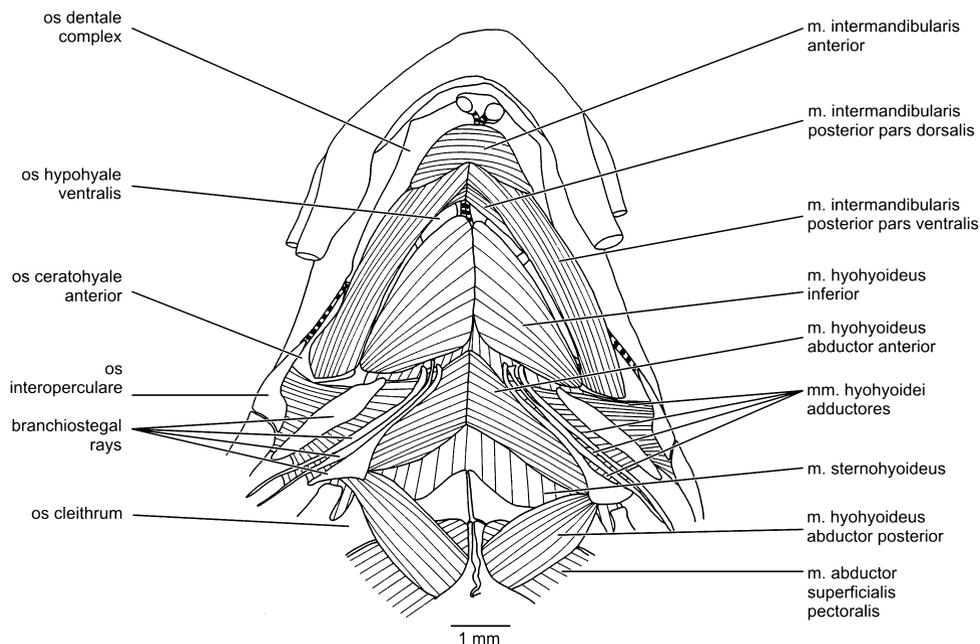


Figure 4. Ventral view of the cranial musculature of *Corydoras aeneus*. (Striping indicates fibre direction.)

The *m. intermandibularis anterior* connects the medial sides of both dentary bones at their rostral margin.

The *m. intermandibularis posterior* is subdivided into a *pars dorsalis* and a *pars ventralis* which merge rostrally and insert on the lower jaw. Both parts follow the same path and are difficult to be discerned through dissection. Serial sections, however, clearly show a subdivision into a dorsal and ventral part. These serial sections also revealed that the muscle was innervated by the inferior mandibular nerve branch of the trigeminal nerve (V) and no myocomma was present. This indicates that the muscle merely consists out of the *m. intermandibularis posterior* and that no *m. protractor hyoidei* part is present.

The *m. extensor tentaculi* originates both from the lateral side of the orbitosphe-noid and the caudal side of the lateral ethmoid bone. Rostrally, the muscle inserts as a single bundle on the caudal margin of the autopalatine, posterior to its articulation with the lateral ethmoid.

Suspensorial musculature (figs. 1, 2)

The *m. levator arcus palatini* originates from the skull at the level of the sphenotic bone and inserts on the laterodorsal surface of the hyomandibula. The *m. adductor arcus palatini* originates from the base of the skull along the lateral side of the parasphenoid bone and inserts on the medial side of both hyomandibula and metapterygoid. Posterior to the *m. adductor arcus palatini*, a *m. adductor*

hyomandibulae is present, originating on the ventral side of the prootic and inserting on the medial surface of the hyomandibula.

Opercular musculature (fig. 2)

The *m. dilatator operculi* is a conical muscle originating from a cavity in the sphenotic and from the hyomandibular bone and running ventroposteriorly to insert, through a tendon, on the anterodorsal side of the opercle, above the articulation with the hyomandibula. The anterior fibres of this muscle are partially continuous with the *m. levator arcus palatini*.

The *m. adductor operculi* originates entirely on the posttemporo-pterotico-supracleithrum. The muscle runs ventrally to insert on a ridge on the dorsomedial side of the opercle.

The *m. levator operculi* is a broad muscle originating on the posttemporo-pterotico-supracleithrum and the prootic. This muscle runs ventrally to insert medially on the operculare on a large ridge that starts just below the rostral side of the insertion ridge of the dilatator operculi and that runs caudoventrally to the middle of the opercle.

Hyoid musculature (fig. 4)

As mentioned, no *m. protractor hyoidei* is present. The *m. hyohyoideus inferior* connects both hyoid arches and the left and right part of this muscle are medially fused through an aponeurosis. The *m. hyohyoideus abductor* in *C. aeneus* originates on the most medial branchiostegal rays, runs rostrally and fuses at the midline just behind the caudal margin of the hyohyoideus inferior. The aponeurosis through which these two halves are fused connects to the midline aponeurosis of the *m. sternohyoideus (q.v.)*. However, a second bundle runs from the branchiostegal rays caudally to insert on the scapulocoracoid. Further, the *mm. hyohyoidei adductores* interconnect all branchiostegal rays, the opercle and the interopercle. Finally, the *m. sternohyoideus* is a large muscle, originating from the cleithrum and running rostrally, inserting on the parurohyal bone and further connecting to the dorsal and ventral hypohyal through a double ligamentous connection. This muscle is split up over its entire length into a right and left half, which medially connect through an aponeurosis.

