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Morphological description of the cephalic region of *Bagrus docmac*, with a reflection on bagridae (teleostei: siluriformes) autapomorphies

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KEYWORDS: Siluriformes, Bagridae, *Bagrus*, cephalic region, autapomorphies, morphology.

ABSTRACT

The cephalic structures of *Bagrus docmac* (Forsskal 1775) are described and compared with those of other bagrids and out-group siluroids as the foundation for a phylogenetic analysis of the Bagridae autapomorphies. From the six characters usually accepted in the literature as bagrid autapomorphies — prominent posterior process of the posttemporal; presence of a retractor posttemporalis muscle; large heavily ossified posttemporal; well-developed posttemporal fossa with a postero-lateral exit; thickened dorso-medial limb of the posttemporal; large, crescentic vomerine head — only the first five can be considered as such, since the shape of the vomer is quite similar to that in some other out-group catfishes. However, one other morphological feature is shown to be a bagrid autapomorphy: the differentiation of the adductor mandibulae A3'-d into a large and a small sub-division, inserted on the posterior and postero-dorsal edges of the coronomeckelian bone, respectively. Bagridae autapomorphies are very likely related to the production of sound and to the reinforcement of the efficiency of mouth closure, and may explain the biological success of bagrids among Ancient World catfishes, and, particularly, on the Asiatic continent.

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Introduction

The Siluriformes, with their 2584 species, represent about 32% of all freshwater fishes (TEUGELS, 1996). They 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).

Among the 34 catfish families, the family Bagridae is one of the most attractive, not only for its large geographical distribution, morphological diversity and economical importance (MO, 1991), but also since the bagrids are, probably, at the basis of the adaptive explosion of the Siluriformes (see for example, JAYARAM, 1966a; CHARDON, 1968; GOSLINE, 1975; MO, 1991). The taxonomic situation of the family has greatly changed through the endeavours of various ichthyologists (for an historical and nomenclature account of the family, see for example, JAYARAM, 1966a; BAILEY & STEWART, 1983; 1984; TAYLOR, 1985; MO, 1991). The classification of MO (1991) is the more commonly accepted one. This author transferred a large number of genera previously considered as Bagridae to four different families: Austroglanidae (new family created by MO), Claroteidae, Amphiliidae and Schilbeidae. As principal argument for this separation, MO described six morphological features (autapomorphies) that define the bagrid fishes, and that distinguish them from all the other Siluriformes: 1) presence of the retractor posttemporalis muscle; 2) well-developed posttemporal fossa with a postero-lateral exit; 3) large heavily ossified posttemporal; 4) presence of a prominent posterior process of the posttemporal; 5) thickened dorso-medial limb of the posttemporal; 6) large, crescentic vomerine head.

The bagrids (*sensu* MO, 1991) have been the subject of numerous morphological studies (DAVID, 1936; HORA, 1936; TILAK, 1965; 1967; VASISHT & UBEROI, 1965; JAYARAM, 1966a, b; 1968; 1971; 1973a, b; 1976; HASHMI, 1967; BHARGAVA, 1971; DESOUTTER, 1975; BAILEY & STEWART, 1983; 1984; MO, 1991). Most studies are dedicated to the head region, and particularly to the cranial osteology. In fact, the only descriptions of the cephalic musculature of some bagrid fishes are those given by TAKAHASI (1925), STIX (1956), VASISHT & AGGARWAL (1972), JAYARAM & SINGH (1982), GHIOT *et al.* (1984) and MO (1991). These descriptions are not very detailed since most studies include a large number of catfish families, or even different Ostariophysi orders.

The aim of this work is 1) to study in detail the osteology and myology of the cephalic region (branchial apparatus excluded) of *Bagrus docmac* (Forskall, 1775), 2) to compare these structures with those of other bagrids and out-group siluroids as the foundation for a phylogenetic analysis of the Bagridae autapomorphies and 3) to discuss the functional and adaptative significance of these autapomorphies.

Material and methods

The fishes studied are from the private collection of our laboratory (LFEM), from the "Musée Royal de l'Afrique Centrale" of Tervuren (MRAC) and from the "Université Nationale du Bénin"

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(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 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 is given below.

Amphilius brevis (Amphiliidae): MRAC 89-043-P-403, 1 (alc); MRAC 89-043-P-2333, 1 (t&a). *Amphilius jacknosi* : LFEM, 2 (alc). *Arius hertzbergii* (Ariidae): FFEM, 1 (alc). *A rmaginops 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 docmac*: MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); 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, 2 (t&a). *Chrysichthys nigrodigitatus* : UNB, 2 (alc); 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). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); LFEM, 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*: MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias (*Pimelodidae): LFEM, 2 (alc), LFEM, 2 (t&a). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (t&a).

Results

The description of the cephalic structures of *Bagrus docmac* is best appreciated from the figures. Only a short description in words is given.

OSTEOLOGY

The nomenclature for the osteologic structures basically follows that used by DAGET (1964).

Os mesethmoideum (o-meth): Unpaired. Forked anteriorly, with a ligament at each of the antero-lateral extremities that supports the premaxillary (**figs 2, 6**).

Os latero-ethmoideum (o-leth): Paired. With a lateral articulation facet for the palatine (**figs 1, 2, 3, 8**).

Os vomerale (o-vm): Unpaired. T-shaped (**fig. 3**), with a ventral toothplate at its rostral end (**fig. 1**).

Fig. 1. Lateral view of the skull of *Bagrus docmac* (MRAC 86-07-P-516). Infraorbital series, ligament between the mesethmoid and the premaxillary and ligaments linking the maxillary to the mandible, premaxillary and metapterygoid were removed.

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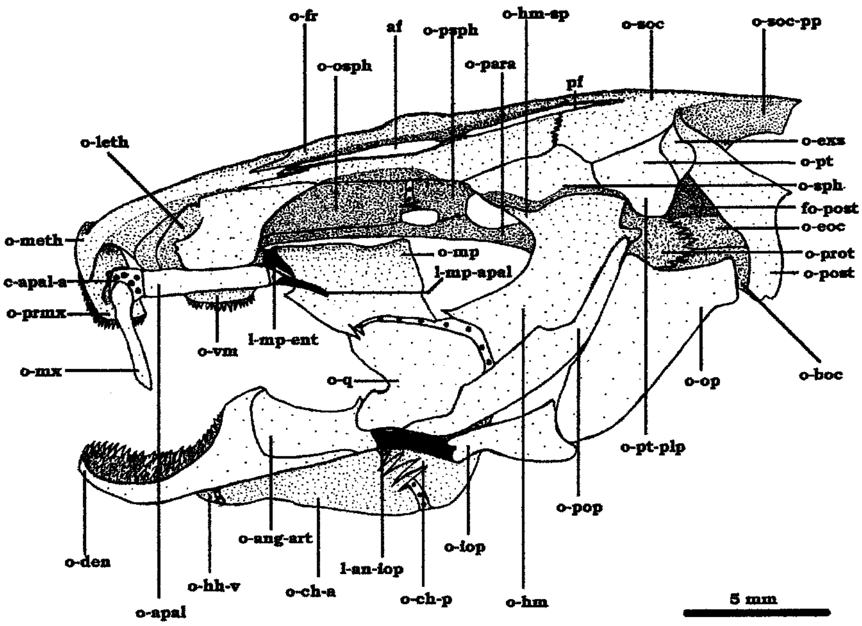


Os orbitosphenoideum (o-osph): Paired. Posterior to the lateral ethmoid (**figs 1,3**).

