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Catfishes as a Case Study for Discussions on General Evolution: The Importance of Functional Uncouplings in Morphological Macroevolution

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Abstract

Many evolutionary biologists have stressed that functional uncouplings play an important role in morphological macroevolution, as they facilitate diversification and speciation by increasing the number of degrees of freedom and allowing more mechanical solutions for functional problems. In the present paper, the importance of functional uncouplings in the evolution of six major catfish structural complexes is briefly discussed, namely those constituted by the mandibular barbels and associated structures, the pectoral girdle complex, the elastic spring apparatus, the suspensorium, the palatine-maxillary system, and the adductor mandibulae complex. The overview of these major structural complexes indicates that functional uncouplings did effectively play an essential role on catfish evolutionary history. The study of this cosmopolitan and particularly diverse group representing about one-third of all freshwater fishes thus supports the importance of functional uncouplings in morphological macroevolution.

Keywords: Catfish, functional morphology, macroevolution, phylogeny, Siluriformes, structural innovation, Teleostei.

Introduction

Galis (1996) pointed out that structural innovation is essentially associated with four main types of morphological events: acquisition of a new structure; loss of a function by a structure that subsequently becomes available for a new function; duplication of a structure; and functional uncoupling. A typical example of the acquisition of a new structure is the osseous fibular crest in theropod dinosaurs and birds (Galis, 1996). This is an ossified sesamoid cartilage rudiment derived from connective tissue subjected to high pressure and tension. Concerning the loss of a function by a structure that subsequently becomes available for a new function, a typical example given by Galis (1996) is the loss of lingual prehension enabling the impressive chemosensory specialisation of the tongue in scleroglossan reptiles. With respect to the duplication of structures, followed by specialisation of the repeated structures for different functions, several examples of this type of structural innovation have been reported in the literature - for example the differentiation of gill arches in fishes and the teeth in mammals (see Galis, 1996). As regards functional uncouplings, these refer to cases when part of a certain complex originally associated with a certain mechanism X gives rise to a complex associated with a mechanism Y, with the remaining of the original complex continuing to perform the original mechanism X. In this way, not only do the organisms now have the possibility to perform the mechanism Y, but this mechanism Y can also be eventually associated with other mechanisms already available (Z, W, etc.). Within the four main types of structural innovations, functional uncouplings seem to be particularly important in morphological macroevolution, as stressed by authors such as, e.g., Schaefer and Rosen (1961), Dullemeijer (1974), Vermeij (1974), Lauder (1981), Barel (1985), Schaefer and Lauder (1986, 1996), Wainwright and Turingan (1993), Gussekloo (2000), or Liem and Summers (2000). According to Vermeij (1974), such functional uncouplings facilitate diversification and speciation by increasing the number of degrees of

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freedom and allowing more mechanical solutions for functional problems.

The present paper provides a new insight into the evolution of six main structural complexes of one of the most diverse vertebrate groups, the Siluriformes (catfishes), and briefly explains how the study of these structural complexes indicates that functional uncouplings have effectively played an essential role in the evolutionary history of this group.

Materials and methods

The Siluriformes, or catfishes, found in North, Central and South America, Africa, Europe, Asia and Australia, with fossils inclusively found in Antarctica, constitute a highly diversified, cosmopolitan group. With 34 families, about 437 genera and more than 2700 species, it includes one-third of all freshwater fishes and is one of the most diverse Vertebrate taxa (e.g., Burgess, 1989; Diogo, 2003; Teugels, 2003). The detailed study of the Siluriformes can, thus, provide useful data, and illustrative examples, for broader discussions on general phylogeny and macroevolution.

The new insight provided in the present paper on the evolution of six major catfish structural complexes is based on the phylogenetic results of Diogo's (2004) extensive cladistic analysis of 440 morphological characters in species of 87 genera representing all 32 extant catfish families. These are briefly summarised in Fig. 1. The six structural complexes are those formed by the mandibular barbels and associated structures, the pectoral girdle complex, the elastic spring apparatus, the palatine–maxillary system, the suspensorium, and the adductor mandibulae complex. The role of functional uncouplings on the evolution of each of these structural complexes will be discussed.

