

Ontogeny of the jaw and maxillary barbel musculature in the armoured catfish families Loricariidae and Callichthyidae (Loricarioidea, Siluriformes), with a discussion on muscle homologies

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The neotropical loricarioid catfishes include six families, the most species-rich of which are the Callichthyidae and the Loricariidae. Loricariidae (suckermouth armoured catfishes) have a highly specialized head morphology, including an exceptionally large number of muscles derived from the adductor mandibulae complex and the adductor arcus palatini. Terminology of these muscles varies among the literature, and no data exist on their ontogenetic origin. A detailed examination of the ontogeny of both a callichthyid and a loricariid representative now reveals the identity of the jaw and maxillary barbel musculature, and supports new hypotheses concerning homologies. The adductor mandibulae muscle itself is homologous to the A1-OST and A3' of basal catfishes, and the A3' has given rise to the newly evolved loricariid retractor veli as well. The A2 and A3'' have resulted in the retractor tentaculi of Callichthyidae and the retractor premaxillae of Loricariidae. Thus, these two muscles are shown to be homologous. In Loricariidae, the extensor tentaculi consists of two separate muscles inserting on the autopalatine, and evidence is given on the evolutionary origin of the loricariid levator tentaculi (previously and erroneously known as retractor tentaculi) from the extensor tentaculi, and not the adductor mandibulae complex. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 155, 76–96.

ADDITIONAL KEYWORDS: adductor mandibulae – *Ancistrus* – *Corydoras* – development – homology – myology – suckermouth catfish.

INTRODUCTION

Research on teleostean ontogeny has generally involved studies concerning external morphology and skeletal development. Only a few authors have investigated the myological transformations (e.g. Jarvik, 1980; Surlemont, Chardon & Vandewalle, 1989; Surlemont & Vandewalle, 1991; Adriaens & Verraes, 1996, 1997a, b, c). Data on the early ontogeny of the musculature might, however, yield important findings in cases where origins or homologies of muscles are unknown or questioned. Also, transformations of musculo-skeletal systems are key factors in changes

in the efficiency of functional units during ontogeny, and, hence, survival of larval teleosts.

Our knowledge of the musculature serving the jaws and the maxillary barbels in ostariophysan teleosts suffers from the variety in number and properties of the muscles, although Takahasi (1925), Winterbottom (1974), Gosline (1989), Adriaens & Verraes (1996), Diogo & Chardon (2000), Wu & Shen (2004) and others have published important contributions toward the understanding of the origin and homologies of these muscles. For the loricarioid catfishes the situation is even more complex, due to the increasing number of separate subdivisions with shifted insertions, added to the often highly mobile and differently orientated jaw bones (Howes, 1983a; Schaefer & Lauder, 1986, 1996; Geerinckx *et al.*, 2007b). As a consequence, the

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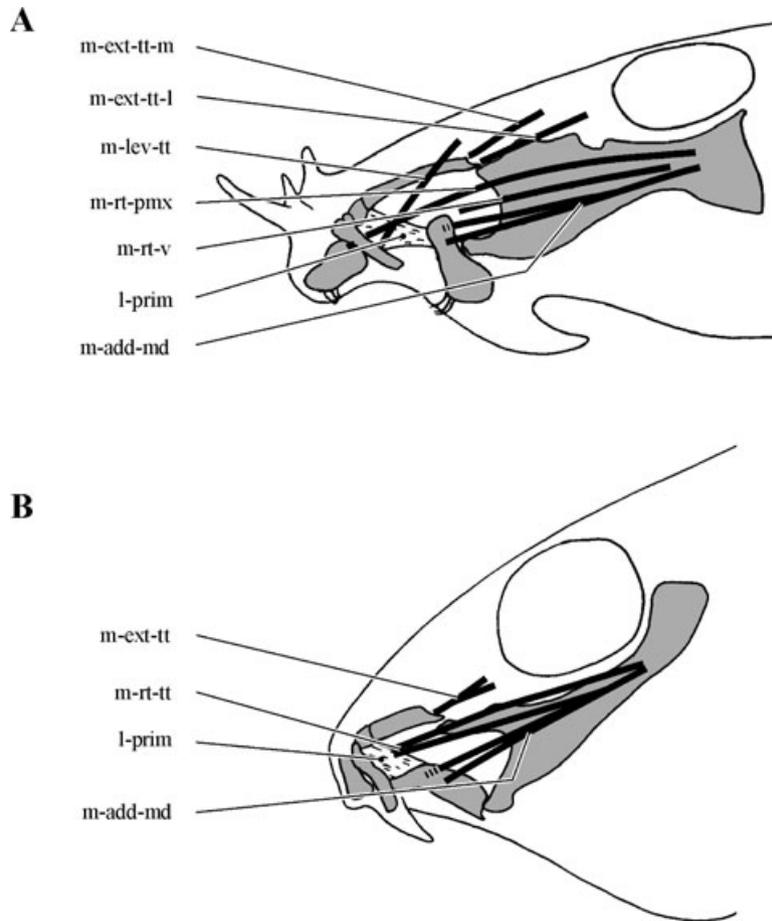


Figure 1. Schematic lateral view of jaw and maxillary barbel musculature in (A) *Ancistrus cf. triradiatus* and (B) *Corydoras aeneus*. Redrawn from Schaefer & Lauder (1986) and adjusted according to Geerinckx *et al.* (2007b). Names as featured in the current paper.

muscular nomenclature is almost as diverse as the musculature itself, and names are usually appointed on the basis of assumed muscle function, which may or may not be coupled to a homology.

This paper focuses on the adductor mandibulae complex, originating from the dorsal adductor part of the mandibular muscle plate, and the extensor tentaculi muscles, originating from the adductor arcus palatini, which is the anteriormost dorsal part of the hyoid muscle plate (Jarvik, 1980). The retractor tentaculi of most siluriforms is considered a derivative of the adductor mandibulae complex (e.g. Eaton, 1948; Howes, 1983b; Adriaens & Verraes, 1996). We studied the ontogeny of the jaw and maxillary barbel musculature of a specialized loricariid, and compared it with that of a more basal callichthyid. The ontogeny of the intermandibularis muscles in a loricariid, also inserting on the lower jaw, has been discussed previously (Geerinckx & Adriaens, 2007).

Loricariid head musculature has been described by Howes (1983a), Schaefer & Lauder (1986), Schaefer

(1997) and Geerinckx *et al.* (2007b) (Fig. 1A). In most Loricariidae, the adductor mandibulae part that acts directly on the lower jaw (muscle *b* of Howes, 1983a) originates on the quadrate, hyomandibula and preopercle, and inserts on the angulo-articular and dentary bones of the lower jaw. The retractor premaxillae (muscle *c* of Howes, 1983a) originates on the hyomandibula, and inserts tendinously on the posterior aspect of the premaxilla. The retractor veli (muscle *d* or retractor palatini of Howes, 1983a) originates on the metapterygoid and sends its tendon into the oral valve. The 'retractor tentaculi' (muscle *a* of Howes, 1983a) has its origin on the anteroventral face of the lateral ethmoid and runs to the maxillary bone. The extensor tentaculi consists of a lateral and a medial part that are completely separated (*e* and *f* of Howes, 1983a). The extensor tentaculi pars lateralis (*e*) runs from a canal-like groove, formed by the lateral ethmoid and the metapterygoid, to the ventrolateral autopalatine process [this groove is not canal-like in those loricariids that lack a well-

Table 1. Specimens used in the present study

SL (mm)	Age (PF)	Method	Staining	Used for
<i>Ancistrus cf. triradiatus</i>				
6.1	4	SS (2 µm)	T	3D reconstruction + drawing
7.0	6	SS (2 µm)	T	Drawing
8.0	7	SS (2 µm)	T	3D reconstruction
10.2	14	SS (2 µm)	T	Observation
12.4	43	SS (2 µm)	T	Observation
33.5	160 (subadult)	SS (5 µm)	T	Observation
70	? (adult)	Dissection	–	Observation
94	? (adult)	Dissection	–	Observation
102	? (adult)	Clearing	AB + AR	Observation
<i>Pterygoplichthys disjunctivus</i>				
62.8	? (subadult)	SS (5 µm)	T	Observation
<i>Otocinclus vestitus</i>				
22.1	? (adult)	SS (5 µm)	T	Observation
<i>Farlowella acus</i>				
155	? (adult)	SS (5 µm)	T	Observation
<i>Corydoras aeneus</i>				
4.9	6	SS (2 µm)	T	Drawing
9.3	16	SS (2 µm)	T	Observation
34	? (adult)	Dissection	–	Drawing
39	? (adult)	SS (5 µm)	T	Drawing

AB, alcian blue; AR, alizarin red S; PF, post-fertilization; SL, standard length; SS, serial sectioning; T, toluidine blue.

developed lateral metapterygoid ridge (Howes, 1983a; Armbruster, 2004)]. The extensor tentaculi pars medialis (*f*) connects the ventromedial autopalatine process with the ventral skull surface and is considered the antagonist of the retractor premaxillae (Alexander, 1965; Howes, 1983a; Geerinckx *et al.*, 2007b). The most relevant accounts on callichthyid musculature have been published by Howes (1983a), Schaefer & Lauder (1986) and Huysentruyt, Geerinckx & Adriaens (2007) (Fig. 1B).

The autopalatine–maxillary mechanism is synapomorphic for catfishes, but some significant structural diversity has been noticed within the group (Gosline, 1975; Ghiot, 1978; Ghiot, Vandewalle & Chardon, 1984; Adriaens & Verraes, 1997b; Diogo & Vandewalle, 2003a). The mechanism in Loricariidae and Callichthyidae is that of the rotating type, and is characterized by a neurocranial articulation at the posterior end of the autopalatine (Huysentruyt & Adriaens, 2005; Geerinckx *et al.*, 2007b).

MATERIAL AND METHODS

Specimens of the loricariid *Ancistrus cf. triradiatus* Eigenmann and the callichthyid *Corydoras aeneus* (Gill) were commercially obtained and bred in aquaria. Embryos and juveniles were sedated in MS-222 and

fixed in a paraformaldehyde/glutaraldehyde solution at different time intervals (Table 1). Specimens were arbitrarily selected, representing the ontogenetic period in which the muscles arise and transform. For both species, the embryonic and juvenile specimens were all fathered by the same male. Toluidine-stained 2- or 5-µm sections were embedded in Technovit 7100, cut with a Reichert-Jung Polycut microtome and examined using a Reichert-Jung Polyvar light microscope. Digital photographs were taken from the serial sections. Graphical three-dimensional reconstructions were made from serial sections of an *A. cf. triradiatus* and a *C. aeneus* specimen, using the software packages Amira 3.1.1 (TGS) and Rhinoceros 3.0 (McNeel). Skeletal structures were studied on *in toto* cleared and stained specimens, following the method of Taylor & Van Dyke (1985). Examination of the specimens was made using an Olympus SZX9 stereoscopic microscope, equipped with a camera lucida for drawing. Adult musculature was studied for comparison, but we refer to Geerinckx *et al.* (2007b) and Huysentruyt *et al.* (2007) for more detailed accounts. In the study of nerve patterns, serial sections of three other loricariid species were used to verify whether the patterns seen in *A. cf. triradiatus* were indeed representative for loricariids in general (see Table 1). We base our written results on the study of a few of the examined (serially

sectioned) specimens, but refer to the other specimens when necessary. Our discussion on the functionality of muscles is based on anatomy only, as no biomechanical studies could be done on such small specimens.

