Belg. J. Zool. — Volume 124 (1994) — issue 2 — pages 139-155 — Brussels 1994

*Manuscript received on 13 June 1994*

# ON THE FUNCTIONAL SIGNIFICANCE OF THE LOSS OF THE INTERHYAL DURING ONTOGENY IN *CLARIAS GARIEPINUS* BURCHELL, 1822 (TELEOSTEI : SILUROIDEI)

by

DOMINIQUE ADRIAENS and WALTER VERRAES
University of Ghent, Institute of Zoology
K.L. Ledeganckstraat 35, B-9000 Gent (Belgium)

## SUMMARY

In larval *Clarias gariepinus* the cartilaginous interhyal is continuous with the dorsal and ventral part of the hyoid arch. During later ontogeny the interhyal becomes reduced and is completely lost in the adult specimens. The connection between the suspensorium and the hyoid is replaced by a stout ligament, the ligamentum hyomandibulo-ceratohyale. It is hypothesised that this will reduce the mobility of the hyoid bar. Some specific lifestyle adaptations of *C. gariepinus* overrule the necessity of highly mobile hyoid bars. Large hyoid bar depressions would destabilise the dorso-ventrally flattened skull when resting on the bottom. As the Clariidae are able to perform aerial respiration, no large hyoid depression is needed for an extensive aquatic respiration. As *C. gariepinus* is not a suction feeding species, no sudden volume increase of the orobranchial cavity is required through a large hyoid depression. Morphological evidence indicating a restricted possibility of the depression of these bars consists of a small skin fold between the hyoid and the lower jaw, allowing a restrained ventral excursion of the rostral tip of the hyoid. Due to the strongly dorso-ventrally flattened skull the suspensorium is relatively small, in its dorso-ventral direction, which restricts the lateral displacement of the caudal tip of the hyoids during depression. A short sternohyoideus muscle connects the hyoid bar to the pectoral girdle, thus enabling a restricted movement of the bar during contraction. The branchiostegal membrane is rather firm and can be little folded and unfolded.

*Keywords* : interhyal, hyoid, *Clarias*, ontogeny, functional morphology

## INTRODUCTION

The interhyal, also referred to as the stylohyal (DAGET, 1964), forms in most teleosts the connection between the dorsal and ventral part of the hyoid arch, respectively the hyosymplecticum and the ceratohyal. In a generalised teleost this interhyal initially consists of a cartilaginous bar-like structure which is already or becomes isolated from the cartilaginous hyoid arch early during ontogeny. In

*C. gariepinus*, and in most Siluroidei, the interhyal remains continuous with both the hyosymplecticum and the ceratohyal (Hoedeman, 1960 ; Howes and Teugels, 1989 ; Arratia, 1990). In a generalised teleost the cartilaginous interhyal becomes ossified during ontogeny, except at its two articulating ends which come in contact with the hyomandibular and the posterior ceratohyal bones. In catfish the interhyal, if present, becomes ossified or remains cartilaginous. An ossified interhyal is present in *Callichthys*. A rudimentary interhyal can be observed in some primitive species, such as *Diplomystes*, *Nematogenys* and *Loricaria*, where the dorsal articulation between the interhyal and the hyomandibular bone is lost (Arratia, 1990). In *C. gariepinus* a reduction of the interhyal occurs during ontogeny until it is completely lost, already in juvenile specimens. The loss of the interhyal seems to be a feature which is present in several groups of Ostariophysi. In the gonorhynchiform *Phractolaemus* (Phractolaemidae) (Daget, 1964) and the cypriniform *Gobio gobio* (Ostariophysi : Cyprinidae) (Vandewalle, 1975) the interhyal is lacking. In the Siluroidei the absence of the interhyal seems to be general, except for some, already mentioned, species (Arratia, 1990).

Commonly, in the adult teleostean situation, the interhyal forms two articulation facets, with the posterior ceratohyal bone and the hyomandibular bone, respectively. In general these articulations are of the ball and socket type, although variation is present in some teleosts. In several cases the interhyal-ceratohyal connection becomes ligamentous (Karrer, 1967 ; Osse, 1969 ; Anker, 1974 ;1989 ; Birdsong, 1975 ; Vandewalle *et al.*, 1982). In *Blennius pholis* (Perciformes : Blenniidae) also the dorsal articulation becomes ligamentous (Vandewalle *et al.*, 1982). In some cases some additional ligaments are present, connecting the interhyal to surrounding structures other than the posterior ceratohyal bone. In *Gasterosteus* (Gasterosteiformes : Gasterosteidae) a ligamentum interhyalo-suspensoriale is present connecting the interhyal to the preopercular bone (Anker, 1974), as is the case in *Microgobius* (Perciformes : Gobiidae) (Birdsong, 1975) and in *Haplochromis* (Perciformes : Cichlidae) (Anker, 1989). In *Ammodytes* and *Embolichthys* (Perciformes : Ammodytidae) a ligament is present between the bony interhyal and the interopercular bone (Pietsch and Zabetian, 1990). In those teleosts where the interhyal seems to be absent, a ligament is present between the suspensorium and the hyoid (Vandewalle, 1975 ; Arratia, 1990). This is also the case for *C. gariepinus* where a stout ligament runs from the hyomandibular bone to the posterior ceratohyal bone. The absence of the interhyal in adult *C. gariepinus* and the presence of a ligament was already noticed by Nawar (1954).

The loss of the interhyal and its replacement by a stout ligament in *C. gariepinus* will probably have an influence on the mobility of the hyoid. As stated by Anker (1989), the interhyal plays an important role in the four bar sytem of the hyoid, the interopercular bone, the lower jaw and the suspensorium. In this system the length of the interhyal is related to the movement range of the hyoid, and thus of the lower jaw. Apart from their role in the opening of the mouth, the hyoid bars play an important role in the depression of the mouth floor and the lateral expansion of the branchial cavity (Aerts, 1991) which is necessary for generating a negative pressure in the mouth cavity.

Arratia (1990) stated that the loss of the interhyal and its replacement by a ligament is a result of the strongly dorso-ventral flattening of the skulls. This paper deals with the functional significance of the loss of the interhyal in *C. gariepinus* and its possible effect on the movements of the hyoid. The interhyal and surrounding structures are studied in three ontogenetic stages of *C. gariepinus*.

## MATERIAL AND METHODS

Specimens of *Clarias gariepinus* Burchell, 1822 of three ontogenetic stages were used to describe the morphology of the interhyal element and surrounding structures. Fertilised 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 moments (8 days and 120 days after fertilization) specimens where sedated in MS 222. An 8 days 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 days 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 days old fish were embedded in Paraplast. The 5 µm thick serial sections were stained with an improved trichrome staining (Mangakis *et al.*, 1964).

