THE ORIGIN AND TRANSFORMATION OF THE PALATINE-MAXILLARY SYSTEM OF CATFISH (TELEOSTEI: SILURIFORMES): AN EXAMPLE OF MACROEVOLUTION

by

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ABSTRACT

Barbels are a general characteristic of Siluriformes, responsible for their popular name "catfish". Among the three types of catfish barbels — mandibular, maxillar and nasal — the maxillary ones are characterized by their connection to a mobile mechanism, the palatine-maxillary system (PMS). Siluriform sister-groups (Gymnotiformes and Characiformes) do not have barbels at all and do not present any structure prefiguring barbels, particularly the maxillary barbels, which are the only ones present in the most primitive catfishes, the diplomystids. So, in the absence of well preserved fossils, a gap remains between the diplomystids and the other ostariophysans. However, starting from the Diplomystidae, it seems possible to hypothesise evolutionary lines leading to more specialised PMS types. The present paper focuses on the evolution of the PMS among catfish. For each morphological transformation, the way it was realised is hypothesized and the probable adaptive advantage it brings is analysed.

KEY WORDS: adaptation, catfish, functional morphology, palatine-maxillary system, macroevolution, maxillary barbels, Siluriformes.

INTRODUCTION

Barbels are a general characteristic of Siluriformes, responsible for their popular name "catfish". Their adaptive value for muddy waters dwellers and nocturnal fish (see ALEXANDER, 1965) was demonstrated experimentally (HERRICK, 1903; BOWEN, 1931; HOAGLAND, 1932; TATEDA, 1961; BIEDENBACH, 1971). Among the three types of catfish barbels — mandibular, maxillar and nasal — the maxillary ones are characterized by their connection to a mobile mechanism, the palatine-maxillary system (PMS), which is constituted by the maxillary, the palatine and

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more or less specialised ligaments and muscles responsible for their move-
ments (GOSLINE, 1975). They are supported by a central rod compris-
ing a dense network of elastin with or without cartilage (GHIOT, 1978;
GHIOT & BOUCHEZ, 1980; BENJAMIN, 1990). The proximal end of
this rod is firmly incrusted in the hollow distal end of the maxillary bone
(GHIOT, 1978; GHIOT & BOUCHEZ, 1980; GHIOT et al., 1984; SKEL-
TON, 1981). Their skin is covered with mucus cells and taste buds (HER-
RICK, 1903; GHIOT, 1978; GHIOT & BOUCHEZ, 1980; BENJAMIN,
1990).

Siluriform sister-groups (Gymnotiformes and Characiformes) do not
have barbels at all and do not present any structure prefiguring barbels,
particularly the maxillary barbels, which are the only ones present in
the most primitive catfishes, the diplomystids (FINK & FINK, 1981;
ARRATIA, 1987; 1992; GRANDE, 1987). In fact, catfish PMS shows
two basic siluriform synapomorphies: 1) the uncoupling of the palatine
from the rest of the suspensorium (REGAN, 1911; ALEXANDER, 1965;
GOSLINE, 1975; ARRATIA & SCHULTZE, 1991; ARRATIA, 1992)
and 2) the differentiation of the adductor arcus palatini in a separate
muscle usually called extensor tentaculi, which, in most cases, abducts
the maxillary barbel (ALEXANDER, 1965; WINTERBOTTOM, 1974;
GOSLINE, 1975; GHIOT, 1978; GHIOT et al., 1984). So, unless well
preserved fossils are described in the future, a gap will remain between the
diplomystids and the gymnotiforms and characiforms. However, starting
from the Diplomystidae, it seems possible to hypothesise evolutionary
lines leading to more specialised PMS types. The present paper focuses
on the evolution of the PMS among catfish. For each morphological
transformation, the way it was realised is hypothesized and the probable
adaptive advantage it brings is analysed.