Results and discussion

1. Structures associated with catfish mandibular barbels

The system formed by catfish mandibular barbels and associated structures was described by authors such as, e.g., Munshi (1960), Singh (1967), Singh and Munshi (1968), Ghiot (1978), Howes (1983a,b, 1985), Ghiot et al. (1984), Mo (1991), Diogo and Chardon (2000a) and Diogo et al. (2003). In a very simplified way, one can describe it as being constituted by the mandibular barbels, their basal cartilages, and some small muscles attaching to these cartilages (Fig. 2A). It thus promotes the movements of the barbels, which are important for functions such as prey detection or obstacle avoidance (for a recent overview, see Diogo et al., 2003).

The small muscles responsible for the movements of the mandibular barbels (Fig. 2A) are the result of differentiation of the cephalic ventral musculature (see e.g., Ghiot, 1978; Howes 1983a,b, 1985; Ghiot et al., 1984; Diogo & Chardon, 2000a; Diogo et al., 2003). Originally, this is essentially func-



Fig. 1. Relationships among the extant catfish families according to the recent cladistic analysis of catfish higher-level phylogeny promoted by Diogo (2004) [for more details, see text].

tionally associated and anatomically linked with the mechanisms of opening/closure of the mouth and abduction/adduction of the suspensorium. Thus, there was an important functional uncoupling within the cephalic ventral musculature. Small muscles differentiated from it promoting the movements of the mandibular barbels, while the remaining ventral muscles (see Fig. 2A) continue to be mainly functionally associated with mouth opening/closure and suspensorium abduction/adduction.

This structural innovation can, for example, be distinguished from a structural innovation by the acquisition of a new structure, since these small muscles are the result of a simple differentiation from the existing ventral musculature. They are not new, neomorphic structures, as are for example sesamoid bones (see Introduction). Also, this structural innovation does not correspond to the loss of a function by a structure that subsequently becomes available for a new function, since the remaining ventral musculature continue, as explained above, to be functionally associated with mouth opening/closure and suspensorium abduction/adduction. Lastly, it also does not correspond to the specialisation of duplicated, repeated structures, as are for example mammalian teeth, since neither the ventral musculature nor any of its muscles were really duplicated. As mentioned above,



the small muscles of the mandibular barbels are simply the result of the differentiation of part of the original ventral muscles, and not of an evolutionary duplication and subsequent specialisation of one of these later muscles.

According to Diogo's (2004) recent phylogenetic analysis of the higher-level phylogeny of the Siluriformes, the differentiation of the small muscles of the mandibular barbels from the ventral musculature, and, thus, the important functional uncoupling referred above, seems to have occurred in the node leading to the clade formed by all extant catfishes excluding loricarioids (i.e., nematogenyids + trichomycterids + callicthyids + scoloplacids + loricariids) and diplomystids (see Fig. 1). Fig. 2. (A) Ventral view of the mandibular barbels and associated structures of the catfish Schilbe mystus. The basal cartilages of the mandibular barbels are shown in black, the small muscles associated with the movements of these barbels are shown in grey. On the left side, all the musculature is exposed, on the right side the mandibular barbels, their basal cartilages, and the most superficial muscles were removed in order to show the most dorsal muscles (M-HH-INF hyohyoideus inferior muscle, M-INTM intermandibularis muscle, M-INTT intertentacularis muscle, MND mandible, MND-B mandibular barbels, M-PR-MND-B protractor of the external mandibular barbel, M-PR-H protactor hyoideus muscle, M-RE-MND-B retractors of the mandibular barbels). (B) Ventral view of the pectoral girdle of the catfish Cranoglanis bouderius. The muscles associated with the movements of the pectoral spines are shown in grey; on the left side all musculature is exposed, on the right side the most superficial muscles were removed in order to show the most dorsal musculature (CL cleithrum, M-AB-PRO abductor profundus muscle, M-AB-SUP abductor superficialis muscle, M-ARR-D-DD, M-ARR-D-VD dorsal and ventral divisions of arrector dorsalis muscle, M-ARR-V arrector ventralis muscle, PEC-RA pectoral rays, PEC-SP pectoral spine, SCA-COR scapulocoracoide). (C) Lateral view of the cephalic region and elastic spring apparatus of the catfish Cranoglanis bouderius. The most lateral fibers of the epaxialis muscle were removed in order top show the protractor of the Müllerian process; this latter process is shown in black, its protractor muscle is shown in grey (M-PR-MUP protractor of the Müllerian process, MUP Müllerian process, NEU neurocranium, PEC-GIRD pectoral girdle, SB swimbladder).