Other juvenile specimens were used for clearing and staining *in toto*, according to Hanken and Wassersug (1981). These where 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), another was used for further observations (TL = 149.90 mm, SL = 132.50 mm, PAL = 68.20 mm). Still another specimen was used for dissection and drawing (TL = 154.05 mm, SL = 136.20 mm, PAL = 71.30 mm).

The serial sections were studied and drawn using a WILD M12 light microscope, equiped 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 the cleared and stained specimens.

## RESULTS

In the examined specimens it is hypothesised that the morphological state of development is more likely to be related to the body length of the fish instead of to the age. It was observed in the specimen of *C. gariepinus* of 120 days (SL = 46.75 mm) that the interhyal is still present, although in a reduced form. In the younger, but larger specimen (age of 100 days, SL = 125.45 mm) the interhyal is already absent. The difference in length of the two specimens is due to the fact that the 100 days old specimen was raised under commercial conditions, thus obtaining perhaps maximal growth. In this paper the ontogenetic development of the interhyal and surrounding structures will be discussed in a non-chronological order, but in relation to increasing standard length.

### 1. Standard length 7.19 mm (8 days) :

In early ontogeny one continuous cartilaginous plate is formed, containing both the mandibular and hyoid arch, except for the pars palatina of the palatoquadratum, as was observed in 5.2 mm specimens by SURLEMONT *et al.* (1989). This part has become isolated from the mandibular arch, which is a typical feature of siluroid fishes (ALEXANDER, 1965 ; GOSLINE, 1975). In the examined specimen of 8 days, the Meckelian cartilage had already become separated from the pars quadrata of the palatoquadratum (Fig. 1). The interhyal, on the contrary, is still a continuous cartilaginous bar between the ventral and dorsal parts of the hyoid arch. Muscles related to the depression and elevation of the hyoid can already be observed. The sternohyoideus muscle, which enables the depression, inserts on a ventral process of the anterior copula. In the 5.2 mm fry, no such an insertion was observed

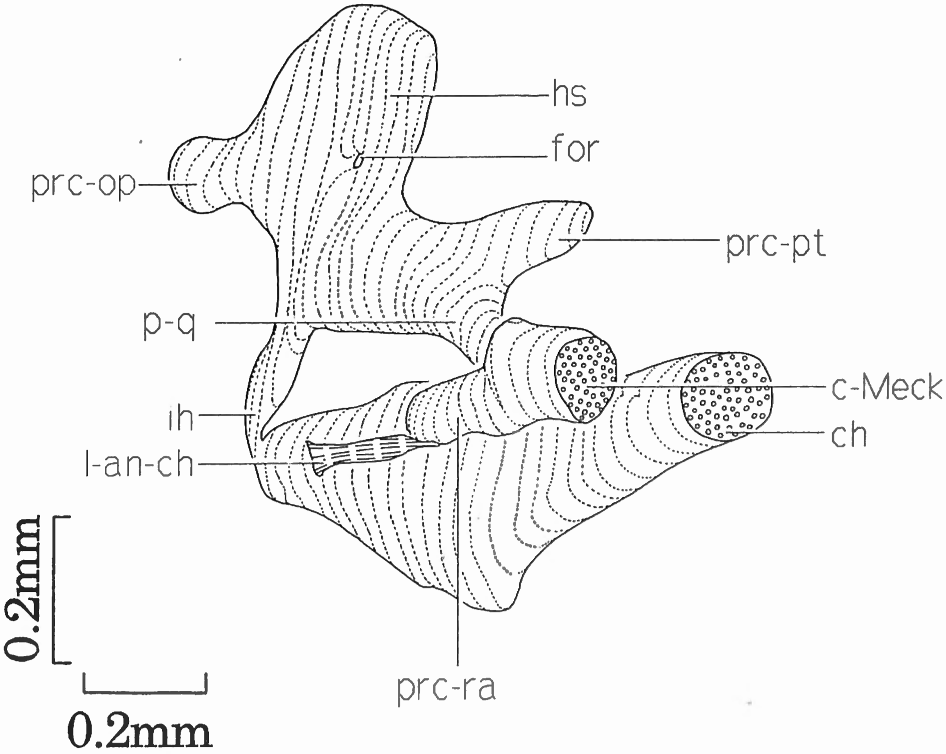

Fig. 1. — Graphical 3D-reconstruction : oblique, anterio-lateral view (right side) of cartilaginous suspensorium, lower jaw (partim) and ceratohyal (partim) of *C. gariepinus* (SL = 7.19 mm) (small circles indicate cartilage) (palatinum not drawn) (Abbreviations see page 152).

yet (SURLEMONT *et al.*, 1989). The elevation muscle, the hyoid protractor muscle, did reach the lower jaw.

No ligament could yet be found between the ceratohyal and the suspensorium but a ligamentum angulo-ceratohyale was already present.