Abbreviations: br-lev-tt, branch to musculus levator tentaculi; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; ch, ceratohyale; hh, hypohyale; hs, hyosymplecticum; infr-r-V-VII, infraorbital root of trigeminal and facial nerves; l-prim, ligamentum primordium; lm-on, lamina orbitonasalis; lm-prc, lamina praecerebralis; m-add-apal, musculus adductor arcus palatini; m-add-md, musculus adductor mandibulae; m-add-md-e, external part of musculus adductor mandibulae; m-add-md-i, internal part of musculus adductor mandibulae; m-ext-tt, musculus extensor tentaculi; m-ext-tt-l, musculus extensor tentaculi pars lateralis; m-ext-tt-m, musculus extensor tentaculi pars medialis; m-lev-apal, musculus levator arcus palatini; m-lev-tt, musculus levator tentaculi; m-rt-pmx, musculus retractor premaxillae; m-rt-tt, musculus retractor tentaculi; m-rt-v, musculus retractor veli; n-I, nervus olfactorius; n-II, nervus opticus; not, notochord; o-aa, os angulo-articulare; o-apal, os autopalatium; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den, os dentale; o-den-mm, os dento-mentomeckelium; o-fr, os frontale; o-hh, os hypohyale; o-hh-d, os hypohyale dorsale; o-hh-v, os hypohyale ventrale; o-io-I/III, os infraorbitale I/III; o-lacr, os lacrimale; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-pmx, os praemaxillare; o-pop, os praeoperculare; o-pvm, os praevomerale; o-q, os quadratum; or-v, oral valve; p-q, pars quadrata of palatoquadratum; pal, palatinum; pr-cor, processus coronoideus; pr-pt, processus pterygoideus; r-bc, ramus buccalis nervus facialis; r-md-V, ramus mandibularis nervus trigeminus; r-md-e, ramus mandibularis externus; r-md-i, ramus mandibularis internus; r-mx, ramus maxillaris nervus trigeminus; r-mx/bc, anastomosed rami maxillaris and buccalis; r-mx/bc/md, anastomosed rami maxillaris, buccalis and mandibularis; sol-n, solum nasi; t-g, tooth germs; t-m, taenia marginalis; tr-cr, trabecula cranii.

RESULTS

In this paper, 'adductor mandibulae' refers to the cheek muscle division(s) inserting on the lower jaw, whereas 'adductor mandibulae complex' refers to the whole set of muscle subdivisions originating from the A1-OST, A2 and A3 parts (there are no A1 and A ω , see below). In the description of *Ancistrus cf. triradiatus*, the loricariid muscle known as the 'retractor tentaculi' (see Introduction) is here referred to as levator tenta-

culi, because of the hypothesis of a non-homology with the retractor tentaculi in *Corydoras aeneus* and other siluriforms, as presented in the Discussion. Argumentation concerning homologies, as well as the use of the nomenclature, is given in the Discussion.

ONTOGENY

Ancistrus cf. triradiatus

6.1-mm SL stage: In this embryonic specimen, more or less 1 day before hatching, most of the cheek musculature is already visible, albeit in a rudimentary state. Observations of living embryos (removed from the egg scale) indicate that only hyoid movements visibly occur in the head. The chondrocranium is only partially formed, but the trabecular bar and main splanchnocranial elements are present (Geerinckx, Brunain & Adriaens, 2005). Notice that in Figure 2 (and Fig. 4) the branchial basket and the developing teeth are not shown. The adductor mandibulae complex consists of four recognizable divisions (Fig. 2A, B). The outermost muscle, the external part of the adductor mandibulae, originates near the anterolateral margin of the hyosymplectic part of the cartilaginous suspensorium, close to the palatoquadrate part. It runs dorsolateral to the palatoquadrate, and ends near, but not on, the dorsolateral aspect of Meckel's cartilage (Fig. 2C).

The second, medioventral muscle, the internal part of the adductor mandibulae, originates anterior to the anterodorsal margin of the palatoquadrate. The origin of this muscle is confluent with the external adductor mandibulae part (Fig. 3C). It almost reaches the posterodorsal face of Meckel's cartilage, slightly medial to the basis of the coronoid process (Fig. 2).

The third muscle, the retractor premaxillae, is situated mediodorsal to the external adductor mandibulae part, their posterior fibres contacting each other (Fig. 3C). The fibres of the retractor premaxillae pass the coronoid process of Meckel's cartilage dorsally, and end just anterior to it (thus having no insertion). On the medioventral aspect of the anteriormost part of the muscle, a developing aponeurosis is seen (Fig. 3A), without any contact to a recognizable structure whatsoever. The premaxilla is only recognizable by the presence of a few tooth germs, borne by a thin sheet, which is barely ossified.

The retractor veli, the fourth, medialmost muscle of the adductor mandibulae complex, originates close to the anterodorsal margin of the palatoquadrate, more or less where the pterygoid process will later develop (Fig. 3B). Except anteriorly, the fibres are continuous with those of the internal adductor mandibulae part, and thus, indirectly, with the external adductor mandibulae and the retractor premaxillae (Fig. 3C). The anterior end of the retractor veli is situated

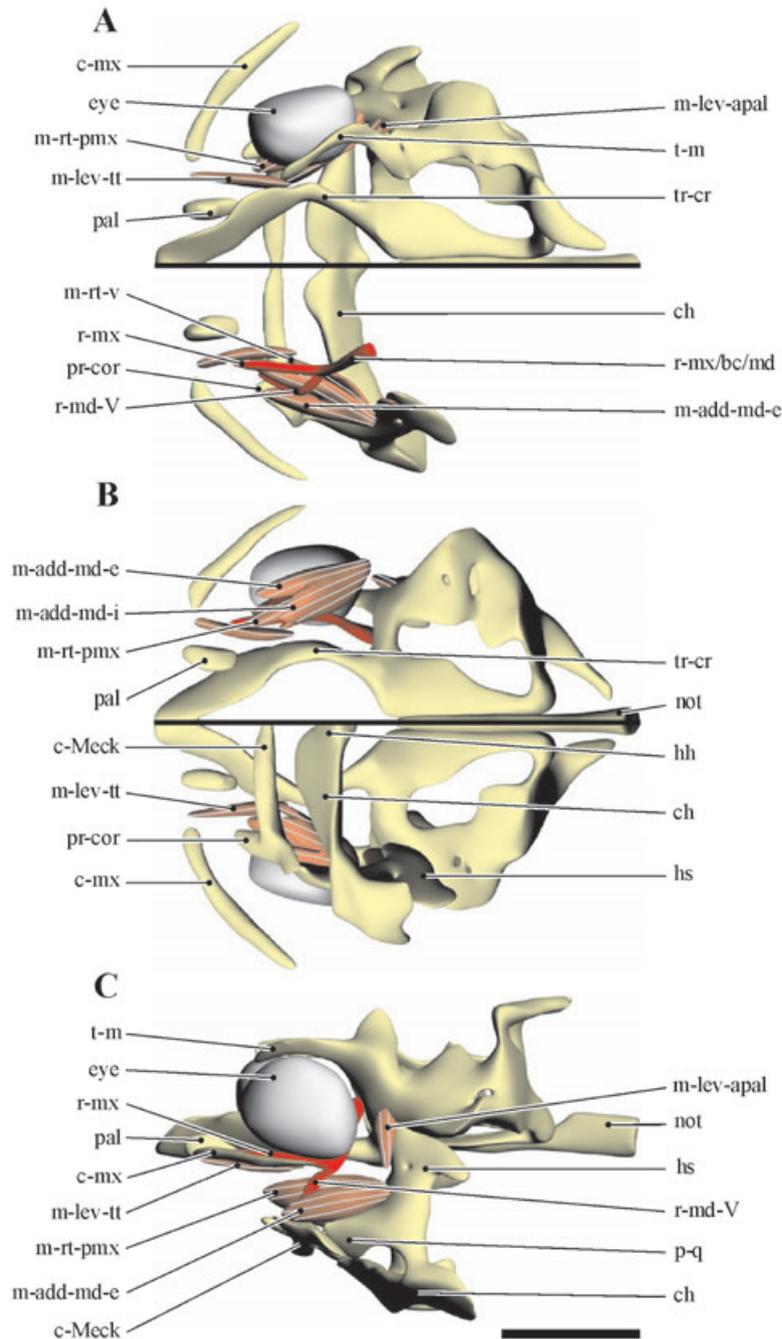


Figure 2. Three-dimensional reconstruction of the head of a 6.1-mm SL *Ancistrus* cf. *triradiatus* embryo. Only the skeleton and the jaw and maxillary barbel musculature are shown. A, dorsal view (left half of neurocranium removed); B, ventral view (left suspensorium, hyoid and mandibular arch removed); C, lateral view. Scale bar = 0.5 mm.

posterodorsal to Meckel's cartilage. Its fibres diverge medially from the rest of the complex, and are directed toward the tissue bordering the oral cavity, at the point where the oral valve is developing.