2. Pectoral girdle complex

The siluriform pectoral girdle has been described by authors such as, e.g., Reed (1924), Hubbs and Hibbard (1951), Alexander (1965), Gosline (1977), Brosseau (1978), Royero (1987), Grande (1987), and Diogo et al. (2001a).

One of the more remarkable anatomical specialisations of catfishes, which presents an inestimable value for palaeontologists, is surely the peculiar transformation of the overall configuration of the pectoral girdle, and specially of the first pectoral ray (Fig. 2B). Contrary to most basal teleosts, in which the pectoral girdle is constituted by a large and variable number of bones and is highly mobile in relation to the neurocranium, in catfishes the pectoral girdle is only composed of three main skeletal elements, the cleithrum, scapulo-coracoid and posttemporo-supracleithrum. The last of these is usually deeply attached to the neurocranium.

The particular configuration of the first pectoral ray (= pectoral spine) and the muscles attached to it (Fig. 2B) are related to a peculiar 'friction-locking' mechanism. When the pectoral spine is abducted, its base, frequently thickened and bearing several ridges, is locked in the pectoral girdle, as a defensive mechanism; the stridulation of the spine base in the pectoral girdle enables the production of sound (see e.g., Reed, 1924; Hubbs & Hibbard, 1951; Alexander, 1965; Gosline, 1977; Royero, 1987). Apart from being essentially associated with a protective function and sound production,

such a mechanism could eventually also be related with terrestrial locomotion, feeding habits or reproductive behaviour (see e.g., Burgess, 1989). One can thus also talk here of a major evolutionary functional uncoupling. In fact, the typical, stout pectoral spine of catfishes, associated with functions such as those referred above, is the result of an evolutionary decoupling from the remaining pectoral rays. These were originally (and continue to be) essentially functionally associated with the general movements of the body. Also, although the various rays forming the pectoral fins of Actinopterygii seem at first sight to have originated by a structural duplication, such a duplication has occurred much before catfishes evolved (see e.g., Pough et al., 1999). Thus, the stout pectoral spine of catfishes is not the result of any duplication of a certain specific pectoral fin ray already existing in these fishes, but simply of a functional uncoupling between one of the existing rays and the remaining ones (see above). Another example of functional uncoupling occurring within catfish evolutionary history is that the arrector dorsalis muscle which is attached to the stout pectoral spine, has become divided into a dorsal and a ventral part (Fig. 2B). This promotes different types of movements of this spine (see e.g., Diogo et al., 2001a).

The recent results of Diogo's work on catfish higherlevel phylogeny indicate that the functional uncoupling between the highly modified first pectoral ray and the remaining ones seems to have occurred in the very first stages of catfish macroevolution. It is present in the most basal extant catfishes, the diplomystids. With respect to the differentiation of the arrector dorsalis muscle into a dorsal and a ventral part separated by a large horizontal lamina of the scapulo-coracoid, this seems to have occurred in the node leading to the clade including all extant catfishes excepting the Loricarioidea (see above) and Diplomystidae (see Fig. 1).

