

# Ontogeny of the suspensorial and opercular musculature in the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes)

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**Abstract** Several morphological features characterizing Loricariidae or suckermouth-armoured catfishes (Siluriformes, Teleostei) are related to their ability to attach onto substrates with their sucker mouth, and to scrape algae and other food items from these substrates. Suspensorial and opercular muscles are among those muscles usually involved in respiration (and feeding). In several loricariids including the genus *Ancistrus*, the opercular musculature is decoupled from the respiratory mechanisms. Results show that the adductor arcus palatini is relatively large throughout the whole ontogeny, while the levator arcus palatini is minute. It develops in association with the dilatator operculi, which exhibits substantial growth only in the juvenile and adult stages. The levator and adductor operculi are connected during early ontogeny, and anterior fibres of the latter muscle differentiate into the adductor hyomandibulae, a muscle previously thought to be absent in loricariids. Relative muscle sizes and orientations, as well as articular transformations and the transition from cartilaginous to bony skeletal elements, indicate ontogenetic transformations in the skeleto-muscular system, affecting and steering functionalities.

**Keywords** Catfishes · Development · Muscle function · Myology · Nerves

## Introduction

The suspensorial and opercular musculature is part of the dynamic apparatus involved in respiration and feeding in

teleost fishes. Muscle activity can result in (1) expansion and contraction of the orobranchial cavity, and (2) expansion and contraction of the opercular cavity. The first set of actions can be referred to as the pressure pump, as contraction of the orobranchial cavity forces water through the gills. Expansion of the opercular cavity sucks water from the former cavity via the gills; this opercular pump has been called the suction pump (Hughes 1960, 1970). The anatomical basis of the first system is most complex, as orobranchial volume changes can be generated by movements of the jaw and hyoid bars (ventrally), the neurocranium (dorsally), and the suspensoria (laterally) (e.g. Schaeffer and Rosen 1961; Elshoud 1978; Lauder and Liem 1980; Lauder 1985; Muller 1987; Aerts 1991). Opercular musculature is also often involved in the mouth-opening mechanism (Elshoud 1978; Aerts et al. 1987; Lauder and Liem 1980). Studies on cranial ontogeny have suggested transformations in the structural basis for respiratory kinematics, tightly coupled to the developmental sequence of participating elements (especially muscles and skeletal structures) (Vandewalle et al. 1985; Surlemont et al. 1989; Surlemont and Vandewalle 1991; Adriaens and Verraes 1997a; Adriaens et al. 2001).

In Loricariidae or suckermouth armoured catfishes (Siluriformes, Teleostei), the suspensorial and opercular musculature is known to present a great degree of variation in size, position and even mere presence (Howes 1983). Loricariidae are a highly specialized, but diverse and speciose family, and typically have a ventrally placed sucker-mouth with an enlarged and posteriorly oriented lower lip and medioventrally rotated lower jaws (Alexander 1965; Schaefer and Lauder 1986; Geerinckx et al. 2007b). The generally well developed adductor arcus palatini ontogenetically arises from the anterior part of the constrictor dorsalis of the hyoid muscle plate; the posterior part of this constrictor

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dorsalis gives rise to the adductor operculi, of which the levator operculi and adductor hyomandibulae are believed to have derived (Schaeffer and Rosen 1961; Winterbottom 1974; Diogo and Vandewalle 2003). The levator arcus palatini and dilatator operculi originate from the constrictor dorsalis of the mandibular muscle plate (Winterbottom 1974).

In several loricariid taxa, including the genus *Ancistrus*, the opercle has probably lost its role in the respiratory mechanism, and has acquired a role in a defensive apparatus in which cheek spines (enlarged odontodes) can be erected (Howes 1983; Geerinckx and Adriaens 2006). In *Ancistrus* species, some of the opercular muscles are greatly enlarged, whereas the presence of the small adductor hyomandibulae has generally been overlooked (Geerinckx et al. 2007b). The role of the suspensorial muscles in the buccal pump system is interesting, as the posterior edge of the hyomandibular is sutured to the neurocranium in many loricariid genera (Armbruster 2004), restricting the mobility of the suspensorium. The present paper describes the ontogeny of the suspensorial and opercular muscles in the bristlenose catfish *Ancistrus* cf. *triradiatus* Eigenmann 1918. The discussion on the functionality of muscles is based on the anatomy only, as no biomechanical studies including EMG could be done on such small specimens.

In all Siluriformes, including loricariids, the anterior-most fibres of the adductor arcus palatini have differentiated into muscles serving the autopalatine–maxillary system (Singh 1967; Gosline 1975). Ontogeny of these muscles in loricariids is discussed by Geerinckx et al. (2008), and is not included in the present paper.

## Material and methods

Specimens of the loricariid *Ancistrus* cf. *triradiatus* were commercially obtained and bred in aquaria. At different time intervals embryos and juveniles were sedated in MS-222 and fixed in a paraformaldehyde–glutaraldehyde solution. Specimens throughout early ontogeny (fathered by the same male) were used to study the morphology of the musculature. Specimens with a standard length of 4.8, 5.2, 6.1, 7.0, 8.0, 10.2 and 12.4 mm were serially sectioned (Technovit 7100 embedding, slide thickness 2 µm, cut with a Reichert-Jung Polycut microtome). All seven specimens were examined, but only three of these specimens (‘stages’) are described in detail in this paper, with reference to the other specimens when relevant. Earlier stages than 6.1 mm are not mentioned, as toluidine does not stain undifferentiated muscle tissue. Two adult specimens (70 mm SL: female, 94 mm SL: male) were used to compare the early ontogenetic to the adult musculature, but we refer to Geerinckx et al. (2007b) for a detailed account on the adult

myology of the species. One subadult of 35 mm SL was serially sectioned as well (slide thickness 5 µm), providing detailed information on the innervation of the muscles. 3D-reconstructions were made from serial sections of the 6.1 and 8.0 mm stages, using the software packages Amira 3.1.1 (T.G.S.) and Rhinoceros 3.0 (McNeel).

