The Structures Associated With Catfish (Teleostei: Siluriformes) Mandibular Barbels: Origin, Anatomy, Function, Taxonomic Distribution, Nomenclature and Synonymy

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THE STRUCTURES ASSOCIATED WITH CATFISH (TELEOSTEI: SILURIFORMES) MANDIBULAR BARBELS: ORIGIN, ANATOMY, FUNCTION, TAXONOMIC DISTRIBUTION, NOMENCLATURE AND SYNONYMY

by

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ABSTRACT

The morphological features of the ventral region of the head of 16 siluriform species were studied in detail and compared with those described in the literature as the foundation for a general survey of the origin, anatomy, function, taxonomic distribution, nomenclature and synonymy of the structures associated with catfish mandibular barbels. The restricted taxonomic distribution of some of these structures indicates that the study of these structures could reveal useful data to infer the phylogenetic relationships between different catfish groups.

KEY WORDS: catfish, comparative anatomy, functional morphology, mandibular barbels, Siluriformes.

INTRODUCTION

The catfish, with their 2584 species, represent about 32% of all freshwater fishes and are "one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade" (TEUGELS, 1996). They owe their name to the presence of barbels surrounding the snout region. These barbels are supported by a central rod, comprising a dense network of elastin, with or without true cartilage (GHIOT & BOUCHEZ, 1980; BENJAMIN, 1990), and their skin is covered with mucus cells and taste buds (WRIGHT, 1884; HERRICK, 1903; LANDACRE, 1910; KAMRIN & SINGER, 1953, 1955; DESGRANGES, 1972; FINGER, 1976, 1978; GROVER-JOHNSON & FARBMAN, 1976). Catfish are mostly nocturnal and inhabit mainly muddy waters (ALEXANDER, 1965). The barbels are used in searching food and avoiding obstacles.

Catfish have three types of barbels: nasal barbels, maxillary barbels and mandibular barbels. Despite their morphological, physiological, ethological, ecological and even taxonomic (GHIOT *et al.*, 1984) importance, the mandibular barbels and associated structures were only studied by a few authors (MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968; GHIOT, 1978; HOWES, 1983; GHIOT *et al.*, 1984). Moreover, most of these authors do not make any reflection on the functional and adaptive significance of the structures studied, and do not compare their results with those available in the literature, using, for example, different names for homologous structures and the same names for different structures.

The aim of this work is to study in detail the structures associated with the mandibular barbels of some catfishes and to compare them with those described in the literature, in order to give a general survey of the ontogenetic origin, morphological diversity, function, taxonomic distribution and synonymy of all the known structures associated with catfish mandibular barbels, and to propose a coherent nomenclature for these structures, paving the way, therefore, for future morphological, functional, ecological, ethological, phylogenetic and taxonomic works dedicated to these fishes.

MATERIAL AND METHODS

The fishes studied are from the private collection of the laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC) and from the Université Nationale du Bénin (UNB). Anatomical descriptions are made after dissection of alcohol fixed or trypsin-cleared and alizarine-stained (following TAYLOR & VAN DIKE'S 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The fresh (fre) or alcohol fixed (alc) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected follows:

Amphilius brevis (Amphiliidae: Amphiliinae): MRAC 89-043-P-403, 1 (alc); MRAC 89-043-P-2298, 1 (alc); MRAC 89-043-P-2333, 1 (alc); MRAC 89-043-P-2372, 1 (alc). *Amphilius jacksoni* (Amphiliidae: Amphiliinae): LFEM uncatalogued, 1 (alc). *Amarginops cranchii* (Claroteidae): LFEM uncatalogued, 1 (alc). *Bagrus bayad* (Bagridae): LFEM uncatalogued 1 (alc); LFEM uncatalogued, 1 (fre). *Bagrus docmac* (Bagridae): MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (alc). *Clarias batrachus* (Clariidae): MRAC 94-020-P-1, 2 (alc). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc); LFEM uncatalogued, 2 (alc). *Clarias meladerma* (Clariidae): MRAC 92-100-P-1, 1 (alc). *Chrysichthys auratus* (Claroteidae): UNB uncatalogued, 3 (alc); UNB uncatalogued, 3 (fre).

Chrysichthys nigrodigitatus (Claroteidae): UNB uncatalogued, 2 (alc); UNB uncatalogued, 4 (fre). *Diplomystes chilensis* (Diplomystidae): LFEM uncatalogued, 1 (alc). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Phractura brevicauda* (Amphiliidae: Doumeinae): MRAC 90-057-P-5145, 1 (alc); MRAC 92-125-P-362, 1 (alc); MRAC 92-125-P-386, 1 (alc). *Phractura intermedia* (Amphiliidae: Doumeinae): MRAC 73-016-P-5888, 1 (alc). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (alc).

RESULTS

The structures associated with the mandibular barbels of five catfish species representing, respectively, the families Bagridae (*Bagrus docmac*), Clariidae (*Clarias gariepinus*), Claroteidae (*Chrysichthys nigrodigitatus*) and the subfamilies Amphiliinae (*Amphilius brevis*) and Doumeinae (*Phractura brevicauda*) of the family Amphiliidae, are described in detail. The two subfamilies of the family Amphiliidae do not constitute a monophyletic group (HE, 1997; DIOGO & CHARDON, in preparation) and should be separated in two different families (remain the amphiliins in the family Amphiliidae and the doumeins are transferred to the new catfish family Doumeidae (DIOGO & CHARDON, in preparation)). Significative differences between the structures present in the five species and those present in the other studied species belonging to the same (sub)families will be mentioned. The choice of the nomenclature followed in the descriptions will be explained in the discussion. In order to simplify the description *Chrysichthys nigrodigitatus* is taken as the example with which the other four described species will be compared.

Chrysichthys nigrodigitatus (fig. 1)

This species presents two pairs of mandibular barbels: the inner one (internal mandibular barbel) and the outer one (external mandibular barbel), situated, in the antero-ventral and antero-ventro-lateral regions of the head (fig. 1a), respectively. Each barbel is associated with one cartilage, which consists of two parts. The first one, the "supporting part", is situated between the base of the barbel and the dentary, to which it is firmly attached by a large number of fibres (fig. 1a, b). The other part, the "moving part", is longer than the first one and situated posteriorly to it (fig. 1a, b). It is on this part that the muscles for the movement of the mandibular barbels insert. These muscles are:

Musculus protractor hyoidei: This muscle joins the hyoid bar to the mandible, and is divided into pars dorsalis, pars lateralis and pars ventralis (fig. 1a). This latter part, which runs from the anterior ceratohyal to a