Os parasphenoideum (o-para): Unpaired. The longest bone of the cranium (**fig. 3**).

Os pterosphenoideum (o-psph): Paired. Posterior to the orbitosphenoid (**figs 1, 3**).

Os sphenoticum (o-sph): Paired. It presents, together with the pterotic, an articulatory facet for the hyomandibula (**figs 1, 3**).

Os pteroticum (o-pt): Paired. There is a large postero-lateral process at its dorsal surface (**figs 1, 2, 3**).

Os prooticum (o-prot): Paired. The foramen of the trigemino-facial nerve complex is situated between this bone, the pterosphenoid and the parasphenoid (**figs 1, 3**).

Os epioticum (o-epot): Paired. Small bone situated on the posterior surface of the neurocranium.

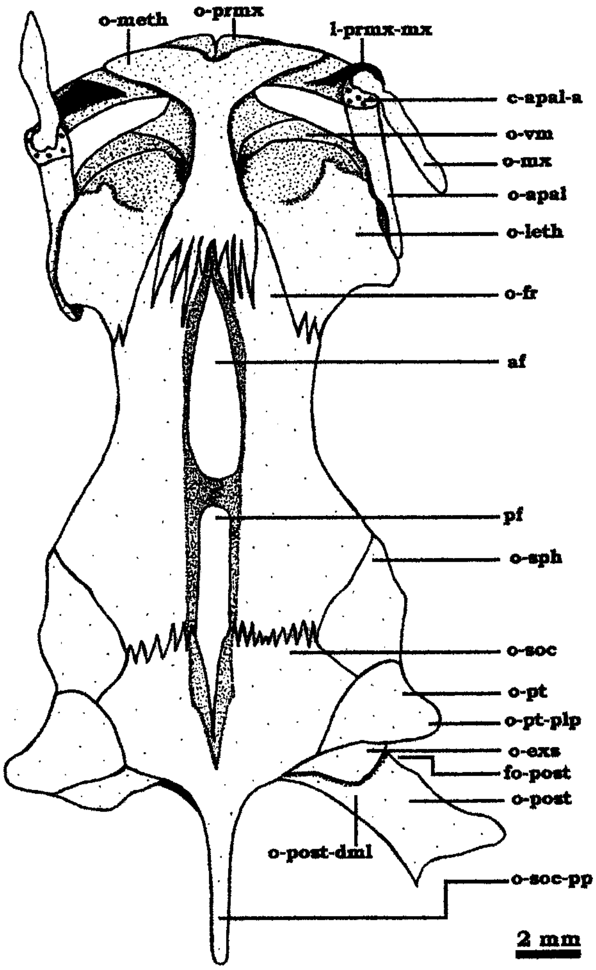
Os exoccipitale (o-eoc): Paired. Lateral to the basioccipital (**fig. 3**).

Os basioccipitale (o-boc): Unpaired. It presents two postero-ventral processes connected by means of a thick ligamentous tissue with the ventro-medial limbs of the posttemporal (**fig. 3**).

Os frontale (o-fr): Paired. The two frontals are largely separated by the well-developed anterior and posterior fontanelles, and are connected with each other medially halfway along their length *via* a bony bridge which separates the fontanelles (**fig. 1, 2**).

Os supraoccipitale (o-soc): Unpaired. Large bone with a long posterior process (**figs 1, 2**).

Fig. 2. Dorsal view of the neurocranium and palatine-maxillary system of *Bagrus docmac* (MRAC 86-07-P-516).



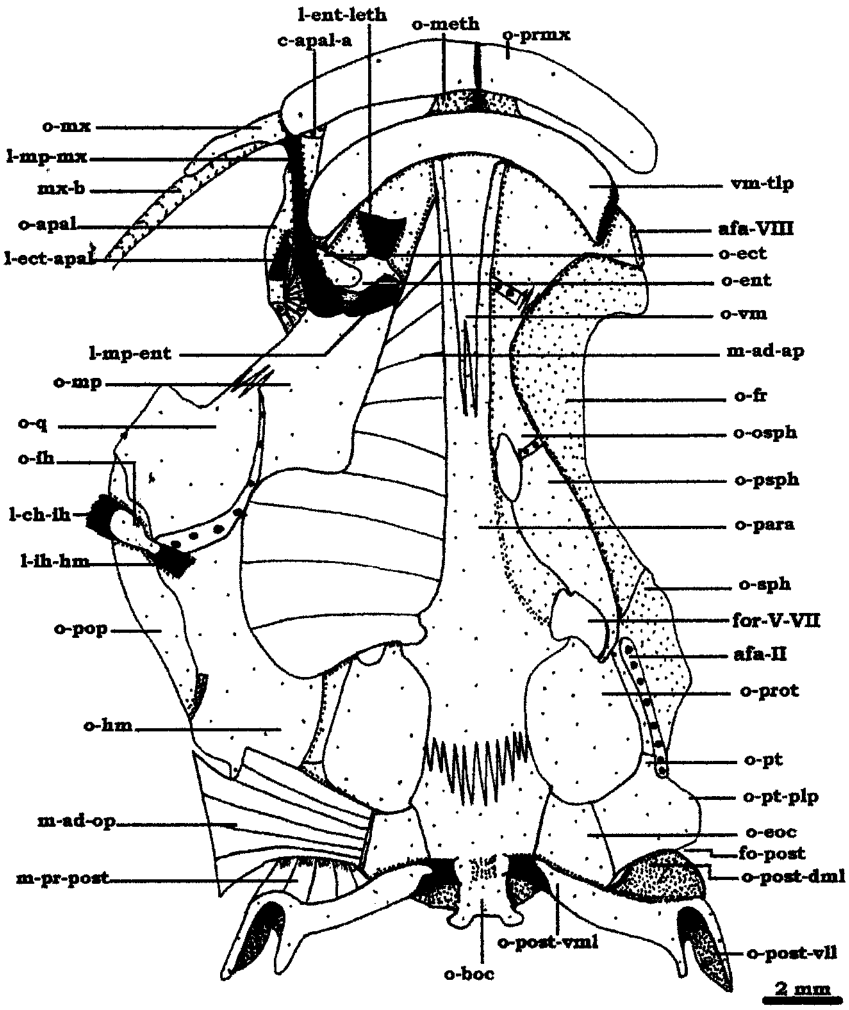
Os extrascapulare (o-exs): Paired. Beneath the extrascapular and the dorso-medial limb of the posttemporal is a large depressed posttemporal fossa bordered mainly by the pterotic, epiotic and supraoccipital (**figs 1, 2, 3**).