## Results

### 6.1 mm SL stage

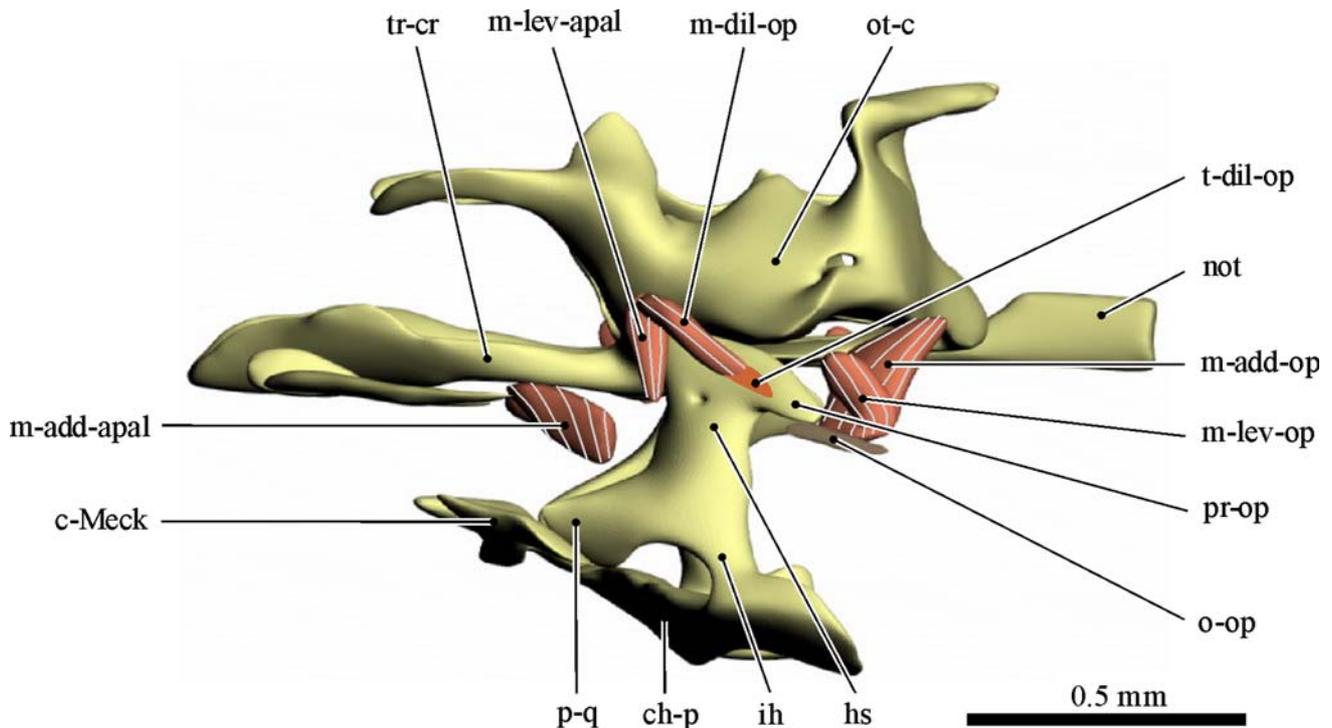
While in earlier stages (4.8 and 5.2 mm SL) no recognizable muscle tissue was present, most suspensorial and opercular muscles can be identified in the 6.1 mm specimen (Fig. 1). Hatching occurs at a standard length of 6.8 mm on average; this specimen was still in the egg when anaesthetized. No ossification is observed on the neurocranium floor or the suspensorium. The adductor arcus palatini is already present between these two structures. The flat muscle clearly lacks any insertion, neither on the neurocranium nor on the suspensorium. The suspensorium is oriented in a vertical plane: a vertical line can be drawn along the neurocranium–hyosymplectic articulation, the interhyal and the hyoid arch (Fig. 1).

The levator arcus palatini has developed as a small muscle against the lateral to rostral side of the hyosymplectic part of the cartilaginous suspensorium. Fibre direction is ventrally from the region lateral to the suspensorium–neurocranium articulation. No insertion is observed. Near its origin some muscle fibres are continuous with the fascia of the dilatator operculi. The latter muscle originates from the same region, but is somewhat larger and runs caudoventrally along the suspensorium, also lacking an insertion. No visible muscle fibres or tendon reach the opercle, which has appeared as a tiny splint of bone near the opercular process of the suspensorium.

The levator operculi and adductor operculi are in contact with each other near their ventral end. Both muscles originate on the ventral floor of the otic capsule of the neurocranium, the levator being more rostromedial than the adductor operculi. The levator operculi, the smallest of both muscles, runs toward the dorsal aspect of the opercle, without effectively reaching it. The adductor operculi almost reaches it somewhat more medially, and is fused to the medialmost fibres of the levator.

### 8.0 mm SL stage

In this specimen the adductor arcus palatini has substantially expanded and has become a broad muscle plate originating from the trabecular bar and inserting on the base of the pterygoid process and the medial edge of the hyosymplectic of the



**Fig. 1** 3D-reconstruction of the head skeleton and hyoid musculature of a 6.1 mm SL *Ancistrus* cf. *triradiatus* embryo. Lateral view the branchial basket is not shown: *c-Meck* cartilago Meckeli, *ch* ceratohyale, *hs* hyosymplecticum, *ih* interhyale, *m-add-apal* musculus adductor arcus palatini, *m-add-op* musculus adductor operculi, *m-dil-op* musculus

dilatator operculi, *m-lev-apal* musculus levator arcus palatini, *m-lev-op* musculus levator operculi, *not* notochord, *o-op* os operculare, *ot-cap* otic capsule, *p-q* pars quadrata of palatoquadratum, *pr-op* processus opercularis, *t-dil-op* tendon of musculus dilatator operculi, *tr-cr* trabecula cranii

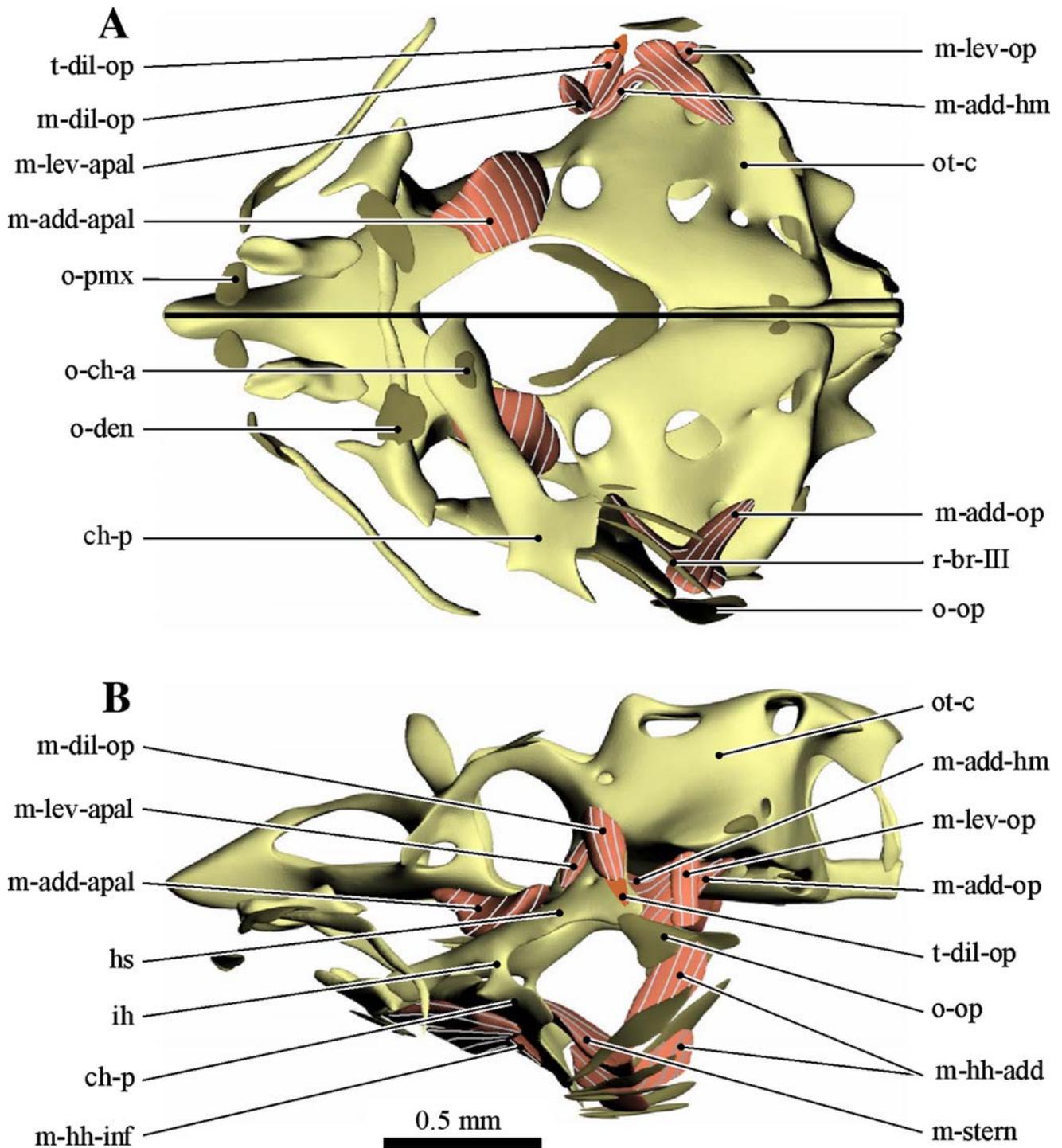
cartilagenous suspensorium (Fig. 2a; at this moment perichondral ossification is just starting to cover some parts of the chondrocranium, but not this region of the suspensorium). The caudalmost fibres have no insertion at all, as they end halfway between the trabecular bar and the suspensorium, the latter still lacking its dorsomedial membranous outgrowth (see 12.4 mm specimen). The muscle reaches the perichondrium of both cartilagenous neurocranium and suspensorium, so the muscle might well be functional by now.