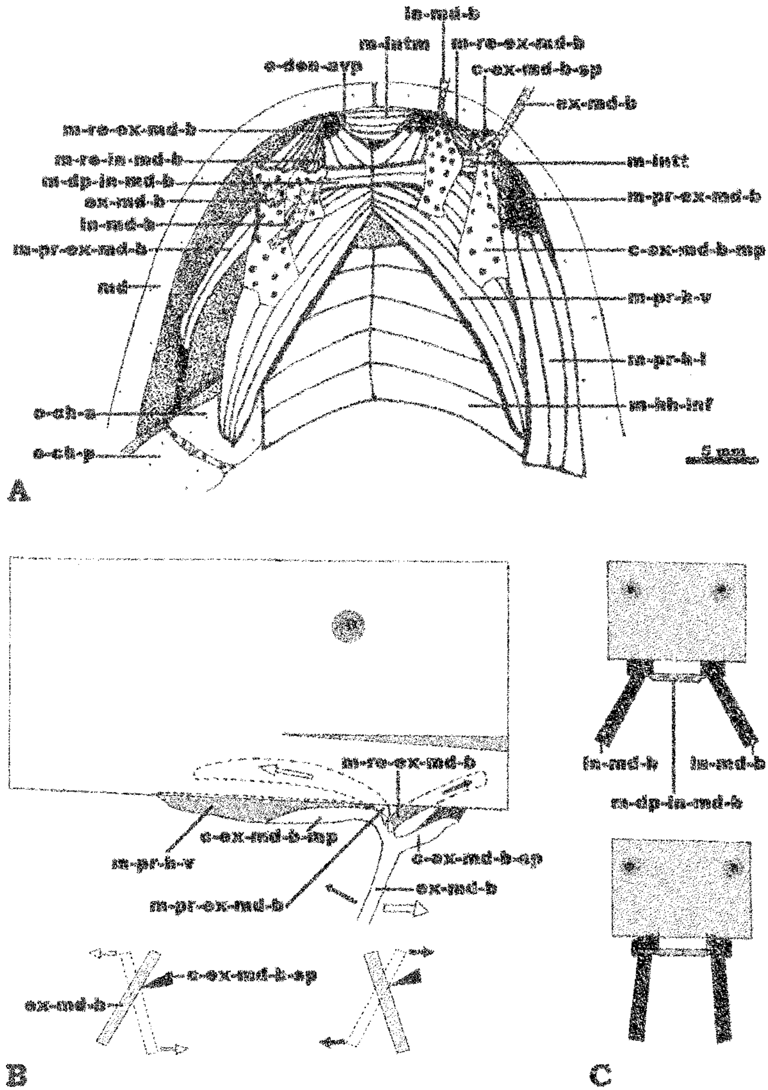

Fig. 1. *Chrysichthys nigrodigitatus*. A: Ventral view of the head. Only the proximal parts of the mandibular barbels are illustrated. On the left side the pars dorsalis and lateralis of the protractor hyoidei and the hyohyoideus inferior were removed and the anterior parts of the cartilages associated with the mandibular barbels were pulled backwards. B: Schemes illustrating our hypothesis concerning the retraction (black arrows) and the protraction (white arrows) of the external mandibular barbels (lateral view) (for explanations, see points II-a and IV-a of the discussion). C: Schemes illustrating our hypothesis concerning the depression of the internal mandibular barbels (frontal view) (for explanations, see point VI-a of the discussion).

medial aponeurosis, lodges the moving parts of the cartilages associated with the mandibular barbels (fig. 1a, b).

Musculus retractor externi mandibularis tentaculi: A small muscle that runs from the dentary (near the symphysis) to the moving part of the cartilage of the external mandibular barbel (fig. 1a, b).

Musculus retractor interni mandibularis tentaculi: A small muscle joining the dentary (near the symphysis) to the moving part of the cartilage of the internal mandibular barbel (fig. 1a).

Musculus protractor externi mandibularis tentaculi: A long muscle that originates on the postero-dorso-lateral face of the anterior ceratohyal and inserts on the moving part of the cartilage of the external mandibular barbel (fig. 1a, b).

Musculus depressor interni mandibularis tentaculi: A small muscle extending between the ventro-medial face of the moving part of the cartilage of the internal mandibular barbel and a medial aponeurosis (fig. 1a, c).

Musculus intertentacularis: A very small muscle situated between the ventro-lateral and the ventro-medial faces of the moving parts of, the internal and external mandibular barbels (fig. 1a), respectively.

Phractura brevicauda (fig. 2)

The most significative differences between the structures associated with the mandibular barbels of this species and those of *Chrysichthys nigrodigitatus* are: 1) The moving parts of the cartilages of the mandibular barbels are thinner in *Phractura*. 2) In *Phractura* the pars ventralis of the protractor hyoidei is divided in two bundles: the lateral one is attached to the moving part of the cartilage of the external mandibular barbel and the inner one inserts on the moving part of the cartilage associated with the internal mandibular barbel. 3) The protractor externi mandibularis tentaculi is originated on both the anterior and posterior ceratohyals.

Bagrus docmac (fig. 3a, b)

The principal differences with *Chrysichthys nigrodigitatus* are: 1) The muscles depressor interni mandibularis tentaculi and intertentacularis are absent (fig. 3a). 2) The supporting parts of the cartilages of the internal and external mandibular barbels are associated (fig. 3a). 3) The retractor externi mandibularis tentaculi is bifurcated anteriorly, and the two branches are separated by both the protractor hyoidei pars dorsalis and the intermandibularis (fig. 3a, b). Such a bifurcation was not observed in the other bagrid species studied (*Hemibagrus wycki*, *Mystus gulio* and *Pseudomystus bicolor*). 4) The moving parts of the cartilages of the mandibular barbels are smaller (fig. 3a) than those of *Chrysichthys*.

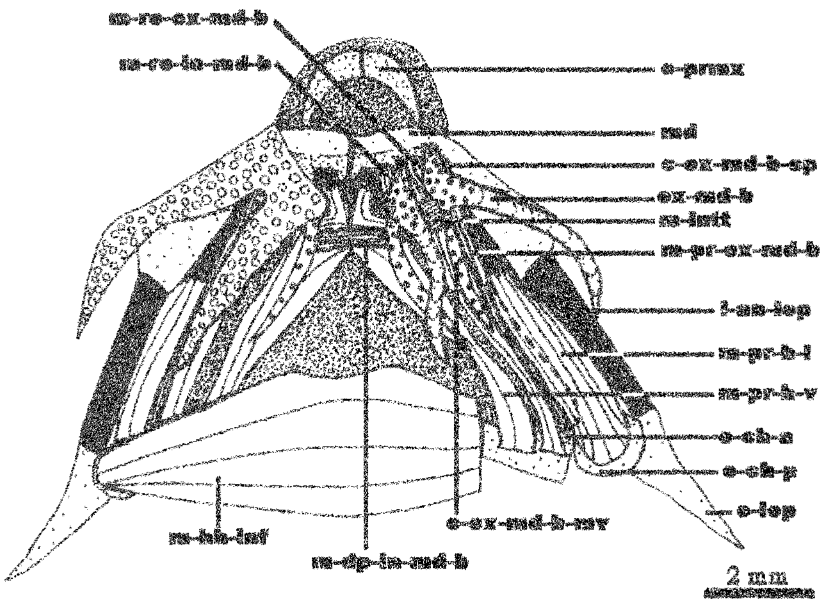

Fig. 2. Ventral view of the head of *Phractura brevicauda*. On the right side the papillae associated to the mandibular barbels were removed.

