PART II

Function and Functional Morphology
Functional Morphology of Catfishes: Movements of Barbels

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INTRODUCTION

Barbels are a general characteristic of Siluriformes (Fig. 7.1A-C), responsible for their popular name “catfish”. Catfish barbels are clearly involved in near-field chemoreception (while nostrils are concerned with far-field: Herrick, 1903) and mechanoreception including gliding and pressure sensitivity, direct contact and rheotactism (Hoagland, 1932; Biedenbach, 1971). They are supported by a central rod, comprising a dense network of elastin (Fig. 7.2A), with or without “elastic/cell-rich cartilage” (terminology according to Benjamin, 1990). Their skin is covered with mucous cells and taste-buds (Wright, 1884; Herrick, 1903; Landacre, 1910; Kamrin and Singer, 1953; Desgranges, 1972; Finger, 1976, 1978; Grover-Johnson and Farbman, 1976; Arratia and Huaquín, 1995), which are probably not only gustatory, but also mechanosensory (Rajbanshi, 1966). It is notable that taste-buds are not at all restricted to barbels, but are also present on the whole body surface and particularly densely spaced on the inner side of the lips (Rajbanshi, 1966). Catfish

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barbels are necessary to initiate feeding responses and contact with food is needed (Biedenbach, 1971). Their adaptive value in muddy-water dwellers and nocturnal fish is evident and was, moreover, demonstrated experimentally (Alexander, 1965). Although catfish barbels seem to be mainly associated with search for food and with avoiding obstacles, they could also be associated with several other functions, such as locomotion, fright reaction, aggression or sexual attraction (for a general overview on this subject see Jayaram, 1978).

Three main types of catfish barbels can be distinguished, namely maxillary barbels, mandibular barbels and nasal barbels (Fig. 7.1). The maxillary barbels, invariably present in catfishes, including the most basal members of the group, the diplomystids, are characterised by their connection to a mobile mechanism, the palatine-maxillary system, which is constituted by the maxilla, the autopalatine and more or less specialised ligaments and muscles responsible for their movements (Alexander, 1965;
Gosline, 1975). They are supported by a central rod, the proximal extremity of which is firmly embedded in the hollow distal end of the maxillary bone (Fig. 7.2A). The mandibular barbels are plesiomorphically absent in catfishes, but present in the great majority of non-diplomystid catfishes, which usually present two pairs (e.g., Fig. 7.1) (Diogo and Chardon, 2000a). They are associated with a basal “elastic/cell-rich cartilage” (see above), which usually consists of an anterior and a posterior part. The anterior part, termed the “supporting part” by Diogo and Chardon (2000a), is usually situated between the base of the barbels and the dentary, to which it is firmly attached by connective tissue (Fig. 7.3A, B). The posterior part, usually longer than the anterior, is termed the “moving part” by Diogo and Chardon (2000a: 457) since “it is on this part that the muscles for movement of the mandibular barbels insert” (Fig. 7.3A, B). The nasal barbels present a rather limited taxonomic distribution within Siluriformes compared with the other two types of barbels (Burgess, 1989). They are characteristically associated with a
**Fig. 7.3.** *Chrysichthys nigrodigitatus* (modified from Diogo and Chardon, 2000a). **A.** Ventral view of the head. Only the proximal parts of the mandibular barbels are illustrated. On the left side of the illustration the pars dorsalis and lateralis of the protractor hyoidei and the hyohyoides inferior were removed and the anterior portions of the ‘elastic/cell-rich cartilages’ associated with the mandibular barbels pulled backwards. **B.** Schemes illustrating retraction (black arrows) and protraction (white arrows) of the external mandibular barbels (lateral view). **C.** Schemes illustrating depression of the internal mandibular barbels (frontal view). Abbreviations: c-ex-md-b-mp, c-ex-md-b-sp: moving and supporting parts of ‘elastic/cell-rich cartilage’ of external mandibular barbel; ch-a, ch-p: anterior and posterior ceratohyals; den-avp: anteroventral process of dentary; dp-in-md-b: depressor interni mandibularis tentaculi; ex-md-b: external mandibular barbels; hh-inf: hyohyoidus inferior; in-md-b: internal mandibular barbel; intm: intermandibularis; intt: intertentacularis; md: mandible; pr-ex-md-b: protractor externi mandibularis tentaculi; pr-h-l, pr-h-v: pars lateralis and ventralis of protractor hyoidei; re-ex-md-b: retractor externi mandibularis tentaculi; re-in-md-b: retractor interni mandibularis tentaculi.
cartilaginous basal frame supported by the surrounding bones of the nasal region (Fig. 7.2B), and are related neither to a mobile mechanism nor to a muscular system (Alexander, 1965; Singh, 1967; Ghiot, 1978; Ghiot et al., 1984; Mo, 1991; Adriaens and Verraes, 1997a). In this chapter we briefly summarise the principal mechanisms and/or muscular systems associated with the different types of movements of catfish barbels.

