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Ontogeny of the cranial musculature in *Corydoras aeneus* *Callichthyidae*, *Siluriformes*

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A complete study of the early ontogeny of the cranial muscles of *Corydoras aeneus* (Callichthyidae) was undertaken and results were compared with those for the loricariid *Ancistrus* cf. *triradiatus*. This comparison reveals a high degree of similarity in the ontogeny of both species' cranial muscles. Both species lack a musculus protractor hyoidei, and the musculus intermandibularis posterior is divided into two different parts that have partly obtained a novel function (serving the lower lip) in *A. cf. triradiatus*. A similar increase in muscular complexity in this species is found in the dorsal constrictor of the hyoid muscle plate. This constrictor gives rise to the same muscles in both *C. aeneus* and *A. cf. triradiatus*, but in *A. cf. triradiatus* the musculus levator operculi later hypertrophies. In *C. aeneus* the musculus extensor tentaculi forms a single muscle diverging posteriorly, whereas in *A. cf. triradiatus* the musculus extensor tentaculi differentiates into two separate bundles. Also, a loricariid neof ormation is present called the musculus levator tentaculi.

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INTRODUCTION

A good starting point of study to detect functional changes as they occur throughout ontogeny, are the higher levels of organization linked to these changes, like the chondrocranium, osteocranium and muscle system (Simonović *et al.*, 1999). The development of the cartilaginous as well as the bony skull has been the subject of various studies on siluriforms in general (Kindred, 1919; Bamford, 1948; Srinivasachar, 1957*a, b*, 1958*a, b*, 1959; Vandewalle *et al.*, 1985, 1997; Tilney & Hecht, 1993; Adriaens & Verraes, 1994, 1997*a*, 1998; Geerinckx *et al.*, 2005) and callichthyids in particular (Ballantyne, 1930; Hoedeman, 1960*a, b, c*). Only in the cases of *Clarias gariepinus* (Burchell) and *Ancistrus* cf. *triradiatus* Eigenmann, however, has the focus of ontogenetic research been extended to the level of the development of the muscular system (Surlemont *et al.*, 1989; Surlemont &

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Vandewalle, 1991; Adriaens & Verraes, 1996, 1997*a, b, c*; Geerinckx & Adriaens, 2007, 2008; Geerinckx *et al.*, 2009). The study of this muscular system from the earliest stages of development could yield valuable information on functional needs placed on the developing organism. Such data are of great value in an evolutionary context because morphogenesis and differentiation are very intense during early life stages and functional constraints of vital importance act on each of those stages (Van Snik *et al.*, 1997). Information on the presence of muscular tissue and on sites of muscle origin and insertion would be indicative of the functionality of these units throughout ontogeny.

To fill this knowledge gap, the aim of this study is to provide a complete description of the ontogeny of the cranial muscles of *Corydoras aeneus* (Gill) (family Callichthyidae), in continuation of previous studies published on the species' development and the ontogeny of the chondrocranium, osteocranium and postcranial skeleton (Huysentruyt *et al.*, 2007, 2008). In addition, *C. aeneus* belongs to the superfamily Loricarioidea, in which an evolutionary trend has been observed that has led to the formation of a suckermouth in two lineages (Astroblepidae and Loricariidae). In the latter family, this has ultimately led to the formation of a highly specialized feeding mechanism (alga scraping). In addition to the presence of this suctorial mouth in these lineages, implications of this specialized apparatus involve tilted lower jaws and new muscle configurations, which greatly increase jaw mobility (Geerinckx *et al.*, 2005). Placed within the evolutionary lineage exhibiting these adaptations, the Callichthyidae appears to be phylogenetically more basal than the Astroblepidae and Loricariidae (Schaefer & Lauder, 1986, 1996) and has a ventrally placed mouth already present but with neither the presence of a sucking disc nor an alga-scraping feeding apparatus. In this context, the study of the morphology and development of *C. aeneus*, compared with a loricariid *A. cf. triradiatus* examined by Geerinckx *et al.* (2005), can also contribute to a better knowledge of the differences in cranial morphology and their effect on the observed variation in feeding ecology within the superfamily Loricarioidea.

MATERIALS AND METHODS

A total of 35 *C. aeneus*, which were obtained through a local pet shop and of which 25 were male, were kept in a tank with a water temperature at 24–26° C, pH level 8–8.5 and hardness of 9–12° dH. Breeding was induced following the protocol of Fuller (2001). Fifty-nine offspring specimens were removed at different ages, killed with an overdose of MS-222 [3-aminobenzoic acid ethyl ester (Sigma-Aldrich; www.sigmaldrich.com)], measured and preserved in paraformaldehyde fixative (4%). Seven specimens were selected based on standard length (L_S) and age (3.3–9.3 mm, and 0, 1, 3, 3, 4, 6 and 13 days post hatching) and were embedded in Technovit 7100 (www.kulzer-technik.de) and 2 µm thick transverse sections were made using a Reichert-Jung Polycut microtome (www.reichert.com), after which they were stained with toluidine blue. These serial sections were digitally photographed and some of them used for 3D reconstructions using Amira 3.1.1 (TGS Europe; www.tgs.com) and Rhinoceros software (Robert McNeel & Associates; www.mcneel.com). Terminology of muscles and their development follows Winterbottom (1974) and Jarvik (1980). A discussion on homology of muscles and some aspects of the innervation pattern is given by Huysentruyt *et al.* (2007).

