A head with a suckermouth :
a functional-morphological study of the head of the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes)

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ABSTRACT. The neotropical loricariid catfishes are highly specialized for adhering to substrates, and can continue breathing and even scrape food from these surfaces while using the mouth for suction. A detailed study integrating bones, muscles and ligaments was performed on *Ancistrus* cf. *triradiatus*, using cleared and stained specimens, dissections and manipulations on fresh specimens, serial sections, and histological examination of key tissues. A limited kinematic study using high-speed video was performed as well.

The suspensorium is a rather rigid structure; the hyoid is more movable and associated muscles are more substantial; it appears to be more important in the buccal pump system. The transverse orientation of the hyohyoideus abductor suggests it can't open the branchiostegal membrane. This movement might be passive. Apart from divisions inserting on the lower and upper jaws, a medial adductor mandibulae division, the retractor veli, inserts on the oral valve. The retractor tentaculi[1] and the lateral part of the completely subdivided extensor tentaculi move the maxillary barbel, a structure that allows controlled inspiration preventing failing of the suction system. Rotational movements of the lower and upper jaws result in scraping the substrate. Antagonistic muscles for the adductor mandibulae divisions inserting on the lower and upper jaws might be a part of the protractor hyoidei and the medial part of the extensor tentaculi. The lower jaws are most mobile, not being linked to the hyoid arch medially. A medial cartilage plug acts as a supporting and gliding device for the lower jaws.

KEY WORDS : Feeding, function, morphology, myology, osteology, respiration.

INTRODUCTION

Many fishes have adopted a behaviour in which adhesion to substrates proves to be advantageous. Three typical features of the body plan that seem to have an adaptive value can be discerned (HORA, 1930) : firstly, a depressed body shape reduces drag of torrential water when lying on a substrate. Paired fins that are closely appressed to the substrate can aid in maintenance of this close contact. Secondly, frictional devices may evolve, such as spines or odontodes on the ventral side of the body and fins, making it less likely an adhering fish is washed away. Thirdly, a suction apparatus can attach a fish more firmly, irrespective of the substrate inclination or the current direction. The latter two mechanisms are also of great value in non-flowing water systems, and (especially the third) allow the adhesion to inclined substrates.

Examples of the latter mechanism in recent teleosts are numerous. Thoracic discs providing both friction and suction, as well as paired fins with adhesive surfaces have been described in Sisoridae and Erethistidae (HORA, 1930; SAXENA & CHANDY, 1966; TILAK, 1976). A suction disc is formed by the pelvic fins in various families, such

as Gobiidae (HORA, 1930), or by the ventral surface of the lower lip in the cyprinid *Garra* (HORA, 1930; SAXENA & CHANDY, 1966). Gyrinocheilidae have a modified gill opening, providing both an inspiratory and an expiratory canal. Consequently, when adhering to a substrate, the mouth can continue to work as a sucking cup (SMITH, 1945; JAYARAM, 1950; BENJAMIN, 1986; ROBERTS & KOTTELAT, 1993; NELSON, 1994). A small ventral mouth with thick, papillated lips, as well as tentacles and minute spines on fin rays ensure adhesion in certain Amphiliidae (HORA, 1930; DIOGO et al., 2000). A ventral suckermouth is also well developed in members of the Mochokidae and Astroblepidae. The latter group can even use the suckermouth for terrestrial movements (JOHNSON, 1912).

Also, in some fishes the coupling of a suckermouth to structural transformations in the jaws or the lips has allowed an evolutionary development of a substrate-scraping device. The single largest group, in which the combination of oral suction and a scraping feeding apparatus is found, is the family of the South American Loricariidae, or suckermouth armoured catfishes. The family is characterized by remarkable features such as a bony armor, a ventrally oriented suckermouth, ventrally tilted lower jaws and new and unique muscle configurations increasing jaw mobility (SCHAEFER & LAUDER, 1986). Not

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[1] This muscle, however, is not homologous to the retractor tentaculi of related and non-related siluriforms. Therefore it has been renamed levator tentaculi in a recent paper (in submission).

only this morphology, but also their status as the largest catfish family [more than 670 species according to a recent count (FERRARIS et al., 2003)] has drawn focus to the group. Among the most important papers discussing loricariid cranial morphology are ALEXANDER (1965), HOWES (1983), SCHAEFER (1987; 1988), SCHAEFER & LAUDER (1986; 1996) and ARMBRUSTER (2004). Accounts on postcranial morphology were given by SHELDEN (1937) and SCHAEFER (1987; 1997), while ALEXANDER (1964) and CHARDON (1968) treated the loricariid Weberian apparatus.

Cranial osteology and myology of the loricariid *Otocinclus vittatus* have been described by SCHAEFER (1997), with a strong systematic and phylogenetic interest. The aim of the present paper is to describe in detail the cranial osteology and myology of one loricariid species, and to discuss those parts of the head involved in suction, respiration and feeding, with an emphasis on functionality of structures rather than their use as systematic characters. The anatomical results are coupled to a limited kinematic data set.

MATERIALS AND METHODS

Ancistrus cf. *triradiatus* Eigenmann 1918, a bristlenose suckermouth armoured catfish, was chosen for this study, as we consider it a generalized loricariid (medium sized, with an intermediate body depth and length). Specimens of both sexes of *A.* cf. *triradiatus* were commercially obtained. Osteology was studied on *in toto* cleared and stained specimens (TAYLOR & VAN DYKE, 1985). Dissections were performed for the study of both hard and soft tissues. Whenever necessary, visualisation of muscle fiber arrangement was enhanced by the use of iodine (BOCK & SHEAR, 1972). Examination of the specimens was done using an Olympus SZX9 stereoscopic microscope, equipped with a camera lucida for drawing. One subadult specimen was selected for serial sectioning. The obtained toluidine stained 5μm sections (Technovit 7100 embedding, cut with a Reichert-Jung Polycut microtome) were studied using a Reichert-Jung Polyvar light microscope. Selected tissue samples (both lips, oral valve and tissue connecting it to the upper jaws, cartilage plug between lower jaws) of another specimen were histologically studied; the 10μm paraffin cut sections were stained with Verhoeff-Van Gieson's stain for elastin and collagen (PEARSE, 1985).

Examined specimens : clearing and staining : 4 (male : 88mm SL, 90mm SL; female : 44mm SL; gender unknown : 36mm SL); dissection : 3 (male : 94mm SL; female : 68mm SL, 74mm SL); serial sections : 1 (gender unknown : 33.5mm SL); histological study : 1 (female : 71mm SL). Some specimens of *Farlowella acus*, *Otocinclus vestitus* and *Pterygoplichthys lituratus* were studied for comparison.

Live observations were carried out in aquaria (including experiments with milk used as dye to visualize water flows during respiration). Filming of three specimens (in lateral, ventral and oblique ventrolateral view) was done with a Redlake Motionscope digital video camera at 200 frames per second. Only each eight frame was analysed (25 frames per second). Observations are qualitative; no markers or length measurements were included. An extensive biomechanical study was not aimed for; such study on *Pterygoplichthys lituratus*, using X-rays and electromyography, is in progress.

RESULTS

Except where noted, osteological terminology follows SCHAEFER (1987), and myological terminology follows WINTERBOTTOM (1974).

Neurocranium (Figs 1-2-3-4)

The anterior half of the long mesethmoid is almost cylindrical and gives the snout region rigidity. Anterolateral cornua are absent, and there is an expanded ventral disc projecting ventrally (Fig. 2). The large lateral process of the lateral ethmoid [antorbital process of SCHAEFER (1987)] has an articular facet for the autopalatine anteriorly, and an articular facet with a supporting ridge for the metapterygoid ventrally.

The anterior part of the frontal is relatively narrow, while the posterior part is broader, reaching the orbit. The sphenotic has a prominent lateral process, enclosing the infraorbital canal. Posterior to the orbit, the sphenotic contributes to the articulation with the hyomandibular (Fig. 2B).

In the skull floor the toothless prevomer is a narrow bone, without well developed lateral wings. It sutures deeply with the mesethmoid (anteriorly) and the parasphenoid (posteriorly), which sutures with the basioccipital as well. The parasphenoid forms a longitudinal protruding ridge on the ventral side of the neurocranium. It has a pair of small lateral wings. A major part of the skull wall and floor lateral to the parasphenoid is occupied by the orbitosphenoid. Together with the pterosphenoid and the prootic it forms the border of the sphenotic fenestra (Fig. 2B). The prootic contributes to the posterior skull floor and, to a lesser degree, to the neurocranium wall, where it bears almost half of the articulation facet for the hyomandibular.

The basioccipital is fused posteriorly with the ossified Baudelot's ligaments into a T-shaped bone (Fig. 4A). Laterally, a certain degree of fusion has occurred with the exoccipital. The ossified Baudelot's ligaments are vertical bony ridges protruding ventrally from the skull floor. They extend toward, and suture with, ventral flanges of the compound pterotics, which are the continuation of this transverse ventral ridge.

A substantial part of the posterior skull roof, skull floor and caudolateral wall of the brain case is taken by the pterotic. Thus it is a double-layered bone, providing ample insertion space for the opercular muscles. Where it contacts the sphenotic and prootic, it forms the caudal edge of the hyomandibular articulation. The pterotic is fused to the more ventrocaudal supracleithrum (or even posttemporo-supracleithrum) of the pectoral girdle. The true nature of this fused bone complex, as well as its relation to the ossified Baudelot's ligament, has not been unambiguously resolved (LUNDBERG, 1975; FINK & FINK, 1996); its development is part of a forthcoming paper. It

will be further referred to as compound pterotic. The epi-occipital [epiotic of SCHAEFER (1997)] is a small element composing part of the caudal neurocranium wall (Fig. 3). Finally, the parieto-supraoccipital lacks a pronounced posterior process. Posteroventrally, a *V*-shaped medial ridge is fused with the fused neural arch of the second and third vertebrae. Moreover, the posterior tip is fused with the neural spine of the sixth vertebra, as in *Hypostomus plecostomus* (ALEXANDER, 1964) (Fig. 3). There is no dorsomedial crest.
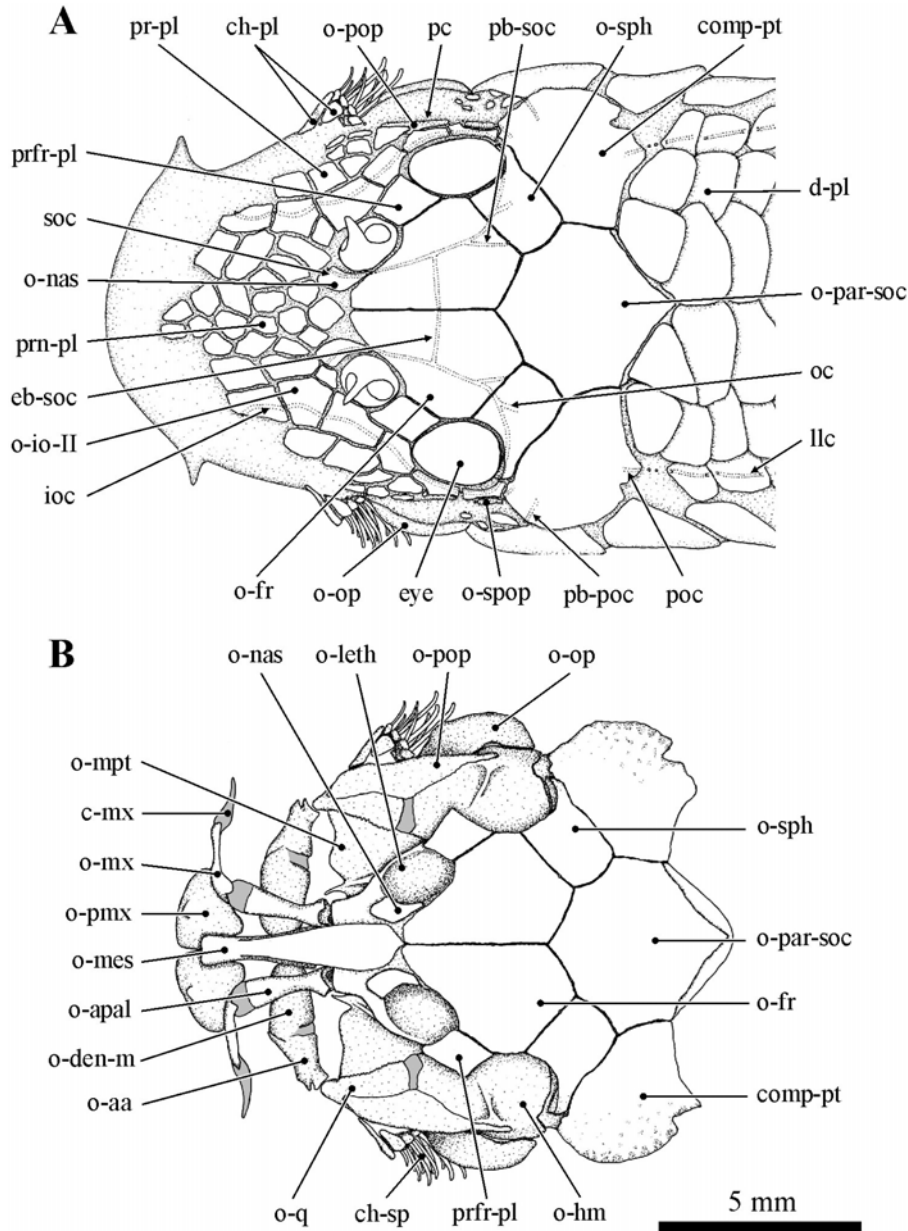