Gill arch musculature (figs. 5, 6)

Dorsally, in *C. aeneus*, gill arches I-IV bear a *m. levator externus*. These muscles originate grouped on the ventrolateral side of the prootics and insert on the respective epibranchial bones. On the third arch, however, the insertion site of the *m. levator externus* has also extended onto the cartilage connecting the epibranchial and infrapharyngobranchial III to the infrapharyngobranchial IV, with some fibres even inserting on the latter bone. Only arches I, II and IV bear a *m. levator internus*.

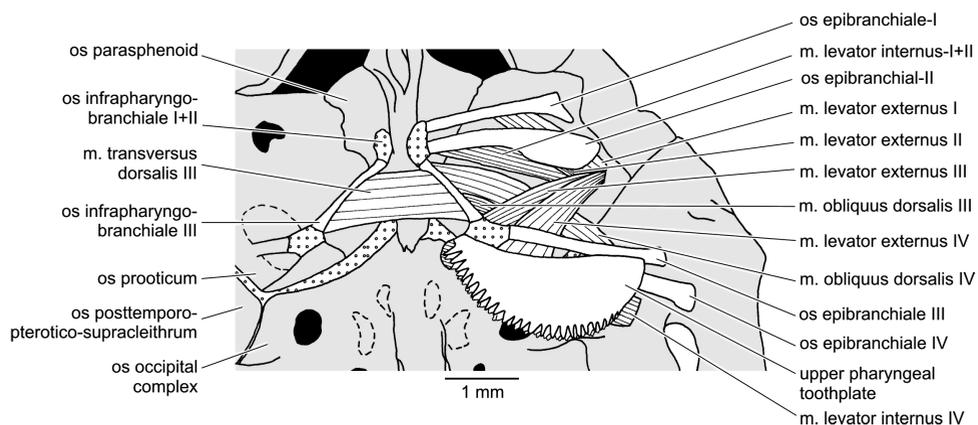


Figure 5. Ventral view of the dorsal gill arch muscles. (Roman numerals numbers indicate gill arch numbers; striping indicates fibre direction.)

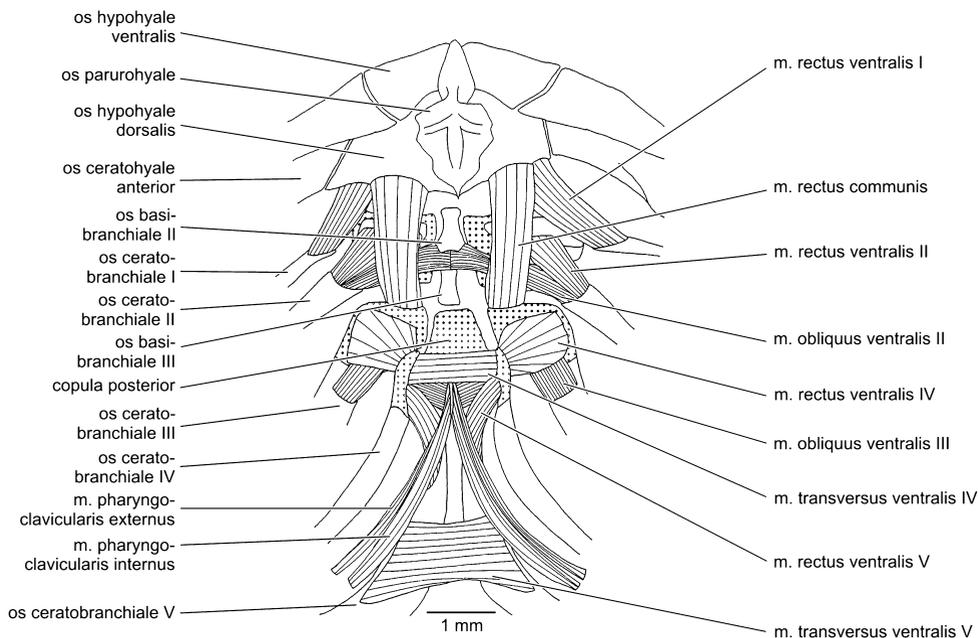


Figure 6. Ventral view of the ventral gill arch muscles. (Roman numerals indicate gill arch numbers; striping indicates fibre direction.)

This muscles is a single muscle in the first two arches, originating on the prootic, on the same site as the *mm. levatores externus*, and inserting on the cartilaginous infrapharyngobranchial I+II and epibranchial II. Since the infrapharyngobranchials of the first two arches are fused, we chose to consider this muscle as the combined *m. levator internus* of the first two arches. On the fourth arch the *m. levator internus* also inserts on the infrapharyngobranchial IV, with the upper pharyngeal toothplate attached, but the site of origin is on the ventromedial part of the posttemporo-

pterotico-supracleithrum. A *m. obliquus dorsalis* is only present on arches III and IV. These muscles interconnect the epibranchials and infrapharyngobranchials of both arches. Only the third arch bears a *m. transversus dorsalis* which interconnects the left and right infrapharyngobranchial. Additionally, the *m. obliquus posterior* connects the ceratobranchial V to the epibranchial IV. It is a short muscle, with its sites of origin and insertion close to the lateral tips of both bones. No *m. retractor dorsalis* or *m. levator posterior* is present. In gill arches I, II, III and IV a *m. adductor arcuum branchialium* is present connecting the ceratobranchials to the epibranchials.

