

## Ontogeny of the maxillary barbel muscles in *Clarias gariepinus* (Siluroidei: Clariidae), with some notes on the palatine-maxillary mechanism

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(With 12 figures in the text)

Siluroids are characterized by the presence of a palatine-maxillary mechanism, which enables a controlled mobility of the maxillary barbels. In *Clarias gariepinus*, the ontogeny of this mechanism is studied and described as well as those muscles related to the maxillary barbel. Two muscles are distinguished: (1) *retractor tentaculi*, connecting the maxilla to the suspensorium, and (2) *extensor tentaculi*, running from the ventro-lateral face of the skull to the posterior half of the palatine. These typical catfish muscles are derived from muscles that are present in generalized teleost fishes. The retractor muscle is believed to be derived from the A<sub>3</sub> muscle of the adductor mandibulae complex. The extensor muscle is formed from the anterior fibres of the adductor arcus palatini. The palatine is rod-like in *C. gariepinus* and articulates with the orbito-nasal lamina in larval specimens and with its ossification, the lateral ethmoid, in juvenile and adult specimens. The articulation occurs via a long cartilaginous strip on the dorsal face of the autopalatine, thereby enabling both a rotation and a restricted sliding.

### Introduction

The siluroid fishes, or catfishes, are all characterized by the presence of barbels surrounding the snout region. Depending on the taxon, the number of barbels varies from one to four pairs (Alexander, 1965). In those species where only one pair occurs, it is the maxillary barbel which is present, e.g. in Diplomystidae, Loricariidae and Callichthyidae (Gosline, 1973, 1975). A small maxillary barbel can be distinguished also in some cyprinoids (e.g. *Cyprinus*, *Gobio* (Cyprinidae)) (Alexander, 1966; Gosline, 1973). In those catfishes carrying four pairs of barbels, the following types can be distinguished: one pair of maxillary, one pair of nasal, and two pairs of mandibular barbels (Fig. 1). The nasal barbels are situated between the anterior and posterior nostrils. The mandibular barbels, a medial and a lateral pair, lie at the ventral side of the lower jaw and are embedded at their bases into the hyoid protractor muscle (Adriaens & Verraes, In prep.). The maxillary barbel is situated on the rostro-lateral face of the snout. This barbel is usually the largest one, being as long as, or even longer than, the whole body length, e.g. in *Pimelodina* (Pimelodidae) (Stewart, 1986). The barbels are supported by a central rod, comprising a dense network of elastin. The surrounding skin is covered with mucous cells and taste buds (Ghiot & Bouchez, 1980). Generally, the barbels are simple but in some taxa they can bear side branches, as in some Mochokidae and all Doradidae (Alexander, 1965).

The maxillary barbels are distinguished from the others by their connection to a mobile mechanism. This palatine-maxillary mechanism is present in all catfish (Gosline, 1975); several

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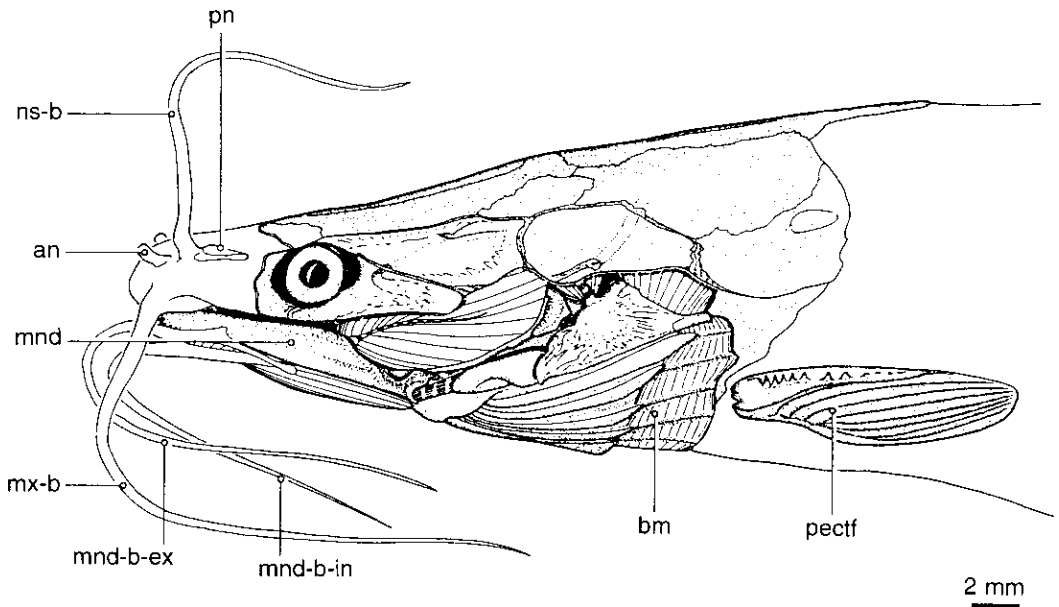


FIG. 1. Skull of *Clarias gariepinus* (142.80 mm SL): lateral view (skin removed) (an = anterior nostril; bm = branchiostegal membrane; mnd = mandibula; mnd-b-ex = external mandibular barbel; mnd-b-in = internal mandibular barbel; mx-b = maxillary barbel; ns-b = nasal barbel; pectf = pectoral fin; pn = posterior nostril).

types of these mechanisms have been described in different siluroid taxa (Eaton, 1948; Alexander, 1965; Singh, 1967; Gosline, 1975; Ghiot, 1978; Ghiot, Vandewalle & Chardon, 1984; Arratia, 1992). Generally, this mechanism consists of a set of elements which partially constitute the feeding apparatus in most non-siluroid teleosts. These elements are the palatine and the maxilla, to which a set of tentacular muscles is attached. The palatine has become isolated from the rest of the suspensorium in siluroids, instead of being connected to the pterygoid region, as in most teleosts. It has a bar-like shape and articulates with the skull, in general at its middle, with its rostral tip connected to the maxilla. This kind of articulation with the skull enables such movements of the rostral tip that make the maxilla rotate. The toothless maxilla has been modified into a socket-like structure, enclosing the base of the central rod of the barbel (Regan, 1911; Eaton, 1948). Consequently, a rotation of the maxilla results in a displacement of the barbel. The mechanism is triggered by a set of muscles that have been derived from other muscles, which are present in non-siluroid fishes (Takahasi, 1925; Winterbottom, 1974). Different strategies have been developed in the muscular pattern of the palatine-maxillary mechanism. In general, a retractor muscle, connected to the maxilla, and an extensor muscle, connected to the palatine, can be distinguished, but other strategies have been described (Alexander, 1965; Singh, 1967; Gosline, 1975).

The benthic life style of most siluroid fishes has affected the evolutionary development of certain elements of the 'Bauplan'. The reduction of the optical sensory organs, resulting in very small eyes, is one of many adaptations to this life style (Alexander, 1965). This reduction has affected the development of the cartilaginous skull, which in siluroids is of the platytrabecular type, instead of the tropitrabecular type of most teleosts (Daget, 1964). In siluroids, the reduced visual sense is partially compensated by the strongly developed barbels that have both a taste and tactile function. The coupling of the sensory function of the barbels to a palatine-maxillary

mechanism increases their importance as sensory organs. The mouth opening and closing mechanism is sometimes coupled to the palatine-maxillary mechanism in such a manner that, when opening the mouth, the maxillary barbel is projected in front of the mouth, which enables pre-sampling of potential food (Alexander, 1965, 1966; Gosline, 1973).