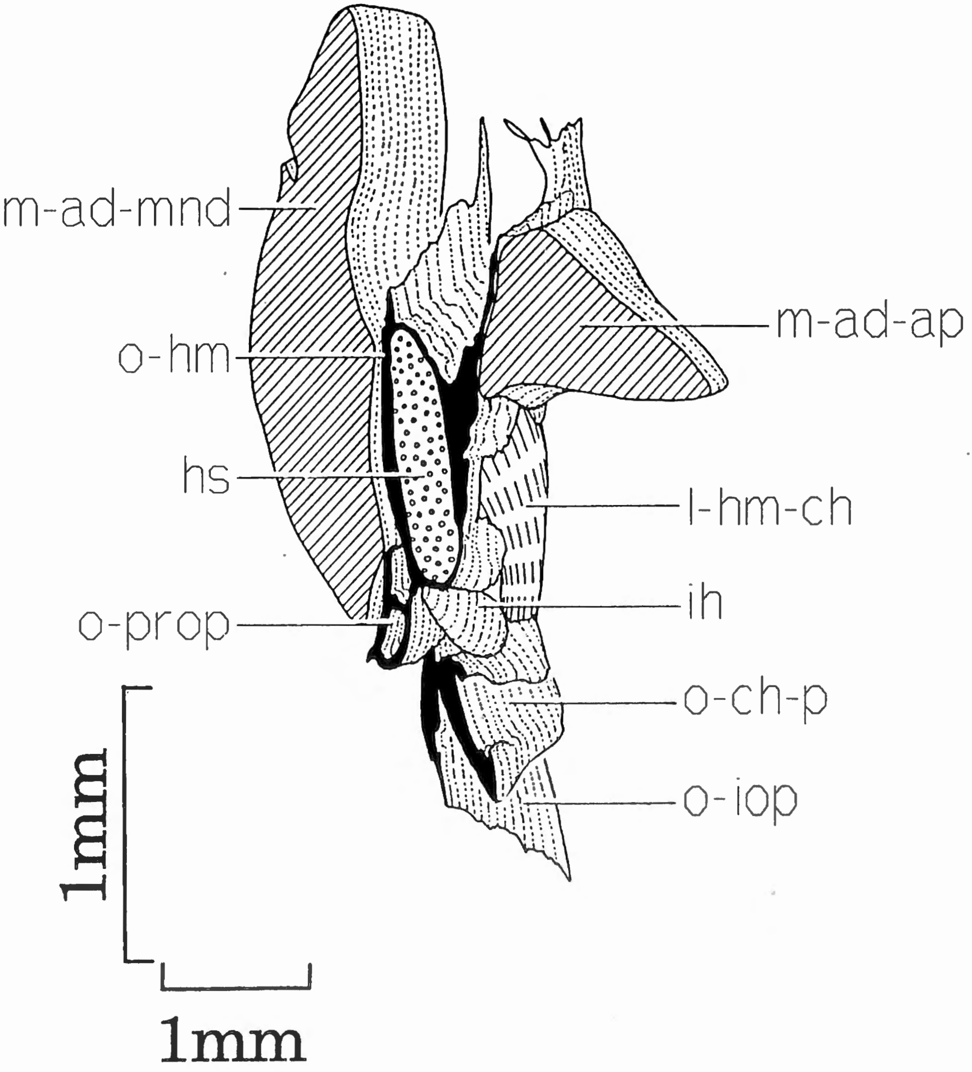

Fig. 2. — Graphical 3D-reconstruction : oblique, posterio-medial view of the suspensorium (right side) at the level of the interhyal and the ligamentum hyomandibulo-ceratohyale of *C. gariepinus* (SL = 46.75 mm) (small circles indicate cartilage, black areas indicate bone, hatched areas indicate muscles).

## 2. Standard length 46.75 mm (120 days) :

At this stage all the suspensorial ossifications are present : the quadrate bone, the metapterygoid bone, a sesamoid bone refered to as the 'entopterygoid' type 4 according to ARRATIA (1992), the hyomandibular bone and the preopercular bone. The symplectic bone is not present, which is a general feature of most siluroid teleosts (ALEXANDER, 1965 ; ARRATIA, 1990). The interhyal has become separated from the ceratohyal (Fig. 2), but seems to be still continuous with the hyosymplecticum. The non-ossified interhyal is situated at the ventro-medial side of the hyomandibular bone, medial to the connection between the latter and the preopercular bone. Ventrally the interhyal articulates with the posterior part of the posterior ceratohyal bone. The histological aspect of the interhyal differs from that of the ceratohyal and the hyosymplecticum. In the latter a lot of extracellullar matrix, surrounding small chondrocytes is present, whereas the interhyal has a small amount of matrix, separating large cells.

Medial to the interhyal a stout ligament is present, connecting the hyomandibular bone to the posterior ceratohyal bone (Fig. 2). This ligamentum hyomandibulo-ceratohyale is attached to the medial face of the hyomandibular bone, ventrally to the posterior insertion of the arcus palatini adductor muscle, and to the dorsal face of the posterior ceratohyal bone, right in front of the articulation with the interhyal (Fig. 2).

The muscles involved in the movements of the hyoids are completely developed and their presence is comparable with the situation in the 125.45 mm specimens. The sternohyoideus muscle is a relative short but broad muscle connecting the shoulder girdle to the hyoid, through the urohyal bone (WINTERBOTTOM, 1974). The muscle is attached to the rostral margin of the cleithral bone, along the whole length of the ventral part (Fig. 3B). Rostrally, the muscle inserts onto the forked urohyal bone. This bone is attached to the rostral tips of the two ventral hypohyal bones through two ligaments, *i.e.* the ligamenta urohyalo-hypohyalia. The hyoid protractor muscle inserts on the ventral face of the posterior part of the anterior ceratohyal bone, and the anterior part of the posterior ceratohyal bone (Fig. 3A). Rostrally the insertion of the muscle is spread out. The superficial fibers insert on the bases of the mandibular barbels, whereas the deeper ones insert on the ventral face of the lower jaws.

The lower jaw is connected to the ceratohyal bone in a direct and an indirect way. The direct connection occurs through the ligamentum angulo-ceratohyale, which has become a stout ligament. It runs from the caudalmost tip of the lower jaw to the lateral face of the posterior ceratohyal bone (Fig. 3B). Indirectly, the lower jaw is connected to the posterior ceratohyal bone through the interopercular bone : a ligamentous connection is present (1) between the angular bone and the interopercular bone and (2) between the interopercular bone and the posterior ceratohyal bone. The ligamentum angulo-interoperculare inserts on the caudalmost tip of the lower jaw, lateral to the ligamentum angulo-ceratohyale (Fig. 3A-B).