MOVEMENTS OF CATFISH MAXILLARY BARBELS

In all catfishes, movements of the maxillary barbels are related to a mobile mechanism, the palatine-maxillary system (Gosline, 1975). However, here we shall differentiate the palatine-maxillary system of Siluriformes into two main types: that found in Diplomystidae and that found in all remaining catfishes, i.e., the Siluroidei (sensu Grande, 1987).

Palatine-maxillary System of Diplomystidae

In diplomystids, the posterior end of the autopalatine is loosely connected with the posterior part of the suspensorium (Fig. 7.4) by sesamoid bones and ligaments (Arratia, 1987, 1992; Diogo and Chardon, 2001). It articulates medially and dorsally with the neurocranium and anteriorly, by means of its rostral cartilaginous head, with the maxilla (Fig. 7.4). Like most teleosts, the maxilla of diplomystids bears teeth (Fig. 7.5) while in all...
other catfishes maxillary teeth are lacking, except in the Eocene fossil *Hypsidoris farsonensis* (Arratia, 1987, 1992; Grande, 1987; Mo, 1991; Diogo and Chardon, 2001). It is linked with the lower jaw by two ligaments (Fig. 7.4), with the primordial ligament joining its proximal end to the coronoid process of the dentary and a thick ligament joining its medial aspect and the lateral face of the mandible. The single muscle associated with the palatine-maxillary system of diplomystids is the extensor tentaculi, derived from the anterior portion of the adductor arcus palatini (Takahasi, 1925; Nawar, 1955; Stix, 1956; Munshi, 1960; Munshi and Singh, 1967; Singh, 1967; Singh and Munshi, 1968; Winterbottom, 1974; Jayaram and Singh, 1982; Howes, 1983a, b, 1985), which extends from the neurocranium to the posterior end of the autopalatine (Fig. 7.4). The palatine-maxillary system of diplomystids, which very likely represents the plesiomorphic condition for siluriforms (Diogo et al., 2000a; Diogo and Chardon, 2000), is rather simple (Fig. 7.5). The extensor tentaculi muscle pulls the autopalatine backward thanks to the mobile articulation between this latter bone and the neurocranium, and thus also pulls the proximal end of the maxilla (Fig. 7.5A, B), which is linked through a cartilaginous joint to the autopalatine (Fig. 7.4). The backward movement of the proximal part of the maxilla results in an anteroventral displacement of its posterior end because of the thick ligament linking its distal extremity to the lower jaw (Fig. 7.5A, B). The maxillary barbel, whose proximal end is firmly embedded in the hollow distal extremity of the maxillary bone (Fig. 7.2A), follows the maxilla and turns to the bottom and forward (Fig. 7.5A, B). Abduction of the maxillary barbel may also result from mouth opening due to the maxillo-mandibularial ligament linking the distal extremity of the maxilla to the lateral surface of the lower jaw (Fig. 7.5A, B), which rotates the maxilla in the same way as in many teleosts with a partially freed maxilla (Alexander, 1965; Gosline, 1975; Diogo et al., 2000a; Diogo and Chardon, 2001). Closure of the mouth would thus promote the opposite movement, that is, adduction of the maxillary barbel (Fig. 7.5A, B). However, adduction of the maxillary barbel is probably not exclusively related to mouth closure. In fact, in an elegant morphofunctional study of the primordial ligament of *Parauchenipterus galeatus*, Royero and Neville (1997: 157) concluded that this ligament “has rubber properties and because of this can store energy during abduction of the maxilla”, with “the stored energy being released when the action of the extensor tentaculi muscle ceases”, thus returning the maxilla and its respective
Fig. 7.5  Scheme illustrating palatine-maxillary system of Diplomystes chilensis (modified from Diogo and Chardon, 2001). A. Maxillary barbel adducted. B. Maxillary barbel abducted. Abbreviations: apal: autopalatine; ex-t: extensor tentaculi; l-mx-md: ligamentum maxillo-mandibulare; l-pri: ligamentum primordium; md: mandible; mx: maxilla; mx-b: maxillary barbel; prmx: premaxilla.
Catfishes