The extensor tentaculi has not yet developed by this time. The posterior end of the palatine carti-

lage, to which the muscle inserts in the older specimens, is just beginning to develop. The levator tentaculi, however, has already developed, well apart from the adductor mandibulae complex (Fig. 3A; also see Fig. 3D). It originates close to the trabecular bar of the skull floor, near the still

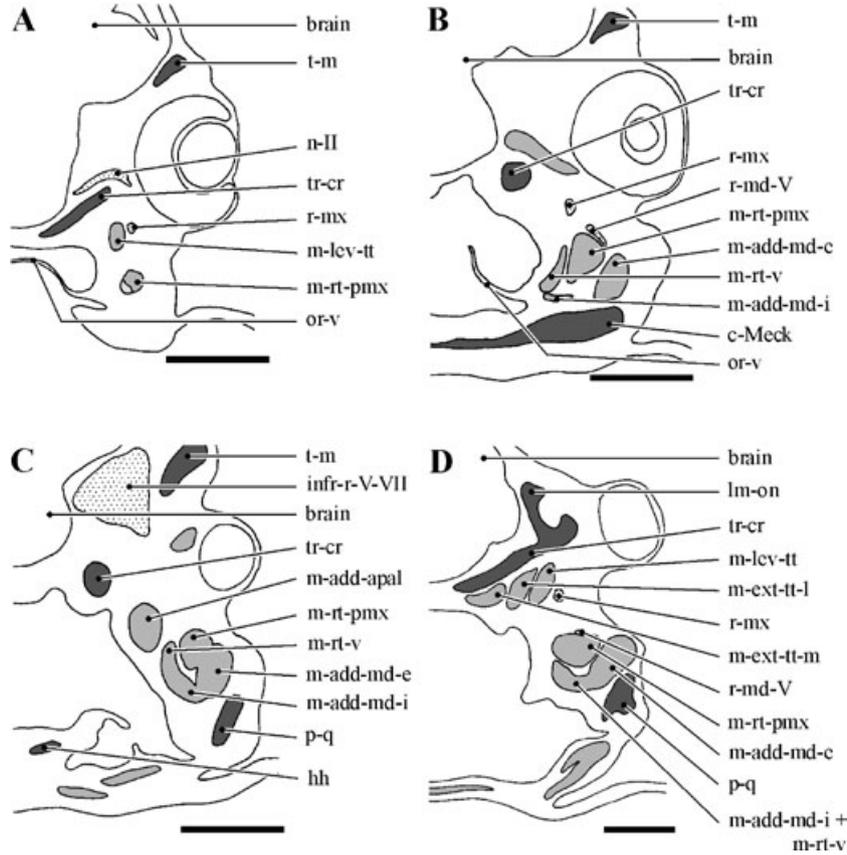


Figure 3. Cross-sections of embryonic *Ancistrus cf. triradiatus*. Only the lower right part of each section is shown. A, anterior to lower jaw; B, at lower jaw; C, posterior to lower jaw (A–C: 6.1 mm SL); D, just posterior to lower jaw (7.0 mm SL) (dark grey indicates cartilage, light grey indicates muscle, stippled areas indicate nerves). Scale bar = 0.2 mm.

rudimentary orbitonasal lamina. It passes just lateral to the palatine cartilage, and ends without a clear insertion between the palatine and maxillary cartilages (Fig. 2B). Only the first anlage (no calcification) of the maxillary bone is seen, anterior to the rostral end of the muscle.

The path of some of the main nerve branches emerging from the infraorbital trunk of the trigemino-facial complex can already be followed. The mandibular branch of the trigeminal nerve separates from the trigemino-facial complex outside the neurocranium, and crosses the retractor premaxillae from medial to lateral (Fig. 3B), subsequently entering the adductor mandibulae complex between the retractor premaxillae and the external adductor mandibulae part. It passes over Meckel’s cartilage just medial to the coronoid process, thus anterior to the rostral end of the internal adductor mandibulae part. The anastomosed maxillary and buccal branches run in a rostral direction, lateroventral of the trabecular bar. They are not adjacent to the adductor mandibulae complex, but lie just lateral to the levator tentaculi (Fig. 3A). In this stage it is not clear where both

branches separate. At the level of the anterior end of the levator tentaculi the fibres diverge, but they are not sufficiently developed to allow further examination of their courses. For the same reason, no muscle innervation can be observed at this stage.

8.0-mm SL stage: In this specimen still few elements are ossifying, those in the cheek region being the dento-mentomeckelium (the dentary is barely fused to the mentomeckelium), the premaxilla and the maxilla. Cheek muscles that were already present have enlarged substantially (Fig. 4A–C). The extensor tentaculi is present as well, having most probably appeared somewhere between the 6.1- and 7.0-mm stages (Figs 3D, 5A).

The external adductor mandibulae part inserts on the lateral portion of Meckel’s cartilage and on its coronoid process, which points rostradorsally. In the posterior half of the muscle, the fibres still cannot be separated from those of the other muscles of the adductor mandibulae complex (Fig. 5B). The origin of the external adductor mandibulae part is on the hyosymplectic part of the suspensorium, up to the insertion

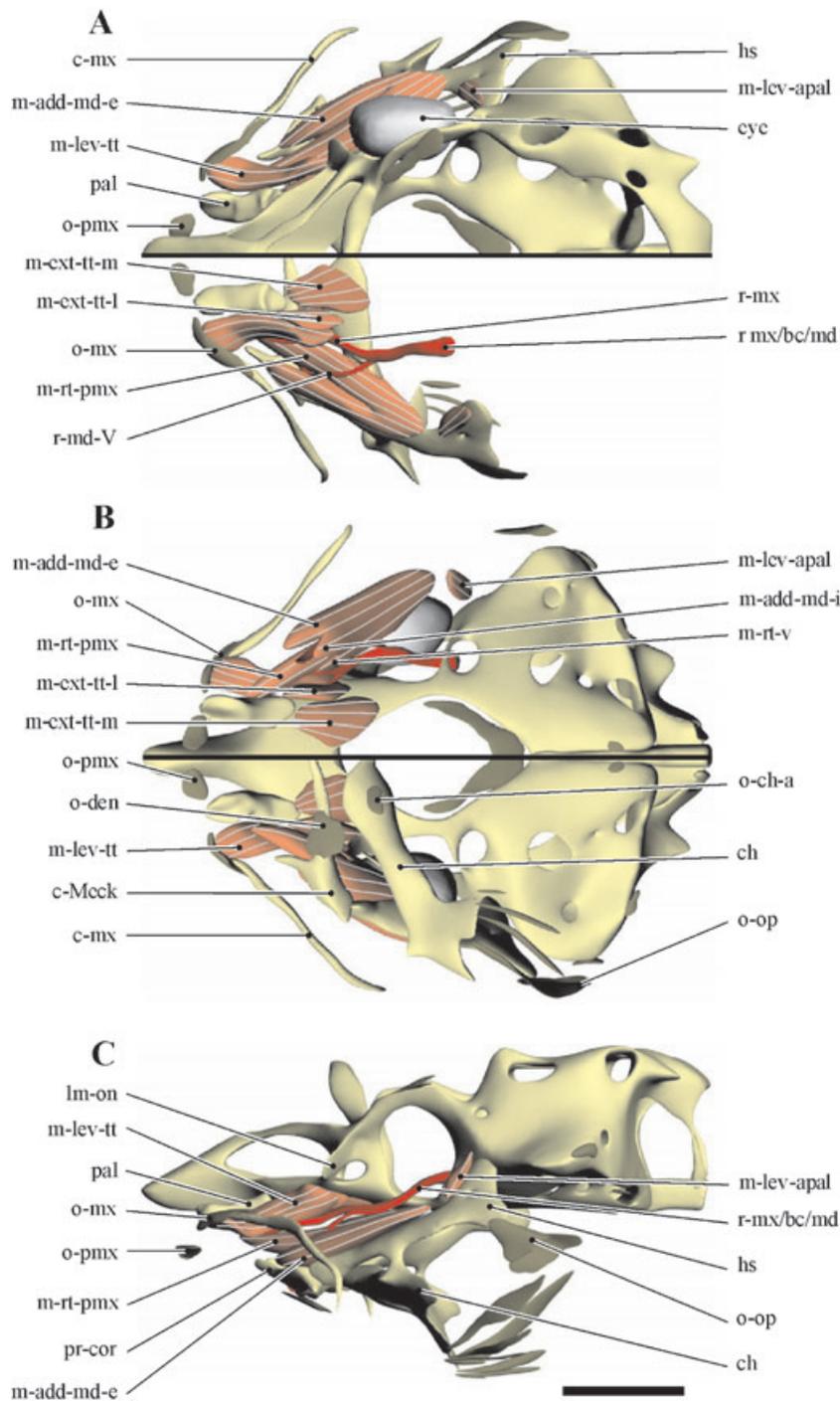


Figure 4. Three-dimensional reconstruction of the head of an 8.0-mm SL *Ancistrus* cf. *triradiatus* free-living embryo. Only the skeleton and the jaw and maxillary barbel musculature are shown, as well as the principal nerve branches in the jaw region (the buccal branches have been omitted). A, dorsal view (left half of neurocranium removed); B, ventral view (left suspensorium, hyoid and mandibular arch removed); C, lateral view. Scale bar = 0.5 mm.

place of the levator arcus palatini, which is situated posteromedial to it. As dense connective tissue connects the muscle to both its insertion surfaces, it can be assumed that the muscle could now well be functional.

The internal adductor mandibulae part now has both its insertions as well. A part of it originates on the lateral aspect of the anterior part of the hyosymplectic cartilage, while an equal portion of the muscle