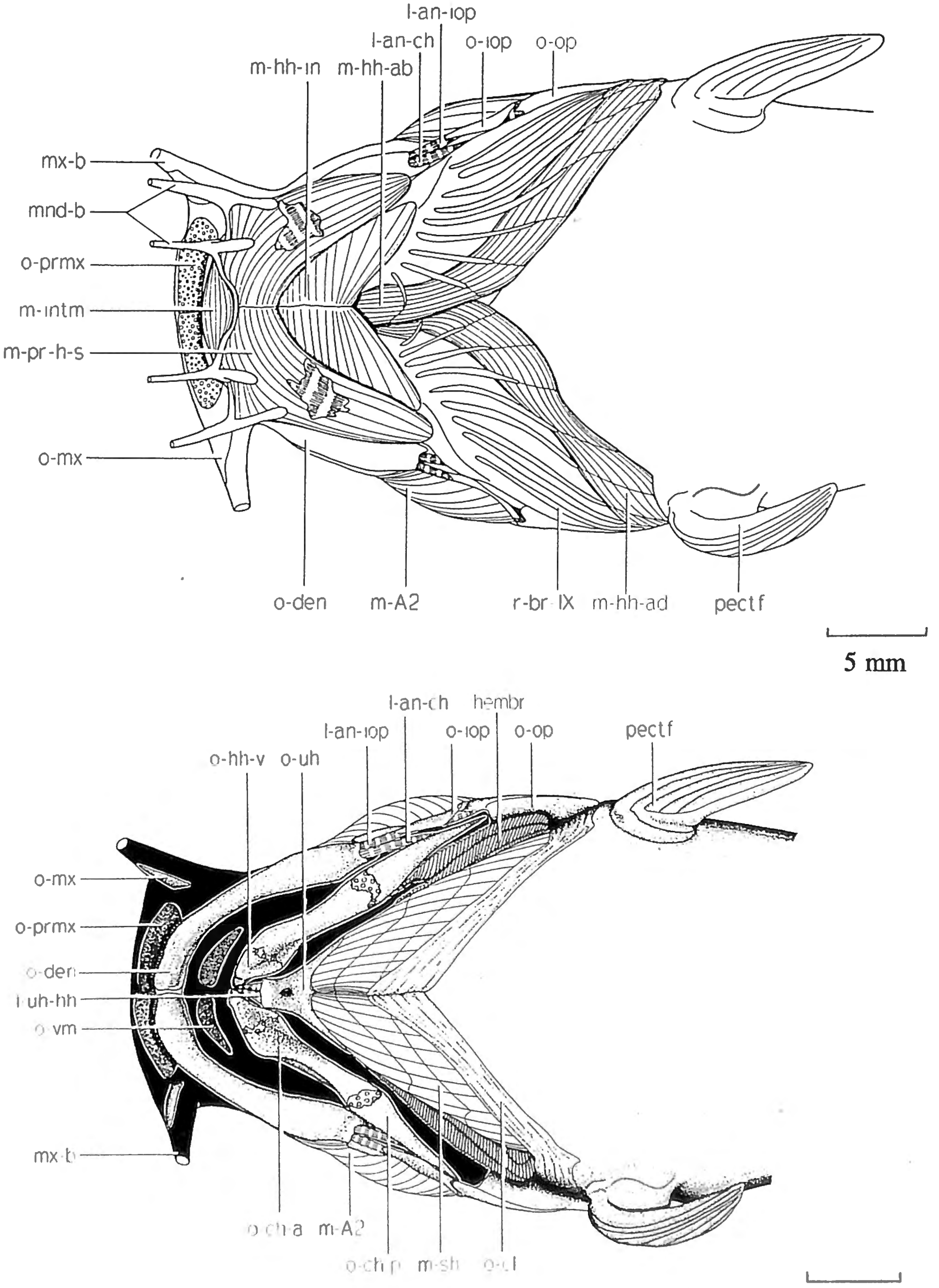

Fig. 3. — Ventral view of a juvenile *C.gariepinus* (SL = 136.20 mm) : A. skin removed ; B. superficial muscles and branchiostegal membrane removed (small circles indicate cartilage).

### 3. Standard length 125.45 mm (100 days) :

At this stage the interhyal has become completely reduced. The only firm connection between the posterior ceratohyal bone and the suspensorium is the strongly developed ligamentum hyomandibulo-ceratohyale (Fig. 4). It is attached to a ridge on the medial face of the hyomandibular bone, and runs up to the dorsal face of the posterior part of the hyoid.
The description of the muscles involved in the depression and elevation of the hyoid is comparable to that given for the 46.75 mm specimens.

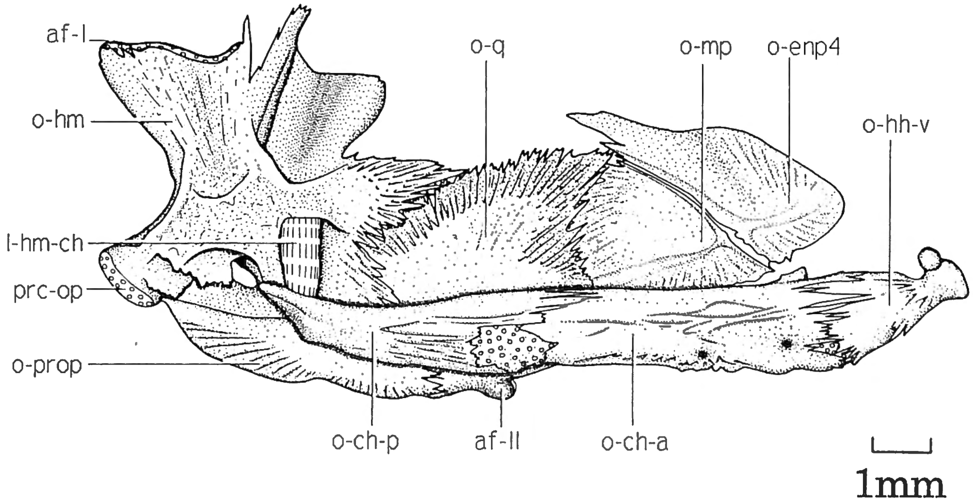

Fig. 4. — Medial view (left side) of suspensorium and hyoid of a juvenile *C. gariepinus* (SL = 136.20 mm) (small circles indicate cartilage).

## DISCUSSION

In juvenile specimens of *C. gariepinus* the ceratohyal is ligamentously connected to the lower jaw and to the interopercular bone. However in larval specimens (7.19 mm) only the former, the ligamentum angulo-ceratohyale, could be distinguished. The latter was not present yet, as well as the interopercular bone itself. The ligamentum angulo-ceratohyale plays an important role in the mouth opening mechanism, partially generated through the retraction of the ceratohyal (MULLER, 1987). This mechanism could eliminate the need for a passive recovery depression of the lower jaw through the cartilaginous connection between the lower jaw and the suspensorium, of its adduction by contraction of the mandibular adductor muscle as was observed in the 5.2 mm fry (SURLEMONT *et al.*, 1989). The ligament was found in most other siluroid fishes as well (SCHAEFER and LAUDER, 1986). In the 46.75 mm specimens the ligament between the ceratohyal and the interopercular bone could be distinguished, as well as the ligament between the interopercular bone and the lower jaw, the latter inserting laterally to the ligamentum angulo-ceratohyale on the lower jaw (Fig. 3A-B). As is the case for the latter, the ligamentum angulo-interoperculare as well plays an important role in the opening of the mouth. The ligament takes part in the four bar mechanism, consisting of the interopercular bone, the opercular bone, the suspensorium and the lower jaw (AERTS and VERRAES, 1984).

A shift can thus be observed in mouth opening mechanisms during ontogeny in *C. gariepinus*, going from a passive recovery depression of the cartilaginous connection between the lower jaw and the suspensorium, to a bar system which depresses the lower jaw by the depression of the hyoid bars, mediated by the sternohyoideus muscle and the ligamentum angulo-ceratohyale. Later in ontogeny a second bar system, the opercular four bar system (opercular bone, interopercular bone, suspensorium and lower jaw), may play a role in the mouth opening which is then coupled to the above mentioned hyoid bar system.