RESULTS

STAGE 1: 3.3 MM L_S (HATCHLING) (FIG. 1)

At hatching, the chondrocranium of *C. aeneus* is still very rudimentary with the neurocranium concentrated around the notochord tip and the splanchnocranium still confined to the hyosymplectic-ptyergoquadrate plate (Arratia, 1992). At this point, a small sheet of muscular tissue, the mandibular muscle plate (*i.e.* the mandibular section of the visceral muscle primordium), is present anterior to this early suspensorium. The sheet is broad dorsally and oriented in a dorso-ventral direction with a slight anteroventral inclination in the lower half, narrowing towards its ventral tip.

STAGE 2: 4.0 MM L_S (FIG. 2)

Shortly after hatching, the neurocranium has expanded rostrally and, at the level of the splanchnocranium, the suspensorium has differentiated into a quadrate and hyosymplectic part and the hyoid arch has been formed. The dorsal part of the mandibular muscle plate has differentiated anteriorly into a musculus levator arcus palatini, which connects the antero-dorsal margin of the hyosymplectic to the anterior margin of the otic capsule, and posteriorly into a musculus dilatator operculi. Both of these muscles remain in close contact with each other and even share some fibres in adult specimens (Huysentruyt *et al.*, 2007). The musculus dilatator operculi also originates on the otic capsule but its insertion site, the opercle, is still absent at this point in development. This way, the muscle has no insertion point yet and is without function at this point in development. Posterior to the suspensorium the constrictor dorsalis and constrictor ventralis of the hyoid muscle plate are present with the former associated with the otic capsule and lying posteromedial to the hyosymplectic. The ventral constrictor (or musculus interhyoideus posterior), on the

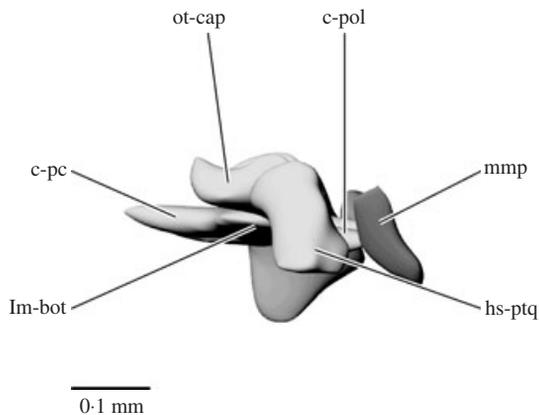


FIG. 1. Right lateral view of a 3D reconstruction of the chondrocranium and associated muscles of *Corydoras aeneus* (3.3 mm L_S). c-pc, cartilago parachordalis; c-pol, cartilago polaris; hs-ptq, hyosymplectic-ptyergoquadrate plate; lm-bot, lamina basiotica; mmp, mandibular muscle plate; ot-cap, otic capsule.