According to Diogo et al. (2000a: 384), the main morphological differences between the palatine-maxillary system of diplomystid and non-diplomystid catfishes are: (1) a de novo ligament joining the maxilla to the premaxilla; (2) the distal end of the maxilla is no longer attached to the lateral surface of the mandible by a strong ligament (Diogo et al., 2000a: fig. 6B). These authors further indicate that the functional implications of these morphological changes are “the new maxillo-premaxillar ligament acts as the fulcrum for maxillary barbel abduction/adduction movements, replacing the maxillo-mandibulary ligament, and, consequently,
conferring a greater freedom to the distal end of the maxilla" (Diogo et al., 2000a: 384).

Abduction of the maxillary barbel in siluroids can be differentiated into two main types—"rocking" and "sliding" (Gosline, 1975), with both types differing significantly from the abduction mechanism described above for diplomystids (Gosline, 1975; Diogo et al., 2000a; Diogo and Chardon, 2001). A rocking palatine-maxillary system is present in siluroids such as clariids, claroteids, auchenipterids, mochokids, sisorids, cranogladinids, erethistids, aspredinids, amphiliids, heteropneustids, plotosids and some ictalurids (McMurrich, 1884; Nawar, 1955; Alexander, 1965; Singh, 1967; Gosline, 1975; Ghio et al., 1984; Adriaens and Verraes, 1997a; Royero and Neville, 1997; Diogo and Chardon, 2000b, 2001; Diogo et al., 2000a, b, 2001; Oliveira et al., 2001; Diogo et al., in press). In these catfishes, contraction of the extensor tentaculi pulls the posterior end of the autopalatine posteromedially, but the firm articulation between the autopalatine and the neurocranium prevents a longitudinal displacement of the autopalatine. Therefore, the back end of the autopalatine essentially moves medially (Fig. 7.7A, B). The anterior end of the autopalatine and the proximal tip of the maxilla associated with it therefore essentially move laterally. This, by the resistance of the premaxillo-maxillary ligament, provokes abduction of the maxilla (Fig. 7.7A, B) and associated barbel. In those siluroids with a sliding palatine-maxillary system, as for example, pimelodids, hepapterids, pseudo-
pimelodids (see Diogo, Chapter 12, this volume), doradids, ariids, schilbeids, pangasiids, bagrids and some ictalurids (Eaton, 1948; Alexander, 1965; Gosline, 1975; Ghiot, 1976, 1978; Ghiot et al., 1984; Diogo et al., 2000a; Diogo and Chardon, 2001), the type of articulation between the autopalatine and the skull enables a significant translation of the autopalatine in an anteroposterior direction (Fig. 7.8A). During the posterior movement of the autopalatine, the proximal tip of the maxilla is retracted and, through the ligamentous connection between the maxilla and the premaxilla, provokes abduction of the maxilla (Fig. 7.8A) and its associated barbel. In some cases, abduction of the maxillary barbel in siluroids could be generated through muscular activity directly on the maxilla. In Callichrous padba, for example, three slips of muscle are

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**Fig. 7.8** Scheme illustrating the palatine-maxillary system of Bagrus docmac (modified from Diogo and Chardon, 2001). A. Dorsal view of anterior region of the cranium showing abduction of the maxillary barbel (on the left side of illustration). B. Frontal view of cranium showing elevation of the maxillary barbel (on right side of illustration). Abbreviations: af-apal-neu: articulatory facet of autopalatine for neurocranium; apal: autopalatine; ex-t-3-4: bundles of extensor tentaculi; l-prmx-mx: ligamentum praemaxillo-maxillare; mx: maxilla; mx-b: maxillary barbel; prmx: premaxilla.
attached on the proximal tip of the maxilla in such a manner that, when contracting, they abduct the maxillary barbel (Singh, 1967).