ANKER (1989) stated that the range of the movement of the hyoid increases with a longer interhyal. The loss of the interhyal and its functional replacement through a ligament must have an effect on the movements of the hyoid. Moreover, the rotation of an interhyal can be related to the abduction of the lower jaws and the abduction and the rotation of the hyoids (ANKER, 1974). The replacement of a skeletal element through a ligament can be functionally interesting when only tensile forces are applied on the ligament. When compressed, the ligament would of course crumple. In the case of *C. gariepinus* this implicates that the ventral excursion of the posterior part of the hyoid, during its forward and backward swinging, could be reduced, so that mainly an anterior-posterior translation is performed (Fig. 5).

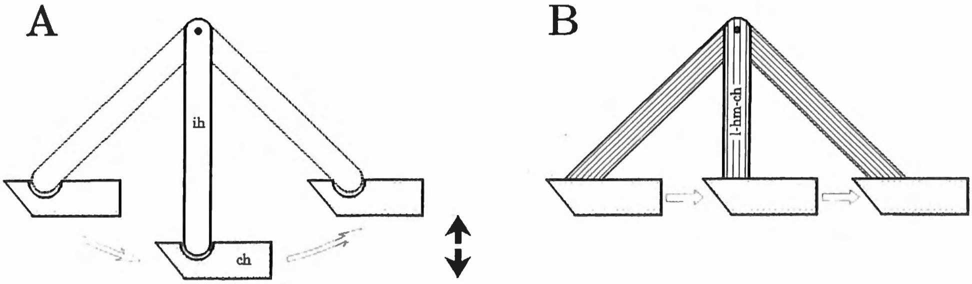

Fig. 5. — Scheme : A. rotation of the interhyal with a ventral excursion of the hyoid ; B. ligament replacing the interhyal with an anterior-posterior translation of the hyoid.

According to SURLEMONT *et al.* (1989) the functional significance of a cartilaginous interhyal, which is continuous with the dorsal and ventral part of the hyoid arch, is related to the mechanical properties of cartilage. Such a connection assists a passive recovery displacement of the depressed hyoid. The depression of the hyoid can be accomplished by the contraction of the sternohyoideus muscle. In the 7.19 mm fry this muscle was already functional, which was not the case in the

5.2 mm fry (SURLEMONT *et al.*, 1989). The hyoids can normally be elevated by the contraction of the hyoid protractor muscle. In the 7.19 mm fry this muscle although the inserts on the lower jaw, as well elevation can then be generated by the elasticity of the cartilage of the interhyal. Once the connection between the interhyal and the ceratohyal is lost, the muscle takes over.

As the interhyal is lacking in adult *C. gariepinus* it could be expected that this would affect the rotation possibilities, more specifically a depression, of the hyoid. Some morphological features supporting this hypothesis where observed :

1. The rostralmost tip of the hyoid is connected to the lower jaw through skin and connective tissue. The degree of depression of the hyoids partially depends on the length of that skin and connective tissue. Cross sections (Fig. 6A) show that the fold between the jaw and the hyoid is rather small, allowing only a small ventral excursion of the hyoid tip. As the depression of the lower jaw itself is restricted by a kind of lateral skin valve between the maxillary barbel and the lower jaw, this will not increase the depression possibility of the hyoid.

2. During depression of the hyoids their posterior tips are abducted. This results in the lateral rotation of the suspensorium (AERTS, 1991). A strong abduction of the suspensoria would require a strongly developed articulation with the skull. In most fish species, where the abduction of the suspensorium, related to the depression of the hyoid, is important, the suspensorium articulates rostrally with the skull through the palatine and the ethmoid part of the neurocranium and caudally through two consecutive ball and socket articulations between the hyomandibular bone and the skull (*e.g.* in Badidae (BARLOW *et al.*, 1968), in Percidae (OSSE, 1969), in Gasterosteidae (ANKER, 1974), in Serranidae (BENMOUNA *et al.*, 1984), in Gobiidae (MESTERMANN and ZANDER, 1984), in Pleuronectiformes (BRILL, 1988), in Cyprinidae (ARRATIA, 1992)). In *C. gariepinus*, and catfish in general, the suspensorium has lost its rostral articulation between the palatine and the skull. As already mentioned, the palatine has become an isolated structure which plays an important role in the movements of the maxillary barbel (ALEXANDER, 1965; GOSLINE, 1975). Also the ball-like articulations are lacking on the hyomandibular bone (Fig. 4). Instead, a hardly distinguishable cartilaginous articulation ridge can be observed. This morphological feature suggests that the rotation possibilities of the suspensorium are reduced. Another fact is that the height of the skull, which is dorso-ventrally flattened, is reflected in the height of the suspensorium. As a decrease in the height of the suspensorium will result in a decrease of the lateral displacement of the posterior tip of the hyoids, this displacement will be restricted in *C. gariepinus*. ALEXANDER (1970) stated that in fish with dorso-ventrally flattened heads the depression of the hyoids plays a relatively more important role for increasing the volume of the orobranchial cavity than in fish with lateral depressed heads, where the abduction of the suspensorium is far more important. Due to the dorso-ventrally flattened skull, a small depression of the hyoids will generate a relatively large increase in volume.

3. Muscular evidence for a reduced depression of the hyoids is present as well. The sternohyoideus muscle is responsible for the depression of the hyoid. In those teleosts where a large depression is needed, the sternohyoideus muscle is rather long