Amphilius brevis (fig. 4a)

The most significative differences with *Chrysichthys nigrodigitatus* are: 1) The external mandibular barbels are not situated in the ventro-lateral, but in the lateral face of the head. 2) The retractor externi mandibularis tentaculi is absent. 3) The well-developed depressor interni mandibularis tentaculi is inserted not only on the medial aponeurosis, but also on the dentary. 4) The protractor externi mandibularis tentaculi originates on the anterior and posterior ceratohyals. 5) *Amphilius brevis* has a small muscle — "muscle 3 of the mandibular barbels" — that runs from the lateral surface of the dentary to the external mandibular barbel. 6) The moving parts of the cartilages associated with the mandibular barbels are smaller than those of *Chrysichthys*.

Clarias gariepinus (fig. 5a)

The principal differences compared to *Chrysichthys nigrodigitatus* are: 1) The intertentacularis muscle is absent. 2) The retractor muscles of both the external and internal mandibular barbels are inserted medially on a cartilaginous complex, and not on the dentary. 3) *Clarias* possesses a small muscle — "muscle 2 of the mandibular barbels" — that originates

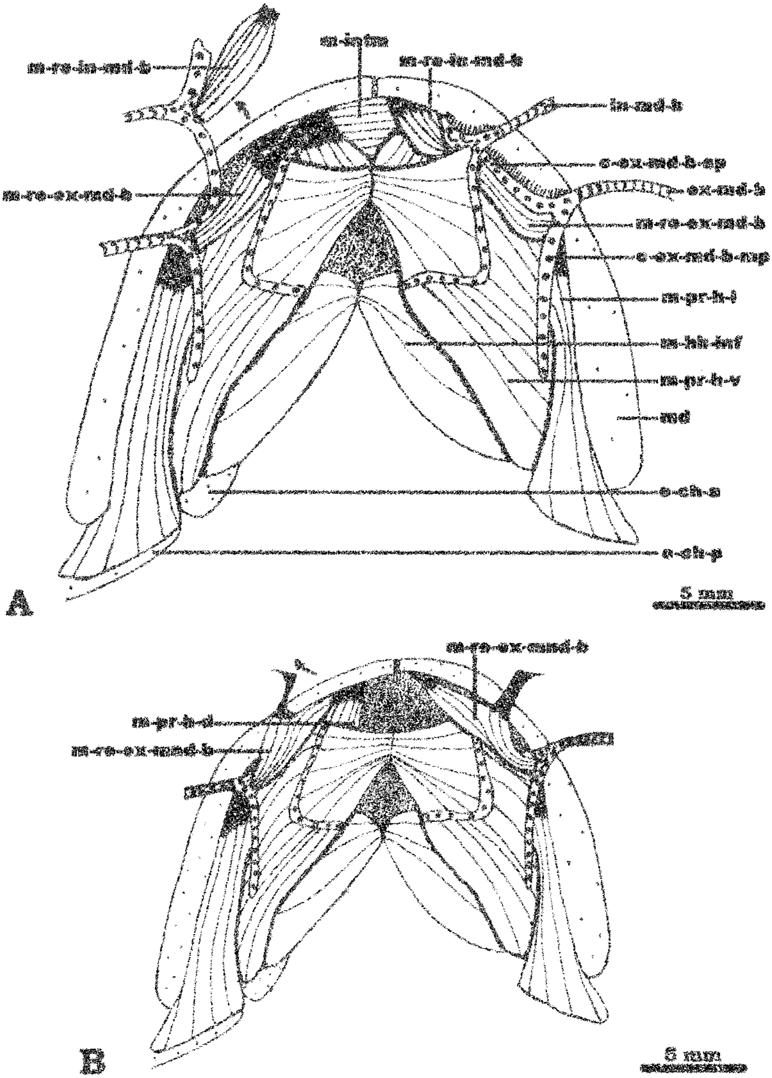

Fig. 3. Ventral view of the head of *Bagrus docmac*. Only the proximal parts of the mandibular barbels are illustrated. A: In the left side the external mandibular barbel, its retractor muscle and the supporting part of the cartilage associated to it were pulled laterally. B: The internal mandibular barbels, their retractor muscles and the intermandibularis were removed. On the right side, the pars dorsalis of the protractor hyoidei was removed.

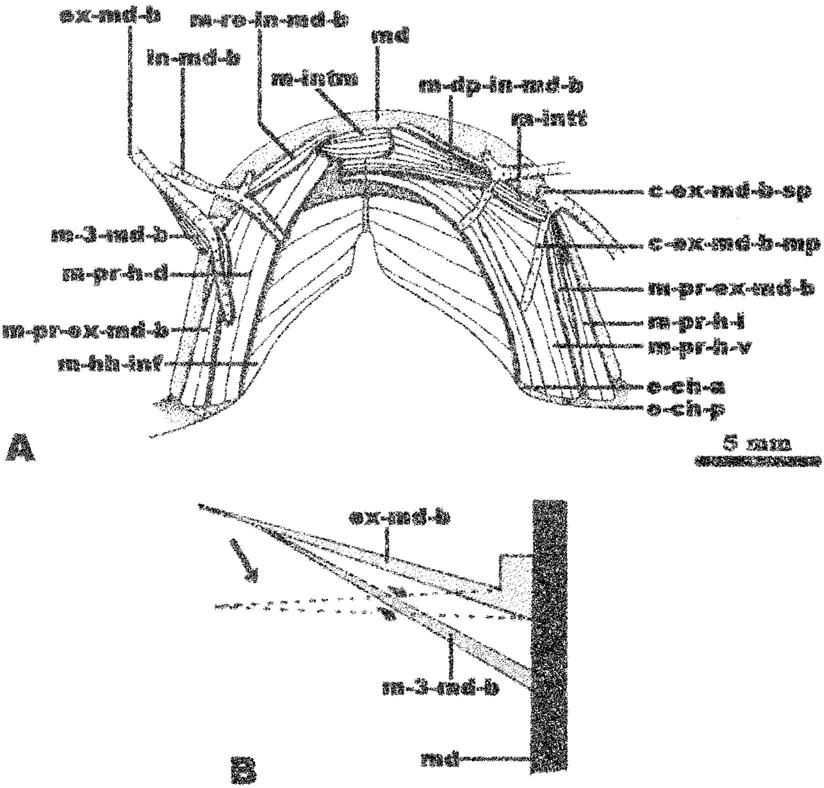

Fig. 4. *Amphilius brevis*. A: Ventral view of the head. Only the proximal parts of the mandibular barbels are illustrated. On the left side the pars ventralis and lateralis of the protractor hyoidei, the intertentacularis and the depressor interni mandibularis tentaculi were removed. B: Scheme illustrating our hypothesis concerning the function of the muscle 3 of the mandibular barbels (for explanations, see point X-a of the discussion).

on the dentary and inserts on the cartilaginous complex. 4) In *Clarias*, both the cartilages associated with the internal mandibular barbels are connected by means of a cartilaginous complex, which is linked to that of the external mandibular barbels.

DISCUSSION

In this chapter the origin, function, taxonomic distribution, nomenclature and synonymy of each of the known structures associated with the mandibular barbels of catfish are discussed.