The direction of the levator arcus palatini has slightly shifted: the muscle now runs rostroventrally instead of ventrally from the neurocranium–suspensorium articulation (Fig. 2b). A clear insertion on the neurocranium is not present, and the muscle is still in contact with the dilatator operculi. Serial sections actually show its origin to be on the fascia of the latter muscle, and, thus indirectly, on the neurocranium. It inserts on the rostrolateral edge of the hyosymplectic. The dilatator operculi originates on the lateral side of the anterior portion of the otic capsule, just dorsal to the articulation of the hyosymplectic to the neurocranium. Insertion is doubtful: a long tendon reaches toward the dorsal aspect of the opercle, but might or might not effectively attach to it. The orientation of the dilatator operculi has become more dorsoventral, compared to the orientation in the 6.1 mm specimen. This is related to allometric growth

of chondrocranium elements. The suspensorium has also elongated and its ventral part has shifted anteriorly (compare Figs. 1, 2b). This marks a major transformation in the chondrocranium bauplan: not only is the anterior region (including most of the suspensorium) elongating, the relative positions of the articulations of the suspensorium with the neurocranium, lower jaw and hyoid have changed.

The levator operculi still is a narrow, vertical muscle band stretching from the lateralmost protuberance of the otic capsule in the direction of the dorsal aspect of the opercle, well posterior to the insertion of the dilatator operculi tendon. Medially, its fascia is still in contact with the fascia of the larger adductor operculi. This latter muscle, without any doubt the largest of the opercular muscles at this moment, has expanded and almost reaches the opercle only slightly more medially than the levator. Interestingly, some anterior fibres of the adductor operculi insert on the opercular process of the suspensorium. Unambiguous insertion of the adductor or levator operculi on the opercle is not yet observed.

A rostradorsal differentiation of the adductor operculi has resulted in a thin muscle band ending in connective tissue near the medial side of the hyosymplectic part of the suspensorium. This band thus runs completely caudorostrally. We identify this muscle as the adductor hyomandibulae



**Fig. 2** 3D-reconstruction of the head skeleton and musculature of a 8.0 mm SL *Ancistrus* cf. *triradiatus* free-living embryo. The branchial basket is not shown. **a** Ventral view (right suspensorium and hyoid bar removed; only suspensorial and opercular musculature shown); **b** lateral view (jaw and maxillary barbel muscles removed). *ch* ceratohyale, *hs* hyosymplecticum, *ih* interhyale, *m-add-apal* musculus adductor arcus palatini, *m-add-hm* musculus adductor hyomandibulae, *m-add-op*

musculus adductor operculi, *m-dil-op* musculus dilatator operculi, *m-hh-add* musculus hyohyoidei adductores, *m-hh-inf* musculus hyohyoideus inferior, *m-lev-apal* musculus levator arcus palatini, *m-lev-op* musculus levator operculi, *m-stern* musculus sternohyoideus, *o-ch-a* os ceratohyale anterior, *o-den* os dentale, *o-op* os operculare, *o-pmx* os praemaxillare, *ot-cap* otic capsule, *r-br-III* radius branchios-tegalis III, *t-dil-op* tendon of musculus dilatator operculi

(see [Discussion](#) for an account on the usage of this name in teleostean myology).

#### 12.4 mm SL stage

Between the 8.0 and 12.4 mm stages most cranial bones have appeared, including all perichondral bones. Most of the cartilage of the neurocranium and suspensorium is covered by a bone layer. The opercle has grown, having become thicker as well as deeper. Origins and insertions of the suspensorial and opercular muscles are on the osteocranium now.

Little has changed in the shape or relative size of the adductor arcus palatini. Origin is on the orbitosphenoid and parasphenoid. The posterior fibres run in a lateral direction, toward a large, membranous medial extension of the hyomandibular bone. The more anterior fibres run more rostro-laterally, reaching both the hyomandibular and the metapterygoid, the latter of which has grown around the cartilaginous pterygoid process.

The levator arcus palatini now has its final origin, i.e. on the lateral extension of the sphenotic (dermosphenotic portion), that was not yet present in the 8.0 and 10.2 mm stages. It has lost the contact to the dilatator operculi. The latter muscle is now provided with a large aponeurosis (Fig. 3a). Muscle fibres diverge from it, both medially and (less) laterally. The medial fibres originate on the perichondral ossification of the otic capsule wall (autopterotic portion of pterotic bone), and the lateral fibres attach on a membranous tissue sheet covering the muscle and lying directly under the skin. Current ossification in this sheet is part of the dermopterotic portion of the pterotic bone.

Both the levator and adductor operculi now insert on the opercle: the levator on the dorsal margin of the bone, posterior to the dilatator operculi insertion, and the adductor medial of this dorsal margin. Origin of the levator operculi is now also on the pterotic instead of on the cartilage of the otic capsule. The adductor operculi now originates rather posteriorly on the neurocranium floor, with a clear tendon that also contacts the adductor hyomandibulae muscle. Origin is on the ventral aspect of the pterotic bone, more or less where the supracleithral ossification of Baudelot's ligament initiates. The supracleithrum is fused to the postero-ventral aspect of the pterotic in loricariids (Geerinckx et al. 2007a). The vertically flattened adductor hyomandibulae, originating on a tissue sheet that is continuous with the tendon of the adductor operculi (Fig. 3a, b), inserts rather loosely on connective tissue attaching to the inner side of the hyomandibular.