3. Elastic spring apparatus

The elastic-spring-apparatus was described by authors such as Bridge and Haddon (1893, 1894), Sörensen (1894), Chranilov (1929), Tavolga (1962), Alexander (1965), Chardon (1968), Taverne and Aloulou-Triki (1974), Howes (1983b, 1985), Royero (1987), Ladich and Bass (1998), Heyd and Pfeiffer (2000), Fine and Ladich (2003), and Parmentier and Diogo (in press).

In short, it is formed by a modified, highly flexible anterior process (the Müllerian process) of the parapophysis of the fourth vertebra and by a protractor muscle inserted on this Müllerian process (see Fig. 2C). When the protractor muscle contracts it pulls the Müllerian process anteriorly. When it relaxes, it allows the Müllerian process to recoil so that the swimbladder emits sound.

The production of sound in catfishes may have a social function. The mochokid *Synodontis*, for example, produce a characteristic 'murmur' in a dangerous situation (Taverne &

Aloulou-Triki, 1974), probably to give alarm to some other fishes. The possibility of producing sound has, thus, very likely, an important evolutionary significance for the different catfish lineages that had acquired it, especially taking into account that these fishes are mainly nocturnal and live in conditions where is greatly reduced visibility (Alexander, 1965). The evolution of an elastic spring apparatus in siluriforms thus again supports the important role of functional uncouplings in structural innovation. The protractor of the Müllerian process, responsible for the movements of this apparatus, and, thus, for the production of sound by the swimbladder, results from the independent differentiation, in different lineages, of existing muscles such as the supracarinalis anterior and/or the epaxialis. These muscles performed (and continue to perform) a rather different function (see e.g., Royero, 1987). According to Diogo's phylogenetic results, this differentiation, and, thus, this important functional uncoupling, has occurred at least five times within catfish evolutionary history, namely in the clade formed by malapterurids + mochokids + auchenipterids + doradids, in the ariids, in the cranoglanidids, in the pseudopimelodin pimelodids, and in some pangasiids (see Fig. 1).

4. Suspensorium

The siluriform suspensorium has been studied by McMurrich (1884a,b), Regan (1911), Starks (1926), De Beer (1937), Alexander (1965), Gosline (1975), Howes (1983b, 1985), Howes and Teugels (1989), Mo (1991), Arratia (1992), De Pinna (1993), Vandewalle et al. (1993), Diogo et al. (2001b), and Diogo and Chardon (2003). As illustrated in the simplified scheme presented in Fig. 3, the main evolutionary transition from a typical teleostean suspensorium (Fig. 3A) and the configuration found in the plesiomorphic diplomystid catfishes (Fig. 3B) is that, in the latter, there is a major decoupling between the autopalatine and the main body of the suspensorium (note: in siluriforms, as in other ostariophysans, the dermopalatine is considered to be plesiomorphically absent, thence the use of the term autopalatine in catfish literature: see e.g., Fink & Fink, 1981). In fact, in diplomystids the autopalatine is no longer firmly attached to the anterior surface of the main body of the suspensorium. Instead, it is linked to it by relatively long ligaments in which are embedded small sesamoid bones (Fig. 3B). This frees the autopalatine to incorporate another major structural complex that is relatively independent from the suspensorium, the palatine-maxillary system. This allows ample movements of the maxillary barbels. Like the mandibular barbels, the maxillary ones are very important for functions such as prey detection or obstacle avoiding. The major decoupling between the autopalatine and the rest of the suspensorium was seemingly acquired in the beginning of catfish evolutionary history, being almost never reverted subsequently (see Diogo, 2004).