MATERIAL AND METHODS

The studied fishes are from the private collection of our laboratory
(LFEM: Laboratory of Functional and Evolutionary Morphology), from
the Université Nationale du Bénin (UNB), the Musée Royal de l'Afrique
Centrale of Tervuren (MRAC), the Muséum National d'Histoire Naturelle
(MNHN) of Paris, and from the National Museum of Natural History of
Washington (USNM). Anatomical descriptions are made after dissection
of fresh, alcohol fixed or trypsin-cleared and alizarine-stained (following
the method of TAYLOR & VAN DIKE, 1985) specimens. Dissections
and morphological drawings were made using a Wild M5 dissecting
microscope equipped with a camera lucida. The fresh (fre), trypsine-
cleared and alizarine-stained (t&a) 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): MRAC 89-043-P-403, 1 (alc); MRAC 89-043-P-2333, 1 (t&a). *Amphilius jacknosi* (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* (Amphiliidae): MNHN 1961-0600, 1 (alc); *Arius hertzbergii* (Ariidae): LFEM, 1 (alc). *Amarginops cranchii* (Claroteidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999 (alc). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); LFEM, 5 (fre); MRAC 86-07-P-516, 1 (t&a). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc); LFEM, 2 (t&a). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 5 (fre); UNB, 2 (t&a). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 3 (fre); UNB, 2 (t&a). *Doumea typica* (Amphiliidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152. *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Genidens genidens* (Ariidae): LFEM, 3 (alc); *Glyptosternum maculatum* (Sisoridae): LFEM, 3 (alc); *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Loricaria cataphracta* (Loricariidae): LFEM, 2 (alc); LFEM, 1 (t&a); *Malapterurus electricus* (Malapteruridae): MRAC 90-057-P-2373, 1 (alc); 90-057-P-2374, 1 (alc); 90-057-P-2375, 1 (t&a); *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Phractura brevicauda* (Amphiliidae): MRAC 90-057-P-5145, 1 (alc); MRAC 92-125-P-386, 1 (t&a). *Phractura intermedia* (Amphiliidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias (*Pimelodidae): LFEM, 2 (alc); LFEM, 3 (fre); LFEM, 2 (t&a). *Plotosus lineatus* (Plotosidae): USNM 200226, 2 (alc); *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (t&a). *Schilbe mystus* (Shilbeidae): MRAC P.58661, 1 (t&a).

RESULTS

The PMS of six catfish species, representing different levels of PMS specialisation, is described in fig. 1.

Diplomystes chilensis (Molina, 1972)

The posterior end of the palatine is loosely associated to the posterior part of the suspensorium by sesamoid bones and ligaments (fig. 1a). It articulates medially and dorsally with the neurocranium and anteriorly, by means of its fore cartilage, with the maxilla (fig. 1a). The maxillary
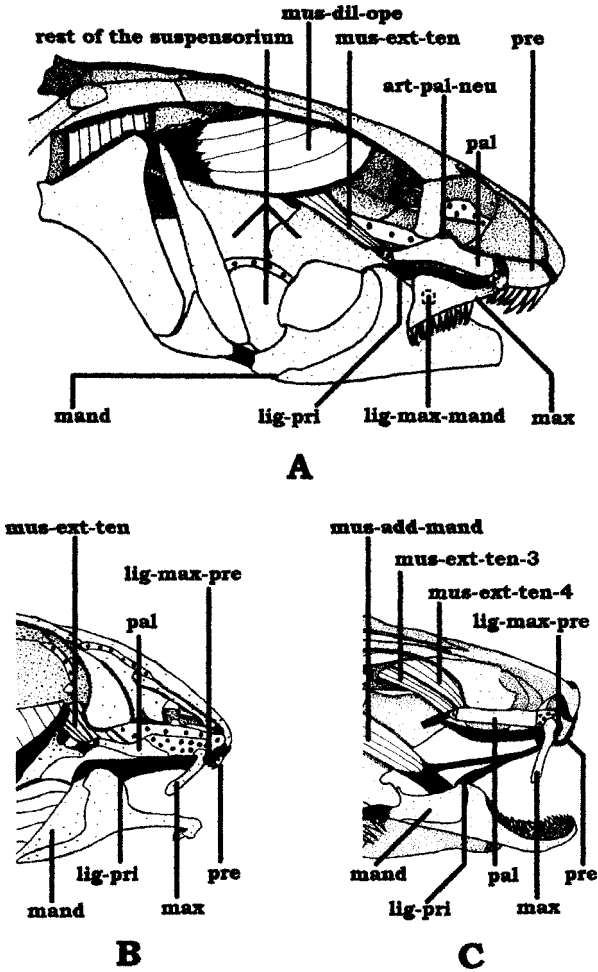
Fig. 1. Lateral view of: A) The cranium of *Diplomystes chilensis*. B) The anterior region of the cranium of *Chrysichthys nigrodigitatus*. C) The anterior region of the cranium of *Bagrus docmak*. Bones are represented by thin dots, cartilages by large black dots, muscles by stripes and ligaments are in plain black. Art-pal-neu: articular facet of the palatine with the neurocranium; lig-max-man: ligamentum maxillo-mandibulare; lig-max-pre: ligamentum maxillo-premaxillare; lig-pri: ligamentum primordiale; mand: mandible; max: maxillary; mus-add-mand: muscle adductor mandibulae; mus-dil-ope: muscle dilatator operculi; mus-ext-ten: muscle extensor tentaculi; mus-ext-ten-3, mus-ext-ten-4: bundles of the muscle extensor tentaculi; pal: palatine; pre: premaxillary.