Os posttemporale (o-post): Paired. It presents four limbs. The dorso-medial limb (**figs 1, 2**) is linked to the extrascapular and supraoccipital by means of extensive ligamentous tissue. The ventro-medial limb (**fig. 3**) is firmly attached to the basiocccipital by a strong and short ligament. The ventro-lateral limb (**fig. 3**) is deeply forked, forming a profound articulating groove for the upper edge of the cleithrum. Finally, a prominent posterior process (**figs 1, 2**) is present on the postero-dorsal surface of the posttemporal. Posteriorly, the posttemporal forms a broadened surface that is associated with the rostral end of the airbladder.

Os operculare (o-op): Paired. Triangular. It articulates antero-dorsally with the hyomandibula and antero-ventrally with the interopercular (**fig. 1**).

Fig. 3. Ventral view of the neurocranium of *Bagrus docmac* (MRAC 86-07-P-516). On the left side the suspensorium and the palatine-maxillary system, as well as the muscles and ligaments associated with these structures, are illustrated. On the right side, the vomerine tooth-plate was partially cut to show the

articulatory facet of the lateral-ethmoid with the palatine. Vomerine and premaxillary teeth were removed.



Os interoperculare (o-iop): Paired. Its anterior and antero-medial surfaces are linked, by means of thick ligamentous tissue to the angulo-articular (**figs 1, 5**) and to the posterior ceratohyal, respectively (**fig. 5**).

Os praeoperculare (o-pop): Paired. Long and thin bone firmly attached to the hyomandibula and to the quadrate (**figs 1, 3, 4**).

Os hyomandibulare (o-hm): The homology, and thus the correct denomination of this bone, as well as of the other suspensorium components of catfish, has been the subject of many controversies (McMurrich, 1884; De Beer, 1937; Hoedeman, 1960a, b; Gosline, 1975; Arratia *et al.*, 1978; Arratia & Menumarque, 1981; 1984; Howes, 1983; 1985; Arratia, 1987; 1990; 1992; Howes & Teugels, 1989; etc.). Here we will describe the suspensorium bones by their most accepted names, which correspond to those proposed by Regan (1911). The paired hyomandibulas articulate dorsally with the paired pterotics and sphenotics, and present an antero-dorsal spine to reinforce this articulation (**figs 1, 3, 4**).

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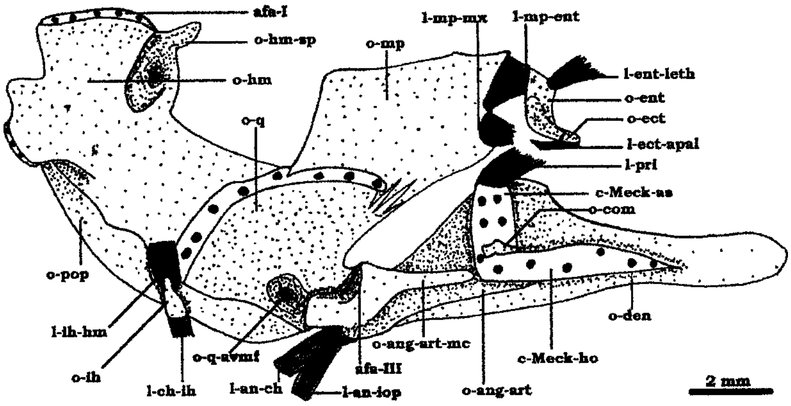
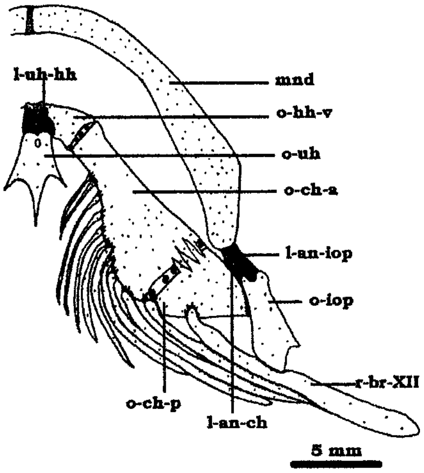
Fig. 4. Medial view of the suspensorium (opercular and interopercular excluded), mandible and ligaments of *Bagrus docmac* (MRAC 86-07-P-512).



Os quadratum (o-q): Paired. Its fore end presents an articulatory facet for the angulo-articular (**fig. 1**) and its antero-ventro-medial surface has a deep concavity to receive the posterior process of the same bone (**fig. 4**). Dorsally, the quadrate is connected by cartilage to the hyomandibula, and by cartilage and a little bony suture to the metapterygoid (**figs 1, 3, 4**).

Fig. 5. Ventral view of the splanchnocranium of *Bagrus docmac* (MRAC 86-07-P-516).



Os metapterygoideum (o-mp): Paired, rectangular bone. It is ligamentously linked to three bones: its antero-dorsal surface is linked to the rear end of the palatine (**fig. 1**), its antero-ventro-lateral extremity to the maxillary (**figs 2, 3, 4**) and its antero-dorso-medial edge to the entopterygoid (**figs 1, 3, 4**).

Os entopterygoideum (o-ent): Paired. Its fore end is attached to the lateral ethmoid by means of a strong ligament (**figs 3, 4**).

Fig. 6. Lateral view of the cephalic musculature of *Bagrus docmac* (MRAC 86-07-P-512). A: All the muscles exposed (for the osteology, see fig. 1). B: Adductor arcus palatini and sections A1 and A2 of the adductor mandibulae were removed. C: Levator arcus palatini and sections A3'-d-1, A3'-d-2 and A3'-v of the adductor mandibulae were removed.

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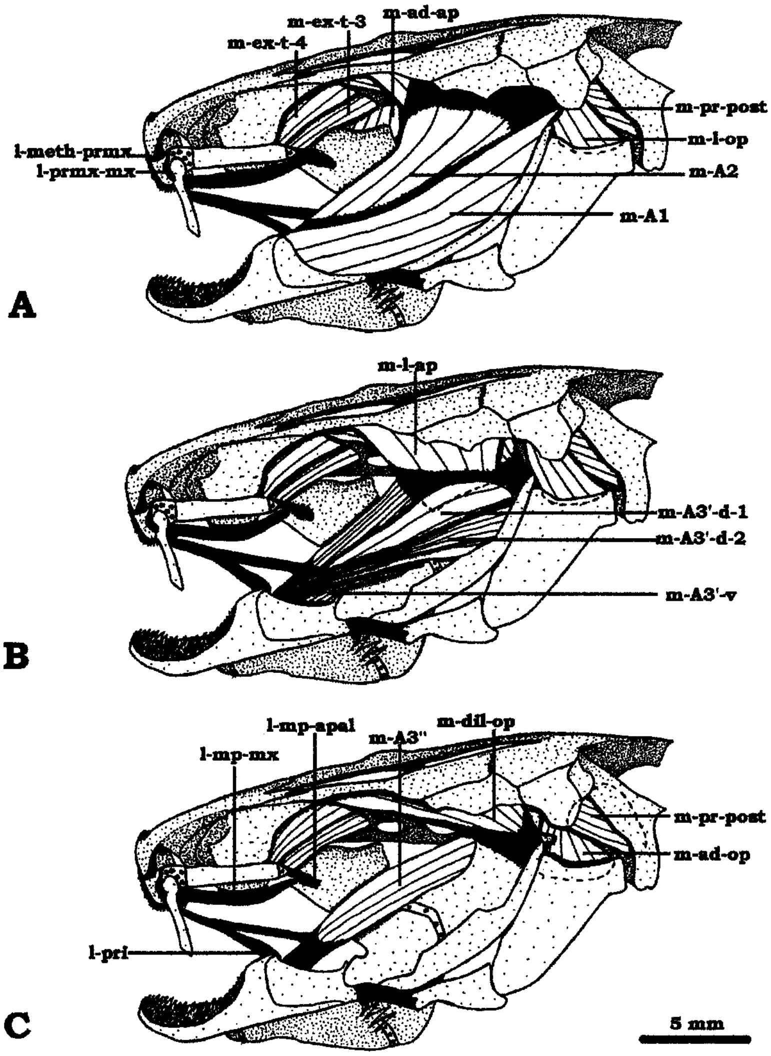