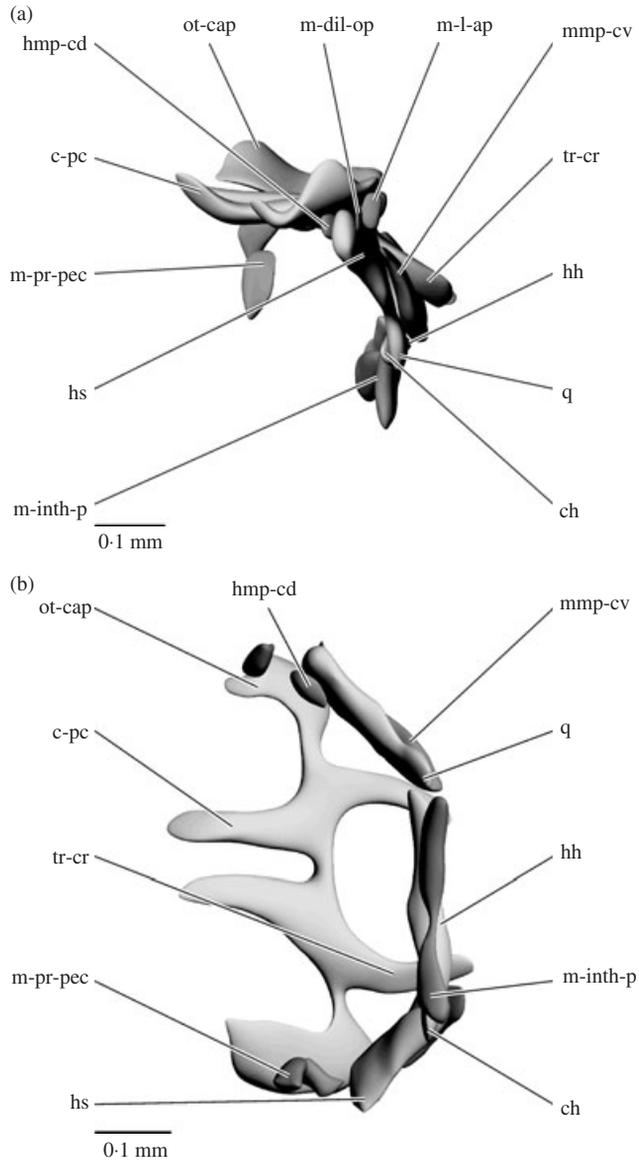


FIG. 2. Reconstruction in 3D of the chondrocranium and associated muscles of *Corydoras aeneus* (4.0 mm L_S): (a) right lateral view and (b) ventral view. ch, ceratohyal; c-pc, cartilago parachordalis; hh, hypohyal; hmp-cd, constrictor dorsalis of the hyoid muscle plate; hs, hyosymplecticum; m-dil-op, musculus dilatator operculi; m-inth-p, musculus interhyoideus posterior; m-l-ap, musculus levator arcus palatini; mmp-cv, constrictor ventralis of the mandibular muscle plate; m-pr-pec, musculus protractor pectoralis; ot-cap, otic capsule; q, quadrate; tr-cr, trabecula cranii.

other hand, is situated just posterior to the early hyoid. At the posterior margin of the neurocranium, the musculus protractor pectoralis is present, originating at the ventroposterior side of the otic capsule.

STAGE 3: 4.4 MM L_S (FIG. 3)

At this stage, the neurocranium has further differentiated. Its roof has closed anteriorly at the level of the ethmoid cartilage and posteriorly where the otic capsules and neurocranial floor have expanded significantly. In the splanchnocranium, a lower jaw is present and ventral to it, the anterior part of the mandibular muscle plate has differentiated into a musculus intermandibularis anterior and posterior. The anterior part is situated and inserts on the anterior margin of the still unpaired cartilaginous lower jaw. The posterior part, however, originates on both ceratohyals, but does not yet insert on the lower jaw and is therefore without function at this point in development. In the larger middle section of the mandibular muscle plate, the dorsal fibres are differentiated into a distinct musculus retractor tentaculi, originating on the anterior side of the suspensorium and inserting on the primordial ligament, near the autopalatine (since this ligament is very thin and irregularly shaped, it is not shown in the reconstruction). The remaining part of the mandibular muscle plate forms the still undifferentiated musculus adductor mandibulae complex that originates on the suspensorium but which, next to an insertion on the primordial ligament, also inserts on the lower jaw. The constrictor dorsalis of the hyoid muscle plate forms a musculus adductor arcus palatini, originating on the trabeculae cranii and inserting on the medial side of the suspensorium. More anteriorly, fibres of this hyoid muscle plate are differentiated further into a musculus extensor tentaculi, which also originates on the trabeculae cranii and inserts on the posterior margin of the autopalatine. More posteriorly, the constrictor dorsalis is differentiated into two parts, which both originate on the ventral side of the otic capsule. The anterior part can be discerned as the musculus adductor hyomandibulae, and the posterior part as the remaining constrictor dorsalis of the hyoid muscle plate. This section, although it inserts on the dorsomedial margin of the operculum, is not yet differentiated into a musculus adductor and musculus levator operculi. Ventrally, the musculus sternohyoideus is now present, connecting the hyoid arch with the pectoral girdle.

STAGE 4: 4.9 MM L_S [FIGS 4 AND 5(a)]

At 4.9 mm L_S the chondrocranium is more rigid anterodorsally through the tæniae marginales, and all parts of the splanchnocranium are more differentiated. The musculus extensor tentaculi is enlarged and inserts on the solum nasi. The musculus retractor tentaculi connects to the primordial ligament (not shown in reconstruction) and the musculus adductor mandibulae is not yet differentiated into an A_2 and A_1 OST- A_3 ' part [Fig. 5(a)]. Further, at the dorsal margin of the opercle the muscle sheet is fully differentiated and a separate musculus levator operculi and musculus adductor operculi are now present.

STAGE 5: 5.3 MM L_S [FIG. 5(b), (c)]

The musculus adductor mandibulae is now fully differentiated into an A_2 and A_1 OST- A_3 ' part [Fig. 5(b)] and, at this stage, the last cranial muscles to develop are the musculus hyohyoideus abductor and adductores [Fig. 5(c)].

STAGE 6 AND 7: 6.3 AND 9.3 MM L_S

No new cranial muscles developed after 5.3 mm L_S .