Adduction of the maxillary barbel in siluroids can be realised in three different major ways. The most simple and direct is through contraction of a retractor tentaculi muscle directly inserted on the maxilla, which is derived from an inner section of the adductor mandibulae (McMurrich, 1884; Eaton, 1948; Alexander, 1965; Howes, 1983a, b, 1985; Schaefer, 1990; Schaefer and Lauder, 1986, 1996; Howes and Fumihiro, 1991; Bornbusch, 1995; Cabuy et al., 1999 Diogo et al, 1999; Diogo and Chardon, 2000c). However, as stated by Diogo and Vandewalle (Chapter-2, this volume), although the retractor tentaculi is present in numerous siluriforms, e.g., callichthyids, ictalurids, malapterurids, doradids, clariids, heteropneustids, sisorids, amphiliids, erethistids, aspredinids or some bagrids, the plesiomorphic condition for siluriforms is clearly that in which this muscle is absent. Therefore, there should be alternative mechanisms to promote adduction of the maxillary barbel in those siluroids lacking a retractor tentaculi. One of these mechanisms is the second elastic mechanism described above for Diplomystidae, in which adduction of the maxillary barbel is associated with the action of the primordial ligament. Another adducting mechanism is present in those siluroids with a sliding palatine-maxillary system, such as ‘pimelodids’ or bagrids. In these latter catfishes a portion of the extensor tentaculi muscle (Fig. 7.9: ex-t-1) is configured in such a way that, during its contraction the palatine is shifted anteriorly and, consequently, the maxilla and maxillary barbel are adducted (e.g., Alexander, 1965; Ghiot, 1978; Ghiot et al., 1984; Ghiot et al., 1984; Diogo et al., 2000a; Diogo and Chardon, 2001).

Apart from a pure extension and retraction of the maxillary barbels, elevation and depression of these barbels are also possible in some siluroids (Alexander, 1965; Ghiot, 1978; Ghiot et al., 1984; Adriaens and Verraes, 1997a; Diogo et al., 2000a, b; Diogo and Chardon, 2001).

Fig. 7.9 Ventral view of right side of anterior region of the cranium of Bagra docmac (modified from Diogo et al., 1999). Abbreviations: af-apal-neu: articulatory facet of autopalatine for neurocranium; apal: autopalatine; ex-t-1-3: bundles of extensor tentaculi.
Elevation results from the rotation-elevation of the distal end of the maxillary through a similar rotation-elevation of the autopalatine initiated by contraction of a bundle of the extensor tentaculi inserted on the posterodorsal surface of the autopalatine (Fig. 7.8B: ex-t-4). Contraction of an antagonist bundle of the extensor tentaculi (e.g., Fig. 7.9: ex-t-2), inserted on the posteroverentral surface of the autopalatine, effects the opposite movement, that is, depression of the maxillary barbel.

MOVEMENTS OF CATFISH MANDIBULAR BARBELS

The structures associated with movements of the mandibular barbels were analysed in some detail in studies such as those of Munshi (1960), Singh (1967), Munshi and Singh (1967), Singh and Munshi (1968), Ghioț (1976, 1978), Howes (1983a), Ghioț et al. (1984), Adriaens and Verraes (1997b), Diogo et al. (1999, 2000b) and Diogo and Chardon (2000b), and a detailed overview on the origin, anatomy, function, taxonomic distribution, nomenclature and synonymy of these structures recently presented by Diogo and Chardon (2000a).

As mentioned in the Introduction, the cartilages associated with catfish mandibular barbels are characteristically divided into a supporting and a moving part (Fig. 7.3A, B). The supporting part attaches anteriorly on the dentary by means of a large number of thin and short fibres (Fig. 7.3A, B) which, according to Diogo and Chardon (2000a: 464) “confer on the mandibular barbels a solid exterior point d’appui, creating an articulatory system somewhat similar to the rocking palatine-maxillary system present in some catfishes” (Fig. 7.3B). 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. 7.3B: white arrows); “if their dorsal extremity is pulled anteriorly, their ventral extremity will be displaced posteriorly” (Fig. 7.3B: black arrows) (Diogo and Chardon, 2000a: 464). Therefore, retraction of the outer mandibular barbel is provoked by contraction of the muscle retractor externi mandibularis tentaculi (Fig. 7.3B: black arrows), which runs from the anteromedial surface of the mandible to the anterodorsal surface of the moving part of the basal cartilage of the external mandibular barbel (Fig. 7.3A, B). Accordingly, retraction of the inner mandibular barbel is provoked by contraction of the retractor interni mandibularis tentaculi, which runs from the anteromedial surface of the mandible to the anterodorsal surface.
of the moving part of the basal cartilage of the inner mandibular barbel (Fig. 7.3A).