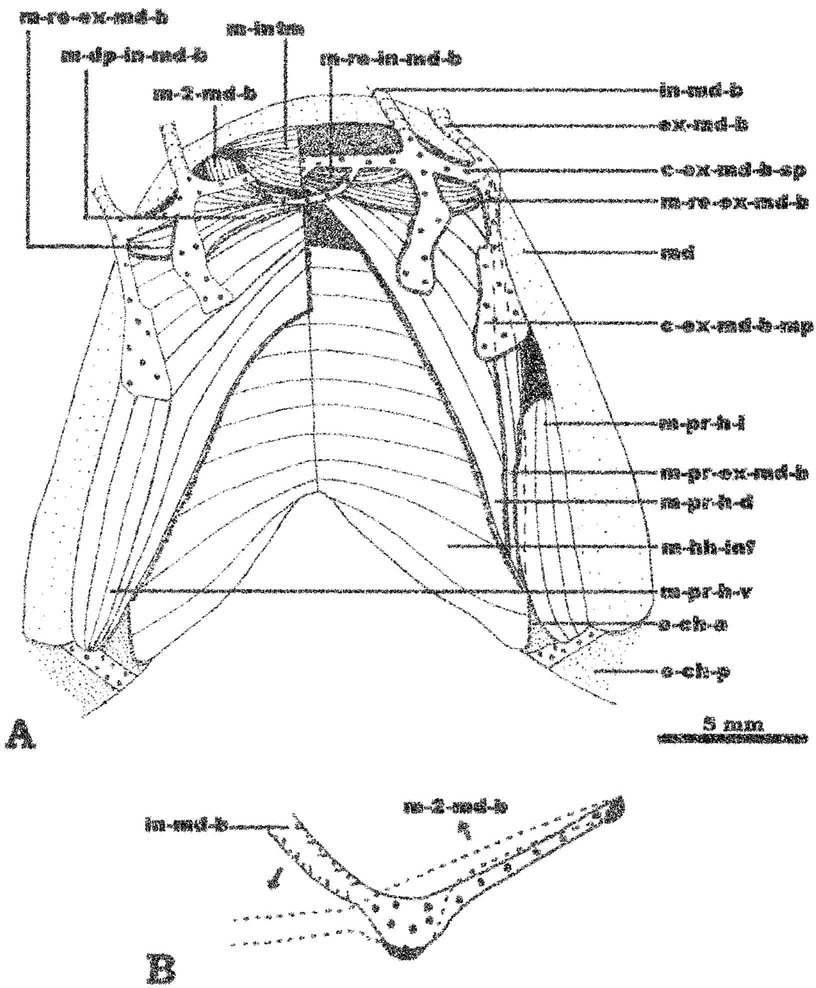

Fig. 5. *Clarias gariepinus*. A: Ventral view of the head. Only the proximal parts of the mandibular barbels are illustrated. In the right side the pars ventralis of the protractor hyoidei, the intermandibularis, the muscle 2 of the mandibular barbels and the depressor interni mandibularis tentaculi were removed. B: Scheme illustrating our hypothesis concerning the function of the muscle 2 of the mandibular barbels (for explanations, see point IX-a of the discussion).

I-Supporting and moving parts of the cartilages associated with the mandibular barbels

I-a-Function: The cartilages associated with the mandibular barbels are normally considered as structures embedded within the protractor hyoidei

(TAKAHASI, 1925; MUNSHI, 1960; ALEXANDER, 1965; SINGH, 1967; SINGH & MUNSHI, 1968; WINTERBOTTOM, 1974; GHIOT, 1978; GHIOT *et al.*, 1984; MO, 1991; ADRIAENS & VERRAES, 1997). This led some authors, as, for example, ALEXANDER (1965), to believe that "though slips of the geniohyoideus (protractor hyoidei) muscle attach to their (the mandibular barbels) bases, they are not very mobile". This consideration is contestable. In fact, the mandibular barbels of specimens of the genera *Chrysichthys*, *Synodontis* and *Clarias*, for example, show a mobility superior to that of the maxillary barbels (personal observation). The explanation seems to be that the cartilages associated with the mandibular barbels do not only support them, but also promote their movements. In fact, these cartilages present two distinct parts. The anterior one attaches anteriorly on the dentary by means of a large number of thin and short fibres (figs 1a, b, 2, 3a, 4a, 5a). It is precisely the connection between this part and the dentary bone that probably explains the large mobility of the mandibular barbels, since it creates a solid exterior point d'appui or 'articulatory system' (fig. 2b) somewhat similar to the 'rocking palatine-maxillary system' (responsible for the movement of the maxillary barbels) present in some catfishes (Gosline, 1975). So, if the dorsal extremity of the mandibular barbels is pulled posteriorly, their ventral extremity, by means of the solid central point d'appui conferred by the supporting part of their cartilages, will be displaced anteriorly (fig. 1b: white arrows); if their dorsal extremity is pulled anteriorly, their ventral extremity will be displaced posteriorly (fig. 1b: black arrows). The other part of the cartilages associated to the mandibular barbels, situated posteriorly to the first one, presents a great mobility. The muscles related to the movements of the mandibular barbels attach (figs 1a, b, 2, 3a, b, 4a, 5a) to it and by the contraction of these muscles, the dorsal extremities of these barbels are displaced (fig. 1b).

I-b-Nomenclature: According to their function (see above), the anterior part of the cartilages associated with the internal and to the external mandibular barbels are called "supporting part of the cartilage associated with the internal mandibular barbel" and "supporting part of the cartilage associated with the external mandibular barbel", respectively. In the same way, the posterior parts of these cartilages are called "moving part of the cartilage associated with the internal mandibular barbel" and "moving part of the cartilage associated with the external mandibular barbel", respectively.

I-c-Taxonomic distribution: The cartilages associated with the mandibular barbels are present in all the other species studied — except *Diplomystes chilensis* (Diplomystidae), which does not possess mandibular barbels, — and also in all those species described in the few works where the structures associated to these barbels are analysed (superficially or with some detail) (TAKAHASI, 1925; MUNSHI, 1960; ALEXANDER, 1965; SINGH, 1967; SINGH & MUNSHI, 1968; GHIOT, 1976, 1978; HOWES, 1983; GHIOT *et al.*, 1984; MO, 1991; BORNBUSCH, 1995; ADRIAENS & VERRAES, 1997). So, it seems probable that such cartilages are present in most (if not all) catfishes that possess mandibular barbels. However, the subdivision of these cartilages in a moving and a supporting part, is more complicated, since, with the exception of this work, the configuration of these cartilages was only studied in detail by GHIOT (1978), HOWES (1983), GHIOT *et al.* (1984), BORNBUSCH (1995) and ADRIAENS & VERRAES (1997). Nevertheless, our observations, together with our interpretations of the descriptions given by these authors, pointed out that this subdivision is present in at least a large number of catfishes.

I-d-Origin: The cartilages associated with catfish mandibular barbels are a *de novo* formation, that is not homologous or even similar to any other structure present in other teleosteans, fishes or animals.

I-e-Synonymy: All the authors have previously considered each cartilage associated with the mandibular barbels as a single structure, without any morphological or functional subdivision, they have called it:
Base des barbillons mandibulaires (GHIOT, 1976; GHIOT *et al.*, 1984), Base of the mental (or mandibular) barbels (TAKAHASI, 1925; MUNSHI, 1960; ALEXANDER, 1965; ADRIAENS & VERRAES, 1997), Cartilaginous basal frame of the mental barbels (MO, 1991), Cartilaginous plate of the mandibular barbels (HOWES, 1983; Bornbush, 1995) [The "cartilaginous plate carrying the barbels" of GHIOT (1978) is not homologous with the cartilages associated with the mandibular barbels of this work (see point VIII)], Cartilaginous rod present at the base of the mandibular barbels (SINGH, 1967; SINGH & MUNSHI, 1968).