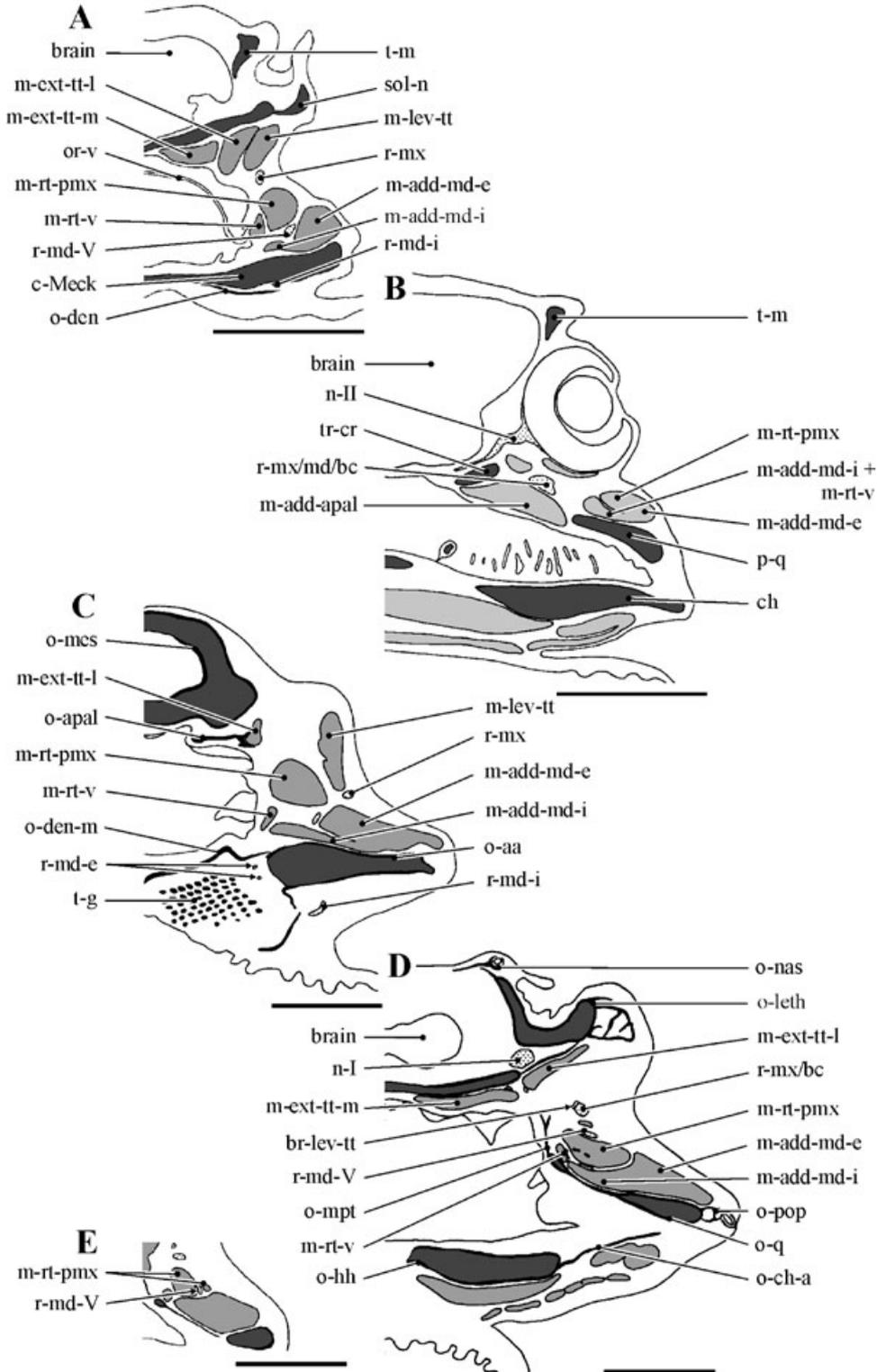


Figure 5. Cross-sections of embryonic *Ancistrus* cf. *triradiatus*. Only the right half of each section is shown (only adductor mandibulae complex in E). A, at lower jaw; B, at posterior side of hyoid bar (A, B: 8.0-mm SL); C, at lower jaw; D, at anterior side of hyoid bar (C, D: 12.4-mm SL); E, at anterior side of hyoid bar (10.2-mm SL) (black indicates bone, dark grey indicates cartilage, light grey indicates muscle, stippled areas indicate nerves). Scale bar = 0.5 mm.

originates on the dorsal tissue sheet extending between this suspensorial part and the now completely developed pterygoid process. It can be supposed that, as long as this sheet is not ossified into the dermal part of the metapterygoid bone, these ventralmost fibres probably are not functional. The muscle appears to have developed an insertion on Meckel's cartilage (Fig. 5A).

The retractor premaxillae is substantially larger than that in younger specimens, and has become more separated from the external adductor mandibulae part. In transsection, the muscle is flattened posteriorly, but more or less round for most of its length. Its fibres originate on the hyosymplectic, medial to those of the external adductor mandibulae part, and anterior to anteromedial to the course and insertion of the levator arcus palatini. The muscle has considerably lengthened, even compared with the other cheek muscles, and now reaches anterior to the lower jaw. Its tendon, developed from the ventromedial aponeurosis, is continuous with the connective tissue sheet that stretches between the developing maxillary and premaxillary bones, and the anterior tip of the palatine cartilage. Considering the location of this connective tissue sheet, it corresponds to the primordial ligament as defined by Gosline (1986: 707). Thus, only indirect tendinous contact exists between the retractor premaxillae and the maxilla or the premaxilla.

The retractor veli is still continuous with the internal adductor mandibulae part for half of its length, with its origin at the basis of the pterygoid process. It can now be clearly observed that anteriorly the fibres run up to the lateral edge of the oral valve, contacting the dense connective tissue that continues inside this valve (Fig. 5A, B).

The extensor tentaculi pars medialis originates near the ventral side of the trabecular bar, at the level of the preorbital basis. It is a horizontally flattened muscle, ending at the posteriomedial face of the palatine cartilage. It is unlikely that the muscle is functional at this moment, as there seems to be no contact between the developing tendon and the palatine cartilage. Caudally, the muscle fibres touch those of the adductor arcus palatini, although there is no continuity between both muscles. The extensor tentaculi pars lateralis is more adjacent to the levator tentaculi (see below) than to the pars medialis. The origin of the extensor tentaculi pars lateralis is near the ventral side of the trabecular bar, at the level of the orbitonasal foramen, but most fibres originate more laterally, ventral to the orbitonasal lamina. The pars lateralis runs further rostrally, compared with the pars medialis, toward the posterolateral edge of the back of the palatine cartilage. It does not seem, however, to reach it, nor does it provide any sign of a

tendinous insertion. There is no contact between the fibres of both retractor tentaculi parts.

The levator tentaculi very much resembles the extensor tentaculi pars lateralis: it lies directly laterally to it, is equally flattened in a vertical plane, and also originates near the ventral side of the orbitonasal lamina. Far posteriorly, the muscles are in contact, but do not merge. The levator tentaculi, however, continues further rostrally along the lateral aspect of the palatine cartilage. The ventral fibres are now directed somewhat laterally, so that, at the level of the anterior palatine end, the muscle is horizontally instead of vertically flattened (Fig. 4A–C). As such, the ventral fibres insert most distally on the maxilla; the dorsal ones insert most proximally, close to the palatine articulation. The levator tentaculi and both extensor tentaculi muscles are already present in the younger 7.0-mm specimen as well, but less developed, and with fibres also close to each other but not confluent (Figs 3D, 5A).

The maxillary and buccal nerve branches are still anastomosed. After separating from the mandibular branch dorsal to the pterygoid process basis, they continue as one strand, mediodorsal to the adductor mandibulae complex, along the lateroventral edge of the levator tentaculi. Two minor branchlets leave the bundle to innervate the levator tentaculi. On arrival on the dorsal surface of the retractor premaxillae, the mandibular branch splits off a medial branch that enters the adductor mandibulae complex dorsomedially, and then continues laterally before descending between the retractor premaxillae and the external adductor mandibulae part. The main branch runs dorsally on the internal adductor mandibulae part where this muscle inserts on the lower jaw, and then runs over Meckel's cartilage before innervating the dentary region and the muscles ventral to it (Fig. 4A–C).

12.4-mm SL stage: As most skeletal structures of the skull start to ossify at a standard length of 9–11 mm, important changes in shape are seen by the time a standard length of 12.4 mm is reached (Geerinckx *et al.*, 2007a). During the onset of this major ossification period, the upper snout region goes through a phase of elongation, while the lower jaw acquires its more or less final shape. These transformations are reflected in the muscular development.

The orientation of the suspensorium has become more rostrocaudal than dorsoventral. The longitudinal axis of the lower jaw is directed medially instead of rostrally (as is the case in most teleosts), and the direction of the muscles inserting onto the lower jaw is perpendicular to it. Coupled to this, an important change during the ontogeny of the jaw musculature in *Ancistrus cf. triradiatus* is the broadening of the

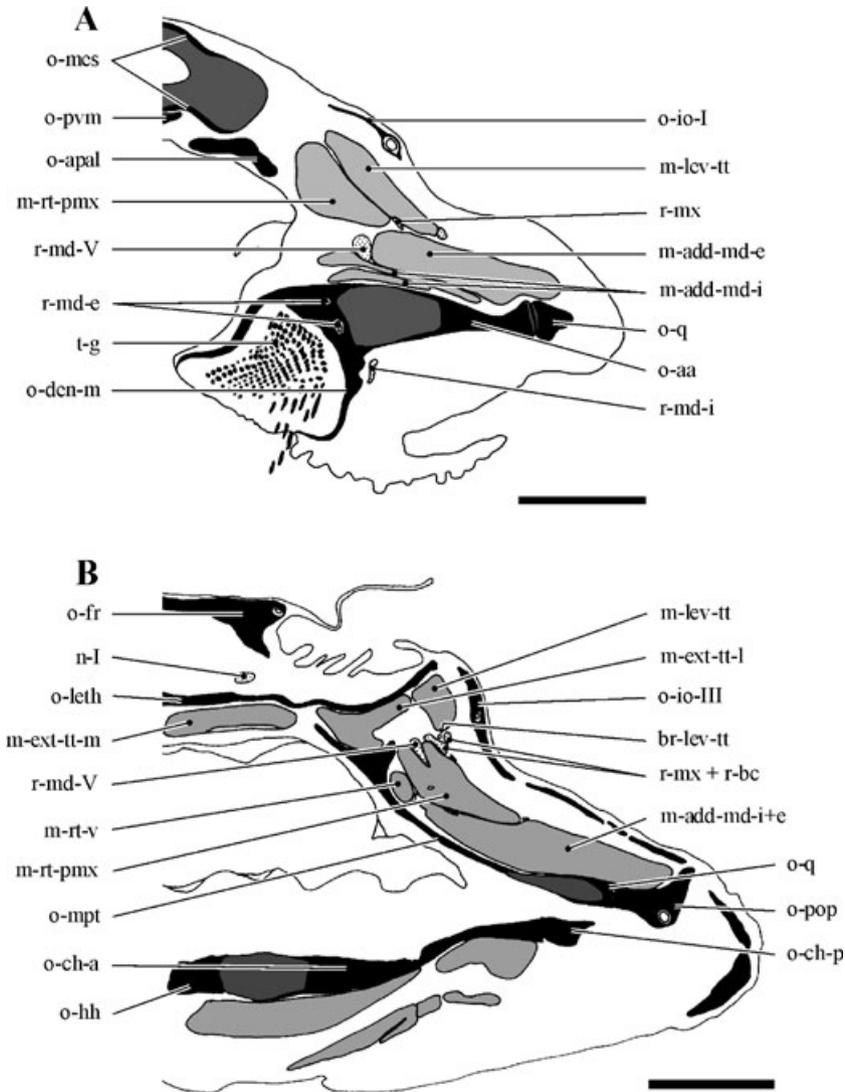


Figure 6. Cross-sections of subadult *Ancistrus cf. triradiatus*. Only the right half of each section is shown. A, at lower jaw; B, at hyoid bar (33.5-mm SL) (black indicates bone, dark grey indicates cartilage, light grey indicates muscle, stippled areas indicate nerves). Scale bar = 1 mm.

external and internal parts of the adductor mandibulae, with the external part lying more dorsal to the internal part, when compared with earlier stages (Fig. 5C, D).

Ossification of the lower jaw has significantly progressed by now, with the final insertion site of the external adductor mandibulae part now being the dorsal aspect of the angulo-articular and the lateral face of the dentary coronoid process. The internal adductor mandibulae part now attaches to the dorso-caudal aspect of the dento-mentomeckelian bone, as well as to the Meckelian fossa, and the medialmost part of the angulo-articular. Near its origin on the suspensorium, the lateralmost fibres of the internal part are still in contact with the external part, but lie

separate along most of their length. The external part originates on the hyomandibula and the dorsal aspect of the preopercle, which has developed by now. The internal part originates on the quadrate and the metapterygoid; only a few fibres insert on the hyomandibula. This already corresponds to the adult configuration. In the internal part, two layers can be discerned, intimately connected at their anterior, tendinous insertion, but well separable posteriorly (Fig. 6A).