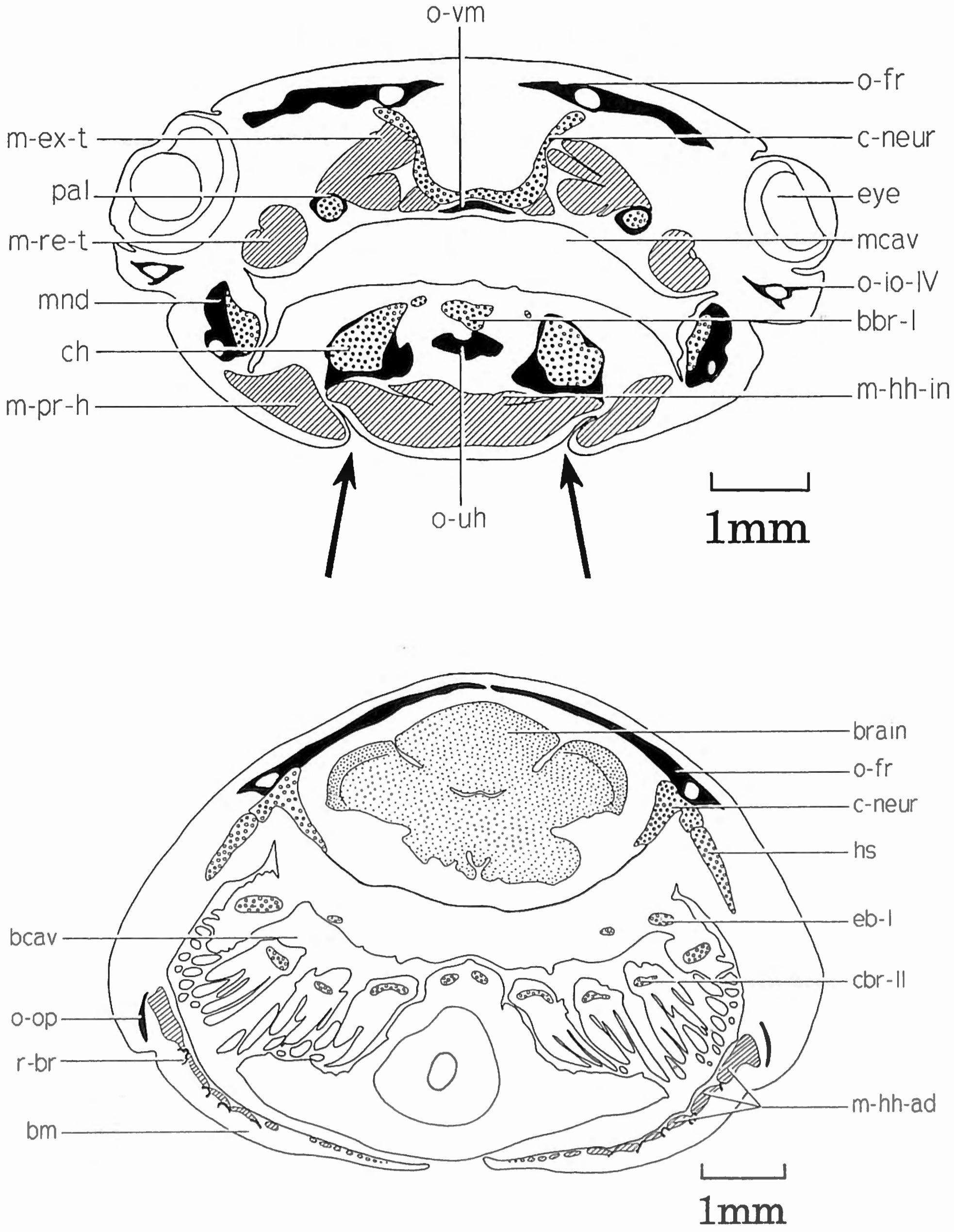

Fig. 6. — Cross section of juvenile *C. gariepinus* (SL = 46.75 mm) : A. at the level of the eyes showing the small fold between the hyoid and the lower jaw (arrows) ; B. at the level of the anterior part of the opercular bone showing the firm, unfolded branchiostegal membrane (small circles indicate cartilage, black areas indicate bone, hatched areas indicate muscles).

and slender (ANKER, 1974; 1989) (*e.g.* in gobies (ADRIAENS, *et al.*, 1993)). In *C. gariepinus* the muscle consists of three myomeres, separated by myocommata. The muscle is enlarged laterally, but is rather short in the anterior-posterior direction (Fig. 3B), which results in a larger contraction force but a reduced displacement of the rostral tip of the hyoid during contraction. What has to be taken in account is the cooperative function of the inferior obliquus muscle, which is a hypaxial body muscle inserting on the posterior border of the cleithral bone. The muscle plays an important role in the retraction of the pectoral girdle, and thus in the retraction of the hyoid through the sternohyoideus muscle (MULLER, 1987). However, cross sections show that in *C. gariepinus* the ventral part of the inferior obliquus muscle is rather small.

4. A large expansion of the orobranchial cavity would require an expanding branchiostegal membrane. This membrane can be extended from the folded situation because the skin is supported by a series of branchiostegal rays. In *C. gariepinus* this membrane is well developed and is rather firm (Fig. 3A). However, cross sections show that the thick branchiostegal membrane is not folded (Fig. 6B), which implicates a restricted expansion possibility of the membrane, and thus of the orobranchial cavity.

5. Aquarium observations of live material show that *C. gariepinus* exert a restricted depression of the hyoid during respiration phases. Also manipulation of fixed material suggests that little depression of the hyoid is possible.

Some additional arguments, related to specific lifestyle adaptations of *C. gariepinus*, contribute to the need of a restricted depression of the hyoid :

1. Like several benthic fishes, *C. gariepinus* has a strongly, dorso-ventrally flattened head. If, when resting on the bottom, the mouth floor should be depressed to a far extent during repiration, the stabilisation by the flattened head would be overridden.

2. A large depression of the hyoid for respiration is probably not required. Clariidae are able to perform aerial respiration by means of a suprabranchial organ, which is a modified, posterior part of the branchial arches (ALEXANDER, 1965; HELLIN et CHARDON, 1981). This structural adaptation enables the species to survive in tropical swamps and other ponds with a low level of oxygen. *Clarias* is also known to make rather important terrestrial excursions between two ponds, which is facilitated by aerial respiration (BABIKER, 1984). The hyoids do play an important role in the transport of the swallowed air. During aerial inspiration at the water surface, the elevated hyoids are depressed, resulting in the suction of the air. Then they are elevated through muscle contraction in order to press the air bubble from the orobranchial cavity into the suprabranchial cavity. A second elevation of the bars is noted during expiration when the bubble is transported from the suprabranchial cavity to the outside through the opercular slits (HELLIN et CHARDON, 1981; VANDEWALLE and CHARDON, 1991). In abnormal *C. gariepinus*, where the hyoid bars were immobilised, VANDEWALLE and CHARDON (1991) noted that these fish were still able to perform aquatic respiration due to only opercular

movements. So neither for terrestrial nor for aquatic ventilation large hyoid depression seems to be needed in *C. gariepinus*.