bears teeth (fig. 1a) like in most teleosts, but such maxillary teeth are lacking in all other catfishes, except in the Eocene fossil *Hypsidoris farsonensis* (GRANDE, 1987; MO, 1991; ARRATIA, 1992). This bone is attached to the lower jaw by two ligaments (fig. 1a): the primordial ligament joining its proximal end to the coronoid process of the dentary and a thick ligament between its medial aspect and the lateral face of the mandible. The extensor tentaculi is the sole muscle associated to the PMS. It extends from the neurocranium to the rear end of the palatine (fig. 1a). Some of its fibres are still mixed with those of the adductor arcus palatini muscle. The way the palatine-maxillary system works is rather simple (fig. 2). The extensor tentaculi pulls the palatine backward thanks to the mobile articulation between this bone and the neurocranium (fig. 1a) and thus also pulls the proximal end of the maxilla (fig. 2a→b), which is linked through a cartilaginous joint to the palatine (fig. 1a). The backward movement of the proximal part of the maxilla provokes an anteroventral displacement of its posterior end because of the thick ligament attaching its distal extremity to the lower jaw (fig. 2a→b). The maxillary barbel, whose proximal end is firmly incrusted in the hollow distal extremity of the maxillary bone (see fig. 1), follows the maxilla and turns to ventral and forward (fig. 2a→b). Such PMS in which maxillary barbel abduction results from a longitudinal movement of the palatine are called "sliding type" by GOSLINE (1975). The abduction of the maxillary barbel may also result from mouth opening thanks to the same thick mandibulo-maxillary ligament (fig. 2a→b), which rotates the maxilla in the same way as in many teleost with a partially freed maxilla (ALEXANDER, 1965; GOSLINE, 1975).

Chrysichthys nigrodigitatus (Lacépède, 1803)