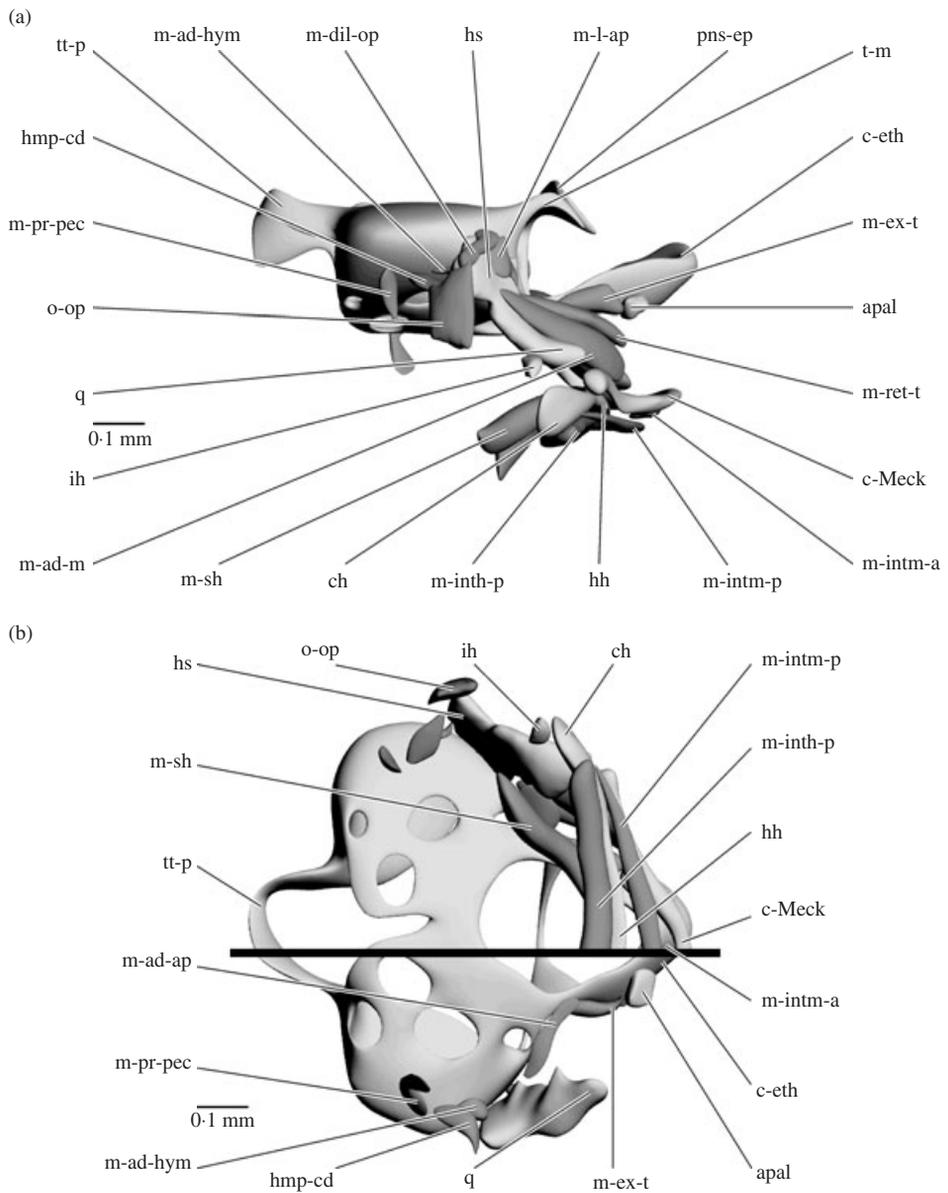


FIG. 3. Reconstruction in 3D of the chondrocranium and associated muscles of *Corydoras aeneus* (4.4 mm L_S): (a) right lateral view and (b) ventral view (opercle, hyoid and associated muscles, lower jaw and associated muscles removed on left side). apal, autopalatinum; c-eth, cartilago ethmoideum; ch, ceratohyal; c-Meck, Meckel's cartilage; hh, hypohyal; hmp-cd, constrictor dorsalis of the hyoid muscle plate; hs, hyosymplecticum; ih, interhyal; m-ad-ap, musculus adductor arcus palatini; m-ad-hym, musculus adductor hyomandibulae; m-ad-m, musculus adductor mandibulae; m-dil-op, musculus dilatator operculi; m-ext-t, musculus extensor tentaculi; m-inth-p, musculus interhyoideus posterior; m-intm-a, musculus intermandibularis anterior; m-intm-p, musculus intermandibularis posterior; m-l-ap, musculus levator arcus palatini; m-pr-pec, musculus protractor pectoralis; m-ret-t, musculus retractor tentaculi; m-sh, musculus sternohyoideus; o-op, os operculum; pns-ep, pons epiphysialis; q, quadrate; t-m, taenia marginalis; tt-p, tectum posterius.