As the relative growth of the dilatator and levator operculi has surpassed that of the adductor operculi, the dilatator is now the largest opercular muscle, and the levator and adductor are of smaller, similar size.

Further ontogeny in juvenile *Ancistrus cf. triradiatus*

The adductor and levator arcus palatini, as well as the adductor operculi, grow more or less isometrically during further growth of *A. cf. triradiatus*. The adductor hyomandibulae remains very small and slender, being almost unrecognizable in adult specimens (in fact, it is easily overlooked without relying on serial sections; Figs. 4a, b, 5). The levator operculi grows relatively large, becoming a pyramidal muscle extending in a cavity of the (compound) pterotic bone. The most drastic growth is observed in the dilatator operculi, allometrically increasing in size during juvenile and even adult growth. Especially in large males, the muscle is housed in a cranial cavity that reaches toward the midline, above the brain, but below the dorsal skull roof. Intense modifications in the skull roof are present.

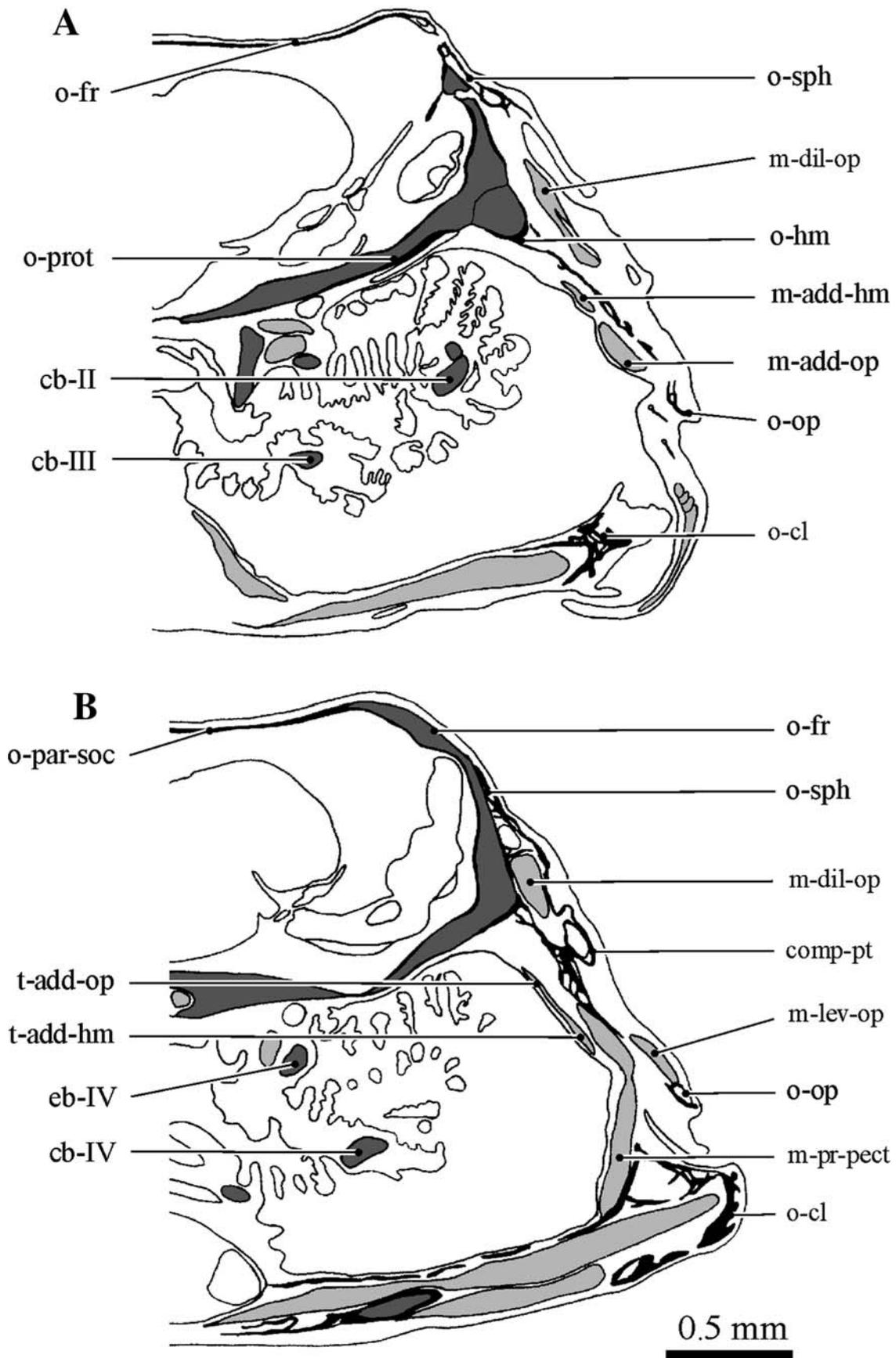
#### Muscle innervations

Serial sections clearly show the innervations of all suspensorial and opercular muscles. The adductor arcus palatini is innervated by a small branch of the hyomandibular trunk of the facial nerve. This branch, aptly named ramus adductor arcus palatini (Atoda 1936), also supplies both parts of the extensor tentaculi [muscles being derived from the adductor arcus palatini (Geerinckx et al. 2008)]. Further along the hyomandibular trunk the opercular branch separates from it, almost immediately splitting in two parts: one supplies the levator operculi, and another enters the adductor operculi as well as the adductor hyomandibulae. A nerve branch separates from the infraorbital trunk (consisting of bundles of both trigeminal and facial nerves) soon after it emerges from the skull. This branch [ramus levator arcus palatini of Atoda (1936)] splits into a lateral branchlet to the levator arcus palatini and a posterior branchlet to the dilatator operculi.

#### Discussion

##### Timing of muscle ontogeny

In *A. cf. triradiatus* most suspensorial and opercular muscles are present in the 6.1 mm SL specimen; only the adductor hyomandibulae has not yet differentiated. None of the present muscles has distinct insertions. It is not clear whether any muscle contractions in this stage could move the chondrocranial elements via the not yet differentiated connective tissue that separates the muscle tissue from the cartilage. The only cranial muscle of which a probable insertion is observed in this stage is the hyohyoideus inferior. Origin is on the hyoid bar, but no anterior insertion is present in the intermandibularis posterior (Geerinckx and



◀ **Fig. 3** Cross sections of a 12.4 mm SL *Ancistrus* cf. *triradiatus* specimen. Only the right part of each section is shown. **a** At articulation between hyomandibular and sphenotic; **b** at posterior end of opercular (black indicates bone, dark grey indicates cartilage, light grey indicates muscle). *cb-II/III/IV* ceratobranchiale II/III/IV, *comp-pt* compound pterotic bone, *eb-IV* epibranchiale IV, *m-add-hm* musculus adductor hyomandibulae, *m-add-op* musculus adductor operculi, *m-dil-op* musculus dilatator operculi, *m-lev-op* musculus levator operculi, *m-pr-pect* musculus protractor pectoralis, *o-cl* os cleithrum, *o-fr* os frontale, *o-hm* os hyomandibulare, *o-op* os operculare, *o-par-soc* os parieto-supraoccipitale, *o-prot* os prooticum, *o-sph* os sphenoticum, *t-add-hm* tendon of musculus adductor hyomandibulae, *t-add-op* tendon of musculus adductor operculi

Adriaens 2007). At this moment, one day before hatching, a weak contraction and expansion of the orobranchial chamber can be observed.