Ventrally, all arches bear a *m. rectus ventralis*, with the exception of arch III. This muscle connects the ceratobranchial of the respective arch to the hypobranchial of the proceeding one, except for the first arch, where this muscle inserts on the dorsal hypohyal. Arch III bears the *m. rectus communis*, which has the same origin as the *m. rectus ventralis* in the other arches, but with its insertion on the dorsal hypohyal. A *m. obliquus ventralis* is only present in arches II and III, connecting the arches' hypobranchials to their ceratobranchials. In arch II, these muscles also insert on the basibranchial, connecting the right and left *m. obliquus ventralis* at this point. A *m. transversus ventralis* was found in arches IV and V, interconnecting the left and right cartilaginous hypobranchial in the fourth arch and the left and right ceratobranchial in the fifth. Further, both the *m. pharyngoclavicularis internus* and *externus* connect the ventral part of the gill basket to the pectoral girdle. Posteriorly, both ceratobranchial V and epibranchial IV are confluent with the *m. sphincter oesophagi*.

Eye musculature (fig. 7)

The extrinsic eye musculature in *C. aeneus* is similar to the pattern commonly found in teleosts. Two oblique muscles, the *m. obliquus superior* and *m. obliquus inferior*

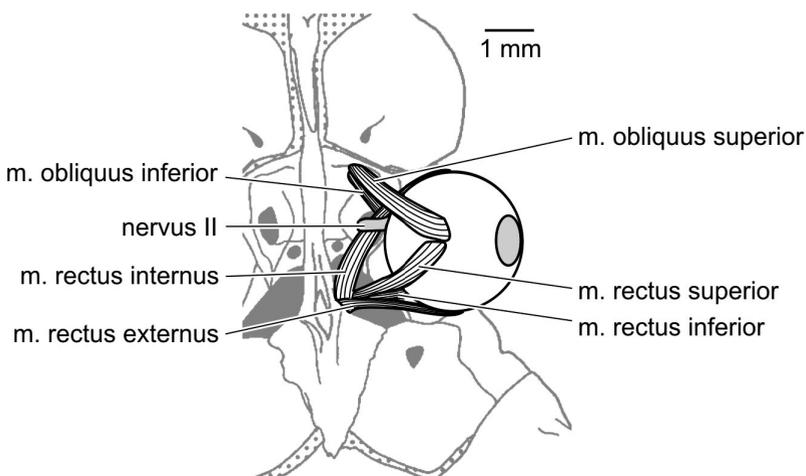


Figure 7. Graphic reconstruction of a ventral view of the eye musculature. (Striping indicates fibre direction.)

originate on the orbitosphenoid bone and insert on the most dorsal and most ventral part of the eyeball respectively. At the same sites respectively, both the *m. rectus superior* and *m. rectus inferior* insert, both originating on the parasphenoid. The last two extrinsic eye muscles, the *m. rectus externus* and the *m. rectus internus* both originate in a large posterior myodome between the prootics and the parasphenoid at the level of the prootic bridge, inserting respectively on the most caudal and most rostral side of the eyeball.

Pectoral musculature (fig. 8)

The pectoral girdle is connected to the splanchnocranium through the *m. sternohyoideus* and to the posttemporo-pterotico-supracleithrum through the *m. protractor pectoralis* (fig. 1). Ventrally, the main muscle mass for movement of the pectoral fin is made up of the *m. abductor pectoralis superficialis pars ventralis*. This muscle originates on the ventrolateral face of the cleithrum and scapulocoracoid and runs backwards where it attaches to the bases of all fin rays except the pectoral spine. Dorsal to this muscle lies the *m. abductor pectoralis superficialis pars dorsalis*, which also inserts on the fin rays, but originates from the scapulocoracoid. Lateral to these muscles lies the *m. arrector pectoralis ventralis*, which originates from the dorsolateral side of the cleithrum and inserts ventrally on the pectoral fin spine. Dorsal to this the *m. arrector pectoralis dorsalis* originates on the dorsomedial side of the cleithrum, runs through a foramen in the cleithrum and inserts on the anterodorsal margin of the pectoral fin spine. Also originating on the dorsomedial face of the pectoral girdle, but on the scapulocoracoid are the *m. adductor pectoralis superficialis* and the *m. adductor pectoralis profundus*, which also pass through a foramen to insert dorsally on the bases of all fin rays except the pectoral spine. Here, the lateral muscle fibres finally insert on the more medial fin rays and the medial fibres insert on the lateral rays, this way resulting in a 'cross-over' of muscle fibres. The pectoral spine is abducted by contraction of the *m. abductor pectoralis profundus*, which also originates on the medial side of the scapulocoracoid, but ventrally, and inserts on the head of this pectoral fin spine. Additionally, the pectoral girdle is connected to the pelvic girdle through the *m. infracarinalis anterior*.

Pelvic musculature (fig. 9)

Ventrally, the pelvic girdle is covered by three separate muscles. The most ventral muscle is the *m. abductor pelvici superficialis*, which originates medially on the pelvic girdle and inserts on all but the most lateral fin ray. Underneath this muscle, but with a more anterior origin lies the *m. abductor pelvici profundus*, which also inserts on all fin rays except the first. Also ventrally lie the *m. arrector pelvici ventralis* and the *m. arrector pelvici dorsalis*, which both originate on the ventrorostral margin of the anterior internal process and insert on the first pelvic fin ray. On the anteromedial margin of the anterior internal process of the pelvic girdle the *m. adductor pelvici superficialis* originates and posterior to this up to