The posterior end of the palatine is indirectly linked to the posterior sus-pensorium through sesamoid bones and ligaments (fig. 3a). The pala-tine articulates mediodorsally with the neurocranium and anteriorly by its large cartilaginous end to the proximal end of the maxilla (figs 1b, 3a). The maxilla is a thin rod-like bone linked to the premaxilla and dentary by ligaments, and free at its distal end (figs 1b, 3a). Like in *Diplomystes*, there is only one muscle associated to the PMS: the extensor tentaculi. However, in *Chrysichthys* this muscle is completely distinct from the ad-ductor arcus palatini and its fibres are oriented obliquely rather than lon-gitudinally (figs 1b, 3a). The mechanism of the PMS remains simple. The extensor tentaculi pulls the posterior end of the palatine and the associ-ated sesamoid bones mediodorsally. The firm articulation of the palatine on the neurocranium prevents a longitudinal displacement of the palatine (fig. 3a→b). The anterior end of the palatine and the proximal tip of the
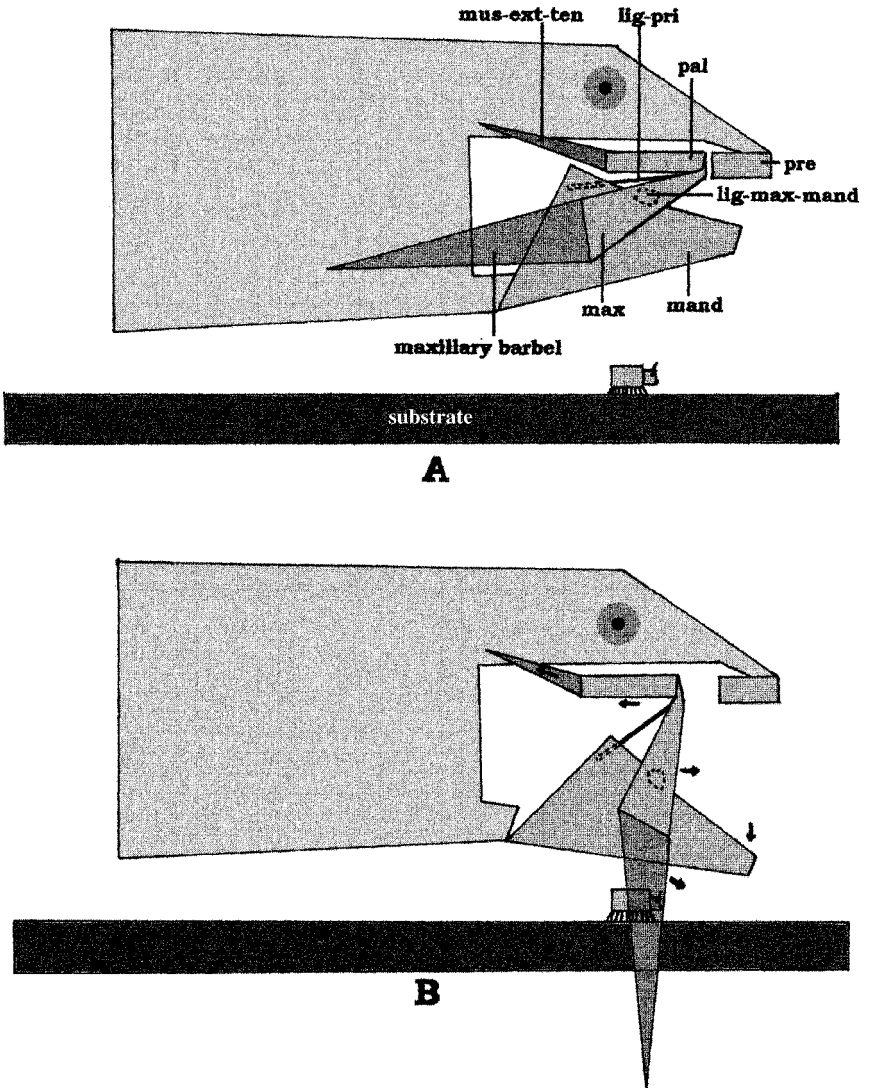
Fig. 2.   Scheme illustrating the PMS of *Diplomystes chilensis* (for explanations, see text):
A) The maxillary barbel is adducted. B) The maxillary barbel is abducted. Lig-max-man:
ligamentum maxillo-mandibulare; lig-pri: ligamentum primordiale; mand: mandible;
 max: maxillary; mus-ext-ten: muscle extensor tentaculi; pal: palatine; pre: premaxillary.
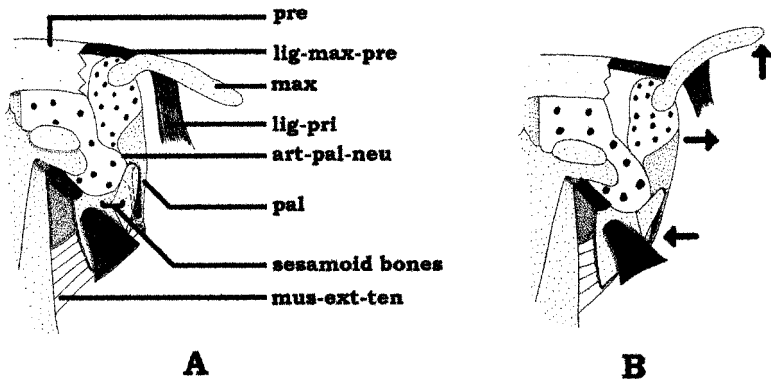
Fig. 3.   Ventral view of the PMS of *Chrysichthys nigrodigitatus* (for explanation, see text): A) The maxillary barbel is adducted. B) The maxillary barbel is abducted. Art-pal-neu: articulatory facet of the palatine with the neurocranium; lig-max-pre: ligamentum maxillo-premaxillare; lig-pri: ligamentum primordiale; max: maxillary; mus-ext-ten: muscle extensor tentaculi; pal: palatine; pre: premaxillary.

maxilla associated with it therefore move latero-ventrally and, thus, be-
cause of the resistance of the premaxillary-maxillary ligament, abduct the
maxilla (fig. 3a→b) and its associated barbel. This kind of PMS with a
rocking movement of the palatine is called "rocking type" by GOSLINE
(1975). The adduction of the maxillary barbel results from mouth closure.
When the anterior tip of the mandible moves upward, the insertion of the
primordial ligament (fig. 1b) moves back, pulling the maxilla and thus
adducting the barbel.

Bagrus docmak (Forsskall, 1775)