3. A sudden volume increase of the orobranchial cavity is necessary for suction feeding fishes. Movement of the hyoids is one of the mechanisms responsible for the production of a large negative pressure in the orobranchial cavity. Three possible movements are important : depression, retraction and elevation. The backward rotation in the plane of the suspensorium is also of great importance for a rapid jaw depression (AERTS, 1991). In generalised suction feeding teleosts, powerful suction is associated with a protrusion of the anterior parts of the mouth, *i.e.* the premaxillary and the maxillary bones (WESTNEAT and WAINWRIGHT, 1989). The premaxillary bone of such teleosts bears a notable ascending process where in biting species the arm is relatively shorter than in suction feeding species (WITTE, 1984). In *C. gariepinus* however, no ascending process can be observed, as the premaxillary bone is a plate-like bone bearing small conical teeth. The maxillary bone has completely lost its function as part of the feeding apparatus, as it has become part of the palatine-maxillary mechanism. This enables the extension and the retraction of the maxillary barbel, with the maxillary bone as a supporting base for the barbel (Fig. 3B) (GOSLINE, 1975). Additionally the vomeral bone also bears many small teeth (Fig. 3B). The lower jaw is equiped with a large battery of both narrow and broad conical teeth wich are usefull for grasping and holding prey. Aquarium observations show that *C. gariepinus* does not exert a powerful suction feeding but is more likely to swim to the given food.

## CONCLUSIONS

Early in ontogeny (SL = 7.19 mm) the interhyal is present in *C. gariepinus* as a cartilaginous structure, continuous with the hyosymplecticum and the hyoid. The depressor muscle of the hyoid, the sternohyoideus muscle, is already developed and functional, but its antagonist, the hyoid protractor muscle, is yet only partially developed. It does insert on the lower jaws but is partially functional. Its function is faciliated by the elastic properties of the cartilaginous interhyal. Later in ontogeny (SL = 46.75 mm), the interhyal becomes separated from the hyoid and is present in a reduced form. The hyoid protractor muscle is completely formed and functional here. The connection between the suspensorium and the hyoid is replaced by a stout ligamentous strap. In the adult situation (SL = 125.45 mm) the interhyal has been lost completely, where the only connection between the suspensorium and the hyoid is the ligamentum hyomandibulo-ceratohyale.

In this paper it is hypothesised that a reduction and loss of the interhyal will have effect on the mobility of the hyoid. Evidence is provided that the loss of the interhyal can result in a restricted depression of the hyoids. Morphological evidence supporting the hypothesis of a restricted depression is : (1) the presence of a small fold between the hyoid and the lower jaw, (2) a restricted abduction of the suspensorium, (3) a relatively short (but broad) sternohyoideus muscle and (4) a branchiostegal membrane which is only capable of a restricted expansion. The reduced depression of the hyoid probably has no important negative effect on gill ventilation because *C. gariepinus* is able to perform aerial respiration. No powerful suction feeding is performed either, as *C. gariepinus* has few protrusible mouth parts and many, small teeth on the lower jaw, the premaxillary and the vomeral bone.

## ABBREVIATIONS

af-I = articulation facet of the hyomandibular bone with the neurocranium
af-II = articulation facet of the quadrate bone with the mandibula
bbr-I = basibranchial I
bcav = branchial cavity
bm = branchiostegal membrane
cbr-II = ceratobranchial II
ch = ceratohyal
c-Meck = cartilago Meckeli
c-neur = cartilaginous neurocranium
eb-I = epibranchiale I
for = foramen truncus hyomandibularis
hembr = hemibranchia
hs = hyosymplecticum
ih = interhyal
l-an-ch = ligamentum angulo-ceratohyale
l-an-iop = ligamentum angulo-interoperculare
l-hm-ch = ligamentum hyomandibulo-ceratohyale
l-uh-hh = ligamentum urohyalo-hypohyale
m-A2 = A2 part of the mandibular adductor muscle
m-ad-ap = arcus palatini adductor muscle
m-ad-mnd = mandibular adductor muscle
mcav = mouth cavity
m-ex-t = tentacular extensor muscle
m-hh-ab = hyohyoid abductor muscles
m-hh-ad = hyohyoid adductor muscles
m-hh-in = inferior hyohyoid muscle
m-intm = intermandibular muscle
mnd = mandibula
mnd-b = mandibular barbel
m-pr-h = hyoid protractor muscle
m-pr-h-s = superficial part of the hyoid protractor muscle
m-re-t = tentacular retractor muscle
m-sh = sternohyoideus muscle
mx-b = maxillary barbel
o-ch-a = anterior ceratohyal bone
o-ch-p = posterior ceratohyal bone
o-cl = cleithral bone
o-den = dental bone
o-enp4 = sesamoid bone ’entopterygoid’ type 4
o-fr = frontal bone

o-hh-v = ventral hypohyal bone
o-hm = hyomandibular bone
o-io-IV = infraorbital bone IV
o-iop = interopercular bone
o-mp = metapterygoid bone
o-mx = maxillary bone
o-op = opercular bone
o-prmx = premaxillary bone
o-prop = preopercular bone
o-q = quadrate bone
o-uh = urohyal bone
o-vm = vomeral bone
pal = palatinum
pectf = pectoral fin
p-q = pars quadrata of the palatoquadratum
prc-op = processus opercularis
prc-pt = processus pterygoideus of the palatoquadratum
prc-ra = processus retroarticularis
r-br = radii branchiostegii

## ACKNOWLEDGEMENTS

We wish to thank Prof. Dr. F. Ollevier and Dr. F. Volckaert of the Laboratory of Ecology and Aquaculture (Catholic University of Leuven) and Mr. W. Fleure (Someren, the Netherlands) for providing the specimens of *C. gariepinus*, and D. Vandenbroeck and G. De Wever for making the serial sections of *C. gariepinus*. This study was supported by a grant of the Institute for Science and Technology (to D. Adriaens) and a FKFO-project (to W. Verraes).

## REFERENCES

Adriaens, D., D. Decleyre and W. Verraes (1993) — Morphology of the pectoral girdle in *Pomatoschistus lozanoi* De Buen, 1923 (Gobiidae), in relation to pectoral fin adduction. *Belg. J. Zool.*, **123(2)** : 135-157.

Aerts, P. (1991) — Hyoid morphology and movements relative to abducting forces during feeding in *Astatotilapia elegans* (Teleostei : Cichlidae). *J. Morph.*, **208** : 323-345.

Aerts, P. and W. Verraes (1984) — Theoretical analysis of a planar bar system in the teleostean skull : the use of mathematics in biomechanics. *Annls Soc. r. zool. Belg.*, **114(2)** : 273-290.

Alexander, R. McN. (1965) — Structure and function in catfish. *J. Zool. (Lond.)*, **148** : 88-152.

Alexander, R.Mc.N. (1970) — Mechanics of the feeding of various teleost fishes. *J. Zool. (Lond.)*, **162** : 145-156.

Anker, G.Ch. (1974) — Morphology and kinematics of the head of the stickleback, *Gasterosteus aculeatus*. *Trans. zool. Soc. Lond.*, **32** : 311-416.