As it is shown in Fig. 3C, in specialised catfishes such as amphiliids and many sisoroids (group formed by amblycipi-



Fig. 3. Scheme illustrating the configuration of the suspensorium of a typical primitive teleost (A) and of the catfishes *Diplomystes* (B), *Amphilius* (C) and *Loricaria* (D), according to the authors' hypothesis on the functional morphology and evolution of catfish suspensorium. Dotted areas represent articulatory facets, black structures represent ligaments, and the hatched oblique line represents the ventral surface of the neurocranium to which the suspensorium articulates (*AF-APAL-NEU* articulatory facet between autopalatine and neurocranium, *AF-PAL-NEU* articulatory facet between palatine and neurocranium, *AF-SUSP-NEU* articulatory facet between main body of suspensorium and neurocranium, *APAL* autopalatine, *L-SUSP-NEU* ligament between suspensorium and neurocranium, *PAL* palatine, *SES-BON* sesamoid bones, *SUSP* main body of suspensorium) [for more details, see text].

tids + akysids + sisorids + aspredinids + erethistids: see Fig. 1) the overall configuration of the suspensorium is still further modified in relation to that of a typical suspensorium of a primitive teleost. In these specialised catfishes, the neurocranial articulatory facet of the autopalatine is essentially situated on the posterior half of this bone (Fig. 3C). This articulatory facet therefore gives a point of support to the rear end of the autopalatine (the fore end of this bone is supported by its narrow connection with the premaxilla), thus allowing a still greater decoupling between the autopalatine and the rest of the suspensorium (Fig. 3C). The ligament connecting the main body of the suspensorium and the ethmoideal region, as well as the sesamoid bones embedded in it, are no longer in contact with the autopalatine (Fig. 3C). The ossification of this ligament is almost complete, seemingly fastening the association between the main body of the suspensorium and the neurocranium. It thus creates a somewhat solid 'second articulatory point' between these two mechanical units. Such a 'second articulatory point' between the main body of the suspensorium and the neurocranium is also found in the highly specialised loricariids, as a result of a completely different, homoplasic morphological configuration (Diogo, 2004). In fact, in loricariids, the anterodorsal margin of the main body of the suspensorium is directly articulated with the ethmoideal region, as schematised in Fig. 3D. Therefore, it can be said that some specialised catfishes, such as loricariids, amphiliids and many sisoroids, independently acquired a suspensorium configuration in which there is an almost complete functional uncoupling of the palatine–maxillary system for moving the maxillary barbels while somehow rebuilding a suspensorial articulation on the skull functionally similar to that seen in primitive teleosts (Fig. 3C,D).

5. Palatine-maxillary system

Catfish maxillary barbels are characterised by their connection to a mobile mechanism, the palatine–maxillary system, which is constituted by the maxilla, autopalatine and more or less specialised ligaments and muscles responsible for their movements. This system was discussed by Eaton (1948), Alexander (1965), Singh (1967), Gosline (1975), Ghiot (1978), Ghiot and Bouchez (1980), Howes (1983a,b, 1985), Ghiot et al. (1984), Royero and Neville (1997), Diogo et al. (2000), Diogo and Chardon (2001), and Diogo et al. (2003).

Siluriform sister-groups, i.e., Gymnotiformes and, in a broader sense, Characiformes, do not have maxillary barbels and do not present any structure prefiguring barbels, and the maxillary barbels present in some cypriniforms do not seem to be homologous to those of catfishes (see e.g., Alexander, 1965, Ghiot & Bouchez, 1980, Arratia, 1992). In fact, the catfish palatine–maxillary system is based on three basic siluriform synapomorphies, as can be seen in the scheme of Fig. 4 summarising, in major lines, some major evolutionary transitions concerning the evolution of this system within the Siluriformes.