In those papers dealing with the palatine-maxillary mechanism, a comparative approach is usually made which may reveal some evolutionary relationship and even historical geographical distribution (Alexander, 1965; Singh, 1967; Gosline, 1975; Ghiot *et al.*, 1984). In this paper, the results of an ontogenetic study of those muscles of the African catfish *Clarias gariepinus* (Clariidae), related to the maxillary barbel, are given. The muscles related to the movements of the mandibular barbels are dealt with in a separate paper (Adriaens & Verraes, In prep.). In the literature, varying nomenclature has been applied for the barbel muscles, as will be discussed briefly. In the present paper, a terminology according to Winterbottom (1974) is used.

### Material and methods

Specimens of *C. gariepinus* (Burchell, 1822) of 2 ontogenetic stages (7.19 mm SL and 144.90 mm SL) were used to describe the myology of the skull. A third stage (46.75 mm SL) was used for further observations. Fertilized eggs were obtained from the Laboratory of Ecology and Aquaculture (Catholic University of Leuven, Belgium) and were raised at a temperature of 25 °C. At different intervals (8 days and 120 days after fertilization), specimens were sedated in MS 222. An 8-day-old specimen (TL = 7.77 mm, SL = 7.19 mm, PAL = 3.76 mm) (PAL = Preanal length) was fixated in a paraformaldehyde-glutaraldehyde solution, the 120-day-old fish (TL = 50.15 mm, SL = 46.75 mm, PAL = 23.90 mm) in a buffered 4% formaldehyde solution. Both were used for serial sectioning. The former was embedded in EPON. The sections of 2 µm were stained with toluidine. The 120-day-old fish were embedded in Paraplast. The 5-µm thick serial sections were stained with an improved trichrome staining (Mangakis, Böwe & Pikova-Müllerova, 1964).

Other juvenile specimens were used for clearing and staining *in toto*, according to Hanken & Wassersug (1981). These were commercially raised specimens with an age of approximately 100 days, obtained from Mr Fleure (Someren, the Netherlands). One specimen was used for drawing (TL = 144.90 mm, SL = 125.45 mm, PAL = 67.10 mm), other specimens were used for further observations (TL = 149.90 mm, SL = 132.50 mm, PAL = 68.20 mm) (TL = 166.90 mm, SL = 144.50 mm, PAL = 78.30 mm) (TL = 163.50 mm, SL = 142.80 mm, PAL = 75.70 mm) (TL = 154.05 mm, SL = 136.20 mm, PAL = 71.30 mm).

The serial sections of the 8-day-old larvae were studied and drawn using a WILD M12 light microscope, equipped with a camera lucida. Three-dimensional reconstructions were made using a commercial software package. A WILD M5 stereo-microscope with camera lucida was used for studying and drawing the cleared and stained specimens.

Discussion on the functionality of the different muscles in this paper is based on anatomical evidence, as well as manipulations of preserved material. No cinematographical or electromyographical analyses have been done. In this paper, when mentioning the functionality of a certain muscle, morphological evidence indicates that the muscle can be functional as it bears both its insertions.

### Results

In *C. gariepinus*, two muscles are found that take part in the palatine-maxillary mechanism: (1) a retractor tentaculi and (2) an extensor tentaculi.

#### *7.19 mm SL specimen*

*Retractor tentaculi* – Already in this larval stage, both maxillary barbel muscles can be distinguished (Fig. 2). The retractor tentaculi is almost completely covered laterally, by the

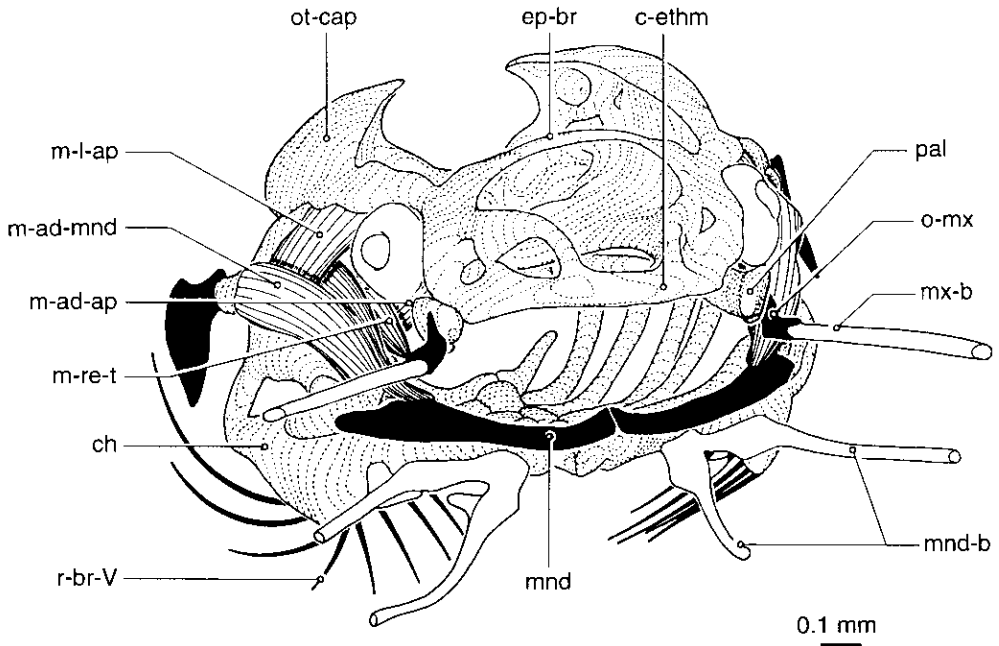


FIG. 2. Graphical 3D reconstruction of the skull of *Clarias gariepinus* (7.19 mm SL): oblique fronto-lateral view (not all skeletal and muscular elements are drawn) (black indicates bones) (c-ethm = ethmoid cartilage; ch = ceratohyal; ep-br = epiphysial bridge; m-ad-ap = adductor arcus palatini; m-ad-mnd = adductor mandibulae; m-l-ap = levator arcus palatini; m-re-t = retractor tentaculi; mnd = mandibula; mnd-b = mandibular barbel; mx-b = maxillary barbel; o-mx = maxilla; ot-cap = otic capsule; pal = palatine; r-br-V = branchiostegal ray V).

adductor mandibulae complex (Adriaens & Verraes, 1996). The muscle originates from the medial face of the cartilaginous suspensorium, at the anterior margin of the hyosymplectic (Figs 3, 4). No ossifications of the hyosymplectic are detected at this stage. The muscle initially runs along the dorsal margin of the pterygoid process, eventually passing along its lateral face. At the level of this process, the muscle runs between the adductor mandibulae  $A_3$  and the adductor arcus palatini (Figs 2, 3a, 4a). Rostrally it inserts on the caudal face of the maxilla via a small tendon. The insertion of the tendon on the maxilla is situated as far as possible from the articulation of the bone with the palatine and the submaxillary cartilage, thereby maximizing the power output during contraction (Figs 3, 5). The maxilla is already well formed and articulates with a cartilaginous complex formed by the palatine and the submaxillary cartilage.

*Extensor tentaculi* – The extensor tentaculi is a relatively small muscle covered by the eye, connecting the palatine to the neurocranium (Fig. 6). This muscle originates from the lateral face of the preorbital bases and partially from the medial face of the orbito-nasal lamina of the cartilaginous skull, precisely posterior to its articulation with the palatine. The dorso-ventrally directed fibres insert on the dorsal face of the posterior half of the cartilaginous palatine (Figs 3, 4, 5). No ossification of the palatine is observed at this stage. The insertion is spread along the posterior half of the palatine, from exactly posterior to its articular facet up to its posterior tip (Figs 5b, c, 6). The palatine articulates with the neurocranium at the orbito-nasal lamina (Fig. 6).