Os ectopterygoideum (o-ect): The lateral extremities of the paired ectopterygoids are ligamentously connected to the paired palatines; their medial edges are firmly attached to the paired entopterygoids (**figs 3, 4**).

Os autopalatinum (o-apal): Paired. Rod-like bone with cartilage at its anterior and posterior ends. It articulates with the maxillary and the lateral ethmoid by its anterior cartilage and by its medial surface, respectively (**figs 1, 2, 3**).

Os maxillare (o-mx): The paired maxillaries support the paired maxillary barbels (**fig. 3**).

Os praemaxillare (o-prmx): Each of the paired premaxillaries is dorsally linked by a strong ligament to the proximal extremity of the paired maxillaries (**figs 2, 3**) and bears ventrally a large tooth-plate (**fig. 1**).

Os angulo-articulare (o-ang-art): Paired. This bone, together with the dentary, coronomeckelian and Meckel cartilage, constitute the mandible (**fig. 4**). The caudal end of the angulo-articular is ligamentously linked to the interopercular and to the posterior ceratohyal (**figs 1, 4, 5**). Its antero-dorsal surface, together with the postero-dorsal surface of the dentary, form a dorsal condyle (processus coronoideus), which is linked by a long and thick ligament (primordial ligament) to the maxillary (**figs 2c, 4**). The ascending portion of the Meckel cartilage (**fig. 4**) is lodged in the primordial ligament.

Os dentale (o-den): The paired, toothed dentaries are firmly connected, by means of a large number of short and thin fibres, to the supporting parts of the cartilages associated with the mandibular barbels (**fig. 9**).

Os coronomeckelium (o-com): Paired. Small bone lodged in the medial surface of the mandible. Posterior and postero-dorsally it bears crests for attachment of the jaw muscle (**figs 4, 7c**).

Os interhyale (o-ih): Paired. The interhyal is a small bone linking the hyoid arch to the suspensorium: dorsally, it is ligamentously linked to the antero-ventro-medial end of the hyomandibula, near to the cartilage between the hyomandibula and the quadrate; ventrally, it is connected by means of ligamentous tissue to the rear end of the posterior ceratohyal (**figs 3, 4**).

Os ceratohyale posterior (o-ch-p): The paired posterior ceratohyals are linked by ligaments to the angulo-articular, interopercular and interhyal (**fig. 5**).

Os ceratohyale anterior (o-ch-a): Paired. Together with the posterior ceratohyal it supports the branchiostegal rays (**fig. 5**).

Os hypohyale ventrale (o-hh-v): Paired. Each ventral hypohyal presents a ventral concavity to receive one of the antero-lateral edges of the urohyal (**fig. 4**).

Os hypohyale dorsale: The paired dorsal hypohyals are small bones situated dorsal to the paired ventral hypohyals.

Os urohyale (o-uh): The urohyal is a single shuttle-like bone lying medially behind the symphysis of the two ventral hypohyals and connected to these bones by means of two short and thick ligaments.

MYOLOGY

For simplicity we follow as much as possible WINTERBOTTOM (1974), although the homologies and nomenclature of the different adductor mandibulae sections of teleostean fishes should be revised fundamentally.

Fig. 7. Medial view of the mandible and adductor mandibulae muscle of *Bagrus docmac* (MRAC 86-07-P-512). A: Adductor mandibulae complex, except section A1, exposed. B: Ligamentum primordium and section A3" of the adductor mandibulae were removed. C: Sections A*ω* and A2 of the adductor mandibulae were removed.

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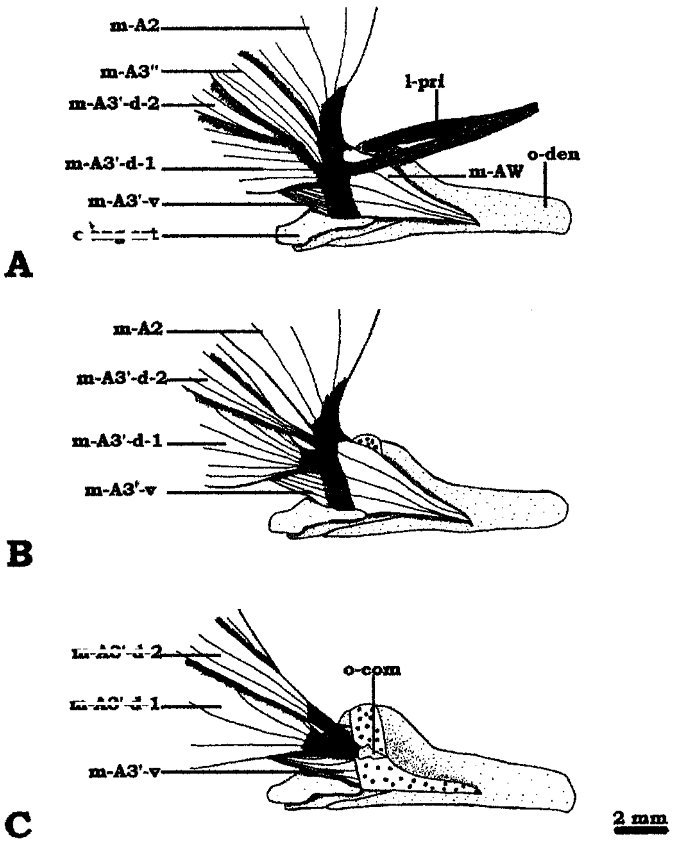

Musculus adductor mandibulae (m-ad-mnd): Paired. This muscle is differentiated in seven divisions. The A1 originates muscularly on the lateral surfaces of the preopercular, quadrate and hyomandibula and inserts tendinously and muscularly on the lateral and posterior surfaces of the angulo-articular (**fig. 6a**). The A2 is linked posteriorly by means of broad tendinous tissue to the dorso-lateral surfaces of the frontal, sphenotic and pterotic (**fig. 6a**) and anteriorly by means of a strong tendon to the medial crest of the angulo-articular and to the back of the A *ν* (**fig. 7b**). The A3' is divided in two bundles. The most ventral one originates tendinously on the postero-lateral surface of the quadrate (**fig. 6**) and inserts muscularly on the medial surface of the angulo-articular (**fig. 7c**). The most dorsal one is differentiated in two subbundles: the smallest originates muscularly on the lateral surface of the preopercular (**fig. 6b**) and inserts tendinously on the postero-dorsal edge of the coronomeckelian (**fig. 7c**); the largest originates muscularly on the lateral surfaces of the quadrate, metapterygoid and hyomandibula (**fig. 6b**) and inserts tendinously on the posterior edge of the coronomeckelian (**fig. 7c**). The A3" originates muscularly on the antero-dorsal surface of the hyomandibula (**fig. 6c**) and inserts, by means of a long forked tendon, on the medial crest of the angulo-articular (**fig. 7a**) and, *via* the primordial ligament, on the proximal extremity of the maxillary (**figs 6c, 7a**). Lastly, the A*ω*, which is lodged in the medial face of the mandible, is attached anteriorly on the ventro-medial surface of the dentary and posteriorly on the tendon of the A2 (**fig. 7c**).