Fig. 1. – A, Dorsal view of the skull of *Ancistrus* cf. *triradiatus* (44mm SL); B, Skin and most dermal plates removed. Cartilage is indicated by grey shading. c-mx, cartilago maxillaris; ch-pl, cheek plates; ch-sp, cheek spines; comp-pt, compound pterotic bone; d-pl, dermal plate; eb-soc, epiphysial branch of supraorbital canal; ioc, infraorbital canal; llc, lateral line canal; o-aa, os anguloarticulare; o-apal, os autopalatinum; o-den-m, os dento-mentomeckelium; o-fr, os frontale; o-hm, os hyomandibulare; o-io-II, os infraorbitale II; 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-par-soc, os parieto-supraoccipitale; o-pmx, os praemaxillare; o-pop, os praeoperculare; o-q, os quadratum; o-sph, os sphenoticum; o-spop, os suprapraeoperculare; oc, otic canal; pb-poc, pterotic branch of postotic canal; pb-soc, parietal branch of supraorbital canal; pc, preopercular canal; poc, postotic canal; pr-pl, postrostral plate; prfr-pl, prefrontal plate; soc, supraorbital canal.
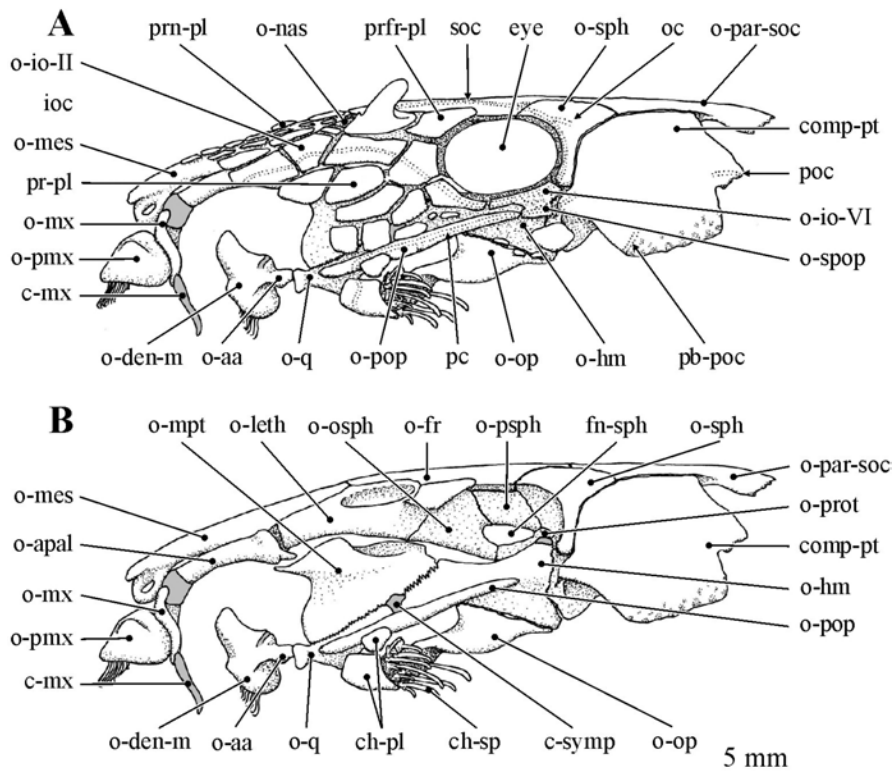
Fig. 2. – A, Lateral view of the skull of *Ancistrus* cf. *triradiatus* (44mm SL); B, Most dermal plates removed. Cartilage is indicated by grey shading. c-mx, cartilago maxillaris; c-symp, cartilago symplecticum; ch-pl, cheek plates; ch-sp, cheek spines; comp-pt, compound pterotic bone; fn-sph, fenestra sphenoidea; ioc, infraorbital canal; o-aa, os anguloarticulare; o-apal, os autopalatinum; o-den-m, os dento-mentomeckelium; o-fr, os frontale; o-hm, os hyomandibulare; o-io-II/VI, os infraorbitale II/VI; 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-osph, os orbitosphenoideum; o-par-soc, os parieto-supraoccipitale; o-pmx, os praemaxillare; o-pop, os praeoperculare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-q, os quadratum; o-sph, os sphenoticum; o-spop, os suprapraeoperculare; oc, otic canal; pb-poc, pterotic branch of postotic canal; pc, preopercular canal; poc, postotic canal; pr-pl, postrostral plate; prfr-pl, prefrontal plate; prn-pl, prenasal platelet; soc, supraorbital canal.
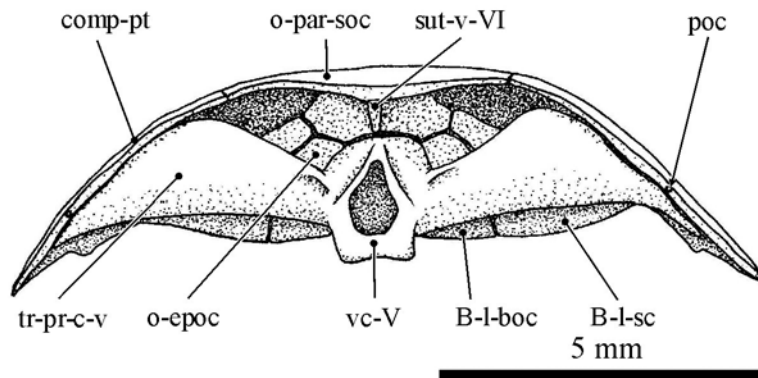
Fig. 3. – Caudal view of the neurocranium of *Ancistrus* cf. *triradiatus* (44mm SL). Cartilage is indicated by grey shading. B-l-boc, Baudelot's ligament pars basioccipitalis; B-l-sc, Baudelot's ligament pars supracleithris; comp-pt, compound pterotic bone; o-epoc, os epioccipitale; o-par-soc, os parieto-supraoccipitale; poc, postotic canal; sut-v-VI, occipital suture with neural spine of sixth vertebra; tr-pr-cv, transverse process of complex vertebra; vc-V, fifth vertebral centrum.
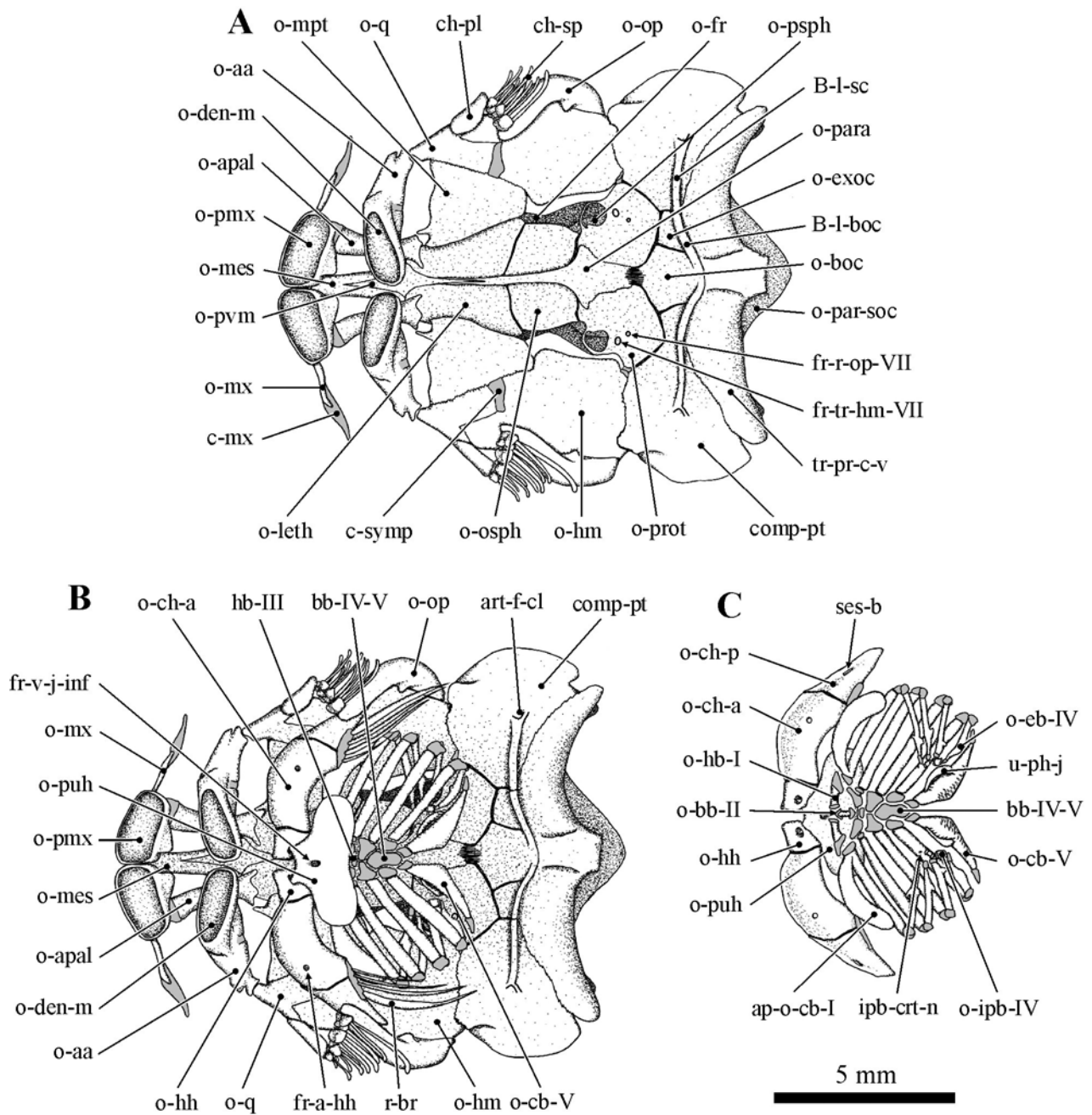
Fig. 4. – A, Ventral view of the skull of *Ancistrus* cf. *triradiatus* (44mm SL), hyoid and branchial arches removed; B, With hyoid and branchial arches; C, Dorsal view of hyoid and branchial arches. Cartilage is indicated by grey shading. ap-o-cb-I, anterior process of os ceratobranchiale I; art-f-cl, articulation facet for cleithrum; bb-IV-V, basibranchialia IV-V (posterior copula); B-l, Baudelot's ligament; c-mx, cartilago maxillaris; c-symp, cartilago symplecticum; ch-pl, cheek plates; ch-sp, cheek spines; comp-pt, compound pterotic bone; fr-a-hh, foramen for artery supplying hyohyoideus inferior; fr-v-j-inf, foramen vena jugularis inferior; hb-III, hypobranchiale III; ipb-crt-n, infrapharyngobranchial-like cartilage nucleus; o-aa, os anguloarticulare; o-apal, os autopalatinum; o-bb-II, os basibranchiale II; o-boc, os basioccipitale; o-cb-V, os ceratobranchiale V; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den-m, os dento-mentomeckelium; o-eb-IV, os epibranchiale IV; o-exoc, os exoccipitale; o-fr, os frontale; o-hb-I, os hypobranchiale I; o-hh, os hypohyale; o-hm, os hyomandibulare; o-ipb-IV, os infra-pharyngobranchiale IV; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-op, os operculare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-par-soc, os parieto-supraoccipitale; o-pmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-puh, os parurohyale; o-pvm, os praevomerale; o-q, os quadratum; r-br, radius branchiostegus; ses-b, sesamoid bone; tr-pr-c-v, transverse process of complex vertebra; u-ph-j, upper pharyngeal jaw.