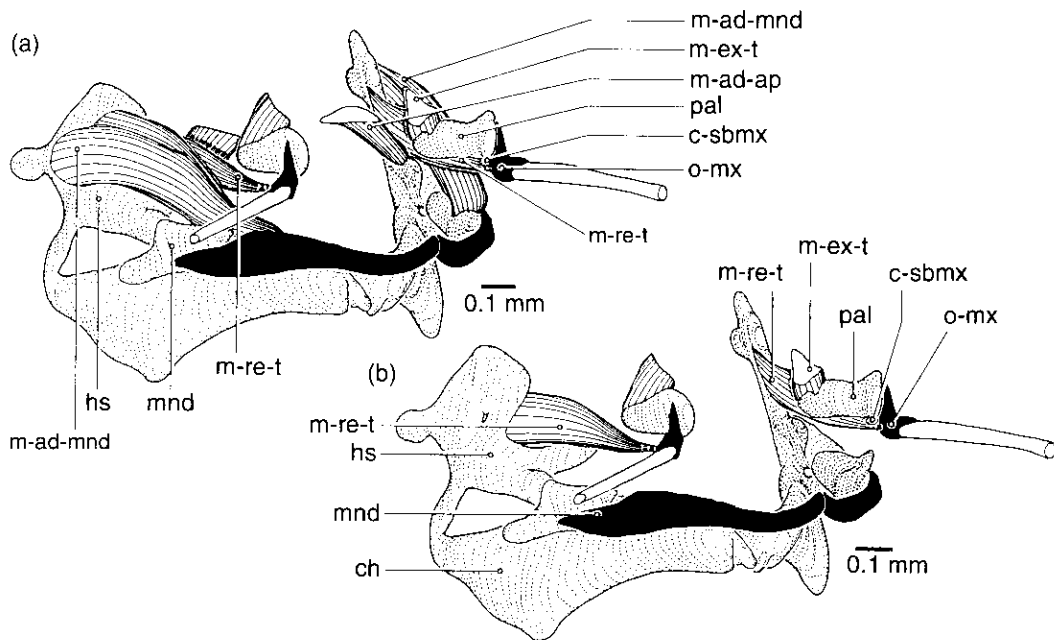


FIG. 3. Graphical 3D reconstruction of the suspensorium, palatine, lower jaw, and hyoid in *Clarias gariepinus* (7.19 mm SL) (oblique anterior view): (a) adductor mandibulae complex, adductor arcus palatini and maxillary barbel muscles drawn; (b) adductor mandibulae complex and adductor arcus palatini muscles removed (black indicates bones) (c-sbm = submaxillary cartilage; ch = ceratohyal; hs = hyosymplectic; m-ad-ap = adductor arcus palatini; m-ad-mnd = adductor mandibulae; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mnd = mandibula; o-mx = maxilla; pal = palatine).

#### 144.90 mm SL specimen

**Retractor tentaculi** - In both the 46.75 mm SL specimen and the 144.90 mm SL specimen, the maxillary barbel musculature is comparable to the adult situation (Nawar, 1955). The retractor tentaculi has become a large muscle originating from the ossified suspensorium and inserting via a long and stout tendon on the maxilla (Figs 7a, b). The origin of the muscle is spread over the hyomandibular, the quadrate and the metapterygoid. From its medial face, the hyomandibular has a rostrally directed, membranous outgrowth (Fig. 8). This plate-like structure increases the insertion surface for the retractor tentaculi, the latter being attached to the major part of the lateral face of this plate. The dorsal fibres of the muscle originate from just below the dorsal margin of the hyomandibular (Fig. 7b). The ventral fibres originate from the quadrate, which lies antero-ventrally to the hyomandibular. The medial fibres originate from the postero-lateral face of the metapterygoid. Posteriorly, the muscle lies against the medial face of the adductor mandibulae A<sub>3</sub>. From this point, it runs anteriorly along the ventro-medial side of the eye and lateral to the palatine and the extensor tentaculi muscle. Anteriorly to the eye, the muscle is covered laterally by the infraorbitals I to III. Eventually the muscle inserts via a well-developed tendon to the posterior face of the maxilla. In both the 46.75 mm SL and 144.90 mm SL specimen, the insertion on this bone is situated on the dorsal part of the posterior face (Fig. 9). Posteriorly, the conspicuous tendon is continued into an aponeurosis, dividing the retractor in a dorsal and a ventral part.

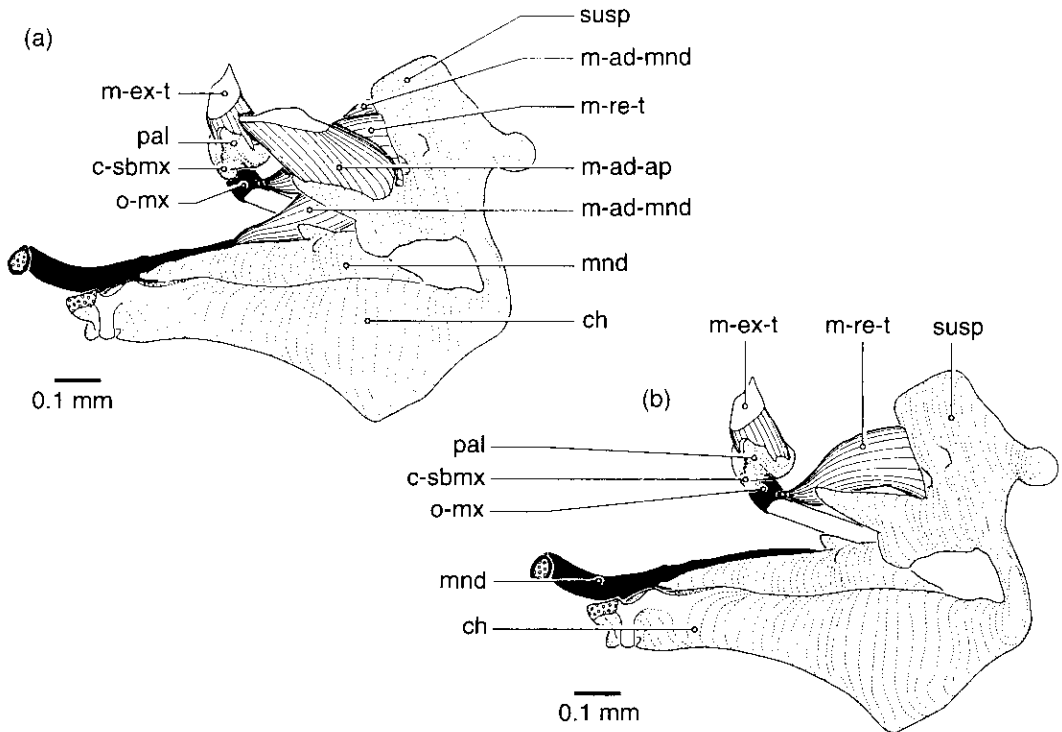


FIG. 4. Graphical 3D reconstruction of the right suspensorium, palatine, lower jaw, and hyoid in *Clarias gariepinus* (7.19 mm SL) (postero-medial view): (a) adductor mandibulae complex, adductor arcus palatini and maxillary barbel muscles drawn, (b) adductor mandibulae complex and adductor arcus palatini muscles removed (black indicates bones, small circles indicate cartilage) (c-sbmx = submaxillary cartilage; ch = ceratohyal; m-ad-ap = adductor arcus palatini; m-ad-mnd = adductor mandibulae; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mnd = mandibula; o-mx = maxilla; pal = palatine; susp = suspensorium).

The maxilla is well developed and articulates with the lateral face of the rostral tip of the ossified palatine, the autopalatine (Fig. 9). The maxilla bears two articulatory condyles at its proximal end that facilitate the previously mentioned articulation. The dorsal condyle bears a ligamentous connection with the antorbital bone. At its distal end, the maxilla has a tube-like socket into which inserts the central rod of the maxillary barbel (Fig. 9). Manipulation of the retractor tentaculi makes the maxilla rotate backward around the rostral tip of the autopalatine, resulting in an adduction of the maxillary barbel. The articulation of the two is held in place during rotation by a cap of connective tissue.