Musculus levator arcus palatini (m-l-ap): Paired. It originates muscularly on the ventro-lateral surfaces of the frontal and sphenotic and inserts tendinously on the dorso-lateral face of the hyomandibula (**fig. 6b**).

Musculus dilatator operculi (m-dil-op): Paired. Medial to the levator arcus palatini (**fig. 6c**). It originates muscularly on the ventral surfaces of the frontal, sphenotic and pterotic and inserts, by means of a thick tendon on the antero-dorsal face of the opercular (medial to the preopercular but lateral to the articulatory facet of the opercular for the hyomandibula).

Musculus levator operculi (m-l-op): Paired. Dorsally it is muscularly linked to the ventro-lateral surface of the pterotic and ventrally it is muscularly associated to the dorsal face of the opercular (**fig. 6b**).

Musculus protractor posttemporalis (m-pr-post): Paired. This muscle was described for the first time by MO (1991), being called "retractor post-temporalis" by this author. The attribution of such a name to designate this muscle is obviously incorrect, since MO (1991: 44) himself recognised that its contraction "can only cause the lateral side of the posttemporal to move anteriorly" (see the **figures 3** and **6** and also the discussion). So, it is proposed that MO's "retractor posttemporalis" be designated, from now on, as "protractor posttemporalis". The protractor posttemporalis, which occupies the major part of the posttemporal fossa, attaches anteriorly on the postero-ventral surface of the pterotic (medially to the levator operculi but laterally to the adductor operculi) and posteriorly on the antero-ventral surface of the posttemporal (**figs 3, 6**).

Musculus adductor operculi (m-ad-op): Paired. Situated medially to the levator operculi and protractor posttemporalis, it originates on the ventromedial surface of the pterotic and inserts on the dorso-medial surface of the opercular, but also on the postero-dorso-medial surface of the hyomandibula (**figs 3, 6c**).

Musculus adductor arcus palatini (m-ad-ap): The paired adductores arcus palatini extend from the lateral sides of the orbitosphenoid, pterosphenoid and parasphenoid to the medial sides of the hyomandibula and metapterygoid (**figs 3, 6a**).

Musculus extensor tentaculi (m-ex-t): Paired. This muscle is differentiated in four sections. The extensor tentaculi 1 extends from the lateral ethmoid to the postero-medial face of the palatine (**fig. 8a, c**). The extensor tentaculi 2 originates on the lateral ethmoid and orbitosphenoid and inserts on the postero-ventral surface of the palatine (**fig. 8a, c**). The extensor tentaculi 3 is attached medially to the orbitosphenoid and laterally to the back of the palatine (**figs 6a, 8a, c**). Lastly, the extensor tentaculi 4, situated dorsal to the other three bundles, originates on the lateral ethmoid, orbitosphenoid and frontal and inserts on the postero-dorsal crest of the palatine (**figs 6a, 8b, c**).

Musculus protractor hyoidei (m-pr-h): Paired. This muscle presents 3 parts. The pars ventralis, in which are lodged the moving parts of the cartilages associated with the mandibular barbels, extends from the postero-ventral surface of the anterior ceratohyal to a medial aponeurosis (**fig. 9a**). The pars dorsalis originates on the postero-ventral side of the anterior ceratohyal and inserts tendinously on the dentary, near the mandibular symphysis (**fig. 9b**). The pars lateralis originates on the postero-ventral surface of the posterior ceratohyal and inserts, by means of a strong tendon, on the ventro-medial face of the dentary (**fig. 9a**).

Fig. 8. Palatine and extensor tentaculi of *Bagrus docmac* (MRAC 86-07-P-512). A: Ventral view. B: Ventral view. Sections 1, 2 and 3 of the extensor tentaculi were removed. C: Medial view. The different sections of

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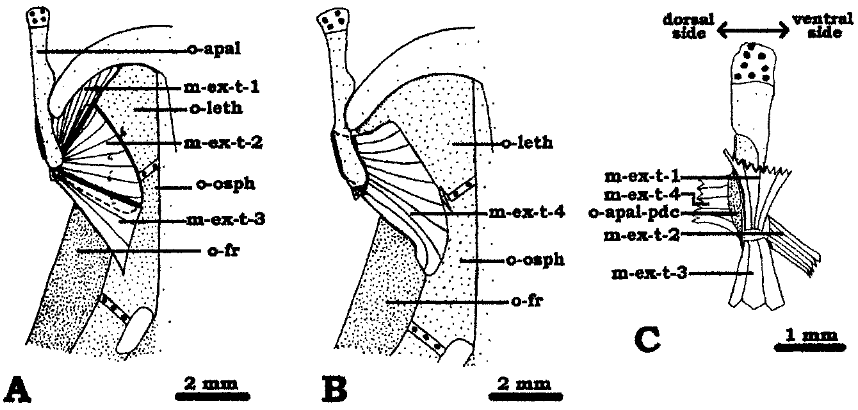
the extensor tentaculi were separated from the neurocranium, in order to show their attachments on the palatine.



Musculus hyohyoideus inferior (m-hh-inf): Paired. Thick muscle that attaches laterally on the ventral surface of the anterior ceratohyal and medially on a medial aponeurosis (**fig. 9a**).

Musculus sternohyoideus: Unpaired. It originates on the anterior region of the cleithrum and inserts on the posterior region of the urohyal.

Musculus intermandibularis (m-intm): Unpaired. Well-developed muscle linking the antero-medial sides of the two dentaries (**fig. 9a**).

Musculus retractor externi mandibularis tentaculi (m-re-mnd-b-ex): Paired. Posteriorly it is attached on the moving part of the cartilage associated with the outer mandibular barbel (**fig. 9a, b**). Anteriorly it is attached, by means of a long, bifurcated tendon, to two different regions of the dentary: one, situated dorsally to the retractor interni mandibularis tentaculi, far from the mandibular symphysis (**fig. 9a**); the other, situated dorsally to the intermandibularis and to the pars dorsalis of the protractor hyoidei, lies quite near the symphysis (**fig. 9b**).

Musculus retractor interni mandibularis tentaculi (m-re-mnd-b-in): Small muscle that originates on the moving part of the cartilage associated with the internal mandibular barbel and inserts tendinously on the dentary (**fig. 9a**).