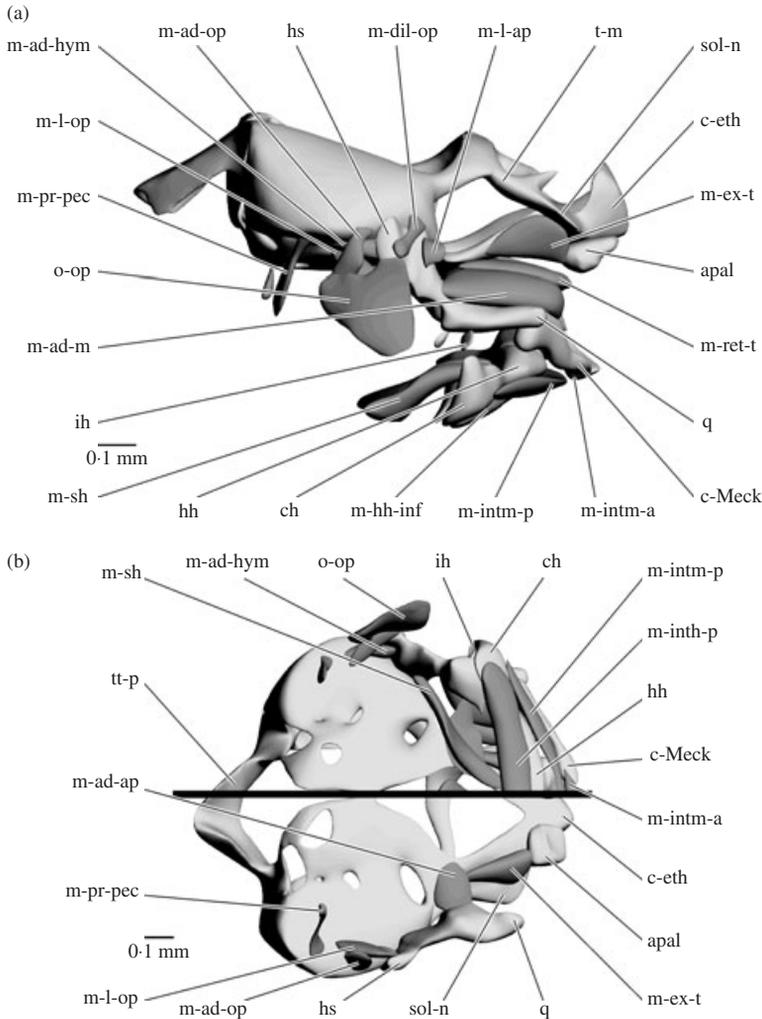


FIG. 4. Reconstruction in 3D of the chondrocranium and associated muscles of *Corydoras aeneus* (4–9 mm L_S): (a) right lateral view and (b) ventral view (opercle, hyoid and associated muscles, lower jaw and associated muscles removed on left side). apal, autopalatinum; c-eth, cartilago ethmoideum; ch, ceratohyal; c-Meck, Meckel's cartilage; hh, hypohyal; hs, hyosymplecticum; ih, interhyal; m-ad-ap, musculus adductor arcus palatini; m-ad-hym, musculus adductor hyomandibulae; m-ad-m, musculus adductor mandibulae; m-ad-op, musculus adductor operculi; m-dil-op, musculus dilatator operculi; m-ext-t, musculus extensor tentaculi; m-hh-inf, musculus hyohyoideus inferior; m-intm-a, musculus intermandibularis anterior; m-intm-p, musculus intermandibularis posterior; m-l-ap, musculus levator arcus palatini; m-l-op, musculus levator operculi; m-pr-pec, musculus protractor pectoralis; m-ret-t, musculus retractor tentaculi; m-sh, musculus sternohyoideus; o-op, os operculum; q, quadrate; sol-n, solum nasi; t-m, taenia marginalis; tt-p, tectum posterius.

DISCUSSION

Very few studies have dealt with the ontogeny of the cranial musculature in teleosts in general and Siluriformes in particular, and the ones that have often fail