II-Musculus retractor externi mandibularis tentaculi

II-a-Function: As explained above, the retraction of the external mandibular barbel is realised by the anterior displacement of the moving part of the cartilage associated with it (fig. 1b: black arrows). This displacement is performed by the contraction of the muscle retractor externi mandibularis tentaculi (fig. 1b: black arrows). This interpretation contradicts those of MUNSHI (1960), SINGH (1967), SINGH & MUNSHI (1968) and GHIOT (1978), who consider this muscle (for the synonymy, see point II-e) to be the protractor, and not the retractor, of the external mandibular barbel. Our interpretation also contradicts that of GHIOT *et al.* (1984), who suggested that the contraction of this muscle provokes a latero-dorsal movement of this barbel. These authors, however, do not give a true functional explanation, but seem to trust mainly on their intuition: "It is difficult to determine the exact function of those five muscles (associated with the mandibular barbels) because the elasticity of the cartilaginous plate carrying the barbels and that of the barbels themselves cannot be appreciated", writes, for example, GHIOT (1978).

We present here three arguments to support our hypothesis. First, from a theoretical biomechanical point of view, based on the anatomy of both the retractor externi mandibularis tentaculi and the cartilage associated to the external mandibular barbel, it seems likely that the retraction of this muscle will provoke the retraction of the external mandibular barbel (see, for example, figs 1b, 3a, 5a). Second, we had the opportunity to study the structures associated with the mandibular barbels of some large fresh specimens of the species *Chrysichthys nigrodigitatus* (about 35 cm of body length) and *Clarias gariepinus* (about 45 cm of body length). When the retractor externi mandibularis tentaculi was artificially stimulated, the ventral extremity of the external mandibular barbel was displaced posteriorly, that is, this barbel was retracted. Finally, as was described in the results section, in *Amphilius brevis* the external mandibular barbels are situated on the lateral, and not on the ventro-lateral surface of the head (fig. 4a). In this species, the retractor externi mandibularis tentaculi probably does not have the same configuration as in the other four species described (fig. 4a, compare with figs 1a, b, 2, 3a, b, 5a). However, *Amphilius* possesses a muscle (muscle 3 of the mandibular barbels: fig. 4a) that is not present in any of the other four species and whose contraction is clearly related to the retraction of the external mandibular barbel (see point X). This seems to indicate that this muscle substitutes functionally the absent retractor externi mandibularis tentaculi, and is related, to the retraction of the external mandibular barbel. It should be noted that despite these arguments, our hypothesis concerning the function of this muscle, as well as of the other muscles discussed in this paper, can only be convincingly demonstrated by electromyography, or, since the very small size of these muscles makes the application of this technique difficults, by electric stimulation.

II-b-Nomenclature: The attribution of the name "musculus retractor externi mandibularis tentaculi" is based to the hypothesized function of this muscle (see point II.a).

II-c-Taxonomic distribution: Most catfish in which the muscles associated with the mandibular barbels were studied with some detail (either by us, or by MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968; GHIOT, 1978; HOWES, 1983; GHIOT *et al.*, 1984) possess a retractor externi mandibularis tentaculi (for the synonymy, see point II-e). There are only three genera where this muscle is absent, namely *Amphilius* (Amphiliidae), *Wallago* (Siluridae) and *Hypophthalmus* (Hypophthalmidae).

The reason why this muscle is absent in *Amphilius* was already explained. The genus *Wallago* does not possess a retractor externi mandibularis tentaculi or any other muscle associated with the mandibular barbels (SINGH, 1967). This could be very likely explained by the fact that silurids (and thus *Wallago*) do not have a strict benthic life-style. They normally reside at some distance from the bottom and their mandibular barbels are not used for substrate exploration (personal observation). The mandibular barbels of these fishes are very small, resembling vestigial structures, and their movements seem to be simply provoked by the brusque movements of the head (personal observation). *Hypophthalmus*, the single genus of the family Hypophthalmidae, does not possess retractores externi mandibularis tentaculi or retractores interni mandibularis tentaculi (HOWES, 1983). However, in this genus, the muscle intermandibularis is separated medially into two bundles, each of them "attached to its respective cartilaginous plate which serves to support the barbel" (HOWES, 1983). These two segments present a configuration similar to that of the retractors of the mandibular barbels of most other catfishes (see HOWES, 1983: fig. 11).

II-d-Origin: SINGH (1967) considers the retractor externi mandibularis tentaculi, as well as the retractor interni mandibularis tentaculi (for the synonymy, see points II-e and III-e) to be derived from the intermandibularis muscle. However, GHIOT (1978) and GHIOT *et al*. (1984) regard these muscles (for the synonymy, see points II-e and III-e) as a differentiation of the muscle protractor hyoidei. This question is very complicated. On the one hand, it seems that these muscles could be derived from the protractor hyoidei, since their shape and the orientation of their fibres are more similar to those of the anterior part of this muscle than to those of intermandibularis muscle (figs 1a, 2, 3a, b, 4a, 5a). On the other hand, there are two arguments that support SINGH's hypothesis. As mentioned above, *Hypophthalmus edentatus* does not possess a retractor externi mandibularis tentaculi or a retractor interni mandibularis tentaculi, but the two bundles of its intermandibularis muscle have a configuration quite similar to that of these muscles. One could, interpret these segments as "undifferentiated" retractors of the mandibular barbels, which supports SINGH's hypothesis. Moreover, this hypothesis also agrees with theoretical idea that decoupling of a muscle normally results in a muscle or bundle whose function remains, at least in the first steps of the differentiation, similar to that of the original muscle (ALEXANDER, 1965). For example, differentiation of the adductor mandibulae (which is related to mouth closure) has resulted in a retractor tentaculi muscle, whose function (the retraction of the maxillary barbels) is, at least in the less specialised catfish, associated to mouth closure (GOSLINE, 1975; Diogo & Chardon, in preparation). As the retraction of the mandibular barbels is usually also related to mouth closure (personal observation), it seems likely, that the retractors of these barbels are derived from the intermandibularis muscle, which is associated to mouth closure (see for example, TAKAHASI, 1925), and not from the protractor hyoidei, which is usually related to mouth opening (see, for example, WINTERBOTTOM, 1974).

II-e-Synonymy: Muscle 2 des barbillons mandibulaires (GHIOT *et al*., 1984), Muscle 2 of the mandibular barbels (GHIOT, 1978), Protractor tentaculi of the external (or first) mental (or mandibular) barbel (MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968). Only some muscles to which these authors give this name do correspond to the muscle retractor externi mandibularis tentaculi in the present work. As pointed out by ADRIAENS & VERRAES (1997), they sometimes confused "some bundles of fibres of the protractor hyoidei with independent muscles associated with the mandibular barbels (some of them being called protractor tentaculi)".