Six infraorbital canal-bearing bones are present on either side. These bones, as well as the canal-bearing nasal, are part of the dermal plating of the snout and cheek region (Figs 1A, 2A). Between both infraorbital series, a total of 24 prenasal plates were counted in the specimen illustrated in the figures (this number varies somewhat among the examined specimens). Ventrolateral to the infraorbitals a group of postrostral plates is present, also varying in number and size, even between both sides of the same specimen (nine at left, eight at right side of drawn specimen; Figs 1A, 2A). The paired, square-shaped prefrontal plate partly covers the lateral process of the lateral ethmoid, bordering the nostril and the orbit.

Splanchnocranium (Figs 1-2-3-4)

The paired autopalatine articulates with the anterior end of the lateral ethmoid. Ventral to the articulation facet (which is directed caudodorsally) two processes are present (Fig. 4A). The tendons of the pars medialis and lateralis of the extensor tentaculi muscle insert on these medial and lateral processes respectively. Anteriorly a large cartilaginous head is present on the autopalatine, on which the bar-shaped maxilla articulates by means of a double medial process, providing two articulatory surfaces. The autopalatine splint, as seen in some other loricariids (SCHAEFER, 1987; 1997), is rudimentary in *Ancistrus* cf. *triradiatus*, fused to the anterolateral side of the autopalatine. The slightly curved maxilla is flattened, providing abundant insertion space for the retractor tentaculi muscle posteriorly. The distal end is fused to the maxillary barbel cartilage, which supports a short barbel. The premaxillae are oval to rectangular basket-shaped and provide space for developing teeth rows. One row of functional teeth (number of teeth per jaw averaging 60 to 80 in adults) inserts on the inner rostral side.

The dento-mentomeckelium and anguloarticular of which the lower jaw consists, are strongly sutured rostrally; a long splint of the dento-mentomeckelium overlies the anguloarticular ventrally. Caudally, the small cartilaginous remnant of the Meckel's cartilage connects both bones. There is no separate coronomeckelian bone. The dento-mentomeckelium resembles the premaxilla in being basket-shaped, and bearing functional and developing teeth rows. As in the premaxilla, the functional teeth (60 to 85 on average) point ventrally, as the whole lower jaw is twisted ventrally and medially. The coronoid process of the dento-mentomeckelium, and, more importantly, the high dorsal ridge of the dento-mentomeckelium and the anguloarticular serve as ample insertion surface for the adductor mandibulae muscle (Fig. 2). Laterally, each anguloarticular articulates with the quadrate; medially, both dento-mentomeckelian bones are loosely embedded in soft tissue containing a cartilaginous plug (Figs 5D-E, 8B). This configuration allows both lower jaws to move independent from each other. The cartilage plug acts as a supporting device for the free medial end of the dento-mentomeckelian bones.

The long, triangulate suspensorium is a very sturdy structure. The quadrate and the hyomandibular are tightly sutured, as well as reinforced by the preopercle that overlies their lateral surfaces, tightly coalesced to both bones (Figs 1B, 2B). Dorsally the small symplectic cartilage is situated between both bones. The hyomandibular articulates with the neurocranium at the point where the prootic, sphenotic and compound pterotic meet. The combined hyomandibular crest for the adductor mandibulae and levator arcus palatini is very conspicuous (Fig. 1B). The restricted mobility of the suspensorium is largely caused by an additional, long and almost suture-like articulation between the posterior edge of the hyomandibular and the compound pterotic (Figs 2B, 4A). Both quadrate and hyomandibular are loosely sutured to the metapterygoid (Fig. 2B). Dorsally this latter bone articulates with the lateral ethmoid, the long articulation being most rigid in the posterior half. The body of the metapterygoid and a dorsolateral lamina extending toward the autopalatine provide a groove-like housing for the pars lateralis of the extensor tentaculi muscle (Fig. 2B). Although the entire suspensorium is rather rigid, some bending along the joints and sutures allows a certain degree of movement toward the medial, while elasticity seems to return it to the resting position.

The hyoid (Fig. 4B-C) consists of paired (ventral) hypohyals, and anterior and posterior ceratohyals [anterohyal and posterohyal of SCHAEFER (1987; 1997)]. The anterior ceratohyal has synchondral joints with the hypohyal and the posterior ceratohyal. The latter joint is reinforced by means of a suture between the anterior laminae of both bones. The posterior ceratohyal has a long hinge with the medial face of the hyomandibular: halfway along the hyomandibular it has a cartilaginous articulation; at the rostral end of the hyomandibular, near the symplectic cartilage, a second, more movable ligamentous connection is present, with ligaments from the posterior ceratohyal to the preopercle and to the symplectic cartilage too. In the latter ligaments a minute sesamoid bone is found (Fig. 4C). An interhyal is not present. The rostral margin of the anterior ceratohyal adheres to the quadrate and metapterygoid with still longer ligamentous fibers. The resulting articulation between the hyoid and the suspensorium is strongest posteriorly. The articulatory configuration restricts the mobility of the hyoid to a, still considerable, oblique dorsoventral movement, reducing or enlarging the oral cavity. The anterior and posterior ceratohyals share a large, cartilaginous ventrocaudal process, with which four branchiostegal rays articulate (Fig. 4B).

The compound parurohyal bone connects the sternohyoideus muscle to the hyoid arch. It bears two rostral articulatory processes, each fitting into a cavity of one hypohyal (Fig. 4B-C). Strong ligaments keep these elements well connected. A mediodorsal ridge of the parurohyal increases the insertion surface for the sternohyoideus muscle.

In *Ancistrus* cf. *triradiatus* only the second and third basibranchials are ossified (ossification of the third is inconspicuous and only present in the largest specimens). Basibranchial I can't be distinguished, and basibranchials IV and V are fused and remain cartilaginous. Basibranchial II is connected to the parurohyal ligamentously. Hypobranchials I and II are separate from their corresponding ceratobranchials, whereas III and IV are fused to them. Hypobranchial V is reduced to such an extent that it can't be discerned from ceratobranchial V. Only

hypobranchial I is ossified. The ossified ceratobranchials I-IV are long and bar-shaped; V is flattened, has gill filaments on the anterior side only, and bears about 35 conical pharyngeal teeth. Ceratobranchial I bears an accessory process, as large as the bone itself (Fig. 4C). This process is loosely attached to the hyomandibular, and bears gill rakers on its posterior side. The process, present in many loricariids, is unique among siluriforms (SCHAEFER, 1987; ARMBRUSTER, 2004). All epibranchials except the fourth bear posterior uncinate processes, of which the third is the largest. Epibranchial I bears an additional small anterior process. Ossified infrapharyngobranchials III and IV are present, articulating with epibranchials II-IV, the prootic and the upper pharyngeal jaws; the latter being paired elongated dermal bones that bear about 25 conical teeth each. Infrapharyngobranchial III is a short bar, whereas IV is more square-formed. In front of infrapharyngobranchial III a minuscule cartilage nucleus can be seen (Fig. 4C). Whether this corresponds to infrapharyngobranchial I or II could not be determined.

Of the opercular bones, only the opercle itself is a separate structure in *Ancistrus* cf. *triradiatus*. The suprapreopercle, a simple canal bone with a ventral flange, fuses with the sixth infraorbital in large specimens, resulting in an apparently "double" canal bone (Fig. 2A). As mentioned above, the preopercle rigidly connects the quadrate and the hyomandibular in all examined specimens. It is an elongated, flattened canal bone overlying the lateral margin of these suspensorial bones, attaching them to the armoured skin. There is no interopercle, nor an interoperculo-mandibular ligament (there is, however, a lateral mandibulo-hyoid ligament). The opercle has a complex shape. It has a long joint with the suspensorium, consisting of a main articulation with a cartilaginous hyomandibular head and opercular socket, a rather stiff, bony articulation more posteriorly, and a tooth-like fortification of the joint more anteriorly (see also GEERINCKX & ADRIAENS, 2006). Movements along this hinge have an effect on the ventral process of the opercle (Fig. 2) that will push the large cheek spines, a set of very large odontodes, to a lateral, erect position. These spines insert on small bony platelets, which are embedded in ligamentous tissue and so articulate with the opercular process. Two cheek plates are present. The anteriormost cheek plate is the larger, and is situated more ventrally. It articulates with the spine-bearing platelets and the quadrate. The resulting cheek-spine mechanism has been described and discussed recently (GEERINCKX & ADRIAENS, 2006).

Jaw musculature (Figs 6-7-8)

Loricariid jaw musculature is highly complex. In addition, the homology between the adductor mandibulae subdivisions as described in loricariids and A1, A2 and A3 sections has been a matter of debate (ALEXANDER, 1965; WINTERBOTTOM, 1974; HOWES, 1983; SCHAEFER, 1997; DIOGO, 2005). Ideally, developmental studies, and a comparative examination of several loricarioid families should be done in order to clarify all possible homologies and de novo formations. At this moment it is most appropriate to describe muscle divisions according to their position, presumed function and (eventual) previous nomenclature in loricariids.

In the jaw muscle complex of *Ancistrus* cf. *triradiatus*, different muscle divisions can be discerned. The main part of the complex is the adductor mandibulae sensu stricto [muscle b of HOWES (1983)]. Two main subdivisions can be discerned. The longest, external bundle originates on the preopercle and on the lateral surface of the hyomandibular, anterior to, and on the prominent lateral hyomandibular ridge, and inserts on the high dorsal ridge of the dento-mentomeckelium and the anguloarticular of the lower jaw. The shorter, more ventral and interior part of the muscle, hidden below the external one, consists of two flat, distinct bundles (Fig. 6B) that originate on the quadrate, the hyomandibular and the metapterygoid. They insert dorsocaudally on the meckelian cartilage and the body of the anguloarticular. Experimentally pulling the adductor mandibulae results in an adduction of the mandible, but also rotates it, so that the teeth row swings anteriorly. This rotation appears to be due to the rather dorsal insertion on the lower jaw of the muscle.

Medial to the dorsal bundle of the adductor mandibulae lies the retractor premaxillae [muscle c of Howes (1983)], which also originates on the hyomandibular. Manipulation of the muscle pivots the premaxilla around its dorsal articulation. The result is analogous to that of the combined adductor mandibulae bundles on the lower jaw: the teeth scrape on the substrate where the fish is lying on.

The third part of the complex is the thin and strap-like retractor veli [muscle d of HOWES (1983); Figs 6B, 7C], originating posteriorly on the metapterygoid, and running medial to the retractor premaxillae. Almost a third of the muscle is composed of the thin aponeurosis, from which the fibers diverge in the oral valve (or velum). The presence of these collagen fibers running in both halves of the oral valve was shown by the Verhoeff-Van Gieson's stain methods. The collagen fibers intermingle at the midline where they enclose a band of elastic tissue running rostrocaudally (Fig. 5B-C), connecting the valve with the cartilage-like tissue between both premaxillae. The soft connective tissue between the autopalatine and the metapterygoid is loosely attached to the aponeurosis, but pulling the muscle has no apparent effect other than retracting the valve backward.