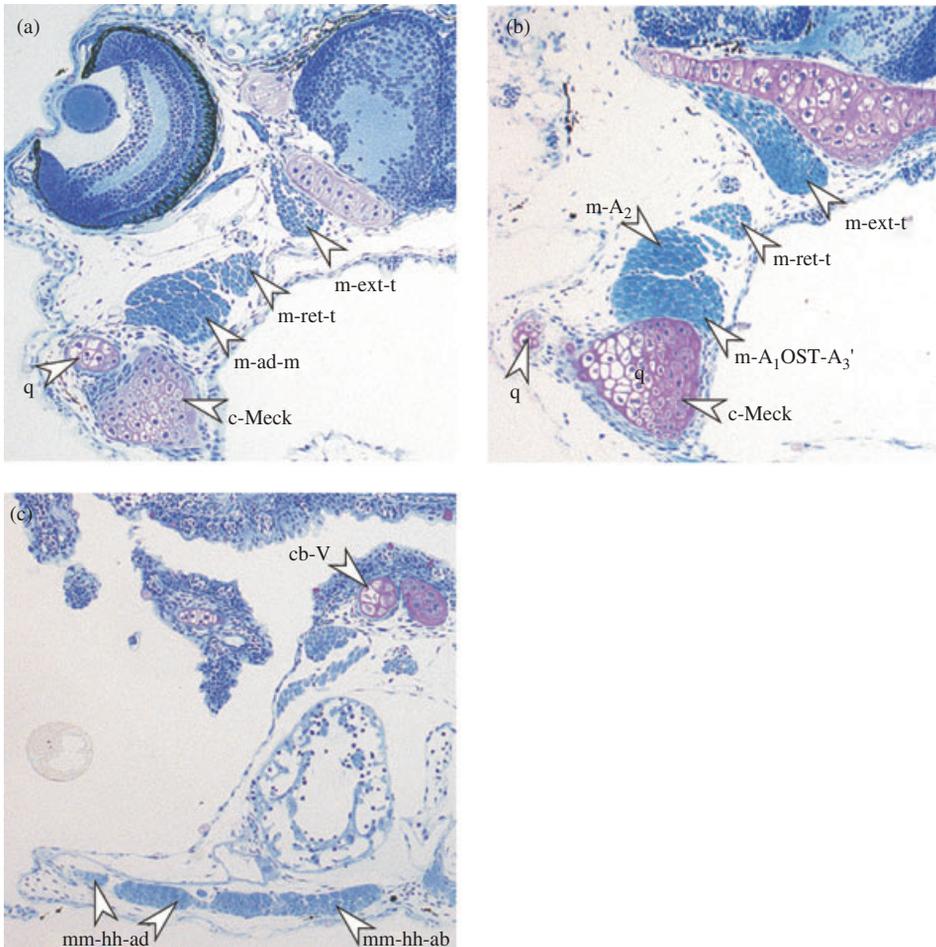


FIG. 5. Histological sections showing aspects of detailed muscular ontogeny: (a) (4.9 mm L_S) section through lower jaw-suspensorium articulation showing an undifferentiated adductor mandibulae, (b) (5.3 mm L_S) section through lower jaw-suspensorium articulation showing further differentiation in the adductor mandibulae and (c) (5.3 mm L_S) section through anterior part of last branchial arch showing differentiation in hyohyoidei muscles. cb-V, ceratobranchial V; c-Meck, Meckel's cartilage; m-A₁OST-A₃', musculus adductor mandibulae A₁OST-A₃'; m-A₂, musculus adductor mandibulae A₂; m-ad-m, musculus adductor mandibulae; m-ext-t, musculus extensor tentaculi; m-hh-ab, musculus hyohyoideus abductor; mm-hh-ad, musculi hyohyoidei adductores; m-ret-t, musculus retractor tentaculi; q, quadrate.

to describe the very earliest stages of ontogeny. As one of very few exceptions, a detailed overview on the developmental pattern of cranial muscle development in *Amia calva* L. was given by Jarvik (1980), based on work done by Allis (1897) and Edgeworth (1928). Given the phylogenetic position of the Amiiformes as a sister group to the Teleostei (Hurley *et al.*, 2007), and given the lack of other studies dealing with the subject, the pattern described by Jarvik (1980) has often been regarded as the plesiomorph teleostean pattern. In this pattern, all of the cranial muscles originate from an ontogenetic primordium of the visceral musculature, with the exception of

the eye musculature and the musculus sternohyoideus, which originate from somatic musculature (Jarvik, 1980; Adriaens & Verraes, 1996). Of the three parts of visceral muscle primordium (mandibular, hyoid and branchial muscle plates) only the first two are dealt with in this study on *C. aeneus*, and the results are compared with those on *A. cf. triradiatus* (Geerinckx & Adriaens, 2008; Geerinckx *et al.*, 2009).