The upper snout elongation appears to affect those muscles inserting on it, i.e. the levator tentaculi (see below) and the retractor premaxillae. The retractor premaxillae has grown further anteriorly, and now reaches the posterior face of the premaxilla, and can

thus be considered functional. Anteriorly, the ventral aponeurosis of the retractor premaxillae has largely lost its contact with the connective tissue part attached to the maxilla; in adults, there is no connection whatsoever. An interesting feature in the 12.4-mm specimen concerns the path of the mandibular nerve branch relative to the retractor premaxillae: in one side of the specimen the nerve branch runs dorsally and laterally to the muscle, as described in the earlier stages, but in the other side it enters and exits the muscle dorsally, locally separating a small group of fibres from the main muscle mass for a short distance (Fig. 5D). The same phenomenon is observed in one side of the 10.2-mm specimen, although here it occurs more laterally (Fig. 5E).

The retractor veli is now clearly discernible from the internal adductor mandibulae part, and has its origin on the metapterygoid, on and just posterior to the basis of the ossified pterygoid process.

The extensor tentaculi pars medialis originates on the ventral faces of the lateral ethmoid and the orbitosphenoid. In larger specimens attachment is also observed on the lateral side of the ventral parasphenoid ridge. The muscle inserts tendinously on the ventromedial process of the autopalatine.

The metapterygoid has now developed a lateral apolamella, which serves as additional insertion space for the extensor tentaculi pars lateralis in larger specimens, but not yet in the 12.4-mm specimen. A round aponeurosis lies in the centre of the muscle, and is continuous with the short tendon attaching to the ventrolateral process of the autopalatine. Both the medial and the lateral part of the extensor tentaculi can be considered functional in this stage.

The lateral migration of the levator tentaculi is the most prominent event occurring between this and the former stage (Fig. 5C). The orbitonasal skull region is broadening; the muscle origin is now on the lateral half of the rostroventral aspect of the lateral ethmoid, a bone that expands rostrally and laterally to accommodate and support the olfactory organ. Also, the maxilla grows allometrically, becoming considerably longer during the early ossification phase (Geerinckx *et al.*, 2007a). Thus, both points of attachment of the muscle are shifting laterally, with the logical consequence that the muscle migrates laterally as well. As a result, the levator tentaculi no longer lies directly against the palatine cartilage, which is now becoming replaced by the autopalatine bone. The anterior end of the muscle has become more flattened, its width increasing as the maxilla elongates.

Except for the irregular path of the mandibular nerve branch, there is no significant difference between the position of the nerves in the cheek region in this specimen and in the adults (Figs 5D, 6B; see below).

Corydoras aeneus

4.9-mm SL stage: The adductor mandibulae complex consists of three subdivisions that are continuous for most of their length: two dorsal and one ventral. It is only little differentiated. Most of it originates on the hyosymplectic part of the suspensorium, lateral and anterior to the insertion of the levator arcus palatini. Some fibres originate on the palatoquadrate part. The ventral division inserts on Meckel's cartilage (without a true tendon), and thus is considered the true adductor mandibulae muscle (Fig. 7B). At this stage, the separation into an internal and an external part is not clear, except anteriorly (Fig. 7B). A dorsolateral and a dorsomedial division pass the lower jaw dorsally, uniting on a ventrally placed aponeurosis that is continuous with the primordial ligament. More caudally these two dorsal divisions of the adductor mandibulae complex are separated by the mandibular branch of the trigeminal nerve. Posterior to the lower jaw, the dorsolateral division is fused to the ventral, true adductor mandibulae muscle.

The extensor tentaculi is a single muscle that originates on the trabecular bar near the orbitonasal lamina, as well as on the medial floor of this lamina. It runs toward the laterocaudal end of the palatine cartilage (Fig. 7B). The (bucco)maxillary branch of the trigeminal nerve runs between the extensor tentaculi and the dorsomedial division of the adductor mandibulae complex (Fig. 7A).

9.3-mm SL stage: The dorsomedial division, medial to the mandibular nerve branch, is now relatively well distinguished from the remainder of the adductor mandibulae complex, except near both insertions, i.e. posteriorly, on the hyomandibula, and anteriorly, near its tendon, where it is joined by the dorsolateral division (Fig. 7C, D). This dorsolateral division, lateral to the mandibular nerve branch, still cannot be separated from the adductor mandibulae inserting on the lower jaw, except for the fact that its fibres extend more anteriorly, fusing with the dorsomedial division (Fig. 7C). The dorsomedial and dorsolateral divisions attach to a ventral aponeurosis that inserts on the primordial ligament. As such, this compound muscle (retractor tentaculi of Howes, 1983a) is penetrated posteriorly by the mandibular nerve branch (e.g. Fig. 8A vs. 8B in adult specimen). In the adductor mandibulae muscle, an external and an internal part can now be distinguished. The mandibular branch runs over the internal part before entering the lower jaw, as it does in *Ancistrus cf. triradiatus*.

The extensor tentaculi now inserts on a ventrolateral process on the posterior tip of the autopalatine. A remarkable observation concerns the neurocranial origin of this muscle. At the level of the nasal organ the muscle becomes significantly broader (Fig. 7C),

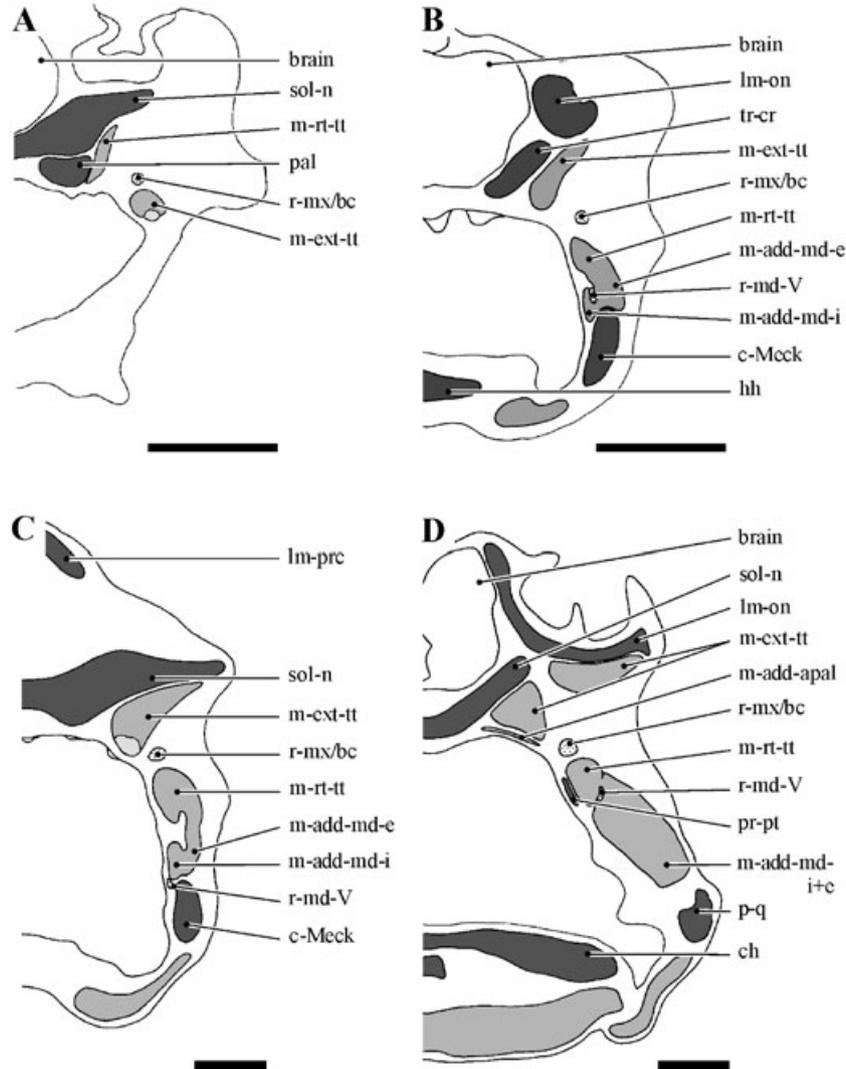


Figure 7. Cross-sections of larval *Corydoros aeneus*. Only the right half of each section is shown. A, anterior to lower jaw; B, at lower jaw (A, B: 4.9-mm SL); C, at lower jaw; D, posterior to lower jaw (C, D: 9.3-mm SL) (black indicates bone, dark grey indicates cartilage, light grey indicates muscle, stippled areas indicate nerves). Scale bar = 0.2 mm.

and the posterior portion of the muscle is split into two parts: a medial one originating on the trabecular bar and the preorbital base, and a laterodorsal one originating almost completely laterally on the ventral aspect of the orbitonasal lamina. This posterior separation is even more pronounced in adult specimens (Fig. 8B; Huysentruyt *et al.*, 2007).

MUSCLE INNERVATIONS AND NERVE POSITIONS

In (sub)adult *Ancistrus cf. triradiatus* and *Corydoros aeneus* the main branches of the infraorbital trunk of the trigeminofacial root are complexly intertwined, but can be identified for most of their course in the serial sections of the 12.4- and 33.5-mm specimens (A.

cf. triradiatus) and the 9.3- and 39.0-mm specimens (*C. aeneus*).

Ancistrus cf. triradiatus

The three main branches of the infraorbital trunk are the maxillary and mandibular branches of the trigeminal nerve and the buccal branch of the facial nerve. The buccal branch separates from the trunk, but re-enters it at the level of the posterior eye margin. Here, the trunk breaks up into two large parts. The ventral one is the mandibular branch, and the dorsal one consists of the anastomosed maxillary and buccal branches, the latter sending off small branchlets laterally (to pit organs and the infraorbital canal). Some of the buccal branchlets stay

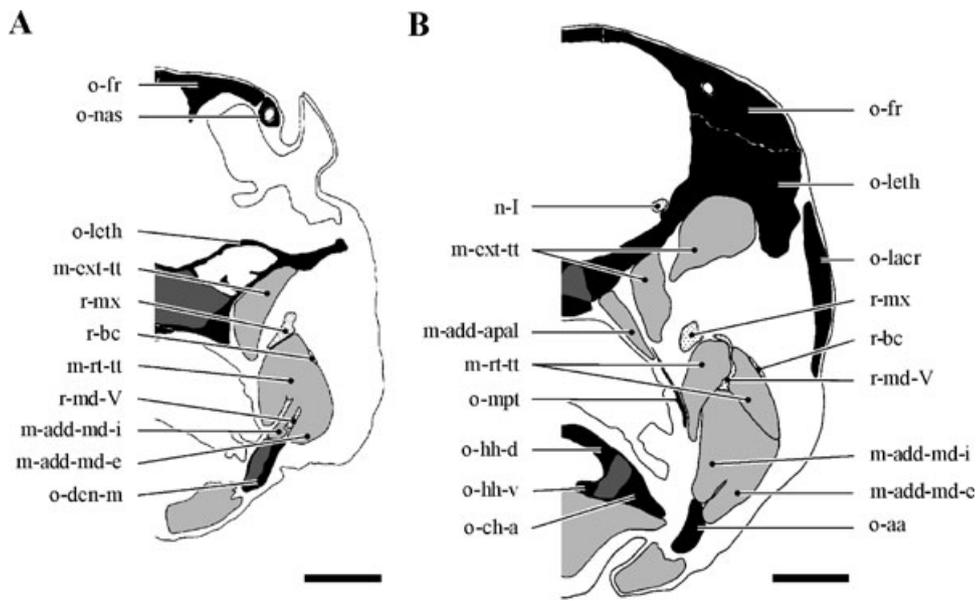


Figure 8. Cross-sections of adult *Corydoras aeneus*. Only the right half of each section is shown. A, halfway along lower jaw; B, at posterior end of lower jaw (39.0-mm SL) (black indicates bone, dark grey indicates cartilage, light grey indicates muscle, stippled areas indicate nerves). Scale bar = 1 mm.