In the 8.0 mm specimen the adductor hyomandibulae has differentiated from the adductor operculi, but lacks an anterior insertion on the suspensorium. The other suspensorial muscles are now provided with both origin and insertion. Insertion of the opercular muscles, however, is still uncertain (dilatator operculi), absent (levator operculi) or absent except for a few fibres attaching to the suspensorium (adductor operculi). In the 12.4 mm specimen all final insertions are present. This sequence in muscle appearance and insertion was also observed in the clariid *Clarias gariepinus* Burchell 1822, the only siluriform of which the muscular ontogeny has been studied into detail thus far: appearance (at 4.7 mm TL) and insertion (at 5.2 mm TL) of the adductor and levator arcus palatini occur first, while the opercular muscles are first seen at 5.2 mm TL (Surlemont et al. 1989; Surlemont and Vandewalle 1991). The dilatator operculi probably attaches to the opercular process of the hyosymplectic in the 5.2 mm TL specimen (Surlemont and Vandewalle 1991), and insertion on the opercle appears not yet completely developed in a 7.2 mm SL specimen (Adriaens and Verraes 1997a). Insertion of the levator operculi on the opercle is effective at 6.8 mm SL. At this stage, the adductor operculi is closely associated with the opercular process of the hyosymplectic (as in *A. cf. triradiatus*); an undubious insertion on the opercle is only observed at 46.8 mm SL (Adriaens and Verraes 1997a). *C. gariepinus* lacks an adductor hyomandibulae.

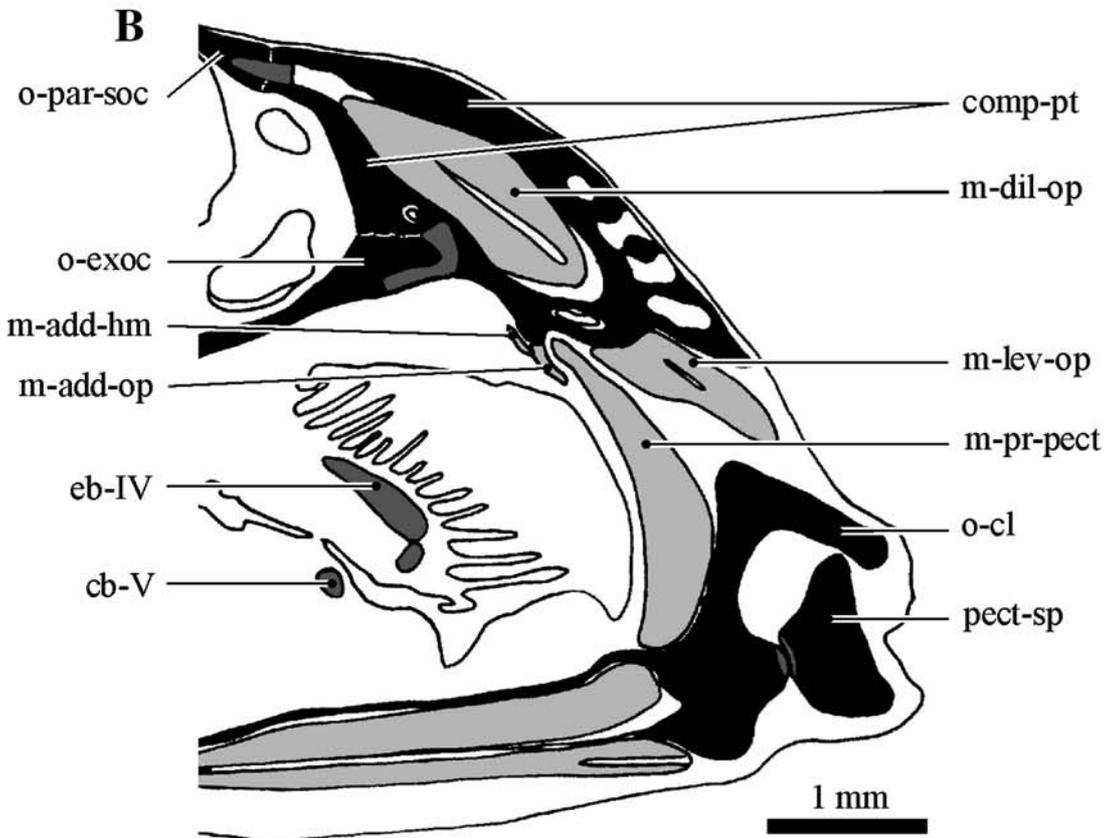
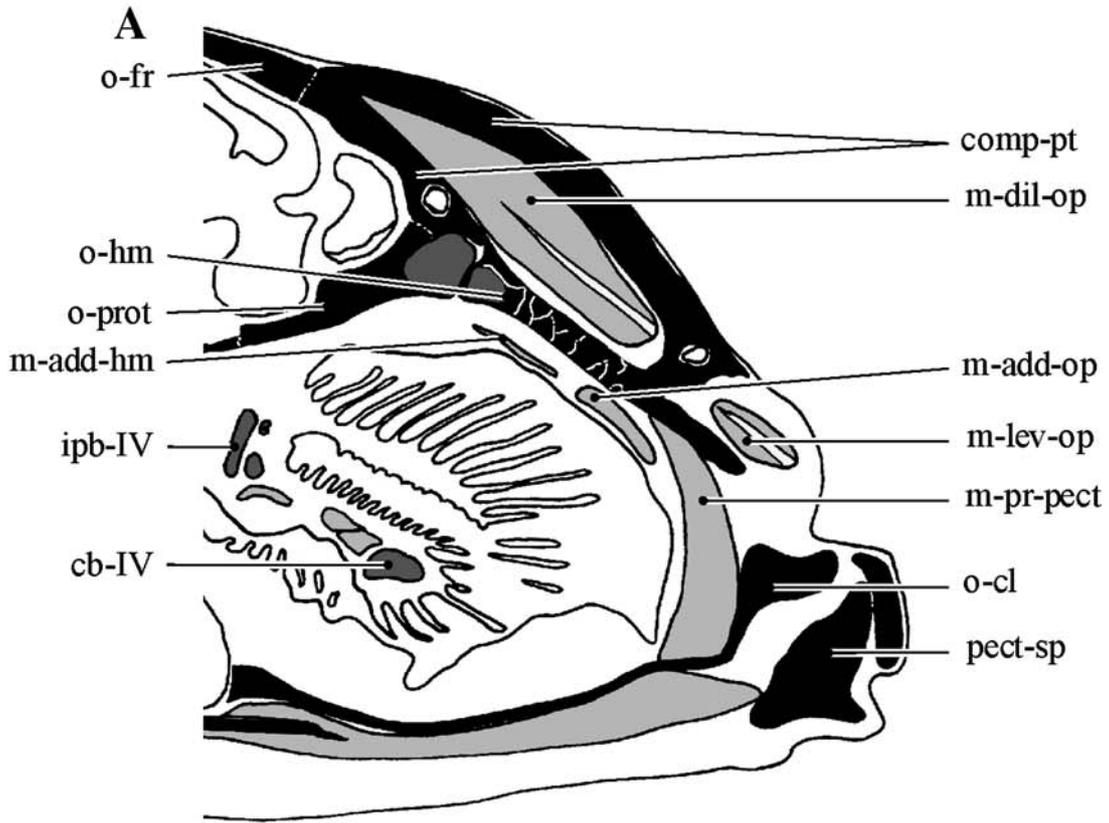
#### Muscle function in *A. cf. triradiatus*