The dorsal retractor tentaculi [muscle a of HOWES (1983); Figs 6A, 7A] overlies the other muscles of the cheek region. It is a broad band-like muscle, originating from an anterior ridge on the ventral side of the lateral ethmoid. Two thirds of the muscle fibers run straight to the posterior face of the maxilla; the other third, comprising the lateroventral fibers, runs in a slightly more lateral direction, inserting closer to the distal tip of the bone. Contraction of the muscle appears to pull the tip of the maxilla in a caudodorsal direction. Due to the position of the bone and the maxillary barbel cartilage (where upper and lower lip meet) the lateral lip tissues are retracted toward the dorsal.
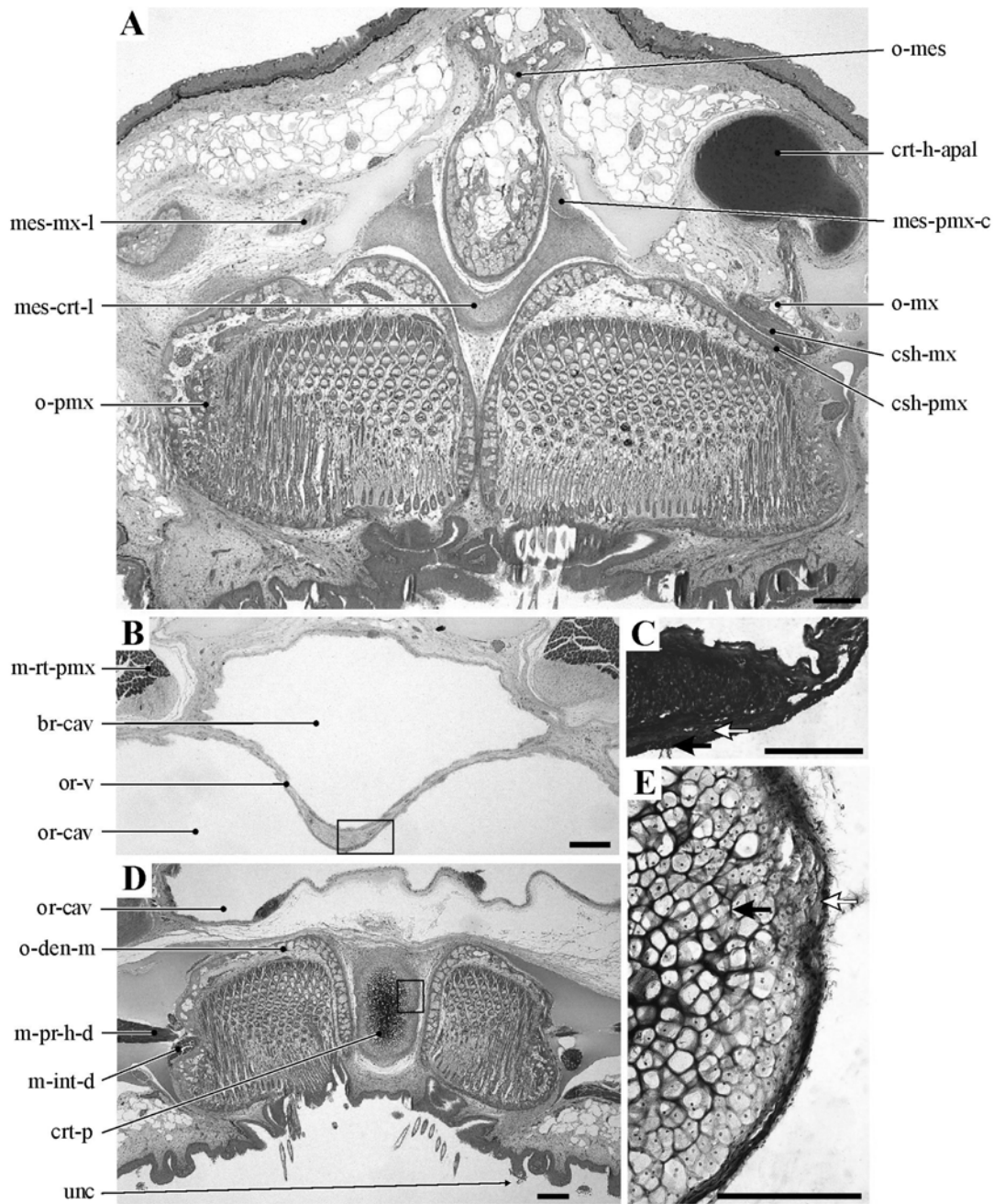
Fig. 5. – A, Section at the level of the premaxillae, showing the mesethmoid-premaxillary cartilage, some of the rostral ligaments and the tissue cushions between the premaxilla and the proximal head of the maxilla. Notice the close contact between both premaxillae. B, Section at the level of the rostral half of the oral valve, indicating the cartilage-like medial band, cut transversely. C, Detail of oral valve (cf. rectangle in fig. B), showing the elastic cartilage band (black arrow) and the collagen fibers (white arrow). D, Section at the level of the dento-mentomeckelian bones, indicating their relation to the cartilage plug attached to the hyoid. Notice the papillae with epidermal brushes or unculi on the lower lip. E, Detail of cartilage plug, showing the elastic cartilage (black arrow) and the thin sheet of perichondral collagen fibers (white arrow). (A, B, D, Technovit sections, toluidine blue stain. C, E, paraffin sections of other specimen, Verhoeff-Van Gieson's stains. Scale bars are 200 μm.) br-cav, branchial cavity; crt-h-apal, cartilaginous head of autopalatine; crt-p, cartilage plug; csh-mx, cushion on maxilla; csh-pmx, cushion on premaxilla; m-int-d, musculus intermandibularis pars dentalis; m-pr-h-d, musculus protractor hyoidei pars dentalis; m-rt-pmx, musculus retractor premaxillae; mes-crt-l, mesethmoid-cartilage ligament; mes-mx-l, mesethmoid-maxillary ligament; mes-pmx-c, mesethmoid-premaxillary cartilage; o-den-m, os dento-mentomeckelium; o-mes, os mesethmoideum; o-mx, os maxillare; o-pmx, os praemaxillare; or-cav, oral cavity; or-v, oral valve or velum; unc, unculi or unicellular keratinized brushes.
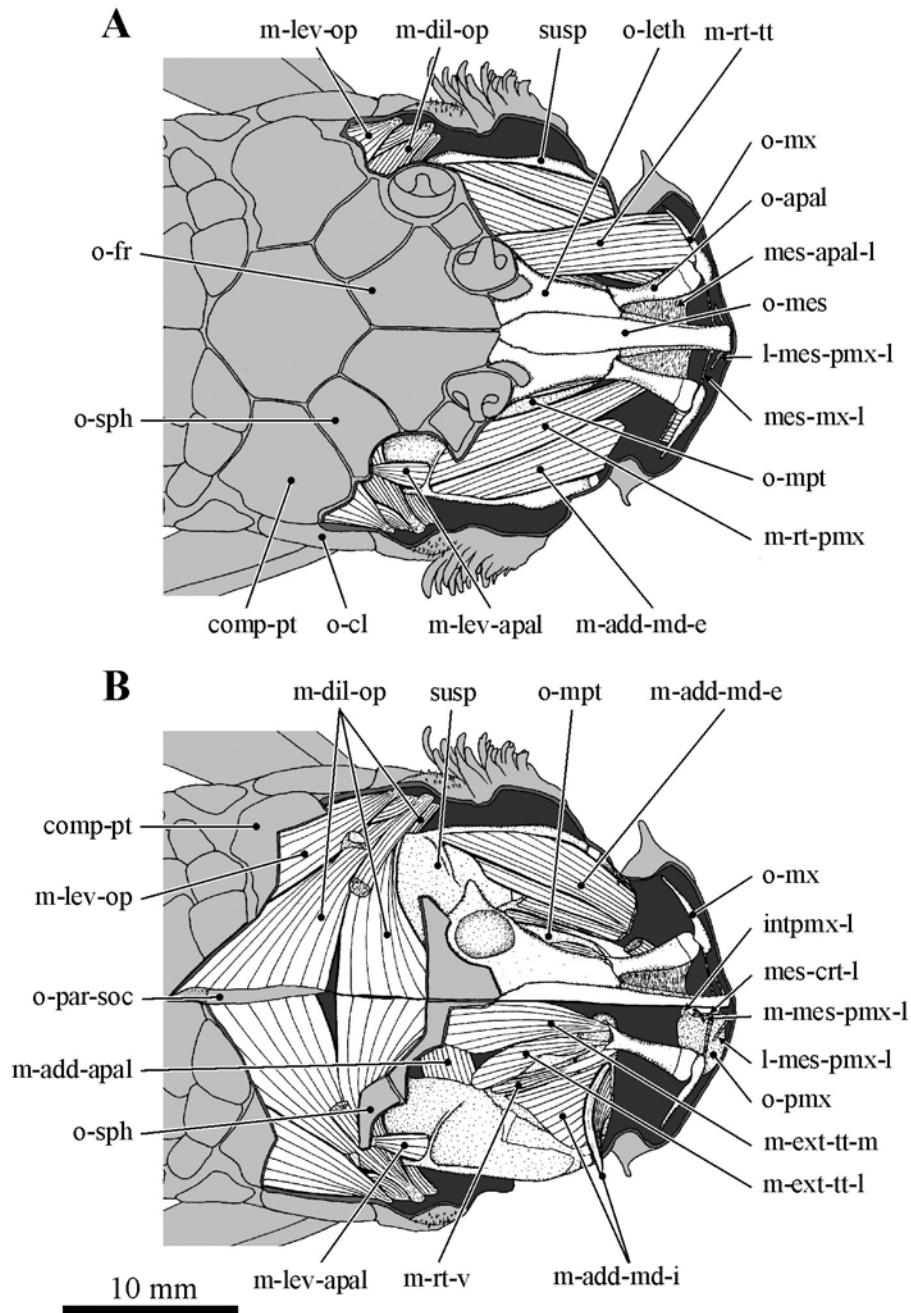
Fig. 6. – Dorsal view of cranial musculature of *Ancistrus* cf. *triradiatus* (94mm SL); A, Part of skin and dermal plates, and right retractor tentaculi muscle removed; B, Dissection showing deeper muscles (medial bundle of right adductor mandibulae muscle partly removed). comp-pt, compound pterotic bone; intpmx-l, interpremaxillary ligament; l-mes-pmx-l, lateral mesethmoid-premaxillary ligament; m-add-apal, musculus adductor arcus palatini; m-add-md-e, external part of musculus adductor mandibulae; m-add-md-i, internal part of musculus adductor mandibulae; m-dil-op, musculus dilatator operculi; 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-op, musculus levator operculi; m-mes-pmx-l, medial mesethmoid-premaxillary ligament; m-rt-pmx, musculus retractor premaxillae; m-rt-tt, musculus retractor tentaculi; m-rt-v, musculus retractor veli; mes-apal-l, mesethmoid-autopalatine ligament; mes-crt-l, mesethmoid-cartilage ligament; mes-mx-l, mesethmoid-maxillary ligament; o-apal, os autopalatinum; o-cl, os cleithrum; o-fr, os frontale; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-par-soc, os parieto-supraoccipitale; o-pmx, os praemaxillare; o-sph, os sphenoticum; susp, suspensorium.
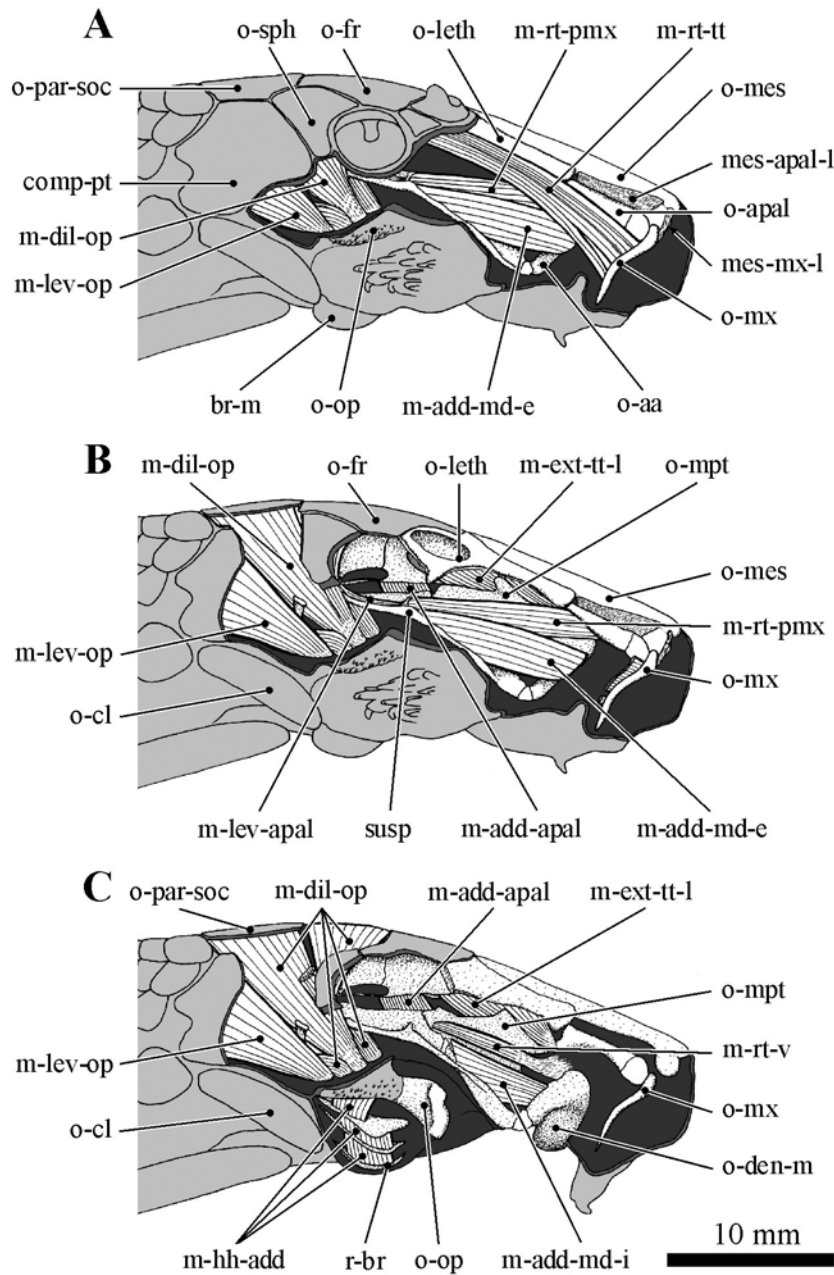
Fig. 7. – Lateral view of cranial musculature of *Ancistrus* cf. *triradiatus* (94mm SL); A, part of skin and dermal plates removed; B-C, Further dissections showing deeper muscles. br-m, branchiostegal membrane; comp-pt, compound pterotic bone; m-add-apal, musculus adductor arcus palatini; m-add-md-e, external part of musculus adductor mandibulae; m-add-md-i, internal part of musculus adductor mandibulae; m-dil-op, musculus dilatator operculi; m-ext-tt-l, musculus extensor tentaculi pars lateralis; m-hh-add, musculi hyohyoidei adductores; m-lev-apal, musculus levator arcus palatini; m-lev-op, musculus levator operculi; m-rt-pmx, musculus retractor premaxillae; m-rt-tt, musculus retractor tentaculi; m-rt-v, musculus retractor veli; mes-apal-l, mesethmoid-autopalatine ligament; mes-mx-l, mesethmoid-maxillary ligament; o-aa, os anguloarticulare; o-apal, os autopalatinum; o-cl, os cleithrum; o-den-m, os dento-mentomeckelium; o-fr, os frontale; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-op, os operculare; o-par-soc, os parieto-supraoccipitale; o-sph, os sphenoticum; r-br, radius branchiostegus; susp, suspensorium.
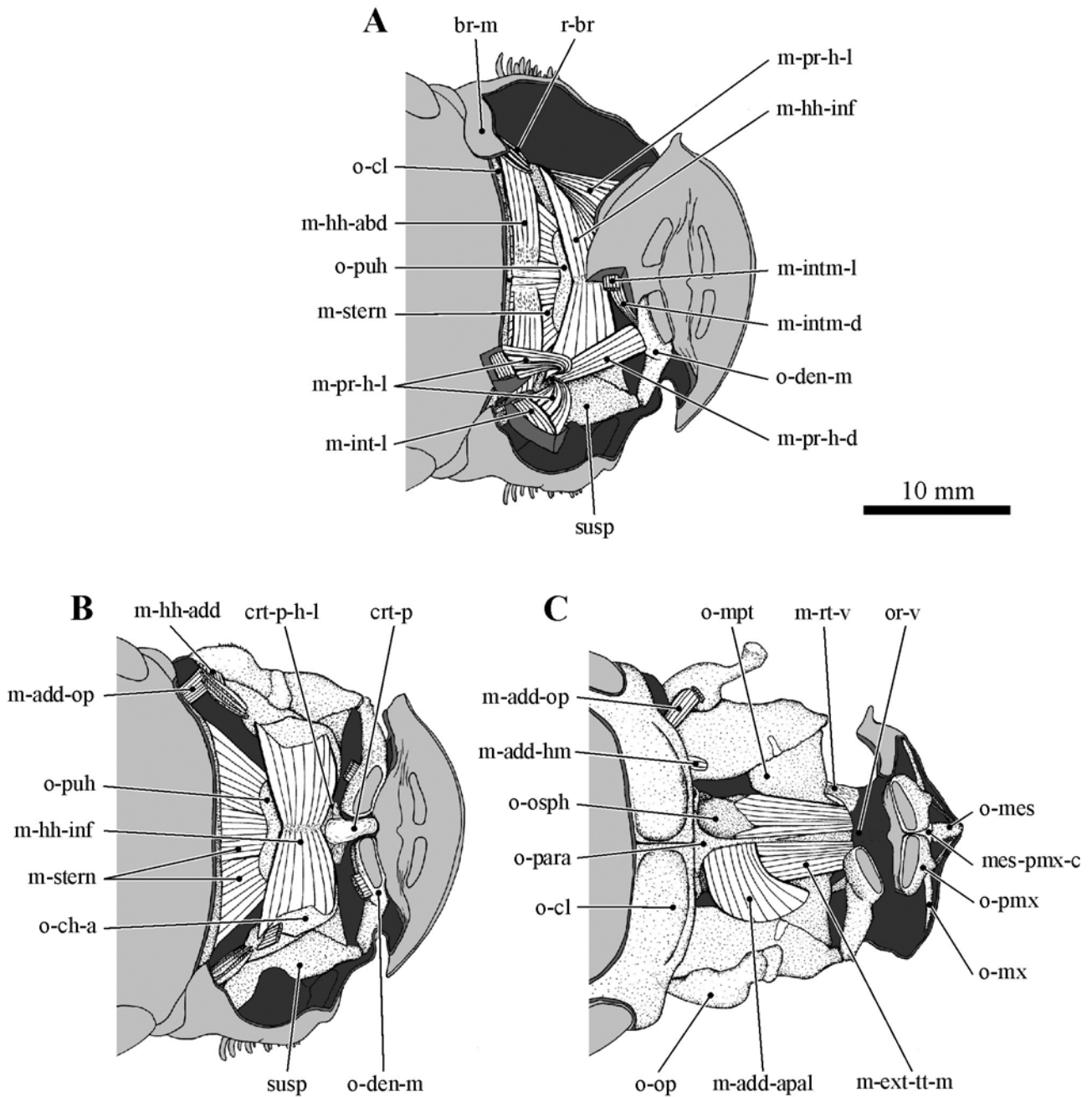
Fig. 8. – Ventral view of cranial musculature of *Ancistrus* cf. *triradiatus* (94mm SL); A, part of skin, left half of lower lip and associated muscles removed; B-C, Further dissections showing deeper muscles. br-m, branchiostegal membrane; crt-p, cartilage plug; crt-p-h-l, cartilage plug-hyoid ligaments; m-add-apal, musculus adductor arcus palatini; m-add-hm, musculus adductor hyomandibulae; m-add-op, musculus adductor operculi; m-ext-tt-m, musculus extensor tentaculi pars medialis; m-hh-abd, musculus hyohyoideus abductor; m-hh-add, musculi hyohyoidei adductores; m-hh-inf, musculus hyohyoideus inferior; m-intm-d, musculus intermandibularis pars dentalis; m-intm-l, musculus intermandibularis pars labialis; m-pr-h-d, musculus protractor hyoidei pars dentalis; m-pr-h-l, musculus protractor hyoidei pars labialis; m-rt-v, musculus retractor veli; m-stern, musculus sternohyoideus; mes-pmx-c, mesethmoid-premaxillary cartilage; o-ch-a, os ceratohyale anterior; o-cl, os cleithrum; o-den-m, os dento-mentomeckelium; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-op, os operculare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-pmx, os praemaxillare; o-puh, os parurohyale; or-v, oral valve or velum; r-br, radius branchiostegus; susp, suspensorium.