III-Musculus retractor interni mandibularis tentaculi

III-a-Function: The relationship between this muscle and the moving part of the cartilage of the internal mandibular barbel is similar to the relationship between the retractor externi mandibularis tentaculi and the moving part of the cartilage of the external mandibular barbel (figs 1a, 2, 3a, 5a). Its contraction will cause the retraction of the internal mandibular barbel. This hypothesis, supported by artificial manipulation of some large fresh specimens of *Chrysichthys nigrodigitatus* and *Clarias gariepinus* (see point II-a), contradicts those of MUNSHI (1960), SINGH (1967), SINGH & MUNSHI (1968) and GHIOT (1978), who believe that this muscle (for the synonymy, see point III-e) is related to protraction, and not retraction, of the internal mandibular barbels. GHIOT *et al*. (1984), suggested that its contraction will provoke a latero-dorsal displacement of these barbels. However, as mentioned above, these authors do not give any explanation to support their hypotheses (see point II-a).

III-b-Nomenclature: The attribution of the name "musculus retractor interni mandibularis tentaculi" to this muscle is based on its assumed function (see point III-a).

III-c-Taxonomic distribution: The taxonomic distribution of this muscle is similar to that of the retractor externi mandibularis tentaculi (see point II-c). In the genus *Amphilius*, only the first one is present (fig. 4a).

III-d-Origin: See point II-d.

III-e-Synonymy: Muscle 3 des barbillons mandibulaires (GHIOT *et al*., 1984), Muscle 3 of the mandibular barbels (GHIOT, 1978), Protractor tentaculi of the internal (or second) mental (or mandibular) barbel (MUNSHI,

1960; SINGH, 1967; SINGH & MUNSHI, 1968). Only some muscles to which these authors give this name do correspond to the muscle retractor interni mandibularis tentaculi described in the present work. As explained before, they confused some fibres of the protractor hyoidei with independent muscles associated with the mandibular barbels (see point II-e). Moreover, SINGH (1967: fig. 7), in his description of the muscles associated with the mandibular barbels of *Clarias batrachus*, uses this name to describe a muscle that clearly corresponds to the "muscle 2 of the mandibular barbels" (fig. 5a) of this work (see point IX).

IV-Musculus protractor externi mandibularis tentaculi

IV-a-Function: This muscle is the antagonist of the retractor externi mandibularis tentaculi: it pulls the moving part of the cartilage associated with the external mandibular barbel posteriorly, pushing this barbel forward (fig. 1b: white arrows). MUNSHI (1960), SINGH (1967) and SINGH & MUNSHI (1968), without giving any explanation, consider this muscle (for the synonymy, see point IV-e) to be a retractor, and not a protractor of the external mandibular barbel. However, a detailed analysis of its configuration, seems to indicate that its contraction causes protraction of the barbel (fig. 1b: white arrows). This hypothesis was supported by the manipulation of some large fresh specimens of the species *Chrysichthys nigrodigitatus* and *Clarias gariepinus*. Moreover, it agrees with the theoretical principle that decoupling of a muscle normally results in a muscle whose function is somewhat similar to the function of the original muscle (ALEXANDER, 1965; see also II-d). The protractor externi mandibularis tentaculi is clearly derived from the protractor hyoidei (see point IV-d). This latter muscle is normally associated to mouth opening (see for example, WINTERBOTTOM, 1974), and since the opening of the mouth is normally related to the protraction of the mandibular barbels (personal observation), it seems likely that the protractor externi mandibularis tentaculi is a protractor, and not a retractor, of the external mandibular barbels.

IV-b-Nomenclature: The name "musculus protractor externi mandibularis tentaculi" is reverse to the function of this muscle (see point IV-a).

IV-c-Taxonomic distribution: This muscle is absent in many of the species in which it was studied in some detail (either by us or by MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968; GHIOT, 1978; HOWES, 1983; GHIOT *et al.*, 1984), namely: in *Wallago attu* (Siluridae) (SINGH, 1967); *Pimelodus clarias*, *Sorubim lima* and *Pseudoplatystoma fasciatum* (Pimelodidae) (GHIOT, 1978); *Hypophthalmus edentatus* (Hypophthalmidae) (HOWES, 1983); *Bagrus bayad* (Bagridae) (GHIOT *et al.*, 1984) and *Bagrus docmac* (Bagridae) (this work). The absence of this muscle in *Wallago attu*, as well as of the other muscles associated with the mandibular barbels, is probably related to its life-style (see point II-c). *Hypophthalmus edentatus* has a "small muscle slip attaching to the outer mandibular barbel" that is a "continuation of the dorsal portion" of the protractor hyoidei (HOWES 1983), which has probably the same functional role as the protractor externi mandibularis tentaculi. In the other five species, the absence of this muscle can probably be explained by the fact that its function is also performed indirectly by the contraction of the pars ventralis of the protractor hyoidei muscle (see point V). However, it should be noticed that the seven species mentioned above only represent a small sample of the catfish species in which the muscles associated with the mandibular barbels were studied in detail, which seems to indicate that this muscle is widely distributed in catfish.

IV-d-Origin: Considering its posterior and anterior attachments, its spatial configuration and the orientation of its fibres, the protractor externi mandibularis tentaculi clearly seems to be derived from the protractor hyoidei muscle (figs 1a, 2, 4a, 5a). This hypothesis is in agreement with those of Edgeworth (1935), MUNSHI (1960), SINGH (1967), SINGH & MUNSHI (1968), GHIOT (1978) and GHIOT *et al.* (1984). In fact, in some species studied here (*e.g.*, *Chrysichthys nigrodigitatus* and *Clarias gariepinus*) some fibres of these muscles are mixed and, as mentioned above (see point IV-c), *Hypophthalmus edentatus* possesses "a small bundle slip" of the protractor hyoidei (HOWES, 1983) that seems to be an "undifferentiated" protractor externi mandibularis tentaculi.

IV-e-Synonymy: Muscle 5, 6 ou 7 (?) des barbillons mandibulaires (GHIOT *et al.*, 1984). In their figure 5b, these authors illustrate 3 muscles (to which they attribute, in the text, the numbers 5, 6 and 7), that correspond to the protractor externi mandibularis tentaculi, depressor interni mandibularis tentaculi and intertentacularis of the present work. However, neither this figure, nor the text, clearly defines which number corresponds to each muscle. Retractor tentaculi of the external (or first) mental (or mandibular) barbel (MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968). Only some muscles to which these authors give this name do correspond to the muscle protractor externi mandibularis tentaculi of this work. As explained before, they confuse some fibres of the protractor hyoidei with independent muscles associated with the mandibular barbels (see point II-e).