In *A. cf. triradiatus* the adductor arcus palatini shows no important positional or size-related transformations during ontogeny. Its early position and insertion are already identical to the adult configuration. The levator arcus palatini is more influenced by changes in shape and position: its fibre direction from the neurocranium changes from slightly caudoventrally (Fig. 1) to essentially rostrally (Fig. 5a). Opposed to its origin, its insertion is never associated to

that of the dilatator operculi, thus contradicting Howes' (1983) description of adult *Ancistrus* sp. The insertion of the adductor and levator arcus palatini on the suspensorium suggests their role in the adduction and abduction of the wall of the orobranchial chamber, as in other siluriforms and most teleosts (Nawar 1955; Osse 1969; Lauder and Liem 1980; Adriaens and Verraes 1997a).

The function of the opercle and associated musculature in *Ancistrus* cf. *triradiatus* differs from the general teleostean situation, in which abduction and adduction of the opercle causes the opercular cavity to expand and constrict, respectively. The opercle and opercular muscles are involved in a mechanism of erectile cheek spines, used as a defensive apparatus. This altered morphology and function was noticed by Alexander (1965) and Howes (1983), and recently described into detail by Geerinckx and Adriaens (2006). The opercular muscles thus have acquired an altered biological function, although the adductor operculi still adducts the opercle, and the dilatator and levator operculi abduct it. The effects of the latter muscles are identical, as the long articular hinge allows opercular movement only in one rotational plane (compare left and right side on Fig. 5b; Geerinckx and Adriaens 2006). It can be observed that the opercle does not move synchronously with the ventrally positioned branchiostegal membrane. This, and the fact that it is used in the defensive cheek-spine apparatus, and not respiration, infers that the opercular muscles appear to have lost their respiratory role (Howes 1983; Geerinckx and Adriaens 2006; Geerinckx et al. 2007b). The biomechanical couple between the opercle and the lower jaw (Elshoud 1978; Aerts and Verraes 1984; Aerts et al. 1987; Westneat 1990) is lost as well, as the interopercle and interoperculo-mandibular ligament are absent in many loricariids including the species of *Ancistrus* (Armbruster 2004; Geerinckx et al. 2007b).

The function of the adductor hyomandibulae is uncertain. The muscle remains very small during later ontogeny. In some papers (e.g. Howes 1983; Schaefer 1997) the name 'adductor hyomandibulae' is erroneously used for the adductor arcus palatini. The true loricariid adductor hyomandibulae is an anterior derivation of the adductor operculi. It was not seen in loricariids by Howes (1983) and Schaefer (1997), but we found it in *Pterygoplichthys lituratus* (Kner 1854) (extremely small), *Farlowella acus* (Kner 1854) and *Otocinclus vestitus* Cope 1872. Among siluriforms, the muscle has also been found in Amblycipitidae, Ariidae, Bagridae, Callichthyidae, Claroteidae, Crangonidae, Plotosidae and Siluridae (Takahasi 1925: 'retractor hyomandibularis'; Diogo and Vandewalle 2003; Huysentruyt et al. 2007). It is not present in the basal siluriform Diplomystidae and Nematogenyidae (Diogo and Vandewalle 2003; Diogo et al. 2006). It appears to have developed independently in several non-siluriform lineages as well (Winterbottom 1974).



◀ **Fig. 4** Cross sections of a 33.5 mm SL *Ancistrus* cf. *triradiatus* specimen. Only the right part of each section is shown. **a** At suture between hyomandibular and compound pterotic; **b** at exoccipital (black indicates bone, dark grey indicates cartilage, light grey indicates muscle). *cb-IV/IV* ceratobranchiale IV/IV, *comp-pt* compound pterotic bone, *eb-IV* epibranchiale IV, *ipb-IV* infrapharyngobranchiale IV, *m-add-hm* musculus adductor hyomandibulae, *m-add-op* musculus adductor operculi, *m-dil-op* musculus dilatator operculi, *m-lev-op* musculus levator operculi, *m-pr-pect* musculus protractor pectoralis, *o-cl* os cleithrum, *o-exoc* os exoccipitale, *o-fr* os frontale, *o-hm* os hyomandibulare, *o-par-soc* os parieto-supraoccipitale, *o-prot* os prooticum, *pect-sp* pectoral spine