The palatine is loosely associated to the rest of the suspensorium by liga-
ments and sesamoid bones and to the neurocranium by a broad articulatory
surface (figs 1c, 5a). Anteriorly, it articulates with the proximal tip of the
maxilla (figs 1c, 5a). The maxilla is linked to the premaxilla, suspenso-
rium and mandible by ligaments (figs 1c, 5a). The muscles associated to
the PMS are the extensor tentaculi and the adductor mandibulae. The first
one is differentiated in four bundles, all of them attaching to the palatine:
bundle 1 is attached to its postero-medial face (fig. 4a), bundle 2 to the
postero-ventral face (fig. 4a), and bundles 3 and 4 to the posterior (figs 1c,
4a, 5a) and postero-dorsal (fig. 1c) faces, respectively. The tendon of the
inner section of the adductor mandibulae is fused to the primordial liga-
ment (fig. 1c). The PMS works as follows. The extensor tentaculi 3 pulls
the palatine backward along its long, sliding articular facet with the neu-
rocranium (fig. 5a). The proximal end of the maxilla linked with the pala-
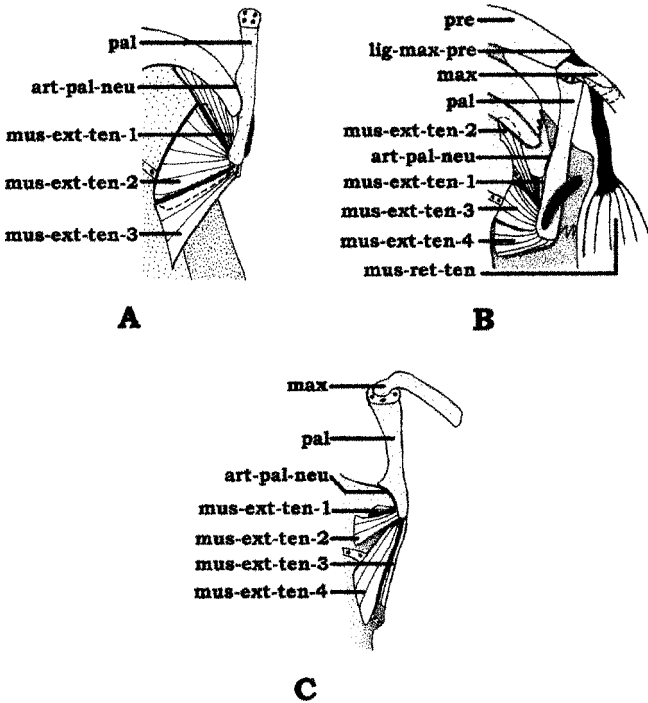tine is thus also pulled posteriorly, but the maxillo-premaxillary ligament

Fig. 4.   Ventral view of the left side of the anterior region of the cranium of: A) *Bagrus docmak*. B) *Clarias gariepinus*. C) *Amphilius brevis*. Art-pal-neu: articulatory facet of the palatine with the neurocranium; lig-max-pre: ligamentum maxillo-premaxillare; max: maxillary; mus-ext-ten-1, mus-ext-ten-2, mus-ext-ten-3, mus-ext-ten-4: bundles of the muscle extensor tentaculi; mus-ret-ten: muscle retractor tentaculi; pal: palatine; pre: premaxillary.

provokes the rotation of the maxilla and the abduction of its distal part (fig. 5a) and of the associated barbel. The adduction of the barbel may result: from the contraction of the extensor tentaculi 1, which is the antagonist of the extensor tentaculi 3 (fig. 4a), and from the contraction of the adductor mandibulae muscle, which, *via* its insertion on the primordial ligament (fig. 1c), pulls the maxilla backward. Elevation and depression of the maxillary barbel are also possible. Elevation results from the rotation-elevation of the distal end of the maxillary by the contraction of the extensor tentaculi 4, which inserts on the postero-dorsal surface of the palatine (fig. 1c; fig. 3b). The extensor tentaculi 2 provokes the opposite movement, that is, the depression of the maxillary barbel, by pulling on the postero-ventral face of the palatine.
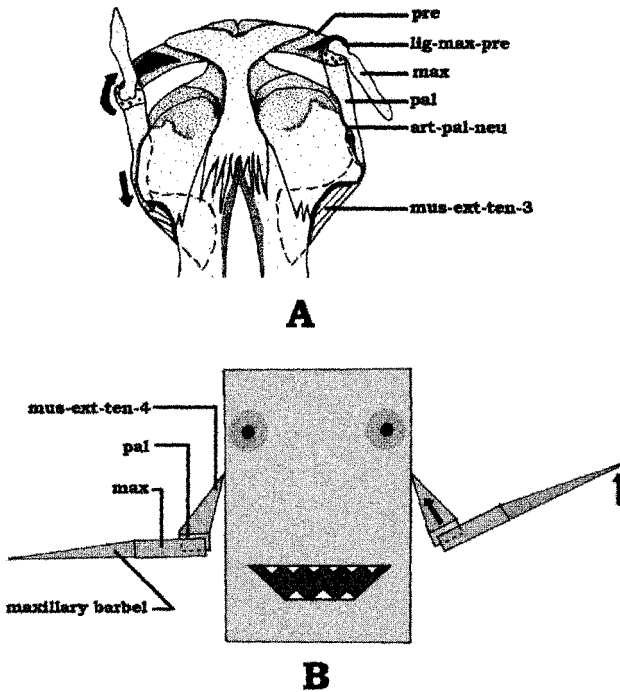
Fig. 5.   Scheme illustrating the PMS of *Bagrus docmak* (for explanation, see text): A) Dorsal view of the anterior region of the cranium showing the abduction of the maxillary barbel (in the left side). B) Frontal view of the cranium showing the elevation of the maxillary barbel (in the right side). Art-pal-neu: articulatory facet of the palatine with the neurocranium; lig-max-pre: ligamentum maxillo-premaxillare; max: maxillary; mus-ext-ten-3, mus-ext-ten-4: bundles of the muscle extensor tentaculi; pal: palatine; pre: premaxillary.