ANKER, G.CH. (1989) — The morphology of joints and ligaments in the head of a generalised *Haplochromis* species : *H. elegans* TREWAVAS 1933 (Teleostei, Cichlidae). III. The hyoid and the branchiostegal apparatus, the branchial apparatus and the shoulder girdle apparatus. *Neth. J. Zool.*, **39(1-2)** : 1-40.

ARRATIA, G. (1990) — Development and diversity of the suspensorium of trichomycterids and comparison with loricarioids (Teleostei : Siluriformes). *J. Morph.*, **205** : 193-218.

ARRATIA, G. (1992) — Development and variation of the suspensorium of primitieve catfishes (Teleostei : Ostariophysi) and their phylogenetic relationships. *Bonner Zoologische Monographien*, **32** : 1-149.

BABIKER, M.M. (1984) — Aspects of the biology of the catfish *Clarias lazera* (CUV. and VAL.) related to its economic cultivation. *Hydrobiologia*, **110** : 295-304.

BARLOW, G.W., K.F. LIEM and W. WICKER (1968) — Badidae, a new fish family — behavioural, osteological, and developmental evidence. *J. Zool. (Lond.)*, **156** : 415-447.

BENMOUNA, H., I. TRABERT, P. VANDEWALLE et M. CHARDON (1984) — Comparaison morphologique du neurocrâne et du splanchnocrâne de *Serranus scriba* (LINNE 1758) et de *Serranus cabrilla* (LINNE 1758), (Pisces, Serranidae). *Cybium*, **8(2)** : 71-93.

BIRDSONG, R.S. (1975) — The osteology of *Microgobius signatus* POEY (Pisces : Gobiidae), with comments on other gobiid fishes. *Bull. Fla. State Mus. Biol. Sci.*, **19(3)** : 135-187.

BRILL, E.J. (1988) — Asymmetry and functional design — the pharyngeal jaw apparatus in soleoid flatfishes (Pisces : Pleuronectiformes). *Neth J. Zool.*, **37(3-4)** : 322-364.

DAGET, J. (1964) — Le crâne des Téléostéens. *Mém. Mus. Natl. Hist. Nat. (Paris)*, **série A 31(2)** : 163-341.

GOSLINE, W.A. (1975) — The palatine-maxillary mechanism in catfishes with comments on the evolution and zoogeography of modern siluroids. *Occ. Paps. Calif. Acad. Sci.*, **120** : 1-31.

HANKEN, J. and R. WASSERSUG (1981) — The visible skeleton. A new double-stain technique reveals the native of the « hard » tissues. *Functional Photography*, **16** : 22-26.

HELLIN, B. et M. CHARDON (1981) — Observations sur le trajet de l'air durant la respiration aérienne chez *Clarias lazera* CUVIER et VALENCIENNES, 1840. *Annls Soc. r. zool. Belg.*, **113(1)** : 97-106.

HOEDEMAN, J.J. (1960) — Studies on callichthyid fishes : 5. Development of the skull in *Callichthys* and *Hoplosternum* (2) (Pisces : Siluriformes). *Bull. aquat. Biol.*, **2(13)** : 21-36.

HOWES, G.J. and G.G. TEUGELS (1989) — Observations and homology of the pterygoid bones in *Corydoras paleatus* and some other catfishes. *J. Zool. (Lond.)*, **219** : 441-456.

KARRER, C. (1967) — Funktionell-anatomische und vergleichende Untersuchung des Schädels vom Hechtkärpfling, *Belonesox belizanus* KNER (Teleostei, Cyprinodontiformes, Poeciliidae). *Zool. Jb. (Anat.)*, **84** : 191-248.

MANGAKIS, N., E. BÖWE and ZD. PIKOVA-MÜLLEROVA (1964) Vorschlag für ein Erfahrungsgemäss guter und schnell arbeitends trichromverfahren. *Zentbl. allg. Path. path. Anat.*, **105(5-6)** : 289-292.

MESTERMANN, K.D. and C.D. ZANDER (1984) — Vergleichende osteologische Untersuchungen an *Pomatoschistus*-Arten (Gobioidei, Pisces). *Zool. Jb. (Anat.)*, **111** : 501-542.

MULLER, M. (1987) — Optimization principles applied to the mechanism of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *J. theor. Biol.*, **126** : 343-368.

NAWAR, G. (1954) — On the anatomy of *Clarias lazera* : I. Osteology. *J. Morph.,* **94** : 551-585.

OSSE, J.W.M. (1969) — Functional morphology of the head of the perch (*Perca fluviatilis* L.) : an electromyographic study. *Neth. J. Zool.,* **19(3)** : 289-392.

PIETSCH, T.W. and C.P. ZABETIAN (1990) — Osteology and interrelationships of the sand lances (Teleostei : Ammodytidae). *Copeia,* **1** : 78-100.

SCHAEFER, S.A. and G.V. LAUDER (1986) — Historical transformation of functional design : evolutionary morphology of feeding mechanisms in loricarioid catfishes. *Syst. Zool.,* **35(4)** : 489-508.

SURLEMONT, C., M. CHARDON and P. VANDEWALLE (1989) — Skeleton, muscles and movements of the head of a 5.2 mm fry of *Clarias gariepinus* (BURCHELL) (Pisces : Siluriformes). *Fortsch. Zool.,* **35** : 459-462, Eds. SPLECHTNA/HILGERS : Trends in Vertebrate Morphology, Gustav Fischer Verlag, Stuttgart, New York.

VANDEWALLE, P. (1975) — Contribution à l'étude anatomique et fonctionelle de la région céphalique de *Gobio gobio* (L.) (Pisces, Cyprinidae). 3. Les os, les muscles et les ligaments. *Forma et Functio,* **8** : 331-360.

VANDEWALLE, P. and M. CHARDON (1991) — A new hypothesis on the air flow in air breathing in *Clarias gariepinus* (Teleostei, Siluriformes). *Belg. J. Zool.,* **121(1)** : 73-80.

VANDEWALLE, P., P. SEILLER et M. CHARDON (1982) — Particularités anatomiques et fonctionnelles de la région céphalique de *Blennius pholis* L. (Pisces ; Blennidae). *Cybium,* **6(4)** : 73-94.

WESTNEAT, M.W. and P.C. WAINWRIGHT (1989) — Feeding mechanism of *Epibulus insidiator* (Labridae ; Teleostei) : evolution of a novel functional system. *J. Morph.,* **202** : 129-150.

WINTERBOTTOM, R. (1974) — A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phila.,* **125(12)** : 225-317.

WITTE, F. (1984) — Consistency and functional significance of morphological differences between wild-caught and domestic *Haplochromis squamipinnis* (Pisces, Cichlidae). *Neth J. Zool.,* **34(4)** : 596-612.