Figure 4A schematizes the plesiomorphic configuration of catfish palatine-maxillary system, found in the basal diplomystids. The numbers 1, 2 and 3 of this Fig. 4A thus represent those three basic siluriform synapomorphies that have been present since the first stages of catfish evolutionary history and were not reverted subsequently. They are found in all extant catfishes. The synapomorphies are: (1) the distal portion of the maxilla serving as the base of the characteristic catfish maxillary barbels; (2) the uncoupling of the autopalatine from the rest of the suspensorium (see above); and (3) the differentiation of the extensor tentaculi, a muscle usually promoting the abduction of the maxillary barbels, from the adductor arcus palatini, which is mainly related to the adduction of the suspensorium. As mentioned above, the maxillary barbels are important for food searching, but also for obstacle detection and/or social behaviour. The loose attachment between the autopalatine and the rest of the suspensorium, associated with the differentiation of the muscle extensor tentaculi, permits the abduction of the maxilla and its barbel to be realised not only by the depression of the lower jaw (as in many other teleosts), but directly by the contraction of this muscle (see Diogo et al., 2003).

As shown in Fig. 4B (innovation 1), the main morphological difference between the palatine-maxillary system of diplomystid and non-diplomystid catfishes is that, in the latter, the distal end of the maxilla is no longer firmly attached to the lateral surface of the mandible by a strong ligament. This feature confers a greater freedom to the maxilla, and, thus, to the important maxillary barbels, and is present in all extant non-diplomystids (Fig. 4B–D).

Other significant morphological difference between diplomystids and the great majority of the siluriforms is the presence, in the latter, of a strong ligament connecting the premaxilla and the maxilla. This acts as the fulcrum for abduction/adduction movements of the maxillary barbel (Fig. 4C, innovation 1). However, contrary to the main morphological innovation described in the paragraph above, this feature is not present in all non-diplomystids examined. It is absent, for example, in catfishes such as nematogenyids and trichomycterids (see Fig. 4B).

Also worthy of mention is the presence, in many catfishes, of an extensor tentaculi muscle that is subdivided in several bundles (Fig. 4C, innovation 2), which confers a wider range of movements to the maxilla and its associated barbel - e.g., elevation or depression (see Diogo et al., 2003). The subdivision of the extensor tentaculi in different bundles probably arrived homoplasically in numerous catfish lineages. It is present in members of several catfish families, such as callichthyids, scoloplacids, astroblepids, loricariids, silurids, some claroteids, malapterurids, mochokids, doradids, auchenipterids, some bagrids, pimelodids, amphiliids, clariids, amblycipitids, sisorids, aspredinids or erethistids (Diogo, 2004). Another major key-innovation homoplasically acquired in different siluriform lineages and also found in several catfish taxa is the differentiation of a retractor tentaculi muscle from the innermost adductor mandibulae section. This attaches, via the primordial ligament (see Fig. 4C), directly onto the maxilla (Fig. 4D). The presence of this muscle allows the adduction of the maxilla and its barbel to



Fig. 4. Scheme illustrating the configuration of the palatine–maxillary system of the catfishes *Diplomystes* (A), *Nematogenys* (B), *Callichthys* (C), and *Scoloplax* (D), according to the authors' hypothesis on the functional morphology and evolution of this system in Siluriformes (*AF-APAL-NEU* articulatory facet between autopalatine and neurocranium, *APAL* autopalatine, *L-MX-MND* ligament between maxilla and lateral surface of mandible, *L-PRI* primordial ligament, *L-PRMX-MX* ligament between premaxilla and maxilla, *M-AD-MND* adductor mandibulae muscle, *M-EX-T* extensor tentaculi muscle, *MND* mandible, *MX* maxilla, *PRMX* premaxilla) [for more details, see text].

be realised directly by the contraction of this muscle. A retractor tentaculi muscle is found in catfishes such as scoloplacids, astroblepids, loricariids, silurids, some schilbids, some ictalurids, malapterurids, mochokids, some doradids, some auchenipterids, some bagrids, some pimelodids, amphiliids, clariids, amblycipitids, akysids, sisorids, aspredinids or erethistids (see Diogo, 2004).