anastomosed to the maxillary branch (all of these minor buccal branches are omitted in the figures). The ventralmost fibres of the mandibular branch descend into the dorsomedial portion of the adductor mandibulae complex, between the retractor premaxillae and the retractor veli. The fibres divide into two portions, the dorsal one innervating the retractor premaxillae, the ventral one serving the internal and external parts of the adductor mandibulae, and the retractor veli (visible on sections, but not indicated on Figs 5D, 6B). The main part of the mandibular branch runs rostroventrally, between the retractor premaxillae (medial) and the external adductor mandibulae part (lateral). In one side of the 33.5-mm specimen, the mandibular branch even enters the retractor premaxillae, splitting the muscle into a large medial part and a somewhat smaller lateral part (Fig. 6B). Apart from this, the two parts cannot be distinguished from each other, neither posterior nor anterior to the nerve course. This is also even more aberrant than the separation of only a few fibres of the retractor premaxillae in the 10.2- and 12.4-mm specimens (see above). The separation of only a few fibres is also observed in the other side of the 33.5-mm specimen. The mandibular branch then runs ventral to the retractor premaxillae and dorsal to the internal adductor mandibulae part (Fig. 6A). Close to the insertion of the latter muscle it splits into a part serving the dentary region, and a part running to the musculature between the lower jaw and the hyoid. Analogous to the papers of Vetter (1878), Juge (1899)

and Atoda (1936) we name the branch that innervates the dentary bone itself the external mandibular branch (although in *Ancistrus* cf. *triradiatus* it is situated most medially, as a result of the medially rotated jaw); the internal mandibular branch is the one that sends branches into the intermandibular and protractor hyoideus muscles. A comparison with *Pterygoplichthys disjunctivus* (Hypostominae), *Otocinclus vestitus* (Hypoptopomatinae) and *Farlowella acus* (Loricariinae) clearly indicates that the mandibular branch in these specimens always runs between the external adductor mandibulae part and the retractor premaxillae, not separating fibres of the latter muscle.

The maxillary branch runs dorsolaterally to the retractor premaxillae, and continues along the lateroventral edge of the levator tentaculi, sending one portion to the premaxillary region in the snout, and a larger portion into the maxillary barbel. The buccal branch sends off several small and larger branchlets along its course in the cheek. Some fibres stay anastomosed to a minor bundle of the maxillary branch, ending in and near the premaxilla, a situation also described in the siluriform *Parasilurus asotus* (Atoda, 1936).

Both parts of the extensor tentaculi are innervated by separate portions of the branch that serves the adductor arcus palatini as well, and that originates from the hyomandibular trunk of the trigeminofacial root (Fig. 6B). The levator tentaculi is innervated by a branch of thick fibres originating from the

anastomosed maxillary–buccal branch (Figs 5D, 6B). They can be traced up to the level of the posterior eye margin, where they seem to lose themselves in two small groups absorbed by the trigeminal part of the nerve complex formed by fibres of the mandibular and maxillary branches.

Except for the mandibular branch of the trigeminal nerve (see above), no significant differences were observed in the nerve positions and innervations in the loricariids *Pterygoplichthys disjunctivus*, *Otocinclus vestitus* and *Farlowella acus*.

Corydoras aeneus

Near their origin, it is hard to discriminate between the buccal and the mandibular and maxillary branches, as several parts of the buccal branch anastomose to the other branches. Along the whole of the length of the adductor mandibulae complex, the well-developed maxillary branch lies mediodorsal to this complex, and lateroventral to the extensor tentaculi, most of its fibres finally entering the maxillary barbel. The adductor mandibulae complex is innervated by a ventral portion of the mandibular branch, which has separated from the maxillary branch immediately after its emergence from the skull. The mandibular branch then enters the complex separating the dorsolateral and dorsomedial divisions (thus splitting the retractor tentaculi in two parts; Fig. 8B). It then continues, rostrally separating the largest external part of the adductor mandibulae and the smaller internal part (Fig. 8A). It then sends off its branchlets to the dentary region and the musculature in the ventral region of the lower jaw. The extensor tentaculi is innervated by the same branch that serves the adductor arcus palatini, and that originates from the hyomandibular trunk of the trigeminofacial root.

DISCUSSION

THE ADDUCTOR MANDIBULAE COMPLEX

Vetter's (1878) terminology of the adductor mandibulae sections can be applied to siluriforms, but has been replaced by more recent terminologies (see below). Vetter's A2-section typically lies ventrolaterally in teleosts, and inserts on the dorsal face of the lower jaw, usually including the dentary coronoid process, and often also the angulo-articular and the Meckelian fossa (Vetter, 1878; Winterbottom, 1974). The more medial A3-section usually inserts on the medial face of the dentary and/or the Meckelian fossa (Vetter, 1878; Winterbottom, 1974). In ostariophysans it always inserts (at least) on the Meckelian fossa (Gosline, 1989; Wu & Shen, 2004). Both sections have been found in siluriforms, and can be discerned as follows (in at least some taxa; Takahasi, 1925): the

external A2-section is fused to an outer portion of the internal A3-section, thus giving rise to the combined A2A3' section, which is separated posteriorly from the inner A3 portion (or A3'') by the course and the insertion of the levator arcus palatini. Takahasi's identification of an A3'-part fused to the A2 is based on the relationship of the muscle to the A ω -section in those cypriniforms and siluriforms examined by him. His configuration and nomenclature have been followed by, for example, Gosline (1989) and Adriaens & Verraes (1996). In some cases the mandibular branch of the trigeminal nerve passes between the A2- and A3-sections, but this is not a general situation (Edgeworth, 1935; Winterbottom, 1974; Gosline, 1989; see below). The A2-section of Vetter (1878) has been named 'external division' (Gosline, 1989), A1-OST (Diogo & Chardon, 2000) and A2 α (Wu & Shen, 2004). Vetter's A3-section most probably corresponds to the 'internal division' of Gosline (1989), although the latter author incompletely described the inner divisions in the basal catfish *Diplomystes*, compared with the work of Diogo & Chardon (2000) and Diogo (2005). Wu & Shen (2004) synonymized their A2 β to the A2 of Diogo & Chardon (2000) and the internal section of Gosline (1989). Alexander (1965) erroneously presumed the presence of an A1-section in the adductor mandibulae part that inserts on the lower jaw in both callichthyids and loricariids; his erroneous terminology was followed by Howes (1983a), Schaefer & Lauder (1986) and Schaefer (1997).

Of the various recent terminologies, Wu & Shen's (2004) uses derivatives of the terms A2 and A3 pointing to the various subdivisions of the adductor mandibulae complex, and avoids any reference to the term A1. An A1 section as observed in acanthomorphs is absent in siluriforms (Adriaens & Verraes, 1996; Diogo & Chardon, 2000; Diogo, 2005). However, it is more appropriate to follow the terminology of Diogo & Chardon (2000), Diogo (2005) and Diogo, Chardon & Vandewalle (2006), given the thoroughness of their comparative work on siluriforms. Note that their A2 is not homologous to the A2 of Vetter (1878). Given the limited systematic range of taxa studied by us, we are not in a position to condemn or reject any of these proposed nomenclatures.

In Diplomystidae, the most basal catfish family, Diogo & Chardon (2000) discern a large, lateral A1-OST with the A2 lying mediodorsal to it. The former muscle inserts on the coronomeckelian and angulo-articular, the latter on the coronomeckelian alone. Concerning the deeper adductor parts, Diogo & Chardon (2000) and Diogo (2005) provide more detail than Gosline (1989). They discriminate a dorsal and a ventral part of the A3' that lie medioventral to the other divisions and insert on the posterior part of the coronomeckelian and the angulo-articular,

respectively. *Diplomystes* also possesses an A₀ stretching between the A₂ tendon and the inner face of the dentary. Although several bundles are present, the adductor mandibulae complex of Diplomyctidae is relatively undifferentiated at the level of its anterior insertions, and it lacks a direct connection to the primordial ligament (Arratia, 1987; Gosline, 1989; Diogo & Chardon, 2000). The course of the mandibular branch of the trigeminal nerve is lateral to all divisions (Gosline, 1989).

Within the loricarioid lineage, Nematogenyidae have been studied by Howes (1983b), Diogo (2005) and Diogo *et al.* (2006). The lateral A₁-OST and A₂ are present, as well as an A₃'-division, situated medially to the uppermost fibres of the A₂. The medial A₃'-section consists of a dorsal and a ventral part, as in Diplomyctidae. The above authors found that *Nematogenys inermis* lacks a retractor tentaculi. Whereas Diogo (2005) states that there is no relationship between the A₃' and the primordial ligament, Howes (1983b: 12) mentions an anterior tissue sheet connected to the upper, inner division (A₃''): 'Stemming from the antero-medial surface of this muscle, and extending across the dorsal surface of the mandible is a thick sheet of connective tissue. This sheet bifurcates, the upper strand attaching to the posterior face of the maxilla, the lower to the distal portion of the maxilla where it forms a sheath around the maxillary barbel.'

In the adductor mandibulae complex of *Trichomycterus rivulatus* (Trichomycteridae), Howes (1983a) mentions the presence of an outer portion inserting on the lower jaw, and a tendon connecting it to connective tissue running to the maxilla. An additional medial section (A₃'?) inserts onto the inner aspects of the dentary. The precise identification of these muscles remains unclear. The association between any of the adductor mandibulae bundles and the maxilla or the primordial ligament is contradicted by Diogo (2005), who investigated some other *Trichomycterus* species and *Hatcheria macraei*. A retractor tentaculi muscle was not found in the trichomycterids examined by Schaefer & Lauder (1986).

In the callichthyid *Corydoras aeneus* we distinguished an external and an internal adductor mandibulae part. Based on its ventrolateral position and insertion on the outer portion of the lower jaw, the external adductor mandibulae part can be considered homologous to the A₁-OST. Based on its ventromedial position and its insertion on the posteromedial face of the lower jaw, the internal adductor mandibulae part can most probably be identified as the A₃', as it takes the place of the A₃' of *Diplomystes* and *Nematogenys*, and the additional medial section of *Trichomycterus*. In *Corydoras*, the A₃' is not divided into a dorsal and a ventral part.