*Extensor tentaculi* – The less conspicuous extensor tentaculi lies between the skull and the dorso-lateral face of the autopalatine (Fig. 7c). The muscle originates from the ventral side of the perichondral part of the lateral ethmoid, dorsal to the lateral tip of the vomer. The lateral ethmoid is the ossification of the rostro-lateral part of the chondrocranium, thereby enclosing the orbito-nasal lamina (Fig. 10) (Daget, 1964). The autopalatine articulates with the lateral ethmoid at this lamina. The insertion of the extensor tentaculi muscle is spread over the medial face of the ossified orbito-nasal lamina. Posteriorly, the origin is situated at the ventral and ventro-lateral face of the lateral ethmoid. In the 46.75 mm SL, the medial fibres also originate from the lateral

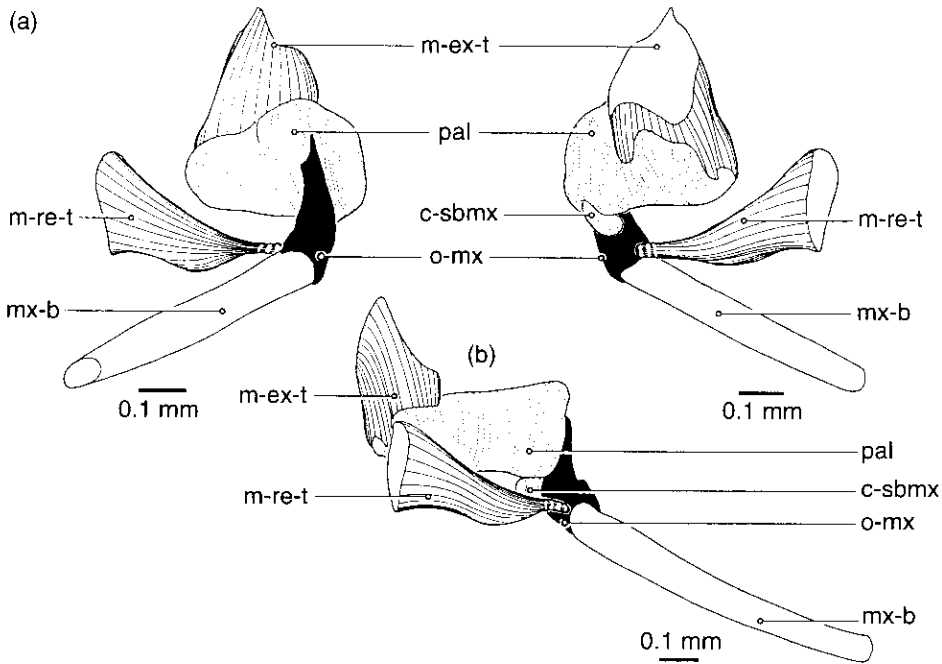


FIG. 5. Graphical 3D reconstruction of the right side musculo-skeletal elements of the palatine-maxillary mechanism in *Clarias gariepinus* (7.19 mm SL): (a) antero-lateral view; (b) postero-lateral view; (c) postero-medial view (black indicates bones) (c-sbmx = submaxillary cartilage; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mx-b = maxillary barbel; o-mx = maxilla; pal = palatine).

face of the ptero- and orbitosphenoids. All the fibres insert on the posterior half of the autopalatine (Fig. 9). The insertion is muscular; however, in the 46.75 mm SL a small tendon accents the anterior fibres. The insertion only occurs posteriorly to the articular facet, at the dorso-lateral face of the autopalatine. Distally, the autopalatine forms a dorso-lateral ridge on which the fibres insert (Fig. 11). From there on, the insertion becomes spread over the dorsal face of the bone. A differentiation of the extensor tentaculi seems to have occurred as a partially distinct medial part and lateral part are present. The lateral part originates from the neurocranium, inserting on the dorso-lateral face of the autopalatine. The medial part does not appear to originate from the skull but from the lateral face of the entopterygoid, at the level of the ligamentous connection between the autopalatine and the entopterygoid. Posteriorly, this medial part is not distinguishable, only one muscle bundle running from the lateral side of the neurocranium (i.e. the orbitosphenoid and pterosphenoid) to the cartilaginous posterior tip of the palatine.

At the articulation zone between the lateral ethmoid and the autopalatine, the former still bears a cartilaginous facet (Fig. 10, arrows). In the middle, the autopalatine bears a distinct articular facet on its dorso-medial face (Fig. 9, af-VII). This facet is small but is antero-posteriorly elongated. The structure of the two articulations suggests that, not only a rotation, but a restricted translation in an antero-posterior direction is also possible. Apart from this direct connection between the lateral ethmoid and the autopalatine, both are, as already mentioned, connected indirectly: the autopalatine is attached to the entopterygoid through a ligamentous

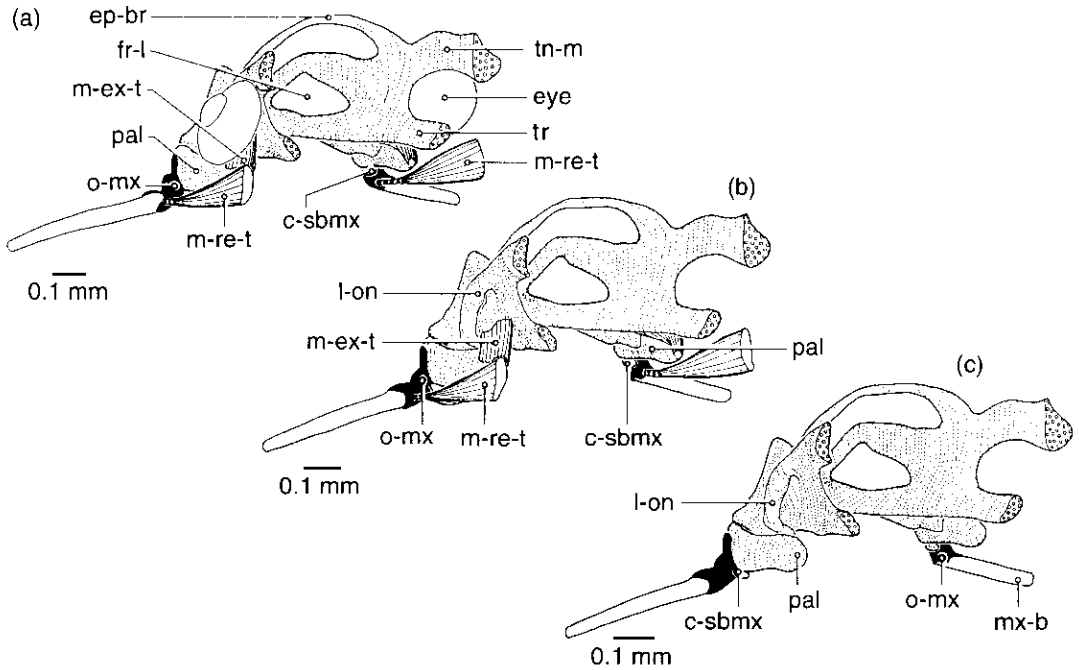


FIG. 6. Graphical 3D reconstruction of the musculo-skeletal elements of the palatine-maxillary mechanism and part of the chondrocranium in *Clarias gariepinus* (7.19 mm SL): (a) postero-lateral view; (b) *idem*, eyes removed; (c) *idem*, muscles removed, showing articulation between palatine and orbito-nasal lamina (black indicates bones, small circles indicate cartilage) (c-sbmx = submaxillary cartilage; ep-br = epiphysal bridge; fr-l = foramen fila olfactoria; l-on = orbito-nasal lamina; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mx-b = maxillary barbel; o-mx = maxilla; pal = palatine; tn-m = taenia marginalis; tr = trabecula).