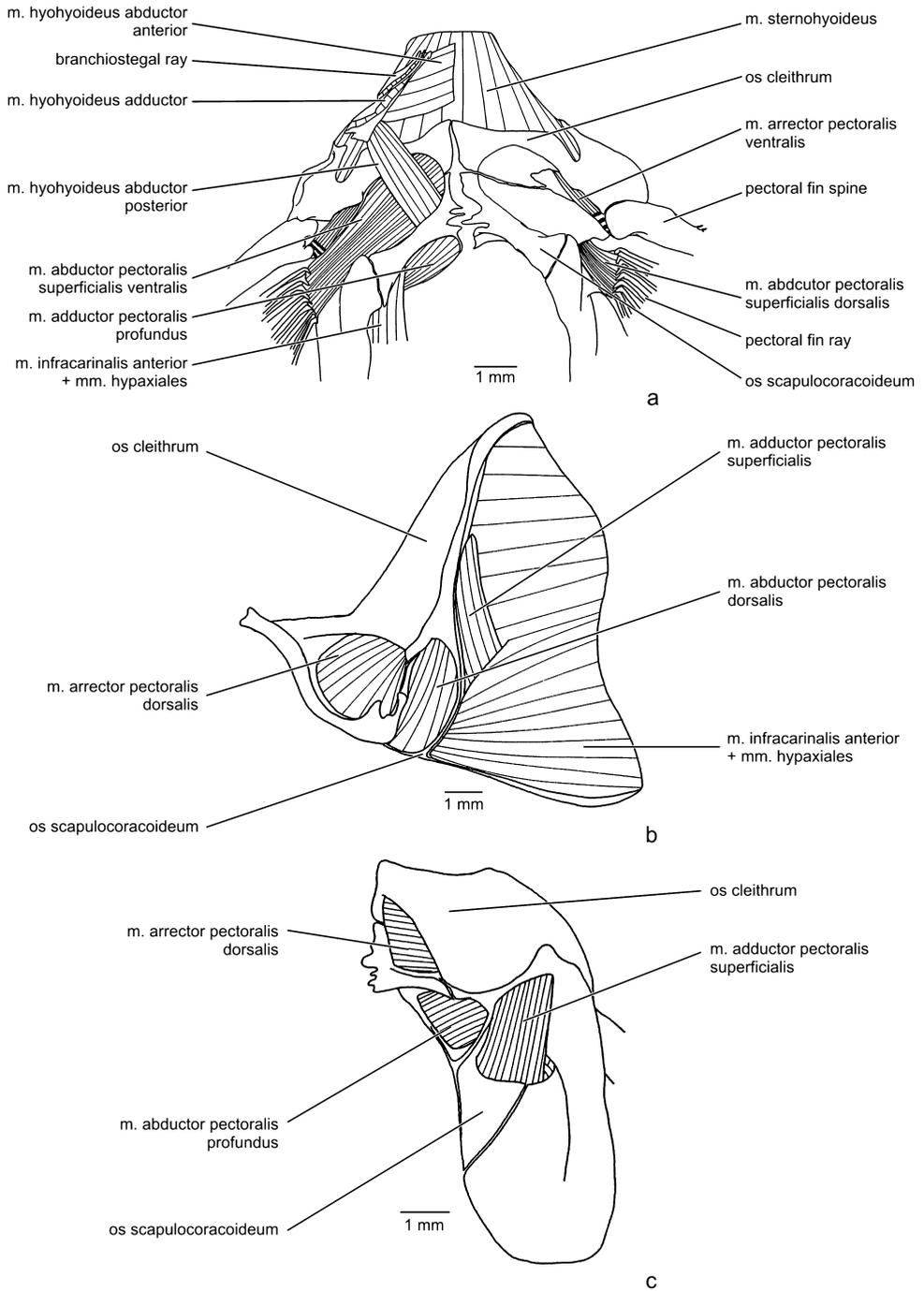


Figure 8. (a) Ventral view of the musculature of the pectoral girdle (adductor profundus and abductor profundus muscle removed on left side). (b) Medial view of the musculature of the right pectoral girdle. (c) Dorsal view of the right pectoral girdle (infracarinalis and hypaxial muscles removed). (Striping indicates fibre direction.)