The ontogeny of the adductor mandibulae complex suggests a double origin of the retractor tentaculi in *Corydoras*: the dorsolateral division is partly confluent with the external adductor mandibulae part or A₁-OST, which inserts on the lower jaw. We identify this division as the A₂ of Diogo (2005). The dorsomedial division, originating anteromedial to the other division, corresponds to the A₃' of Nematogenyidae. Diogo (2005) also stated that the callichthyid retractor tentaculi results from the A₃'', without, however, an involvement of the A₂. The mandibular branch of the trigeminal nerve, running between the A₂ and the A₃'', is discussed below.

Some authors have hypothesized an A₁ origin of the siluriform retractor tentaculi (Takahasi, 1925; Edgeworth, 1935). The most supported idea, however, states that the retractor tentaculi originates from an inner division of the adductor mandibulae complex (McMurrich, 1884; Lubosch, 1938; Eaton, 1948; Alexander, 1965; Howes, 1983b; Adriaens & Verraes, 1996, 1997b; Diogo, 2005). A retractor tentaculi muscle is present in several siluriform families such as Clariidae, Ictaluridae, Cranoglanididae and Bagridae, and is believed to originate from the A₃' (Nawar, 1955; Adriaens & Verraes, 1996; Diogo, 2005). Both Howes (1983b) and Diogo (2005) support the idea that the muscle has been derived independently in several siluriform lineages, via a connection with the primordial ligament. The absence of a retractor tentaculi in the basal loricarioid families Nematogenyidae and Trichomycteridae, as well as in Diplomyctidae, suggests that the retractor tentaculi has independently evolved within the loricarioid lineage.

Clarias gariepinus is the only siluriform for which the ontogeny of the musculature has been studied so far (e.g. Adriaens & Verraes, 1996). A re-evaluation of their data reveals that their retractor tentaculi might not be truly homologous to the retractor tentaculi of *Corydoras aeneus* (i.e. in *C. gariepinus* having originated from more ventral fibres of the complex). In both species, the retractor tentaculi is a medial derivative of the adductor mandibulae complex that might have evolved independently (see above). The ontogenetic evidence on *C. gariepinus* suggests that the composition of the adductor mandibulae complex may well correspond to the general siluriform pattern of Diogo & Chardon (2000) and Diogo (2005), which is corroborated by the results of the current study. A lateral A₁-OST (A₂A₃'β of Adriaens & Verraes, 1996) and A₂ (A₂A₃'α) can be distinguished. With respect to the medial adductor part, a comparison with the configuration in *Diplomystes*, *Nematogenys* and *Ancistrus* suggests that the superficial and deeper A₃' parts of Adriaens & Verraes (1996) are homologous to the dorsal and ventral part of the A₃' of the former

species (also in *C. garipepinus*, one part lies more dorsal to the other). As the more medial retractor tentaculi during ontogeny shows no affinities with the A2, but with the A3', we hypothesize that it must be derived from this A3' (and thus is not homologous to the A3'' of loricarioids). Thus, the retractor tentaculi might have different evolutionary origins within the siluriforms.

In Callichthyidae, the retractor tentaculi provides a biomechanical coupling between the maxilla, the suspensorium and the lower jaw via a tendinous insertion on the primordial ligament (Howes, 1983a; Schaefer & Lauder, 1986). Moreover, a novel connection has also been established between the primordial ligament and the premaxilla. This bone has become highly mobile as the tight connection to the neurocranium has been loosened: a functional coupling between the retractor tentaculi and the premaxilla has thus been created (Schaefer & Lauder, 1986).

The portion of the loricariid adductor mandibulae complex that effectively inserts on the lower jaw, as observed in *Ancistrus* cf. *triradiatus*, consists of two divisions. In order to compare these two divisions to divisions in *Corydoras* and other siluriforms, the fact that the loricariid lower jaw has rotated medially has to be taken into account when considering differences in jaw muscle topographies. Both loricariid lower jaws point toward each other. As a spatial consequence of this rotation, the external adductor mandibulae part would come to lie dorsal to the internal adductor part, in order to maintain their insertions on the lower jaw.

We hypothesize homology between the external adductor mandibulae muscle in *Ancistrus* and *Corydoras*, and, hence, the A1-OST. This hypothesis is supported by the similar posterior and anterior insertions, i.e. the hyomandibula and the preopercle, and the dorsolateral aspect of the angulo-articular and the lateral face of the dentary coronoid process. Also, the muscle lies well lateral to the mandibular nerve branch in both *Ancistrus* and *Corydoras*. The internal part of the adductor mandibulae of *Ancistrus* and *Corydoras* is considered homologous with the A3' of *Diplomystes* and the other above-mentioned siluriforms, based on the origin on the suspensorium and the insertion on the dorsomedial aspect of the lower jaw, including the Meckelian fossa. Additionally, in both species the mandibular nerve branch lies on the anterior tendon of this internal adductor part before passing down the Meckelian fossa. The dorsal and ventral portions of the internal part, observed in the 12.4-mm and all larger specimens of *Ancistrus* (Fig. 6A), might correspond to the dorsal and ventral parts of the A3' in *Diplomystes* (Diogo & Chardon, 2000; Diogo, 2005) and *Nematogenys* (Diogo *et al.*, 2006).

The loricariid retractor veli has been hypothesized to be a medial derivative of the adductor mandibulae complex (Howes, 1983a; Schaefer & Lauder, 1986). The muscle was first described as the 'muscle of oral valve' by Gradwell (1971). It was called retractor palatini by Howes (1983a), and is featured as such in the papers of Schaefer & Lauder (1996), Schaefer (1997), Diogo & Vandewalle (2003b) and Diogo (2005). A non-homologous retractor palatini was described earlier in balistoids, as an anterior portion of the adductor arcus palatini, inserting on the autopalatine (Lubosch, 1929; Hofer, 1938). Based on this, and on functional considerations (i.e. the fact that it retracts the oral valve and not the autopalatine; see also Gradwell, 1971), Geerinckx *et al.* (2007b) proposed the new name retractor veli for this newly differentiated muscle in loricariids. This retractor veli even differentiates into two separate bundles in *Otocinclus vestitus* (Geerinckx *et al.*, 2007b). Considering that (1) the muscle is absent in Callichthyidae and other non-loricariid loricarioids, (2) the innervating nerve branchlet separates from the branch innervating the internal adductor mandibulae part (A3') and (3) the latter muscle and the retractor veli are continuous for most of their length during early ontogeny of *Ancistrus*, it seems most plausible that it is a medial derivative of this adductor part.

We hypothesize homology between the loricariid retractor premaxillae (*Ancistrus*) and the medial half (A3'') of, or even the whole (A2 + A3''), callichthyid retractor tentaculi (*Corydoras*). Several arguments support this hypothesis. (1) Both muscles are connected to the premaxilla. The callichthyid retractor tentaculi has a connection to the premaxilla via a dorsal extension of the primordial ligament (Schaefer & Lauder, 1986; Huysentruyt *et al.*, 2007). The loricariid retractor premaxillae is directly attached to the premaxilla. (2) The anterior tendon continues as an aponeurosis in the ventral to ventromedial aspect of the retractor tentaculi or premaxillae muscle in *Corydoras* and *Ancistrus*, respectively. (3) In both species the muscle arises as the dorsalmost part of the adductor mandibulae complex, and is situated lateral to the pterygoid process of the cartilaginous suspensorium, reaching beyond the coronoid process of Meckel's cartilage. In early ontogeny the lateral fibres of the muscle originate on the hyosymplectic and are in contact with those of the external adductor mandibulae part; the medial fibres originate anteromedially to the other parts on the hyosymplectic. (4) Innervation of both muscles is similar: the first branchlet to separate from the branch that innervates the whole adductor mandibulae complex is the one serving the retractor tentaculi (*Corydoras*) or the retractor premaxillae (*Ancistrus*). The main branch innervating the complex originates from the mandibular branch,

and is present in other teleosts as well: siluriform examples are given by Atoda (1936), Mithel (1964a), Winterbottom (1974) and Adriaens & Verraes (1996). (5) The last argument relates to the relative position of the retractor tentaculi or premaxillae, and the buccomaxillary nerve branch. In larval and adult *Corydoras*, and in embryonic *Ancistrus*, the position of this anastomosed branch is dorsomedial to the muscle. In adult *Ancistrus* this nerve cord migrates laterally, along with the levator tentaculi (see below).

Opposed to the buccomaxillary nerve branch, which invariably runs outside the adductor mandibulae complex, we do not want to overestimate the use of the course of the mandibular branch of the trigeminal nerve to prove homologies of adductor muscle parts. The nerve crosses or enters the adductor mandibulae complex differently in different taxa. It has proved its usefulness in several studies (e.g. Wu & Shen, 2004; Diogo, 2005), but sometimes relative positions are too variable to be reliable (Edgeworth, 1935; Mithel, 1964a; Gosline, 1989). The paths of nerves can be modified according to topographical changes of the innervated muscle bundles. This might affect the validity of the use of the course of the mandibular nerve branch for homology assessments within the adductor mandibulae complex (Nakae & Sasaki, 2004). As mentioned above, although the mandibular nerve branch in *Ancistrus* passes lateral to the retractor premaxillae in some cases, it runs through the muscle in others (e.g. Fig. 5D, E). Even individual left/right variation is observed. In all examined specimens of *Corydoras* the mandibular nerve branch runs between both halves of the retractor tentaculi.

Thus, it is impossible to use the mandibular nerve branch to identify adductor mandibulae sections in *Ancistrus* unambiguously. Also, the rather posterior position of the levator arcus palatini in *Ancistrus*, and its absence in several other loricariids (Diogo, 2005), inhibits any definite identification. The position of the insertion of this suspensorial muscle has been used to discriminate between adductor parts in other siluriforms (Takahasi, 1925; Adriaens & Verraes, 1996). In *Ancistrus*, the retractor premaxillae thus consists of the A2 + A3'', or, perhaps, of the A3'' alone.

The presence of a retractor premaxillae and an (indirectly) antagonistic muscle originating from the medial fibres of the extensor tentaculi in loricariids (see Alexander, 1965; Geerinckx *et al.*, 2007b) can be linked to a novel protrusion mechanism that evolved in the loricarioid lineage. The antagonistic muscle acts on the premaxilla via the autopalatine [extensor tentaculi pars medialis (Alexander, 1965; Howes, 1983a; Geerinckx *et al.*, 2007b)]. An ascending process on the premaxilla is typical for those teleosts with a protractile upper jaw (Eaton, 1935). Such a process is present on the premaxilla in Loricariidae, but absent

in most siluriforms. The mechanism of loricariids is, however, different from the protrusion mechanisms described by Motta (1984), and even largely decoupled from the movements of the maxilla (Alexander, 1965; Geerinckx *et al.*, 2007b).