V-Musculus protractor hyoidei

This muscle is normally associated to mouth opening (WINTERBOTTOM, 1974). However, in catfish, its pars ventralis is also related to the movements of the mandibular barbels (WINTERBOTTOM, 1974; GHIOT, 1978; HOWES, 1983; GHIOT *et al.*, 1984; MO, 1991; ADRIAENS & VERRAES, 1997). GHIOT (1978), GHIOT *et al.* (1984) and ADRIAENS & VERRAES (1997) divide the pars ventralis in different functional and morphological sections. This division is questionable. In almost all catfish where the muscles associated to the mandibular barbels were studied in detail (either by us or by MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968; GHIOT, 1978; HOWES, 1983; GHIOT *et al.*, 1984), with exception of the species *Phractura brevicauda* and *Phractura intermedia*, the pars ventralis of the protractor hyoidei is composed of a single and undifferentiated mass of fibres, constituting a single and homogeneous bundle, in which the moving parts of the cartilages associated to the mandibular barbels are lodged (figs 1a, b, 3a, 4a, 5a; see also MUNSHI, 1960, SINGH, 1967, SINGH & MUNSHI, 1968, WINTERBOTTOM, 1974; HOWES, 1983 and MO, 1991). It does not seem likely that GHIOT's (1978), GHIOT *et al.*'s (1984) and ADRIAENS & VERRAES'S (1997) different sections of the pars ventralis of the protractor hyoidei can contract independently, causing different types of movements of the mandibular barbels. In fact, the relationship between this pars ventralis and the moving parts of the cartilages of these barbels is similar to the relationship between the protractor externi mandibularis tentaculi and the moving part of the cartilage associated with the external mandibular barbel (fig. 1b). It is probable, that the pars ventralis of the protractor hyoidei works as a single functional unit, related to the protraction of the mandibular barbels. This hypothesis was supported by the manipulation of some large fresh specimens of the species *Chrysichthys nigrodigitatus* and *Clarias gariepinus*.

For a discussion of nomenclature, taxonomic distribution, origin and synonymy of the protractor hyoidei muscle, see WINTERBOTTOM (1974: 243, 244, 245).

VI-Musculus depressor interni mandibularis tentaculi

VI-a-Function: This muscle is inserted on the ventro-medial face of the moving part of the cartilage associated with the internal mandibular barbel (figs 1a, c, 2, 4a, 5a). Its contraction is expected to result in the depression of the internal mandibular barbels (fig. 1c). This hypothesis was supported by the artificial contraction of this muscle in some large fresh specimens of *Chrysichthys nigrodigitatus* and *Clarias gariepinus*.

VI-b-Nomenclature: The attribution of the name "muculus depressor interni mandibularis tentaculi" to this muscle is due to its probable function (see point VI-a).

VI-c-Taxonomic distribution: The depressor tentaculi was only described in *Hypophthalmus edentatus* (HOWES, 1983) and *Chrysichthys longibarbus* (GHIOT *et al.*, 1984) (for the synonymy, see point VI-e). The lack of previous descriptions could be related to its very small size, and to the difficulty to detect it, and not to its absence. However, its presence in all the species studied by us, with exception to those of the family Diplomystidae (which do not possess mandibular barbels) and Bagridae, the fact that it is present in four catfish families (Claroteidae, Clariidae, Hypophthalmidae and Amphiliidae) that do not constitute a monophyletic group (CHARDON, 1968; MO, 1991; DIOGO & CHARDON, in preparation) and the fact that these families inhabit the Asiatic (Clariidae), African (Clariidae, Amphiliidae and Claroteidae) and South American (Hypophthalmidae) continents, seems to indicate that it is widely distributed in catfish.

VI-d-Origin: We agree with GHIOT *et al*. (1984) that this muscle (for the synonymy, see point VI-e) is probably derived from the protractor hyoidei, not only due to the configuration of these two muscles, but also because in *Clarias* and *Amphilius*, some of the fibres of these two muscles are deeply mixed. HOWES (1983) considers the depressor interni mandibularis tentaculi of *Hypophthalmus edentatus* (for the synonymy, see point VI-e) a differentiation of the hyohyoideus muscle (this author also gives an alternative hypothesis, in which this muscle is interpreted as a differentiation of the protractor hyoidei). However, the depressor interni mandibularis tentaculi and the hyohyoideus are usually separated by the protractor hyoidei (see, for example, figs 1a, 4a, 5a), which seems to indicate that the first one is not derived from the hyohyoideus, but from the protractor hyoidei.

VI-e-Synonymy: Hmd ("bundle of fibres that attaches to the base of the inner mandibular barbel") (HOWES, 1983), Muscle 5, 6 ou 7 (?) des barbillons mandibulaires (GHIOT *et al*., 1984) (see point IV-e).

VII-Musculus intertentacularis

VII-a-Function: The function of this muscle (figs 1a, 2, 4a) is probably to connect the internal and external mandibular barbels of the same side. This hypothesis was supported by the manipulation of some large fresh specimens of *Chrysichthys nigrodigitatus* and is also supported by the fact that, among the species studied here, this muscle is only present in those species where the cartilages of the internal and external mandibular barbels are not cartilaginously associated (*Amphilius brevis*, *Amphilius jacknosi, Amarginops cranchii*, *Chrysichthys auratus*, *Chrysichthys nigrodigitatus*, *Phractura brevicauda* and *Phractura intermedia*) (figs 1a, 2, 4a, compare with figs 3a, 5a).

VII-b-Nomenclature: The name "musculus intertentacularis" refers to the anatomy and function of this muscle (see point VII-a). It should be remembered that this muscle is the only one that really connects any type of catfish barbels, since the depressor interni mandibularis tentaculi does not connect the internal mandibular barbels of both sides, but each of them to a medial aponeurosis (figs 1a, 2, 4a, 5a).

VII-c-Taxonomic distribution: It is very hard to appreciate the taxonomic distribution of this muscle, since it is extremely small, and may not have been observed by other authors: it was only described in *Chrysichthys longibarbus* (GHIOT *et al.*, 1984) (for the synonymy, see point VII-e). This muscle seems to be absent in those catfishes with a cartilaginous association between the cartilages of the internal and external mandibular barbels of the same side, like, for example, clariids (fig. 5a) and bagrids (fig. 3a).

VII-d-Origin: We agree with GHIOT *et al.* (1984), who considers this muscle (for the synonymy, see point VII-e) to be derived from the protractor hyoidei, not only because of the configuration of the two muscles (figs 1a, 2, 4a) but also because in *Clarias gariepinus* some fibres of the two are deeply mixed.

VII-e-Synonymy: Muscle 5, 6 ou 7 (?) des barbillons mandibulaires (GHIOT *et al.*, 1984) (see point IV-e).

VIII-Cartilaginous plate carrying the mandibular barbels and muscles 1, 4 and 5 of these barbels

All four structures — cartilaginous plate and the three muscles — were only observed by GHIOT (1978) in some pimelodid catfishes and are not homologous with any of the structures described above.

VIII-a-Function: GHIOT's (1978) hypothesis concerning the function of these four structures should be regarded cautiously, since this author does not give any morphological, functional or experimental argument to support it (see point II-a).

VIII-b-Nomenclature: The nomenclature proposed by GHIOT (1978) seems appropriate since the function of these four structures is not, for the present, clear (see point VII-a), and no conflicts in any nomenclature do occur.

VIII-c-Taxonomic distribution: These four structures were found only in three pimelodid species, namely *Pimelodus clarias*, *Sorubim lima* and *Pseudoplatystoma fasciatum* (GHIOT, 1978). They could represent autapomorphic features of this family, or, more likely, of the subfamily Pimelodinae, to which these three species belong (TEUGELS, 1996), since this the family "Pimelodidae" is probably not monophyletic (LUNDBERG & MCDADE, 1986).