#### Ontogeny of muscle function in *A. cf. triradiatus*

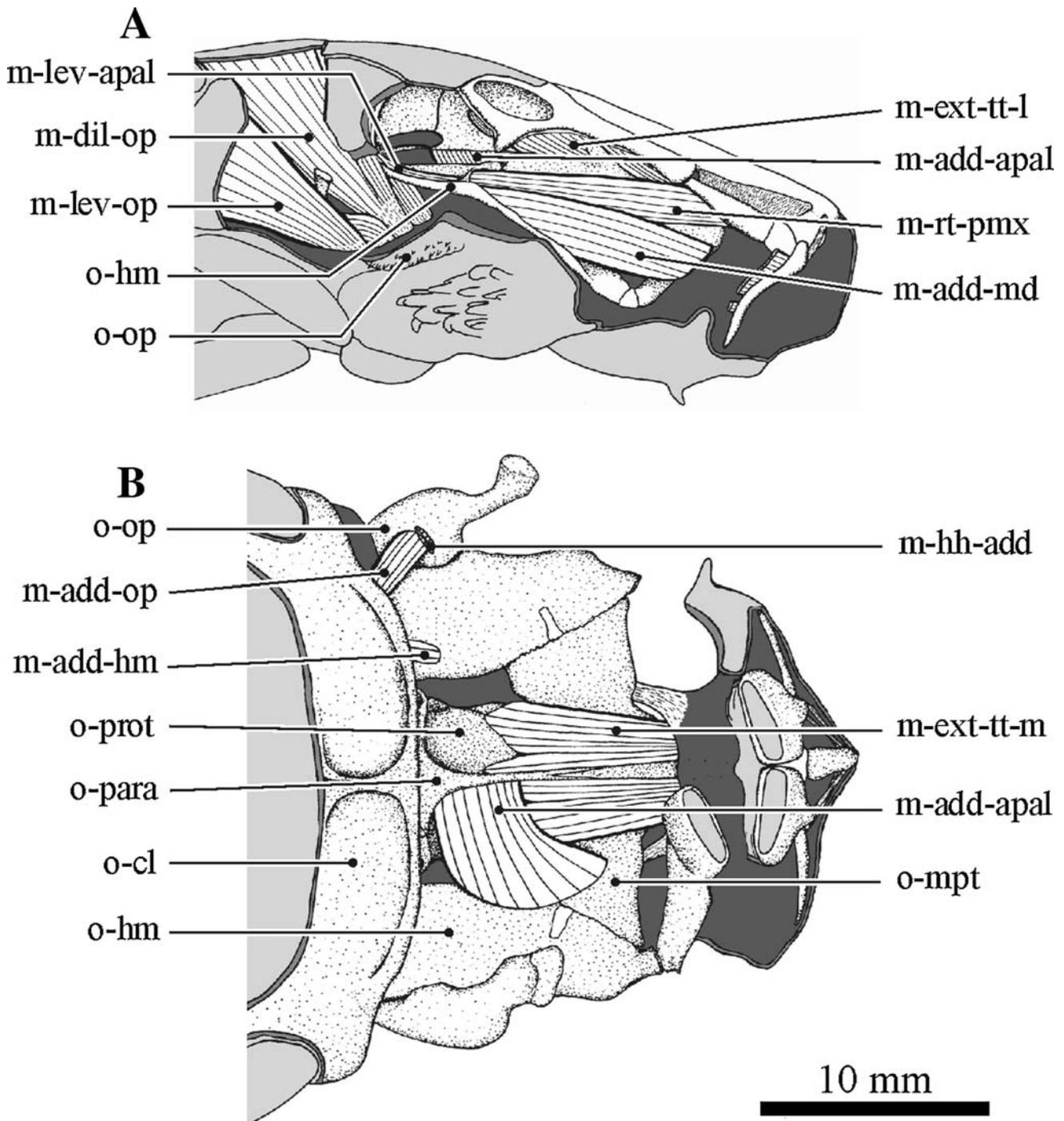
The relative volume of the suspensorial musculature during early ontogeny of *Ancistrus* cf. *triradiatus* (e.g. 8.0 mm specimen) is interesting: the adductor arcus palatini is very large, and the levator arcus palatini is very small, with a fibre direction (line of action) that is not ideal to abduct the suspensorium. Of the larger hyoid muscles, the hyohyoideus inferior is more substantial and has its insertions earlier than the sternohyoideus (Geerinckx and Adriaens 2007). Thus, the musculature responsible for a compression of the orobranchial chamber at the level of the hyoid and suspensorium [hyohyoideus inferior, adductor arcus palatini, possibly (temporarily) adductor operculi] seems more substantial and functional earlier than the antagonistic musculature responsible for the orobranchial expansion (sternohyoideus, levator arcus palatini). We observed actual movements of the hyoid bar and suspensoria from about 6.0 mm SL on. The expansion phase might well profit from the elastic properties of the cartilaginous skeleton. The contribution of the cartilage elasticity has been suggested for *Clarias gariepinus* as well (Vandewalle et al. 1985; Surlemont et al. 1989). The zones of articular cartilage, containing hypertrophied cartilage cells with little matrix, are highlighted in Fig. 6. In other teleost species such cartilage tissue has been found in joints and symphyses subject to compression (Anker 1989; Benjamin 1990; Aerts 1991). A hypothetical respiratory cycle would include a compression phase in which the hyohyoideus inferior and adductor arcus palatini would contract: the articular cartilage between the hyosymplectic and the neurocranium (1) and the interhyal cartilage (2) would bend; the hyoid symphyseal cartilage (3) would bend and compress (especially posteriorly). In the expansion phase, the elasticity of the chondrocranium, as well as the action of the (still small) sternohyoideus and levator arcus palatini, could bring the hyoid bar and suspensoria back to their original position.

Newly hatched larvae of *A. cf. triradiatus* immediately cling to vertical or even totally inclined surfaces in the nest cavity [parental care is common in *Ancistrus* species (Burgess 1989)]. Only the suckermouth is used for attachment, so suction is particularly important. Considering the

relatively weakly developed sternohyoideus and levator arcus palatini during early ontogeny (compared to the antagonistic muscles), we assume it might well be impossible to maintain this lower pressure inside the orobranchial cavity without the cartilage elasticity. Apparently, possible adhesive properties of the papillose surface of the only partly developed lips are not enough to maintain attachment, as is suggested by experiments with an anaesthetizing substance (MS-222), that halts muscle activity. Suction fails immediately.

During ontogeny, several major transformations occur that influence the mode of respiration: the proceeding development of the cranial muscles and ligaments, and their insertions, the ossification of the skeletal elements, and the lengthening of the skull, including the change in shape and position of the suspensorium (compare Figs. 1, 2b). In the 6.1 mm specimen the articulation points (1–3 in Fig. 6) are all in one vertical plane. During further ontogeny points 2–3 shift anteriorly. The same has been observed for *Clarias gariepinus* (Vandewalle et al. 1985, Fig. 1). Compared to adult *A. cf. triradiatus*, the hyoid symphysis has shifted significantly more anteriorly in adult *C. gariepinus*. In the latter species, Vandewalle et al. (1985) correlated this shift to a reduction of the buccal cavity and a parallel enlargement of the opercular fold and branchiostegal membrane. In adult *A. cf. triradiatus* the smaller branchiostegal membrane and more posterior position of the (rotated) lower jaw and lip are probably related to the more posterior position of the hyoid arch. A functional consequence of the smaller branchiostegal membrane (and the fact that the opercle may not be involved in respiratory movements) is the absence of a forceful suction pump system in adult (and larval) *A. cf. triradiatus*, compared to *C. gariepinus* and many other bottom-living teleosts (Hughes 1970; Adriaens and Verraes 1997a). This is also reflected in the small size of the branchiostegal musculature (Geerinckx et al. 2007b).