The intermandibularis muscle consists of two separate divisions (Fig. 8A). The dorsalmost, here called pars dentalis, connects the posterior aspects of both lower jaws, inserting in a groove along the teeth-bearing dento-mentomeckelian bones. Medially, where the contralateral halves meet in a slim raphe, they attach firmly to the inner tissue of the lower lip. The effect of this muscle is not clear, but it appears to pull the mandibles together and rotate them backward, which causes the lower lip to purse toward the substrate. The pars labialis of the intermandibularis is a separate division, attached to both lateral sides of the inner lower lip tissue ventral and caudal to the pars dentalis. Laterally, the fibers run into the connective tissue posterior to the basis of the maxillary barbel. Contrary to the pars dentalis, some muscle fibers do cross the midline, and there is no raphe. Manipulation of this muscle part leads to pursing of the lower lip. There is no muscular contact between the intermandibularis and the subdivisions of the protractor hyoidei.

Hyoid musculature (Fig. 8)

The protractor hyoidei muscle, often referred to as geniohyoideus (OSSE, 1969; SCHAEFER & LAUDER, 1986; SCHAEFER, 1997) consists of two completely separate subdivisions having different directions and insertions (Fig. 8A). Terminology in literature can be confusing, as the names often refer to the relative position of these subdivisions, but these can vary from taxon to taxon. Hence names referring to the insertions are given here. A separate, band-like subdivision is the protractor hyoidei pars dentalis [part a of HOWES (1983); lateral division of SCHAEFER (1997)], connecting the ventral side of the posterior ceratohyal to the ventrocaudal side of the dento-mentomeckelium. Pulling the pars dentalis retracts and rotates the mandibles around their axis and brings the teeth rows in a position ready for scraping; the movement of the mandibles automatically retracts the lower lip somewhat. The hyoid stays almost motionless. Another subdivision is the pars labialis [part b of HOWES (1983); medial division of SCHAEFER (1997)]. It runs between the posterior ceratohyal and the lower lip tissue. It diverges in several small bundles before reaching the lip. The effect appears to be on the lower lip only : it is flattened and retracted dorsally. Again, no significant movement of the hyoid is observed.

The largest ventral muscle is the unpaired hyohyoideus inferior (or hyohyoides inferior), lying ventral to the hyoid arch (Fig. 8B). It is narrower at the midline, where a medial raphe connects both halves. Fiber direction is from the medial raphe toward the lateral attachment on the ventral side of the anterior and posterior ceratohyals. As suggested by manipulation, any contraction elevates the hyoid, reducing the branchial cavity. An additional, indirect effect, probably caused mainly by the caudalmost fibers, appears to be on the proximal ends of the branchiostegal rays that articulate with the hyoid arch. As a result, the branchiostegal membrane is opened slightly.

The antagonist of the hyohyoideus inferior is the sternohyoideus muscle that diverges from the dorsal surface of the parurohyal to the anterior edge of the cleithrum of the pectoral girdle. The muscle is much broader than long. As the pectoral girdle is an almost immobile struc-

ture in *Ancistrus* cf. *triradiatus*, the only effect of manipulating the sternohyoideus is the retraction and depression of the hyoid arch. Although some movement of the cartilage plug anterior to the hyoid arch is observed, no effect is seen on the mandibles. The almost cylindrical plug of cartilage is connected to the ventral face of the hypohyals, projecting rostrally, between both dento-mentomeckelia. The cartilage is elastic, while no collagen is seen except for a very thin perichondral layer. No collagen fibers attach to the dento-mentomeckelian bones (Fig. 5D-E).

The two medialmost branchiostegal rays are kept close to each other by means of short ligamentous fibers. The second and the third, and the third and the fourth, respectively, are interconnected by short muscles, running from the lateral edge of the medial to the dorsal surface of the more lateral ray. From the ventral face of the fourth, lateralmost and broadest ray, an additional, narrowing muscle attaches to the medial aspect of the opercle. These three different muscles are collectively referred to as the hyohyoidei adductores (Figs 7C, 8B). They force the branchiostegal rays together and toward the opercle which results in an adduction of the branchiostegal membrane and, hence, the closure of the gill opening.

The first, medial branchiostegal ray provides insertion for the hyohyoideus abductor, a flat and straight transverse muscle projecting toward the midline, which it does not reach (Fig. 8A). At four fifths of its length it continues as a thin aponeurosis and connects to the ventral fascia of the sternohyoideus, thus only forming indirect contact with its counterpart. Pulling one or both abductors unambiguously closes the branchiostegal membrane.

Suspensorial musculature (Figs 6-7-8)

The levator arcus palatini is a minute muscle running obliquely from the sphenotic (medial to the emergence of the preopercular canal) to the hyomandibular, where it inserts on the posterior side of the ridge that also forms the attachment site for the adductor mandibulae. Attachment is muscular and relatively broad on the hyomandibular and tendinous and slim on the sphenotic (Figs 6B, 7B). These observations contradict HOWES' (1983) statement that the muscle joins the dilatator operculi in *Ancistrus*. The muscle is too small to allow manipulation, but probably can only slightly elevate the well-attached suspensorium.

A prominent adductor arcus palatini connects the medial face of the suspensorium (hyomandibular and metapterygoid) with the base of the neurocranium. Origin is on the ventral ridge of the parasphenoid as well as a large surface of the orbitosphenoid. Manipulation of the muscle brings the suspensorium to a more medial position.