Pimelodus clarias (Bloch, 1795)

The PMS is identical to that of *Bagrus docmak* except that the tendons of the adductor mandibulae are completely distinct from the primordial ligament.

Clarias gariepinus (Burchell, 1822)

The palatine is associated to the posterior part of the suspensorium by ligaments and sesamoid bones and articulates with the neurocranium and the premaxilla (fig. 4b). This latter bone is linked by a small ligament to the maxilla (fig. 4b). Two muscles are integrated in the PMS: the extensor tentaculi and the retractor tentaculi. The first one is differentiated in five bundles, all of them attaching to the palatine

(fig. 4b): bundles 1 and 2 are attached to its postero-medial face, bundle 3 to its postero-ventral face, and bundles 4 and 5, respectively, to its posterior and postero-dorsal faces. The retractor tentaculi, differentiated from the adductor mandibulae (TAKAHASI, 1925; ALEXANDER, 1965; WINTERBOTTOM, 1974; DIOGO & CHARDON, in press), originates on the suspensorium and inserts on the maxillary (fig. 4b). Abduction of the maxillary barbels is realised by the 2 and 4 bundles of the extensor tentaculi, in a "rocking type" mechanism similar to that of *Chrysichthys nigrodigitatus* (fig. 4b). The adduction of the barbels is provoked by the retractor tentaculi (fig. 4b), which pulls the maxilla backward. Their depression and elevation result from the contraction of, respectively, the 3 and 5 bundles of the extensor tentaculi, which work like the extensor tentaculi 2 and 4 of *Bagrus docmak* (see above).

Amphilius brevis (Boulenger, 1902)

The PMS is very similar to that of *Clarias gariepinus*. Two differences are noticeable (fig. 4c): the neurocranium articulatory facet of the palatine lies on its posterior extremity, and the palatine is completely separated from the rest of the suspensorium.

DISCUSSION

Our hypothesis concerning the evolution of catfish PMS is illustrated in figure 6. The six different steps schematised in this figure (fig. 6a, b, c, d, e, f) are not the elements of one single evolutionary lineage, but represent evolutionary levels of PMS specialisation in not directly related species of different catfish lineages (for catfish phylogeny see, for example, MO, 1991; DE PINNA, 1993). For each step, innovations and supposed adaptive advantages are pointed out.

Diplomystes chilensis (fig. 6a)