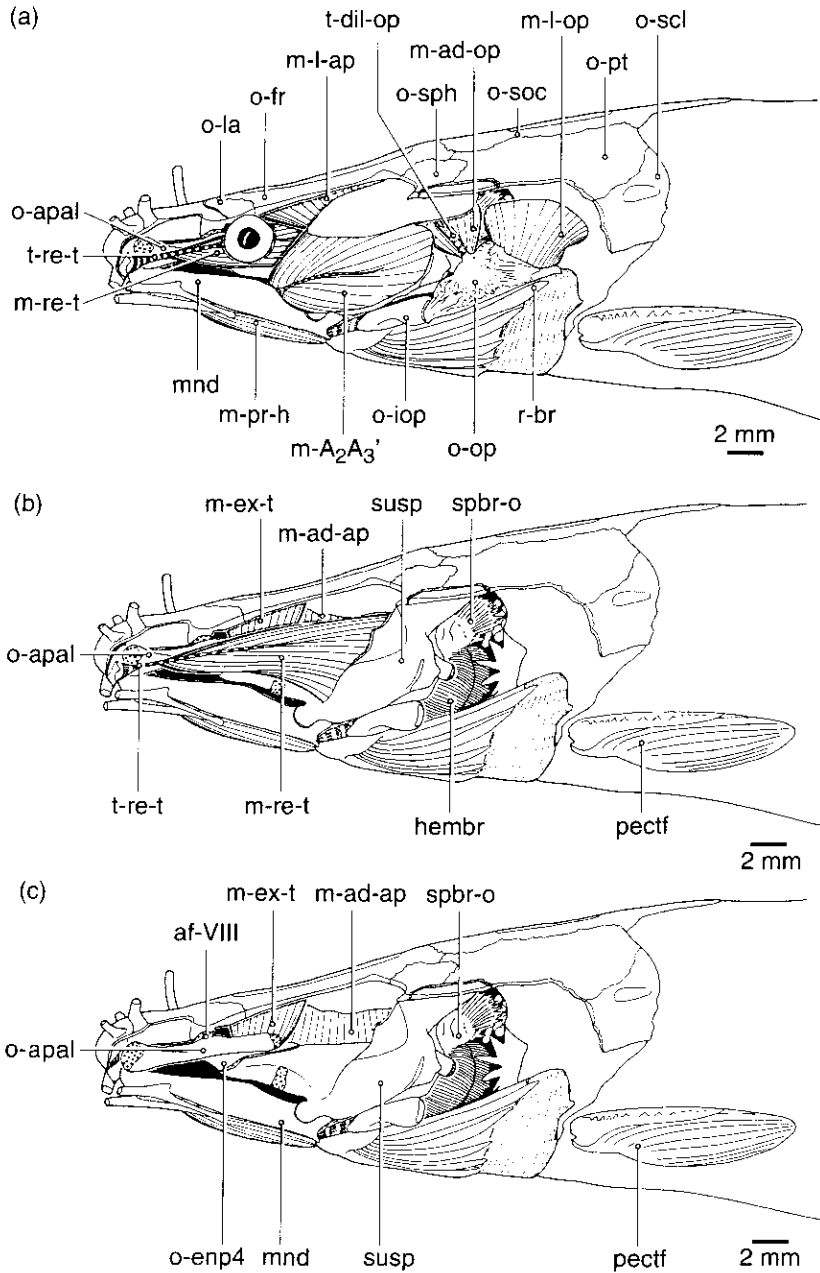
strap. Additionally, a ligamentous link is present between the entopterygoid and the lateral ethmoid. These connections indicate that the entopterygoid in *C. gariepinus* corresponds to the sesamoid 'entopterygoid' type four of Arratia (1992).

### Discussion

The structure and the origin of the elements related to the palatine-maxillary mechanism have been investigated to a great extent, however, much confusion remains. The homology of the

FIG. 7. Skull of *Clarias gariepinus* (142.80 mm SL) (lateral view): (a) adductor mandibulae complex exposed; (b) retractor tentaculi exposed; (c) extensor tentaculi exposed (af-VIII = articularity facet of the lateral ethmoid bone with the autopalatine; hembr = hemibranchia; m-A<sub>2</sub>A<sub>3</sub>' = adductor mandibulae A<sub>2</sub>A<sub>3</sub>'; m-ad-ap = adductor arcus palatini; m-ad-op = adductor operculi; m-ex-t = extensor tentaculi; m-l-ap = levator arcus palatini; m-l-op = levator operculi; m-pr-h = protractor hyoidei; m-re-t = retractor tentaculi; mnd = mandibula; o-apal = autopalatine; o-enp4 = sesamoid 'entopterygoid'; o-fr = frontal; o-iop = interopercular; o-la = lateral ethmoid; o-op = opercular; o-pt = pterotic; o-scl = supracleithrum; o-soc = supraoccipital; o-sph = sphenotic; pectf = pectoral fin; r-br = branchiostegal ray; spbr-o = suprabranchial organ; susp = suspensorium; t-dil-op = tendon of the dilatator operculi; t-re-t = tendon of the retractor tentaculi).





retractor muscle of the maxillary barbel is one of these much discussed topics. Several hypotheses have been proposed concerning homology, but the general agreement exists that the muscle is derived from a part of the adductor mandibulae complex, based on evidence of innervation (see below). However, there is still discussion as to which part of the complex gave rise to the barbel

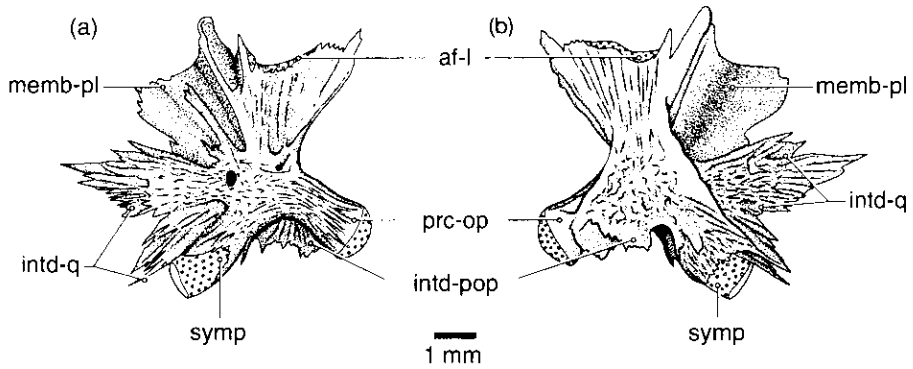


FIG. 8. Hyomandibular of *Clarias gariepinus* (125.45 mm SL): (a) medial view; (b) lateral view (small circles indicate cartilage) (af-I = articulatory facet of the hyomandibular with the sphenotic; intd-pop = interdigitating surface for the preopercular; intd-q = interdigitating surface for the quadrate; memb-pl = membranous plate of the hyomandibular; prc-op = opercular process; symp = symplectic).

retractor muscle. In general, two hypotheses are proposed: (1) the retractor tentaculi is derived from the  $A_1$  muscle; and (2) it is derived from the  $A_3$  muscle.