DISCUSSION

MO (1991) states that the family Bagridae is defined united by six autapomorphies: 1) presence of the protractor posttemporalis (MO's "retractor posttemporalis" , see above) muscle; 2) well-developed posttemporal fossa with a postero-lateral exit; 3) large heavily ossified posttemporal; 4) prominent posterior process of the posttemporal; 5) thick dorso-medial limb of the posttemporal; 6) large, crescentic vomerine head.

Fig. 9. Ventral view of the ventral cephalic musculature of *Bagrus docmac* (MRAC 86-07-P-512). A: On the left side, the internal mandibular barbel, its retractor muscle and the cartilage associated to it were pulled laterally. B: Internal mandibular barbels, their retractors and supporting parts of the cartilages associated to them, as well as the intermandibularis muscle, were removed. On the right side, the pars dorsalis of the protractor hyoidei was also removed.

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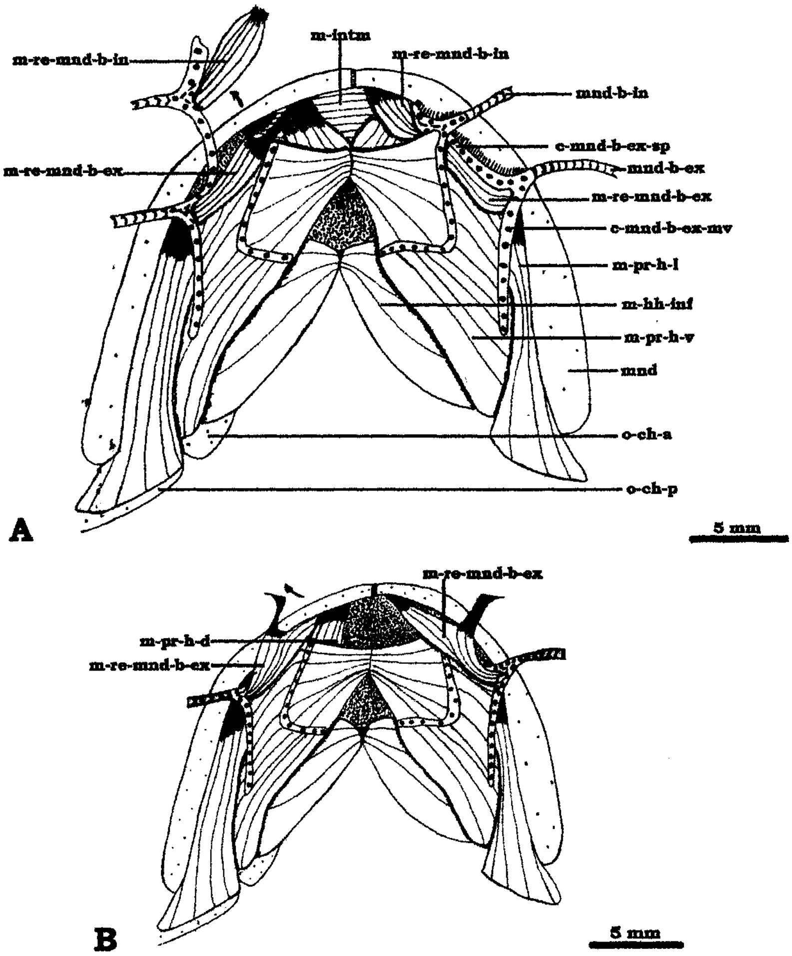

These six morphological features are present in *Bagrus docmac* , as well as in all the other bagrids studied in this work. H owever, the last one — a large, crescentic vomerine head — is not exclusively present in bagrid fishes. In fact, the vomer of some clariids (*e.g. Clarias* , *Uegitglanis*, DAVID, 1936: fig. 1; POLL, 1942: fig. 4; ALEXANDER, 1965: fig. 14; TILAK, 1963b: fig. 3; VANDEWALLE *et al.*, 1993: fig. 3; ADRIAENS & VERRAES, 1998: fig. 12c), silurids (*e.g. Silurus*, CERNÝ, 1988: fig. 5; KOBAYAKAWA, 1989: figs 5b, 19b, 22b, 24b, 26b, 24b; 1992: figs 1b, 3b), sisorids (*e.g. Nangra*, TYLAK, 1963a: fig. 2) and claroteids (*e.g. Chrysichthys*, GHIOT *et al.*, 1984: fig. 3b; JAYARAM & SINGH, 1984: fig. 2) have a large, crescentic anterior head quite similar to that found in the Bagridae.

MO (1991: 46) argued that "such an enlarged, crescentic vomer head is viewed as apomorphic because of its restricted distribution in the Siluroidei (*. . .*), a similar vomer also occurs in *Silurus* and *Clarias* , but (*. . .*) because there is other evidence (his phylogenetic results) indicating that Clariidae and Siluroidei are phylogenetically remote to the *Bagrus*-like (Bagridae), it is assumed that the latter developed this condition independently (...), therefore, the vomer having an enlarged, crescentic anterior portion is considered synapomorphic for the *Bagrus*-like genera". This argumentation is contestable. First, a large, crescentic vomerine head is not only present in bagrids, clariids and silurids, but also in at least some sisorids and claroteids (see above). Second, MO's use of the term "autapomorphic" and "synapomorphic" is, at least in this particular

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case, incorrect. An "autapomorphy", by definition (HENNIG, 1966: 90), is a derived character that was acquired by and is restricted to a phyletic line after it branched off from its sister group, and that can be used phylogenetically to separate this phyletic line from all the others. As this character is only found in the organisms of this lineage it is considered as a "synapomorphy" of these organisms, that is, a derived feature which only they possess. So, even if we accept that the large, crescentic vomerine head was independently acquired in the different families mentioned above, it can not be considered an Bagridae autapomorphy, since it is found in different catfish groups (in fact, there is no phylogenetic sense to consider the derived characters resulting from parallel or convergent evolution as autapomorphic features of all the different taxa that acquired them). Moreover, it is not clear that the large, crescentic vomerine head has been acquired independently in the different catfish families mentioned above, since the claroteids and/or clariids, for example, have been considered several times (*contra* MO, 1991) as near relatives of the bagrids (see, for example, REGAN, 1911; DAVID, 1936; POLL, 1957; JAYARAM, 1966a, b; 1968; 1971; 1973a, b; 1976; CHARDON, 1968; JAYARAM & SINGH, 1982; 1984; GHIOT *et al.*, 1984; etc.). Therefore, we believe that from the six Bagridae autapomorphies proposed by MO (see above), only the first five should be really considered as such.

However, our observations on *Bagrus docmac* reveal three other morphological features that, by their rarity, could constitute potential autapomorphies: 1) the marked bifurcation (**fig. 9b**) of the tendon of the retractor externi mandibularis tentaculi; 2) the deep perforation (**fig. 4**) of the antero-ventro-medial surface of the quadrate; 3) the differentiation of the adductor mandibulae A3'-d in two sub-divisions, with the smallest attached to the postero-dorsal surface of the coronomeckelian and the largest attached to the posterior end of the same bone (**figs 6b, 7c**).