MANDIBULAR MUSCLE PLATE

The small sheet of muscular tissue present at hatching in *C. aeneus* is situated anterior to the suspensorium, which suggests this muscle sheet is the early mandibular muscle plate. This is confirmed by the fact that, at 4.9 mm L_S , the different muscular units developing from this plate are all innervated by parts of the mandibular trunk of the trigeminal nerve (V), a diagnostic character of the mandibular muscle plate (Edgeworth, 1935; Jarvik, 1980). Shortly after hatching, at 4.0 mm L_S , a dorsal section splits off, forming the musculus dilatator operculi and musculus levator arcus palatini. This is in accordance with the constrictor dorsalis of the mandibular muscle plate as described by Winterbottom (1974) and Jarvik (1980). In *A. calva*, the remaining part of the mandibular plate further gives rise to the musculus palatomandibularis, a compound musculus adductor mandibulae, and a ventral musculus intermandibularis (Jarvik, 1980). Later, in *A. calva*, the musculus palatomandibularis forms the musculus nasalis, preorbitalis and parabasalis, all of which are absent in teleosts, with the exception of a preorbital muscle described in two species of cobitids (Takahasi, 1925; Winterbottom, 1974; Jarvik, 1980). Takahasi (1925) has further proposed the hypothesis that at least part of this musculus palatomandibularis has been incorporated into the A_1 part of the adductor mandibulae complex in teleosts. Given this, a primitive musculus palatomandibularis is believed to be absent in teleosts and the ventral part of the muscle plate at this point is designated as the constrictor ventralis. In *C. aeneus*, at 4.4 mm L_S , this constrictor ventralis further differentiates into a musculus intermandibularis anterior and posterior (Edgeworth, 1935; Winterbottom, 1974). In teleosts the musculus intermandibularis posterior is generally believed to have fused to the musculus interhyoideus anterior forming the compound musculus protractor hyoidei, based on an observed double innervation of this intermandibular muscle by both the mandibular trunk of the trigeminal nerve (V) and the hyoid trunk of the facial nerve (VII), and based on the presence of a myocomma in the muscle (Winterbottom, 1974). Since serial sections revealed the intermandibular muscle in *C. aeneus* to be innervated only by the inferior mandibular nerve branch of the trigeminal nerve (V) and since no myocomma was present, however, the intermandibular muscle, in this case, merely consists of the musculus intermandibularis posterior in *C. aeneus* and no musculus protractor hyoidei part is present (Huysentruyt *et al.*, 2007). This is also the case in *A. cf. triradiatus* (Geerinckx & Adriaens, 2007). The musculus intermandibularis posterior of other adult non-loricarioid siluriforms generally has a secondary subdivision, with some bundles serving the mandibular barbel base (Diogo & Chardon, 2000). In adult *C. aeneus*, such a subdivision is also present, although no insertion on the mandibular barbels is found (Huysentruyt *et al.*, 2007). These subdivisions of the musculus intermandibularis posterior are also found in *A. cf. triradiatus* but, given the rotation of the lower jaw in this species and the subsequent orientation of these bundles in combination with the absence of mandibular barbels in loricariids, Geerinckx & Adriaens (2007) have termed them

the labial and dental parts of the musculus intermandibularis posterior. Nonetheless, it seems plausible that these bundles in loricariids are homologous to the subdivisions found in *C. aeneus*, but in loricariids they partly obtained a novel function, serving the lower lip.

In *C. aeneus*, at 4.4 mm L_S , the remaining part of the adductor division of the mandibular muscle plate differentiates into a dorsal musculus retractor tentaculi, inserting only on the primordial ligament, and a more ventral compound musculus adductor mandibulae. At 5.3 mm L_S , the latter splits up further into a dorsomedial A_2 part, which also inserts on the primordial ligament and a compound A_1 OST- A_3' , diverging anteriorly into an A_1 OST bundle inserting on the dorsolateral side of the lower jaw, and an A_3' bundle inserting on the dorsomedial side. The fact that the musculus retractor tentaculi is also derived from the adductor division of the mandibular plate supports the hypothesis of homology of this muscle to part of the A_3'' , as already suggested by various authors (Lubosch, 1938; Alexander, 1965; Howes, 1983; Adriaens & Verraes, 1996, 1997*d*; Diogo & Chardon, 2000; Diogo, 2005; Huysentruyt *et al.*, 2007).

In *A. cf. triradiatus*, the adductor mandibulae complex consists of the same bundles as *C. aeneus*, with the addition of a musculus retractor veli (Geerinckx *et al.*, 2009). The bundle homologous to the musculus retractor tentaculi, on the other hand, is present, but its insertion point has shifted from the primordial ligament directly onto the premaxilla. Given this, and since in various studies on loricariids the term musculus retractor tentaculi was already mistakenly used for what Geerinckx *et al.* (2009) called the musculus levator tentaculi (Howes, 1983; Schaefer & Lauder, 1986, 1996; Diogo & Vandewalle, 2003), Geerinckx *et al.* (2009) proposed the term musculus retractor premaxillae for this muscle.

HYOID MUSCLE PLATE

In *C. aeneus*, the hyoid muscle plate starts to develop shortly after the appearance of the mandibular muscle plate. In the specimens examined, at its time of first appearance, the plate is already split up into a constrictor dorsalis and constrictor ventralis. In *A. calva*, the constrictor ventralis differentiates into a musculus interhyoideus anterior and musculus interhyoideus posterior in later development (Jarvik, 1980). Since the musculus interhyoideus anterior is then believed to further differentiate into part of the musculus protractor hyoidei in *A. calva* (Edgeworth, 1935; Winterbottom, 1974), which is absent in *C. aeneus* (Huysentruyt *et al.*, 2007), the ventral part of the intermandibular muscle present in *C. aeneus* can be assumed homologous with the musculus interhyoideus posterior of *A. calva*. This is also confirmed by the fact that this muscle plate further differentiates into the musculus hyohyoideus inferior, the musculus hyohyoideus abductor and the musculi hyhoidei adductores, all of which are believed to differentiate from the musculus interhyoideus posterior (Winterbottom, 1974; Jarvik, 1980). Jarvik (1980) further describes the constrictor dorsalis as differentiating into a single anterior muscle, the musculus adductor hyomandibulae, and two posterior muscles, the musculus adductor operculi and musculus levator operculi. At 4.4 mm L_S , however, only two muscle bundles were found in *C. aeneus*. Given their position and the fact that the anterior bundle inserts on the medial side of the hyosymplectic, this anterior bundle is considered homologous with the musculus adductor hyomandibulae. The posterior bundle is still homologous