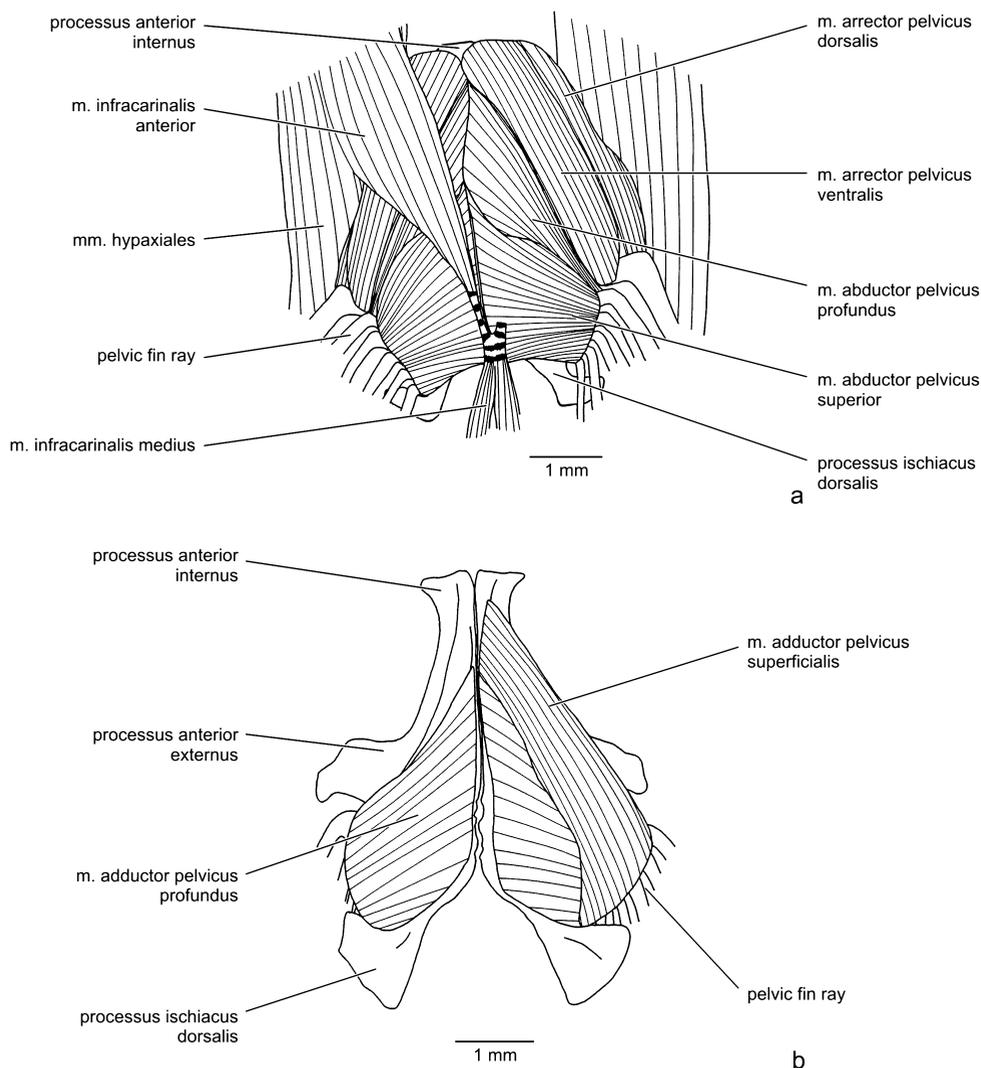


Figure 9. (a) Ventral view of the musculature of the pelvic girdle. (b) Ventral view of the musculature of the pelvic girdle. (Arrector muscles, abductor muscles, hypaxials and infracarinalis muscle removed; striping indicates fibre direction.)

the posterior margin of the girdle, the *m. adductor pelvici profundus* has its origin. Both these muscles insert on all pelvic fin rays. The pelvic girdle further attaches to the anal fin through the *m. infracarinalis medius* and to the pectoral girdle through the *m. infracarinalis anterior*.

Unpaired fin and body musculature (figs. 10, 11 and 12)

The caudal fin musculature mainly consists of a *m. flexor dorsalis* and a *m. flexor ventralis*, which both originate on the third preural vertebral centre and insert on

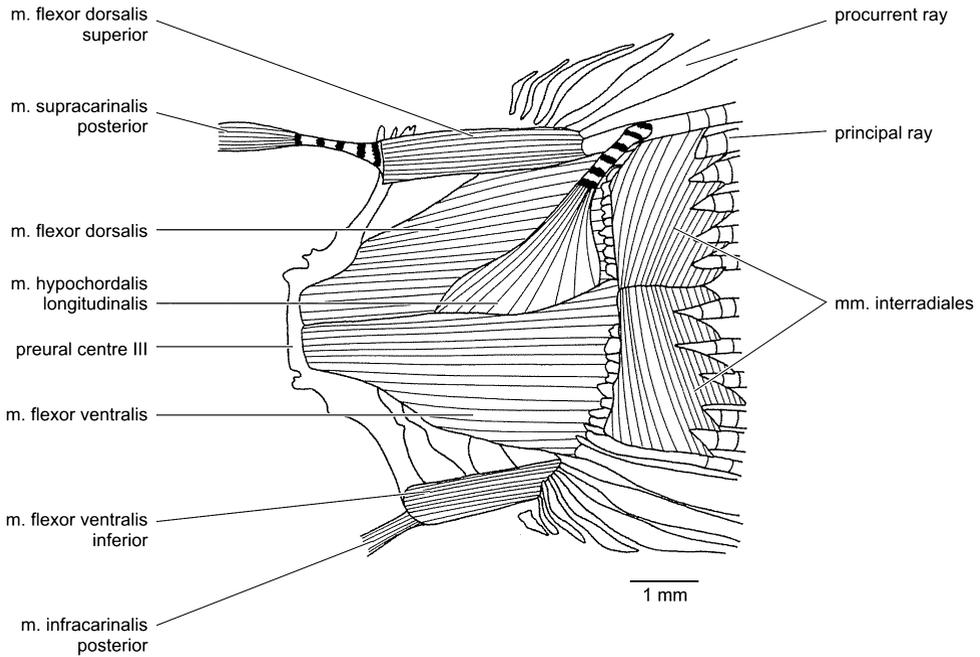


Figure 10. Left lateral view of the caudal fin musculature. (Striping indicates fibre direction.)

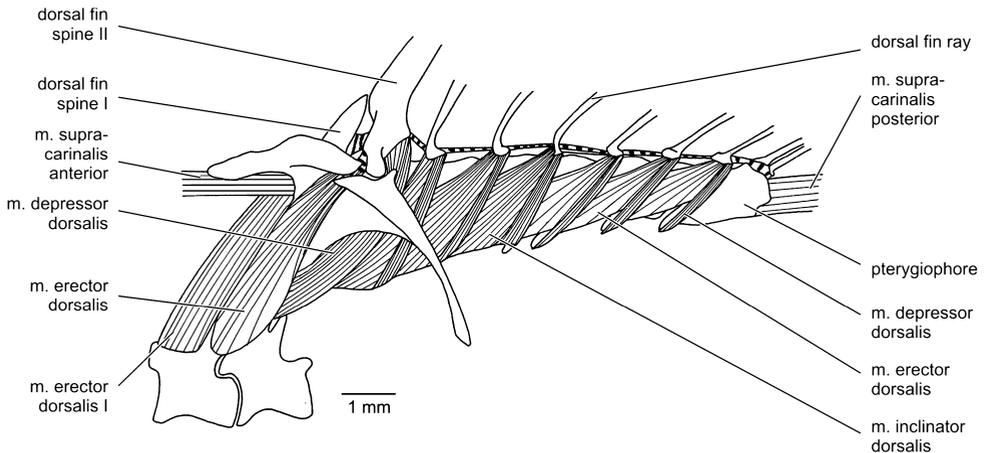


Figure 11. Left lateral view of the dorsal fin musculature. (Erector muscles removed on last 4 fin rays; latin numbers indicate ray/spine number; striping indicates fibre direction.)