In siluriforms the extensor tentaculi is a muscle derived from the adductor arcus palatini and the antagonist of the retractor tentaculi (WINTERBOTTOM, 1974). In *Ancistrus* cf. *triradiatus*, as in other loricariids (HOWES, 1983; SCHAEFER, 1997), the extensor tentaculi is divided in two completely separate elements, which we will refer to as the pars lateralis and pars dentalis (Fig. 8C). The extensor tentaculi pars lateralis [muscle e of HOWES (1983)] inserts on the ventrolateral process of the autopalatine. The muscle is circular in transsection and has an anterior aponeu-

rosis continuing halfway inside the muscle itself. Fibers radiate from this aponeurosis. Insertion space for this "circularly pinnate" muscle is provided by a bony canal formed by the ventral face of the lateral ethmoid and a groove formed by the lateral face and a lateral process of the metapterygoid. Pulling the muscle in fresh specimens results in a lateroventral swinging of the autopalatine and a corresponding ventral movement of the tip of the maxilla, as both are coupled through their articulation and the mesethmo-maxillary ligament. The maxillary barbel and the lateral parts of the lips are consequently pushed against the substrate.

The second segment, the extensor tentaculi pars medialis [muscle f of Howes (1983)], is a more flattened muscle connecting the longer ventromedial process of the autopalatine with the lateral ethmoid, the orbitosphenoid and the lateral side of the ventral parasphenoid ridge. The tendon inserting on the autopalatine continues as a ventral aponeurosis to which the slightly dorsally oriented fibers attach. The effect of pulling the muscle is a ventral movement of the autopalatine. The autopalatine-maxillary articulation pushes the caudal edge of the premaxilla downward, pivoting the premaxilla around its ligamentous articulation with the mesethmoid. Due to the configuration of the articulation, effect on the distal tip of the maxilla itself is negligible. The abduction of the premaxilla brings the teeth in a position ready for scraping. The extensor tentaculi pars medialis can thus be considered the antagonist of the retractor premaxillae.

The small and extremely thin adductor hyomandibulae originates from the ventral floor of the compound pterotic (together with the adductor operculi), and loosely inserts on connective tissue at the medial side of the hyomandibular (Fig. 8C). Given its size, it is not easy to manipulate it, or to even speculate about its function. The name adductor hyomandibulae has been used for the adductor arcus palatini in loricariids (Howes, 1983; Schaefer, 1997). This is erroneous, as both muscles are not homologous (Winterbottom, 1974; Diogo & Vandewalle, 2003).

Opercular musculature (Figs 6-7-8)

The largest opercular muscle is the dilatator operculi, which has its origin on a large surface on the posterior part of the neurocranium and inserts via a thick aponeurosis on the dorsal side of the opercle, lateral to the articulation with the hyomandibular (Figs 6B, 7C). Its different bundles originate mainly on the compound pterotic, parieto-supraoccipital, sphenotic and the posterior margin of the hyomandibular. Due to the configuration of the hyomandibular-opercular articulation, any force exerted via the aponeurosis rotates the opercle dorsally, erecting the long cheek spines. In large adults some bones of the skull roof and walls show expanded ventral or medial laminae separating the dilatator operculi from the braincase.

Immediately posterior to the insertion of the dilatator operculi on the opercle, the short and sturdy aponeurosis of the levator operculi inserts. It has a broad origin on the compound pterotic. The effect of pulling this muscle is identical to that of the dilatator operculi. Experimental tension on both muscles indicates no role in the opening of the branchiostegal membrane.

The antagonist of these muscles is the adductor operculi (Fig. 8C). It has its tendinous origin on the ventral transverse rim of the compound pterotic contacting the Baudelot's ligament. It inserts muscularly on the medial side of the opercle just posterior to the insertion of the lateralmost division of the hyohyoidei adductores.

The musculature of the branchial basket is not discussed here. See Schaefer (1997) for a description of the branchial muscles in *Otocinclus* and Fernandes et al. (1995) for a short account on the gill filament muscles in *Hypostomus* and *Rhinelepis*.

Ligaments in the rostral region

The mesethmoid, lacking the lateral cornua typical for most siluriforms but bearing a ventral disc-like process, influences the mobility of the upper jaw. The mesethmoid-premaxillary cartilage or meniscus rests on the ventral edge of the mesethmoid disc like a small cap and forms two articulatory cups for the premaxillae (Fig. 8C). It is *V*-shaped in transsection (Fig. 5A). Strong connective tissues and ligaments in the rostral region ensure the relative position of these elements. The mesethmoid-cartilage ligaments connect the rostral tip of the mesethmoid with both posterodorsal sides of the mesethmoid-premaxillary cartilage, running along both sides of the mesethmoid disc (Fig. 6B). The lateral mesethmoid-premaxillary ligaments attach to the anterodorsal side of both premaxillae and the rostral end of the mesethmoid, thus running more or less horizontally (Fig. 6A). The medial mesethmoid-premaxillary ligaments run vertically from the anterior face of the premaxillae to the mesethmoid disc right above it (Fig. 6B). The paired mesethmoid-maxillary ligament, as mentioned above, connects the maxilla, close to its ventral head, to the mesethmoid, immediately behind the other ligament attachments (Figs 6A, 7A). The short interpremaxillary ligament is an unpaired ligament, running transversely behind the mesethmoid-premaxillary cartilage. It keeps both premaxillae closely apposed to each other, restricting their relative movement. The mesethmoid-autopalatine ligament is a broad ligament between the mesethmoid shaft and the autopalatine; the anteriormost fibers are longest, and also contact the autopalatine-maxillary articulatory tissue (Figs 6A, 7A). The paired rostromaxillary and ventral labial ligaments as seen by Schaefer (1997) in *Otocinclus vittatus* are not observed in *Ancistrus* cf. *triradiatus*.

Kinematics (Figs 9-10)

Respiratory cycles while sucking onto a vertical glass wall took approximately 250 to 400ms (with a water temperature of 23°C). The fishes preferred to support themselves with their tail on the bottom of the aquarium. In a first phase the oral cavity expands by a depression of the hyoid (and lower jaw region), and a slight abduction of the suspensoria (Figs 9, 10A). During this expansion phase the oral valve is open, and the branchiostegal membrane is closed (Fig. 10A, E). At maximal expansion the oral valve is closing. Complete closure is observed only well after the onset of elevation of the hyoid and lower jaw region, and adduction of the suspensoria (Fig. 10F). Movements of these latter elements are synchronous. At maximal constriction of the oral cavity the oral valve is

still closed; it bulges out ventrally, probably due to the water pressure inside the mouth. It starts to open again only when a new expansion phase starts. During constriction the branchiostegal membrane opens, allowing water to flow out (Fig. 10B, F). This water flow could be visualized by the use of diluted milk. At maximal constriction the branchiostegal membrane starts to close again (Fig. 10C). The same milk experiment also shows the inflow of water through the narrow openings created in the lateral lip tissue by an elevation of the maxillary barbel. The opening and closure of this inflow opening coincides with the same movements of the oral valve (Fig. 10D). Sometimes only one of both sides of the lips is opening. During the whole cycle, opercular movements are restricted to a very small in- and outward movement, synchronous with the suspensorial movements.
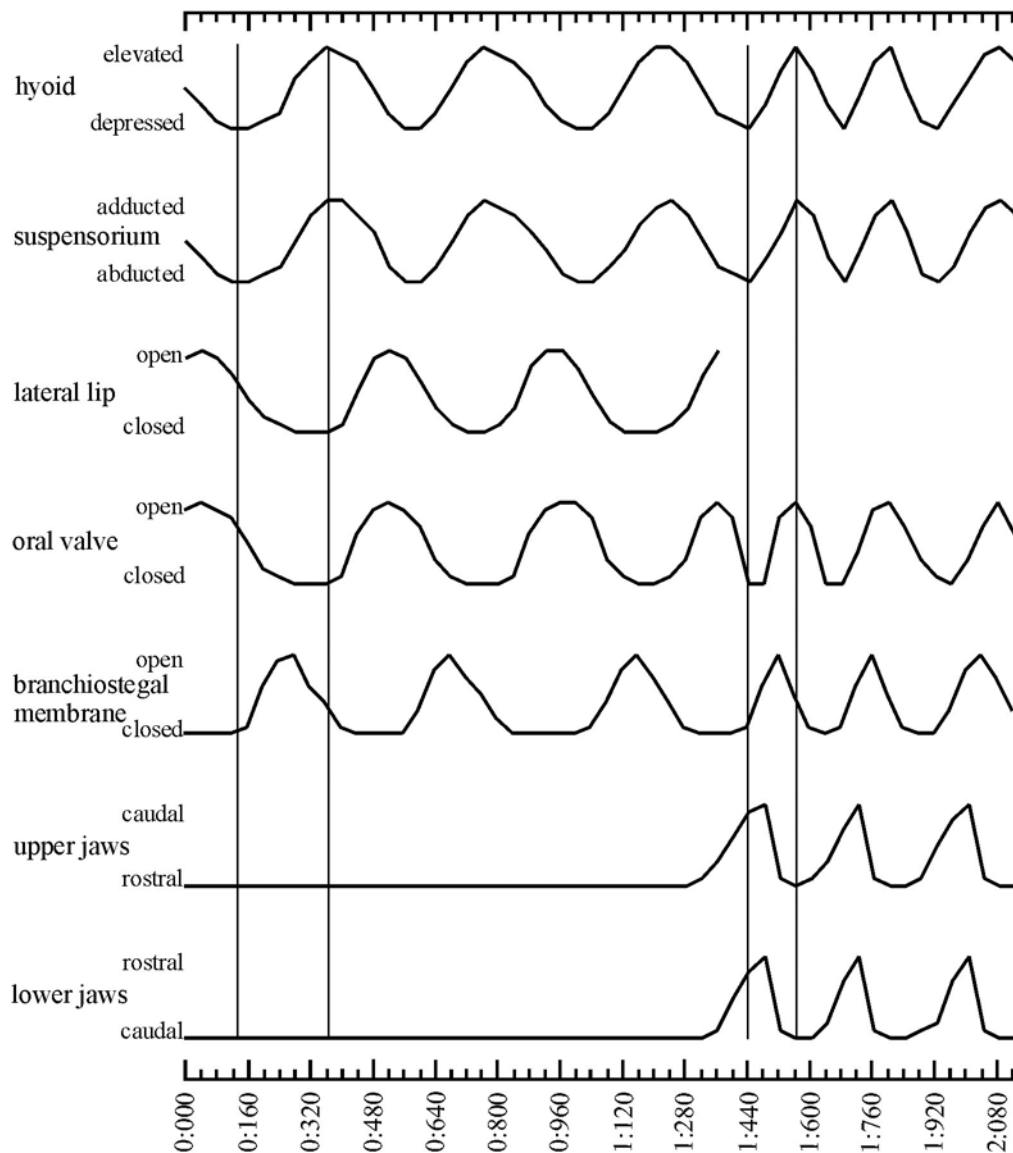

Fig. 9. – Graphs showing movements of some elements involved in respiration and feeding of *Ancistrus* cf. *triradiatus* during two seconds. Three respiratory cycles are followed by three cycles in which scraping occurs. Vertical reference lines indicate maximal oral expansion and constriction during first and fourth cycle. Graphs do not show distance of movements. Slight up and down motion of the lower jaws is not recorded; feeding movements inhibit unambiguous observation of lateral lip movements.
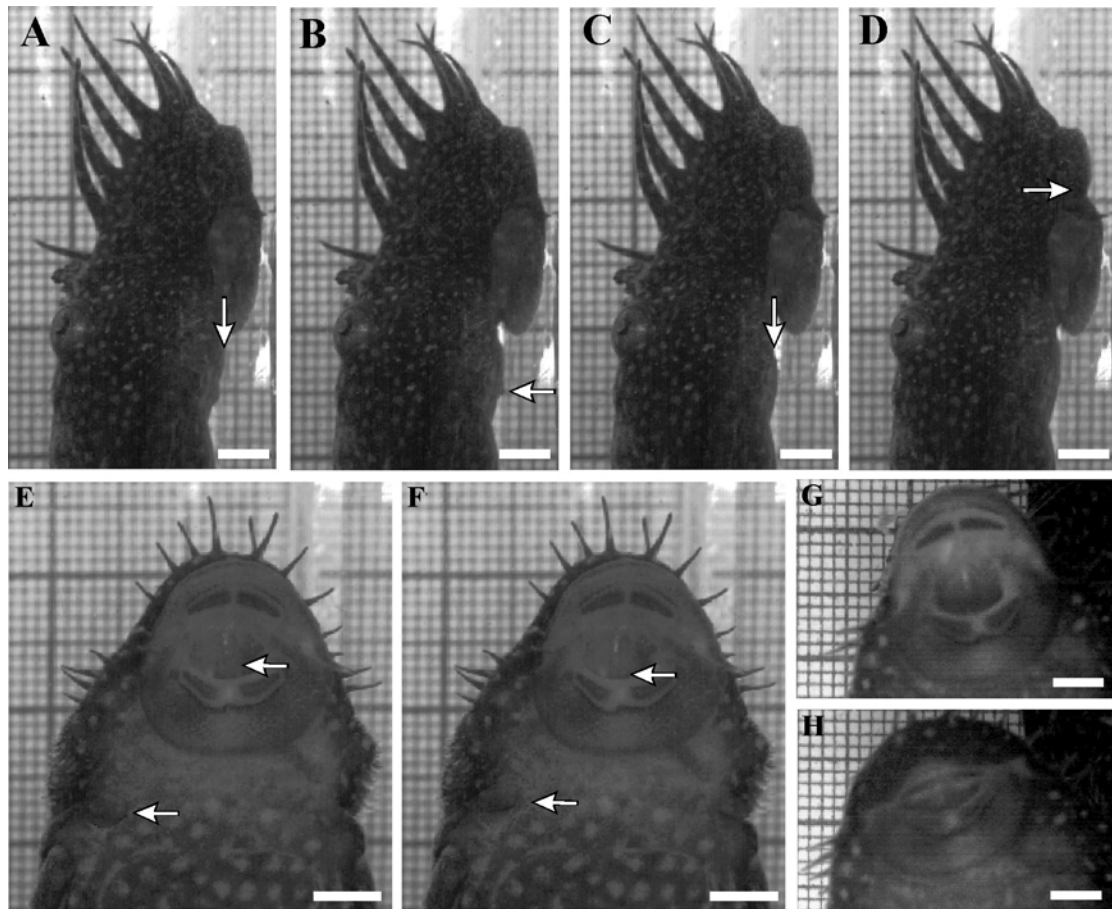
Fig. 10. – Images from respiratory and feeding cycles from two specimens (A-D; E-H). A-D, respiration (lateral view). A, maximal hyoid depression; B, complete opening of branchiostegal membrane; C, maximal hyoid eleva- tion D, inflow via lip opening; E-F, respiration (ventral view). E, oral valve open (branchiostegal membrane closed); F, oral valve closed (moved caudally) (branchiostegal membrane open). G-H, feeding (ventral view). G, upper and lower jaws diverge; H, jaws scrape (move back and rotate). Scale bars are 5mm.