to the posterior portion of the constrictor dorsalis in *A. calva*, which, at this stage in early ontogeny, does not differentiate into a musculus adductor operculi and musculus levator operculi. In addition, in teleosts the anterior part of this muscle plate further differentiates, giving rise to the musculus adductor arcus palatini, which, in turn, gives rise anteriorly to the musculus extensor tentaculi (Winterbottom, 1974; Diogo & Vandewalle, 2003). It has also been argued that the musculus adductor arcus palatini has evolved from a shifted position of the musculus adductor hyomandibulae (Winterbottom, 1974). In several teleosts, however, both a musculus adductor arcus palatini and a musculus adductor hyomandibulae are frequently found (Winterbottom, 1974), as in *C. aeneus*. Winterbottom (1974) has argued that in these cases, the musculus adductor hyomandibulae is a secondary derivative of the anterior fibres of the musculus adductor operculi or of the posterior fibres of the musculus adductor arcus palatini. Diogo & Vandewalle (2003), in their overview on siluriform cranial muscles, accept the former possibility, but provide no arguments for this choice. The data for *C. aeneus* now show that at 4.4 mm L_S , the dorsal constrictor is divided into a musculus extensor tentaculi, a musculus adductor arcus palatini, a musculus adductor hyomandibulae and a dorsal muscle associated with the opercle which later differentiates into a musculus levator operculi and musculus adductor operculi part. Therefore, the possibility of the musculus adductor hyomandibulae being a secondary derivative of the musculus adductor operculi in this case is rejected, since the former differentiates earlier in ontogeny than the latter. The other option where the musculus adductor hyomandibulae is derived from the posterior part of the musculus adductor arcus palatini would therefore seem more plausible here.

In comparison with *A. cf. triradiatus*, a similar pattern of development in the hyoid muscle plate is found in *C. aeneus*, but with an increase in complexity, as is the case in the mandibular muscle plate. This way, the dorsal constrictor in *A. cf. triradiatus* gives rise to the same muscles as in *C. aeneus*. The musculus levator operculi, in *A. cf. triradiatus*, however, later hypertrophies, resulting in the formation of large fossae in the neurcranial roof (Geerinckx & Adriaens, 2008). Additionally, in *A. cf. triradiatus* and some other loricariids, the musculus extensor tentaculi is differentiated into two separate bundles (as opposed to a single muscle diverging posteriorly in *C. aeneus*) and a loricariid neof ormation is present called the musculus levator tentaculi (Diogo, 2005; Geerinckx *et al.*, 2009). This fits the evolutionary trend of an increased differentiation of the constrictor dorsalis of the hyoid muscle plate in teleosts, in which anterior fibres of the musculus adductor arcus palatini give rise to new muscles in various groups. In loricarioids, the musculus extensor tentaculi arises and later splits up into two separate bundles with a subsequent differentiation of the musculus levator tentaculi in Loricariidae. In Acanthuridae, Balistidae and Ostraciidae, the anterior portion of the musculus adductor arcus palatini gives rise to a musculus retractor arcus palatini and in the balistid genus *Balistes*, it differentiates into a musculus retractor palatini.

The ontogeny of the musculus adductor hyomandibulae in *A. cf. triradiatus*, however, differs substantially from the situation found in *C. aeneus*. In *A. cf. triradiatus*, this muscle appears at a later stage of ontogeny than the musculus adductor arcus palatini and musculus adductor operculi. In addition, it appears in close contact with the muscularis adductor operculi (Geerinckx *et al.*, 2009), which, in this case, would confirm the hypothesis of Winterbottom (1974) and Diogo & Vandewalle (2003) that it is a secondary derivative of the musculus adductor operculi. This would imply that

the musculus adductor hyomandibulae in *A. cf. triradiatus* is not homologous with the same muscle in primitive species like *A. calva*. Given the results found in both *C. aeneus* and *A. cf. triradiatus*, and the fact that, in more primitive lineages like *A. calva*, a musculus adductor hyomandibulae and no musculus adductor operculi are present, it would seem that multiple pathways towards the formation of a musculus adductor hyomandibulae exist in teleosts. Given the function of this muscle and its consistent origin on the otic region of the neurocranium and insertion on the dorso-medial side of the suspensorium, however, the use of the name musculus adductor hyomandibulae seems justifiable on both a functional and morphological, but not a phylogenetic (*i.e.* homology) basis.

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