the bases of the principal fin rays. In addition, dorsal to this muscle lies the *m. flexor dorsalis superior* which originates on the neural spine of the third preural vertebra and inserts on the dorsal proximal fin rays and the upper principal fin ray. Also, ventrally a *m. flexor ventralis inferior* is present, which originates on the haemal spine of the third preural vertebra and inserts on the ventral proximal fin rays. Additionally, on the hypurals I, II and the parhypural, the *m. hypochordalis*

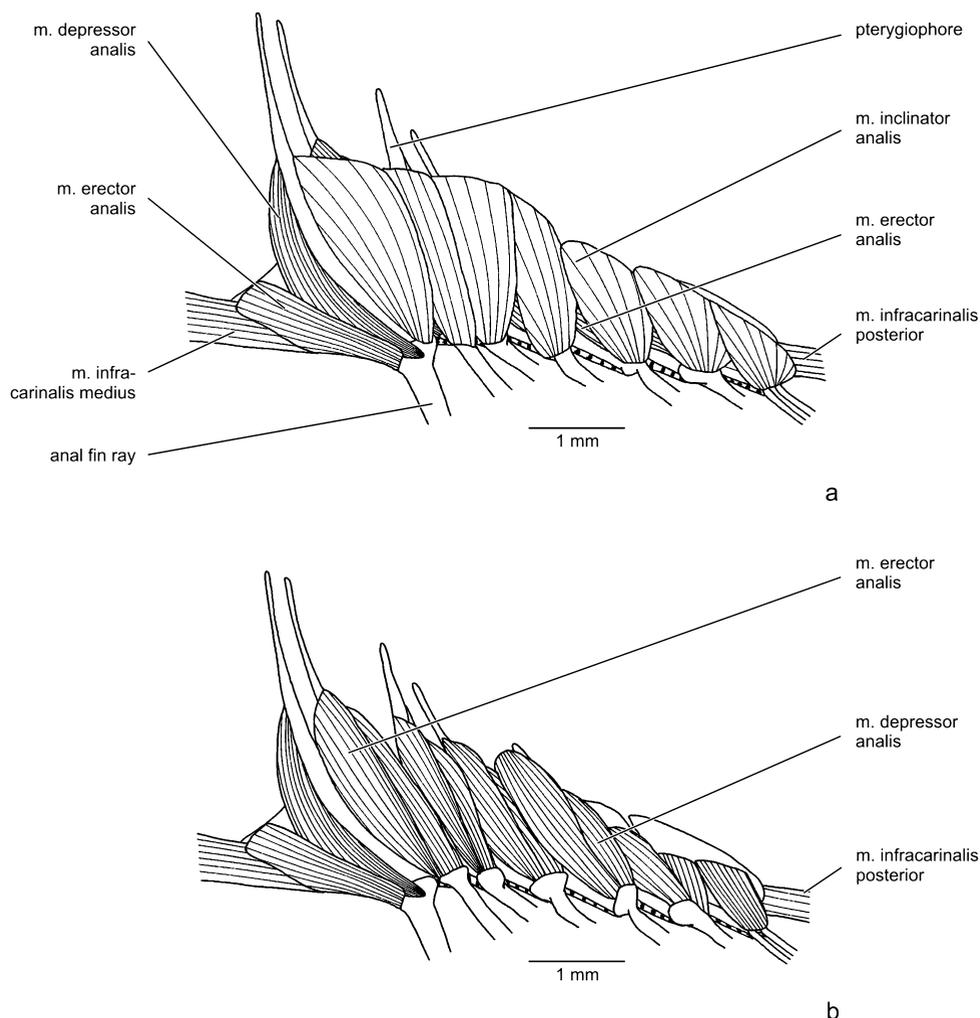


Figure 12. (a) Left lateral view of anal fin musculature. (b) Left lateral view of anal fin musculature. (Inclinator muscles removed; striping indicates fibre direction.)

longitudinalis originates, which ligamentously inserts on the upper principal fin ray. Further, the principal fin rays are interconnected through the *mm. interradians*, which insert on the lepidotrichia shafts, distal to the insertion of the flexor muscles. Dorsally, the posterior margin of the dorsal fin is connected to the neural spine of the third preural vertebra by the *m. supracarinalis posterior*, which inserts on this spine through a tendon. Ventrally, the haemal spine of the third preural vertebra is connected to the anal fin by the *m. infracarinalis posterior* through a muscular insertion.

Three types of muscles control the movement of the dorsal fin: the *mm. erectores dorsales*, the *mm. inclinatores dorsales* and the *mm. depressores dorsales*. The

first two types of muscles, of which the *mm. inclinatores dorsales* lie more lateral and cover the *mm. erectores dorsales*, originate from the anteroventral part of the pterygiophore supporting the preceding fin ray, while the *m. depressor dorsalis* of each fin ray has its origin on the ventral side of the pterygiophore of the corresponding fin ray. On the first dorsal fin spine only a *m. erector dorsalis* inserts which originates on the anterodorsal side of the ninth vertebra. A *m. erector dorsalis* also inserts on the second dorsal fin spine, which also originates on the ninth vertebra, albeit on the posterodorsal side. Additionally this second spine bears a *m. depressor dorsalis* which originates on the anterodorsal side of the tenth vertebra and runs posterior to the transverse process to insert on the spine's posterior margin. Posteriorly, the dorsal fin is connected to the third preural vertebra through the *m. supracarinalis posterior*. Anteriorly, the dorsal fin connects to supraoccipital bone through the *m. supracarinalis anterior*.