(1) The fact that the retractor tentaculi inserts on the maxilla has led to the idea that the retractor muscle would be homologous with that part of the adductor mandibulae complex

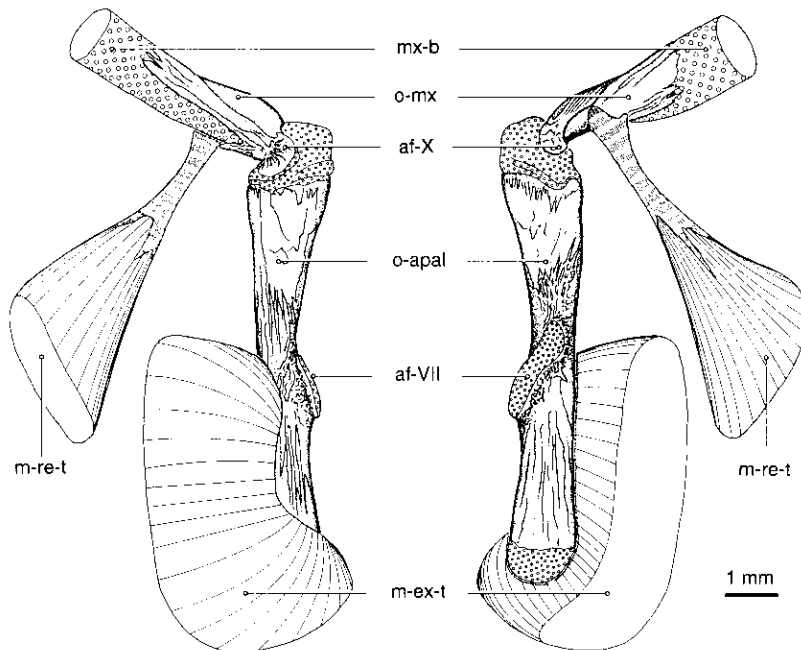


FIG. 9. Right side musculo-skeletal elements of the palatine-maxillary mechanism of *Clarias gariepinus* (125.45 mm SL): (a) ventral view; (b) dorsal view (small circles indicate cartilage, circles in maxillary barbel indicate elastine network) (af-VII = articular facet of the autopalatine with the lateral ethmoid; af-X = articulatory facet of the maxilla with the autopalatine; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mx-b = maxillary barbel; o-apal = autopalatine; o-mx = maxilla).

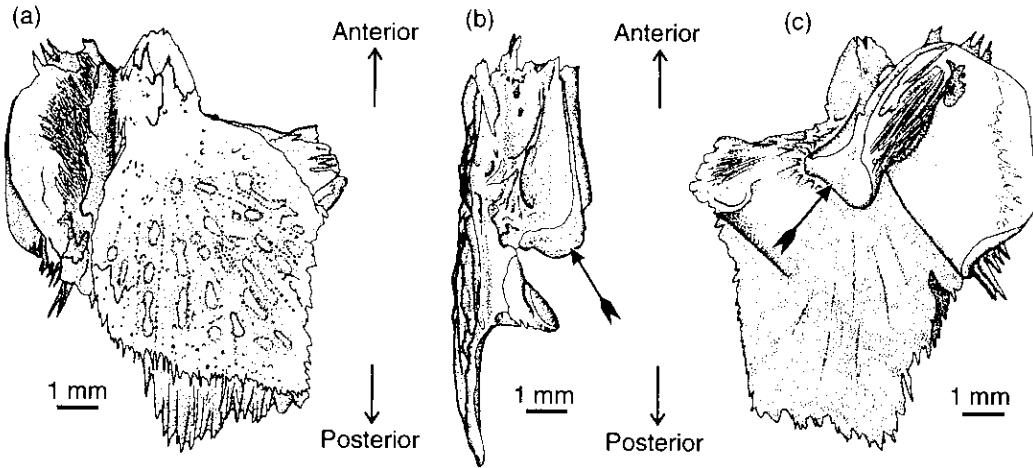


FIG. 10. Lateral ethmoid of *Clarias gariepinus* (174.50 mm SL): (a) dorsal view; (b) lateral view; (c) ventral view (arrows indicate articular facet with autopalatine).

which normally inserts on the maxilla, i.e. the  $A_1$  part. In generalized ostariophysans, the  $A_1$  muscle is the superficial part of the complex which inserts on the posterior or lateral margin of the maxilla (Winterbottom, 1974), directly (as in Cypriniformes, Gonorhynchiformes, and some primitive Characiformes), or through a primordial ligament (as in other Characiformes) (Fink & Fink, 1981). The latter ligament generally connects the maxilla with the lower jaw. A contraction of this  $A_1$  muscle will generate a backward rotation of the maxilla, coupled to an elevation of the lower jaw (Motta, 1984; Gosline, 1986). Takahasi (1925), who investigated the cranial muscles of different otophysans, found different configurations of the adductor mandibulae complex and the retractor muscle. The  $A_1$  muscle (Takahasi's maxillaris part), is the most superficial part of the complex in cyprinoid fishes, as observed in *Opsariichthys* (Cyprinidae). In this species, the

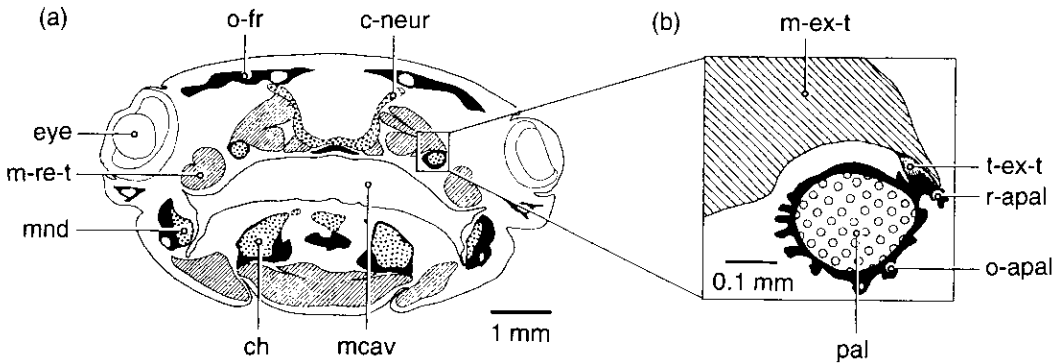


FIG. 11. Serial section of *Clarias gariepinus* at the level of the eyes (46.75 mm SL): (a) overview; (b) detail of dorso-lateral ridge of the autopalatine (black indicates bones, small circles indicate cartilage, shading indicates muscles) (c-neur = cartilaginous neurocranium; ch = ceratohyal; m-ex-t = extensor tentaculi; m-re-t = retractor tentaculi; mcav = mouth cavity; mnd = mandibula; o-apal = autopalatine; o-fr = frontal; pal = palatine; r-apal = insertion ridge of the autopalatine for the extensor tentaculi; t-ex-t = tendon of the extensor tentaculi).

muscle is well developed, consisting of a dorsal  $A_{1\alpha}$  part and a ventral  $A_{1\beta}$  part. Rostrally, the fibres are attached to a primordial ligament which runs from the articular and dentary to the maxilla. In siluroids, however, different patterns of the maxillaris are observed. Although in some cases the maxillaris seems to be reduced completely (e.g. *Liobagrus*: Amblycipitidae, *Pseudobagrus*: Bagridae and some Trichomycteridae (Schaefer & Lauder, 1986)), it is generally present. Surprisingly, when present, the muscle, connected tendinously to the maxilla, lies medial to the mandibularis section, the latter corresponding to the  $A_2$  and  $A_3$  muscles. Takahasi (1925) hypothesized that the ventral part of the  $A_1$  muscle, the  $A_{1\beta}$ , migrated ventrally along the primordial ligament, eventually inserting only on the lower jaw, thereby fusing with the mandibularis. The dorsal part, however, the  $A_{1\alpha}$ , kept its insertion to the maxilla through the primordial ligament. The loss of the connection of the primordial ligament with the lower jaw results in a tendinous connection between the  $A_{1\alpha}$  and the maxilla and no connection between the latter and the lower jaw, as is the case for *Parasilurus* (Siluridae). Takahasi (1925) described a complete gradient of muscle patterns from which he concluded that the retractor tentaculi of Siluroidei is homologous with the  $A_{1\alpha}$  of Cyprinoidei.