The overall discussion presented in the above paragraphs thus allows us to say that functional uncouplings also played (as in the other structural complexes previously discussed) an important role in the evolution of the palatine-maxillary system within catfishes. The uncoupling of the anterior portion of the adductor arcus palatini in an extensor tentaculi muscle (Fig. 4A), together with the uncoupling between the suspensorium and the autopalatine, allows the abduction of the maxilla and its barbel to be performed not only by the depression of the lower jaw as in other teleosts, but also by direct contraction of extensor tentaculi. The loss of the firm ligamentous connection present in diplomystids between the mesial surface of the maxilla and the lateral surface of the mandible subsequently allowed, in most non-diplomystids, the maxilla to be relatively uncoupled from the movements of the mandible (Fig. 4B). The mobility of the maxilla and its associated barbel were additionally even reinforced by the functional uncoupling, in several catfish groups, between the retractor tentaculi and the adductor mandibulae, as explained above (Fig. 4D). Also, in order to better assist the movements of the maxillary barbels, the extensor tentaculi muscle became subdivided, in numerous catfish taxa, in different bundles (Fig. 4C, D) allowing a wider range of possible movements of these barbels.

6. Adductor mandibulae complex

The siluriform adductor mandibulae complex has been discussed by McMurrich (1884a,b), Jaquet (1898), Takahasi (1925), Stix (1956), Dubale and Shah (1959), Alexander (1965), Munshi (1960), Munshi and Singh (1967), Singh and Munshi (1968), Winterbottom (1974), Jayaram and Singh (1982), Howes (1983a,b, 1985), Gosline (1989), Diogo and Chardon (2000b) and Diogo and Vandewalle (2003).

As stressed by authors such as Takahasi (1925), Winterbottom (1974) or Gosline (1989), the general evolution of the adductor mandibulae complex in teleosts was also basically a history of functional uncouplings, with an almost undifferentiated mass of fibres giving a sometimes impressive number of different bundles related to different parts of the mandible, and even to other structures (e.g., maxilla). Within catfishes, functional uncouplings have also played a relevant role in adductor mandibulae evolution. One of the major keyinnovations concerning the evolution of the adductor mandibulae complex in Siluriformes is the independent differentiation, in several taxa, of a retractor tentaculi muscle directly attached on the maxilla (Fig. 4D). The evolutionary advantage of the presence of such a muscle is that it allows the adduction of that bone, and, thus, of the maxillary barbel, to be realised more efficiently by means of its direct contraction. This contraction, in contrast to that of the main adductor mandibulae complex, is thus not mainly associated with the opening/closure of the mouth, but rather with a direct adduction of the maxillary barbels. Thus, again, this is a typical evolutionary decoupling in which a complex (the adductor mandibulae complex) originally essentially associated with a certain mechanism X (mouth opening/closure) is uncoupled: one part derived from it (the retractor tentaculi) performs a new mechanism Y (the adduction of the maxilla by direct muscular contraction); the other part (the remaining adductor mandibulae complex) continues to perform the original mechanism X (mouth opening/closure). In this way, not only has the organism now the possibility of performing the new mechanism Y, but this can also be eventually associated with certain other already available mechanisms (Z, W, etc.). This, as referred in the Introduction, facilitates diversification and speciation by increasing the number of degrees of freedom and allowing a wider range of possible mechanical solutions for functional problems.

General comments

In this paper, we briefly analyzed the importance of functional uncouplings in the evolution of six catfish major structural complexes, namely those formed by the mandibular barbels and associated structures, the pectoral girdle complex, the elastic spring apparatus, the suspensorium, the palatine-maxillary system, and the adductor mandibulae complex. In a certain way, one could say that catfish macroevolutionary history is, in part, effectively a history of functional uncouplings, with such uncouplings having effectively played an important role in the macroevolution of all these six structural complexes. The study of siluriforms therefore strongly supports the importance of functional uncouplings in morphological macroevolution. This cosmopolitan and diverse group of fishes thus seems to constitute, in effect, a particularly interesting case study for broader discussions on theoretical biology and general macroevolution.

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