Respiratory cycles accelerate during feeding (Fig. 9). In addition, extensive rotation of both lower and upper jaws occurs. During the constriction phase the mandibles not only depress, but also move posteriorly. An additional rotation of the jaws along their axis brings the teeth rows even further posteriorly. At the same time, the premaxil- lae protrude anteriorly by a rotation around their hinge to the mesethmoid disc (Fig. 10G). During the subsequent expansion phase the mandibles move and rotate so that the tooth row scrapes the glass surface in an anterior direction. An analogous action occurs in the premaxillae : the tooth row scrapes the surface in a posterior direction. At peak expansion the teeth of lower and upper jaws almost touch each other (Fig. 10H). The rough, papillose surface of the large lower lip moves posteriorly and ante- riorly together with the lower jaw. Fishes often proceed somewhat anteriorly during each cycle, so that a fresh substrate can be fed upon. Opening of the lateral lip tissue is less pronounced and difficult to observe during feeding. The extensive jaw movements might well allow a suffi- cient inflow of water. Often (but not always) body and tail movements accompany the feeding sequences.

DISCUSSION

Anatomical observations, aided by the manipulation of muscles in fresh specimens, yielded some remarkable morphological considerations. Together with the limited kinematic data set functional hypotheses could sometimes be formulated. Here we group the morphological struc- tures and kinematic facts in six known functional mecha- nisms present in loricariids, providing a comprehensive overview of elements, movements, and possible func- tional-morphological links. The morphological basis of some typical loricariid structures or systems is also dis- cussed and compared to non-loricariids.

The buccal pump system

In *Ancistrus* cf. *triradiatus*, oral expansion has a double function : inflow of water and food, and the maintenance of the suction power when adhering to a substrate. In fishes with a depressed head, the hyoid depression gene- rally has a greater share in the buccal pump system than the suspensorium abduction (ALEXANDER, 1970; GOSLINE, 1973; ADRIAENS & VERRAES, 1997a). The sternohyoideus

and hyohyoideus inferior muscles, respectively depressing and elevating the hyoid arch in many fishes (e.g., BALLINTIJN & HUGHES, 1965), are among the largest and most vascularized muscles in *A.* cf. *triradiatus*, indicating their importance in this system. The articulation between the hyoid arch and the suspensorium is long and strong, compared to several other teleosts (ANKER, 1974; AERTS, 1991; HUNT VON HERBING et al., 1996). The large suspensorium is rigid (the metapterygoid is connected to the other bones with sutures), and anchored to the skull via the posterior hyomandibular-pterotic suture and the dorsal connection of both the metapterygoid and the hyomandibular to the neurocranium. It is also connected with the tough, armoured skin at the level of the preopercle, even more reducing its mobility. These connections can all be considered reinforcements of the hyoid-suspensorium system [some are characteristic for loricariids or the more apomorphic loricariid taxa (SCHAEFER, 1990; ARMBRUSTER, 2004)], and might be adaptations to the high forces probably generated during suction while adhering to a substrate.

The ossified Baudelot's ligaments, vertical ridges between the basioccipital and the supracleithral part of the compound pterotic, form an ossified posterior wall of the branchial cavity, which ALEXANDER (1965) regarded as an adaptation to withstand the negative pressure caused by the suction, hydrostatically isolating the orobranchial cavity from the intestinal cavity. The relative resilience of the suspensorium and the strengthening of the suspensorial-neurocranial connection could be interpreted in a similar way : a weaker and more movable suspensorium would be susceptible to collapsing when extreme suction is needed.

Figures 6B and 8C clearly show that the masses of the two muscles inserting on the suspensorium are far from equal : the adductor arcus palatini is large, while the levator arcus palatini is almost rudimentary. It can be hypothesized that the relatively large adductor arcus palatini can cause a slight adduction of the suspensorium, and that elevation is mainly a result of the return of the suspensorium to its original position. Our manipulations during dissection and the absence of the levator arcus palatini in some loricariids (ALEXANDER, 1965; HOWES, 1983) corroborate this hypothesis. During dissection, elastic properties of the skin and the ligamentous tissue in the hyomandibular-pterotic suture appeared to be the main cause of such passive elevation, rather than the bending of the bony suspensorium itself, which was suggested by ALEXANDER (1965). This also explains the presence of a relatively robust adductor arcus palatini, needed to overcome the resilience of the suspensorium.

Whether the buccal pump system is able to maintain a negative pressure in the oral cavity has since long been a matter of debate. HORA (1930) believed that the lips could not function as a sucker while respiration continued, since the inflowing water would cause the system to fail. ALEXANDER (1965) demonstrated that respiration and suction can function simultaneously, and that both actions continue when the fish is pulled away from the substrate (a vertical aquarium glass). Our results indicate that inflowing water was limited to a thin stream passing under the sucker immediately posterior to each maxillary barbel, a

phenomenon also observed by VANDEWALLE et al. (1986) in *Hypostomus punctatus*.

The branchiostegal membrane

Water leaves the orobranchial cavity through the branchiostegal opening. It does not enter there, as initially supposed by REGAN (1904), but is inhaled via the mouth. The functioning of the muscles associated with the branchiostegal membrane in *Ancistrus* cf. *triradiatus* can not easily be understood. As indicated by manipulation, contraction of the hyohyoidei adductores closes the branchiostegal membrane. SCHAEFER (1997) did not mention this muscle in his myological account on *Otocinclus*, but we found it in *O. vestitus*.

In non-loricariid siluriforms like *Clarias gariepinus* the paired hyohyoideus abductor opens the branchiostegal membrane, inserting on the medialmost branchiostegal ray and originating directly on the hyoid arch, or indirectly, via a medial aponeurosis, thus running more or less rostrocaudally (ADRIAENS & VERRAES, 1997b). Remarkably, in *A.* cf. *triradiatus* the muscle runs completely transversely (Fig. 8A), so that experimental contraction closes the membrane instead of opening it, the muscle having become a functional adductor. The angle between the hyohyoideus abductor and the fibers of the sternohyoideus on which they attach is 90°; hence no interaction of functions is assumed. Also, due to its shortness, the sternohyoideus can't induce a significant change in orientation of the hyohyoideus abductor. Two possible mechanisms might cause the abduction of the membrane in *A.* cf. *triradiatus* : it might have become a passive movement, induced by the high pressure in the branchial cavity caused by the contraction of the hyohyoideus inferior, or it might be initiated by the posterior part of the latter muscle, attaching to the posterior ceratohyal, near the articulation of the first branchiostegal ray. Manipulation suggested that movements of the hyoid have a slight effect on the position of the rays. SCHAEFER (1990) observed that in some loricariids, this part of the hyohyoideus inferior inserts on the branchiostegal rays themselves.

Our anatomical study and observations suggest the movements of the opercle in the respiratory cycle are negligible. It is moved very slightly by the movements of the suspensorium, with which it articulates. In *A.* cf. *triradiatus*, it has a prominent role in the erection of the large cheek spines (HOWES, 1983; GEERINCKX & ADRIAENS, 2006).

Movements of maxillary barbels and lips

Initiation of suction requires a close adhesion of the upper and lower lips to the substrate. In the most plausible theoretical scenario the outer edges of the suction disc, formed by the fused lips, are pushed against the substrate. A subsequent creation of a negative pressure by expansion of the oral cavity (posterior to the valve) enables transferring water from the cavity anterior to the oral valve. A fish adopting a sucking position brings the less mobile upper lip against the substrate by literally swimming against it or pushing the head downward. Pulling both parts of the intermandibularis muscle appears to result in a pursing of the lower lip. Antagonistic movement, i.e. retracting the lower lip toward the body, is most

probably achieved by contraction of the protractor hyoidei pars labialis, as suggested by manipulations (see also The lower jaws).

The maxillae of most loricariids support only small maxillary barbels. It appears that their main function has become to mediate the movements of the lateral lip tissue in which they are embedded. The retractor tentaculi muscle lifts this part of the lips from the substrate, as in many siluriforms (WINTERBOTTOM, 1974), allowing water to enter the oral cavity. Experiments with diluted milk showed that when the fish clings to a vertical substrate water often enters only one side of the mouth, and only this side of the lip is seen moving. This suggests the independent contraction of the left or right retractor tentaculi. VANDEWALLE et al. (1986) hypothesized that the elevation of the lateral lip tissue is mostly caused by lateral movements of the lower jaws. We found, however, no anatomical link connecting both elements. The lateral motion of the lower jaws is negligible when compared to their dorsoventral movements during respiration. Also, when only one of both lip sides is elevated, no visible asymmetry in the movements of the lower jaws is present. The closing of the lip furrow by the action of the levator arcus palatini, suggested by the same authors, is highly improbable, not only because of the absence of an anatomical link, but also because the levator arcus palatini is absent in several loricariids (HOWES, 1983). Our hypothesis, based on the anatomy of *Ancistrus* cf. *triradiatus*, that the extensor tentaculi pars lateralis may close the lip opening, should ideally be tested by electromyographical experiments. The extensor tentaculi [not subdivided in catfishes other than loricariids (SCHAEFER, 1990; DIOGO, 2005)] is responsible for a downward or forward movement of the maxillary barbel in most catfishes (ALEXANDER, 1965; GOSLINE, 1975). The origin of the pars lateralis in the lateral ethmoid-metapterygoid groove is unique among siluriforms, and might have evolved several times within the loricariid family (HOWES, 1983).

The autopalatine-maxillary mechanism of *A.* cf. *triradiatus* and other loricariids is comparable to the situation seen in the African mochokid *Euchilichthys*, also having a sucker-like mouth. Here too, the cartilaginous rostral tip of the autopalatine is situated on top of the premaxilla, the extensor tentaculi muscle is directed completely rostrocaudal, and the line between the lateral ethmoid-autopalatine joint and the muscle insertion on the autopalatine is almost vertical instead of horizontal (GOSLINE, 1975).

The oral valve

The oral valve of loricariids attaches to the anterodorsal mouth roof, and, when closed, separates a small anterior cavity from the larger oral cavity. The muscle we name retractor veli has previously been called muscle d or retractor palatini (HOWES, 1983; SCHAEFER, 1997; DIOGO & VANDEWALLE, 2003). It is, however, not homologous to the retractor palatini of LUBOSCH (1929, in WINTERBOTTOM, 1974) and HOFER (1938), which is a derivative of the adductor arcus palatini in some perciform and tetraodontiform fishes. Contrary to HOWES' (1983) claim, ALEXANDER (1965) did not name it retractor premaxillae, but omitted it. The muscle is unique for loricariids (SCHAEFER, 1990). Its function has at best been vaguely

described, based on dissection of preserved specimens. It would insert on a "complexly divided connective tissue sheet" (HOWES, 1983 : 313), attached to the autopalatine, the premaxilla, and the lower jaw, and would pull the autopalatine ventrally in preserved specimens. However, our manipulation of the muscle in fresh specimens of *Ancistrus* cf. *triradiatus* revealed no ventral movement of the autopalatine.