Lateral to all other muscles of the anal fin lie the *mm. inclinatores anales*, which originate on the pterygiophores and insert laterally on the fin rays bases. Underneath these muscles lie the *mm. erectores anales* and the *mm. depressores anales*. Both these muscles originate on the pterygiophores and insert on the fin rays, the *mm. erectores anales* anteriorly and the *mm. depressores anales* posteriorly. Posteriorly, the *m. infracarinalis posterior* connects the anal fin to the third preural centre and anteriorly, the *m. infracarinalis medius* connects the anal fin to the pelvic girdle.

DISCUSSION

Next to structural changes in the morphology of the *m. hyohyoideus inferior*, the presence of a cartilage plug between the lower jaw and the hyoid in Astroblepidae and Loricariidae, and the shift and neoformation of several ligamentous connections in the jaw region, the Loricarioidea differ structurally from the plesiomorphic siluriform situation found in Diplomystidae as described by Diogo and Chardon (2000) at the level of the jaw musculature. Because of this, the superfamily Loricarioidea has been considered “a clade showing a pattern of progressive increase in the mechanical complexity of structures associated with feeding”, with consequent homology ambiguities (Schaefer and Lauder, 1986, 1996).

A first example of this is the nature of the dorsal division of the *m. adductor mandibulae* inserting onto the maxillary bone, the so-called A_1 (Winterbottom, 1974; Gosline, 1986, 1993). Since such a muscle in ostariophysans is believed to have evolved independently from the A_1 in eurypterygians (Fink and Fink, 1996), a true A_1 part, as present in Acanthomorpha, is absent in Ostariophysi (Adriaens and Verraes, 1996; Diogo and Chardon, 2000; Wu and Shen, 2004). Alexander (1965), however, did recognise an A_1 part in Callichthyidae and Loricariidae, an error later adapted by Howes (1983), Schaefer and Lauder (1986) and Schaefer (1997). Diogo and Chardon (2000) chose to name the different muscle bundles according to their position, giving the more lateral bundles inferior numbers. This way, they named this dorsolateral section in Ostariophysi A_2 (medial to A_0 and A_1). Following the

same logic, they suggested the term A_1OST for the ventrolateral cheek muscle inserting on the dorsal face of the lower jaw (the term OST was added to avoid confusion with the acanthomorph A_1). Wu and Shen (2004), on the other hand, avoided the use of the term A_1 in their terminology, using only derivatives of the A_2 and A_3 terms. Still we believe the terminology proposed by Diogo and Chardon (2000) to be more appropriate, given the thoroughness of their comparative work on siluriforms, a group dealt with in a rather limited way by Wu and Shen (2004). However, it must be noted that in the terminology of Diogo and Chardon (2000) the term A_1 in A_1OST is somewhat misleading due to the lack of any relation of this muscle with the maxillary, as already stated by Wu and Shen (2004); as well as that their A_2 is not homologous to the A_2 as described by Vetter (1878), and maybe the term A_2OST would have been more appropriate.

Given this, we identified the dorsolateral division of the *m. adductor mandibulae* in *Corydoras aeneus* as the A_2 according to the definition by Diogo and Chardon (2000). In *C. aeneus*, in contrast to other non-loricarioid catfishes, this muscle has shifted its insertion onto the *lig. primordium*, through which it indirectly inserts on both upper and the lower jaw, altering the entire jaw mobility (Howes, 1983; Schaefer and Lauder, 1986). Next to this, in *C. aeneus*, the *m. retractor tentaculi* also inserts on the *lig. primordium*, a muscle we believe to be homologous to, or derived from the A_3'' , as already suggested by various authors (Lubosch, 1938; Alexander, 1965; Howes, 1983; Adriaens and Verraes, 1996, 1997; Diogo and Chardon, 2000; Diogo, 2005).

In the ventral region of this cheek muscle complex, the *m. adductor mandibulae* is composed of two separate bundles: one attaching to the lower jaw laterally and a second one attaching to the lower jaw on the medial side. Given the ventrolateral position of the former bundle we identified it as the A_1OST . The latter bundle was identified as the A_3' , based on its medial position. Gosline (1989, 1993) and Adriaens and Verraes (1996) also confirm the presence of a compound lower jaw muscle in catfishes, and conclude that this muscle is the composed A_2A_3' , as suggested earlier by Takahashi (1925). Given the synonymy between the A_2 as described by Takahashi (1925) to the A_1OST as described by Diogo and Chardon (2000), this conclusion also fits our findings and we put this compound muscle in homology with the A_1OST-A_3' . This insertion of the A_1OST-A_3' directly onto the medial surface of the dentary is considered a derived state in Siluriformes (Diogo, 2005). Diogo (2005), also claims that in *Corydoras*, the insertion of the A_3' is lateral to that of the A_2 and A_3'' , and that the A_3'' inserts partially on the mandible and partially on the *lig. primordium*. When regarding the A_3'' as the *m. retractor tentaculi*, the latter statement is indeed correct, but our observations contradict the lateral position of the A_3' as it is situated on the medial side of the A_2 . Wu and Shen (2004) do not mention a further subdivision of the A_3 and place the A_3 in synonymy with the A_3' as described by Takahashi (1925). They, however, do not mention the *m. retractor tentaculi* in their survey, and since this is believed to be homologous to the A_3'' , retaining the name A_3' for the medial bundle in *C. aeneus* seems justifiable. Finally,

in *C. aeneus* both an A_0 and A_ω are absent, a condition common in Siluriformes (Alexander, 1965; Diogo, 2000).