VIII-d-Origin: We agree with GHIOT (1978) and GHIOT *et al.* (1984) that the muscles 1, 4 and 5 of the mandibular barbels are probably derived from the protractor hyoidei and that the cartilaginous plate carrying the mandibular barbels is a neo-formation.

VIII-e-Synonymy: No other name has been attributed to these structures, which were only described by GHIOT (1978).

IX-Muscle 2 of the mandibular barbels

IX-a-Function: A hypothesis concerning the function of this muscle is illustrated in the figure 5b. The two small black areas represent the fixed points of the cartilage associated with the internal mandibular barbel: the left one, situated between the two barbels, is firmly attached to the dentary bone by means of a large number of short and thin fibres (fig. 5a); the right one represents the medial region of the cartilaginous complex of *Clarias gariepinus*. When the muscle 2 is contracted, the cartilage situated between the internal barbel and the medial line to which it is associated is pulled antero-laterally, provoking the retraction of the internal barbel. This hypothesis, which was supported by artificial stimulation of the muscle in two large fresh specimens of *Clarias gariepinus*, contradicts that of SINGH (1967), which attributed, without giving any explanation, the name "protractor tentaculi" to this muscle (for the synonymy, see point IX-e). In the absence of more available data on the subject, our functional hypothesis should be regarded in a very prudent way.

IX-b-Nomenclature: The attribution of the name "muscle 2 of the mandibular barbels" is due to the uncertainty concerning its function (see point IX-a) and to its very limited taxonomic distribution (see point IX-c). Note that the "muscle 2 of the mandibular barbels" of GHIOT (1978) and the "muscle 2 des barbillons mandibulaires" of GHIOT *et al*. (1984) were synonymized with the retractor externi mandibularis tentaculi (see point II-E).

IX-c-Taxonomic distribution: This muscle was found only in three *Clarias* species — *C. batrachus*, *C. gariepinus* and *C. meladerma* — which seems to indicate that it could represent an autapomorphic character of the this genus or of the family Clariidae. This question can only be answered by the study of other species of the genus Clarias, of the family Clariidae as well as of other catfish families.

IX-d-Origin: SINGH (1967) considers the muscle 2 (for the synonymy see point IX-e) as a differentiation of the intermandibularis. Due to the scarce available data about this subject, we prefer to wait for studies on the embryological development and the nervous innervation of this muscle, before giving any comment about its origin.

IX-e-Synonymy: Protractor tentaculi of the second mandibular barbel (SINGH, 1967). Of all the muscles which this author named so, only the first of the three "protractor tentaculi" mentioned in his description of *Clarias batrachus* corresponds to the muscle 2 of the mandibular barbels in the present work.

X-Muscle 3 of the mandibular barbels

X-a-Function: The contraction of this muscle (short arrows) provokes the retraction of the external mandibular barbel (long arrow) (fig. 4b).

X-b-Nomenclature: This muscle — which was found only in the species *Amphilius brevis* (fig. 4a) and *Amphilius jacksoni* (see point X-c) — is associated with the retraction of the external mandibular barbel (see point X-b), but is not homologous to the muscle retractor externi mandibularis tentaculi (see point X-d) of other catfishes (see, for example, figs 1a, 2, 3a, b, 5a). Therefore, we called it "muscle 3 of the mandibular barbels." Note that the "muscle 3 of the mandibular barbels" of GHIOT (1978) and the "muscle 3 des barbillons mandibulaires" of GHIOT *et al*. (1984) were synonymized with the retractor interni mandibularis tentaculi (see point III-e).

X-c-Taxonomic distribution: This muscle was found only in the species *Amphilius brevis* and *Amphilius jacksoni*, which may be explained by the fact that, in amphiliids, the external mandibular barbels are situated in the lateral (fig. 4a), and not in the ventral region of the head (see point II-a).

X-d-Origin: This muscle seems not to be homologous to the retractor externi mandibularis tentaculi of the other catfishes. Their shape, spatial position, structural relations and fibre orientation are quite different. The retractor externi mandibularis tentaculi is usually attached to the antero-dorsal face of the dentary, close to the mandibular symphysis, and to the antero-dorsal face of the moving part of the cartilage of the external mandibular barbel (figs 1a, b, 2, 3a, b, 5a), while the muscle 3 of the mandibular barbels is attached to the lateral face of the dentary and to the posterior surface of the proximal extremity of the external mandibular barbel (fig. 4a). Due to the scarce available data about this muscle, we prefer to wait for studies on it embryological development and nervous innervation before making other commentaries about its origin.

X-e-Synonymy: Since this muscle was only described in the present work, no synonyms have been used.

General conclusions

Of all the 13 known structures associated to the mandibular barbels hitherto discussed, seven seem to be commonly present in catfish, namely: 1) the cartilages of these barbels, comprising a moving and a supporting part; 2) the retractor externi mandibularis tentaculi; 3) the retractor interni mandibularis tentaculi; 4) the protractor externi mandibularis tentaculi; 5) the protractor hyoidei (pars ventralis); 6) the depressor interni mandibularis tentaculi; 7) the intertentacularis. The other six structures appear to be present only in specific catfish lineages, namely:

the cartilaginous plate carrying the mandibular barbels and the muscles 1, 4 and 5 of these barbels in the Pimelodinae (or Pimelodidae?), the muscle 2 of the mandibular barbels in *Clarias* (or Clariidae?) and the muscle 3 of the mandibular barbels in *Amphilius* (or Amphiliinae?). The limited distribution of these six structures seems to indicate that the study of the structures associated with the mandibular barbels could probably be useful to infer the phylogenetic relationships between different catfish groups. We are conscious that, despite this work, there are a large number of questions concerning the origin, function and taxonomic distribution of these structures that need to be answered, and that only further studies concerning their embryological development, anatomy and innervartion, as well as experimental studies, can clear these questions. We hope, however, that this work will pave the way for such studies, and that it will be useful in future morphologic and phylogenetic research on siluriform fishes.

LIST OF ABBREVIATIONS

c-ex-md-b-mp	cartilago externi mandibularis tentaculi: moving part
c-in-md-b-sp	cartilago interni mandibularis tentaculi: supporting part
l-an-iop	ligamentum angulo-interoperculare
m-dp-in-md-b	musculus depressor interni mandibularis tentaculi
m-hh-inf	musculus hyohyoideus inferior
m-intm	musculus intermandibularis
m-intt	musculus intertentacularis
m-pr-ex-md-b	musculus protractor externi mandibularis tentaculi
m-pr-h-d	musculus protractor hyoidei pars dorsalis
m-pr-h-l	musculus protractor hyoidei pars lateralis
m-pr-h-v	musculus protractor hyoidei pars ventralis
m-re-ex-md-b	musculus retractor externi mandibularis tentaculi
m-re-in-md-b	musculus retractor interni mandibularis tentaculi
m-2-md-b	muscle 2 of the mandibular barbels
m-3-md-b	muscle 3 of the mandibular barbels
md	mandibula
ex-md-b	external mandibular barbel
in-md-b	internal mandibular barbel
o-ch-a	os ceratohyale anterior
o-ch-p	os ceratohyale posterior
o-den-avp	os dentale: antero-ventral process
o-iop	os interoperculare
o-prmx	os praemaxillare

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