In siluriforms, an A0-section can be present (e.g. Takahasi, 1925; Gosline, 1989; Wu & Shen, 2004; Diogo, 2005) or absent (e.g. Gosline, 1989; Adriaens & Verraes, 1996; Diogo, 2005). Based on the definitions given by Vetter (1878) and Winterbottom (1974) it can be stated that there is no sign of an A0 in early or adult stages of both *Corydoras aeneus* and *Ancistrus* cf. *triradiatus*.

Within the loricarioid clade, the myology of the two remaining families, Astroblepidae and Scoloplacidae, is less well known. As a consequence, only a tentative and incomplete comparison of their jaw musculature can be made here.

No detailed information exists about the nature of the A1-OST and A3' of the adductor mandibulae portion inserting on the lower jaw in astroblepids. A retractor premaxillae is present (Schaefer & Lauder, 1996), with the lower fibres not entirely separated from the outer adductor complex (Howes, 1983a), indicating a composition possibly homologous to A2 + A3'' (cf. the loricariid retractor premaxillae and the callichthyid retractor tentaculi). Howes' (1983a) statement that fibres of the retractor premaxillae would originate on the lateral ethmoid seems inconsistent with his accompanying figure, and is opposed by other authors, who describe a suspensorial origin (Diogo, 2005; S. A. Schaefer, pers. comm.).

Little is known of the scoloplacid cranial musculature. Schaefer (1990) described an adductor part inserting on the lower jaw (without reference to any possible subdivisions) and a retractor premaxillae with a long tendon inserting on the premaxilla. Defining homologies with the A2- and A3-divisions of other loricarioids requires a more detailed examination of scoloplacid musculature. According to Diogo (2005), the origin of the retractor premaxillae is on the suspensorium. Both authors describe a 'retractor tentaculi' originating on the lateral ethmoid; this muscle will be discussed in the next section.

THE EXTENSOR TENTACULI AND LEVATOR TENTACULI
Our proposed homology of the callichthyid retractor tentaculi and the loricariid retractor premaxillae implies non-homology between the callichthyid retractor tentaculi and the loricariid 'retractor tentaculi' of Howes (1983a), Schaefer & Lauder (1986, 1996), Schaefer (1997), Diogo & Vandewalle (2003b) and Geerinckx *et al.* (2007b), identical to the 'adductor tentaculi' of Alexander (1965) and 'muscle a' of Howes (1983a). Hence, we propose the name 'levator

tentaculi' for this muscle, a name that, to our knowledge, is not taken for any other teleost muscle (Winterbottom, 1974; Diogo & Vandewalle, 2003b). Additionally, it aptly describes the motion of the maxilla, the rudimentary maxillary barbel and the associated lateral lip tissue, which is elevated from the substrate (to which loricariids can attach with their sucker-like mouth) (Geerinckx *et al.*, 2007b; our pers. observ.). In the following discussion we will provide additional evidence for this hypothesis of non-homology.

The extensor tentaculi is generally present in siluriforms, and can be a single or a subdivided muscle (Diogo & Vandewalle, 2003b). It is a single muscle in Diplomystidae and Nematogenyidae, with some fibres intermingled with those of the adductor arcus palatini (Diogo, 2005), of which it is an anterior derivative (Takahasi, 1925; Alexander, 1965; Winterbottom, 1974; Gosline, 1975; Adriaens & Verraes, 1997b). Origin is on the neurocranium, usually (at least) on the ventral aspect of the lateral ethmoid, as in Trichomycteridae, Callichthyidae and Astroblepidae (Howes, 1983a; Schaefer & Lauder, 1986; our pers. observ.). Whereas the whole of the adductor mandibulae complex originates from the dorsal, masticatory part of the mandibular muscle plate and is innervated by a portion of the mandibular branch of the trigeminal nerve, the adductor arcus palatini and the extensor tentaculi are derived from the constrictor hyoideus dorsalis muscle plate, and are innervated by the palatine branch of the hyomandibular trunk of the facial nerve (Mithel, 1964a; Alexander, 1965; Singh, 1967; Jarvik, 1980). Innervation of the levator tentaculi of *Ancistrus* and other examined loricariids is discussed below.

In Callichthyidae, Scoloplacidae and Astroblepidae, Diogo (2005) noted the differentiation of the extensor tentaculi into two elongated ventral bundles attaching to the postero-ventrolateral surface of the autopalatine, and an additional dorsal bundle essentially orientated dorsoventrally and attaching to the posterodorsal surface of this bone. We found only one instead of two ventral bundles in *Corydoras aeneus* (Fig. 7D). The complete separation of the ventral bundle of the extensor tentaculi into two separate muscles, i.e. a pars medialis and a pars lateralis, is a character observed in loricariids only (Howes, 1983a; Diogo, 2005; Geerinckx *et al.*, 2007b). Here, both parts, which appear to be separated from early ontogeny onward, are innervated by two portions of the palatine branch of the hyomandibular trunk of the facial nerve.

The following is a summary of evidence from our results, to support the non-homology of the loricariid levator tentaculi and any part of the adductor mandibulae complex, as well as the close affinity of

the former muscle to the extensor tentaculi. First, the dorsolateral part of the extensor tentaculi of *Corydoras* originates on the same place as the levator tentaculi of *Ancistrus*, i.e. far laterally on the lateral ethmoid (Fig. 8B) or the orbitonasal lamina during early stages (Fig. 7D).

Second, during early ontogeny the levator tentaculi of *Ancistrus* develops separate from the adductor mandibulae complex, but adjacent to the extensor tentaculi pars lateralis. This is clearly visible on Figures 2, 3A–D, 4 and 5A.

Third, the lateralmost fibres of the extensor tentaculi of *Corydoras* insert on the lateral aspect of the autopalatine (e.g. Fig. 7A), with part of the tendon even extending slightly further anteriorly along that bone. A shift of these muscle fibres via the connective tissue connecting the autopalatine to the dorsolateral soft palate and the maxilla seems more parsimonious than the shift of the origin of the callichthyid retractor tentaculi from the suspensorium to the lateral ethmoid and an additional *de novo* development of the loricariid retractor tentaculi from the adductor mandibulae complex.

Fourth, the relative position of the extensor tentaculi (and levator tentaculi) to the anastomosed buccomaxillary nerve branch and the adductor mandibulae complex in *Corydoras* and (embryonic) *Ancistrus* is identical. In both species the buccomaxillary nerve branch is situated dorsomedial to the adductor mandibulae complex, but (ventro)lateral to the extensor tentaculi bundles and the levator tentaculi (present in *Ancistrus* only) (Figs 3A–D, 4, 5A–C, 6A, 7A–D, 8A–B). This evidence can be overlooked in adult *Ancistrus*, as during ontogeny, the levator tentaculi migrates and expands laterally (Fig. 3A vs. 5C), while the adductor mandibulae complex expands somewhat medially, as a spatial consequence of the more medial jaw position (Geerinckx *et al.*, 2007a, b). The anastomosed buccomaxillary nerve branch migrates laterally as well, still retaining its relative position to the levator tentaculi.

The innervation of the loricariid levator tentaculi remains somewhat puzzling. Based on dissections, Howes (1983a) concluded that innervation occurs by a branchlet of the maxillary branch of the trigeminal nerve, entering the ventral surface of the muscle. Serial sections showed us that a thin nerve branch indeed enters it at its ventrolateral side, immediately splitting into two small branchlets innervating the muscle. The very large axons originate from the anastomosed buccomaxillary branch, and can be traced back some distance, to the level where also the mandibular branch forms part of the nerve. (The same innervation was observed in *Pterygoplichthys*, *Otocinclus* and *Farlowella*.) As the mandibular and buccomaxillary branches are undistinguishably connected

here, it is unclear to which of these two branches the axons belong. The infraorbital trunk and even the roots of the trigeminal (V) and facial (VII) nerves are intimately intermingled, as in other siluriforms and teleosts (Berkelbach, 1915). Comparison with the paths of the nerves in the cheek region in other siluriforms revealed that, first, separation, anastomosis and branching patterns of the mandibular, maxillary and buccal branches vary within the order, and, second, a possible homologue of the branch innervating the levator tentaculi could not be found in *Silurus*, *Parasilurus*, *Mystus*, *Wallago*, *Bagarius*, *Clarias* and *Corydoras* (Juge, 1899; Atoda, 1936; Mithel, 1964a, b; our pers. observ.). The fact that the levator tentaculi is not innervated by the palatine branch of the hyomandibular trunk (as is the extensor tentaculi) does not support or oppose our hypothesis. An examination of the innervation pattern in the related Scoloplacidae and Astroblepidae could possibly resolve this question.

Based on the above-mentioned argumentation and literature data, we subsequently hypothesize the homology of the 'retractor tentaculi' of Scoloplacidae and Astroblepidae (Howes, 1983a; Schaefer, 1990; Diogo, 2005) and the loricariid levator tentaculi. Both are broad muscles, originate on the neurocranium and cover the retractor premaxillae dorsally. The position of this muscle in Scoloplacidae, as figured by Schaefer (1990: 200), infers that it might well be an intermediate configuration between the dorsolateral extensor tentaculi division of Callichthyidae and the levator tentaculi of Loricariidae ('retractor tentaculi' of Astroblepidae). The shape of the muscle is an additional argument, as the muscle has extended only slightly beyond the posterior end of the autopalatine, and a long tendon crosses the retractor premaxillae dorsally and connects to the maxilla (Schaefer, 1990). Consequently, the name levator tentaculi might be a better term for this muscle in scoloplacids and astroblepids.

Within loricariids, the levator tentaculi can have slightly different orientations, and is sometimes more separated from the extensor tentaculi than in *Ancistrus* (*Otocinclus*, *Hypoptopoma*, *Farlowella*) (Howes, 1983a; our pers. observ.). In these cases the lateral ethmoid, and thus the origin of the muscle, has extended far laterally (*Otocinclus*, *Hypoptopoma*), or the origin of the muscle has shifted rostrally (*Farlowella*).

If the levator tentaculi has indeed originated from dorsolateral fibres of the extensor tentaculi, one could speculate on evolutionary key innovations that could have led toward the loricariid muscle configuration. A hypothetical ancestral configuration would probably have included a retractor tentaculi as in *Corydoras*, retracting the barbel, and perhaps already having an

indirect effect on the premaxilla. The extensor tentaculi would have been broad, as in *Corydoras*, but with lateral fibres inserting even more on the anterior part of the autopalatine and the tissue surrounding the autopalatine–maxillary articulation. Or contact with the maxilla could have been established by means of a long tendon, as in scoloplacids (see above). The tissue that connects the autopalatine to the dorsolateral soft palate in *Corydoras*, and that is continuous with the autopalatine–maxillary articular tissue, could have generated such tendon. Without a detailed microscopic–histological examination of, in particular, scoloplacid and astroblepid representatives, such hypotheses remain speculative. They are, however, justified, as the homology of the loricariid retractor premaxillae and the callichthyid retractor tentaculi implies an alternative, novel origin of the levator tentaculi within the loricarioids.

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