Innovations represent catfish plesiomorphic characters, since diplomystids are the most primitive siluriform and are very probably close to the ancestor of all catfishes (see, for example, REGAN, 1911; CHARDON, 1968; ARRATIA, 1987; 1992; GRANDE, 1987; MO, 1991). 1) The maxillary barbels, which are not present in catfish sister-groups (Gymnotiformes and Characiformes; FINK & FINK, 1981) and are not homologous of those of cyprinids (ARRATIA, 1987); 2) The palatine just loosely attached to the rest of the suspensorium (REGAN, 1911; ALEXANDER, 1965; GOSLINE, 1975); 3) The extensor tentaculi muscle resulting
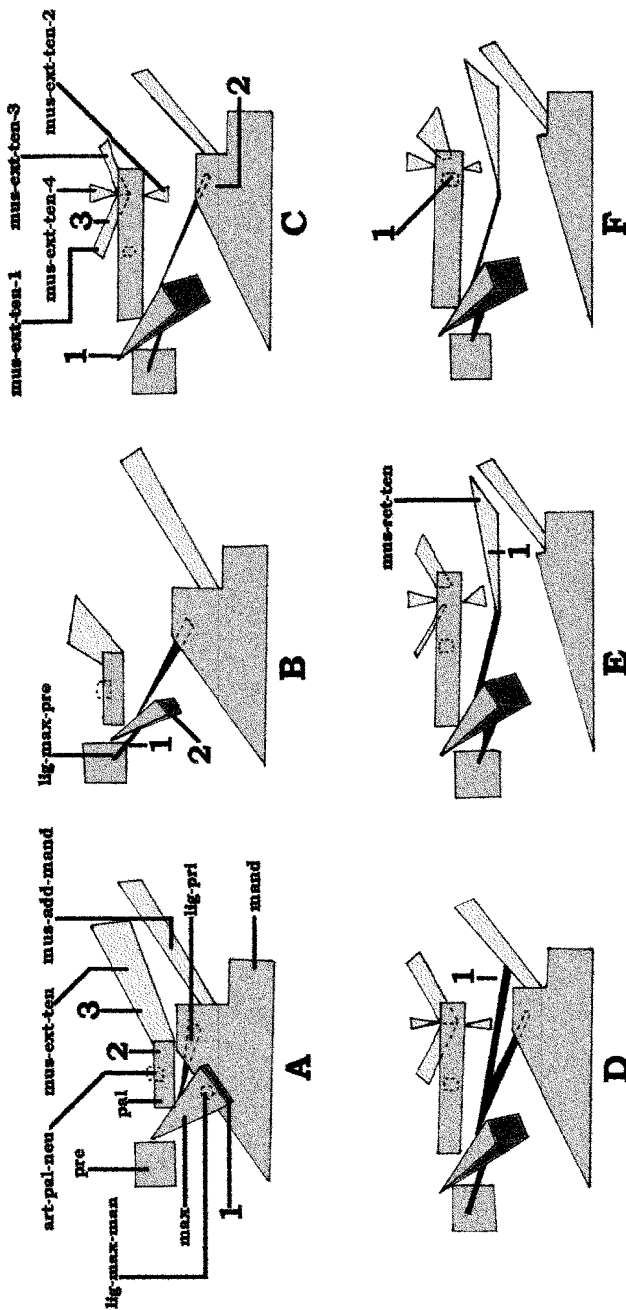
Fig. 6. Scheme illustrating our hypothesis on the evolution of the PMS in catfish (for numbers and further explanation, see text): A) *Diplomystes chilensis*. B) *Chrysichthys nigrodigitatus*. C) *Pimelodus clarias*. D) *Bagrus docmak*. E) *Clarias gariepinus*. F) *Amphilius brevis*. Art-pal-neu: articulatory facet of the palatine with the neurocranium; lig-max-man: ligamentum maxillo-mandibulare; lig-max-pre: ligamentum maxillo-premaxillare; lig-pri: ligamentum primordiale; mand: mandible; max: maxillary; mus-add-mand: muscle adductor mandibulae; mus-ext-ten: muscle extensor tentaculi; mus-ext-ten-1, mus-ext-ten-2, mus-ext-ten-3, mus-ext-ten-4: bundles of the muscle extensor tentaculi; mus-ret-ten: muscle retractor tentaculi; pal: palatine; pre: premaxillary.

from the differentiation of the anterior part of the adductor arcus palatini (ALEXANDER, 1965; WINTERBOTTOM, 1974; GOSLINE, 1975).

Adaptive advantages: The maxillary barbels are useful in food searching, in obstacles detection and in social behaviour (HERRICK, 1903; BOWEN, 1931; HOAGLAND, 1932; TATEDA, 1961; BIEDENBACH, 1971). The loose attachment between the palatine and the rest of the suspensorium, associated with the differentiation of the extensor tentaculi muscle, permits that the abduction of the maxilla and its associated barbel is realised not only by the depression of the lower jaw, but also directly by contraction of this muscle (fig. 2a→b).

Chrysichthys nigrodigitatus (fig. 6b)

This species belongs to the Claroteidae, which is considered a generalised catfish family (MO, 1991; DIOGO & CHARDON, 2000).

Innovations: 1) A *de novo* ligament joining the maxilla to the premaxilla, which is present in most catfishes; 2) The distal end of the maxilla is no longer attached to the lateral face of the mandible by a strong ligament.

Adaptive advantages: The new maxillo-premaxilla ligament acts as the fulcrum for maxillary barbel abduction/adduction movements, replacing the maxillo-mandibulary ligament, but conferring a greater freedom to the distal end of the maxilla (fig. 3a→b). Consequently, the exploration range of the maxillary barbel in food searching and obstacles detection is increased.

Pimelodus clarias (fig. 6c)

Pimelodids are considered as generalised, but somewhat more specialised than claroteids (MO, 1991; DIOGO & CHARDON, 2000).

Innovations: 1) The proximal end of maxilla is dorsal and no longer posterior to the premaxilla; 2) The mandible is dorsoventrally depressed; 3) The extensor tentaculi is divided into several bundles.

Adaptive advantages: The dorsal position of the proximal end of the maxilla relative to the premaxilla greatly increases its mobility and allows an almost 180° abduction (see, for example, fig. 5a). The differentiation of the 2 and 4 bundles of the extensor tentaculi muscle moreover allows depression and elevation of the barbels (see above). The skull and mandible are more flattened in *Pimelodus clarias* (a benthic species as are most catfishes, ALEXANDER, 1965), than in the not fully benthic *Diplomystes chilensis* (ARRATIA, 1987) and *Chrysichthys nigrodigitatus* (DIOGO & CHARDON, 2000). The mandibular depression is related to the

flattening of the skull, which is probably advantageous to benthic catfishes (ALEXANDER, 1965). With such a flattened skull, the maxillary barbel adduction mechanism of *Chrysichthys* (see above) would be inefficient. However, another adduction mechanism is created by the differentiation of the bundle 1 of the extensor tentaculi (see above).