A marked bifurcation of the tendon of the retractor externi mandibularis tentaculi was not described previously in the literature and is not present in any out-group siluroid studied here. However, the fact that this bifurcation is only present in *Bagrus docmac* and *Bagrus bayad* (the only species of the genus *Bagrus* studied), and in no other bagrid studied, makes that it is not a Bagridae autapomorphy.

A perforation of the quadrate is absent in some archaic bagrid genera, like, for example, *Rita* (see descriptions of JAYARAM, 1971) or *Leiocassis*, and is only present in the most specialised ones, for example *Mystus* , *Hemibagrus* or *Bagrus* (for a phylogenetic account on the relationships between bagrid genera see, for example, JAYARAM, 1966a, b; 1968; 1971; 1973a, b; 1976; MO, 1991). Moreover, similar perforations are also found in some out-group catfishes, like, for example, in *Silurus* (KOBAYA KAWA , 1989: figs 6b, 27b, 35b) or in *Heptapterus* (ARRATIA, 1992: fig. 34b). Therefore, an antero-ventro-medial concavity of the quadrate can not be considered a bagrid autapomorphy.

The few studies concerning the cephalic musculature of bagrid fishes (see introduction) make it difficult to judge the phylogenetic significance of the differentiation of the adductor mandibulae A3'-d in two subdivisions, inserted on the postero-dorsal and posterior edges of the coronomeckelian, respectively. H owever, in spite of this difficulty, our observations on the different bagrid genera and comparisons with out-group siluroids (studied by us or described in the literature) indicate that this character is, very likely, a Bagridae autapomorphy. In fact, it is only present in bagrids, and, among these fishes, it is widely distributed and present from the

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most archaic genera, (*e.g. Leiocassis*), to the most specialised ones (*e.g.*, *Mystus*, *Hemibagrus* or *B agrus*).

In summary the family Bagridae is characterized by six autapomorphies: 1) presence of the protractor posttemporalis muscle; 2) well-developed posttemporal fossa with a postero-lateral exit; 3) large heavily ossified posttemporal; 4) presence of a prominent posterior process of the posttemporal; 5) thick dorso-medial limb of the posttemporal; 6) differentiation of the adductor mandibulae A3'-d in a large and a small subdivision, inserted on the postero-dorsal and posterior edges of the coronomeckelian bone, respectively. A reflection on the functional and adaptative significance of these autapomorphies.

MO (1991) considers the presence of a protractor posttemporalis muscle in bagrid fishes to be "functionally linked with activities of the branchial basket since anterior movement of the posttemporal would inevitably pull the ascending portion of the cleithrum with it and consequentially cause the anterior end of the pectoral girdle to turn ventrally (...), this movement would presumably expand the branchial basket". MO's hypothesis seems very unlikely. The articulation between the posttemporal and the cleithrum in bagrids, like in most other catfishes (see for example, ALEXANDER, 1965; CHARDON, 1968; ARRATIA, 1987), allows large movements of these bones with respect to each other. In fact, it is precisely this freedom of movement that permits, without any corresponding movement of the posttemporal, the retraction of the cleithrum (**fig. 10a→b**), and thus of the pectoral girdle, when the mouth is opened by the "hyoid mechanism" (see for example, ADRIAENS & VERRAES, 1997; 1998). So, as the articulation between the posttemporal and the cleithrum allows the ventral part of the cleithrum to move posteriorly without movement of the posttemporal (**fig. 10a→b**), it also permits an anterior displacement of the ventral part of the latter without movement of the cleithrum (**fig. 10c→d**). Therefore, the hypothesis that the contraction of the protractor posttemporalis would principally be associated to a ventral displacement of the anterior end of the pectoral girdle, and especially that this displacement, *via* the sternohyoideus muscle, could "cause the expansion of the branchial basket", seems very unlikely.

Fig. 10. Scheme illustrating our hypothesis c oncerning the functional and adaptive significance of the protractor posttemporalis, as well as the other four autapomorphies related to the posttemporal region of bagrid fishes. Lateral view; for explanations, see discussion. A: The posttemporal and the cleithrum are in their normal positions. B: The cleithrum is retracted. C: The posttemporal and the cleithrum are in their normal positions. D: The posttemporal is protracted (due to contraction of the protractor posttemporalis muscle).

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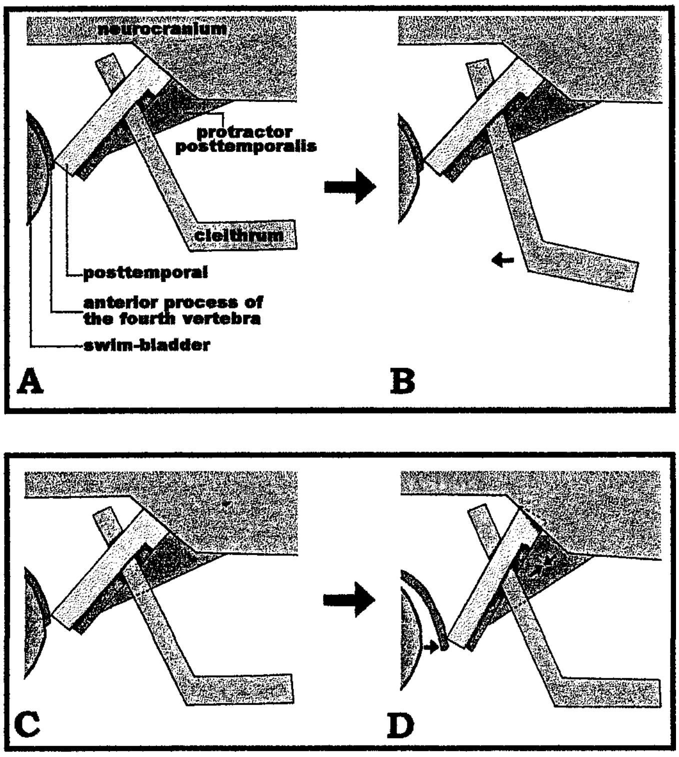

Based on anatomical evidence and artificial manipulation it seems to us much more probable that the presence of a retractor posttemporalis, as well as the other four Bagridae autapomorphies related to the posttemporal region are related to a specialisation that is also found in a large number of other catfish families: the elastic-spring apparatus, which is associated with the production of sound. In ariid, malapterurid, ictalurid, pangasid, auchenipterid, doradid and mochokid catfishes (SÖRENSEN, 1894; BRIDGE & HADDON, 1894; CHRANILOV, 1929; SCHNEIDER, 1961; TAVOLGA, 1962; ALEXANDER, 1965; CHARDON, 1968; TAVERNE & ALOULOU-TRIKI, 1974; HOWES, 1983; 1985; etc.) a muscle originates on the dorsal fin and/or nuchal shields and/or occipital region and inserts on the anterior part of the parapophysis of the fourth vertebra. "When this muscle contracts it pulls the anterior process of the parapophysis forwards (the elastic spring), enlarging the swimbladder: when it relaxes, it allows the spring to recoil, (. . .), the swimbladder is thus caused to pulsate, emitting sound" (ALEXANDER, 1965). This sound-producing mechanism was already demonstrated experimentally by TAVOLGA (1962). The five bagrid autapomorphies mentioned above seem to be related to this mechanism. The contraction of the protractor posttemporalis, which is lodged on the well-developed posttemporal fossa and attached on the ventral surface of the thick dorso-median limb of the large posttemporal (**figs 3, 6**), will protract this bone, and thus the anterior process of the fourth vertebra to which it is associated posteriorly (**fig. 10c→d**). The relaxation of the protractor posttemporalis muscle, will provoke a rapid, strong posterior movement of the posttemporal (**fig. 10d→c**), and, consequently, of the anterior process of the fourth vertebra, against the fore end of the swimbladder (**fig. 10d→c**). The swimbladder and the anterior process of the fourth vertebra may therefore work like a drum and drumstick respectively, producing sound.