Protraction of the external mandibular barbel is provoked by the antagonist of the retractor externi mandibularis tentaculi, that is, by the protractor externi mandibularis tentaculi (Fig. 7.3B: white arrows). This runs from the hyoid arch to the anterodorsal margin of the moving part of the cartilage associated with the external mandibular tentaculi (Fig. 7.3A, B). According to Diogo and Chardon (2000a), the pars ventralis of the protractor hyoidei (e.g., Fig. 7.3A) is also related with protraction of the external mandibular barbel. As a protractor interni mandibularis tentaculi has never been reported in siluriforms, protraction of the internal mandibular barbel is probably exclusively related with contraction of the pars ventralis of the protractor hyoidei muscle (Diogo and Chardon, 2000a).

Apart from a pure retraction and protraction of the mandibular barbels, some other movements of these barbels are possible in some catfishes (Ghiot, 1978; Ghiot et al., 1984; Adriaens and Verraes, 1997a; Diogo et al., 1999, 2000b; Diogo and Chardon, 2000a, b). In fact, some catfishes present, in addition to the muscles mentioned above, a depressor interni mandibularis tentaculi and an intertentacularis (Diogo and Vandewalle, this volume). According to Diogo and Chardon (2000a), the depressor interni mandibularis tentaculi promotes depression of the internal mandibular barbels (Fig. 7.3C), while the intertentacularis promotes the approximation between the internal and the external mandibular barbels of the same side.

MOVEMENTS OF CATFISH NASAL BARBELS

As mentioned in the Introduction, the nasal barbels of catfishes (Fig. 7.2B) are related neither to a mobile mechanism nor to a muscular system (Alexander, 1965; Ghiot, 1978; Ghiot et al., 1984; Mo, 1991; Adriaens and Verraes, 1997a). According to Ghiot et al. (1984: 270), the movements of these barbels are exclusively related with movements of the head and/or the water surrounding the fish, "with the position of the barbels being restored due to simple elasticity".

GENERAL COMMENTS

Catfishes exhibit three main types of barbels, namely, maxillary barbels, mandibular barbels and nasal barbels. Of these three barbel types, the
maxillary are the most widespread within the Siluriformes, being present from the first stage of catfish evolution (the presence of maxillary barbels constitutes a catfish synapomorphy: e.g., Arratia, 1992; de Pinna, 1993, 1998; Diogo et al., 2000a; Diogo and Chardon, 2001). This could explain why the mechanisms associated with movements of these barbels are clearly more diverse than those associated with movements of the mandibular barbels, which arrived in a later stage of catfish evolution (the presence of mandibular barbels constitutes, very likely, a synapomorphy of non-diplomystid catfishes: e.g., Diogo and Chardon, 2000a). Indeed, while there is a single mechanism associated with protraction/retraction of the mandibular barbels (Fig. 7.3B), there are several different ways of performing abduction/adduction of the maxillary ones (Figs. 7.5, 7.7, 7.8A) (see above). With respect to the nasal barbels, they present, as noted above, a rather limited taxonomic distribution within Siluriformes compared to the other two types of barbels, and are related neither to a mobile mechanism nor to a muscular system.

Acknowledgements

We are pleased to acknowledge the helpful criticism, advice and assistance of G.G. Teugels, P. Laleyé, J. Williams, G. Duhamel, R.P. Vari, S.H. Weitzman, G. Arratia, L. Taverne, M. Gayet, C. Oliveira, F. Meunier, S. He, O. Otero, T.X. de Abreu, D. Adriaens, F. Wagemans and E. Parmentier. This project received financial support from the PRAXIS XXI/BD/19533/99 (“Fundação para a Ciência e a Tecnologia”, Portuguese Government) grant to R. Diogo.

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