Next to this, the subdivision of the *m. extensor tentaculi* in *C. aeneus* is a character already mentioned by Diogo (2005) as a derived siluriform state but which was not reported by Schaefer and Lauder (1986, 1996). This subdivision of the *m. extensor tentaculi* fits the general trend of an increase in morphological complexity of the functional design through decoupling present throughout the loricarioid evolution (Schaefer and Lauder, 1986, 1996). The definition of decoupling in this case can be stated as the repetition of individual elements as redundant design components, followed by the specialization of one or more of these elements as a mechanistic basis for the evolution of novel structure/function (Schaefer and Lauder, 1996). In these loricarioids, such a decoupling has mainly occurred at the level of the jaws. The upper jaws have been decoupled from the cranium, while the lower jaw has been decoupled from the opercular series, increasing mobility and independency of both upper and lower jaw (Schaefer and Lauder, 1996). Next to this, the lower jaws and hyoid musculature have become decoupled from their plesiomorphic bilaterally constrained midline attachments and a new redundant linkage was acquired (Schaefer and Lauder, 1996). All these factors, combined with the increase in myological complexity at the level of the *m. adductor mandibulae* has ultimately facilitated the evolution of a suckermouth in astroblepids and loricariids and the evolution of an algae scraping feeding apparatus in the latter family.

Another example in which an evolutionary pattern of increased morphological complexity through decoupling is present throughout the loricarioid lineage involves the opercular system. This way, in the family of the Loricariidae, the opercle has been decoupled from the lower jaw and has lost his function in expiration (Geerinckx and Adriaens, 2006). Within this family, in the Ancistrini-tribe, this has ultimately led to the formation of an erectile opercle, armoured with large denticles, acting as a defensive mechanism (Geerinckx and Adriaens, 2006). One of the most important innovations in this process has been the development of a hypertrophied *m. dilatator operculi*, which has ultimately led to the formation of several myodomes in the skull bones in *Ancistrus* cf. *triradiatus* Eigenmann, 1918, thus forming a 'secondary skull roof' (Geerinckx and Adriaens, 2006).

In *C. aeneus*, the *m. dilatator operculi* is not hypertrophied nor is it split into several different bundles. This corresponds to the plesiomorphic condition for Siluriformes as described by Diogo (2005), who only mentions a subdivided *m. dilatator operculi* in members of the Aspredinidae and Trichomycteridae. He, however, does not mention this for loricariids, though only two species of *Hypoptopoma* Günther, 1868 were included in the study. However, in *C. aeneus*, the *m. dilatator operculi* does extend rostrally, originating in a cavity in the sphenotic bone, a situation which is not mentioned in the study by Diogo (2005). In his study, the origin of the *m. dilatator operculi* on the dorsal surface on the neurocranium is mentioned as a derived character state in Trichomycteridae and members of the genus *Plotosus* (Lacepède, 1803) but the presence of a sphenotic cavity was not detected in any of the studied

siluriforms. As in *A. cf. triradiatus*, the cavity in *C. aeneus* splits up the sphenotic bone in a deeper and outer layer, although both situations differ structurally. In *C. aeneus* the deeper layer of this cavity is formed by perichondral part of this bone (the autosphenotic), where the outer layer is formed by the dermsphenotic part (as shown from preliminary ontogenetic data). In the skull bones where a myodome is formed in *A. cf. triradiatus*, however, the myodome is positioned in between layers of mixed origin, since canals of the lateral line system are present in the deeper layers (Geerinckx and Adriaens, 2006). Therefore, both cavities in *A. cf. triradiatus* and *C. aeneus* cannot be considered homologous and the term myodome was not applied to the situation in *C. aeneus*. In addition, in its most narrow sense the term 'myodome' is restricted to those cavities housing the external eye muscles in teleosts (Rojo, 1991). In a broader sense, as applied by Geerinckx and Adriaens (2006) the term applies to a cavity formed in a bone housing a muscle, which is clearly the case in the *A. cf. triradiatus* skull, but not in the *C. aeneus* sphenotic, where the dermosphenotic merely forms an outgrowth covering the *m. dilatator operculi*.

Nonetheless, the rostral expansion of the *m. dilatator operculi* in *C. aeneus*, combined with the more oblique direction of the opercle-hyomandibular articulation, implies an increase in efficiency in the dilatation of the opercle. Next to this, the anterior bundle of the *m. hyohyoidei abductor* has shifted its orientation to the transverse plane, acting as an adductor of the branchiostegal membrane. A similar state is found in *A. cf. triradiatus*, in which the *m. hyohyoidei abductor* has also shifted its direction medially, acting as an adductor of the branchiostegal membrane, whereas fibres of the *m. hyohyoideus inferior* assist in the abduction (Geerinckx and Adriaens, submitted). This way, the closing of the branchiostegal membrane is at least partially decoupled from the opercle in both species, a factor which could have facilitated the alteration of the opercle into a defensive mechanism in *A. cf. triradiatus*.

This hypothesis would again fit the general hypothesis of increased morphological complexity through decoupling, which shows the importance of decoupling combined with shifts in function as a common evolutionary pathway for accomplishing innovative structural design. It is our belief that further investigation of not only the adult morphologies, but also extensive ontogenetic and functional comparative research of several loricarioid lineages will elucidate the full impact of such an evolutionary pathway and quantify their role in the evolution of these extremely successful and diverse taxa.

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