Bagrus docmak (fig. 6d)

Bagrids are considered more specialised than claroteids (MO, 1991; DIOGO *et al*., 1999; DIOGO & CHARDON; 2000) and are probably related to pimelodids (MO, 1991; DE PINNA, 1993).

   Innovations: 1) One tendon of the adductor mandibulae fuses with the primordial ligament and inserts on the maxilla.

   Adaptive advantages: The maxillary barbel is adducted by contraction of the adductor mandibulae, which inserts directly on the maxilla (fig. 1c), pulling it backward. That mechanism is clearly more efficient than the indirect adduction by the extensor tentaculi 1, which retracts the maxilla through the palatine bone and maxillo-premaxillo ligament (see above).

Clarias gariepinus (fig. 6e)

This species belongs to the family Clariidae, which is considered spe-cialised (ALEXANDER, 1965; CHARDON, 1968; GOSLINE, 1975; MO, 1991).

   Innovations: 1) The retractor tentaculi clearly results from the differen-tiation of the most internal bundle of the adductor mandibulae and forward migration of its tendon *via* the primordial ligament (ALEXANDER, 1965; HOWES, 1983; DIOGO & CHARDON, in press). Such a muscle is present in some other catfish families (ALEXANDER, 1965; GOSLINE, 1975; FINK & FINK, 1981; HOWES, 1983).

   Adaptive advantages: The differentiation of the retractor tentaculi asso-ciated with the loss of the primordial ligament completely uncouples the abduction/adduction of the maxillary barbel from mouth opening/closure, and allows independent specialisation of both the PMS and the mandible. The retractor tentaculi, directly inserting on the maxilla (fig. 4b), is much more efficient for adducting the latter bone and its associated barbel than the extensor tentaculi 1, which may explain the reduction of that bundle (fig. 4b).

Amphilius brevis (fig. 6f)

Amphiliids are one of the most specialised catfishes (HARRY, 1953; CHARDON, 1968; Mo, 1991).

Innovations: 1) The neurocranial articulation of the palatine lies on its posterior part.

Adaptive advantages: The palatine gains from the neurocranial articulation a firm posterior support, which makes the connection between this bone and the rest of the suspensorium by means of sesamoid bones and ligaments useless and may explain the disappearance of these structures (see DIOGO & CHARDON, 1998). This structural modification increases the mobility of the palatine and the efficiency of the PMS, and the abduction range of the maxillary barbel: a small medial movement of the posterior end of the palatine, via its "rocking" articulation with the neurocranium (fig. 4c), results in an large lateral displacement of its anterior tip, and, thus, in an ample abduction of the maxilla and its associated barbel.

GENERAL CONCLUSIONS

GALIS (1996) states that structural innovation is associated to four main types of morphological events: 1) structural uncouplings; 2) acquisition of new structures; 3) loss of a function by a structure that subsequently becomes available for a new function; and 4) duplication of structures. In the particular case of this study, the types 1 (uncoupling between the palatine and the rest of the suspensorium; uncoupling of the adductor arcus palatini, resulting in the differentiation of the extensor tentaculi; uncoupling between the maxillary and the mandible; uncoupling of the extensor tentaculi in various bundles; uncoupling of the adductor mandibulae, resulting in the differentiation of the retractor tentaculi), 2 (the maxillary barbels and the ligaments between the premaxilla and the maxilla are *de novo* formations), and 3 (the palatine and the maxillary have lost their ancestral function, to become incorporated in the PMS) certainly played a important role in PMS evolution. The present study however demonstrates the importance of one more evolutionary process for innovation: simple shape changes and/or in displacement of articulations or muscle and ligament insertions on a structure. Four of the eleven innovations observed in PMS evolution pertain to that category: the elevation of the proximal end of the maxilla relative to the premaxilla (fig. 6C: 1); mandible flattening (fig. 6C: 2); the antero-dorsal migration of one of the tendons of the adductor mandibulae into the primordial ligament (fig. 6D: 1); the backward migration of the neurocranial articulation facet of the palatine (fig. 6F: 1).

PMS evolution provides a good example of adaptive macroevolution: the evolution of catfish PMS seems to be the result of several gradual, non dramatic morphological innovations, all of them with (probably) an important functional adaptive significance. Such examples remain too rare (see GALIS, 1996), and are useful in the controversy between functional morphologists and authors arguing in favour of the neutral theory of evolution even at the macroevolutionary level (see CASINOS, 1990)

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