Our observations corroborate the thesis that in bottom-living teleosts with a dorsoventrally flattened skull (“a broad head”) the hyoid movements contribute more to the volume changes of the orobranchial cavity, compared to teleosts with narrower heads (Alexander 1970; Gosline 1973; Adriaens and Verraes 1997b). The suspensorium of loricariids is relatively weakly movable, due to the tight connection of the metapterygoid to the lateral ethmoid (Alexander 1965; Arratia 1990), the dorsal interdigitation of the hyomandibular to the prootic, and (in many loricariids) the posterior suture of the hyomandibular to the compound pterotic (Howes 1983; Armbruster 2004; Geerinckx and Adriaens 2006). Observation of adults (and larvae) clearly shows that suspensorial movements are considerably less than hyoid movements. It might well be possible that the depression and elevation of the hyoid bar are responsible for most of the suspensorial movements. Such interactions have been found in many

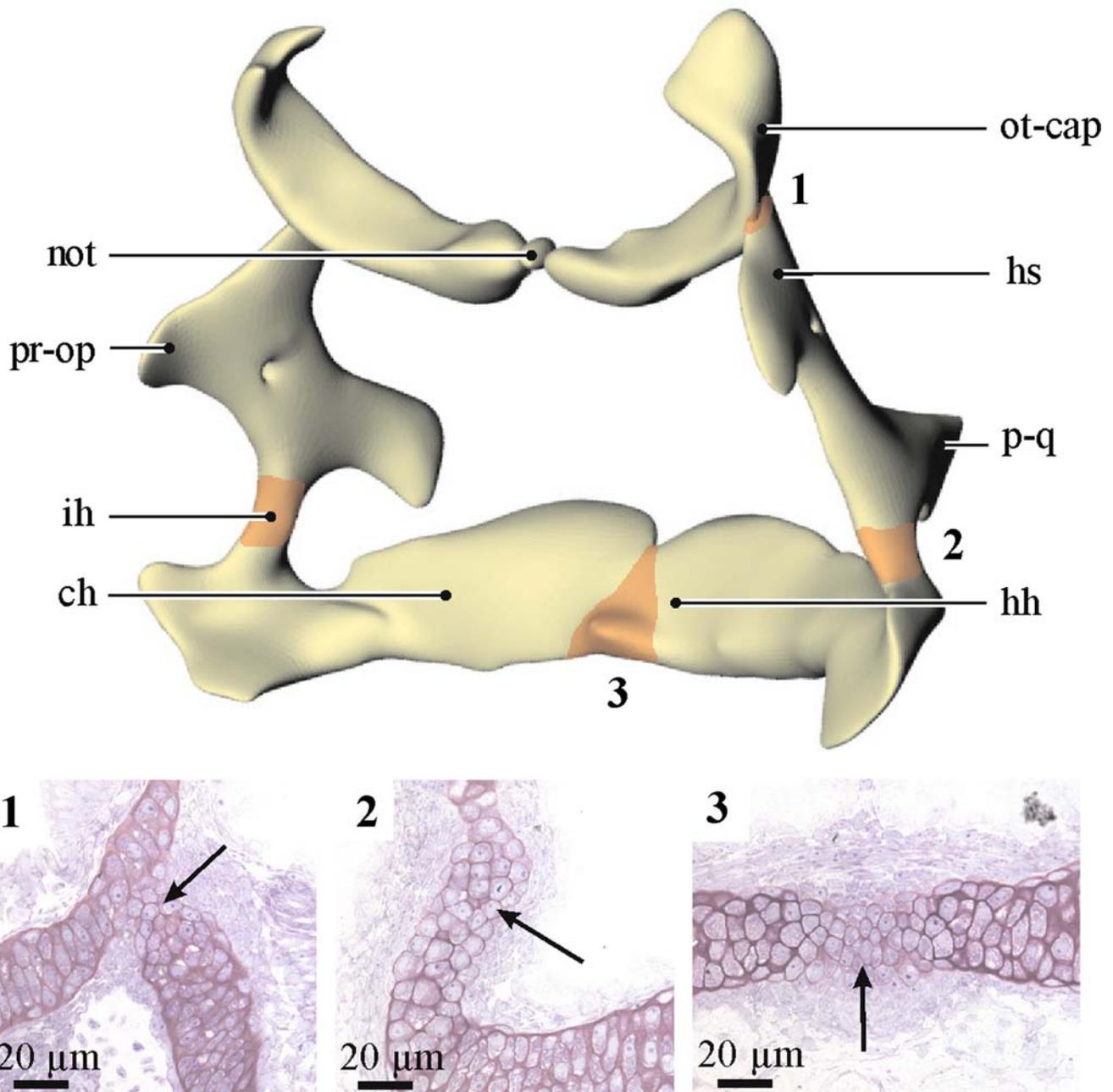


**Fig. 5** **a** Lateral view, and **b** ventral view of a dissection showing the suspensorial and opercular musculature of *Ancistrus* cf. *triradiatus* (94 mm SL). *m-add-apal* musculus adductor arcus palatini, *m-add-hm* musculus adductor hyomandibulae, *m-add-md* musculus adductor mandibulae, *m-add-op* musculus adductor operculi, *m-dil-op* musculus dilatator operculi, *m-ext-tt-l/m* musculus retractor tentaculi pars lateralis/

medialis, *m-hh-add* musculus hyohyoidei adductores (mostly removed), *m-lev-apal* musculus levator arcus palatini, *m-lev-op* musculus levator operculi, *m-rt-pmx* musculus retractor premaxillae, *o-cl* os cleithrum, *o-hm* os hyomandibulare, *o-mpt* os metapterygoideum, *o-op* os operculare, *o-para* os parasphenoideum, *o-prot* os prooticum

teleosts (e.g. Alexander 1969, 1970; Anker 1974; Elshoud-Oldenhavé and Osse 1976; Elshoud 1978; Müller 1989; Aerts 1991; Hunt von Herbing et al. 1996). The ontogenetic replacement of the cartilaginous interhyal by a sesamoid

bone in a more ligamentous hyoid-suspensorial connection (Geerinckx et al. 2007a) may reflect a change in cranial kinetism [the significance of the interhyal has been stressed before (e.g. Anker 1974; Lauder 1980; Adriaens and Verraes



**Fig. 6** Oblique posterior view of a 3D-reconstruction of the suspensoria and hyoid of a 6.1 mm SL *Ancistrus* cf. *triradiatus* embryo. Only a small section of the neurocranium is reconstructed. Zones with hypertrophied cartilage cells with little matrix are highlighted, and indicated by arrows in the details of cross sections of the 6.1 mm SL

larva, shown below. 1 Suspensorial–neurocranial articulation, 2 interhyale, 3 hyoid symphysis. See [Discussion](#) for details. *ch* ceratohyale, *hh* hypohyale, *hs* hyosymplecticum, *ih* interhyale, *not* notochord, *ot-cap* otic capsule, *p-q* pars quadrata of palatoquadratum, *pr-op* processus opercularis

1994)]. The consequences of the weak mobility of the adult suspensorium have been discussed by Alexander (1965) and Geerinckx et al. (2007b). The rigidity of the suspensorium might be important to resist the forces exerted by powerful suction when attaching to a substrate. It might also reinforce the suspension of the hyoid. A certain elasticity of the bony suspensorium itself has however been suggested (Alexander 1965; Anker 1974).

The complex interaction between the suspensorium and the hyoid probably differs significantly between larval and adult specimens. Changes in articulation points might be as important as changes in the connected elements: the increasing rigidity of the suspensorium–neurocranial contact, the loss of the interhyal and the formation of a sesamoid bone probably are key transformations in the change in respiratory kinesis that is expected to occur during

ontogeny of *A. cf. triradiatus*. These changes, as well as the sequence of muscle and bone development and ligament formation and the positional changes of the suspensorium, are all adaptations to the specific functional requirements of teleosts throughout their ontogeny (Liem 1991; Adriaens et al. 2001). In loricariids, this is undoubtedly dominated by the ontogenetic and evolutionary transformations toward a suckermouth with a scraping feeding mode.

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