The sound production by some catfishes may have a social function (SCHNEIDER, 1961). The mochokid *Synodontys*, for example, produce a characteristic "murmur" in a dangerous situation (TAVERNE & ALOULOU-TRIKI, 1974), probably to alarm other fishes. The ability to produce sound represent, very likely, an important adaptation for the different siluroid lineages that have acquired it. These fishes are mainly nocturnal and inhabitants of aquatic habitats with a very reduced visibility (ALEXANDER, 1965).

The differentiation of the adductor mandibulae A3'-d in a large and a small sub-division could be related to a reinforcement of the adductor mandibulae. Adult bagrids, unlike most siluroids, feed mainly on other adult fishes and require a large biting force (CORBET, 1961; ALEXANDER, 1965).

In conclusion, bagrid catfishes are defined by six autapomorphies: the presence of the protractor posttemporalis muscle, well-developed posttemporal fossa with a postero-lateral exit, large heavily ossified posttemporal, presence of a prominent posterior process of the posttemporal, thick dorso-medial limb of the posttemporal and differentiation of the adductor mandibulae A3'-d in a large and a small sub-division, inserted, respectively, on the postero-dorsal and posterior edges of the coronomeckelian bone. These autapomorphies are probably related to sound production (the first five) and to the reinforcement of the adductor mandibulae (the last one), and may be responsible for the biological success of the Bagridae in the Ancient World, and, particularly, on the Asiatic continent.

LIST OF ABBREVIATIONS

af	anterior fontanella
afa-I	articulatory facet of the os hyomandibulare with the os sphenoticum and the os pteroticum
afa-II	articulatory facet of the os sphenoticum and the os pteroticum with the os hyomandibulare
afa-III	articulatory facet of the os angulo-articulare with the os quadratum
afa-VIII	articulatory facet of the os latero-ethmoideum with the os autopalatinum
c-apal-a	cartilago autopalatinum anterior
c-Meck-as	cartilago Meckeli: ascending part
c-Meck-ho	cartilago Meckeli: horizontal part
c-mnd-b-ex-mp	cartilago externus mandibularis tentaculi: moving part
C-mnd-b-ex-sp	cartilago externus mandibularis tentaculi: supporting part
fo-post	fossa postemporalis
for-V-VII	foramen trigemino-facialis
l-an-ch	ligamentum angulo-ceratohyale
l-an-iop	ligamentum angulo-interoperculare
l-ch-ih	ligamentum ceratohyalo-interhyale
l-ect-apal	ligamentum ectopterygoideo-autopalatinum
l-ent-leth	ligamentum entopterygoideo-lateroethmoideum

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l-ih-hm	ligamentum interhyalo-hyomandibulare
l-meth-prmx	ligamentum mesethmoideo-praemaxillare
l-mp-apal	ligamentum metapterygoideo-autopalatinum
l-mp-ent	ligamentum metapterygoideo-entopterygoideum
l-mp-mx	ligamentum metapterygoideo-maxillare
l-pri	ligamentum primordium
l-prmx-apal	ligamentum praemaxillo-autopalatinum
l-prmx-mx	ligamentum praemaxillo-maxillare
l-uh-hh	ligamentum urohyalo-hypohyale
m-A1	musculus adductor mandibulae A1
m-A2	musculus adductor mandibulae A2
m-A3'-d-1	musculus adductor mandibulae A3' pars dorsalis: part 1
m-A3'-d-2	musculus adductor mandibulae A3' pars dorsalis: part 2
m-A3'-v	musculus adductor mandibulae A3' pars ventralis
m-A3"	musculus adductor mandibulae A3"
m-AW	usculus adductor mandibulae Aω
m-ad-ap	musculus adductor arcus palatini
m-ad-op	musculus adductor operculi
m-dil-op	musculus dilatator operculi
m-ex-t-1	musculus extensor tentaculi: part 1
m-ex-t-2	musculus extensor tentaculi: part 2
m-ex-t-3	musculus extensor tentaculi: part 3
m-ex-t-4	musculus extensor tentaculi: part 4
m-hh-inf	musculus hyohyoideus inferior
m-intm	musculus intermandibularis
m-l-ap	musculus levator arcus palatini
m-l-op	musculus levator operculi
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-pr-post	musculus protractor posttemporalis
m-re-mnd-b-ex	musculus retractor externi mandibularis tentaculi
m-re-mnd-b-in	musculus retractor interni mandibularis tentaculi
mnb	mandibula
mnd-b-ex	external mandibular barbel
mnd-b-in	internal mandibular barbel

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mx-b	maxillar barbel
o-ang-art	os angulo-articulare
o-ang-art-mc	os angulo-articulare: medial crest
o-apal	os autopalatinum
o-apal-pdc	os autopalatinum: postero-dorsal crest
o-boc	os basioccipitale
o-ch-a	os ceratohyale anterior
o-ch-p	os ceratohyale posterior
o-cl	os cleithrum
o-com	os coronomeckelium
o-den	os dentale
o-ect	os ectopterygoideum
o-ent	os entopterygoideum
o-eoc	os exoccipitale
o-exs	os extrascapulare
o-fr	os frontale
o-hh-v	os hypohyale ventrale
o-hm	os hyomandibulare
o-hm-sp	hyomandibular spine
o-ih	os interhyale
o-iop	os interoperculare
o-leth	os latero-ethmoideum
o-meth	os mesethmoideum
o-mp	os metapterygoideum
o-mx	os maxillare
o-op	os operculare
o-osph	os orbitosphenoideum
o-para	os parasphenoideum
o-pop	os praeoperculare
o-post	os posttemporale
o-post-dml	os posttemporale: dorso-medial limb
o-post-vll	os posttemporale: ventro-lateral limb
o-post-vml	os posttemporale: ventro-medial limb
o-post-vp	ventral process of the os posttemporale
o-prmx	os praeomaxillare
o-prot	os prooticum

o-psph	os pterosphenoideum
o-pt	os pteroticum
o-pt-plp	os pteroticum: postero-lateral process
o-q	os quadratum
o-q-avmf	os quadratum - antero-ventro-medial fossa
o-soc	os supraoccipitale
o-soc-pp	posterior process of the os supraoccipitale
o-sph	os sphenoticum
o-uh	os urohyale
o-vm	os vomerale
pf	posterior fontanella
r-br-XII	radius branchiostegus XII
vm-tlp	vomerine tooth plate

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