(2) The fact that the  $A_1$  muscle normally is situated at the lateral position of the muscle complex, and the fact that the retractor tentaculi generally lies medial to the complex, has led to the assumption that the retractor tentaculi would be derived from the deeper part of the complex, as was noted by Eaton (1948). Alexander (1965) thus stated that the adductor tentaculi, as he called the retractor tentaculi, was derived from the  $A_3$  muscle instead of the  $A_1$  one. Howes (1983) demonstrated the possible evolutionary shift from an undifferentiated  $A_3$  muscle, inserting on the medial face of the lower jaw, to a differentiated medial part of the  $A_3$  muscle, the retractor tentaculi, which formed a *de novo* insertion on the primordial ligament. In the primitive siluroid *Diplomystes* (Diplomystidae), an inner division of the adductor mandibulae complex is attached both to the lower jaw via a tendon covering the dorsal face of the lower jaw, and to both the maxilla and the lower jaw by a sheet of connective tissue. In *Tandanus* (Plotosidae), the primordial ligament has lost its muscular attachments, thereby solely connecting the maxilla to the lower jaw (Howes, 1983). In this species, both the  $A_1$  and  $A_2$  muscles insert directly on the lower jaw, which is considered to be the plesiomorph condition by Howes (1983), although the opposite was stated by Fink & Fink (1981). In *Pimelodus* (Pimelodidae) and *Clarotes* (Claroteidae), a homologous ligament is present, connecting the maxilla with the coronoid process of the dentary, but an extension of the ligament, running up to the fascia of the medial division of the adductor mandibulae complex is present as well. In *Megalonema* (Pimelodidae) the primordial ligament is posteriorly branched; the medial branch being attached to the medial part of the adductor mandibulae complex, the lateral branch being connected to the lower jaw (Howes, 1983). In *Corydoras* (Callichthyidae), the primordial ligament is formed by a connective tissue sheet which runs from the coronoid process of the lower jaw to both the maxilla and the premaxilla (Schaefer & Lauder, 1986). Here, a shift of the dorsal extension of the primordial ligament has occurred from the maxilla to the highly mobile premaxillae. The  $A_1$  muscle inserts on the lateral aspect of the lower jaw, as well as to the connective tissue to which the retractor tentaculi muscle is connected also. An analogue division of the medial part of the adductor complex, inserting on the maxilla, has also been reported in non-siluroids (e.g. *Aphredoderus*, Aphredoderidae, Perciformes) (Eaton, 1935).

A detailed morphological study of the ontogeny of the adductor mandibulae complex in *C. gariepinus* suggests the absence of the  $A_1$  muscle (Adriaens & Verraes, 1996). The functional adductor mandibulae then comprises the complex of: (1) the fused  $A_2$  and  $A_3$  muscle parts; and

(2) a medial  $A_3''$  part. Both the  $A_3$  parts ( $A_3'$  and  $A_3''$ ) are separated by the levator arcus palatini. It can thus be suggested that the  $A_1$  muscle is lost in *C. gariepinus*, whereas the retractor tentaculi is derived from the  $A_3''$  part of the adductor mandibulae complex.

The origin of the extensor tentaculi seems to be less doubtful. It is generally accepted that the extensor muscle is derived from the adductor arcus palatini (Takahasi, 1925; Alexander, 1965; Winterbottom, 1974; Gosline, 1975; Fink & Fink, 1981), which originates from the lateral margin of the parasphenoid and inserts on the dorsal margin of the suspensorium. Takahasi (1925) distinguished three portions: (1) the hyomandibular, (2) the pterygoid, and anteriorly (3) the palatine portion. Apparently, the decoupling of the palatine from the rest of the suspensorium in siluroids has resulted in the isolation of those fibres inserting on it from the rest of the adductor arcus palatini.

Different nomenclature has been applied to indicate the tentacular muscles, especially for the extensor tentaculi, which is frequently referred to as the 'abductor tentaculi' (Nawar, 1955; Alexander, 1965). Gosline (1975) refers to the muscle as the 'palatine part of the adductor arcus palatini'.

As mentioned above, the innervation of the tentacular muscles basically reveals their true origin. In larval *C. gariepinus*, the ramus mandibularis of the trigeminal nerve runs antero-posteriorly from the ventral face of the cartilaginous lower jaw to the coronoid process where it rises along the lateral side of the jaw. It then passes medially to the process, between the latter and the adductor mandibulae complex to the lateral side of that muscle complex. From there, it rises to the dorsal side of the adductor mandibulae muscles and eventually above the retractor tentaculi muscle. Posterior to the eye, a side branch penetrates between the adductor mandibulae complex and the retractor tentaculi muscle. In the 46.75 mm SL specimen, the ramus has a comparable path (Adriaens & Verracs, 1996). Posteriorly, it lies against the medial side of the adductor mandibulae  $A_3''$ , dorso-laterally to the retractor tentaculi. During early ontogeny, it is the adductor part of the mandibular muscle plate that becomes innervated by the ramus mandibularis. This part will eventually form the adductor mandibulae complex (Jarvik, 1980). The extensor tentaculi, on the other hand, is formed by the constrictor dorsalis part of the hyoid arch musculature (Munshi & Singh, 1967; Winterbottom, 1974; Jarvik, 1980). The innervation occurs through the ramus hyomandibularis of the nervus facialis, which also innervates the adductor arcus palatini (Alexander, 1965).

Different evolutionary trends have been detected in the palatine-maxillary mechanism within the siluroids. A basic mechanism, where only the maxilla is functional, is present both in siluroids and non-siluroid ostariophysans. In some cyprinoid teleosts, the maxilla bears a small barbel at its ventral margin (e.g. *Cyprinus*, *Gobio* (Cyprinidae)). In these fishes, the  $A_1$  muscle is attached to the maxilla through the primordial ligament. Opening of the mouth will make the maxilla rotate forward, resulting in a forward and ventral displacement of the barbel. Contraction of the  $A_1$  muscle will, together with other muscular activity for mouth closure, return the maxilla and barbel to their original position (Motta, 1984). In siluroids, however, the displacement of the maxillary barbel is possibly due to the mobility of the palatine (Gosline, 1973). A basic siluroid construction occurs in the 'primitive' catfish *Diplomystes* (Diplomystidae). In this species, a toothed, non-modified maxilla is connected to the maxillary barbel only through surrounding tissue (Gosline, 1975). During mouth opening, the maxillary barbel is displaced in an antero-ventral direction instead of an antero-lateral direction, as is the case in more specialized catfish. In general, two major types of palatine-maxillary mechanisms can be distinguished: (1) the sliding type, and (2) different rotating types (Gosline, 1975). In the sliding types, the articulation between

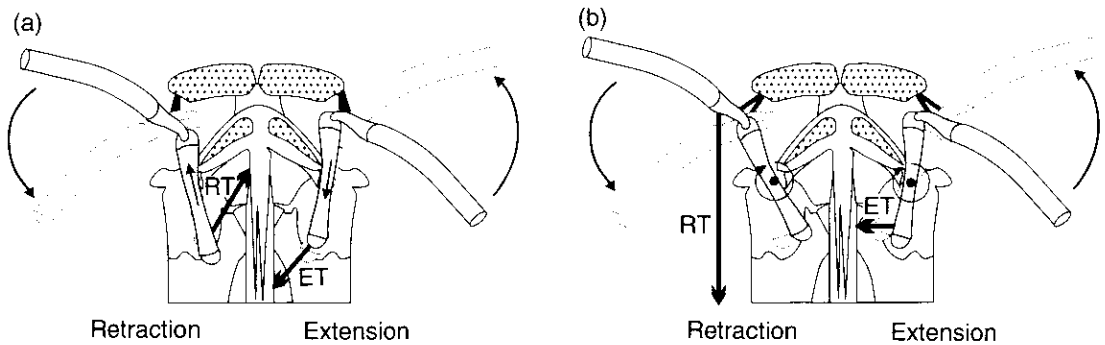


FIG. 12. Scheme of two major types of palatine-maxillary mechanisms in catfishes: (a) sliding type; (b) rotating type (ET = extensor muscle; RT = retractor muscle).