GRADWELL (1971) described a "muscle of oral valve" in several loricariids : *Hypostomus punctatus*, *Hemiancistrus annectens*, *Rineloricaria microlepidogaster*, *Ancistrus occidentalis* and *Otocinclus mariae*. It would insert on the lateral sides of the oral valve, and originate "on the dorsal surface of the skull, anterior to the eyes and lateral to the nares" (GRADWELL, 1971 : 837). His biomechanical analysis proved it to contract at the moment the valve closed. In spite of the questionable description of the muscle origin mentioned in his text, his figures corroborate our assumption that it is the retractor veli. The retractor palatini of HOWES (1983) and the muscle of the oral valve of GRADWELL (1971) are presented as separate muscles in the myological review of DIOGO & VANDEWALLE (2003), but are identical. Apart from *A.* cf. *triradiatus*, we also observed this muscle in *Pterygoplichthys lituratus*, *Farlowella acus* and *Otocinclus vestitus*. In *F. acus* it inserts on the valve via two tendons, while in *O. vestitus* two separate retractor veli divisions are present, only connected posteriorly. The dorsal division inserts more anteriorly on the valve. In breathing specimens of *A.* cf. *triradiatus* it can be observed that the valve is closed at the moment the hyoid elevates (Fig. 9). The exact movements of the valve, both rostrocaudally and dorsoventrally, are difficult to explain, as retractor veli activity, elastic recoil and water pressure and flow probably have a combined effect.

The upper jaws

The high mobility of the premaxillae must be one of the most important evolutionary innovations encountered in the loricarioid lineage, and is a synapomorphy for callichthyids, scoloplacids, astroblepids and loricariids (HOWES, 1983; SCHAEFER, 1990; DIOGO, 2005). SCHAEFER & LAUDER (1986; 1996) listed this release of constraint as one of the decoupling events observed in the evolution leading to the loricariids. In most siluriforms the premaxillae are firmly attached to the lateral cornua of the mesethmoid; structural and functional changes of the premaxilla and maxilla have lead to the inability to perform protrusion (ADRIAENS & VERRAES, 1997a). However, the development of a small dorsal premaxillary process and the disappearance of the mesethmoid cornua have triggered an important shift in the relation between the neurocranium and the upper jaw, enabling a novel protrusion mechanism. Our results suggest this mechanism is most probably mediated by the extensor tentaculi pars medialis and the retractor premaxillae in loricariids. The latter muscle, derived from the adductor mandibulae complex and constituting a key innovation in the loricarioid lineage (SCHAEFER & LAUDER, 1986), has a direct insertion on the premaxilla in astroblepids and scoloplacids as well, and an indirect connection via a connective sheet in callichthyids (SCHAEFER, 1990; SCHAEFER & LAUDER, 1986;

1996), which also have a dorsal premaxillary process (HUYSENTRUYT & ADRIAENS, 2005), and show some degree of premaxilla protrusion (ALEXANDER, 1965).

The vertical ventral mesethmoid disc, present in all loricariids, and, to a lesser degree, astroblepids (SCHAEFER, 1990), is important for the movements of the premaxillae. The mesethmoid-premaxillary cartilage, a meniscus forming a double articulatory cup, keeps the premaxillae in place, aided by the series of ligaments that assist and direct their movements (Fig. 5A). Consequently, contraction of the retractor premaxillae swings the premaxilla teeth row caudally, thus scraping the substrate. The effect of the assumed antagonistic extensor tentaculi pars medialis is more complex : the muscle unambiguously pulls the rostral tip of the autopalatine ventrally. When manipulating the autopalatine in this direction, the autopalatine-maxilla joint pushes against the posterior part of the premaxilla. Both the premaxilla and the maxilla (the part ventral to the joint) are provided with a strong tissue cushion in the region where they touch (Fig. 5A). The ligamentous suspension of the premaxilla makes it rotate about a transverse horizontal axis instead of merely being pushed forward. As a result the premaxilla protrudes, and swings its teeth row rostrally. Dissection and manipulation of this apparatus showed no significant effect on the movement of the tip of the maxilla. Independent motion of each premaxilla seems to be limited by the short interpremaxillary ligament.

The lower jaws

The evolutionary rotation of the lower jaws to a medial position with the teeth pointing rostroventrally, as well as the loss of both the interoperculo-mandibular ligament and the medial connection between both dento-mentomeckelian bones, have laid open new possibilities concerning rotational mobility (SCHAEFER & LAUDER, 1986). During normal respiration in *Ancistrus* cf. *triradiatus* a slight up-and-down motion of the lower jaws and the adjacent lower lip tissue is seen, probably anatomically and functionally coupled to the hyoid movements. Whether this movement is (partly) caused by the adductor mandibulae muscle remains to be verified. Only at feeding the lower jaws are seen rotating and scraping the substrate, more or less synchronously with the upper jaws. In the most probable hypothetical scenario the adductor mandibulae and protractor hyoidei muscles act as antagonists. The scraping movement, in which the teeth are moved rostrally, would be achieved by a contraction of the adductor mandibulae (dissection and manipulation confirmed that the most dorsal part certainly has to be involved). The protractor hyoidei pars dentalis may then perform the antagonistic movement of swinging the lower jaw and its teeth row back caudally. The protractor hyoidei pars labialis can be considered the retractor of the lower lip.

The cartilage plug, attached to the hyoid arch at the midline, and protruding into the space behind and between the lower jaws, is hypothesized to be a supporting device for the dento-mentomeckelian bones, preventing them from being merely pulled caudally. Their caudal motion is restricted, and the effect of contraction of the adductor mandibulae, inserting on the dorsocaudal aspect

of the jaws, is partly transformed in a rotation around the longitudinal axis of the jaws. The consequence is that the teeth can scrape a larger surface. Previously, SCHAEFER & LAUDER (1986; 1996) appointed a different function of the cartilage plug : it was suggested to act as a novel anatomical link between the hyoid and the lower jaws, unique to loricariids, allowing the sternohyoideus muscle to retract the lower jaws via the hyoid arch. This is contradicted by the present study on *Ancistrus* cf. *triradiatus*, as the plug attachment to the hyoid arch is relatively strong, while it is not strongly attached to the lower jaws (Figs 5D-E, 8B). The dento-mentomeckelian bones move and roll against the plug, but are not attached to it. Hence, any force exerted by the sternohyoideus retracts the hyoid arch, and, to a lesser extent, the attached cartilage plug, but has no significant effect on the mandibles. This was shown by manipulation of freshly killed and dissected specimens (tissue characteristics are strongly altered in preserved specimens). Another argument is histological : the cartilage plug connected to the hypohyals consists of elastic cartilage, ideal for a supporting, gliding device, but inappropriate for the efficient transmission of pulling forces in the caudal direction, a mechanism that would benefit more from a tendinous ligament. The mandibulo-hyoid ligament attaches to the lateralmost aspect of the angulo-articular, and its role in retraction of the medially pointed lower jaw seems very slim. The lower lip is moved rostrally and caudally together with the lower jaws. Unicellular keratinized projections or unculi form numerous brushes on thick epidermal papillae that may aid during substrate scraping (Fig. 5 D). These have been observed in other loricariids as well (ONO, 1980 ; ROBERTS, 1982).

The remarkable habitus of loricariids evoked GREGORY (1933 : 196) to state that "in these heavily armoured forms the siluroid skull attains its highest specialization." Considering the results of the present paper, in addition to the works of ALEXANDER (1965), HOWES (1983), SCHAEFER (1987 ; 1997), SCHAEFER & LAUDER (1986 ; 1996) and others, it can be concluded that this has not been an idle statement. On the contrary, the loricariid head is one of the most impressive examples of structural diversification and refinement shaped by evolution.

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ABBREVIATIONS USED IN FIGURES

ap-o-cb-I	anterior process of os ceratobranchiale I
art-f-cl	articulation facet for cleithrum
bb-IV-V	basibranchialia IV-V (posterior copula)
B-l	Baudelot's ligament
br-cav	branchial cavity
br-m	branchiostegal membrane
c-mx	cartilago maxillaris
c-symp	cartilago symplecticum
ch-pl	cheek plates
ch-sp	cheek spines
comp-pt	compound pterotic bone
crt-h-apal	cartilaginous head of autopalatine
crt-p	cartilage plug
crt-p-h-l	cartilage plug-hyoid ligaments
csh-mx	cushion on maxilla
csh-pmx	cushion on premaxilla
d-pl	dermal plate
eb-soc	epiphysial branch of supraorbital canal
fn-sph	fenestra sphenoidea
fr-a-hh	foramen for artery supplying hyohyoideus inferior
fr-r-op-VII	foramen ramus opercularis nervus facialis
fr-tr-hm-VII	foramen truncus hyomandibularis nervus facialis
fr-v-j-inf	foramen vena jugularis inferior
hb-III	hypobranchiale III
intpmx-l	interpremaxillary ligament
ioc	infraorbital canal
ipb-crt-n	infrapharyngobranchial-like cartilage nucleus
l-mes-pmx-l	lateral mesethmoid-premaxillary ligament
llc	lateral line canal
m-add-apal	musculus adductor arcus palatini
m-add-hm	musculus adductor hyomandibulae
m-add-md-e	external part of musculus adductor mandibulae
m-add-md-i	internal part of musculus adductor mandibulae
m-add-op	musculus adductor operculi
m-dil-op	musculus dilatator operculi
m-ext-tt-l	musculus extensor tentaculi pars lateralis
m-ext-tt-m	musculus extensor tentaculi pars medialis
m-hh-abd	musculus hyohyoideus abductor
m-hh-add	musculi hyohyoidei adductores
m-hh-inf	musculus hyohyoideus inferior

m-intm-d	musculus intermandibularis pars dentalis
m-intm-l	musculus intermandibularis pars labialis
m-lev-apal	musculus levator arcus palatini
m-lev-op	musculus levator operculi
m-mes-pmx-l	medial mesethmoid-premaxillary ligament
m-pr-h-d	musculus protractor hyoidei pars dentalis
m-pr-h-l	musculus protractor hyoidei pars labialis
m-rt-pmx	musculus retractor premaxillae
m-rt-tt	musculus retractor tentaculi
m-rt-v	musculus retractor veli
m-stern	musculus sternohyoideus
mes-apal-l	mesethmoid-autopalatine ligament
mes-crt-l	mesethmoid-cartilage ligament
mes-mx-l	mesethmoid-maxillary ligament
mes-pmx-c	mesethmoid-premaxillary cartilage
o-aa	os anguloarticulare
o-apal	os autopalatinum
o-bb-II	os basibranchiale II
o-boc	os basioccipitale
o-cb-V	os ceratobranchiale V
o-ch-a	os ceratohyale anterior
o-ch-p	os ceratohyale posterior
o-cl	os cleithrum
o-den-m	os dento-mentomeckelium
o-eb-IV	os epibranchiale IV
o-epoc	os epioccipitale
o-exoc	os exoccipitale
o-fr	os frontale
o-hb-I	os hypobranchiale I
o-hh	os hypohyale
o-hm	os hyomandibulare
o-io-II/VI	os infraorbitale II/VI
o-ipb-IV	os infrapharyngobranchiale IV
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-osph	os orbitosphenoideum
o-para	os parasphenoideum
o-par-soc	os parieto-supraoccipitale
o-pmx	os praemaxillare
o-pop	os praeoperculare
o-prot	os prooticum
o-psph	os pterosphenoideum
o-puh	os parurohyale
o-pvm	os praevomerale
o-q	os quadratum
o-sph	os sphenoticum
o-spop	os suprapraeoperculare
oc	otic canal
or-cav	oral cavity
or-v	oral valve or velum
pb-poc	pterotic branch of postotic canal
pb-soc	parietal branch of supraorbital canal
pc	preopercular canal
poc	postotic canal
pr-pl	postrostral plate
prfr-pl	prefrontal plate
prn-pl	prenasal platelet
r-br	radius branchiostegus
ses-b	sesamoid bone
soc	supraorbital canal
susp	suspensorium
sut-v-VI	occipital suture with neural spine of sixth vertebra
tr-pr-c-v	transverse process of complex vertebra
u-ph-j	upper pharyngeal jaw
unc	unculi or unicellular keratinized brushes
vc-V	fifth vertebral centrum