the palatine and the skull enables a translation of the palatine in an antero-posterior direction. During the posterior movement of the palatine, the proximal tip of the maxilla is retracted. Through the connection between the distal point of the maxilla and the premaxilla, via connective tissue or via a distinct ligament, the maxilla rotates in such a way that the maxillary barbel is abducted (Fig. 12). The opposite action is generated through the anterior translation of the palatine. In the rotating types, the maxillary barbel is abducted through an exorotation of the rostral tip of the palatine, coupled to an endorotation of the caudal tip. Adduction results from the opposite action. The muscles responsible for these actions may differ between taxa as two functional units control the ab- and adduction of the maxillary barbel. First, the abduction of the barbel generally is generated through a muscular action on the palatine. Thereby muscles connect the caudal half of the palatine with the skull in such a way that, when contracting, this part of the palatine is shifted backward (e.g. *Ameiurus nebulosus*: Ictaluridae) or rotates medially (e.g. *Clarias gariepinus*, *Bagrus bayad*, *Chrysiichthys longibarbis*: Bagridae) in the sliding type and the rotating type, respectively (Ghiot *et al.*, 1984). Exceptionally, the abduction of the barbel is generated through muscular activity to the maxilla. In *Callichrous pabda*, three slips of muscle are attached on the proximal tip of the maxilla in such a manner that, when contracting, the maxillary barbel is abducted. In this species, no muscle is attached to the posterior half of the palatine (Singh, 1967). Second, the adduction of the barbel generally is accomplished through a retractor muscle, connecting the maxilla to the suspensorium. In this situation, the distal tip of the abducted maxilla is retracted during contraction. As a result, the proximal tip of the maxilla is displaced in an anterior direction, thereby pulling the palatine anteriorly in the sliding type (e.g. *Ameiurus*), or rotating the rostral half of the palatine medially in the rotating type (e.g. *Clarias gariepinus*, *Bagrus bayad*, *Chrysiichthys longibarbis*: Bagridae) (Ghiot *et al.*, 1984). Again, exceptions are noted where the palatine induces the retraction of the maxillary barbel and some, or all, fibres of the muscle inserting on the palatine are directed antero-posteriorly in such a way that, during contraction, the palatine is shifted anteriorly (e.g. *Bagrus bayad*: Ictaluridae, *Pimelodus clarias*: Pimelodidae) (Alexander, 1965; Ghiot, 1978; Ghiot *et al.*, 1984). *Chrysiichthys* is another exception where no muscle, responsible for the retraction of the barbel, is present. In this species, the elasticity of the tissue surrounding the palatine induces the retraction of the barbel. In the different rotating types, the rotation of the palatine is probably associated with a restricted sliding, as can be deduced from the shape of its articulations.

Apart from a pure retraction and extension of the maxillary barbel, further specializations of the mechanism have enabled some species to perform a depression and elevation of the barbels as well, noted in the catfish *Pimelodus* by Alexander (1965) and Ghiot (1978). In this species, the extensor tentaculi can be subdivided into five different muscle parts: (1) a latero-anterior, (2) a latero-medial, (3) a latero-posterior, (4) a tentacular abductor, and (5) a tentacular adductor part. Owing to the spread insertion on the palatine, a rotation of the bone around its longitudinal axis is permitted. One of these parts, the tentacular adductor, inserts to the ventral side of the palatine. When contracting it will, apart from a forward sliding, also perform a rotation of the palatine, which results in a depression of the barbel. When combined with the contraction of the barbel abducting muscle, the barbel can only be depressed. On the other hand, three of these muscles are inserted on the dorsal side of the palatine (1-3), which enable an elevation of the barbel during contraction.

In *C. gariepinus*, the palatine-maxillary mechanism is of the rotating type, but a restricted sliding probably occurs. This can be deduced from the shape of the elongated articulatory facet on the dorsal face of the autopalatine (Fig. 9, af-VII). A distinct ligamentous connection is found between the maxilla and the premaxilla. The fact that the extensor tentaculi seems to be divided into lateral and medial parts, as was observed in the 46.75 mm specimens, might contribute to a restricted mobility for depression and elevation of the maxillary barbel.

In some species, the palatine-maxillary mechanism does not function independently. It may be that the mechanism is coupled with other mechanisms. As already mentioned, in the primitive situation it is coupled to the mouth opening and closing mechanism, which provides pre-sampling of food. This is profitable for species with short maxillary barbels, which rotate ventrally instead of laterally. In most catfish, however, the maxillary barbels are well developed and highly mobile in a lateral direction. In these, the barbels can be placed in front of the head, thereby functioning as a food or obstacle detector. It is observed that *C. gariepinus* constantly moves its maxillary barbels when swimming around.

In *Bagrus bayad*, a ligamentous connection is present between the metapterygoid and the palatine (Ghiot *et al.*, 1984). This connection may affect the position of the palatine when, during respiration, the branchial cavity becomes enlarged partially through abduction of the suspensorium. In *C. gariepinus*, a ligamentous connection between the suspensorium and the palatine is observed as well. The sesamoid 'entopterygoid' type four of Arratia (1992) is attached to the posterior part of the palatine via a ligament which inserts on the medial face of the palatine and runs ventrally to the extensor tentaculi.

The anterior tip of the palatine lies against the lateral face of the olfactory sac. This sac bears several diverticula in *Clarias gariepinus*, as is noted in the 46.75 mm SL specimen. The rotation of the rostral tip of the palatine during ab- and adduction of the maxillary barbel may affect the volume of the nasal sac. During the retraction of the barbel, the rostral tip is displaced medially, resulting in a decrease in volume of the nasal cavity. The lateral displacement of the rostral tip during the abduction of the barbel will create a negative pressure in the cavity, which will then refill with water. This process was demonstrated in a *Clarias* species by Alexander (1965), who used Indian ink to demonstrate a flow of fluids through the nasal sacs during ab- and adduction of the maxillary barbels.

In the 46.75 mm SL specimen of *C. gariepinus*, an articulation is present between the dorsal side of the palatine rostral tip and the antorbital. The latter bone, however, seems to be attached to the base of the nasal barbel. Consequently, the displacements of the palatine may generate some movement in the nasal barbels.

### Conclusions

Already during early ontogeny, the palatine-maxillary mechanism can become functional. In a 7.19 mm SL *C. gariepinus* larva, both skeletal elements (palatine, maxillary bone, orbito-nasal lamina) and muscular elements (retractor tentaculi and extensor tentaculi) are present. Although no ossifications of the related cartilaginous elements are observed, the muscles insert on them. Morphological evidence, as well as data from literature, suggest that, in *C. gariepinus*, the retractor tentaculi is derived from the adductor mandibulae A<sub>3</sub>, whereas the A<sub>1</sub> is lost.

Later during ontogeny, the orbito-nasal lamina and palatine ossify, thus forming the lateral ethmoid and the autopalatine. These bones articulate with each other via a well-developed articulatory facet. The shape of this facet suggests that during ab- and adduction of the maxillary barbel, the palatine rotates in this facet but a restricted sliding is possible as well. The muscular configuration corresponds to the one found in many siluroids: a retractor tentaculi running from the suspensorium to the posterior face of the maxillary bone, and an extensor tentaculi interconnecting the lateral face of the skull (at the level of the lateral ethmoid) to the posterior half of the palatine. Some differentiation in the extensor muscle suggests the possibility of a restricted depression and elevation of the maxillary barbel.

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